

RESEARCH ARTICLE

Herbarium specimens reveal increasing herbivory over the past century

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Abstract

1. Predicting how ecological interactions will respond to global change is a major challenge. Plants and their associated insect herbivores compose much of macroscopic diversity, yet how their interactions have been altered by recent environmental change remains underexplored.
2. To address this gap, we quantified herbivory on herbarium specimens of four plant species with records extending back 112 years. Our study focused on the northeastern US, where temperatures have increased rapidly over the last few decades. This region also represents a range of urban development, a form of global change that has shown variable effects on herbivores in the past studies.
3. Herbarium specimens collected in the early 2000s were 23% more likely to be damaged by herbivores than those collected in the early 1900s. Herbivory was greater following warmer winters and at low latitudes, suggesting that climate warming may drive increasing insect damage over time. In contrast, human population densities were negatively associated with herbivore damage.
4. To explore whether changes in insect occurrence or abundance might explain shifts in herbivory, we used insect observational records to build climate occupancy models for lepidopteran herbivores (butterflies and moths) of our focal plant species.
5. These models show that higher winter temperatures were associated with higher probability of insect herbivore presence, while urbanization was associated with reduced probability of herbivore presence, supporting a link between insect herbivore occurrence and herbivory mediated through environment.
6. *Synthesis.* Using a temporal record of plant herbivory that spans over a century, we show that both temperature and urbanization influence insect damage to plants, but in very different ways. Our results indicate that damage to plants by insect herbivores will likely continue to increase through time in the northeastern US as global temperatures rise, but that urbanization may disrupt local effects of winter warming on herbivory by excluding certain herbivores. These changes may scale to shape ecosystem processes that are driven by herbivory, including plant productivity.

KEYWORDS

climate change, global change ecology, herbarium, herbivory, historical data, museum specimen, urbanization, warming

1 | INTRODUCTION

Global change is altering plant life histories. Leafout and flowering occur earlier now than historically, and plants are moving upwards in elevation or polewards in latitude as the climate warms (Parmesan, 2007; Pau et al., 2011). These shifts in space and time could have important community and ecosystem consequences, particularly if the species closely associated with plants are not responding synchronously (van Asch & Visser, 2007; Visser & Holleman, 2001). However, interactions between plants and their associates, and species interactions more generally, are understudied in the context of long-term anthropogenic environmental change because long-term data on these interactions are relatively rare (Magurran et al., 2010).

Here, we used pressed plant specimens from the northeastern US to determine how herbivory has changed over the last 112 years. While herbarium specimens have been used to quantify long-term changes in plant phenology (Davis, Willis, Connolly, Kelly, & Ellison, 2015; Miller-Rushing, Primack, Primack, & Mukunda, 2006; Primack, Imlres, Primack, Miller-Rushing, & Tredici, 2004) and morphology (Law & Salick, 2005; Leger, 2013), they are used much less often to investigate changing interactions between plants and their antagonists. Changes in these antagonistic relationships could have consequences for ecosystem structure and function. For example, insect herbivory is a major driver of plant coexistence (Carson & Root, 2000), biomass production (Belovsky & Slade, 2000), nutrient turnover and retention (Classen, Chapman, Whitham, Hart, & Koch, 2007), animal composition (Brown, Whitham, Ernest, & Gehring, 2001), and ecosystem trajectories (Belovsky & Slade, 2000; Brown et al., 2001; Carson & Root, 2000; Classen, Chapman, Whitham, Hart, & Koch, 2013; Gandhi & Herms, 2010). Additionally, long-term herbivory data from herbarium specimens could inform pest management by revealing trends over time, thus allowing us to determine if monitoring of certain crop or forest plants should become more frequent as global change progresses and whether new pest control strategies might be needed.

Predictions for how climate warming across seasons and years may affect herbivory are complex (Bale et al., 2002), and empirical assessment of herbivory change is limited because there are few existing long-term (>10 year) observational or experimental datasets (Turcotte et al., 2014). In experimental settings, insect survival and fecundity increase with warmer temperatures (Angilletta, 2009). We might thus predict that herbivory should increase with climate warming unless temperatures exceed thermal optima of the herbivores (Deutsch et al., 2008). However, warming in winter could increase insect mortality by reducing snow pack, which exposes insects to very low temperatures, and/or by disrupting winter diapause (Bale & Hayward, 2010). Total herbivore damage may be further complicated by a number of additional interacting factors, including changes in insect predation (Thomson, Macfadyen, & Hoffmann, 2010), plant and insect phenology (Visser & Holleman, 2001), and community composition (Carvalho et al., 2014). As a result of these or other mechanisms, patterns of herbivory across latitude and elevation are highly variable (Moles, Bonser, Poore, Wallis, & Foley, 2011; Moreira, Petry, Mooney, Rasmann, & Abdala-Roberts,

2018). As a consequence, spatial variation in herbivory might not reliably capture how herbivory has changed over time and with recent anthropogenic transformation of habitats and climate.

Over the past few decades, it has become clear that, alongside climate change, urbanization may have profound effects on interactions between plants and their insect herbivores. Urbanization is increasing at unprecedented rates (United Nations, 2008), and its effects on herbivore damage to plants remain poorly described. A number of studies show that certain leaf-feeding insects are excluded from urban habitats, which may reduce herbivory (Fattorini, 2011; Kozlov et al., 2017). However, some herbivores may benefit from urbanization if they are able to escape their natural enemies (Hanks & Denno, 1993) or if the urban heat island effect increases population sizes (Dale & Frank, 2014, 2017; Meineke, Dunn, Sexton, & Frank, 2013; Meineke, Youngsteadt, Dunn, & Frank, 2016). There remains, therefore, large uncertainty about whether the relationship between herbivory and urbanization can be generalized, and how climate change and urbanization may interact to influence the effects of insect herbivores on their plant hosts.

In the northeastern US, mean yearly temperatures have risen 0.8°C from the early to the late 20th century. Winter temperature, a key determinant of insect herbivore survival (Bale et al., 2002), has increased by 0.9°C, more than other seasons (USGCRP, 2017). Some urban areas within the region, such as in the Boston metropolitan area, have expanded rapidly (Jedwab & Vollrath, 2015), whereas other parts of the region remain largely rural. Here, we examine trends in herbivore damage over this time span across four plant species with varied life histories and broad geographical distributions. First, we tested whether insect herbivory was associated with warmer temperatures and urbanization. Second, we explored a proximate, biotic driver of changing herbivory over time—*insect herbivore presence*—with occupancy models constructed from the present-day insect herbivore observations collected by citizen scientists. Although we do not have matching temporal data on the insect herbivores, if shifts in insect herbivore populations are driving changes in herbivory, we would predict that insect herbivore occupancy should be positively associated with the same suite of climate variables driving herbivory change through time. Effects of urbanization are more difficult to predict and might add to or counteract effects of climate change on herbivory.

2 | METHODS

2.1 | Assessing effects of temperature and urbanization on insect herbivory preserved in herbarium specimens

2.1.1 | Study region and focal plant species

New England encompasses much of the northeastern USA and includes the states of Maine, Vermont, New Hampshire, Massachusetts, Connecticut, and Rhode Island. The climate is

variable and characterized by a strong latitudinal gradient in temperature and varied geography, including mountains in Maine, Vermont, and New Hampshire. Detailed information on the climatic history of this region is included in Appendix S1 and Figure S1.

We sampled herbivore damage on four focal taxa in this region: shagbark hickory [*Carya ovata*], swamp white oak [*Quercus bicolor*], showy tick trefoil [*Desmodium canadense*], and wild lowbush blueberry [*Vaccinium angustifolium*]. These species are native to the northeastern United States and are subject to natural herbivory in the wild but were identified by local experts (David E. Boufford and Walter T. Kittredge) as only rarely subject to herbivory within herbaria. Our focal plant species span a broad range of life histories and are eaten by different insect herbivores, some of which are specialized. *Desmodium canadense* is an understory herb that is a host plant for many butterflies and moths. *Carya ovata* is a common canopy tree that provides food for a variety of wildlife. *Vaccinium angustifolium* is a low-lying shrub used for commercial blueberry production. *Quercus bicolor* is a canopy tree used as a timber species. These species are located on distant branches of the angiosperm phylogeny, including Fagales (*Q. bicolor*, *C. ovata*), Ericales (*V. angustifolium*), and Fabales (*D. canadense*), and thus represent highly divergent evolutionary histories. The primary insect herbivore species associated with these plants in our study region are listed in Table S1.

2.1.2 | Quantifying herbivory on herbarium specimens

We quantified herbivory on all specimens collected in New England and preserved within the Harvard University Herbaria, excluding duplicate specimens—those collected on the same day and in the same location as a specimen already sampled—and those without county-level location data or full collection dates (year, month, and day). In total, we quantified herbivory on 123 *C. ovata*, 89 *Q. bicolor*, 149 *D. canadense*, and 215 *V. angustifolium* specimens (Figure 1), spanning the years from 1896 to 2008. None of the specimens we examined were type specimens, and the species we included in our study were selected to be common and thus well-represented in herbaria.

We scored herbivory by overlaying a grid of 5 cm by 5 cm cells, and scoring presence (1) or absence (0) of damage in five randomly selected grid cells, ensuring that selected cells had at least one-fourth leaf cover (Meineke, Davis, & Davies, 2018). We focused on “chewing”—leaf removal by herbivores with mandibles, likely including Lepidoptera (butterflies and moths), Coleoptera (beetles), and Orthoptera (grasshoppers and their relatives)—because it was the most common type of herbivory on specimens and is the subject of most ecological studies on herbivory (Turcotte et al., 2014). When leaves overlapped within a grid cell, we carefully lifted upper leaves to check for herbivory on the leaves below. Chewing herbivory on recently collected specimens is often measured as leaf area removed using image processing program, such as ImageJ [<https://imagej.nih.gov/ij/index.html>]. However, such approaches do not cross over well to herbarium specimens. For example, herbarium specimens frequently have overlapping leaves that are fixed to specimen sheets.

These vouchers can be carefully manipulated and inspected for the presence or absence of herbivory—as we did here—but do not allow us to accurately calculate leaf area. We scored herbivory by examining specimens under a microscope, allowing us to document evidence of herbivory even where the percentage of leaf removed was small, and to better determine whether leaf damage occurred before the specimen was collected or subsequently in the herbarium (see below). Digitized specimens that might be used for image processing to calculate leaf area are typically not high resolution enough to differentiate between these two types of damage. Our scoring of herbivory using a grid-based system allows us to derive data on the intensity of herbivory while avoiding challenges posed by measuring leaf area.

A challenge in quantifying herbivory on herbarium specimens is that a suite of herbivores feed on pressed plants after they are collected. Thus, postcollection damage must be distinguished from damage caused before a specimen was collected. We differentiated between damage by herbivores within herbaria and damage by herbivores on living specimens by the morphology of the damage. We found in this analysis and in a previous study (Meineke et al., 2018) that live plants generally form toughened, necrotic wounds around herbivore damage, but this is not present on specimens damaged indoors postcollection. For examples of outdoor damage to live plants (the type of damage of interest in this study) and indoor insect damage to specimens after collection, see Figure S2. Given that collectors aim to collect unblemished specimens, our analysis likely represents a downbiased and therefore conservative estimate of total herbivory. Nonetheless, estimates are comparable among species and across years under the assumption that collector bias has remained relatively consistent across years.

Shifting collection practices—for example, an increased tendency to include damaged specimens in more recent time periods—could give the appearance of changing herbivory through time. We therefore consulted with curators at several herbaria, and although anecdotal, they reported no knowledge of systematic changes in collection methods that should affect herbivory on specimens. In addition, we note that these biases are not expected to apply to analyses of temperature and urbanization (see below) because (we assume) collectors are not more likely to collect damaged specimens in warmer/cooler or more/less urbanized locations.

To further explore potential for collection bias, we recorded the collector identity for each specimen, and then subset the data to collectors that collected five or more specimens. This yielded a total of 32 collectors. We then tested for an effect of collector on herbivory using a generalized linear model with a logit link function in the *lme4* package (Bates, Mächler, Bolker, & Walker, 2015) in R (R Core Team, 2016) with proportion of grid cells with chewing damage as the response (see additional details on model construction below) and collector identity as the predictor.

2.1.3 | Associating temperature and urbanization data with herbarium specimens

To examine relationships between climate and herbivory, we extracted various temperature predictors from the PRISM Climate

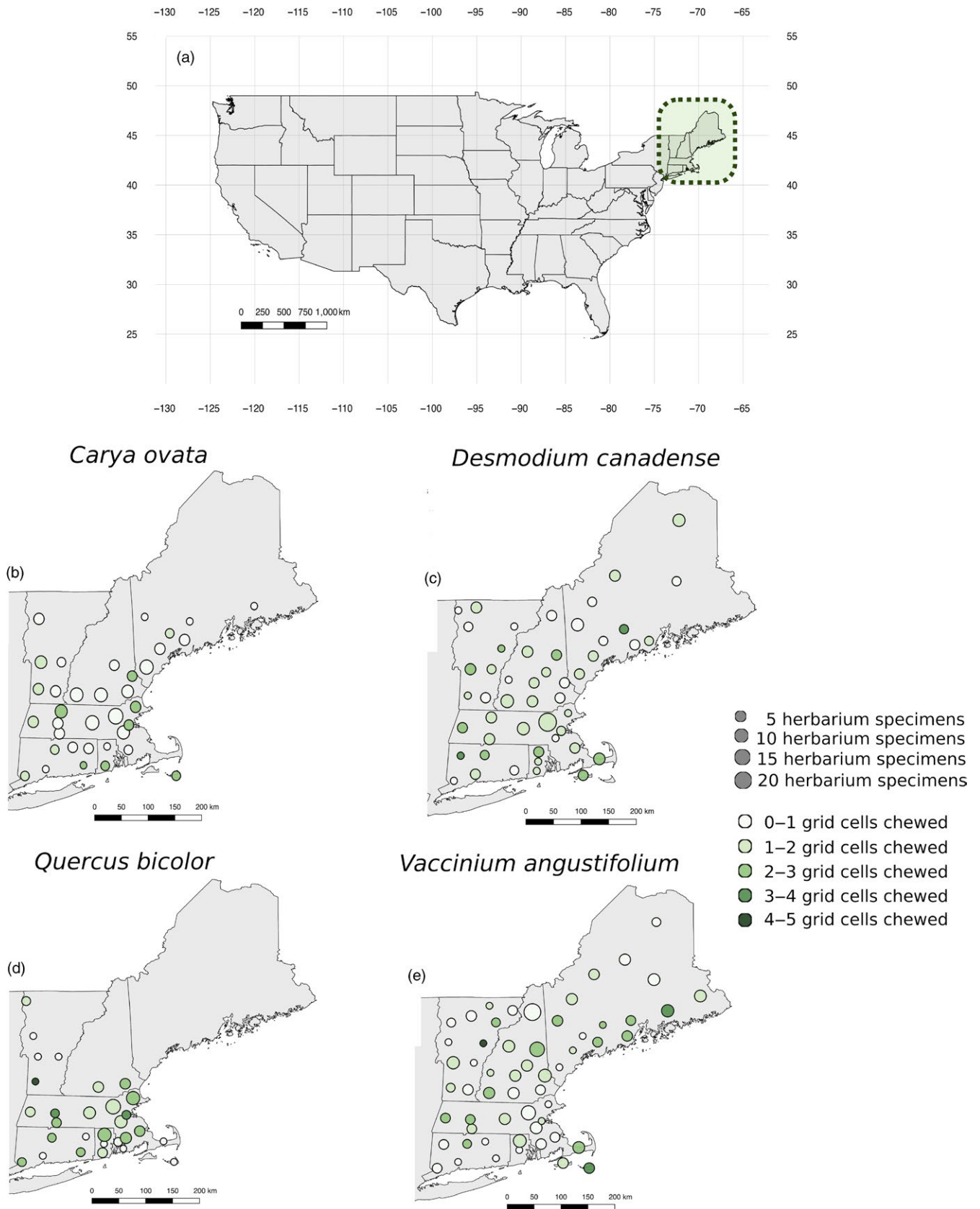


FIGURE 1 Sampling intensity and herbivory for four focal plant species. Data points represent county centroids. Point size corresponds to the number of herbarium specimens from which herbivory data were extracted. Colour represents the average number of grid cells with chewing herbivory

Group, 2004 gridded data [www.prism.oregonstate.edu], all of which were county-level means corresponding to each specimen collection date (Park & Davis, 2017). To broadly represent temperatures during overwintering and spring development of insect herbivores, we extracted mean temperatures from January to March during the year when a specimen was collected. Plant and insect phenology are sensitive to both winter chilling and spring temperatures (Bale & Hayward, 2010; Primack et al., 2004). This climate predictor is designed to capture a range of mechanisms, including early season phenology and winter mortality. One potential benefit of higher early spring temperatures for insect fitness is faster development out of young, vulnerable stages wherein insects are more susceptible to natural enemies (e.g., Culler, Ayres, & Virginia, 2015). To more directly capture effects of winter mortality on insects, we extracted mean temperatures in the three coldest months of the year ("coldest quarter": December, January, and February, with December extracted from the year before a specimen was collected). To represent the potential effects of summer temperature, including heat wave effects on insect mortality, we extracted mean temperatures of the three warmest months in the current and prior year ("warmest quarter": June, July, and August). We included the prior year because many specimens were collected in spring or early summer, prior to the onset of high summer temperatures in the current year. Finally, to represent overall temperatures experienced by insects and plants throughout the year, we extracted mean annual temperatures. This suite of predictors matches the climatic data available for herbivore occurrences (see below).

As a proxy for urban development, we used human population density estimated by county and year with data from the most recent US Census (https://www.census.gov/data.html). As census data are collected every 10 years, we matched each specimen to the nearest decadal population estimate.

2.1.4 | Statistical analyses of the effects of temperature and urbanization on herbivory preserved in herbarium specimens

We explored the relationship between herbivory and environment (mean annual temperature, mean temperature during the warmest quarter, mean temperature during the warmest quarter of the prior year, mean temperature during the coldest quarter, January through March mean temperature, and human population density) with logistic regression fit to the scoring of herbivory in each grid cell. We used generalized linear models with logit link functions in the *lme4* package (Bates et al., 2015) in R (R Core Team, 2016) and proportion of grid cells with chewing damage as the response. We specified a binomial distribution in each model. For all analyses, $n = 123$ *C. ovata*, 89 *Q. bicolor*, 149 *D. canadense*, and 215 *V. angustifolium* specimens.

We generated three sets of models, in which all predictors were specified as fixed effects:

- First, we built a model with year, plant species identity, and the year \times species identity interaction to explore herbivory change over time ($n = 576$).

- Second, we generated a set of global models to simultaneously assess the effects of year, temperature (five variables), and location. These global models included the following predictors: plant species, year the specimen was collected, associated temperature variables for the year of collection, human population density (as a proxy for urbanization), day of year (because specimens collected later in any given year should have more herbivory), and latitude and longitude (as spatial covariates). As temperature predictors were colinear (evaluated using Variance Inflation Factors), we constructed separate global models for each temperature predictor ($n = 5$ models), and compared models using AIC. We contrasted the residual deviances across models (see Faraway, 2016) with and without key predictors to quantify how much of the variation in herbivory was uniquely explained by time, space, and temperature.
- Third, to better illustrate how individual species responded to the environmental predictors (temperature, urbanization), we built separate matching models for each plant species including the full suite of predictor variables (year, temperature, human population density, day of year, latitude, and longitude).

2.2 | Assessing the effects of temperature and urbanization on insect herbivore occupancy

We used HOSTS, a database of Lepidoptera host plants collated from primary literature ([https://www.nhm.ac.uk/hosts]; Robinson, Ackery, Kitching, Beccaloni, & Hernández, 2010) to identify insect herbivore species associated with our focal plants in the continental USA. We focus here on the order Lepidoptera (moths and butterflies) as they are the most frequently collected and recorded insect taxa and have the most complete data on host associations and occurrence. We extracted occurrence data within New England from the Global Biodiversity Information Facility (GBIF [https://gbif.org]) for each herbivore species. All records were collected between 1990 and 2015 and classified as research-grade observations from iNaturalist [www.inaturalist.org], a crowd-sourcing platform that sources natural history observations from the public. Species with fewer than 30 records were excluded from subsequent analyses because it is challenging to fit species distribution models with fewer than 30 records (Wisz et al., 2008). The final dataset included 6,853 records for 69 herbivore species, 47 of which were herbivores of *Q. bicolor*, 16 of *V. angustifolium*, five of *D. canadense*, and one of *C. ovata* (Table S1). These included one nonnative species, the gypsy moth, *Lymantria dispar*, which is invasive and was introduced from Europe to Massachusetts, US in 1868 or 1869 (Liebhold, Halverson, & Elmes, 1992; Liebhold, Mastro, & Schaefer, 1989). To our knowledge, all other herbivore species included in this analysis were native to the study region.

We modelled the presence of each herbivore species (hereafter "occupancy models") using generalized linear models (GLMs) fit using the best predictors of herbivore damage, as estimated in the models described above: mean temperature of the coldest quarter,

extracted from WorldClim 2.0 data (Fick & Hijmans, 2017; [www.worldclim.org]) at 30-s resolution (about one square kilometre), and human population density (extracted data from the US Census American Community survey from 2011 to 2015 [https://www.census.gov/programs-surveys/acs/]). Twenty-five percent of the occurrence records were assigned for testing, and the remaining 75% were used to train the models. Pseudoabsences were generated by randomly extracting $1.5 \times$ the number of observations from the background data (Barbet-Massin, Jiguet, Albert, & Thuiller, 2012; Phillips et al., 2009), delimited as New England.

We used ANOVAs to compare the regression coefficients from the GLMs for insect herbivores grouped by host plant. Regression coefficients were weighted by the model AUC score (Fielding & Bell, 1997), a measure of reliability of the estimates from the climate occupancy models. Thus, more reliable models contributed more to parameter estimation. Post hoc comparisons among pairs of host plant species were made using Tukey's Honest Significant Difference.

3 | RESULTS

3.1 | Assessment of bias in herbarium specimens

We found no evidence for collector bias (Figure S3; $Z = 3.57$, $p = 0.850$, from the GLM of herbivory and collector); that is, different collectors were equally likely to collect specimens damaged by herbivores. The number of specimens of each species declined through time, but we see no reason why this should bias the data towards revealing more or less herbivory in recent specimens than in older specimens. However, herbarium specimens for the different plant species had variable coverage among predictor variables (Figure S4; year, temperature, human population density, latitude, and longitude). Notably, *V. angustifolium* specimens covered lower urbanization intensities than the other species; *Quercus bicolor* specimens covered a smaller range of temperatures than specimens of the other species; and *D. canadense* specimens covered the widest range of latitudes.

3.2 | Effects of temperature and urbanization on herbivory preserved in herbarium specimens

The percentage of specimens with recorded chewing herbivory (all cells combined) ranged from 40% to 74%, depending on plant species (Figure S5; *C. ovata*: 39.8%; *V. angustifolium*: 62.3%; *D. canadense*: 71.8%; *Q. bicolor*: 74.2%). The probability of insect herbivory on specimens across all four plant species increased by 23% over the 112 years between 1896 and 2008 (Figure 2a; $Z = 0.15$, $p = 0.003$, from the GLM of herbivory and years). We found no support for a significant interaction between species and year (including interaction: AIC = 2,094; excluding interaction: AIC = 2,090), indicating that changes in herbivory through time were similar for all four species.

The global model, including environmental predictors, with the lowest AIC included January through March mean temperature as the best of the temperature predictors (January through

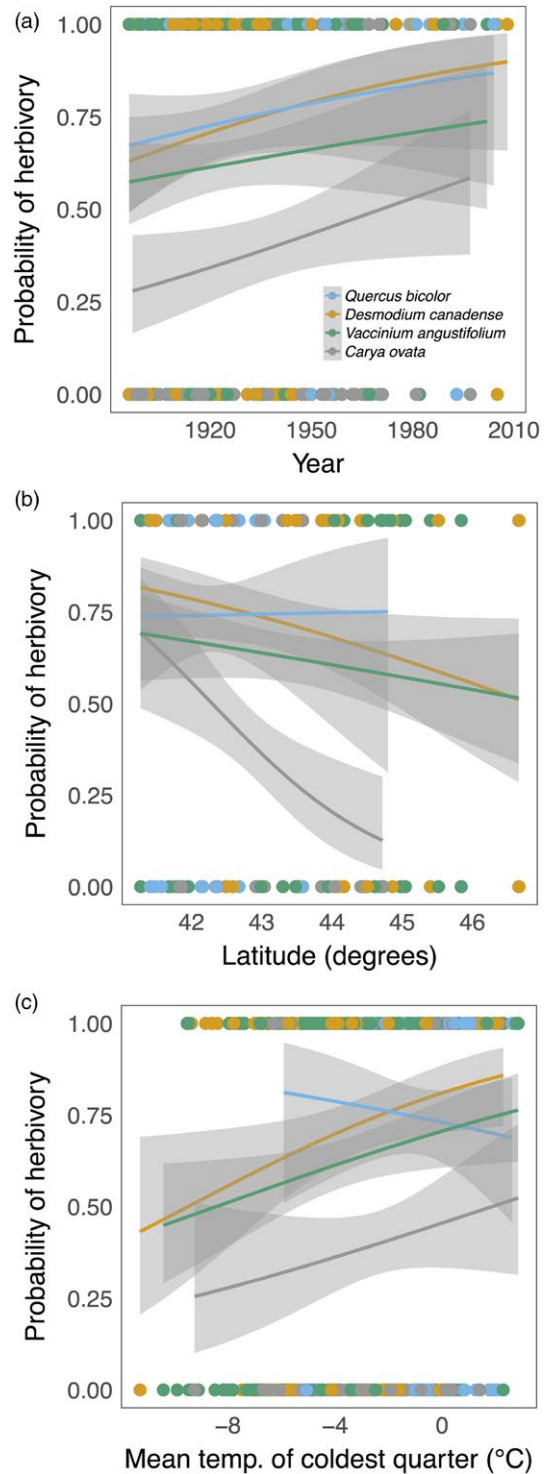


FIGURE 2 Insect herbivory preserved in herbarium specimens across year, space, and temperature. Herbivory increased significantly over (a) years, (b) with decreasing latitude, and (c) with increasing winter temperature (though plots were similar for all temperature predictors. See Figure S6.) Points represent herbarium specimens. Lines are best fit slopes and grey areas represent 95% confidence intervals

March mean: AIC = 2,033; cold quarter mean: AIC = 2,037; warm quarter mean: AIC = 2,037; mean annual: AIC = 2,038; prior warm quarter mean: AIC = 2,039), and we present this model

here (Table 1; see Table S2 and Figure S6 for models including the alternative temperature predictors). Herbivory increased with decreasing latitude (Figure 2b; $Z = -2.04$; $p = 0.041$) and increasing temperature (Figure 2c; $Z = 2.62$; $p = 0.009$) and decreased with increasing human population density (Figure 3; $Z = -3.80$, $p < 0.0001$). Contrasting model residual deviances revealed that temperature could explain up to 40% of the variability in herbivory observed across latitude and years (see Table S3 for further details).

Herbivory also increased as growing seasons progressed (day of year: $Z = 5.85$, $p < 0.0001$) and varied among plant species (for all species $p < 0.0001$; Table S2).

The direction of the relationships revealed by individual species models (Figure 2) matched those in the global models, but better illustrate the changing strength of predictors among host species. For *C. ovata*, the strongest effect was increasing herbivory with decreasing latitude (Figure 2b); for *D. canadense*, it was increasing herbivory over years (Figure 2a) and with decreasing latitude (Figure 2b); for *Q. bicolor*, it was increasing herbivory over years (Figure 2a); and for *V. angustifolium*, it was increasing herbivory over years (Figure 2a) and with increasing temperature (Figure 2b) and decreasing herbivory with increasing human population density (Figure 3). For all model statistics, see Table 2.

3.3 | Effects of temperature and urbanization on insect herbivore occupancy

Herbivore occupancy models indicated that mean temperature in the coldest quarter was positively associated with occurrence of 66 of the 69 total herbivore species (Figure 4a,b). The three exceptions

TABLE 1 Statistics for the full (global) model of herbivory on herbarium specimens with the best fitting climatic predictor, January through March mean temperature

Predictor	Estimate \pm SE	Z	p
Intercept	-0.99 \pm 0.21	-4.724	<0.0001
Year	0.19 \pm 0.04	4.542	<0.0001
Human population density	-0.18 \pm 0.05	-3.802	<0.0001
January through March mean temperature	0.22 \pm 0.08	2.621	0.009
Day of year	0.27 \pm 0.05	5.851	<0.0001
Latitude	-0.19 \pm 0.09	-2.041	0.041
Longitude	0.01 \pm 0.06	0.201	0.841
Species ID: <i>Desmodium canadense</i>	0.77 \pm 0.14	5.489	<0.0001
Species ID: <i>Quercus bicolor</i>	1.04 \pm 0.15	6.762	<0.0001
Species ID: <i>Vaccinium angustifolium</i>	0.93 \pm 0.13	6.868	<0.0001

were all insect herbivores associated with *Q. bicolor*. However, the effects of temperature in the coldest quarter on occupancy of herbivores grouped by host plant were not statistically distinguishable ($F_{3,65} = 0.42$, $p = 0.741$).

In total, 36 of 69 herbivore species responded significantly to urbanization, 22 of which responded negatively, while 14 responded positively (Figure 4c). The effects of urbanization on insect herbivore occupancy differed significantly when herbivores were grouped by host plant species (Figure 4c,d; $F_{(3,65)} = 3.57$, $p = 0.019$). Six of the 16 herbivores of *V. angustifolium* and 16 of the 47 herbivores of *Q. bicolor* were negatively associated with human population density (from the GLMs of herbivore occurrence and human population density; all $p < 0.05$). Two of the herbivores associated with *V. angustifolium*, eight associated with *Q. bicolor*, three associated with *D. canadense*, and the only species associated with *C. ovata* showed positive responses to urbanization. The one species associated with *C. ovata* responded positively to urbanization.

4 | DISCUSSION

4.1 | Herbivory change over the past century

Using herbarium specimens spanning 112 years of rapid global change in the northeastern USA, we found a significant increase in herbivory over the past century. This trend is consistent across four ecologically and phylogenetically distinct host plant species with very different herbivore communities. We suggest our observation of increasing herbivory through time is most likely driven by insect herbivore responses to warmer winter and early spring temperatures. Two environmental drivers—temperature and urbanization—explain much of the trend in herbivory through time, but they have opposing effects. Over space and time, higher temperatures were associated with greater herbivory and higher probabilities of occupancy for 66 of 69 known insect herbivore associates. In contrast, high human population density was associated with lower herbivory and reduced occupancy for most insect herbivores that showed significant responses. In this region of the US, warming is projected to surpass 2°C by 2040 and is expected to be greater in winter than in summer (Karmalkar & Bradley, 2017). Our results indicate that damage to plants by insect herbivores may continue to increase with climate change but that, locally, urbanization may counteract this more general trend.

4.2 | Abiotic and biotic drivers of herbivory

Our analyses indicate that warming winter temperatures may drive increasing herbivory over time. Herbivory preserved in herbarium specimens was positively associated with mean winter to early spring temperature and decreasing latitude. Almost half (40%) of the variation in herbivory through time and across latitudes could be explained by temperature. These findings support theory as well as some empirical evidence suggesting that herbivory is largely driven by winter temperature at mid latitudes (Bale et al., 2002). As winters

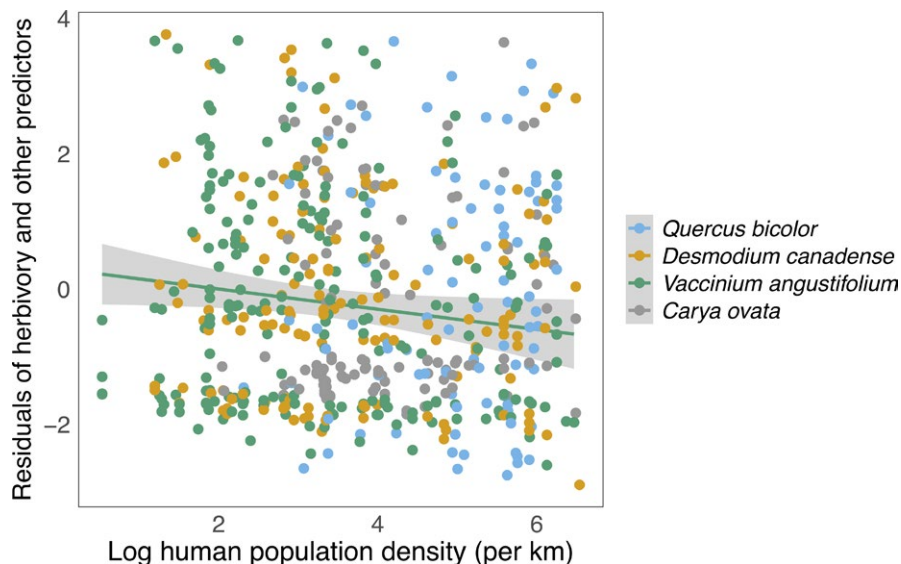


FIGURE 3 Residual analysis displaying effects of human population density on herbivory preserved in herbarium specimens. Because of the strong effects of other variables, we calculated residuals from the global models, including year, winter temperature, latitude, longitude, plant species, and day of year as predictors. The residuals from this model are presented here in the vertical axis to represent the variation in herbivory not explained by these predictors. The trend line shown is for *Vaccinium angustifolium*, the only species for which human population density was a significant predictor of herbivory on herbarium specimens. Notably, this is also the species with the largest range of human population densities represented by herbarium specimens (see x axis range). Comparable plots for the predictor variables displayed in Figure 2 (year, latitude, and temperature) are available in Figure S7. The line is a best fit slope and the grey area represents the 95% confidence interval

in the northeastern US are projected to warm more than other seasons (Karmalkar & Bradley, 2017), we suggest herbivory may continue to increase in the future.

We found compelling circumstantial evidence that insect herbivores known to feed on our focal plants also prefer warmer winters. The vast majority (66/69) of herbivore species examined had higher occupancy probabilities where winter temperatures were warmer. Occupancies of the other three species were not significantly related to winter temperatures, but the trend was also positive. While the association between winter temperatures and herbivore occurrence was estimated using contemporary data across space, we suggest this relationship is likely to be reflected in patterns through time. First, herbivore ranges may have extended northward in response to milder winters (Battisti et al., 2005; Breed, Stichter, & Crone, 2013). Second, resident herbivore species have become more abundant due to greater survival in milder winters (for a review of insect responses to winter temperature, see Bale & Haywood, 2010), and are therefore more frequently observed.

Our data are also consistent with the possibility that shifting phenology might contribute to growing herbivory pressure. There is strong evidence indicating that many butterfly species are flying earlier in the UK, US, Canada, and Spain (Diamond et al., 2014; Gordo & Sanz, 2005; Kharouba, Paquette, Kerr, & Vellend, 2014; Roy & Sparks, 2000). Butterfly species that emerge earlier may have more generations within a year now than they did several decades ago (Altermatt, 2010), allowing more rapid population growth. Warming early in the growing season could also restructure phenological interactions so that they are more synchronous than they were

historically (see Singer & Parmesan, 2010), which may increase herbivory if host plants avoid herbivore damage by timing leaf-out to be asynchronous with herbivore emergence. Warmer early springs might also alter phenological matching between herbivores and their natural enemies, reducing natural biological control of herbivores, as lower trophic levels may be more sensitive to climatic warming than higher trophic levels (Meineke, Dunn, & Frank, 2014; Thackeray et al., 2010). Some evidence suggests that this is the case for Lycaenid butterflies in our study region, which have advanced their flight more than has been shown for birds, which are their potential predators (Polgar, Primack, Williams, Stichter, & Hitchcock, 2013).

Independent from its effect on phenology, warming may affect herbivores indirectly through altering host plant nutritional quality. In some cases, warming can induce water stress that alters plant nutritional quality, which can increase herbivore egg production on water stressed relative to unstressed plants (Dale & Frank, 2017). However, if this were the case here, we would expect that higher summer temperatures (which commonly drive plant water stress) would be most closely associated with greater herbivore damage, contrary to results from our model comparisons.

While warming may have driven increasing herbivory over time, urbanization was associated with reduced herbivory. This negative relationship was consistent with our herbivore occupancy models. Herbivore species that responded significantly were more likely to show significant negative than positive associations with human population density. It is possible that herbivores that showed positive responses (14/69) favour urban areas because of factors such as the urban heat island effect (Dale & Frank, 2014; Meineke et al., 2013),

TABLE 2 Herbivory model statistics for models of individual plant species

Predictor	Estimate ± SE	Z	p
<i>Carya ovata</i>			
Intercept	-0.83 ± 0.56	-1.487	0.137
Year	0.06 ± 0.13	0.489	0.625
Human population density	-0.21 ± 0.14	-1.560	0.119
January through March mean temperature	0.27 ± 0.18	1.451	0.147
Day of year	0.39 ± 0.12	3.144	0.001
Latitude	-0.40 ± 0.18	-2.219	0.026
Longitude	-0.29 ± 0.16	-1.815	0.069
<i>Desmodium canadense</i>			
Intercept	-0.75 ± 0.32	-2.353	0.019
Year	0.28 ± 0.08	3.381	0.0007
Human population density	-0.02 ± 0.08	-0.277	0.782
January through March mean temperature	-0.28 ± 0.16	-1.726	0.084
Day of year	0.25 ± 0.08	2.956	0.003
Latitude	-0.44 ± 0.18	-2.381	0.017
Longitude	0.12 ± 0.11	1.099	0.272
<i>Quercus bicolor</i>			
Intercept	-1.73 ± 0.65	-2.649	<0.008
Year	0.33 ± 0.10	3.129	0.002
Human population density	0.24 ± 0.13	1.867	0.062
January through March mean temperature	-0.00 ± 0.14	-0.021	0.923
Day of year	-0.14 ± 0.11	-1.307	0.191
Latitude	-0.00 ± 0.12	-0.033	0.974
Longitude	-0.14 ± 0.13	-1.071	0.284
<i>Vaccinium angustifolium</i>			
Intercept	0.11 ± 0.27	0.425	0.671
Year	0.16 ± 0.07	2.174	0.030
Human population density	-0.32 ± 0.08	-3.964	<0.0001
January through March mean temperature	0.74 ± 0.15	5.000	<0.0001
Day of year	0.52 ± 0.08	6.835	<0.0001
Latitude	0.10 ± 0.17	0.586	0.558
Longitude	-0.06 ± 0.09	-0.690	0.490

Note. Parameters for models of herbivory on herbarium specimens including all predictors. Significant predictors for each species are in bold

natural enemy release (Meineke et al., 2014), or higher host plant quality on urban compared to rural plants (Hanks & Denno, 1993). However, overall patterns in our data add to mounting evidence that urban development locally reduces diversity in Lepidoptera, which are major herbivores. We focused on Lepidoptera in this study because they are well-represented in observations. Future studies could extend efforts to collect long-term data for other herbivorous taxa, such as beetles and grasshoppers, to determine if there is a more general reduction in herbivore diversity and damage with urbanization.

Trends in herbivory through time across the four focal plant species were remarkably consistent. The relative importance of the different

abiotic variables, however, varied among plant species. Different plant-herbivore relationships are likely sensitive to different drivers. For example, *Q. bicolor* did not show significant trends towards increasing herbivory with increasing temperature or decreasing latitude, even though the vast majority of herbivore species associated with *Q. bicolor* are more likely to occur where temperatures are warmer. Factors other than temperature and herbivore occurrence might thus be stronger drivers of herbivory in this host species. Geographical and temporal variation in driver intensity across the host range might also contribute to explaining different responses among species. For example, the negative association between herbivore damage and human

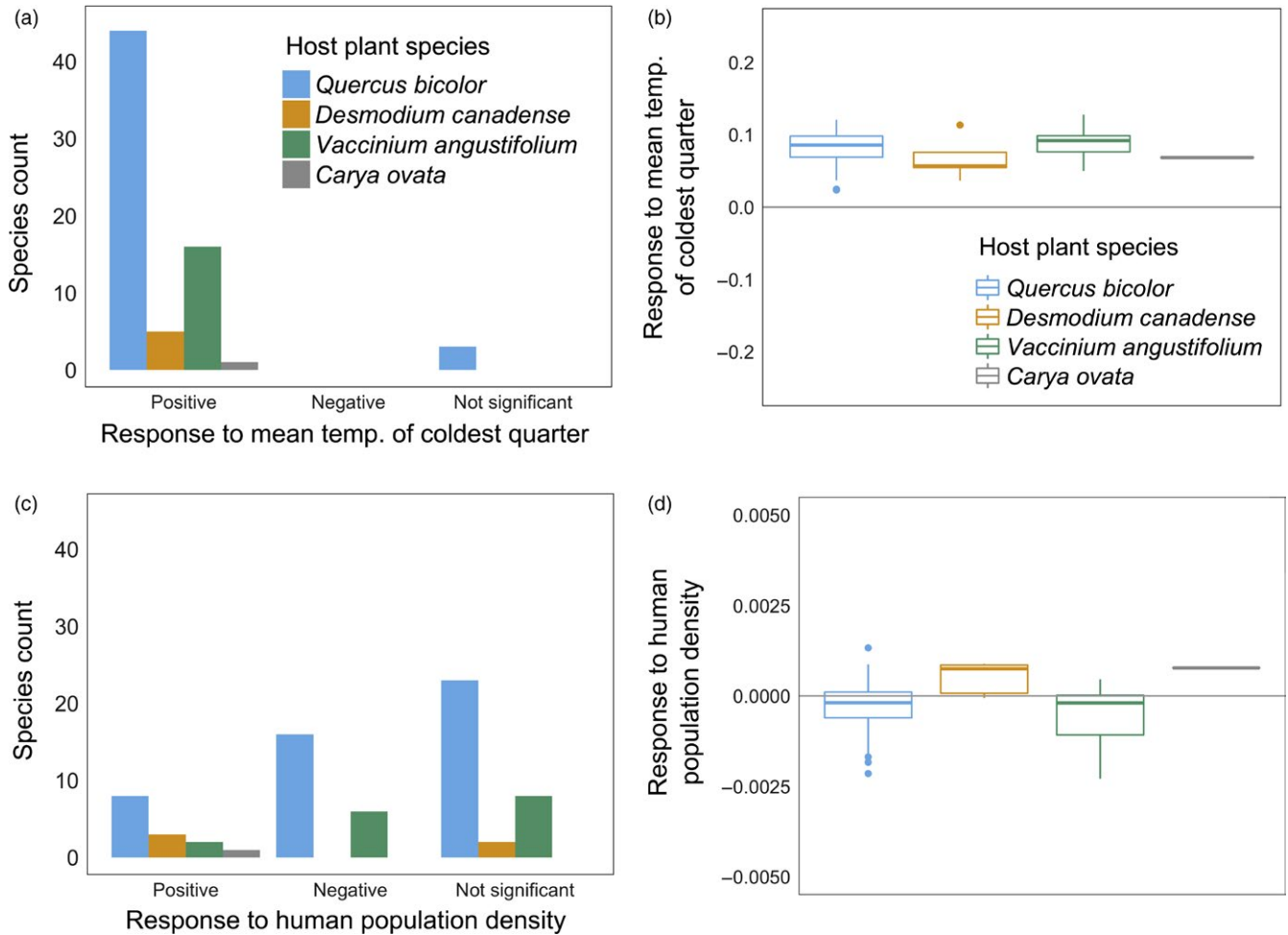


FIGURE 4 Effects of temperature and human population density on insect herbivore occupancy. (a) The number of insect herbivore (butterfly and moth) species with occupancies showing positive, negative, or nonsignificant responses to winter temperature. (b) Boxplot displaying median slopes of herbivore responses to winter temperature. (c) The number of insect herbivore (butterfly and moth) species with occupancies showing positive, negative, or nonsignificant responses to human population density. (d) Boxplot displaying median slopes of herbivore responses to human population density

population density was strongest for *V. angustifolium*. This species has a larger range than *Q. bicolor* and *C. ovata* that captures a larger urbanization gradient (see Figure 3), providing a greater opportunity to detect the effects of human population density.

4.3 | Benefits and drawbacks of museum specimens for characterizing species interactions

Herbarium specimens collected by botanists provide long-term estimates of herbivory that span the timeframe of anthropogenic environmental change, filling a major data gap. Observational studies tend to span much shorter timeframes, with herbivory studies rarely spanning more than 1–2 years (Turcotte et al., 2014). Field warming experiments are also typically short-term and often address effects on herbivores rather than herbivory (but for one exception, see Jamieson, Schwartzberg, Raffa, Reich, & Lindroth, 2015). We suggest that data from herbarium specimens may provide opportunities to assess herbivory across unprecedented temporal, spatial, and

phylogenetic scales (for a more detailed discussion of herbarium data for studying global change, see Meineke et al., 2018). In addition, equivalent data from herbarium specimens on plant–pollinator interactions (e.g., from pollen preserved in specimens; Pauw & Hawkins, 2011) and plant–pathogen interactions (e.g., from pathogen DNA or morphology; Antonovics, Hood, Thrall, Abrams, & Duthie, 2003) may be used to further tailor land management strategies to changing environmental conditions.

However, data from herbaria present challenges that require careful consideration (e.g., see Meyer, Weigelt, & Krefl, 2016; Daru et al., 2018; Meineke et al., 2018). The spatial resolution of older specimens is coarse and, in our data, limited to the county level within the US. In addition, plant collectors tend to avoid damaged specimens, and thus, absolute values of herbivore damage are likely underestimates. Nonetheless, we have shown that it is possible to detect meaningful variation in herbivory that can be contrasted between species and time periods. While collecting biases could in theory confound interpretations—for example, if more recent collectors

are more likely to collect specimens with herbivore damage, leading to an apparent increase in herbivore damage through time—we find no evidence to support any such bias. And, importantly, we can see no reason why collection of damaged specimens should be correlated with temperature or urbanization. In addition, we note that we observe increasing herbivory with day of year (which is independent from trends in change in herbivory over years). As herbivory is cumulative through the growing season, these data indicate that, even if collectors show bias towards selecting more intact specimens, we are still able to detect expected temporal trends in herbivory preserved within herbarium collections.

One exciting prospect is that long-term herbivory data from herbarium specimens may provide the opportunity to compare effects of contemporary temperature change to predictions from fossils. Fossils are one source of long-term data that may help in generating predictions of how plant–herbivore interactions will respond to projected anthropogenic change. Fossils show that herbivory increased in magnitude and diversity during warmer epochs (Currano et al., 2008; Currano, Labandeira, & Wilf, 2010). It is currently unclear how reliably responses to temperature across epochs should predict effects of the rapid, anthropogenic change we are experiencing today. Because herbarium specimens, like fossils, can be scored for the presence and absence of herbivory, it should be possible to answer this question and assess whether patterns across millennia can predict effects of recent global change. Comparing herbivory on herbarium specimens and fossils would require adjusting the methods we have developed here to derive comparable fossil and herbarium data on herbivory that could be placed on a common axis. Our results hint that herbivory responses to contemporary and paleontological climate change might be congruent.

5 | CONCLUSIONS

We found that herbivory has increased over the past 112 years for four species in the northeastern US. Our results contribute to a growing body of research demonstrating how climate change (Suttle, Thomsen, & Power, 2007; Tylisanakis, Didham, Bascompte, & Wardle, 2008) and urbanization (Meineke et al., 2014; Theodorou et al., 2016) might disrupt species interactions. There is an urgent need for a greater focus on the impacts of global change on interacting species because models of species' responses are unlikely to provide accurate predictions without including information on their associates (Gilman, Urban, Tewksbury, Gilchrist, & Holt, 2010). We demonstrated that herbarium specimens contain data that can be used to better inform such predictions. To the extent that patterns across the past century predict the future, we may expect herbivory in nonurban areas to continue increasing with warming winters in the northeastern US. This ecological trend could increase damage to plants that are of ecological, economic, and/or cultural importance. To reduce costs associated with increasing herbivory, we suggest frequent monitoring of crop and forest plants in this region—such as *V. angustifolium* from our study—as the climate continues to warm.

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AUTHORS' CONTRIBUTIONS

E.K.M., T.J.D., and A.T.C. conceived of the project. E.K.M. and T.J.D. designed herbivory quantification and sampling. E.K.M. collected the data. E.K.M., T.J.D., and N.J.S. performed statistical analyses. E.K.M. wrote the paper. All authors contributed substantially to drafts and gave approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.fm23dq6> (Meineke, 2018).

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SUPPORTING INFORMATION

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

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