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Effects of climate change and other anthropogenic impacts on plant phenology and wildlife health in North America

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GRADUATE SCHOOL OF ARTS AND SCIENCES

Dissertation

**EFFECTS OF CLIMATE CHANGE AND OTHER ANTHROPOGENIC
IMPACTS ON PLANT PHENOLOGY AND WILDLIFE HEALTH
IN NORTH AMERICA**

by

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B.A., Williams College, 2015
M.A., Boston University, 2022

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requirements for the degree of
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DEDICATION

For Mom and Dad

butterfly whispers
gently pretending
swimming in the moon sea
we were happy

yellow light upon spring wings
like when the flowers never came
night nesting on mountain dreams
too wild to understand

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Nothing gets done alone. Quite literally, I was not the only one to contribute to this work, although my name is on it here. But in a broader sense, we are all embedded in our communities, and I am endlessly grateful to the people I've come to know during the time this research happened.

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IN NORTH AMERICA
TARA KING MILLER**

Boston University Graduate School of Arts and Sciences, 2022

Major Professor: Richard Primack, Ph.D., Professor of Biology

ABSTRACT

Plants and wildlife are being affected by climate change and human activities. We need to understand the patterns in these impacts to develop management strategies and policy solutions that will help us conserve ecosystems. Climate change is shifting the timing of key life stages in plants, but we do not fully understand the extent and implications of phenological shifts – or changes in the timing of seasonal events – for understudied stages like fruiting or for potential mismatches between plants in different canopy levels. Human activities and climate change impact and harm wildlife in many ways, from wildlife-vehicle collisions and lead poisoning to hurricanes and infectious diseases, but it has been difficult to form a comprehensive picture of these threats across many species and regions, and to discern which factors pose the greatest threat to at-risk species. Here, I collected and curated data from herbarium specimens and wildlife rehabilitation records to advance our understanding of the effects of climate change and human activities on plants and wildlife in North America. First, I found that metrics of first, peak, and last fruiting dates were strongly correlated between two historical datasets, suggesting that field observations and herbarium collections capture similar

orders of fruiting times among plant species in New England. However, I found differences in the exact timing of first and last fruiting dates, indicating that researchers should match methodology when selecting historical records of phenology for present-day comparisons, especially when the exact timing is important. Next, I found that native trees, native shrubs, and non-native shrubs advanced their leaf-out or flowering times faster than native wildflowers advanced their flowering times with warming temperatures. As climate warming progresses, some native wildflower species, especially in warmer regions, are likely to be affected by phenological mismatch and lose access to early-season sunlight. Last, I found that human disturbances accounted for the largest proportion of wildlife injury and sickness in animals admitted to wildlife rehabilitation centers, and I identified the predominant reason for admittance for many species; these reasons included vehicle collisions, fishing incidents, and window or building collisions. I recommended possible interventions to help conserve wildlife, including using or changing wildlife road crossings, fishing and hunting regulations, lead and pesticide regulations, and disaster management plans. In this research, I compiled and analyzed innovative, newly-digitized data sources to provide new insights into the effects of climate change and human activities on plants and wildlife in North America.

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LIST OF ABBREVIATIONS

$^{\circ}\text{C}$	Degrees Celsius
β_0	Bayesian regression model result of intercept estimate
β_1	Bayesian regression model result of slope estimate
β_{FD}	Bayesian regression model result of slope estimate for flowering date
β_{LOD}	Bayesian regression model result of slope estimate for leaf-out date
χ^2	Chi-square
Apr	April
Aug	August
BU	Boston University
CI (in Chapter 2)	Confidence interval
CI (in Chapter 3)	Credible interval
D.C.	District of Columbia
Dec	December
df	Degrees of freedom
DOY	Day of year
EDDMapS	Early Detection & Distribution Mapping System
F	F-value
FD	Flowering date
Feb	February
FL	Florida
Jan	January

Jul	July
Jun	June
km	Kilometer
LOD	Leaf-out date
MA	Massachusetts
Mar	March
MCMC	Markov chain Monte Carlo
n	Sample size
N	Sample size
No.	Number
NOAA	National Oceanic and Atmospheric Administration
Nov	November
n.s.	Not significant
NWS	National Weather Service
NY	New York
Oct	October
<i>P</i>	p-value
PA	Pennsylvania
r	Pearson's correlation coefficient
R ²	R-squared
rehab	Rehabilitation
sd	Standard deviation

SE Canada	Southeast Canada
Sep	September
<i>t</i>	t-value
US	United States
U.S.	United States
USA	United States of America
WILD-ONe	Wildlife Incident Log/Database and Online Network
WNV	West Nile virus
WRMD	Wildlife Rehabilitation Medical Database

CHAPTER ONE: INTRODUCTION

Plants and wildlife are being affected by climate change and human activities (Cleland et al., 2007; Miller-Rushing and Primack, 2008 -- Scanes et al., 2018; Maxwell et al., 2019; Grade et al., 2019). We need to understand the patterns in these impacts to develop management strategies and policy solutions that will help us conserve ecosystems for decades to come.

In contrast to climate-driven changes in leaf-out and flower phenology, which have been well-studied (Primack et al., 2004; Menzel et al., 2006; Cleland et al., 2007; Bertin, 2008; Miller-Rushing and Primack, 2008; Panchen et al., 2012; Polgar et al., 2013; Everill et al., 2014; Ellwood et al., 2019), climate-driven changes in fruiting phenology have been relatively neglected in ecological research (Bertin, 2008; Gallinat et al., 2015). Fruiting is vitally important to the reproductive success of plants and to many animals which rely on wild fruits for nutrition (Primack, 1987; Willson and Whelan, 1993; Parrish, 1997; Tiffney, 2004; Smith et al., 2013). Several studies have found that fruiting times are advancing with warmer temperatures (Menzel et al., 2006; Sherry et al., 2007; Gordo and Sanz, 2010; Panchen and Gorelick, 2015), although not in all cases (Menzel et al., 2006; Sherry et al., 2007). Historical phenology records have been instrumental for studying changes in leaf out and flowering times, but fewer historical data sources exist to investigate similar patterns for wild fruits. This research requires that historical records provide a reliable baseline for comparison, and one way to assess the comparability of observations and herbarium specimens is to determine if they provide similar baseline information, such as differences or similarities in fruiting times. The

extent to which historical records reflect similar or different patterns can indicate the resilience of these patterns to methods of collection, how much these patterns might depend on spatial and temporal scaling, and what methods should be used to compare these groups in the present-day to detect true shifts due to climate change or other aspects of a changing environment. It is important for researchers to know how to work with these differences in historical datasets to investigate the effects of climate change on fruiting phenology.

Plants are important indicators of climate change, as plant species in temperate ecosystems demonstrate a strong trend of shifting their spring phenology – or timing of seasonal events – earlier with warmer temperatures (Bertin, 2008; Cleland et al., 2007; Ellwood et al., 2019; Everill et al., 2014; Menzel et al., 2006; Miller-Rushing & Primack, 2008; Panchen et al., 2012; Polgar et al., 2013; Primack et al., 2004; Stuble et al., 2021). Species vary in their phenological sensitivity, with some species demonstrating greater or lesser shifts with each degree of spring warming (Heberling et al., 2019b; Lee & Ibáñez, 2021a; Park et al., 2018; Reeb et al., 2020). These different rates of response could lead to phenological mismatches, where alignment in the timing of ecological relationships is disrupted (Kharouba & Vellend, 2015; Kharouba et al., 2018; Mayor et al., 2017; Renner & Zohner, 2018). A recent study in Concord, Massachusetts, USA found that canopy trees are advancing their leaf-out times faster than understory wildflowers are in response to warming temperatures (Heberling et al., 2019b). This difference found in phenological sensitivity between trees and wildflower is resulting in a shrinking period of full early-spring sunlight for wildflowers, and thus a likely decline in their ability to

photosynthesize and store carbon (Heberling et al., 2019b). Many early-blooming forest wildflowers rely on the period of full sunlight exposure before canopy trees leaf out in order to perform most of their photosynthesis and carbon gain for the year (Augspurger & Salk, 2017; Heberling et al., 2019a; Kudo et al., 2008; Lapointe, 2001). Few studies have compared phenological mismatches among plants occupying different forest layers (but see Heberling et al. 2019b, Lee & Ibáñez 2021a, and Routhier & Lapointe, 2002, suggesting that such mismatches may be common but understudied), and most studies of phenological mismatches have been limited to small geographic areas (Heberling et al., 2019a; Kharouba & Vellend, 2015; Post & Forchhammer, 2008). It is also yet untested whether non-native species are also contributing to or affected by phenological mismatch among forest layers. As climate warming intensifies, it is important to understand how the phenology of different plant species will respond, and if different responses correspond to understory plants receiving more or less sunlight.

Human activities and climate change impact and harm wildlife in many ways, from wildlife-vehicle collisions and lead poisoning to heat stress and infectious diseases (Gunson et al., 2011; Pain et al., 2019; Piatt et al. 2020; Camacho et al., 2016). We need to understand the prevalence, patterns, and impacts of the threats to wildlife in order to conserve wildlife populations. We need to ascertain which species are most at risk and which threats to address first to conserve at-risk species and populations. Wild animals are important as indicators of ecosystem health and function (Burger and Gochfeld, 2004; Morrison, 1986), as food sources (Borgerson et al., 2019), for cultural significance and medicinal use (Adeola, 1992; Hernandez et al., 2015), tourism (Hou et al., 2020), and

more. Many threats to wildlife, such as lead poisoning and infectious diseases, also impact human health (Bellinger et al., 2013; Gallana et al., 2013). However, it has been difficult to form a comprehensive picture of the trends in these impacts across many species and regions, and to discern which impacts pose the greatest threat to at-risk species. We can use wildlife rehabilitation (rehab) records to learn about these threats to wildlife across North America, make connections to human health, and recommend solutions and remediation that will improve both wildlife and human health.

In this dissertation, I used data from herbarium specimens and wildlife rehabilitation records to advance our understanding of the effects of climate change and human activities on plants and wildlife in North America. I captured impacts on large geographic and taxonomic scales: Chapter 2 examines the fruiting phenology of 67 species across New England; Chapter 3 studies the leaf-out and flowering phenology of 21 species across eastern North America; and Chapter 4 looks at the wildlife health of 1,126 species across the continental U.S. and southern Canada. This research used innovative, newly-digitized data sources to provide new insights into the effects of climate change and human activities on plants and wildlife.

Chapter Overviews

Chapter Two: Comparing fruiting phenology across two historical datasets: Thoreau's observations and herbarium specimens

Fruiting remains under-represented in long-term phenology records, relative to leaf and flower phenology (Bertin, 2008; Gallinat et al., 2015). Herbarium specimens and historical field notes can fill this gap (Meineke et al., 2018; Lang et al., 2019), but

selecting and synthesizing these records for modern-day comparison requires an understanding of whether different historical data sources contain similar information, and whether similar, but not equivalent, fruiting metrics are comparable to one another. For 67 fleshy-fruited plant species, I compared observations of fruiting phenology made by Henry David Thoreau in Concord, Massachusetts (1850s) to phenology data gathered from herbarium specimens collected across New England (mid-1800s—2000s). These two fruit phenology datasets—Thoreau’s field observations and data from herbarium specimens—represent an opportunity to compare fruiting patterns and metrics in different historical datasets. Thoreau’s observations capture fruiting phenology as first, peak, and last fruiting dates; similar, but not equivalent, metrics from herbaria are the earliest, mean, and latest specimens of the season among all of the specimens collected of a species. To identify whether fruiting times and the order of fruiting among species are similar between datasets, I compared dates of first, peak, and last observed fruiting (recorded by Thoreau), and earliest, mean, and latest specimen (collected from herbarium records), as well as fruiting durations.

Chapter Three: Warming temperatures are linked to phenological mismatch among native and non-native trees, shrubs, and wildflowers across the Eastern Deciduous Forest of North America

Deciduous trees, shrubs, and forest wildflowers may be advancing their leaf-out phenology at different rates in response to a warming climate (Heberling et al., 2019b). A mismatch between understory and overstory phenology may lead to a reduction of understory light levels in the early spring, which is a critical period when many spring-

blooming wildflowers achieve highest photosynthetic rates (Augspurger & Salk, 2017; Heberling et al., 2019a; Heberling et al., 2019b; Kudo et al., 2008; Lapointe, 2001). However, the extent of this phenomenon beyond a single site or region is largely unknown. Herbaria are increasingly being used to study how phenology is changing in the context of climate change (Meineke et al., 2018; Lang et al., 2019). The temporal, spatial, and taxonomic breadth of herbarium specimens make them a strong resource in understanding broad trends in phenological change (Heberling and Isaac, 2017; Meineke et al., 2019). Using 3,083 herbarium specimens collected between 1829 and 2019 across eastern North America, I assessed leaf-out and flowering times of 10 tree species (6 native, 4 non-native), 4 shrub species (2 native, 2 non-native), and 7 wildflower species (6 native, 1 non-native). I paired phenological data with historical climate data to quantify differences in phenological sensitivity to spring temperature across canopy strata, across species' geographical ranges, and between native and non-native species.

Chapter Four: Wildlife rehabilitation records for use in ecological research and conservation

Wildlife faces many threats from human activities and human-driven climate change, including hunting and fishing (Golden et al., 2016; Grade et al., 2019), vehicles (Gunson et al., 2011), human infrastructure (Loss et al., 2014; Loss et al., 2014), industrial and agricultural activities (Lemly et al., 2000; Trail, 2006), infectious diseases (Camacho et al., 2016), and extreme weather events (Maxwell et al., 2019). We need to understand the prevalence, patterns, and impacts of these threats to conserve wildlife populations. Wildlife rehabilitation (rehab) centers admit and treat injured and sick

wildlife, with the aim of returning them to the wild. Wildlife rehab centers collect data on animals admitted, including information on species, condition, location found, and outcome (Pyke and Szabo, 2018). Past studies have used rehab records to assess threats to wildlife, but these studies have usually covered only a small geographic area, a single species or small group of species, and/or a single category of threats (Janssen et al., 2020; Kelly and Sleeman, 2003; Ana et al., 2017). Now that records from wildlife rehab centers are becoming digitized, it is increasingly possible to access these data remotely and compile digitized datasets from software databases and individual centers that span much of North America. Reviews have proposed areas of research that wildlife rehab data may be used to study (Trocini et al., 2008; Pyke and Szabo, 2018), but no studies have comprehensively examined the ability of wildlife rehabilitation data to answer a variety of research questions at large geographic scales for a wide range of species. Such studies are particularly important to determine if certain iconic and endangered species face unique threats and if local threats to a species are part of a larger geographic phenomenon. Here, I used 674,320 digitized wildlife rehabilitation records from 94 centers across the USA and Canada to learn about threats that wildlife face and to assess which categories of research questions can be answered with rehab data. I used these findings to make recommendations to help conserve wildlife populations and improve wildlife health.

**CHAPTER TWO: COMPARING FRUITING PHENOLOGY ACROSS TWO
HISTORICAL DATASETS: THOREAU'S OBSERVATIONS AND HERBARIUM
SPECIMENS**

ABSTRACT

Fruiting remains under-represented in long-term phenology records, relative to leaf and flower phenology. Herbarium specimens and historical field notes can fill this gap, but selecting and synthesizing these records for modern-day comparison requires an understanding of whether different historical data sources contain similar information, and whether similar, but not equivalent, fruiting metrics are comparable to one another.

For 67 fleshy-fruited plant species, we compared observations of fruiting phenology made by Henry David Thoreau in Concord, Massachusetts (1850s) to phenology data gathered from herbarium specimens collected across New England (mid-1800s—2000s). To identify whether fruiting times and the order of fruiting among species are similar between datasets, we compared dates of first, peak, and last observed fruiting (recorded by Thoreau), and earliest, mean, and latest specimen (collected from herbarium records), as well as fruiting durations.

On average, earliest herbarium specimen dates were earlier than first fruiting dates observed by Thoreau; mean specimen dates were similar to Thoreau's peak fruiting dates; latest specimen dates were later than Thoreau's last fruiting dates; and durations of fruiting captured by herbarium specimens were longer than durations of fruiting observed

by Thoreau. All metrics of fruiting phenology except duration were significantly, positively correlated within ($r: 0.69-0.88$) and between ($r: 0.59-0.85$) datasets.

Strong correlations in fruiting phenology between Thoreau's observations and data from herbaria suggest that field and herbarium methods capture similar broad-scale phenological information, including relative fruiting times among plant species in New England. Differences in the timing of first, last, and duration of fruiting suggest that historical datasets collected with different methods, scales, and metrics may not be comparable when exact timing is important. Researchers should strongly consider matching methodology when selecting historical records of fruiting phenology for present-day comparisons.

INTRODUCTION

In contrast to climate-driven changes in leaf-out and flower phenology, which have been well-studied (Primack et al., 2004; Menzel et al., 2006; Cleland et al., 2007; Bertin, 2008; Miller-Rushing and Primack, 2008; Panchen et al., 2012; Polgar et al., 2013; Everill et al., 2014; Ellwood et al., 2019), climate-driven changes in fruiting phenology have been relatively neglected in ecological research (Bertin, 2008; Gallinat et al., 2015). Fruiting is vitally important to the reproductive success of plants and to many animals which rely on wild fruits for nutrition (Primack, 1987; Willson and Whelan, 1993; Parrish, 1997; Tiffney, 2004; Smith et al., 2013). Several studies have found that fruiting times are advancing with warmer temperatures (Menzel et al., 2006; Sherry et al., 2007; Gordo and Sanz, 2010; Panchen and Gorelick, 2015), although not in all cases

(Menzel et al., 2006; Sherry et al., 2007). Historical phenology records have been instrumental for studying changes in leaf out and flowering times, but fewer historical data sources exist to investigate similar patterns for wild fruits.

Herbaria are increasingly being used to study how phenology is changing in the context of climate change (Meineke et al., 2018; Lang et al., 2019). The temporal, spatial, and taxonomic breadth of herbarium specimens make them a strong resource in understanding broad trends in phenological change (Heberling and Isaac, 2017; Meineke et al., 2019). Herbarium specimens and historical field notes can fill gaps in our understanding of fruiting phenology by providing historical dates representing the beginning, middle, and end of fruiting, but their methodological eccentricities could present challenges for interpreting, comparing, and synthesizing the information those different data sets provide.

As researchers increase efforts to understand changes in fruiting phenology, it is important to determine how we can use and compare historical datasets. Historical datasets collected with different methods, comprised of different fruiting metrics, and collected across different geographical scales may reflect different ecological patterns (Pearse et al., 2017). If there are method, metric, or scale issues that limit comparison, then researchers need to be careful and deliberate in collecting present-day data with similar methods, metrics, and scales for comparison with these historical datasets. For instance, if herbaria and field observations capture different historical patterns, then historical herbarium records would not be an accurate historical basis to compare with present-day observations. Studies have successfully compared field observations and

herbarium records of flowering dates (Panchen et al., 2012; Davis et al., 2015), however there is less certainty that these data sources are comparable for fruiting phenology.

One challenge for synthesizing field observations and herbarium records is that these methods rely on different fruiting metrics (e.g. peak fruiting date vs. mean fruiting date), which may or may not be comparable. Potential field observation metrics include first fruiting date (Menzel et al., 2006; Sherry et al., 2007; Gordo and Sanz, 2010; Ettinger et al., 2018; Gallinat et al., 2018 b), peak fruiting date (Sherry et al., 2007; Ettinger et al., 2018; Gallinat et al., 2018 a; Gallinat et al., 2018 b), last fruiting date (Sherry et al., 2007; Gordo and Sanz, 2010; Gallinat et al., 2018 b), and the total duration of fruiting (Sherry et al., 2007). However, there are still gaps in our understanding of community fruiting patterns of plants in the wild and during longer time periods, and historical data from observations in the wild and herbarium specimens collected from wild plants can help to fill those gaps. Herbarium collections are based on different methods than are used to make field observations; for example, collectors are not always gathering specimens with the intention to capture first fruiting dates or other phenophases, whereas field observations are often conducted to do just that. Herbarium specimens are collected more frequently in spring and summer, so they may fail to accurately capture the end of fruiting seasons (Daru et al., 2017). In addition, herbaria contain a range of specimens that can be used to infer different metrics: earliest specimen to be collected in the season among all of the specimens, mean date of collection among all of the specimens, and last specimen collected among all of the specimens, instead of start, peak, and end of fruiting over the course of a season at a location. It is not clear

whether metrics using herbarium specimens are comparable to field observation metrics, as they do not directly capture the same phenophases. There are few historical datasets on wild fruits available, so it is important for researchers to know how to work with these differences and synthesize or choose between historical datasets.

Researchers have successfully used historical observations to identify how different functional groups have shifted with climate change in relation to one another and to explore the ecological consequences of those shifts (Heberling et al., 2019b). This research requires that historical records provide a reliable baseline for comparison, and one way to assess the comparability of observations and herbarium specimens is to determine if they provide similar baseline information, such as historical differences or similarities between fruiting times for woody and herbaceous species. While woody and herbaceous species differ in their leaf-out (Rich et al., 2008; Rollinson and Kaye, 2012) and flowering times (Miller-Rushing and Primack, 2008), it is unknown whether these functional groups differ in their fruiting times in temperate ecosystems (but see Giorgetti et al. 2000 for a comparison from a semiarid region). The extent to which these historical records reflect similar or different patterns among groups can indicate the resilience of these patterns to methods of collection, how much these patterns might depend on spatial and temporal scaling, and what methods should be used to compare these groups in the present-day to detect true shifts due to climate change or other aspects of a changing environment.

To assess the comparability of different historical datasets for fruiting phenology, we compared observations made by Henry David Thoreau to data collected from herbarium specimens. Observations made by Thoreau in Concord, Massachusetts in the 1850s have been used to study the effects of climate change on leaf-out, flowering, and bird migration (Miller-Rushing and Primack, 2008; Ellwood et al. 2010; Polgar et al., 2013). In 2001, a previously unpublished collection of Thoreau's fruiting observations of wild plants was released (Thoreau, 2001), expanding the opportunities for the use of Thoreau's data to include investigations of fruiting phenology. Herbarium specimens, which contain vast amounts of information on plant species and their phenological life stages (Davis et al., 2015; Willis et al., 2017a), can also serve as a source of fruit phenology data (Gallinat et al., 2018 a). Specimens are rapidly being digitized for easier access (Soltis, 2017; Daru et al., 2018; Yost et al., 2018; Panchen et al., 2019) and can enable researchers to examine fruiting records from a larger geographical range and longer timespan than is feasible with field studies (Willis et al., 2017a).

These two fruit phenology datasets—Thoreau's field observations and data from herbarium specimens—represent an opportunity to compare fruiting patterns and metrics in different historical datasets. Thoreau's observations capture fruiting phenology as first, peak, and last fruiting dates; similar, but not equivalent, metrics from herbaria are the earliest, mean, and latest specimens of the season among all of the specimens collected of a species. The datasets are similar in that they both assessed large numbers of the same species in New England, however they differ in geographical and temporal range and collection method. Previous work using herbarium specimens showed that while fruiting

times became slightly later (0.1 days/year) over 165 years in New England, geographical location is not a significant predictor of fruiting times (Gallinat et al., 2018 a). We therefore focus here on methodological differences between data sources, though we also acknowledge and consider the effects of sampling differences on the results of our comparison.

While the different metrics used in herbarium-based data and field observations could capture different ecological patterns, novel statistical tools have the potential to minimize these differences. The Weibull method developed by Pearse et al. (2017) is a technique for estimating true first dates from existing observations, using a Weibull distribution. When collecting data on phenological events, there is a low likelihood of capturing the very first event—for instance, it may occur at an earlier time or in a different location than where data are collected. The Weibull method uses existing observations to estimate when the true first date may be and has primarily been used to estimate first flowering dates (Pearse et al., 2017). Here, we test this new method with herbarium fruiting data to estimate “true” earliest fruiting dates, and test whether these dates are more similar to Thoreau’s observed first fruiting dates than are the earliest herbarium specimen dates.

In this study, we address the following questions:

- 1) How does the order of fruiting, for the same species, compare between Thoreau's field observations and herbarium specimens?

- 2) How strongly correlated are the metrics of fruiting phenology within each dataset, and how do similar but not equivalent metrics compare across datasets (e.g. first fruiting vs. earliest herbarium specimen date, and peak fruiting vs. mean specimen date)?
- 3) Does the Weibull method for estimating true first dates from herbarium data increase the comparability of these data with Thoreau's field observations?
- 4) Are the differences or similarities in fruiting phenology between woody and herbaceous species similar between these two datasets?

Answers to these questions will allow future researchers to optimize use of historical datasets when studying how fruiting phenology responds to climate change.

MATERIALS AND METHODS

Metrics of fruiting phenology

For herbarium specimens, we use the date of the earliest and latest ripe fruit observation across all seasons, and we calculate mean fruiting date for each species across all specimens in all years. Thoreau provides fruiting observations from Concord in a style that we can readily interpret as first (first observation), peak ("prime"), or last ("finished," "last through") fruiting dates, though he does not provide any description of his methods of observation or reporting. For some species he does not provide the year of observation, whereas for other species he lists one or more years of observation. The duration of fruiting is calculated as the time from first fruiting date to last fruiting date. The progression of fruiting stages provided by both Thoreau's records and herbarium specimens does not reflect measurements of individuals or species within a single fruiting

season; instead, these observations are drawn from different individuals across the range of years and locations.

Thoreau's observations

Henry David Thoreau made observations of fruiting phenology in and near Concord, Massachusetts over an 11-year period from 1850 to 1860. We compiled Thoreau's observations of first fruiting dates from his book *Wild Fruits* (Thoreau, 2001) for 72 native plant species that have fleshy fruits. Of these species, he also recorded peak dates for 31 species and last dates for 29 species. Thoreau generally recorded one date per species for each metric of first, peak, and last dates. When Thoreau recorded imprecise dates (e.g., "middle July" or "end of August"), we assigned dates using a standard rubric (Table 2.1). Thoreau recorded exact dates for all first dates, 29 of 31 peak dates, and 3 of 29 last dates.

Herbarium specimens

For the same species that Thoreau observed, we inspected herbarium specimens in person and online for most woody species and exclusively online for herbaceous species and the remaining woody species (Figure 2.1). We accessed digitized versions of specimens from the Consortium of Northeastern Herbaria (<http://portal.neherbaria.org>), Harvard University Herbarium (<http://huh.harvard.edu>), University of Connecticut Herbarium (<http://bgbaseserver.eeb.uconn.edu>), and iDigBio portal (<https://www.idigbio.org/portal>). Thirty-one of the study species had already been

evaluated for phenology and included in a recent study (Gallinat et al., 2018 *a*), and for an additional 41 species, we evaluated the presence of fruits using the same protocols: fruits were determined to be ripe based on a combination of color, size, and apparent texture when the specimen was pressed. If the specimen had ripe fruits, we recorded the date, location, collector, and herbarium. We collected data from specimens across New England (Massachusetts, Rhode Island, Connecticut, Vermont, New Hampshire, and Maine) (Figure 2.2) and across the timespan of available specimens (mid-1800s to early 2000s) (Figure 2.3).

We excluded specimens that were collected at the same location on the same day in order to not overrepresent areas with high sampling effort. We excluded three species that Thoreau monitored which have fruit year-round and for which it is difficult to determine if the fruits on the specimens are from the previous year or the current year: *Gaultheria procumbens*, *Juniperus virginiana*, and *Mitchella repens*. We also excluded two species for which it is difficult to distinguish ripe from unripe fruits: *Peltandra virginica* and *Symplocarpus foetidus*.

For the final analyses, we used 67 species, of which 65 were native species and 2 were non-native species, with data collected from 3,432 herbarium specimens of these same species. Of the specimens, 2,264 were from woody plants, and 1,168 were from herbaceous plants. Species' herbarium specimen sample sizes ranged from 20 (*Sassafras albidum*) to 181 (*Vaccinium angustifolium*). For comparisons with Thoreau's observations, we included 67 species in analyses of first fruiting, 31 species in analyses of peak fruiting, and 29 species in analyses of last fruiting and duration.

Data analysis

All analyses were conducted using R Statistical Software, version 3.5.1 (R Core Team, 2018). We conducted Shapiro-Wilk normality tests of the data. All data were normal except for Thoreau's observations of peak dates, last dates, and durations; when we analyzed these data using non-parametric Wilcoxon signed-rank tests, results were identical to paired T-tests. Here, for simplicity of interpretation, we present results from paired T-tests for all analyses.

We conducted paired T-tests to compare the differences between Thoreau's observations of first date, peak date, last date, and duration, and the date of the earliest specimen, mean, latest specimen, and duration of herbarium specimens for each species (duration of herbarium specimens is time from the earliest to the latest specimen). To understand if any differences in variance may affect differences in fruiting times, we ran F-tests to test for equal variance in these four fruiting metrics between the two datasets. To determine the correlations for each metric of fruiting phenology between the two datasets, we calculated Pearson's correlation coefficients for all species together. We also calculated the correlations between first, peak, and last dates for Thoreau's observations, and earliest, mean, and latest specimens for the herbarium specimens, for all species together within each dataset.

To test whether geographic and temporal biases of these historical datasets affected the ecological patterns they captured, we conducted additional analyses with data restricted to similar geography and years. Due to the longer timespan and larger

geographical area encompassed by the herbarium specimens, we conducted analyses comparing the differences between fruiting times and correlations between Thoreau's observations and the herbarium specimens using 1) only herbarium specimens collected before 1950, and 2) only herbarium specimens collected in Massachusetts, Connecticut, and Rhode Island. These analyses did not produce different results from the full dataset, as the geographical differences and the differences over time were relatively minor in comparison to the differences among species. As a result, we used the full herbarium dataset for all analyses and interpretation.

To test whether Weibull "true" first dates were more similar to Thoreau's observations than were earliest specimen dates, we used the *phst* package (Pearse et al., 2017) to calculate Weibull first date estimates from the herbarium specimens. The Weibull method uses existing observations to produce an estimate of the first date with 95% confidence intervals. The estimate is affected by the distribution and number of observations underlying the estimate. For example, a greater number of observations clustered closer to the observed first date will result in an estimate that is closer to the observed first date and smaller confidence intervals. As confidence intervals could not be calculated for *Vaccinium corymbosum*, this species was excluded from analyses using confidence intervals. To identify how different the herbarium-based Weibull estimates were from earliest specimen dates, we calculated correlations. To test whether Weibull estimates or earliest specimen dates have a stronger relationship with Thoreau's dates, we compared the correlations between 1) Thoreau's observed first dates and the Weibull first dates and 2) Thoreau's observed first dates and the herbarium earliest specimen dates.

To compare fruiting phenology between woody and herbaceous species, we ran non-paired T-tests comparing the two groups for each phenophase, within each dataset. We compared between woody and herbaceous species for first date, peak date, last date, and duration for Thoreau's observations, and earliest specimen, mean specimen date, latest specimen, and duration for the herbarium specimens. We excluded *Rubus pubescens* from this analysis, as it is a subshrub or herbaceous perennial and does not fall easily into either group.

RESULTS

Comparing fruiting sequence between Thoreau's observations and the herbarium specimens

Three of the four comparable metrics of fruiting time are significantly positively correlated between Thoreau's observations and the herbarium specimens. We found that the most highly-correlated metric of fruiting between the two datasets is last fruiting date/latest herbarium specimen ($r = 0.85$, $P < 0.001$) (Table 2.2). The next most correlated is peak fruiting date/mean herbarium specimen ($r = 0.78$, $P < 0.001$), followed by first fruiting date/earliest herbarium specimen ($r = 0.59$, $P < 0.001$). Duration is not significantly correlated between the two datasets ($P > 0.05$).

These correlations demonstrate strong consistency in the sequence of fruiting. Species like *Fragaria virginiana*, *Amelanchier* sp., and *Vaccinium angustifolium* consistently fruit early in the season (first fruit in June), while *Aralia racemosa*, *Ilex*

verticillata, and *Nyssa sylvatica* start fruiting late in the season (first fruit in August or September) in both datasets (Figure 2.4).

Differences in fruiting times between Thoreau's observations and the herbarium specimens

In comparing Thoreau's observations and data from herbarium specimens for the different metrics of fruiting, we found that, on average, the earliest herbarium specimens are 28 days earlier than Thoreau's observed first fruiting dates ($t = 10.96$, $df = 66$, $P < 0.001$), and the latest herbarium specimens are 18 days later than Thoreau's observed last fruiting dates ($t = 4.63$, $df = 28$, $P < 0.001$; Table 2.3). Peak fruiting dates and mean herbarium specimens are not significantly different between the two datasets ($t = 0.97$, $df = 30$, $P = 0.34$). Thus, average duration of fruiting is 39 days longer for the herbarium specimens ($t = 7.29$, $df = 28$, $P < 0.001$).

Some species, like *Rubus occidentalis* and *Sambucus canadensis*, have similar first fruiting dates and earliest herbarium specimens in both datasets. Other species show large differences between the two datasets. The earliest specimen of *Solanum ptychanthum* is 79 days earlier than Thoreau's first fruiting date for this species; the earliest *Lindera benzoin* specimen is 75 days earlier, and the earliest *Myrica pensylvanica* specimen is 64 days earlier. Although the earliest herbarium specimens are earlier on average, there are a few species with earlier dates in Thoreau's observations. For example, *Gaylussacia baccata* has a first fruiting date 17 days earlier in Thoreau's observations. There are similar differences for last fruiting dates and latest herbarium

specimens. *Sassafras albidum* and *Crataegus macrosperma* have similar last fruiting dates and latest herbarium specimens in each dataset. On the other hand, the latest *Rubus pubescens* specimen is 63 days later than Thoreau's observed last fruiting date, and the latest *Myrica pensylvanica* specimen is 46 days later. Meanwhile, *Smilax rotundifolia* has a last fruiting date 30 days later in Thoreau's observations.

By testing for equal variance in first fruiting date vs. earliest herbarium specimen, peak fruiting date vs. mean herbarium specimen, last fruiting date vs. latest herbarium specimen, and fruiting duration across the two datasets, we found that the only metric for which variances are statistically different is first fruiting date/earliest specimen ($F = 1.64$, $df = 66$, $P = 0.046$; Table 2.4), with Thoreau's observations having greater variance.

Comparing fruiting metrics within Thoreau's observations and the herbarium specimens

Within datasets, different fruiting metrics (e.g., Thoreau's observations of first, peak, and last fruiting dates) are significantly positively correlated to one another, and relationships among metrics are stronger in Thoreau's observations than the herbarium specimens (Table 2.5). For both datasets, the highest correlation is between first date or earliest specimen and peak date or mean specimen (Thoreau: $r = 0.88$, $P < 0.001$; Herbarium: $r = 0.77$, $P < 0.001$). The next highest correlation is between peak or mean and last date or latest specimen (Thoreau: $r = 0.77$, $P < 0.001$; Herbarium: $r = 0.47$, $P < 0.001$). The lowest correlation, though still highly significant, is between first date or earliest specimen and last date or latest specimen, with the herbarium specimens having a

much lower correlation than Thoreau's observations (Thoreau: $r = 0.74$, $P < 0.001$; Herbarium: $r = 0.40$, $P < 0.001$).

Weibull first fruiting dates

Applying the Weibull method to the herbarium data results in first fruiting date estimates that are four days earlier, on average, than the herbarium earliest specimen dates ($t = 8.90$, $df = 66$, $P < 0.001$; Table 2.6), and the two are strongly correlated ($r = 0.98$, $P < 0.001$; Table 2.6). For most species, Weibull dates are only a few days earlier than earliest specimen dates; however, there are some exceptions: the Weibull first fruiting date is 23 days earlier for *Myrica pensylvanica* and 19 days earlier for *Sassafras albidum*. The first dates Thoreau observed are more strongly correlated with the earliest herbarium specimens ($r = 0.59$, $P < 0.001$) than with the Weibull estimated first dates ($r = 0.48$, $P < 0.001$). Most of the Thoreau's first dates (92%) occur later and fall outside of the 95% confidence intervals (CIs) for the Weibull estimated first dates.

Differences in fruiting times between woody and herbaceous species

In comparing the fruiting times of woody and herbaceous species, we found largely the same results when using Thoreau's observations and the herbarium specimens. With Thoreau's observations, there were no significant differences between woody and herbaceous species' fruiting times for first date ($t = 0.10$, $df = 32$, $P = 0.921$), peak date ($t = 1.20$, $df = 22$, $P = 0.244$), last date ($t = 1.06$, $df = 13$, $P = 0.303$), and fruiting duration ($t = 2.00$, $df = 26$, $P = 0.057$; Table 2.7). Similarly, with the herbarium

specimens, there were no significant differences between woody and herbaceous species' fruiting times for earliest specimen date ($t = 0.21$, $df = 28$, $P = 0.837$), mean specimen date ($t = 0.29$, $df = 14$, $P = 0.778$), and latest specimen date ($t = 1.78$, $df = 10$, $P = 0.107$). In contrast to Thoreau's observations, the herbarium specimens indicate that woody species did have significantly longer fruiting durations ($t = 2.61$, $df = 13$, $P = 0.022$).

DISCUSSION

Historical records can be invaluable to understanding changes in phenology over time and in relation to climate change. Historical records of wild fruiting times are particularly rare, and, as with all historical records, should be selected and synthesized for phenology research with an understanding of how their methodological qualities and sampling issues might affect the ecological patterns they capture. Here, we find that two historical datasets of fruiting phenology—herbarium specimens collected from 1849-2016, and observations made by Henry David Thoreau from 1850-1860—reflect broadly similar patterns in the order of fruiting times and differences between herbaceous and woody plant species in New England. However, we find that the exact timing of different fruiting stages (defined with similar, but not equivalent, metrics) differs for some species between the two datasets, in some cases widely. We find that Weibull estimates of first “true” fruiting dates calculated from herbarium specimens do not increase comparability between the two data sets. Given the differences between these datasets, we recommend researchers consider, as much as possible, matching methodology, including the data source, phenophase metrics, and scaling, when selecting historical records of fruiting

phenology for present-day comparisons. Where this is not possible, researchers should be aware of these issues and how they might affect the outcome of their study.

Consistency of fruiting sequence and duration between datasets

First date and earliest specimen, peak date and mean specimen, and last date and latest specimen are highly correlated between Thoreau's observations and the herbarium specimens. These relationships indicate that there is a very consistent order of fruiting across species, and that this pattern is robust to differences in collection method and phenophase metric. Both historical datasets appear to be capturing a real biological trend in fruiting patterns: the sequence of fruiting for these 67 species is relatively consistent across New England. A consistent trend in the order of fruiting times in woody plants across states in New England was also found by Gallinat et al. (2018a) for many of the same species. Other studies in this region have similarly found that there is a consistent order to when species leaf out (Polgar et al., 2013; Everill et al., 2014; Panchen et al., 2014) and flower (Miller-Rushing and Primack, 2008; Ellwood et al., 2013). Our study builds on previous results by additionally including herbaceous species, using two different methods, and demonstrating that the order of fruiting across species remains consistent when herbaceous species are considered.

Surprisingly, we found that between the two datasets, last fruiting dates and latest specimens were more strongly correlated than did first and earliest, or peak and mean fruiting dates. We expected peak or mean dates to be the most consistent because mean phenological values tend to be less affected by sample size or variability (Miller-Rushing

et al., 2008). In addition, peak flowering dates have been shown to be more comparable between field observations and herbarium specimens than first dates (Davis et al., 2015). Furthermore, Gallinat et al. (2018b) found a stronger correlation between first fruiting and start of peak fruiting than between end of peak and last fruiting, when comparing across recent years and locations of botanical gardens in the U.S., Germany, and China.

It is possible that the stronger correlation between last dates and latest specimens in our study reflects a consistent order in which fruits are consumed by wildlife. Last dates may combine information on both fruiting order and frugivore feeding preferences. For example, fruits with higher antioxidant contents like arrowwood (*Viburnum dentatum*) may reliably be eaten first, whereas less-desirable fruits like winterberries (*Ilex verticillata*) may consistently be left until later in the season (Bolser et al., 2013), which could be reflected in later field observations and specimen collections. Other studies support this trend of preference for certain fruits, indicating for example that birds select fruits with higher lipid content (Stiles, 1980; Greenberg and Walter, 2010).

A future study could determine if this correlation between last fruiting dates and latest herbarium specimens is driven by frugivore feeding preference, phenology, or abundance and nutritional quality of fruits of different species. Studies should also compare fruiting data to bird migration and feeding data to understand how the timing of fruiting coincides with the timing of bird migration, and the impacts any potential mismatches could have on plant and bird populations

Duration of fruiting is not significantly correlated between the two datasets. This may be due to differences in the frequency and duration of sampling, which should be

considered when interpreting historical data on fruiting times. Collectors of herbarium specimens are not looking for the very first and last fruit, whereas Thoreau was.

Differences in fruiting times between Thoreau's observations and the herbarium specimens

The exact timing of fruiting frequently differed between the two datasets. The herbarium specimens have consistently earlier earliest specimens, later latest specimens, and longer durations than Thoreau's observations. The herbarium specimens represent a greater number of years and a greater geographical range; however, our analyses suggest that this is not the main reason for the difference in fruiting times. When we compare Thoreau's observations to herbarium specimens temporally restricted to before 1850 or geographically restricted to southern New England, the results are nearly the same as when comparing all of the herbarium specimens. Further, the results of our equal variance tests indicate that these differences are not due to the herbarium data having greater variance in fruiting dates. On the other hand, the herbarium specimens and Thoreau's observations have peak dates that are not significantly different. In contrast to our findings, Davis et al. (2015) found that field studies captured first flowering dates three days earlier on average than herbarium specimens. The difference in first and last fruiting dates may be attributable to differences in the frequency and duration of sampling, which should be considered when interpreting historical data on fruiting times. These metrics may not be equivalent when comparing the timing of the start and end of fruiting.

Comparison of fruiting metrics within datasets

We found that, within datasets, the different fruiting metrics—first date, peak date, and last date for Thoreau’s observations and earliest specimen, mean specimen, and latest specimen for the herbarium specimens—are mostly highly correlated with one another (r : 0.69–0.88, except herbarium earliest and latest fruiting $r = 0.40$). This finding echoes previous findings of relationships among fruiting stages at botanical gardens (Gallinat et al., 2018b) and other studies which have found that the timing of plant phenophases are correlated (Schwartz and Reiter, 2000; Ettinger et al., 2018). These correlations indicate that the three metrics of fruiting phenology within each dataset capture some redundant information. However, Miller-Rushing et al. (2008) caution that first flowering dates are more variable than peak dates. First dates are dependent on population size, sample size, and sampling frequency. In our analysis, we found that the herbarium specimens have consistently earlier earliest specimens and later latest specimens than Thoreau’s observed first and last dates, whether we used the whole data set or if we just used only the herbarium specimens collected before 1950. Similarly, the results hold when we only use specimens from southern New England. These consistent results further support the conclusion that the beginning and end of a phenophase are more influenced by differences in frequency and duration of sampling. Therefore, we recommend comparing peak or mean fruiting dates when investigating the timing of a phenophase, particularly if a study is merging data from different breadths of space and time. However, peak and mean fruiting metrics were not the most strongly correlated

across datasets (particularly compared to end of fruiting metrics), indicating that peak and mean probably do not capture identical information. When choosing datasets, the most accurate and useful comparisons will still likely be between datasets with similar methods, metrics, and scaling.

Evaluating the Weibull method

We found that estimates of first fruiting dates calculated from the herbarium data using the Weibull method were, on average, four days earlier than corresponding earliest specimen dates, but the order of fruiting remained the same. Small windows of time may have important biological implications for some species. For example, in *Frangula alnus*, later fruits were more likely to be dispersed by birds (Bolmgren and Eriksson, 2014).

There were a few species for which the Weibull first fruiting date was more than a week earlier (10-20 days) than the earliest specimen date. These larger shifts may be due to a smaller sample size and greater variation in the spread of the samples for these species. For example, *Myrica pensylvanica*'s first date shifts 23 days earlier, and it has a sample size of 30 herbarium specimens; *Sassafras albidum*'s first date shifts 19 days earlier, and it has a sample size of 20. In contrast, some of the other species are represented by over 100 samples.

We also compared first fruiting dates observed by Thoreau to the earliest specimens gathered from herbarium specimens and to those generated using a Weibull approach on the herbarium dates. If Thoreau's observations were more strongly correlated with the Weibull first fruiting dates, it could suggest that applying this tool

improves the proximity of herbarium-based estimates to field-based estimates. However, we found that Thoreau's first dates were more strongly correlated with the herbarium earliest specimens than with the Weibull first dates. Future research should clarify if the small differences in first fruiting dates found when comparing the herbarium specimens and Weibull method estimates are biologically important.

Comparing fruiting times of woody and herbaceous species

Thoreau's observations and the herbarium specimens produced similar results for whether woody and herbaceous species differ in their fruiting phenology. Using each dataset, we found that woody and herbaceous species did not differ significantly in fruiting timing for any of the metrics, except duration using the herbarium specimens, which indicated that woody species fruited for longer periods. Herbaceous and woody species started fruiting at about the same time. Woody species fruited later, but not significantly so, than herbaceous species, on average (13 days for Thoreau's observations and 23 days for the herbarium specimens). Using Thoreau's observations, fruiting duration was 14 days longer for woody species, although this difference was not significant. On the other hand, using the herbarium specimens, woody species' fruiting duration was 22 days longer, and this difference was significant. Differences in statistical results may be due to the small number – 7 – of herbaceous species included in these analyses of end of season metrics. Overall, these two historical datasets appear to be comparable when comparing woody and herbaceous species, and future studies should be

able to use these historical data as baselines for comparison to identify whether these groups have shifted their fruiting times in relation to one another.

CONCLUSIONS

Historical records of wild fruiting times are rare and valuable resources for understanding how fruiting times are changing; they should be selected and synthesized for phenology research with an understanding of how their methodological qualities might affect the ecological patterns they capture. This study demonstrates that two different historical datasets—Thoreau’s observations and herbarium specimens—capture very similar information about the order in which woody and herbaceous species fruit in New England. The high correlations of metrics within datasets confirm findings from previous studies and helps validate these historical datasets. The high correlations between the metrics of fruiting in Thoreau’s observations and the herbarium specimens suggest that we may successfully use and compare different methodologies for studying the order in which species fruit. Differences among species are large and consistent enough to clearly emerge regardless of the two methods used here. On the other hand, these datasets do not reflect consistent fruiting timing for the same species, with the earlier earliest and later latest herbarium specimens. Therefore, different historical datasets with similar, but not equivalent, methods may not provide the same information about the timing of the beginning and end of the fruiting season. We find that Weibull estimates of first “true” fruiting dates calculated from herbarium specimens do not increase comparability between the two datasets. Nonetheless, we find that the datasets

do identify similar patterns between the fruiting phenology of herbaceous and woody species. Given that the results from these datasets are not altogether consistent, we recommend researchers strongly consider matching methodology, including the data source, phenophase metrics, and scaling, when selecting historical records of fruiting phenology for present-day comparisons.

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TABLES AND FIGURES

Table 2.1: Standard rubric for assigning dates for Thoreau’s descriptions of fruiting timing. All dates from January and February of the following year were characterized as December 31 (DOY 365) to indicate in the analyses that these fruiting events were late in the season, not extremely early in the season.

Thoreau's Description	Assigned Date	Day of Year (DOY)
"Middle July"	July 15	196
"Late July"	July 30	211
"Through July"	July 30	211
"August"	August 15	227
"Middle August"	August 15	227
"End of August"	August 30	242
"Till September"	September 1	244
"Early September"	September 5	248
"Into September"	September 10	253
"Middle September"	September 15	258
"Through September"	September 30	273
"Early October"	October 5	278
"Through October"	October 30	303
"November"	November 15	319

Table 2.2: Pearson’s correlations between Thoreau and herbarium data for different metrics of fruiting. Significance is indicated by *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, and n.s. = not significant. N is the number of species included.

Metric of Fruiting	r	n	Significance
First/Earliest	0.59	67	***
Peak/Mean	0.78	31	***
Last/Latest	0.85	29	***
Duration	0.34	29	n.s.

Table 2.3: Differences between Thoreau and herbarium fruiting metrics. Differences are mean herbarium dates minus Thoreau dates. Negative values indicate earlier herbarium dates, and positive values indicate later dates or longer durations for the herbarium data. Significance is indicated by *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, and n.s. = not significant. N is the number of species included.

Metric of Fruiting	Difference in means (95% CI)	n	Significance
First/Earliest	-28.2 (-23.0 to -33.3)	67	***
Peak/Mean	-3.0 (-9.2 to 3.3)	31	n.s.
Last/Latest	18.4 (10.3 to 26.6)	29	***
Duration	39.1 (28.1 to 50.1)	29	***

Table 2.4: F-values from tests of equal variance between the Thoreau and herbarium data for different metrics of fruiting. F-values are ratios of the Thoreau variance / herbarium variance. Values greater than 1 indicate that the variance is greater in the Thoreau dataset. Significance is indicated by *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, and n.s. = not significant. N is the number of species included.

Metric of Fruiting	F-value (95% CI)	Significance	n
First/Earliest	1.64 (1.01 to 2.67)	*	67
Peak/Mean	1.38 (0.66 to 2.85)	n.s.	31
Last/Latest	1.84 (0.86 to 3.91)	n.s.	29
Duration	1.40 (0.66 to 2.99)	n.s.	29

Table 2.5: Pearson’s correlations between metrics of fruiting within the Thoreau and herbarium datasets. Significance is indicated by *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, and n.s. = not significant. N is the number of species included.

Metric of Fruiting	Dataset	r	n	Significance
First & Peak	Thoreau	0.88	31	***
Earliest & Mean	Herbarium	0.77	67	***
Peak & Last	Thoreau	0.77	16	***
Mean & Latest	Herbarium	0.69	67	***
First & Last	Thoreau	0.74	29	***
Earliest & Latest	Herbarium	0.40	67	***

Table 2.6: Differences in mean first dates and correlations of first dates between the Weibull method, Thoreau dataset, and herbarium dataset. The difference subtracts the second dataset listed from the first. A positive number means that the *second* dataset listed has *earlier* first dates. Significance is indicated by *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, and n.s. = not significant. N is the number of species included.

Dataset Comparison	Difference in means (+/- 95% CI)	Significance (means)	n	r	Significance (r)
Herbarium-Weibull	4.4 (3.4 to 5.4)	***	67	0.98	***
Thoreau-Weibull	32.6 (26.9 to 38.3)	***	67	0.48	***
Thoreau-Herbarium	28.2 (23.0 to 33.3)	***	67	0.59	***

Table 2.7: Differences between woody and herbaceous species fruiting metrics in the Thoreau and herbarium datasets. Differences are mean woody dates minus mean herbaceous dates. Negative values indicate earlier dates or shorter durations for woody species, and positive values indicate later dates or longer durations for woody species. Significance is indicated by *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, and n.s. = not significant. N is the number of species included.

Metric of Fruiting	Dataset	Difference in means (95% CI)	Significance	Woody n	Herbaceous n
First	Thoreau	0.7 (-13.2 to 14.5)	n.s.	48	18
Earliest	Herbarium	1.2 (-10.7 to 13.2)	n.s.	48	18
Peak	Thoreau	-11.5 (-31.4 to 8.4)	n.s.	21	10
Mean	Herbarium	-2.9 (-24.5 to 18.7)	n.s.	21	10
Last	Thoreau	13.4 (-13.1 to 39.9)	n.s.	21	7
Latest	Herbarium	23.1 (-6.0 to 52.2)	n.s.	21	7
Duration	Thoreau	14.3 (-0.4 to 29.0)	n.s.	21	7
Duration	Herbarium	22.0 (3.7 to 40.3)	*	21	7



Figure 2.1: Image of a digitized *Clintonia borealis* herbarium specimen with ripe fruits, accessed online through the Consortium of Northeast Herbaria (<http://portal.neherbaria.org/portal>). The specimen was collected on August 5, 1931 in Cornwall, Connecticut (Catalog No.: CONN00123819). Fruits were determined to be ripe using a combination of color, size, and apparent texture when the specimen was pressed.

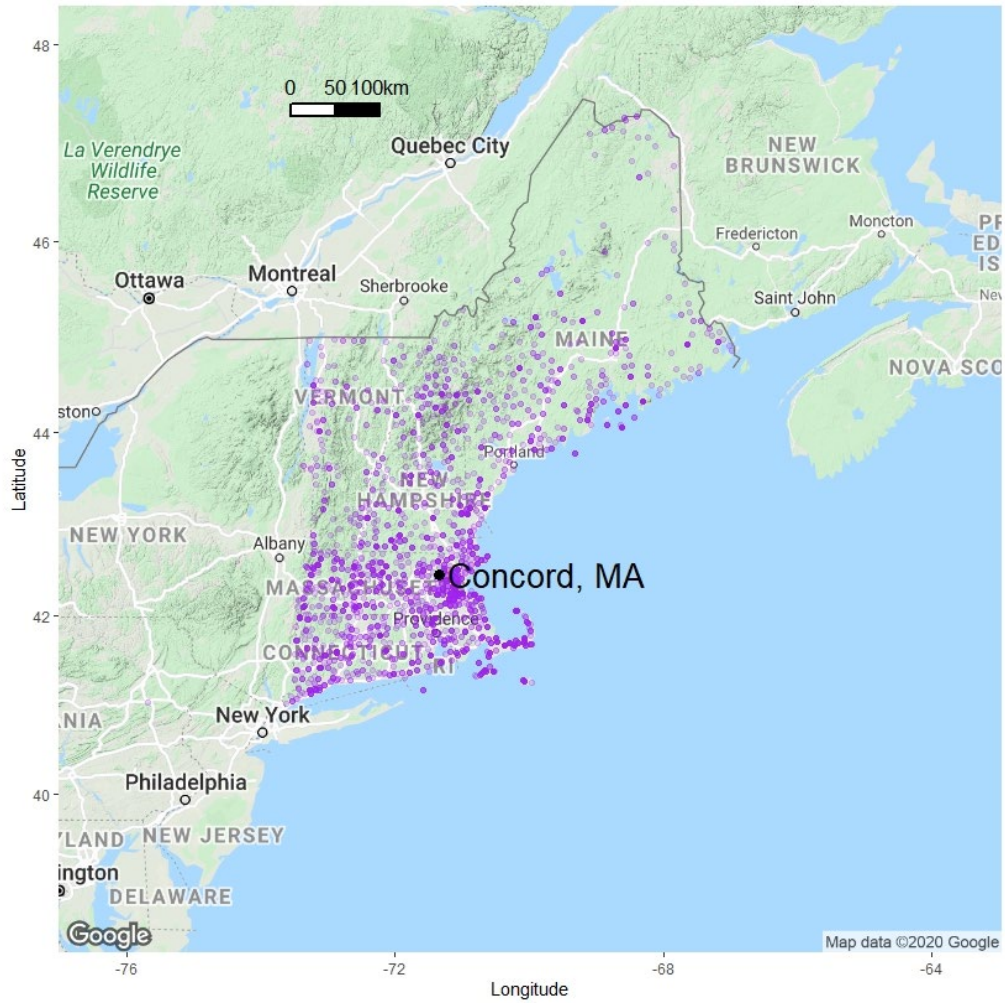


Figure 2.2: Map of the locations of the herbarium specimens in New England. Darker color indicates that points are overlapping and more specimens are found in that area. The black dot labeled “Concord, MA” indicates where Thoreau recorded his observations. Base map from Google Maps ©2020.

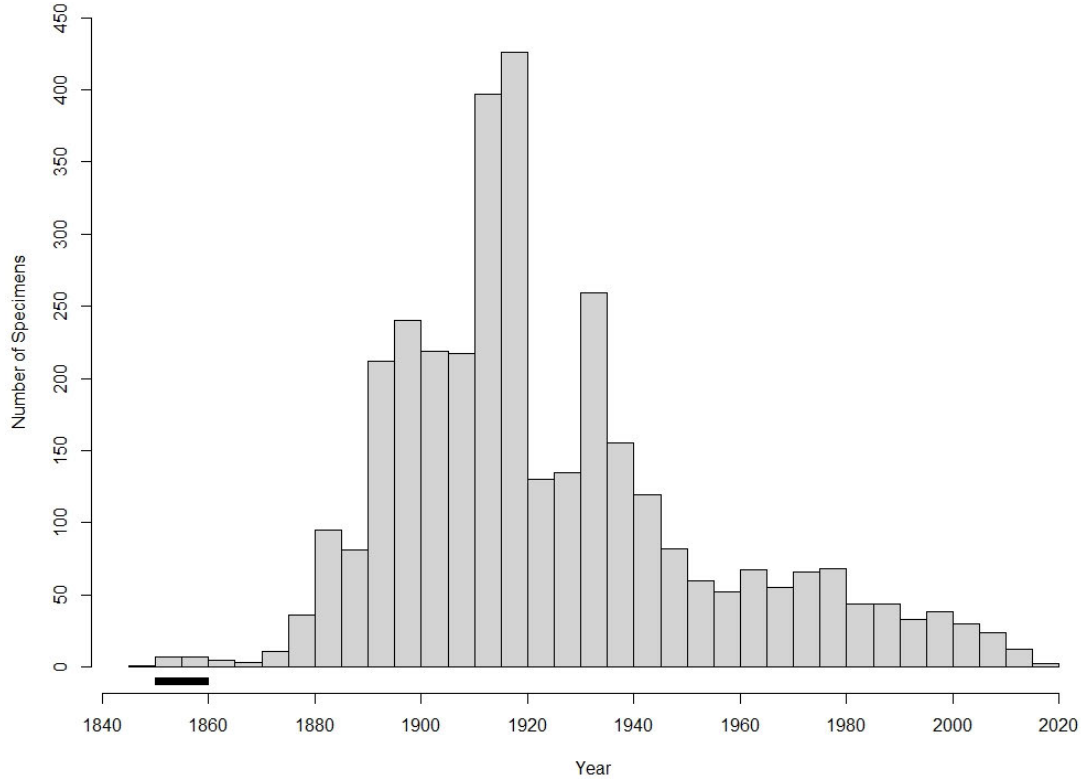


Figure 2.3: Histogram of the number of herbarium specimens collected ($n = 3,432$) by year, from 1849 to 2016. The black bar represents the timespan (1850 to 1860) when Thoreau recorded his observations.

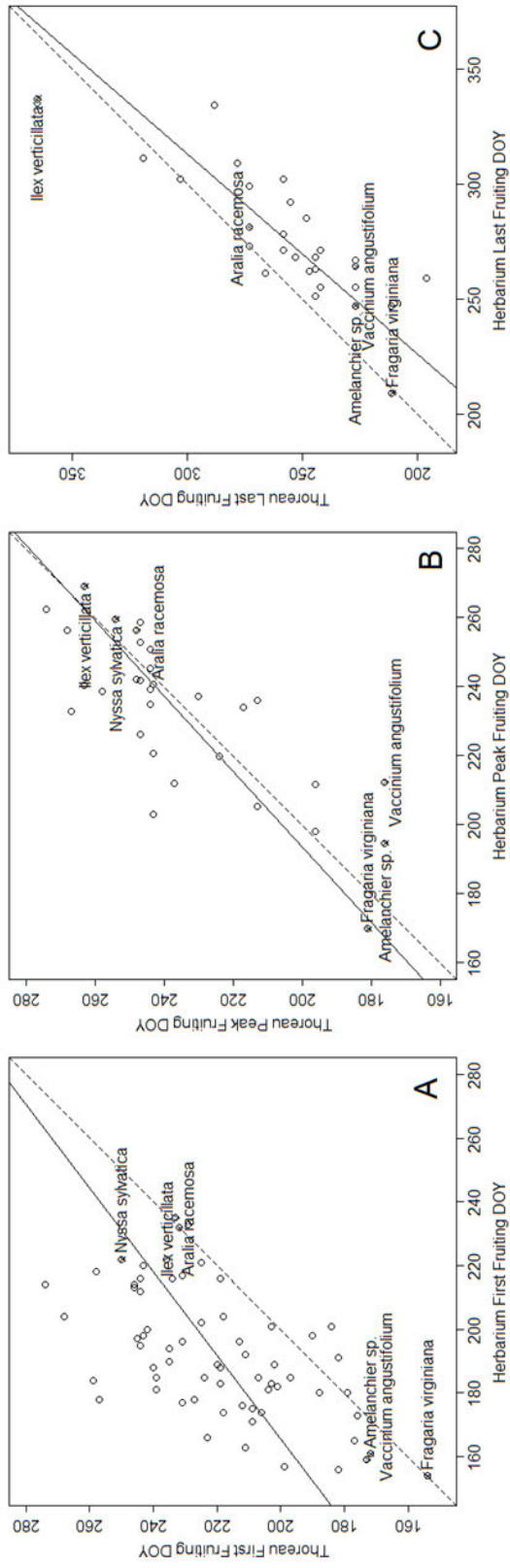


Figure 2.4: Linear regressions comparing Thoreau's observations and the herbarium specimens for (A) first fruiting dates ($y=0.76x+73.9$, $P < 0.001$, $R^2 = 0.34$), (B) peak fruiting dates ($y=0.91x+23.1$, $P < 0.001$, $R^2 = 0.59$), and (C) last fruiting dates ($y=1.15x-60.2$, $P < 0.001$, $R^2 = 0.71$). Three typically early-fruiting species (*Amelanchier* sp., *Fragaria virginiana*, and *Vaccinium angustifolium*) and three late-fruiting species (*Aralia racemosa*, *Ilex verticillata*, and *Nyssa sylvatica*) are labeled. The dotted lines are 1:1 lines, and the solid lines are linear regression lines.

**CHAPTER THREE: WARMING TEMPERATURES ARE LINKED TO
PHENOLOGICAL MISMATCH AMONG NATIVE AND NON-NATIVE TREES,
SHRUBS, AND WILDFLOWERS ACROSS THE EASTERN DECIDUOUS
FOREST OF NORTH AMERICA**

NATIVE LAND ACKNOWLEDGEMENT

This research studies plants found in deciduous forest ecosystems across the eastern United States. We acknowledge that our institutions and study sites are located within the ancestral and unceded homelands of many Indigenous communities. Below, we recognize the specific location where we work and the specific communities who first called this site their home. We also recognize that land acknowledgements are not enough to rectify the violence, forcible displacement, and treaty violations by early European colonists and US federal, state, and governments on Indigenous peoples. However, we hope our land acknowledgement will offer recognition and respect to the people who lived and worked on these lands, create public awareness about the history of where we work, promote the decolonization of ecology and conservation biology, and serve as a call that more work needs to be done to promote social justice in our profession and in our nation.

Suffolk County, Massachusetts

The Boston University main campus in Boston, MA is located on lands once occupied by the Massachusett (*Mass-adchu-es-et*) people, the Pawtucket people, and the

Wampanoag people (Wôpanâak). English colonizers and the United States and Massachusetts Commonwealth governments decimated the Indigenous people through forcible removal, forced assimilation, land grabbing, and genocide. Many people of these and other Indigenous Nations still live in Massachusetts today.

Allegheny County, Pennsylvania

The University of Pittsburgh main campus and the Carnegie Museum of Natural History (CMNH) in Pittsburgh, PA are located on lands once occupied by the Monongahela people (autonym unknown), the Seneca (*O-non-dowa-gah*) people--one of the Six Nations of the Haudenosaunee (hoe-den-ah-show-nee)--and the Lenape (*Lenni-Lenape* or Delaware) people, the Wyandot (*Wandat*) people, the Shawnee (*Shaawanwaki*) people, and the [Osage Nation](#) (*Wahzhazhe*). These lands are home to many nations and peoples, in part, because of continued colonial expansion that forced entire nations to move westward to avoid violence and extirpation. European colonists violated multiple treaties and used the Indian Removal Act of 1830 to forcibly remove the Seneca (now the [Seneca-Cayuga Nation](#)), Lenape (now the [Delaware Nation](#) and [Delaware Tribe of Indians](#)), Wyandot (now the [Wyandotte Nation](#)), and Shawnee (now the [Absentee-Shawnee Tribe of Indians of Oklahoma](#), [Eastern Shawnee Tribe of Oklahoma](#), and [Shawnee Tribe](#)) to what is now Oklahoma, where many of their descendants live today. A related group of Seneca are the [Seneca Nation of Indians](#) who today live in Salamanca, New York.

We encourage our readers to use the Native Land Digital map (<https://native-land.ca/>) that seeks to map the Indigenous territories, treaties, and languages from around the world.

ABSTRACT

Deciduous trees, shrubs, and forest wildflowers may be advancing their leaf-out phenology at different rates in response to a warming climate. A mismatch between understory and overstory phenology may lead to a reduction of understory light levels in the early spring, which is a critical period when many spring-blooming wildflowers achieve highest photosynthetic rates. However, the extent of this phenomenon beyond a single site or region is largely unknown.

Using 3,083 herbarium specimens collected between 1829 and 2019 across eastern North America, we assessed leaf-out and flowering times of 10 tree species (6 native, 4 non-native), 4 shrub species (2 native, 2 non-native), and 7 wildflower species (6 native, 1 non-native). We paired phenological data with historical climate data to quantify differences in phenological sensitivity to spring temperature across canopy strata, across species' geographical ranges, and between native and non-native species.

Predicted phenological mismatches between native trees and wildflowers differed across large spatial scales, with wildflower populations in warmer regions of North America more likely to be affected. Overall, native tree species leafed out 3.6 days earlier per °C spring warming, while native wildflower species advanced their flowering times by 3.2 days per °C. Native trees and wildflowers in the warmer, southern part of their

ranges advanced their spring phenology 2 and 1.5 times faster, respectively, than those in colder, northern locations. The phenological sensitivity of non-native plants was less variable across their ranges. Non-native trees and shrubs exhibited greater phenological sensitivity than native wildflowers. Notably, phenological sensitivities differed substantially among wildflower species, suggesting that certain species are more likely to be affected by phenological mismatch as climate warming progresses.

Synthesis: Our results provide new insight into novel phenological responses within and among species across a wide geographical range and the potential impact of competition and interactions with non-native invasive species. This research highlights the value of newly-available digitized museum collections in phenological research to cover longer time periods, wider spatial areas, and a greater diversity of species than otherwise possible.

INTRODUCTION

Plants are important indicators of climate change, as plant species in temperate ecosystems demonstrate a strong trend of shifting their spring phenology – or timing of seasonal events – earlier with warmer temperatures (Bertin, 2008; Cleland et al., 2007; Ellwood et al., 2019; Everill et al., 2014; Menzel et al., 2006; Miller-Rushing & Primack, 2008; Panchen et al., 2012; Polgar et al., 2013; Primack et al., 2004; Stuble et al., 2021). Species vary in their phenological sensitivity, with some species demonstrating greater or lesser shifts with each degree of spring warming (Heberling et al., 2019b; Lee & Ibáñez, 2021a; Park et al., 2018; Reeb et al., 2020). These different rates of response could lead

to phenological mismatches, where alignment in the timing of ecological relationships is disrupted (Kharouba & Vellend, 2015; Kharouba et al., 2018; Mayor et al., 2017; Renner & Zohner, 2018).

A recent study in Concord, Massachusetts, USA, building on the observations of environmental philosopher Henry David Thoreau from the 1850s, found that canopy trees are advancing their leaf-out times faster than understory wildflowers are in response to warming temperatures (Heberling et al., 2019b). Many early-blooming forest wildflowers rely on the period of full sunlight exposure before canopy trees leaf out in order to perform most of their photosynthesis and carbon gain for the year (Augspurger & Salk, 2017; Heberling et al., 2019a; Kudo et al., 2008; Lapointe, 2001). This difference in phenological sensitivity is resulting in a shrinking period of full early-spring sunlight for wildflowers, and thus a likely decline in their ability to photosynthesize and store carbon (Heberling et al., 2019b). However, it remains untested if this phenological mismatch is widespread across eastern North America. As climate warming intensifies, it is important to understand how the phenology of different plant species will respond, and if different responses correspond to understory plants receiving more or less sunlight. Wildflowers are important for their ecological roles in cycling key nutrients in the ecosystem, contributing to forest species diversity, and providing nutrition to pollinators and animals (Gallinat et al., 2020; Gilliam, 2007; Whigham, 2004).

Phenological mismatches resulting from different rates of change have been documented across trophic levels (Kharouba & Vellend, 2015; Kharouba et al., 2018; Mayor et al., 2017; Post & Forchhammer, 2008). However, few studies have compared

phenological mismatches among plants occupying different forest layers (but see Heberling et al. 2019b, Lee & Ibáñez 2021a, and Routhier & Lapointe, 2002, suggesting that such mismatches may be common but understudied), and most studies of phenological mismatches have been limited to small geographic areas (Heberling et al., 2019a; Kharouba & Vellend, 2015; Post & Forchhammer, 2008). Early spring light is also important for tree seedling survival (Lee & Ibáñez, 2021b), and a recent study has found earlier leaf out in seedlings under climate change to be critical to tree recruitment (Lee & Ibáñez, 2021a).

Long-term data necessary to study these dynamics are limited, though herbaria are increasingly being used to study how phenology is changing in response to climate change (Davis et al., 2015; Heberling et al., 2019c; Lang et al., 2019; Meineke et al., 2018; Reeb et al., 2020; Zohner & Renner, 2014). Recent mass digitization of herbarium specimens has enabled easy access to millions of records of plant occurrence and phenology through time (Daru et al., 2017; Heberling et al., 2019c; Panchen et al., 2019; Soltis, 2017; Yost et al., 2018). Researchers can now use this vast, digital resource to conduct studies of changing phenology across large geographic ranges for thousands of species with an efficiency not previously possible (Ellwood et al., 2019; Heberling & Isaac, 2017; Meineke et al., 2019; Willis et al., 2017a). Park et al. (2018) showed that for widely-distributed plant species, populations had greater phenological sensitivity in the southeastern USA compared to the northeastern USA. Kopp et al. (2020) found that phenological sensitivity was greater at western latitudes and lower elevations in the Pacific Northwest region of North America. Song et al. (2021) found greater

phenological sensitivity at lower latitudes in eastern Asia. These prior studies indicate that species frequently differ in phenological sensitivity across their ranges. Such within-species variation further suggests that phenological mismatch may vary across regions, but this has rarely been studied (but see Routhier & Lapointe, 2002).

Deciduous forests are commonly invaded by shade-tolerant woody shrubs (Martin et al., 2009), which also form a canopy over wildflowers. Non-native plants that have been introduced to new regions have evolved in different climate conditions and thus may have unique sensitivities to environmental cues that differ from native plants (Zohner & Renner, 2014). For example, many non-native plant species in North America occupy different phenological niches compared to native plants (Fridley, 2012; Gallinat et al., 2018; Gallinat et al., 2020; Reeb et al., 2020), and Reeb et al. (2020) found that native and non-native species had different phenological sensitivities to temperature and precipitation in Pennsylvania. These changing dynamics could impact whether non-native species outcompete and shade out native wildflowers. However, it is yet untested whether non-native species are also contributing to or affected by phenological mismatch among forest layers.

In this study, we use herbarium specimens to examine a potential phenological mismatch between overstory trees and understory wildflowers in temperate deciduous forests of eastern North America. This ecosystem is currently heavily invaded by non-native plants (Martin et al., 2009) with predicted increases in introductions of new non-native plants (Allen & Bradley, 2016; Seebens et al., 2017). Therefore, we also

investigate the phenological sensitivity of non-native invasive trees, shrubs, and wildflowers and compare these to native species. We hypothesize the following:

1. Native understory wildflowers across eastern North America are at risk of reduced early-spring sunlight exposure due to phenological mismatches with shrubs and overstory trees.
2. Non-native species have greater phenological sensitivity to warming temperatures than native species, further contributing to mismatches.
3. Plant species in North America have greater phenological sensitivity to temperature in warmer locations than in colder locations.
4. The order in which species leaf out or flower changes as spring temperatures increase.

Overall, we ask whether understory native wildflowers across eastern North America are losing early-spring light access due to phenological mismatches with overstory native or non-native woody species and will continue to be shaded out earlier with ongoing warming.

MATERIALS AND METHODS

Herbarium specimens

We collected leaf-out date (LOD) or flowering date (FD) from herbarium specimens collected in eastern North America for 21 species that are common in deciduous forests and have large ranges spanning much of the eastern half of the continent (Table 3.1). We selected species which are widespread and common across

much of the Eastern Deciduous Forest Biome of North America and well represented in the herbarium record: six native overstory tree species (*Acer rubrum*, *Acer saccharum*, *Carya glabra*, *Fagus grandifolia*, *Quercus alba*, *Quercus rubra*), two native midstory shrub species (*Lindera benzoin*, *Vaccinium corymbosum*), and six native perennial herbaceous, spring-blooming wildflower species (*Anemone quinquefolia*, *Dicentra canadensis*, *Dicentra cucullaria*, *Erythronium americanum*, *Hepatica americana*, *Sanguinaria canadensis*). We chose non-native species which are considered invasive in at least ten U.S. states (EDDMapS, 2021) that also span forest strata: four invasive tree species (*Acer platanoides*, *Populus alba*, *Pyrus calleryana*, *Ulmus pumila*), two invasive midstory shrub species (*Berberis thunbergii*, *Euonymus alatus*), and one invasive understory wildflower (*Ficaria verna*). We selected these native and non-native species because they leaf out at around the same time as they flower. Therefore, for wildflowers and shrubs, our phenological scorings for flowering status also capture leaf-out times. In fact, many of the wildflower and shrub specimens had young leaves on them. However, we did not score wildflower and shrub species directly for leaf-out times, as it is not possible on most specimens to distinguish young leaves from mature leaves. In contrast, for trees, we found that it was possible to distinguish young leaves from mature leaves, owing in part to the greater size of tree leaves. Further, many herbarium specimens of trees with young leaves also have open flowers. As pointed out in other studies, leaf out and flowering are highly-correlated phenological events (Ettinger et al., 2018), and they have been used as proxies for each other (Heberling et al., 2019b).

We accessed all available digitized specimen records (with images) from the Consortium of Northeastern Herbaria (<https://portal.neherbaria.org>), the New York Botanical Garden William and Lynda Steere Herbarium (<https://sweetgum.nybg.org>), the Mid-Atlantic Herbaria Consortium (<https://midatlanticherbaria.org>), the Southeast Regional Network of Expertise and Collections (<https://sernecportal.org>), the Consortium of Midwest Herbaria (<https://midwestherbaria.org>), Canadensys (<https://data.canadensys.net>), and the Acadia University E.C. Smith Herbarium (<https://procyon.acadiau.ca>).

Tree species were evaluated for early, young leaves. Early leaves were determined using a combination of characteristics, including size, translucency, visual texture, and the presence or absence of flowers (Everill et al., 2014). Shrub and wildflower species were evaluated for functional flowers using a combination of characteristics, including shape, openness, color, and the presence or absence of leaves or fruits. For specimens included in the study, we recorded the date, location, collector, and herbarium. We used geographic coordinates provided with the specimens, or if they weren't available, we georeferenced the specimens to the centroid of the most precise geographic unit provided (address, then city or town, then county; Ellwood et al., 2019) using 'geocode' in R package *ggmap* (Kahle & Wickham, 2013). We scored a total of 3,797 herbarium specimens from over 100 herbaria across the eastern United States and Canada. However, we eventually excluded 714 scored specimens because we were unable to find matching climate data, leaving us with 3,083 specimens in the final analysis.

Specimens dated from 1829 to 2019 and were collected from Florida, USA to Quebec, Canada (Figure 3.1). We collected an average of 7 specimens per species from each state or province, with the number of specimens ranging from 0 to 80 across our study region. Greater sample sizes for some species were due to the inclusion of data from existing datasets (Ellwood et al., 2019; Everill et al., 2014). Common geographic and temporal herbarium specimen collection biases are also present in our dataset (Daru et al., 2017; Meineke & Daru, 2021).

Climate data

We collected historic climate data for each specimen from the National Oceanic and Atmospheric Administration's Global Historical Climatology Network. We extracted temperature data for each specimen in the year it was collected from the nearest weather station within a 25-km radius using the R packages *ggmap* (Kahle & Wickham, 2013) and *rnoaa* (Chamberlain, 2017). We calculated monthly average temperatures for all months in the dataset by averaging daily minimum and maximum temperatures for all days in a month. We excluded herbarium specimens with incomplete temperature records from the analysis.

Dividing specimens by spring temperature

In order to compare phenological sensitivity across regions, we divided our specimens into three spring temperature groupings (Cold, Medium, and Warm) based on the average spring (March and April) temperature in the year a specimen was collected.

In a method similar to Love and Mazer (2021), we split the specimens into three equal-sized groups of those with the coldest, medium, and warmest temperatures, then determined the temperature cut-offs dividing those groups and rounded to the nearest whole degree. This division of the dataset resulted in the Cold temperature group as locations with an average spring temperature of less than 6°C, the Medium temperature group as locations with an average spring temperature of greater than or equal to 6°C and less than or equal to 10°C, and the Warm temperature group as locations with an average spring temperature of greater than 10°C. The Cold, Medium, and Warm temperature groups had similar sample sizes among native species ($N \sim 285$ each for trees, shrubs, and wildflowers) and non-native species ($N \sim 55$ each for trees, shrubs, and wildflower). There is some geographical overlap among the temperature groups due to the presence of some colder high elevation sites further south, some warmer coastal sites further north, and due to interannual temperature variation, with occasional cold springs further south and warm springs further north (Figure 3.2). A visual inspection of the spring temperature classifications demonstrates that our approach was generally robust to abnormally cold or warm outlier years skewing the classification of specimens into temperature groups.

Data analysis

All analyses were conducted using R statistical software, version 3.5.1 (R Core Team, 2018). We used Bayesian linear regression, performed in JAGS (Plummer, 2003) using *r2jags* (Su & Yajima, 2015), to model relationships between average spring

temperature (which we define throughout as the mean of March and April temperatures in the year the specimen was collected) and the day of year of early-spring phenology (leaf-out for trees and flowering for shrubs and wildflowers). To determine the best temperature predictor variable for early-spring phenology of our specimens, we compared linear regressions of day of year for leaf-out or flowering phenology (LOD or FD) and different combinations of average monthly temperatures (Heberling et al., 2019b). We used R^2 values to determine that an average of March and April temperatures was the best or among the best predictors of early-spring phenology for all of our subgroups of data (including native species, non-native species, trees, shrubs, wildflowers, and Cold, Medium, and Warm-temperature subdivisions). We used mean spring temperature because of its documented correlation with plant phenology (Miller-Rushing & Primack, 2008; Panchen et al., 2012) and our ability to directly compare results with those of previous phenological studies in the eastern U.S. (e.g., Ellwood et al., 2013; Heberling et al., 2019b, Park et al., 2018; Willis et al., 2017b).

We performed regressions separately for native trees, native shrubs, native wildflowers, non-native trees, non-native shrubs, and non-native wildflower, including random intercepts for species and year (Table 3.2). We also modeled phenological responses of trees, shrubs, and wildflowers to temperature separately for subdivisions by temperature grouping (i.e., Cold, Medium, and Warm) and for each individual species, including year as a random effect. We used these models to estimate changes in the sequence of phenological events across groups and species at spring temperatures of 0 °C, 10 °C, and 20 °C. We conducted analyses to confirm that our conclusions were robust

to different time periods. All prior distributions were non-informative. Normal distribution priors with mean zero and variance 10^5 were used for fixed effect parameters, and random effect standard deviations were sampled from a uniform prior (0,100). We ran our final models with three parallel Markov chain Monte Carlo (MCMC) chains for 50,000 iterations, discarding the initial 10,000 for burn-in. Trace plots and the Gelman–Rubin diagnostic (< 1.1) were used to confirm convergence (Gelman & Hill, 2007). Across models, we consider two groups to be statistically significant if the 95% credible intervals from parameter posterior distributions do not overlap.

RESULTS

Native trees shift phenology more with spring warming than native wildflowers

Native trees advanced their leaf-out dates (LOD) significantly faster than native wildflowers advanced their flowering dates (FD) in response to warmer spring temperatures. The six native tree species leafed out 3.6 days earlier per °C increase in mean spring temperature, while the six native wildflower species flowered 3.2 days/°C earlier (Figure 3.3). The models predict that native wildflowers flower 16 days earlier than native trees leaf out at average spring temperatures of 0 °C, but only 7 days earlier at average spring temperatures of 20 °C. We compare phenology at 0 °C and 20 °C to capture the range of spring temperatures in the dataset and highlight how phenology may shift as the climate warms.

Individual species differed in their sensitivity to spring warming. *Fagus grandifolia* and *Acer rubrum* were the most-sensitive native tree species, advancing their

leaf-out 4.0 and 3.7 days/°C, respectively (Figure 3.4). *Quercus alba* and *Acer saccharum* were the least-sensitive native tree species, advancing leaf-out 3.2 and 3.3 days/°C, respectively. *Erythronium americanum* and *Sanguinaria canadensis* were the most-sensitive native wildflower species, both advancing their flowering 3.5 days/°C. *Anemone quinquefolia*, *Dicentra canadensis*, and *Dicentra cucullaria* were the least-sensitive native wildflower species, advancing their flowering only 2.6, 2.8, and 2.8 days/°C, respectively.

Phenological sensitivity across species' ranges

Native trees in the Warm spring temperature group advanced their leaf-out phenology about two times faster for each degree of warming compared to native trees in the Medium or Cold temperature groups (Figure 3.5). Native wildflowers in the Warm and Medium spring temperature groups were more sensitive to spring warming than those in the Cold temperature group, although modelled slope β_{LOD} or β_{FD} credible intervals overlap. Native shrubs were more sensitive in the Medium temperature group, but not significantly so. Non-native trees and the non-native wildflower did not differ significantly in their sensitivity across Cold, Medium, and Warm spring temperature groups, although the non-native wildflower did exhibit a trend of increasing sensitivity from Cold to Warm temperature groups. Non-native shrubs were more than two times more sensitive in the Medium compared to the Cold temperature group, and had intermediate sensitivity in the Warm temperature group. Native trees were significantly about 1.5 times more sensitive to spring warming than native wildflowers in the Warm

spring temperature group, but there was no significant difference between native trees and wildflowers in the Cold temperature group.

Non-native species phenological sensitivity

Non-native trees, shrubs, and wildflowers did not differ significantly in their phenological sensitivity to warming compared to their native counterparts; although non-native trees were slightly more sensitive than native trees, native shrubs were slightly more sensitive than non-native shrubs, and the non-native wildflower was slightly more sensitive than native wildflowers (Figure 3.3). Non-native plants had much greater variability in their phenological sensitivity.

Individual non-native species also differed in their phenological sensitivity, although the credible intervals were large and only one difference was statistically significant (Figure 3.4). *Pyrus calleryana* was the most-sensitive non-native tree species, advancing its leaf-out 4.4 days/°C of spring warming. *Populus alba* was the least-sensitive non-native tree species, advancing leaf-out 2.9 days/°C of spring warming. Of the non-native shrubs, *Berberis thunbergii* was more sensitive than *Euonymus alatus*, advancing their flowering times 4.3 and 3.7 days/°C, respectively. The non-native wildflower *Ficaria verna* advanced its flowering 3.6 days/°C.

Order of early-spring phenology changes with warming

Based on fitted model estimates, the order of early-spring phenological events – leaf-out and flowering – changed at different spring temperatures. At colder average

spring temperatures (0 °C), the native wildflowers were the first to flower, followed by the leaf-out and flowering of the non-native wildflower, non-native trees, native shrubs, native trees, and then non-native shrubs (Figure 3.6A). Non-native shrubs flowered on average 23 days later than native wildflowers and 7 days later than native trees. At warmer average spring temperatures (20 °C), native shrubs were the first to leaf out, followed by the leaf-out and flowering of the non-native wildflower, non-native trees, native wildflowers, native trees, and then non-native shrubs. Non-native shrubs flowered on average 16 days later than native shrubs and 1 day later than native trees.

From 0 °C to 20 °C, the gap between native wildflowers flowering and native trees leafing out decreased from 15 to 8 days. The gap between native wildflowers and non-native trees early phenology decreased with warming. Native wildflowers flowered about 8 days before non-native trees at 0 °C but non-native trees leafed out about 1 day before native wildflowers at 20 °C. Non-native shrubs flowered about 22 days after native wildflowers at 0 °C, and this gap decreased to about 9 days at 20 °C.

At the species level, the order of phenology also changed at different spring temperatures, based on the fitted model estimates for individual species. *Vaccinium corymbosum* (native shrub) shifted from being one of the latest species to flower at 0 °C to being the in the middle at 20 °C (Figure 3.6B). *Populus alba* (non-native tree) shifted from being in the middle at 0 °C to being one of the latest species at 20 °C. *Pyrus calleryana* (non-native tree), *Lindera benzoin* (native shrub), *Hepatica americana* (native wildflower), and *Ficaria verna* (non-native wildflower) remained four of the earliest species across temperatures. Three of the native wildflowers – *Anemone quinquefolia*,

Dicentra canadensis, and *Dicentra cucullaria* – shifted to being later in the order at higher temperatures.

DISCUSSION

Native trees shift phenology more with spring warming than native wildflowers

We evaluated over 3,000 digitized herbarium specimens to assess differences in spring leaf out and flowering sensitivities and resulting changes to spring phenology order across forest layers and across the ranges of 21 species. We found that native trees advanced their leaf-out times with increased spring temperatures faster than native wildflowers advanced their flowering times. Though interesting regional variation exists, this study demonstrates that earlier findings at a single site in Concord, Massachusetts (Heberling et al., 2019b) are consistent with a general phenomenon across eastern North America. This phenological mismatch means that wildflowers are likely to experience reduced sunlight access for photosynthesis in the early spring in coming decades, and these impacts may lead to declines in the abundance of native wildflower populations as the climate warms (Augspurger & Salk, 2016; Heberling et al., 2019b; Nault & Gagnon, 1993).

A loss of wildflower species from the forest understory would have widespread ecological and conservation impacts. Wildflowers comprise a key component of the species-diverse herbaceous forest layer, impact the regeneration and success of overstory plants, mediate carbon cycling, maintain key nutrients in the ecosystem (e.g., nitrogen, phosphorus), and provide nutrition to many animals (Gallinat et al., 2020; Gilliam, 2007;

Gilliam, 2014; Whigham, 2004). In addition to their ecological roles, spring-blooming wildflowers are important for food, medicine, nature appreciation, and cultural heritage, particularly for Indigenous communities (Applequist, 2021; Burkhart & Jacobson, 2009; Foster & Duke, 2000; Herrick, 1995; Hirsch, 2018; Kuhnlein & Turner, 1991; Meeker & Elias, 1993).

Therefore, it is important to quantify the different responses to climate change among species in order to better understand the extent of mismatches and which species might be more or less successful as the climate warms. Wildflower species that are more sensitive to temperature (e.g., *Erythronium americanum*) may be less impacted by advancing tree canopy leaf out than wildflower species which are less sensitive (e.g., *Anemone quinquefolia*). In addition, a wildflower population located in a forest where the dominant tree species is less sensitive to temperature (e.g., *Quercus alba*) may have more sunlight access and ability to photosynthesize than if the wildflowers were in a forest area where the dominant tree species is more sensitive (e.g., *Fagus grandifolia*), and thus shades them over sooner.

Overall, we did find the same general pattern and similar rates of sensitivity to temperature variation as the earlier Heberling et al. (2019b) study from Concord. However, our findings differ in the amount of difference between the phenological sensitivity of trees and wildflowers. Heberling et al. (2019b) found that native tree species advanced their leaf-out times by 4.4 days/°C spring warming on average and wildflower species advanced their flowering times by 2.2 days/°C, whereas we found that, at the broader continental scale, native tree species advanced their leaf-out times by

3.6 days/°C spring warming on average and wildflower species advanced their flowering times by 3.2 days/°C. Nevertheless, given that our two studies used different types of data (field observations vs. herbarium specimens), and covered different geographical regions (Concord, MA vs. eastern North America), species, and time periods, it is striking that the overall pattern and the direction and magnitude of sensitivity are similar. In contrast, we found that native shrub phenological sensitivity was similar to that of native trees. This is consistent with results from other studies which found that woody understory plant phenology is equally as or more sensitive to warming when compared to that of canopy trees (Lee and Ibáñez, 2021a; Lee and Ibáñez, 2021b).

Phenological sensitivity across species' ranges

Phenological sensitivity differed across native species' latitudinal ranges in eastern North America. Native trees and wildflowers were more sensitive to temperature in the Warm temperature group (predominantly in the southeastern USA) in comparison with the Cold temperature group (predominantly in the northeastern USA), although this difference was not significant for wildflowers. This implies that phenological mismatches will be greater for native wildflowers in the southeastern U.S. – wildflowers in the warmer, southern locations will have fewer days of full sunlight access before they are shaded over, compared to wildflowers in the colder, northern sites. Other studies have found similar trends of species phenological sensitivity increasing at lower latitudes (Park et al., 2018; Song et al., 2021; Zhang et al., 2015). Both Park et al. (2018) and Zhang et al. (2015) suggest that plants in southern regions may have adapted to have greater

sensitivity because the climate is more stable and less variable, and thus there is a greater payoff of tracking spring temperatures when there is less risk of late-spring frost damage.

In contrast to native trees, non-native species did not differ in phenological sensitivity across their latitudinal range. One reason for this may be that all of the non-native plants in our study were intentionally introduced by humans for ornamental horticultural purposes, and many have reduced genetic variability that could limit their ability to adapt to local environments (Ebeling et al., 2011). Instead, it is hypothesized that human selection of plants for ornamental purposes can increase phenotypic plasticity (Matesanz et al., 2010; Richards et al., 2006). Thus, these non-native species may not have adapted to the highly-variable northeastern U.S. climate and may have maintained similar phenological sensitivity across their range. An alternative reason is that the ranges of our non-native species are more limited, with fewer occurrences in the Southeast (EDDMapS, 2021), which may have reduced our ability to detect latitudinal differences.

Non-native species phenological sensitivity

We did not find significant differences between the phenological sensitivity of native and non-native plants. Our results differ from other studies, which largely found that non-native species have more plastic phenology and are advancing more with warming temperatures than are native species (Calinger et al., 2013; Willis et al., 2010; Wolkovich et al., 2013; Wolkovich & Cleland, 2014; Zettlemyer et al., 2019; but see Wilsey et al., 2018 for greater phenological sensitivity in native species). However, many of these studies differed from ours in methodology (experimental field or twig warming

studies) and geographic scope. We also had smaller sample sizes of non-native plants relative to native plants. Further work is needed to determine if the comparability we found in phenological sensitivity between native and non-native plants is due to genuine similarity or due to our choice of species, methods, or sample size. Non-native trees have greater phenological sensitivity than native wildflowers, thus posing a threat to native wildflower fitness, particularly in areas where non-native trees are the dominant canopy trees. In addition, the greater sensitivity of non-native shrubs compared to native wildflowers suggests that in warmer climates the impact of non-native shrub shading may increase with warming.

Order of early-spring phenology changes with warming

The order of early-spring phenology changed from colder to warmer temperatures, with the more-sensitive groups advancing in the order, and the less-sensitive groups falling back in the order. The two native shrubs shifted from fourth- to first-earliest of the six groups. The native wildflowers shifted from first to fourth in the order.

In general, species which are more sensitive and advance in the order are likely to benefit from increased access to sunlight. The species which advanced the most in the order are *Vaccinium corymbosum*, *Pyrus calleryana*, *Berberis thunbergii*, *Fagus grandifolia*, *Ulmus pumila*, *Lindera benzoin*, *Acer rubrum*, *Carya glabra*, and *Euonymus alatus*. It is possible that these species will have the competitive advantage of earlier and longer access to sunlight in the early spring under conditions of climate warming

(Alexander & Levine, 2019; Cleland et al., 2012; De Frenne et al., 2011; Willis et al., 2008; Willis et al., 2010). *Pyrus calleryana* and *Lindera benzoin* are two of the earliest-leafing and earliest-flowering species, so their phenology may become comparatively even earlier at warmer temperatures. This may be an advantage, or it is possible that these earliest species will suffer from increased frost damage (Augspurger & Salk, 2016; Inouye, 2008) and herbivory (Meineke et al., 2021). Zohner et al. (2020) suggest that late spring frost risk is decreasing in North America, but increasing in Europe and Asia. These dynamics should be considered when projecting which species are likely to thrive or decline under future climate change conditions.

The species which moved back the most in the order of spring activity are *Anemone quinquefolia*, *Dicentra canadensis*, *Dicentra cucullaria*, *Populus alba*, and *Acer platanoides*. It is possible that these species will suffer competitively under warming climate conditions. They may have less access to early-spring sunlight and less ability to synthesize and store carbon.

CONCLUSIONS

The results of this study may be used to inform recommendations for conserving native wildflower populations. Wildflower species which are less phenologically sensitive to climate warming and flower later are more likely to be at risk of decline (e.g., *Anemone quinquefolia*, *Dicentra canadensis*, *Dicentra cucullaria*), and tree and shrub species which are more phenologically sensitive and leaf out early in the spring (e.g., *Acer rubrum*, *Fagus grandifolia*, *Pyrus calleryana*, *Ulmus pumila*, *Lindera benzoin*) are

more likely to shade out wildflowers. This dynamic is likely to be particularly salient in the Southeastern U.S. where conservation professionals and managers may seek out further resources to guide management options, which may include thinning out trees and shrubs to maintain early sunlight access for wildflowers (e.g., Maynard-Bean & Kaye, 2019 for non-native shrub removal) or managed relocation for wildflower species threatened by shading (Karasov-Olson et al., 2021).

Our results provide new insight into phenological responses within and among species across a wide geographical range and the potential impact of competition and interactions with non-native invasive species. This research highlights the value of newly-available digitized museum collections in phenological research to cover longer time periods, wider spatial areas, and a greater diversity of species than otherwise possible. This field of study would benefit from further analyses to determine how generalizable these results are to other species, regions, and ecosystems. It remains unclear if these phenological patterns are similar in other temperate deciduous forests of the world, as these patterns may differ due to biogeography (Zohner et al., 2017). Similar studies could also be conducted in different ecosystems to assess if these trends in phenological sensitivity and mismatch also apply to other ecosystems, such as chaparral or boreal forests, or are controlled by other climatic variables like moisture (Keatley et al., 2002; Kramer et al., 2000; Song et al., 2020). Furthermore, to elucidate the mechanisms of these phenological mismatches, physiological experiments could be conducted to test whether different levels of the canopy are responding to different temperature cues, such as air or soil temperature, or are relying more on photoperiod.

Understanding differences in the temperature cues for different levels of the canopy could help us anticipate future mismatches as climate conditions continue to change. Further, understanding the changes in other ecosystems and the roles of other climate variables can help us to understand the magnitude of the potential mismatches and plan conservation responses.

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TABLES AND FIGURES

Table 3.1: The scientific names, common names, sample sizes (n), growth form classification, and native/non-native classification of the 21 study species. Latitudinal range describes the lowest and highest latitude of a collected herbarium specimen in the study.

Scientific name	Common name	n	Growth form	Origin	Latitudinal range (°N)
<i>Acer rubrum</i>	Red maple	310	Tree	Native	29.7 – 46.8
<i>Acer saccharum</i>	Sugar maple	141	Tree	Native	30.2 – 48.6
<i>Carya glabra</i>	Pignut hickory	110	Tree	Native	27.2 – 43.0
<i>Fagus grandifolia</i>	American beech	153	Tree	Native	29.7 – 46.2
<i>Quercus alba</i>	White oak	163	Tree	Native	29.8 – 44.5
<i>Quercus rubra</i>	Red oak	124	Tree	Native	33.3 – 47.0
<i>Lindera benzoin</i>	Northern spicebush	255	Shrub	Native	28.6 – 44.5
<i>Vaccinium corymbosum</i>	High-bush blueberry	262	Shrub	Native	27.3 – 46.1
<i>Anemone quinquefolia</i>	Wood anemone	181	Wildflower	Native	33.0 – 47.4
<i>Dicentra canadensis</i>	Squirrel corn	141	Wildflower	Native	34.9 – 46.9
<i>Dicentra cucullaria</i>	Dutchman's breeches	176	Wildflower	Native	34.5 – 46.7
<i>Erythronium americanum</i>	Yellow trout lily	188	Wildflower	Native	32.3 – 46.8
<i>Hepatica americana</i>	Round-lobed hepatica	147	Wildflower	Native	32.4 – 47.7
<i>Sanguinaria canadensis</i>	Bloodroot	216	Wildflower	Native	30.2 – 48.0
<i>Acer platanoides</i>	Norway maple	65	Tree	Non-native	34.5 – 46.8
<i>Populus alba</i>	White poplar	20	Tree	Non-native	32.6 – 45.5
<i>Pyrus calleryana</i>	Callery pear	55	Tree	Non-native	30.4 – 41.8
<i>Ulmus pumila</i>	Siberian elm	28	Tree	Non-native	35.0 – 46.9
<i>Berberis thunbergii</i>	Japanese barberry	132	Shrub	Non-native	32.9 – 45.5
<i>Euonymus alatus</i>	Burning bush	99	Shrub	Non-native	34.9 – 43.2
<i>Ficaria verna</i>	Lesser celandine	117	Wildflower	Non-native	34.8 – 44.5

Table 3.2: Bayesian regression model results of slope (β_1) and intercept (β_0) estimates with 2.5 and 97.5 credible intervals (CI).

Origin	Growth form	Species	Temperature group	β_1 mean	β_1 2.5 CI	β_1 97.5 CI	β_0 mean	β_0 2.5 CI	β_0 97.5 CI
Native	Trees	NATIVE TREES	All	-3.607	-3.76	-3.46	150.56	147.36	153.80
		<i>Acer rubrum</i>	All	-3.743	-4.02	-3.45	144.62	137.38	152.04
		<i>Acer saccharum</i>	All	-3.286	-3.59	-2.99	143.47	135.84	151.58
		<i>Carya glabra</i>	All	-3.693	-4.16	-3.22	159.34	149.64	168.72
		<i>Fagus grandifolia</i>	All	-3.979	-4.37	-3.61	151.54	141.19	161.53
		<i>Quercus alba</i>	All	-3.196	-3.52	-2.85	152.59	143.85	160.55
		<i>Quercus rubra</i>	All	-3.500	-3.87	-3.13	151.00	143.42	158.38
Shrubs	NATIVE SHRUBS	All	-4.258	-4.49	-4.03	147.89	140.76	155.08	
		<i>Lindera benzoin</i>	All	-3.783	-4.11	-3.44	131.95	126.90	137.15
		<i>Vaccinium corymbosum</i>	All	-4.546	-4.85	-4.26	161.80	152.64	170.88
Wild-flowers	NATIVE WILD-FLOWERS	All	-3.222	-3.38	-3.06	135.18	132.05	138.50	
		<i>Anemone quinquefolia</i>	All	-2.561	-2.99	-2.12	139.33	132.55	146.27
		<i>Dicentra canadensis</i>	All	-2.845	-3.27	-2.43	137.14	132.08	142.29
		<i>Dicentra cucullaria</i>	All	-2.843	-3.24	-2.45	131.85	125.42	138.87
		<i>Erythronium americanum</i>	All	-3.538	-3.87	-3.20	136.30	128.71	143.98
		<i>Hepatica americana</i>	All	-3.303	-3.84	-2.74	129.17	123.22	135.12
		<i>Sanguinaria canadensis</i>	All	-3.484	-3.72	-3.24	130.82	121.43	140.60
Non-native	Trees	NON-NATIVE TREES	All	-3.682	-4.11	-3.26	143.48	136.67	150.12

	<i>Acer platanoides</i>	All	-3.028	-3.50	-2.56	140.54	135.19	146.51
	<i>Populus alba</i>	All	-2.925	-4.13	-1.71	145.06	119.76	170.82
	<i>Pyrus calleryana</i>	All	-4.359	-5.27	-3.49	138.64	121.06	155.96
	<i>Ulmus pumila</i>	All	-3.979	-4.97	-2.99	148.64	136.00	160.30
Shrubs	NON- NATIVE SHRUBS	All	-3.933	-4.39	-3.50	157.88	151.32	164.73
	<i>Berberis thunbergii</i>	All	-4.258	-4.77	-3.73	151.89	145.75	157.49
	<i>Euonymus alatus</i>	All	-3.731	-4.48	-2.99	164.60	156.44	172.74
Wild- flower	NON- NATIVE WILD- FLOWER	All	-3.638	-4.36	-2.93	135.82	123.37	147.34
	<i>Ficaria verna</i>	All	-3.638	-4.36	-2.93	135.82	123.37	147.34
Native Trees	NATIVE TREES	Cold	-2.616	-3.15	-2.06	145.67	141.88	149.48
	NATIVE TREES	Medium	-3.129	-4.47	-1.77	148.30	137.12	159.26
	NATIVE TREES	Warm	-4.943	-5.39	-4.50	168.99	161.44	176.18
Shrubs	NATIVE SHRUBS	Cold	-2.764	-3.70	-1.85	142.07	133.59	150.31
	NATIVE SHRUBS	Medium	-4.659	-6.25	-3.03	151.94	136.27	167.65
	NATIVE SHRUBS	Warm	-3.781	-4.51	-3.07	140.38	126.05	154.65
Wild- flowers	NATIVE WILD- FLOWERS	Cold	-2.422	-2.90	-1.94	132.37	128.76	136.16
	NATIVE WILD- FLOWERS	Medium	-3.513	-4.40	-2.63	138.20	130.60	145.51
	NATIVE WILD- FLOWERS	Warm	-3.505	-4.36	-2.63	138.35	125.95	151.12

Non-native	Trees	NON-NATIVE TREES	Cold	-1.674	-3.02	-0.30	137.57	129.35	145.31
		NON-NATIVE TREES	Medium	-3.151	-5.03	-1.20	140.65	124.71	155.87
		NON-NATIVE TREES	Warm	-2.580	-	-1.42	129.58	112.54	146.55
						3.729			
	Shrubs	NON-NATIVE SHRUBS	Cold	-2.614	-4.19	-1.04	152.37	141.70	162.71
		NON-NATIVE SHRUBS	Medium	-5.909	-7.52	-4.39	172.61	159.07	186.59
		NON-NATIVE SHRUBS	Warm	-4.126	-6.67	-1.70	160.99	129.89	192.00
	Wild-flower	NON-NATIVE WILD-FLOWER	Cold	-1.818	-5.08	1.33	129.00	102.43	156.53
		NON-NATIVE WILD-FLOWER	Medium	-3.308	-6.38	-0.08	133.49	104.50	160.94
		NON-NATIVE WILD-FLOWER	Warm	-3.534	-6.36	-0.75	132.52	93.04	171.13

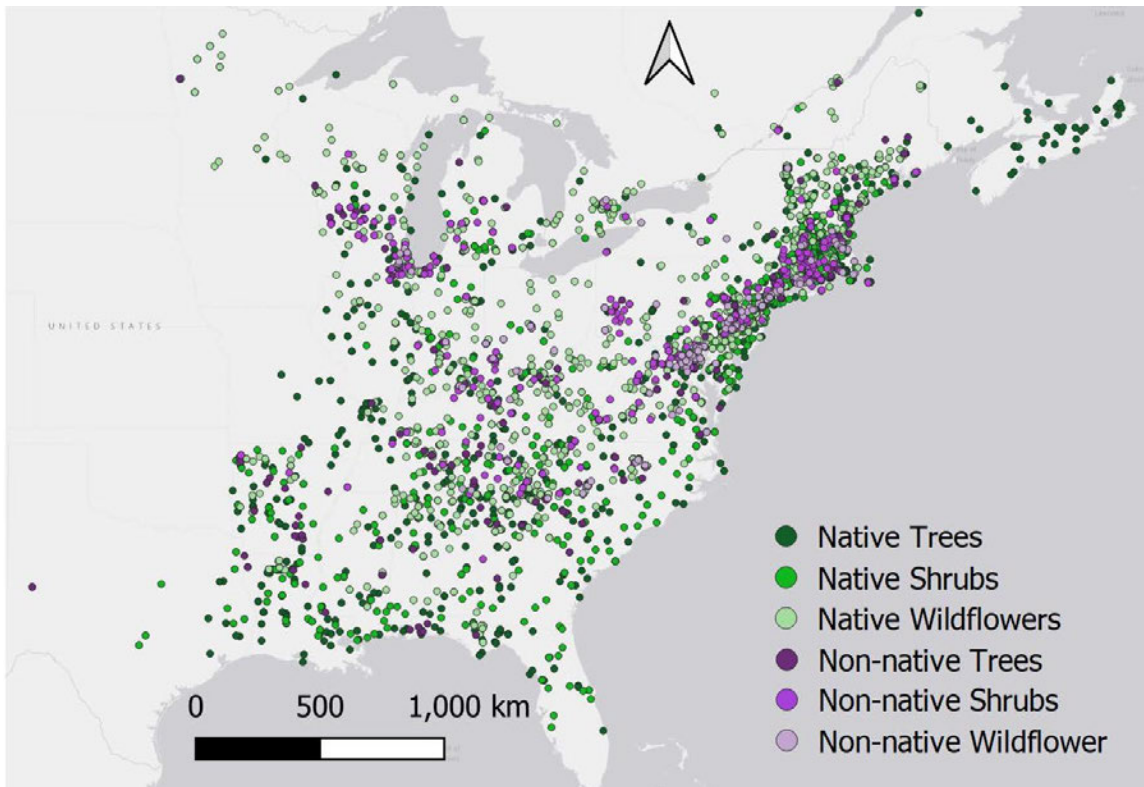


Figure 3.1: Map of herbarium specimen collection locations in eastern North America by growth form and origin.

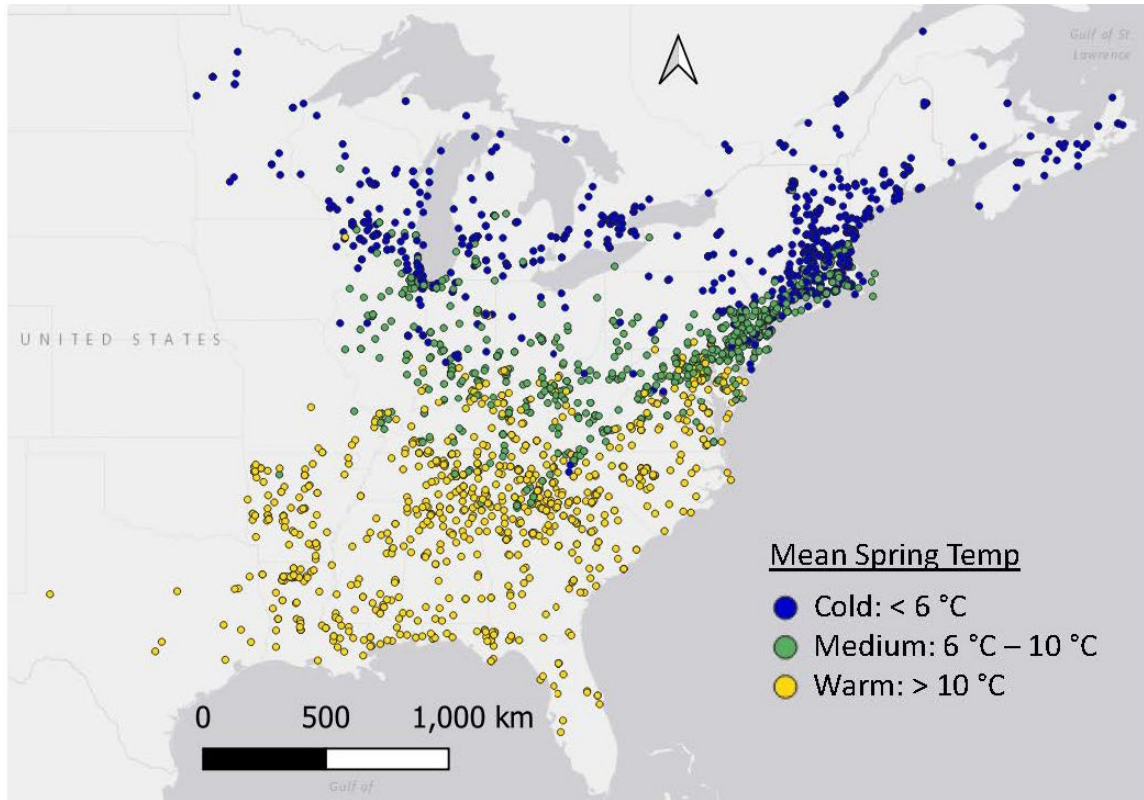


Figure 3.2: Map of herbarium specimen collection locations in eastern North America by mean spring (March/April) temperature groups.

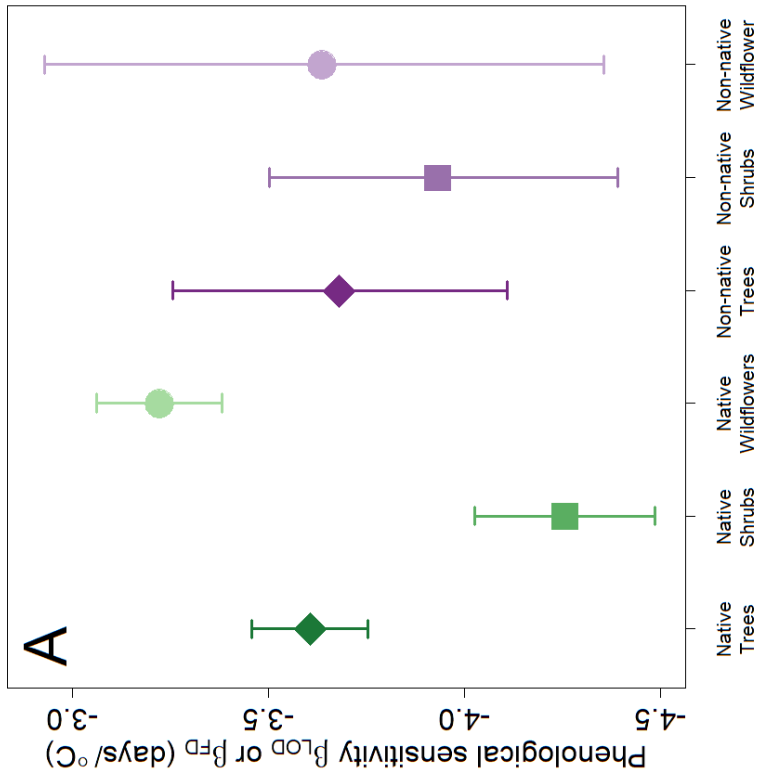
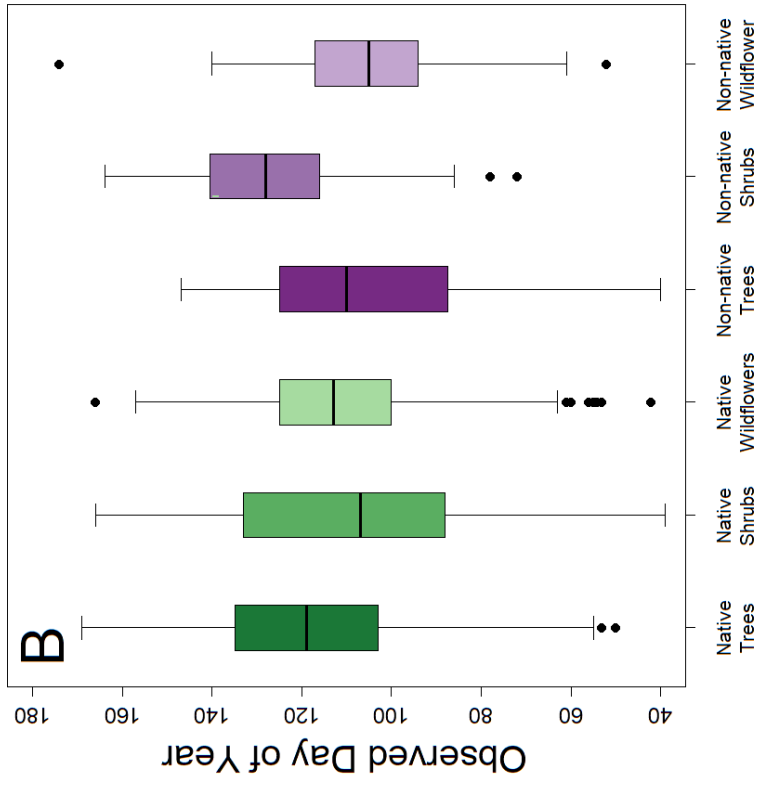


Figure 3.3: Forest plant species exhibited different modeled phenological sensitivity (LOD for trees, FD for shrubs and wildflowers) to mean spring temperature (A) and different observed mean dates and ranges of leaf out or flowering (B) based on their growth form (overstory tree, midstory shrub, or understory wildflower) or their origin (native or non-native) using herbarium records across eastern North America. Points in 2A represent the model slope estimates for β_{LOD} or β_{FD} . Non-overlapping 95% credible intervals in 2A indicate model results which are statistically significantly different. Green colors represent native species and purple colors represent non-native species.

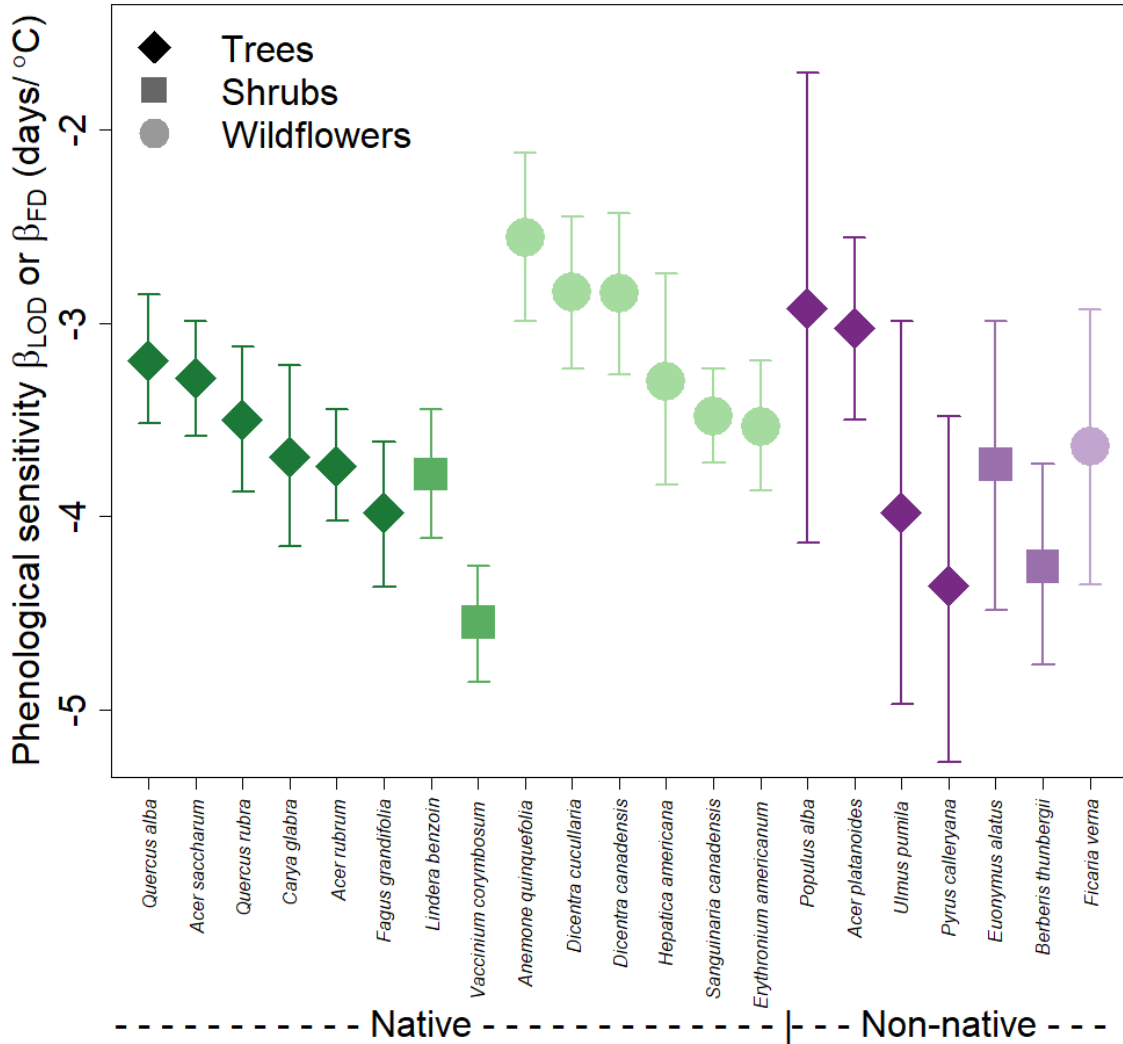


Figure 3.4: Individual forest plant species exhibited different phenological sensitivity to warming temperatures. Points represent the slope estimates (with 95% credible intervals) for β_{LOD} (trees) or β_{FD} (shrubs, wildflowers) from species-specific models. Non-overlapping credible intervals indicate parameter posterior estimates which are statistically significantly different. Green colors represent native species and purple colors represent non-native species.

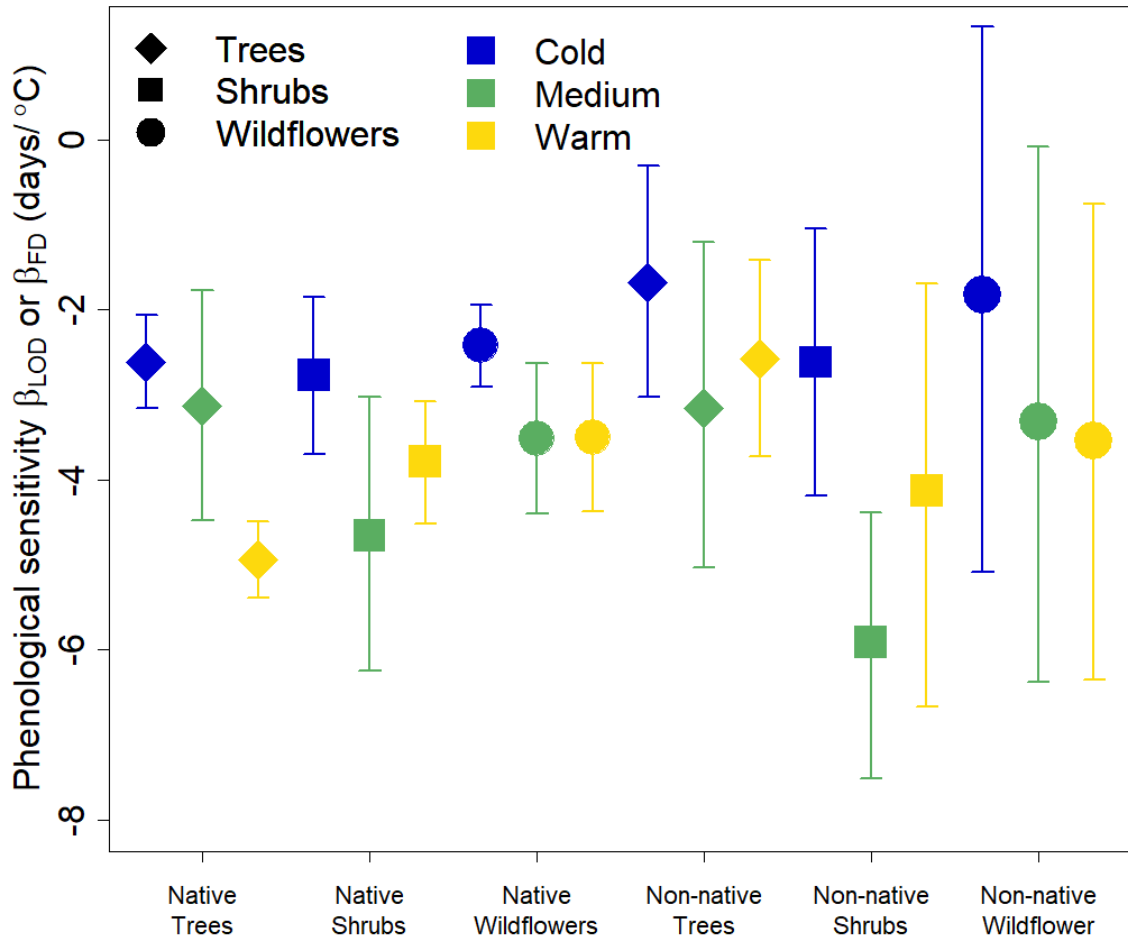


Figure 3.5: Forest plant species had different phenological sensitivity to warming temperatures based on their collection location's average spring temperature (Cold, Medium, or Warm), growth form (canopy tree, midstory shrub, or understory wildflower), or origin (native or non-native) in a study of herbarium records collected across eastern North America. Points represent slope estimates β_{LOD} or β_{FD} (with 95% credible intervals) by sites grouped by long-term mean spring temperatures. Non-overlapping credible intervals indicate parameter posterior estimates which are statistically significantly different.

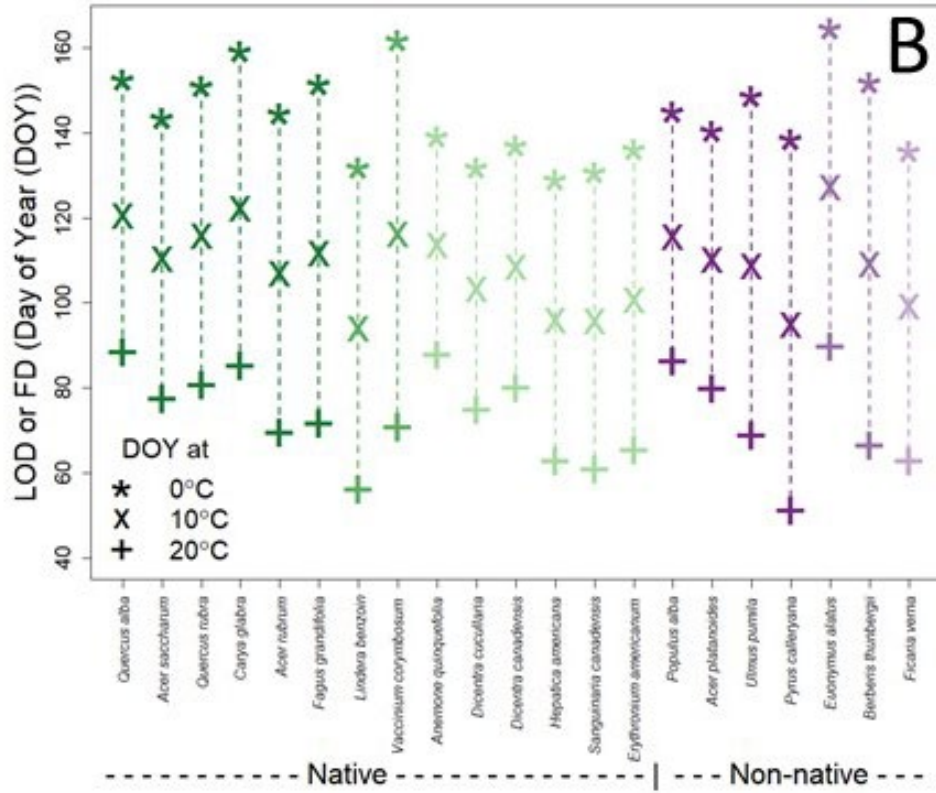
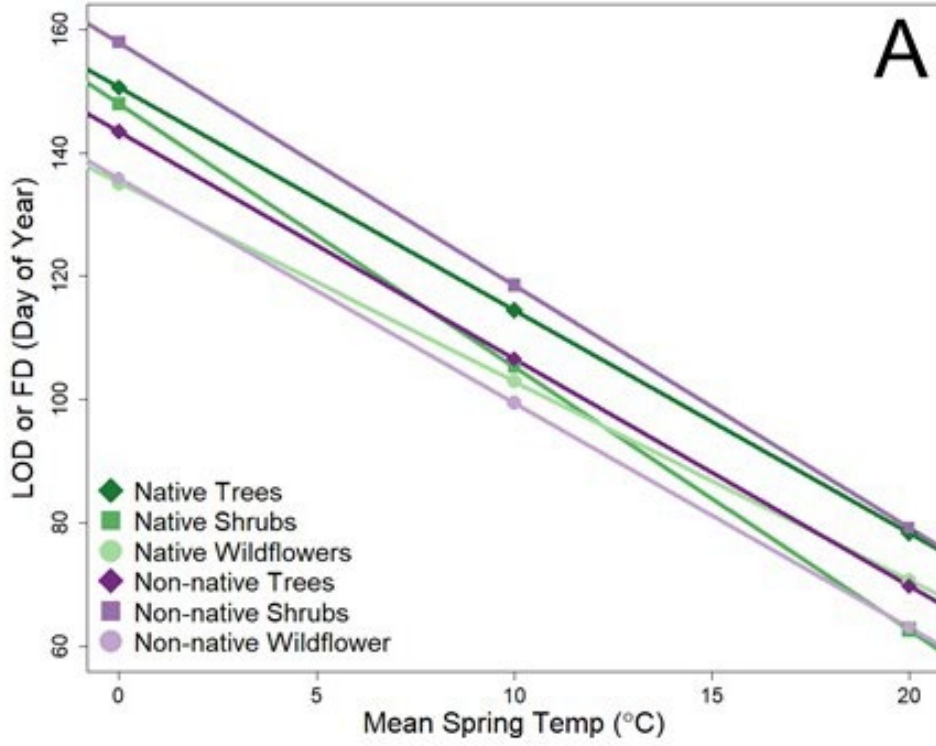


Figure 3.6: The order of early-spring phenology for forest plant species by growth form and origin groups (A) and individual species (B) changed across different average spring temperatures. Points represent fitted model estimates of LOD (trees) and FD (shrubs, wildflowers) at spring temperatures of 0 °C, 10 °C, and 20 °C. Green colors represent native species and purple colors represent non-native species.

CHAPTER FOUR: WILDLIFE REHABILITATION RECORDS FOR USE IN ECOLOGICAL RESEARCH AND CONSERVATION

NATIVE LAND ACKNOWLEDGEMENT

This research studies animals found across the United States and southern Canada. We acknowledge that our institutions and study sites are located within the ancestral and unceded homelands of many Indigenous communities. Below, we recognize the specific location where we work and the specific communities who first called this site their home. We also recognize that land acknowledgements are not enough to rectify the violence, forcible displacement, and treaty violations by early European colonists and US federal, state, and local governments on Indigenous peoples. However, we hope our land acknowledgement will offer recognition and respect to the people who lived and worked on these lands, create public awareness about the history of where we work, promote the decolonization of ecology and conservation biology, and serve as a call that more work needs to be done to promote social justice in our profession and in our nation.

The Boston University main campus in Boston, MA is located on lands once occupied by the Massachusett (*Mass-adchu-es-et*) people, the Pawtucket people, and the Wampanoag people (Wôpanâak). English colonizers and the United States and Massachusetts Commonwealth governments decimated the Indigenous people through forcible removal, forced assimilation, land grabbing, and genocide. Many people of these and other Indigenous Nations still live in Massachusetts today.

We encourage our readers to use the Native Land Digital map (<https://native-land.ca/>) that seeks to map the Indigenous territories, treaties, and languages from around the world.

ABSTRACT

Wildlife faces many threats from human activities and human-driven climate change, including hunting and fishing, vehicles, human infrastructure, industrial and agricultural activities, infectious diseases, and extreme weather events. We need to understand the prevalence, patterns, and impacts of these threats in order to conserve wildlife populations.

Wildlife rehabilitation (rehab) centers admit and treat injured and sick wildlife, with the aim of returning them to the wild. Wildlife rehab centers collect data on animals admitted, including information on species, condition, location found, and outcome. Past studies have used rehab records to assess threats to wildlife, but these studies have usually covered only a small geographic area, a single species or small group of species, and/or a single category of threats.

Here, we use 674,320 digitized wildlife rehabilitation records from 94 centers across the USA and Canada to learn about threats that wildlife face and to assess which categories of research questions can be answered with rehab data. We use these findings to make recommendations to help conserve wildlife populations and improve wildlife health.

We identified key threats by examining conditions causing animals to be brought to wildlife rehab centers. Overall, human disturbances accounted for the largest proportion of wildlife injury and sickness. We identified the primary reason for admittance for many species, which were predominantly anthropogenic factors such as fishing incidents for brown pelicans, window or building collisions for big brown bats, and vehicle collisions for many raptor and reptile species.

We also identified seasonal patterns in lead and pesticide exposure. Lead cases peaked in winter, likely due to animals ingesting lead ammunition from shot carcasses after hunting seasons. Pesticide cases peaked in summer, indicating that animals may be exposed when rodenticides are used to control “pest” populations. In examining possible effects of human-driven climate change, we found that more animals arrived at rehab centers in the week after an extreme weather event compared to the week before, but only for certain types of weather events in certain locations: e.g., hurricanes and floods in southern Florida. Wildlife rehabilitators were able to return about a third of treated animals back to the wild.

Overall, we identified several major drivers of injured and sick wildlife arriving at rehab centers. These findings point to possible interventions to help conserve wildlife, such as wildlife road crossings, fishing and hunting regulations, lead and pesticide regulations, and disaster management plans.

INTRODUCTION

Wild animals are facing many anthropogenic threats from human activities and human-driven climate change, including vehicle collisions (Gunson et al., 2011), hunting and fishing (Golden et al., 2016; Grade et al., 2019), buildings and power lines (Loss et al., 2014b; Loss et al., 2014c), domestic cats and dogs (Mcruer et al., 2017; Young et al., 2011), habitat destruction (Scanes et al., 2018), industrial and agricultural activities (Lemly et al., 2000; Trail, 2006), lead and pesticide poisoning (Pain et al., 2019; Tesfahunegny and Muluaalem, 2016), infectious diseases (Camacho et al., 2016), and extreme weather events (Maxwell et al., 2019). We need to understand the prevalence, patterns, and impacts of these threats on wildlife in order to conserve wildlife populations. We need to ascertain which species are most at risk and which threats to address first to conserve at-risk species and populations. Wildlife is important as an indicator of ecosystem health and function (Burger and Gochfeld, 2004; Morrison, 1986), as food sources (Borgerson et al., 2019), for cultural significance and medicinal use (Adeola, 1992; Hernandez et al., 2015), for tourism (Hou et al., 2020), and more. Many threats to wildlife, such as lead poisoning and infectious diseases, also impact human health (Bellinger et al., 2013; Gallana et al., 2013). We can use wildlife rehabilitation (rehab) records to learn about these threats to wildlife, make connections to human health, and recommend solutions and remediation that will improve both wildlife and human health.

Wildlife rehabilitation centers are centers which admit and treat injured and sick wildlife, with the aim of returning them to the wild. Wildlife rehab centers collect data on

the animals admitted, and these records often include information on the species, condition, location found, age, and more. Some studies have used wildlife rehab records to assess threats to wildlife, but these studies have usually been limited to a smaller geographic area (e.g., New York City in Cai and Calisi, 2016; Minnesota in Ana et al., 2017; Ciudad Real province, Spain in Camacho et al., 2016) and/or a single species or smaller group of species (e.g., bald eagles in Cruz-Martinez et al., 2012; pigeons in Cai and Calisi, 2016; Fringillidae and Passeridae birds in Gourlay et al., 2014; foxes in Kelly and Sleeman, 2003). Further, many studies focus solely on a single category of threats, such as cat interactions (Mcruer et al., 2017), pathogens or diseases (Ana et al., 2017; Camacho et al., 2016; Gourlay et al., 2014; Kelly et al., 2021), or lead poisoning (Cai and Calisi, 2016; Cruz-Martinez et al., 2012; Kramer and Redig, 1997; Yaw et al., 2017). See Table 1 in Pyke and Szabo (2018) for a summary of the numbers of species, individuals, and years included in studies which have used wildlife rehab records.

Studies which have comprehensively examined all the factors causing wildlife to be brought to rehab centers have generally only reported data from a single wildlife center (Burton and Doblár, 2004; Janssen et al., 2020; Molina-López et al., 2017) or often only one species at one center (Kelly and Sleeman, 2003). Notable exceptions are Hanson et al. (2021), who studied rehab records of multiple taxa from many centers across New York from 2012 to 2014; Kelly et al. (2014), who analyzed rehab records of golden eagles, turkey vultures, and ravens from multiple centers across California from 2007 to 2009; and Kelly et al. (2021), who looked at disease detection modeling using records from many centers across California.

To our knowledge, no studies have looked simultaneously at many species or taxonomic groups across the United States and Canada to form a comprehensive, unified picture of the threats that are impacting wildlife health. In the past, such studies would have been difficult as the records were primarily in the form of paper records which could not be readily accessed and analyzed. Now that records from wildlife rehab centers are becoming digitized, it is increasingly possible to access these data remotely and compile digitized datasets that span much of North America. Reviews have proposed areas of research that wildlife rehab data may be used to study (Trocini et al., 2008; Pyke and Szabo, 2018), but no studies have comprehensively examined the ability of wildlife rehabilitation data to answer a variety of research questions at large geographic scales for a wide range of species. Such studies are particularly important to determine if certain iconic and endangered species face unique threats and if local threats to a species are part of a larger geographic phenomenon.

Here, we use a dataset of 674,320 digitized wildlife rehabilitation records from 94 centers across the USA and Canada to learn about the threats that wildlife is facing, what threats are experienced by different species, and how effective wildlife rehab centers are at treating animals.

We will use wildlife rehabilitation records to address the following six categories of research questions. One goal of this study is to assess if these questions can be addressed using this large body of newly-digitized data.

- 1) What general factors are impacting wildlife in the United States and Canada?
What threats are there to individual species, particularly iconic and endangered species?
- 2) Do threats to wildlife vary by geographic region?
- 3) When and which species are affected by chemical pollution and toxicants (specifically, lead and pesticides)?
- 4) Where are infectious diseases (specifically, West Nile virus) appearing, in which species, and how quickly do they spread?
- 5) How are wildlife impacted by extreme weather events?
- 6) What percent of the animals brought to wildlife rehab centers are released? How does that vary by taxonomic group and other factors?

Our overall goal in this study is to use these findings to make recommendations to help conserve wildlife populations and improve wildlife and human health.

MATERIALS AND METHODS

Wildlife rehabilitation dataset compilation and categorization

We collected digitized records of wildlife admitted to wildlife rehabilitation (rehab) centers and compiled them into a dataset. Of the total 675,186 records, 84% were provided as a spreadsheet by the Wildlife Incident Log/Database and Online Network (WILD-ONe) database (created by the Wildlife Center of Virginia, Waynesboro, Virginia, USA; www.WILD-ONe.org), and the remaining 16% of records were provided as separate spreadsheets by individual centers which had been contacted with a request

for data. The initial dataset had 675,186 animal patient records from 132 wildlife rehab centers. We excluded centers which had fewer than 100 records, resulting in a final dataset of 674,320 records from 94 wildlife rehab centers (Table 4.1). The timeframe of records spans from 1975 to 2019, with the vast majority (95%) of the records from 2011 to 2019, due to recent switches to digital record keeping. Some of these digitized records were previously paper records that were transcribed into spreadsheets, but the majority of these digitized records had been directly entered into digital spreadsheets or recordkeeping software in recent years. There are records from 47 U.S. states and the District of Columbia and 8 Canadian provinces (Figure 4.1). The dataset includes 1,102 species, of which 56.1% are birds, 39.6% mammals, 3.4% reptiles, 0.1% amphibians, and 0.8% unclassified or other. Information included in the record for each animal may include some of (but not necessarily all of) the following: unique identifying number, genus, species, subspecies, age class, location found, date admitted, description of condition or reason for admittance, diagnosis, treatment, center where admitted, and disposition (or outcome). Personal identifiable information of rescuers was excluded.

The descriptions of the conditions of the wildlife and reasons for admittance varied widely (based on state reporting requirements and each center's protocol), so we developed a unique categorization schema to standardize the "Reason for Admittance" field across the dataset. We created 27 categories informed by previous publications (Gourlay et al., 2014; Janssen et al., 2020; Kelly and Sleeman, 2003; Kelly et al., 2014; Kelly et al., 2021; Molina-López et al., 2017; Hanson et al., 2021; Romero et al., 2019), the advice of wildlife rehabilitation practitioners, familiarity with the descriptions in the

dataset, and the threats we were interested in studying (e.g., lead). We then determined keywords to classify records into each category. We used ‘case_when’ in R package *dplyr* (Wickham et al., 2020) to classify each record into a “Reason for Admittance” category based on the presence and hierarchy of keywords: for example, if a keyword for two different categories was detected (e.g., both lead and toxicant), the record would be classified into the category which was higher on the hierarchy (e.g., lead). For this classification, we used columns which contained information about animal condition, circumstances of rescue, symptoms, and diagnoses. Many of the descriptions which were vague or more variable ended up in categories such as “sick/unwell,” “injured,” and “unknown/other.” Descriptions and symptoms were generally clear and consistent for categories such as vehicle collisions, hunting or fishing injuries, toxicant poisoning, and infectious diseases. For lead and pesticides, records were classified if they indicated the *presence* of lead or a pesticide, not necessarily above a clinically-determined level. For West Nile virus, records were classified based on a rehabber or veterinarian’s designation, which was based on symptoms, species, time of year, and sometimes, but not always, a diagnostic test (C. Kelley, personal communication).

Geographical and meteorological data

We georeferenced the location where animals were found to the centroid of the most precise geographic unit provided (address, then city or town, then county; Ellwood et al., 2019) using ‘geocode’ in R package *ggmap* (Kahle and Wickham, 2013).

For regional analyses, we grouped states and provinces into the following regions: West (Alberta, Arizona, British Columbia, California, Colorado, Idaho, Manitoba, Montana, New Mexico, Oregon, Saskatchewan, Utah, Washington, and Wyoming), Plains (Arkansas, Iowa, Kansas, Louisiana, Missouri, Nebraska, Oklahoma, South Dakota, and Texas), Great Lakes (Illinois, Indiana, Kentucky, Michigan, Minnesota, Ohio, Wisconsin), Southeast Canada (Nova Scotia, Ontario, Prince Edward Island, Quebec), Northeast (Connecticut, Massachusetts, Maine, New Hampshire, New York, Rhode Island, Vermont), Mid-Atlantic (Washington D.C., Delaware, Maryland, New Jersey, Pennsylvania, Virginia, West Virginia), Southeast (Alabama, Georgia, Mississippi, North Carolina, South Carolina, Tennessee), and Florida. There were no records from Alaska, Hawaii, North Dakota, or several other Canadian provinces. Regions were designed to group together animals found in similar ecoregions, maintain clear spatial clusters of animal locations, follow commonly-understood regional designations (e.g., Northeast), and maintain political (state/province) boundaries. Regions were also made to maintain large enough sample sizes for robust analyses (> 40,000 records in each region).

For analyses of the effects of extreme weather events on wildlife, we extracted information on the type, date, and location of events from the National Oceanic and Atmospheric Administration's (NOAA) Storm Events Database (<https://www.ncdc.noaa.gov/stormevents/>). We collected information on hurricanes and tropical storms in southern Florida (Broward, Miami-Dade, and Palm Beach Counties) from 1996 to 2019, extreme heat events in southern Florida from 2001 to 2017, flood

events in southern Florida from 1997 to 2018, flood events in Delaware from 2013 to 2019, extreme heat events in Delaware from 2013 to 2018, high wind events in Delaware from 2013 to 2019, and high wind events in western New York (Erie County) from 2015 to 2019 (NWS, 2021). Extreme weather event data were collected for years for which there were data for both weather events and rehab records.

Statistical analysis

All analyses were conducted using R statistical software, version 4.0.2 (R Core Team, 2020). For analyses of trends over time, we conducted linear regressions comparing the year to the number or proportion of cases (e.g., lead cases or West Nile virus cases). For analyses comparing the disposition of animals by taxonomic class, we conducted chi-square tests.

For analyses of the impact of extreme weather events, we compared the number of animals admitted in the 7 days before an event and the 7 days after the event (including the day of the event in “after”). Each analysis was conducted using wildlife rehab records and extreme weather events records from a restricted geographical area (e.g., three counties including and surrounding Miami; the state of Delaware). We separately analyzed different types of extreme weather events, including hurricanes and tropical storms, extreme heat events, and flood events. In order to avoid overlap and influence from prior events, we considered events within 13 days of each other to be a combined event; for these cases, we compared the number of animals admitted *per day* in the 7 days before the first event to the number of animals admitted *per day* in the

intervening days and the 7 days after the last event (in some cases, multiple events within several days of each other were combined). For each analysis of a type of extreme weather event in a specific location, we conducted a paired t-test to compare the number of animals admitted to wildlife rehab centers in the 7 days before and 7 days after each extreme weather event. In cases with data from over a decade, we also split the data into two groups of earlier years (1996-2004) and later years (2005-2018) and conducted a separate paired t-test for each group.

RESULTS

Common species admitted to wildlife rehab centers

In this dataset, the five most common species admitted to wildlife rehab centers were, in order, the eastern cottontail rabbit (n=76,994), eastern grey squirrel (n=60,459), Virginia opossum (n=45,380), American robin (n=25,644), and raccoon (n=23,563) (see Table 4.2 for species' scientific names). Of the 21 most common species, 16 were birds and 5 were mammals. The most common species admitted to rehab centers varied slightly by region, with many of the most common species appearing in all or most regions (e.g., eastern cottontail, eastern grey squirrel, Virginia opossum, mallard duck). Some species were the most commonly admitted in only one region (e.g., American crow in the West, red squirrel in Southeast Canada, common box turtle in the Mid-Atlantic, big brown bat in the Great Lakes, white-footed mouse in the Northeast, barred owl and black vulture in the Southeast, brown pelican and laughing gull in Florida, and white-winged dove and

fox squirrel in the Plains). Two non-native species were commonly admitted in many regions: the European starling and house sparrow.

Reason for admittance

We grouped the categories of reason for admittance into seven umbrella groups:

Human Disturbance (vehicle collision, other human disturbance, dog, window or building, cat, fishing, shot, electrocuted), **Orphaned** (juvenile animals found alone at an age still requiring parental care), **Injured or Sick** (injured, sick/unwell, neurologic, trauma, abnormal behavior, dead on arrival), **Natural Disturbance** (other natural disturbance, predator, fell from nest), **Infectious Disease** (parasite, other infectious disease, West Nile virus, bacteria, infection, mange), **Toxicant** (other toxicant, lead, pesticide), and **Unknown or Other**. Overall, Human Disturbance was the most common reason for animals to be admitted (39.8% of cases), followed by Orphaned (20.1%), Unknown or Other (17.1%), Injured or Sick (15.0%), Natural Disturbance (4.7%), Infectious Disease (2.8%), and Toxicants (0.6%). Of the Human Disturbance category, vehicle collisions were the most common reason for animals to be admitted (12.0%). Vehicle collisions were highest from May to July and disproportionately affected reptiles.

When grouping species into taxonomic class, as birds, mammals, or reptiles (with other classes excluded due to low sample sizes), the proportions of different reasons for admittance varied (Figure 4.2A). Human Disturbance remained the largest category for all three classes, but it was a far greater proportion for reptiles. Orphaned animals were a greater proportion of the mammals than of the birds or reptiles. A greater proportion of

birds were reported as injured or sick in comparison with mammals or reptiles. The prevalence of these reason for admittance categories varied slightly by region (e.g., there were more animals affected by human disturbance in the Great Lakes, and more orphaned animals in Southeast Canada), but the overall patterns were largely similar (Figure 4.2B).

There was more variation at the species level in the reasons that wild animals were brought to rehab centers. We selected nine iconic species to highlight. The predominant reasons for these species arriving at rehab centers were vehicle collisions for the great horned owl, red-tailed hawk, bald eagle, eastern screech owl, common box turtle, and red fox; fishing for the brown pelican; window or building collisions for the big brown bat; and abnormal behavior for the common loon (Figure 4.3A). We also highlighted six endangered (or threatened) species with 10 or more records. The predominant reasons for these species to arrive at rehab centers were injuries for the piping plover, vehicle collisions for the gopher tortoise and wood stork; abnormal behavior for the loggerhead sea turtle and green sea turtle; and fishing incidents for the Kemp's ridley sea turtle (Figure 4.3B).

Lead

The majority of lead cases (70%) were specified as confirmed or suspected, and the remaining 30% lacked information on whether they were confirmed or suspected. Of those specified, 72% were confirmed with the presence of lead. There was a clear seasonal pattern in lead cases, with more cases in the winter, fewer in the summer, and intermediate numbers in the spring and fall (Figure 4.4A). The number of lead cases at

wildlife rehab centers increased significantly over time, from 3 cases in 2010 to 107 cases in 2019 (p -value < 0.001). However, when taken as a proportion of total animals admitted per year, there was no significant increase in lead cases over time (p -value = 0.90; lead cases typically 0.06-0.12% of total cases per year). Bald eagles were by far the species in which lead was detected the most, with bald eagles comprising 39% of the lead cases (Figure 4.4B). The species most-commonly affected by lead varied slightly by region, with many of the same species predominantly affected across several regions (e.g., bald eagle, turkey vulture, black vulture, red-tailed hawk, common loon, Canada goose, mallard), and some species in which lead was detected more often only in certain regions (e.g., golden eagle in the West, Virginia opossum in the Great Lakes, mute swan in the Northeast).

Pesticides

The majority of pesticide cases (89%) were specified as confirmed or suspected, and of those, 43% were confirmed with the presence of a pesticide. Of the total pesticide cases, 86% were suspected to be rodenticides. There was a seasonal pattern in pesticide cases, with slightly more cases from late spring to early fall, and slightly fewer (but still a steady number) in the early spring, late fall, and winter (Figure 4.5A). The number of pesticide cases at rehab centers increased significantly over time, from 6 in 2011 to 93 in 2019 (p -value < 0.001). When taken as a proportion of total animals admitted per year, pesticide cases increased slightly but non-significantly over the past decade (p -value = 0.35; pesticide cases typically 0.06-0.10% of total cases per year). Red-tailed hawks and

eastern grey squirrels were the species comprising the most pesticide cases (12.4 and 11.6%, respectively) (Figure 4.5B). The species affected by pesticides varied slightly by region, with most of the same species predominantly affected across several regions (e.g., red-tailed hawk, eastern grey squirrel, eastern chipmunk, eastern cottontail, great horned owl), and a few species in which pesticides were detected more often only in certain regions (e.g., white ibis in Florida, plains pocket gopher in the Plains, bald eagle in the Mid-Atlantic, ring-billed gull in the Great Lakes).

West Nile virus

The majority of West Nile virus (WNV) cases (89%) were specified as confirmed or suspected, and of those, 52% confirmed the presence of WNV. There was a strong seasonal pattern in WNV cases, with most cases in July, August (peak), and September (Figure 4.6A). There was very large interannual variation in the number of WNV cases at rehab centers. WNV cases did not significantly increase over time (p -value = 0.17), nor did they significantly increase when taken as a proportion of the total number of animals admitted per year (p -value = 0.68; WNV cases typically 0.10-0.28% of total cases per year). American crows, red-tailed hawks, and great horned owls were the species comprising the most WNV cases (45.8, 20.1, and 12.5%, respectively) (Figure 4.6B). The species affected by WNV varied slightly by region, with most of the same species predominantly affected across several regions (e.g., American crow, red-tailed hawk, great horned owl, Cooper's hawk, barred owl, bald eagle), and a few species in which WNV was detected more often only in certain regions (e.g., snowy owl in Southeast

Canada, raccoon in the Great Lakes, American kestrel in the Plains, fish crow in the Mid-Atlantic, eastern grey squirrel in the Northeast). By 2013, WNV was already present at centers which tested for WNV across the Northeast, Mid-Atlantic, and Great Lakes.

Extreme weather events

The effects of extreme weather events on the number of animals admitted to rehab centers appeared to vary based on the location and the type of weather event. There were no significant effects of extreme heat, flood, or high wind events in Delaware, high wind events in western New York, or extreme heat events in southern Florida (Table 4.3). There were significantly more animals admitted to rehab centers following hurricane and tropical storm events and flood events in southern Florida. Compared to the week before an event, on average, six more animals were admitted the week after a hurricane or tropical storm, and three more animals were admitted following a flood. These effects were stronger in recent years, possibly due to the increasing intensity and frequency of extreme weather events (NAS, 2016; Ummenhofer and Meehl, 2017). When divided into two time periods (1996-2004 and 2005-2018 for hurricanes and tropical storms, 1997-2004 and 2005-2018 for floods), only the 2005-2018 time period had significant results, and these results indicated a greater increase in animals admitted after extreme weather events compared to the results for the entire time period. Compared to the week before an event, on average, nine more animals were admitted after a hurricane or tropical storm and four more animals were admitted after a flood for the 2005-2018 time period. Following a storm or flood event in southern Florida, more mammals, particularly

opossums, and more double-crested cormorants and northern mockingbirds were brought to rehab centers. Compared to the week before the event, animals brought in after were more likely to be orphaned or have fallen from a nest.

Disposition

Overall, 32.5% of animals were released back to the wild, 29.7% died at rehab centers, 28.9% were euthanized, and 8.9% were transferred, active cases, or another outcome. The outcomes were fairly similar across different taxonomic classes. For birds, mammals, and reptiles, 32-33% were released, 24-31% died, and 28-29% were euthanized (Figure 4.7). For amphibians, more were euthanized (35.0%), and fewer died (21.5%). Mammals had the highest release rate (33.3%), and amphibians had the lowest release rate (31.5%). However, none of these differences are statistically significant ($\chi^2 = 2.93$, $df = 6$, $p\text{-value} = 0.82$).

DISCUSSION

We evaluated six categories of research questions to determine which questions can be addressed with wildlife rehabilitation (rehab) records and to make recommendations to help conserve wildlife populations and improve wildlife and human health.

Threats to wildlife – overall and by species

An important caveat is that the information collected by rehab centers does not necessarily reflect what is happening in wildlife populations as a whole. Our conclusions here are limited to which animals arrive at rehab centers, and there are biases in which species and conditions show up. For example, people may be more likely to pick up a charismatic animal, like a bald eagle, compared to a common animal, like a pigeon. People may be less likely to pick up an animal perceived as dangerous, like a bear, or a disease risk, like a raccoon. People will be more likely to encounter animals which are near houses, roads, etc., and thus will be more likely to pick up animals which get sick or injured in proximity to people. This dynamic will also affect which conditions are more likely to show up at wildlife rehab centers – for example, people are more likely to encounter an animal which got hit by a car and less likely to encounter an animal which got sick in the middle of the woods. These biases and others not stated here should be kept in mind and clearly communicated when analyzing rehab records.

We identified key threats to wildlife by examining conditions that caused animals to be admitted to wildlife rehab centers. Overall, human disturbance accounted for the largest proportion of wildlife illness and injury. This pattern is consistent with other studies: Burton and Doblak (2004) found that human activities accounted for most of the animals admitted to a rehab center in Columbus, Ohio, and Janssen et al. (2020) found that human and urbanization-related stressors were the most common stressors to rescued animals in Adelaide, South Australia. First, the predominance of human disturbance in rehab records may be partially due to the nature of wildlife rehabilitation – animals will

be found more often in areas near humans where they may be affected by human activities. Second, even if the impact of human activities is biased to be larger than it would be in a random sample of sick and injured wildlife, these records still indicate that human activities are having a large, negative impact on wildlife. Last, it means that a significant portion of what is impacting wildlife is within our control. We can take steps to reduce our impact and improve wildlife health. At the same time, we can also improve human health. For example, wildlife-vehicle collisions result in human injuries, as well as wildlife injuries (Gunson et al., 2011; Loss et al., 2014a; Shilling and Waetjen, 2015). Wildlife-vehicle collisions were the largest proportion of human disturbance-related cases, and therefore, we can reduce the number of human and wildlife injuries with wildlife-vehicle collision mitigation measures, such as overpasses and underpasses with fencing, roadside vegetation management, reducing speed limits, and installing flight deflectors along roadsides to force birds to fly above vehicle height (Gunson et al., 2011; Loss et al., 2014a; Shilling and Waetjen, 2015). By mitigating our impact on wildlife, we can also improve the health and safety of people and reduce the cost of vehicle accidents.

Toxicants and infectious diseases represented smaller proportions of the animals admitted (0.6% and 2.8% respectively), but these categories receive a lot of attention in research (Franson and Pain, 2011; Plaza et al., 2019; Gourlay et al., 2014). One reason may be that these threats also impact human health (Bellinger et al., 2013; Cai and Calisi, 2016; Kwan et al. 2010; Pimentel, 2005). Another reason may be the potential to create change and solutions through regulations and policy (Kanstrup et al., 2018; Mörner et al. 2002; Rich et al., 2020).

A major strength of this dataset is in the vast number of species we can study (over 1,000). We focused on a handful of iconic, threatened, or endangered species. A key takeaway is that conditions related to human disturbance were the most common reasons for admittance for many species. These were most often vehicle collisions, window or building collisions, and fishing incidents. We recommend that addressing these threats be prioritized in conservation and management efforts with measures such as road crossings, window collision deterrents (e.g., nets, decals) and window design modifications, and public education related to the use and disposal of fishing gear (Dau et al., 2009; Loss et al., 2014a; Shilling and Waetjen, 2015). This dataset can be a tool for local wildlife managers to examine threats to particular species. We recommend keeping in mind the biases of this dataset, but it can be a good place to begin identifying threats.

Regional analyses – differences and similarities in threats to wildlife

We found slight regional differences in the reasons that animals were admitted to rehab centers. For example, a greater proportion of animals were affected by window or building collisions in the Great Lakes, vehicle collisions in the Southeast, toxicants in the Mid-Atlantic, and orphaning in Southeast Canada. One possible explanation for the regional differences is that some species were admitted in greater or lesser numbers in different regions. For example, there were more bats admitted in the Great Lakes, and window or building collisions were a top reason of admittance for bats. Some centers specialize in certain species. Further, regional differences in presence or abundance of animals may also explain differences in the species in which toxicants or diseases were

commonly detected. For example, lead was detected in golden eagles in the West, and West Nile virus was detected in snowy owls in Southeast Canada, where those species are more common (Holt et al., 2020; Katzner et al., 2020). Another possible explanation for the regional differences is that we used an incomplete dataset. Not all centers across the U.S. and Canada are represented in this dataset, so the records here may present a biased sampling of species and/or conditions in different regions. These biases in species abundance and data sampling should be accounted for when making comparisons between regions.

Toxicants

We used lead and pesticides as examples of toxicants that can be studied using wildlife rehab records. The strengths of this dataset are in identifying species in which toxicants are commonly detected and in identifying seasonal patterns in toxicant exposure. We found that lead is most commonly detected in raptors and waterfowl, and pesticides are most commonly detected in raptors and small mammals. We found that 39% of the animals which were identified with lead present were bald eagles; this may be partially due to higher testing and detection efforts for this species. Other studies confirm high rates of lead presence in eagles (Franson and Russell, 2014; Hanley et al., 2022; Slabe et al., 2022). Eagles have long been a focus of the effects of lead and the interest of the public and research communities (Cruz-Martinez et al., 2012; Kramer and Redig, 1997). These studies corroborate our findings of frequent lead detection in eagles, and further, the focus on bald eagles implies that other species likely have higher exposure

and impact from lead, but it is being detected less often. Pesticides are even more likely to go un- and under-detected because the testing is more expensive, the equipment is less common in rehab centers, and confounding symptoms can make diagnosis difficult (Hudson et al., 1984; C. Kelly, personal communication).

Our findings of seasonal patterns support known and suspected sources of toxicant exposure. Lead cases peaked in winter, likely due to animals ingesting lead ammunition from shot carcasses (especially deer) after hunting seasons (Cruz-Martinez et al., 2012; Golden et al., 2016; Kramer and Redig; 1997; Warner et al., 2014). Other studies found a similar seasonal pattern with elevated lead levels in eagles in the late autumn and winter (Cruz-Martinez et al., 2012; Franson and Russell, 2014). On the other hand, Cai and Calisi (2016) found that lead cases in pigeons in New York City peaked in the summer, indicating that atmospheric or particulate lead may be a greater lead source in cities. Other sources of lead likely include fishing gear (Grade et al., 2019) and contaminated sediment (Sileo et al., 2001). Pesticide cases peaked in summer, indicating that animals may be exposed particularly when rodenticides (which were the vast majority of the pesticide cases) are used to control “pest” populations during growing seasons (Elliott et al., 2014; Rich et al., 2020; Watt et al., 2005).

The impacts of toxicants range from individual to population level. Recent studies have concluded that lead poisoning likely suppresses population growth rates in bald and golden eagles (Hanley et al., 2022; Slabe et al., 2022) and common loons (Grade et al., 2018). Pesticides contributed to the precipitous decline of many bird species (Blus, 1996) and still pose an extinction threat to vulture species (Finkelstein et al., 2012; Plaza et al.,

2019). Further, studies have found that toxicants can weaken animals' immune systems and make them more susceptible to diseases (Riley et al., 2007; Sánchez et al., 2020). Toxicants can also contribute to other forms of injury, for example, by affecting behavior and making birds more likely to collide with a vehicle or building (Kramer and Redig, 1997; G. Mertz, personal communication).

The limitations of this dataset are in identifying trends in toxicant exposure over time. Many confounding factors make it difficult to draw accurate conclusions about changes over time. These factors include changes in the following: public awareness of rehabilitation centers, public opinion of wildlife conservation and rehabilitation, behavioral patterns that may lead to finding and bringing in wildlife, wildlife population sizes and distributions, numbers of digitized records, finances at rehab centers, diagnostic and detection tools and capacity, the education and awareness of rehabilitation professionals, and more (A. Lewis and Y. Acosta, personal communication). We recommend that future studies examine ways to control for these factors and others in order to better explain changing patterns over time in wildlife rehab records.

To mitigate the impacts of lead poisoning, we recommend changing federal and state regulations, where necessary, to phase out lead ammunition for hunting and lead fishing gear and to institute buy-back programs for existing lead hunting and fishing gear (Cruz-Martinez et al., 2012; Bellinger et al., 2013; Grade et al., 2018; Hanley et al., 2022). To improve the detection of pesticide poisoning, we recommend education for rehabbers about the symptoms and funding for diagnostic equipment.

Infectious diseases

We used West Nile virus (WNV) as an example of an infectious disease that can be studied using rehab records (Ana et al., 2017). The strengths (identifying species affected and seasonal patterns) and limitations (explaining trends over time) are similar to those with studying toxicants. We found that WNV is most commonly detected in corvids and raptors, and cases peaked in August, which concurred with other studies of WNV in birds (Ana et al., 2017; Kwan et al., 2010). Another limitation of using rehab records to study WNV is that diagnostic criteria are not standardized across centers. Some centers use symptoms, some use diagnostic tests, and some use both (Ana et al., 2017; Camacho et al., 2016; C. Kelley, personal communication). As a mosquito-borne arbovirus, WNV transmission may be affected by climate-related factors in multiple ways.

We found that this particular dataset was weak when attempting to pinpoint the geographical appearance or spread of WNV. We could not draw conclusions about the geographic appearance or spread of WNV without further information on the testing capacities of individual centers. At this point, we are uncertain whether new detection of WNV in a location indicates the spread of the disease to that new location, or the acquiring of new testing capacity. However, Kelly et al. (2021) demonstrated a system of using rehab cases as an early disease detection system, indicating that, while rehab records may not be a useful tool for studying past trends in WNV, they may become a powerful tool for identifying current and future disease emergence.

Climate change impacts – extreme weather events

In examining possible effects of human-driven climate change, we found that more animals arrived at rehab centers in the week after an extreme weather event compared to the week before, but only for certain types of weather events in certain locations: e.g., hurricanes and floods in southern Florida. Other studies have found negative impacts on wildlife health, mortality, and reproduction due to extreme weather events, including cyclones, droughts, high rainfall, floods, cold waves, heat waves, and marine heat waves (Cohen et al., 2020; Maxwell et al., 2019; Piatt et al., 2020; Pruvot et al., 2019).

The differences we found in which types of events had a significant effect may be due to how different events affect animals. For example, the effects of heat stress may manifest over a longer period of time than the week following a heat wave (which is the time period we examined) (Piatt et al., 2020; Pruvot et al., 2019). That may be why we do not see significant differences in the number of animals admitted before and after heat events. In contrast, a hurricane may have a more sudden and severe impact on animals, possibly resulting in many animals being brought to rehab centers directly following a storm (Bugoni et al., 2007; Talbot and Dauzat, 2014). However, Pruvot et al. (2019) identified a mass die-off of bats following a heat wave, and Piatt et al. (2020) linked mass marine bird mortality to a marine heat wave. These contrasting findings suggest that heat is still an important factor to assess for its impacts on wildlife, and the severity and location of the event may be important.

We recommend that the impacts of extreme weather events be accounted in disaster management plans and species management plans, particularly for vulnerable species which have limited geographic ranges. Increased government and grant funding should be allocated to wildlife rehab centers in preparation for treating more animals as climate change progresses.

Disposition

We found that outcomes of rehabilitation were fairly similar across different taxonomic classes. Across birds, mammals, and reptiles, the most common outcome was releasing the animal back to the wild, followed by death and then euthanasia. The rates of release we found were lower than those reported in Molina-López et al. (2017) and Hanson et al. (2021), and higher than those reported in Janssen et al. (2020), which indicates that there is variation in outcomes across rehab centers. Our findings indicate that rehab is a relatively successful venture, and that the resources put into rehab are able to return about a third of treated animals back to the wild. Further research should examine whether outcomes differ by species and by condition (e.g., see Hanson et al., 2021).

Recommendations

We recommend standardizing recordkeeping and criteria for diagnosis across wildlife rehab centers. This effort will require communication across state agencies, which regulate wildlife rehabilitation, and may require changing regulations in some

states to create standardized and consistent terminology. Database software such as WILD-ONE and Wildlife Rehabilitation Medical Database (WRMD) can provide rehabbers with tools to input and store records in a standardized format. Digitizing older, paper records will also provide opportunities to study patterns further back in time.

We found that conditions related to human disturbance, particularly vehicle collisions, window or building collisions, and fishing incidents, were the most common reasons that many animals were brought to rehab centers. We recommend that addressing these threats be prioritized in conservation and management efforts with measures such as road crossings and fencing, window collision deterrents and window design modifications, and public education and disposal of fishing gear. Further, to mitigate the impacts of lead poisoning, we recommend changing federal and state regulations, where necessary, to phase out lead ammunition for hunting and lead fishing gear and to institute buy-back programs for existing lead ammunition and gear.

We recommend using wildlife rehab records as an excellent place to start examining and identifying management and conservation priorities. If little is known about what is affecting a species, rehab records can help to identify places to start and focus future research.

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TABLES AND FIGURES

Table 4.1: Characteristics of the dataset

Field	n
Records	674,320
Wildlife rehabilitation centers	94
Years	45 (1975—2019)
U.S. States	47 (+ D.C.)
Canadian Provinces	8
Species	1,102

Table 4.2: Species common names and scientific names of animals mentioned in text

Common Name	Scientific Name
<u>BIRDS</u>	
American crow	<i>Corvus brachyrhynchos</i>
American kestrel	<i>Falco sparverius</i>
American robin	<i>Turdus migratorius</i>
Bald eagle	<i>Haliaeetus leucocephalus</i>
Barred owl	<i>Strix varia</i>
Black vulture	<i>Coragyps atratus</i>
Blue jay	<i>Cyanocitta cristata</i>
Brown pelican	<i>Pelecanus occidentalis</i>
Canada goose	<i>Branta canadensis</i>
Common loon	<i>Gavia immer</i>
Cooper's hawk	<i>Accipiter cooperii</i>
Double-crested cormorant	<i>Phalacrocorax auritus</i>
Eastern screech owl	<i>Megascops asio</i>
European starling	<i>Sturnus vulgaris</i>
Fish crow	<i>Corvus ossifragus</i>
Golden eagle	<i>Aquila chrysaetos</i>
Great horned owl	<i>Bubo virginianus</i>
House sparrow	<i>Passer domesticus</i>
Laughing gull	<i>Leucophaeus atricilla</i>
Mallard	<i>Anas platyrhynchos</i>
Mute swan	<i>Cygnus olor</i>
Northern mockingbird	<i>Mimus polyglottos</i>
Piping plover	<i>Charadrius melodus</i>
Red-shouldered hawk	<i>Buteo lineatus</i>
Red-tailed hawk	<i>Buteo jamaicensis</i>
Ring-billed gull	<i>Larus delawarensis</i>
Snowy owl	<i>Bubo scandiacus</i>
Turkey vulture	<i>Cathartes aura</i>
White-winged dove	<i>Zenaida asiatica</i>
White ibis	<i>Eudocimus albus</i>
Wood stork	<i>Mycteria americana</i>
<u>MAMMALS</u>	
Big brown bat	<i>Eptesicus fuscus</i>
Eastern chipmunk	<i>Tamias striatus</i>
Eastern cottontail	<i>Sylvilagus floridanus</i>
Eastern grey squirrel	<i>Sciurus carolinensis</i>
Eastern woodrat	<i>Neotoma floridana</i>

Fox squirrel	<i>Sciurus niger</i>
Plains pocket gopher	<i>Geomys bursarius</i>
Raccoon	<i>Procyon lotor</i>
Red fox	<i>Vulpes vulpes</i>
Red squirrel	<i>Sciurus vulgaris</i>
Virginia opossum	<i>Didelphis virginiana</i>
White-footed mouse	<i>Peromyscus leucopus</i>
<u>REPTILES</u>	
Common box turtle	<i>Terrapene carolina</i>
Gopher tortoise	<i>Gopherus polyphemus</i>
Green sea turtle	<i>Chelonia mydas</i>
Kemp's ridley sea turtle	<i>Lepidochelys kempii</i>
Loggerhead sea turtle	<i>Caretta caretta</i>

Table 4.3: The location and type of extreme weather events affected the number of wild animals arriving at wildlife rehab centers in the week before and the week after the event. Significance differences were calculated using paired t-tests, comparing the number of animals that arrived in the week before and the week after an extreme weather event for a series of events of the same type (e.g., floods or hurricanes/tropical storms) and in the location (e.g., Delaware or southern Florida). Significant results are in bold, and a statistically significant negative number in the “Difference in Means” column means that more animals were admitted in the week *after* the extreme weather event compared to the week before the event. Years included in the analyses varied by the timespan of the available weather data and wildlife rehab records. Analyses with 20 or more years were subsequently broken down into analyses of two time periods (earlier years and later years).

Location	Type of Extreme Weather Event	Years	n (events in analysis)	Difference in Means (animals admitted 7 days before vs 7 days after) (95% CI)	p-value	Significance
Southern FL	Heat	2001-2017	8	3.9 (-4.9 to 12.7)	0.333	n.s.
Southern FL	Hurricanes, tropical storms	1996-2018	26	(-)6.0 (-10.7 to -1.2)	0.015	*
		1996-2004	10	(-)0.6 (-2.6 to 1.4)	0.515	n.s.
		2005-2018	16	(-)9.3 (-16.7 to -1.9)	0.017	*
Southern FL	Floods	1997-2018	74	(-)2.6 (-5.0 to -0.3)	0.027	*
		1997-2004	22	(-)0.7 (-2.5 to 1.2)	0.453	n.s.
		2005-2018	52	(-)3.5 (-6.7 to -0.2)	0.036	*
Delaware	Heat	2013-2018	7	0.7 (-14.9 to 16.3)	0.915	n.s.
Delaware	Floods	2013-2019	40	(-)0.8 (-5.0 to 3.5)	0.725	n.s.
Delaware	High winds	2013-2019	11	(-)1.3 (-3.5 to 0.9)	0.228	n.s.
Western NY	High winds	2015-2019	17	(-)7.47 (-22.8 to 7.9)	0.317	n.s.

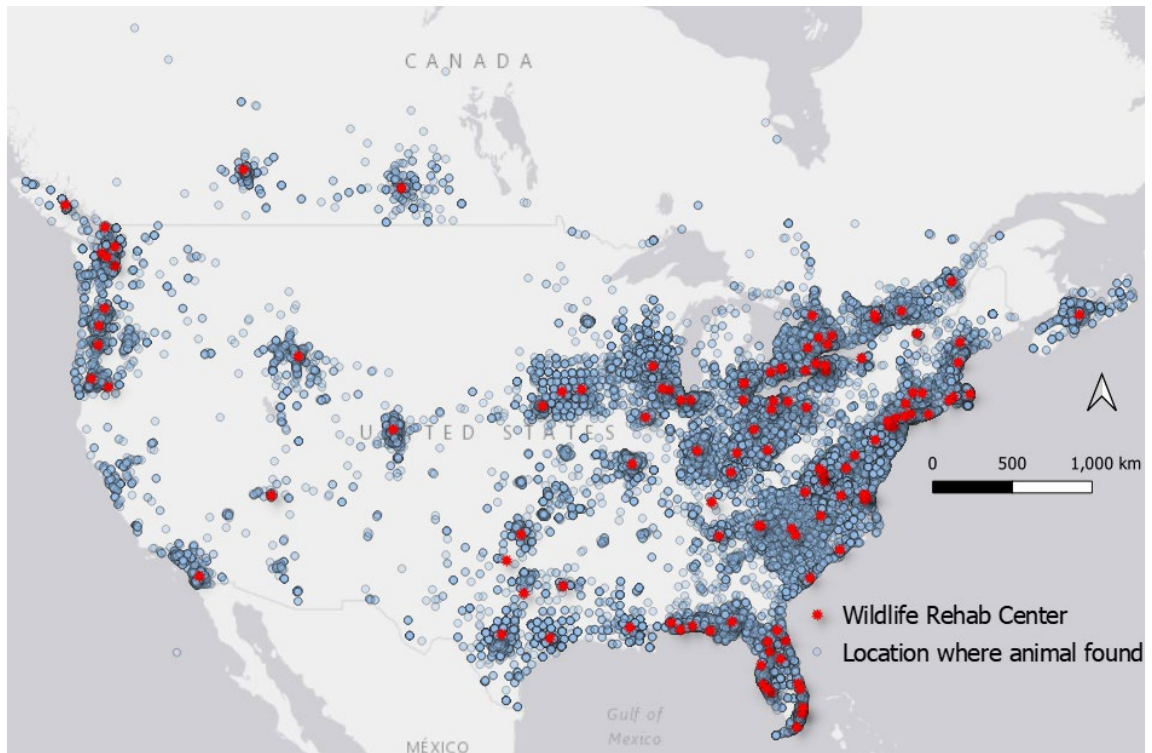


Figure 4.1: Locations of wildlife rehabilitation centers (red stars) and locations where animals were found (blue dots, transparency = 70%). Wildlife records which were not able to be georeferenced to street, town, or county level do not appear on this map. The bold lines outline the eight regions, and the number of wildlife rehab records in each region are as follows: West $n=43,089$; Plains $n=50,889$; Great Lakes $n=168,550$; Southeast Canada $n=54,203$; Northeast $n=85,324$; Mid-Atlantic $n=119,755$; Southeast $n=41,762$; and Florida $n=108,067$.

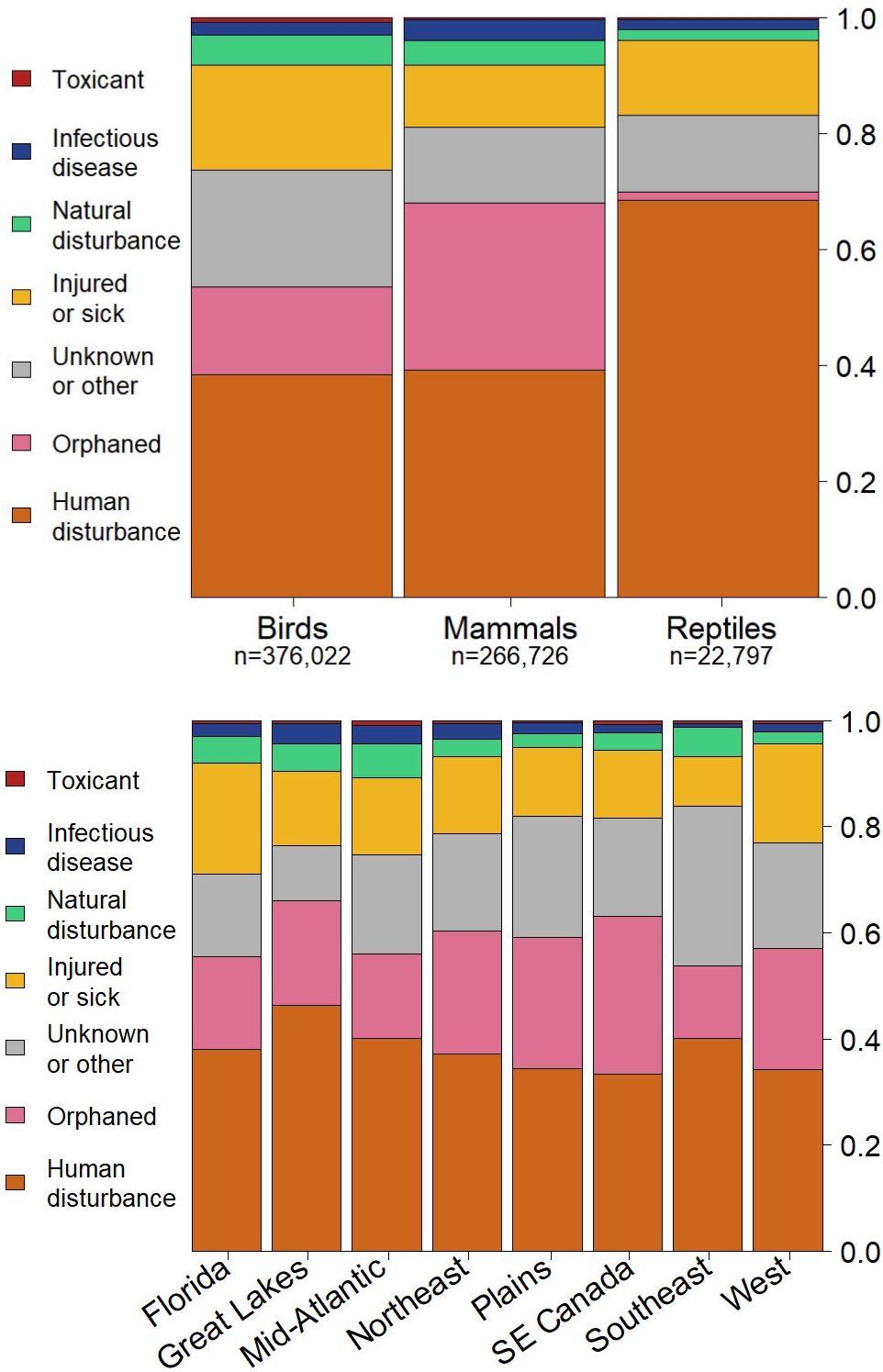


Figure 4.2: The predominant reasons that wild animals arrived at wildlife rehab centers varied by taxonomic class (A) and region (B). Reason for admittance is shown by the

seven umbrella groups. The number of wildlife rehab records in each region are as follows: Florida n=106,053; Great Lakes n=168,550; Mid-Atlantic n=119,752; Northeast n=85,322; Plains n=50,887; Southeast (SE) Canada n=54,142; Southeast n=41,742; and West n=43,071.

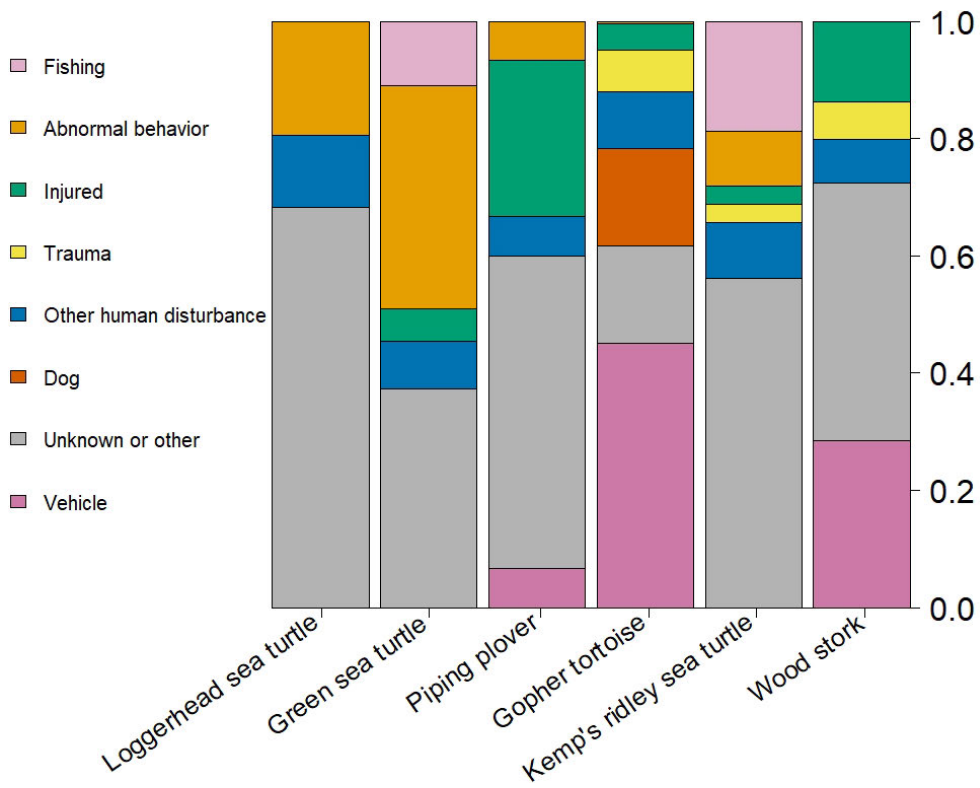
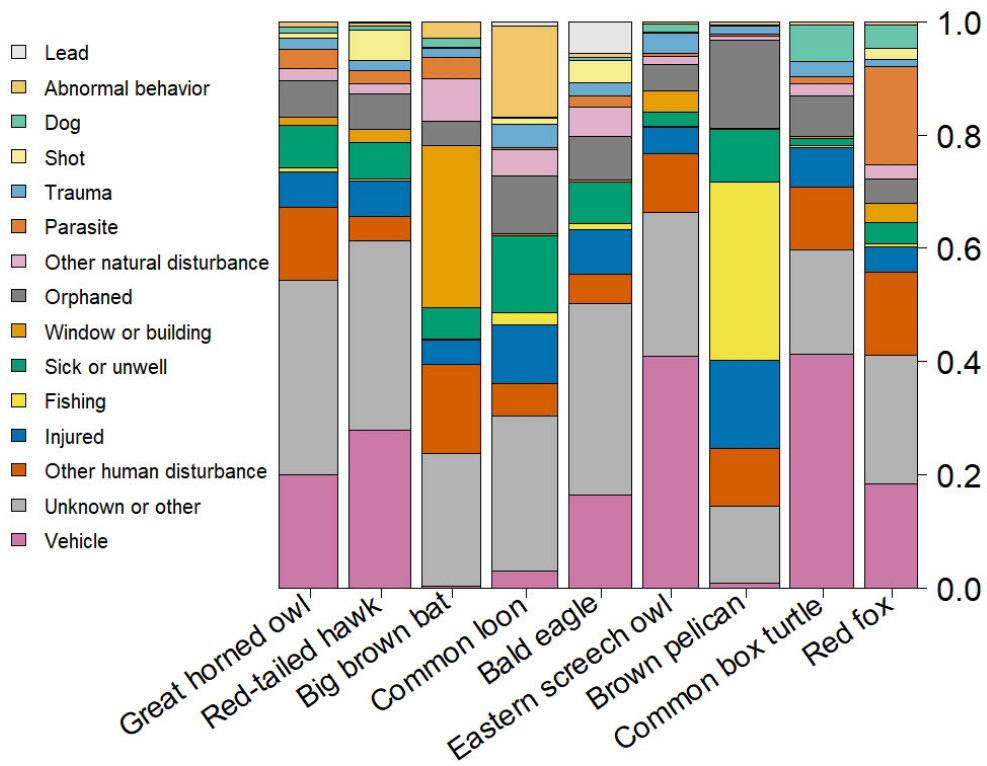


Figure 4.3: The predominant reasons that wild animals arrived at wildlife rehab centers varied by species for nine iconic species (A) and six endangered or threatened species (B). Reason for admittance is shown by a selection of the 27 reasons for admittance categories. (A) includes only the 15 most common reasons for admittance for those nine species, and (B) includes the eight most common reasons for those six species. The number of wildlife rehab records for each species are as follows: Great horned owl n=7,726; Red-tailed hawk n=13,760; Big brown bat n=7,764; Common loon n=1,674; Bald eagle n=3,645; Eastern screech owl n=8,329; Brown pelican n=11,936; Common box turtle n=5,514; Red fox n=2,167 (A); and Loggerhead sea turtle n=41; Green sea turtle n=145; Piping plover n=15; Gopher tortoise n=1,293; Kemp's ridley sea turtle n=32; and Wood stork n=109 (B).

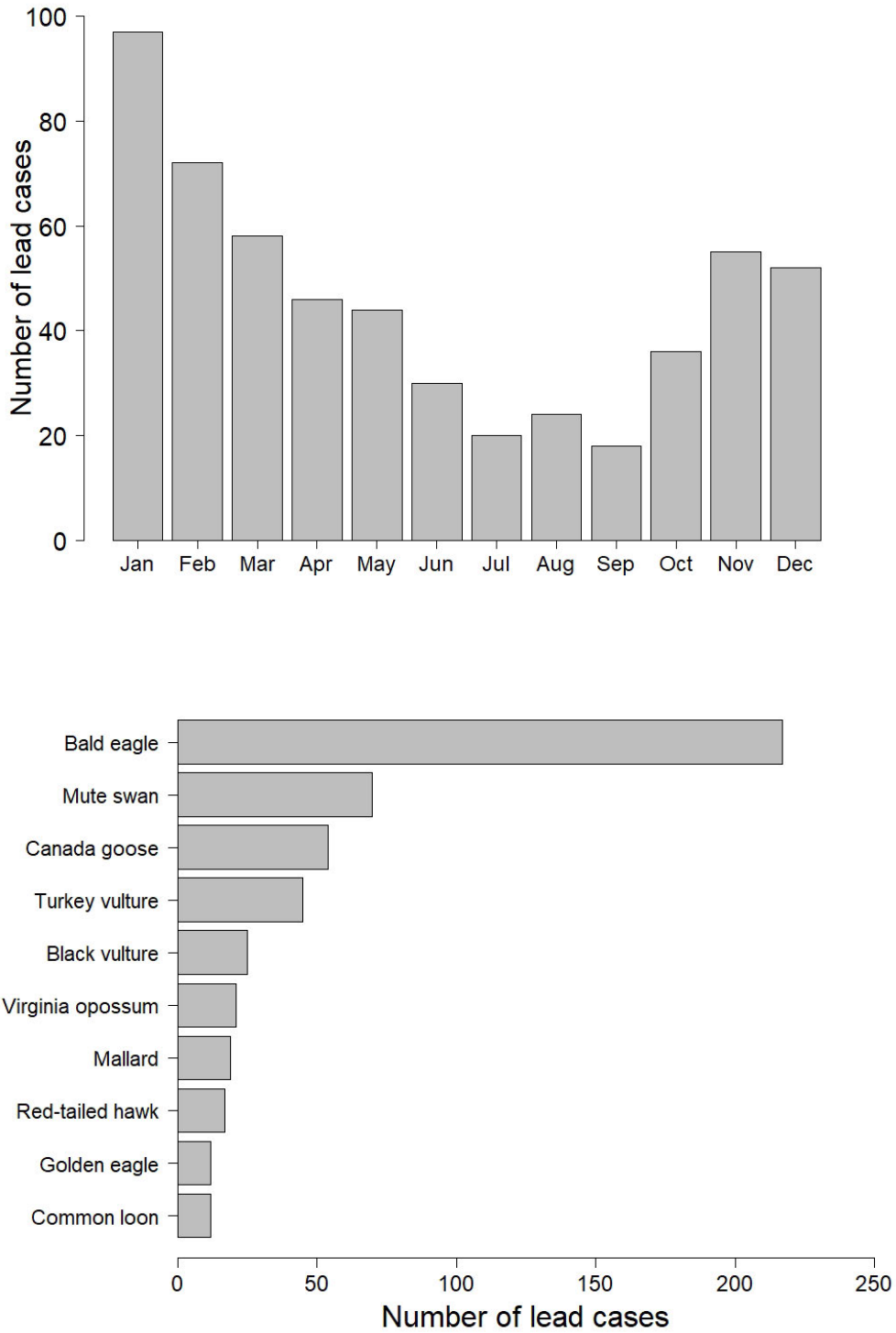


Figure 4.4: Lead cases exhibited strong trends in the seasonality of detected lead cases by month (A), and the species in which lead was most frequently detected (B).

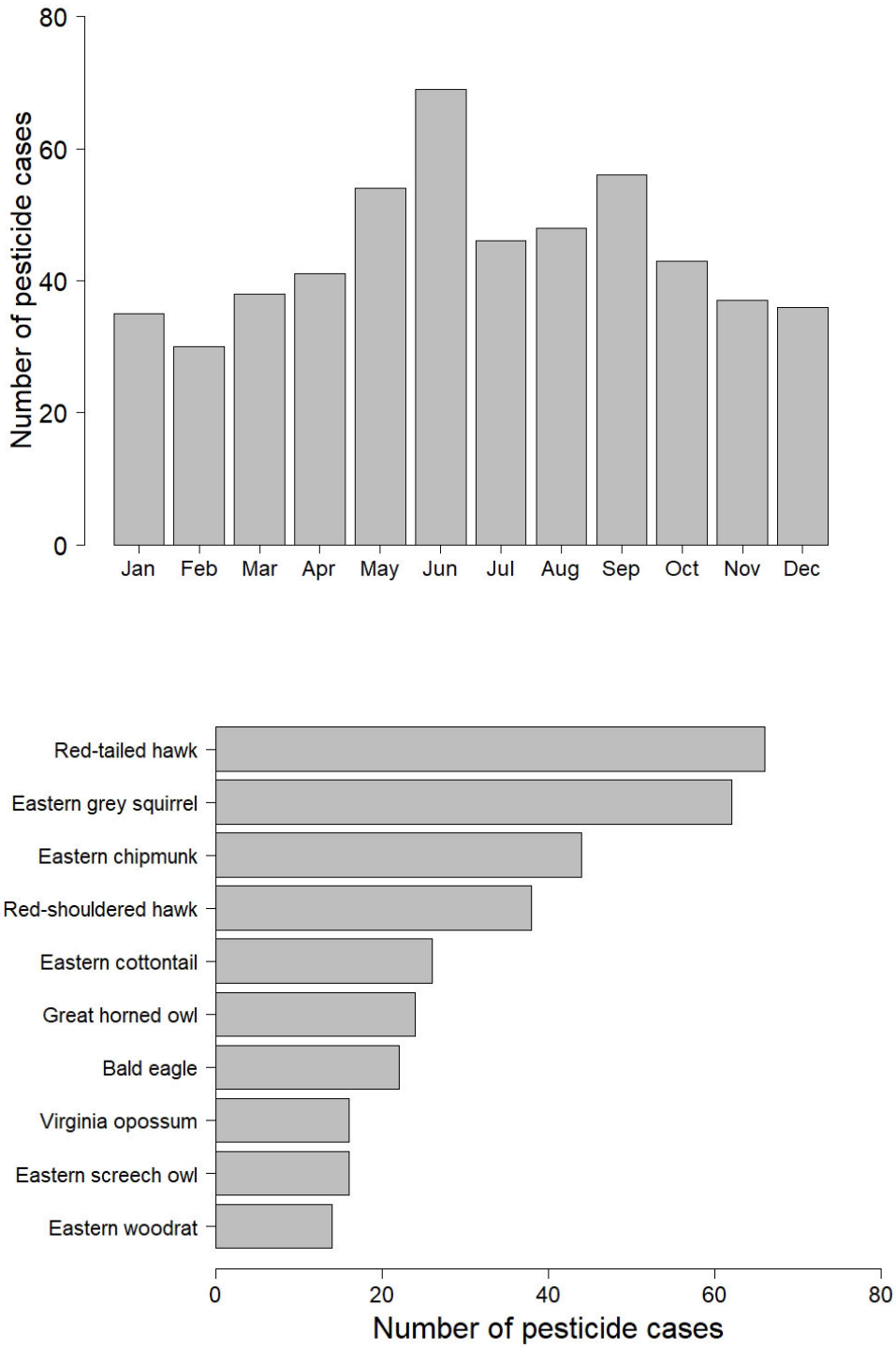


Figure 4.5: Pesticide cases exhibited strong trends in the seasonality of detected pesticide cases by month (A), and the species in which pesticides were most frequently detected (B).

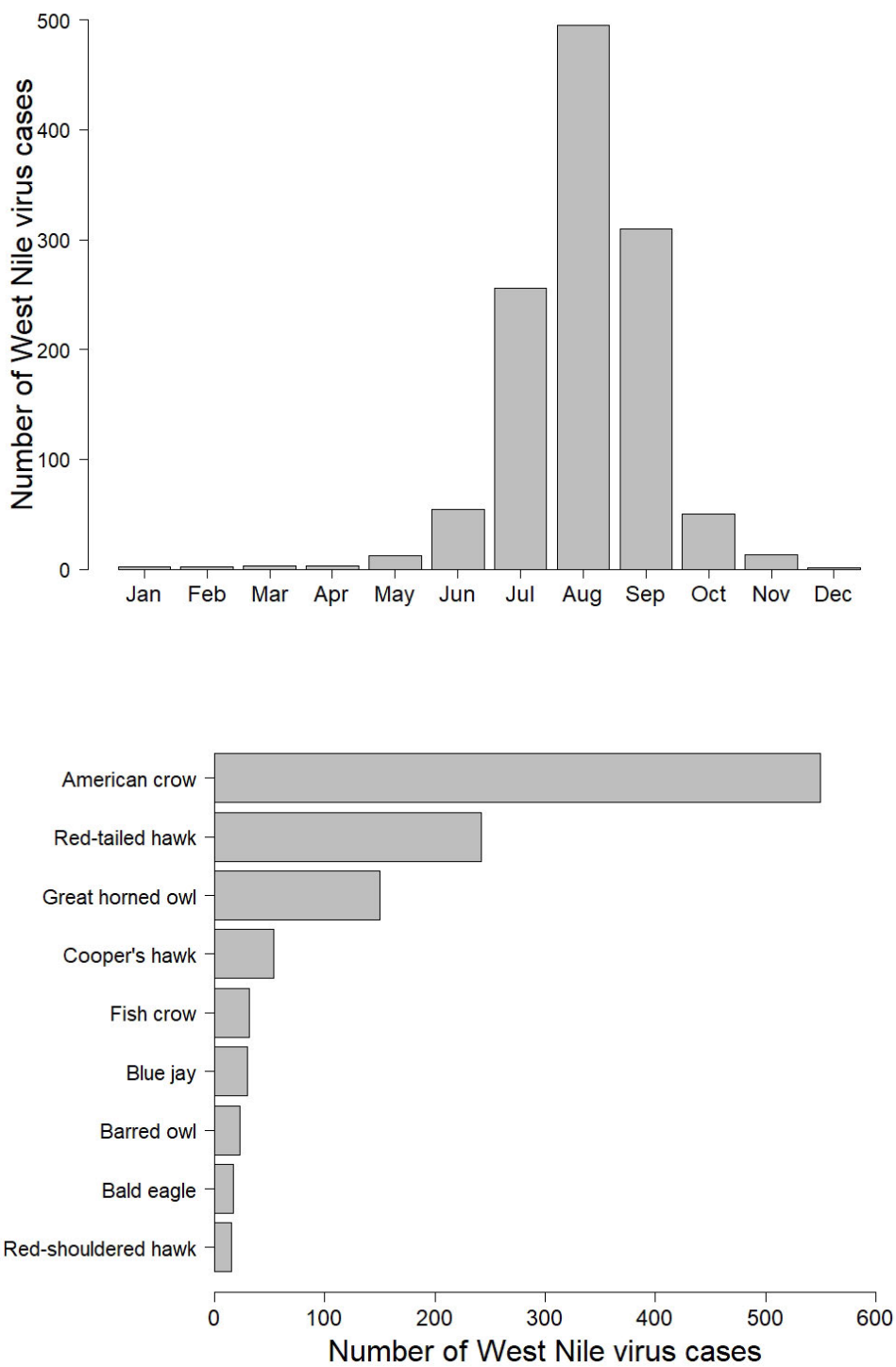


Figure 4.6: West Nile virus (WNV) cases exhibited strong trends the seasonality of detected WNV cases by month (A), and the species in which WNV was most frequently detected (B).

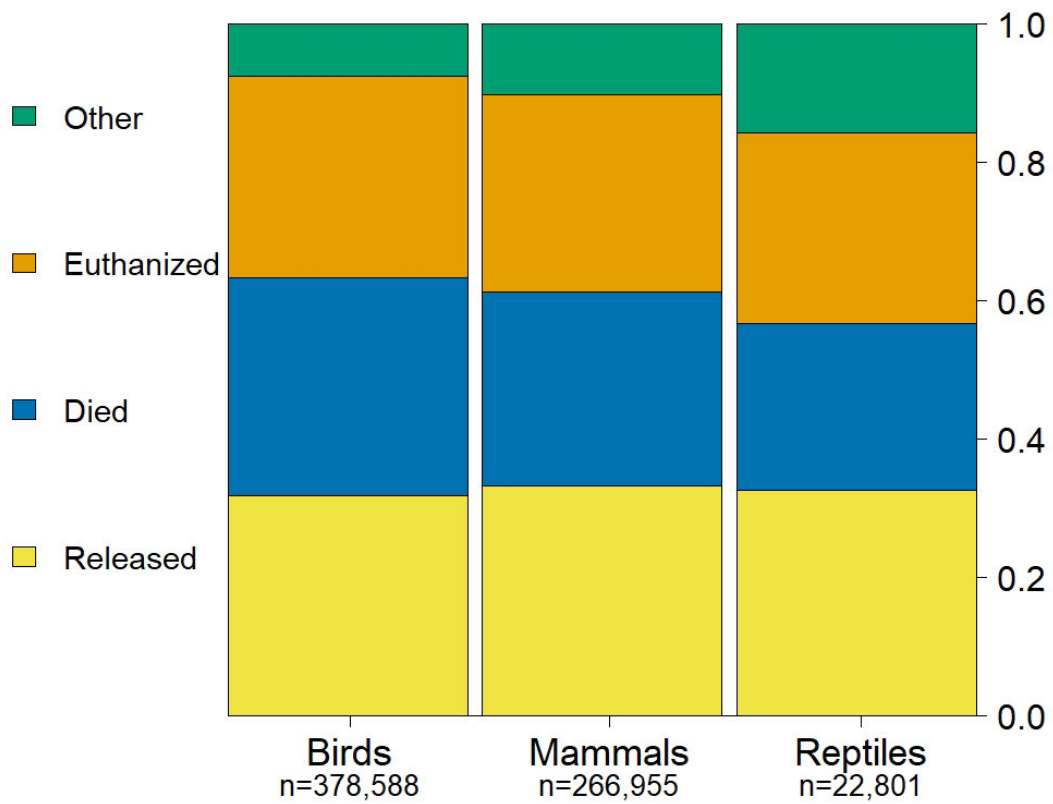


Figure 4.7: The disposition (or outcome) of wild animals at wildlife rehab centers varied by taxonomic class. “Other” includes active cases, animals which were transferred to other facilities, and other cases.

CHAPTER FIVE: CONCLUSIONS

The goal of this dissertation was to fill key gaps in our knowledge about 1) how climate change is shifting the timing of key life stages in plants for understudied stages like fruiting or for interactions and potential mismatches between plants in different canopy levels, and 2) how human activities and climate change are impacting wildlife across many species and regions and to discern which factors pose the greatest threat to at-risk species.

I did this by using data from herbarium specimens to compare historical records of fruiting phenology and to examine phenological sensitivity of trees, shrubs, and flowers, and by using wildlife rehabilitation records to analyze patterns in threats to wildlife across North America.

Chapter Two: Comparing fruiting phenology across two historical datasets: Thoreau's observations and herbarium specimens

On average, earliest herbarium specimen dates were earlier than first fruiting dates observed by Thoreau; mean specimen dates were similar to Thoreau's peak fruiting dates; latest specimen dates were later than Thoreau's last fruiting dates; and durations of fruiting captured by herbarium specimens were longer than durations of fruiting observed by Thoreau. All metrics of fruiting phenology except duration were significantly, positively correlated within and between datasets. Strong correlations in fruiting phenology between Thoreau's observations and data from herbaria suggest that field and herbarium methods capture similar broad-scale phenological information, including relative fruiting times among plant species in New England. Differences in the timing of

first, last, and duration of fruiting suggest that historical datasets collected with different methods, scales, and metrics may not be comparable when exact timing is important. Researchers should strongly consider matching methodology when selecting historical records of fruiting phenology for present-day comparisons.

Chapter Three: Warming temperatures are linked to phenological mismatch among native and non-native trees, shrubs, and wildflowers across the Eastern Deciduous Forest of North America

Predicted phenological mismatches between native trees and wildflowers differed across large spatial scales, with wildflower populations in warmer regions of North America more likely to be affected. Overall, native tree species leafed out 3.6 days earlier per °C spring warming, while native wildflower species advanced their flowering times by 3.2 days per °C. Native trees and wildflowers in the warmer, southern part of their ranges advanced their spring phenology 2 and 1.5 times faster, respectively, than those in colder, northern locations. The phenological sensitivity of non-native plants was less variable across their ranges. Non-native trees and shrubs exhibited greater phenological sensitivity than native wildflowers. Notably, phenological sensitivities differed substantially among wildflower species, suggesting that certain species are more likely to be affected by phenological mismatch as climate warming progresses. My results provide new insight into novel phenological responses within and among species across a wide geographical range and the potential impact of competition and interactions with non-native invasive species. This research highlights the value of newly-available digitized

museum collections in phenological research to cover longer time periods, wider spatial areas, and a greater diversity of species than otherwise possible.

Chapter Four: Wildlife rehabilitation records for use in ecological research and conservation

I identified key threats by examining conditions causing animals to be brought to wildlife rehab centers. Overall, human disturbances accounted for the largest proportion of wildlife injury and sickness. I identified the predominant reason for admittance for many species: e.g., fishing incidents for brown pelicans, window or building collisions for big brown bats, and vehicle collisions for many raptor and reptile species. I also identified seasonal patterns in lead and pesticide exposure. Lead cases peaked in winter, likely due to animals ingesting lead ammunition from shot carcasses after hunting seasons (Cruz-Martinez et al., 2012; Golden et al., 2016; Kramer and Redig; 1997; Warner et al., 2014). Pesticide cases peaked in summer, indicating that animals may be exposed when rodenticides are used to control “pest” populations (Elliott et al., 2014; Rich et al., 2020; Watt et al., 2005). In examining possible effects of human-driven climate change, I found that more animals arrived at rehab centers in the week after an extreme weather event compared to the week before, but only for certain types of weather events in certain locations: e.g., hurricanes and floods in southern Florida. Overall, I identified several major drivers of injured and sick wildlife arriving at rehab centers. These findings point to possible interventions to help conserve wildlife, such as using or changing wildlife road crossings, fishing and hunting regulations, lead and pesticide

regulations, and disaster management plans (Dau et al., 2009; Shilling and Waetjen, 2015; Grade et al., 2018; Hanley et al., 2022).

Future Research Directions

Chapter Two: Comparing fruiting phenology across two historical datasets: Thoreau's observations and herbarium specimens

Future research could determine if the correlation between last fruiting dates and latest herbarium specimens is driven by frugivore feeding preference, phenology, or abundance and nutritional quality of fruits of different species. Studies should also compare fruiting data to bird migration and feeding data to understand how the timing of fruiting coincides with the timing of bird migration, and the impacts any potential mismatches could have on plant and bird populations.

Chapter Three: Warming temperatures are linked to phenological mismatch among native and non-native trees, shrubs, and wildflowers across the Eastern Deciduous Forest of North America

This field of study would benefit from further analyses to determine how generalizable these results are to other species, regions, and ecosystems. It remains unclear if these phenological patterns are similar in other temperate deciduous forests of the world, as these patterns may differ due to biogeography (Zohner et al., 2017). Similar studies could also be conducted in different ecosystems to assess if these trends in phenological sensitivity and mismatch also apply to other ecosystems, such as chaparral or boreal forests, or are controlled by other climatic variables like moisture (Keatley et al., 2002; Kramer et al., 2000; Song et al., 2020). Furthermore, to elucidate the

mechanisms of these phenological mismatches, physiological experiments could be conducted to test whether different levels of the canopy are responding to different temperature cues, such as air or soil temperature, or are relying more on photoperiod. Understanding differences in the temperature cues for different levels of the canopy could help us anticipate future mismatches as climate conditions continue to change. Further, understanding the changes in other ecosystems and the roles of other climate variables can help us to understand the magnitude of the potential mismatches and plan conservation responses.

Chapter Four: Wildlife rehabilitation records for use in ecological research and conservation

Many confounding factors make it difficult to draw accurate conclusions about changes over time using this dataset. These factors include changes in public awareness of rehabilitation centers, changes in public opinion of wildlife conservation and rehabilitation, changes in behavioral patterns that may lead to finding and bringing in wildlife, changes in wildlife population sizes and distributions, changes in numbers of digitized records, changes in finances at rehab centers, changes in diagnostic and detection tools and capacity, changes in the education and awareness of rehabilitation professionals, and more. Future studies should examine ways to control for these factors and others in order to better explain changing patterns over time in wildlife rehab records. I recommend using wildlife rehab records to start examining and identifying management and conservation priorities. If little is known about what is affecting a species, rehab records can help to identify places to start and focus future research.

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CURRICULUM VITAE

