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Phenological sensitivity to temperature mediates herbivory

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Abstract

Species interactions drive ecosystem processes and are a major focus of global change research. Among the most consequential interactions expected to shift with climate change are those between insect herbivores and plants, both of which are highly sensitive to temperature. Insect herbivores and their host plants display varying levels of synchrony that could be disrupted or

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enhanced by climate change, yet empirical data on changes in synchrony are lacking. Using evidence of herbivory on herbarium specimens collected from the northeastern United States and France from 1900 to 2015, we provide evidence that plant species with temperature-sensitive phenologies experience higher levels of insect damage in warmer years, while less temperature-sensitive, co-occurring species do not. While herbivory might be mediated by interactions between warming and phenology through multiple pathways, we suggest that warming might lengthen growing seasons for phenologically sensitive plant species, exposing their leaves to herbivores for longer periods of time in warm years. We propose that elevated herbivory in warm years may represent a previously underappreciated cost to phenological tracking of climate change over longer timescales.

Introduction

Recent shifts in plant phenology capture the global fingerprint of climate change (Cleland et al., 2007; Parmesan & Yohe, 2003; Root et al., 2003). Many plants flower, leaf-out, and fruit earlier now than in the recent past due to anthropogenic climate warming (Rosenzweig et al., 2008). These shifts may scale to affect myriad processes, from local food web dynamics (Walther, 2010) to global carbon cycling (Piao et al., 2007; Xia et al., 2014). Phenological tracking of climate is typically assumed to benefit plants. For instance, plants that track early spring in warm years may be able to take advantage of the extended growing season and increased access to resources (Cleland et al., 2012; Springate & Kover, 2014), whereas observations indicate that species that fail to track warming temperatures over time experience population declines (Willis et al., 2008).

While changing plant phenology has been studied for decades (Schwartz, 2003), it remains unclear how shifts in phenology induced by recent warming may modify ecological relationships among closely interacting species, such as between plants and their associates. In particular, there is concern that differential phenological sensitivities to warming might result in phenological mismatches, in which the timing of cyclic life-history events that overlapped historically become asynchronized (Parmesan, 2006; Visser et al., 2006) or that previously adaptive asynchronies will be disrupted (Singer & Parmesan, 2010). A growing number of observational studies have examined evidence for phenological mismatches (Edwards & Richardson, 2004; Kharouba et al., 2018; Kharouba & Vellend, 2015; Post & Forchhammer, 2007), but long-term data to describe species interactions remain rare, and traditional statistical models are underpowered to detect the subtle signal of shifting asynchrony against a background of large inter-annual variability (Kharouba et al., 2018). Across biological systems, mixed evidence indicates that lower trophic levels may have, on average, advanced their phenologies at a faster pace than higher trophic levels (Thackeray et al., 2010). Yet there are numerous examples in which phenology of associated species appear to be shifting similarly (Bartomeus et al., 2011; Willmer, 2012).

Both insect and plant development are sensitive to temperature (Bale et al., 2002; Cleland et al., 2007), though the specific cues plants and associated insects use to time life history events may differ (Singer & Parmesan, 2010), and include photoperiod, chilling, ‘forcing’, and precipitation (Hegland et al., 2009). For the vast majority of insect and plant species, the combined and relative contributions of these cues have not been well characterized (Chuine & Régnière, 2017). Iconic interactions, such as those between the oak-caterpillar-great tit, reveal consequences of phenological change across trophic levels and provide an understanding of mechanistic drivers within a few systems (e.g., Visser et al., 2006). However, it remains difficult to generalize across diverse insect-plant associations (Forister et al., 2015; Visser & Gienapp, 2019). Therefore, there remains considerable debate as to the expected extent of phenological mismatch between insect herbivores and their host plants under future climate projections, its fitness consequences, and how to generalize across taxa (Gillespie et al., 2013; Liu et al., 2011; Schwartzberg et al., 2014; Visser & Gienapp, 2019).

Here, we use the unique temporal record preserved in herbaria to compile an unprecedented dataset on insect herbivory –as a measure of the strength of ecological interactions– on commonly collected pressed vascular plants distributed widely across the northeastern USA and France, two areas which have warmed more than the global average since the acceleration of anthropogenic climate change (Intergovernmental Panel on Climate Change, 2015) (and see “Methods”). Herbaria capture a variety of plant-insect interactions spanning space and time, yet have only recently emerged as a source for studying these symbioses (Heberling & Isaac, 2017; Meineke, Davis, et al., 2018). Using this historical record, encompassing 36 plant taxa and spanning 115 years, we evaluate how climate variation and phenological sensitivity to shifting temperatures mediate herbivore interactions. Rather than attempting to quantify changing synchrony of pairwise interactions, we assess the ecological impact of shifting trophic interactions directly by analysing interannual variation in a readily identifiable generalized form of herbivory damage, foliar chewing by mandibulate insect herbivores. Chewing damage observed from fossilised plant leaves has been used to infer ancient plant-herbivore interaction strengths, e.g., (Currano et al., 2008; Wilf et al., 2001); here, using orders of magnitude more data, we evaluate how potential changes in trophic synchrony might affect a key driver of plant fitness and evolution over deep time (Farrell et al., 1991; Futuyma & Agrawal, 2009; Labandeira et al., 1994).

Plant phenology may mediate herbivory in myriad ways. We can envisage many scenarios by which individual plant-herbivore interactions might be modified, for example, through temperature mediated impacts on synchrony between early-season caterpillars and their host trees (Forkner et al., 2008; Pureswaran et al., 2019; Schwartzberg et al., 2014; Visser & Holleman, 2001). For other plants, herbivory may accumulate linearly or step-wise throughout the growing season. Here, we consider the aggregate shifts in accumulated herbivore damage through the growing season that may result from changes in synchrony. For example, with climate change, plants that leaf out earlier in warm years may tend to experience an enemy-free window at the start of the extended growing season. This enemy-free period would occur during a vulnerable development time when plant leaves have yet to accumulate sufficient defenses against herbivores—thus reducing herbivory and, potentially, the effect of herbivores on plant fitness (Fig. 1a). However, if herbivores emerge concurrently or prior to plant leaf-out, herbivory may remain constant or increase with extended growing seasons (Fig. 1b). Similarly, if novel herbivores fill the niche of early-season feeders, plants that extend their growing seasons in warmer years may experience increased herbivory relative to those same plants in cooler years and other species with less phenologically sensitive responses to warming (Fig. 1c). While obviously an oversimplification, these alternative scenarios clearly illustrate how herbivory may be mediated by phenology of both plant and herbivore, and the uncertainties in making future projections.

Our unique dataset from herbarium specimens provides a singular long-term record of species interactions that allows us to document how herbivory damage has co-varied with shifting plant phenology without the need for (largely unavailable) data on the identity of specific insect herbivore-plant interactors or the phenology of emergence and feeding activity of insect herbivores, many of which are larvae in their mandibulate phases and rarely monitored in terms of phenology or demography over the timescales represented by museum specimens.

Methods

Geographic extent

We examined patterns of herbivory on herbarium specimens collected from the northeastern USA (Massachusetts, Connecticut, and Rhode Island) and France over 115 years. Both regions have seasonal climates in which the timing of leaf-out and flowering are strongly associated with spring temperatures (Wolkovich et al., 2013). Importantly, georeferenced herbarium specimens are also plentiful, span the time period from prior to anthropogenic warming in the 1970s until the present day, and are extensively mobilized online (northeastern USA: Consortium of Northeastern Herbaria [http://portal.neherbaria.org/portal/]; France: Muséum National D'histoire Naturelle Herbier [https://science.mnhn.fr/institution/mnhn/collection/p/item/search/form?lang=en_US]).

Climate data

To describe long-term climates of our study regions, we extracted mean monthly temperatures from PRISM for the northeastern USA [http://prism.oregonstate.edu] and minimum and maximum daily temperatures from Berkeley Earth for France [http://berkeleyearth.org/data/]; the latter were averaged to arrive at mean daily temperatures. While the northeastern USA experiences higher mean temperatures in summer and lower mean temperatures in winter, January and July are the coldest and warmest months, respectively, for both regions. We calculated long-term mean average monthly temperature for January and July, alongside mean annual temperatures from 1951 to 1980, after which the distortion of anthropogenic climate warming becomes more pronounced. Temperatures were averaged by month and then by county for the northeastern US, and by department for France. Mean average January temperatures were -3.18± 2.70°C in the northeastern USA, and 5.44± 2.28°C in France. Mean average July temperatures were 21.47± 1.18°C in the northeastern USA and 18.64± 1.54°C in France. Thus, despite France extending over a larger range of latitudes, the temperature variability across counties in the northeastern USA and departments in France were similar. The average rate of warming since 1960 is 2.87± 0.23°C/ century in the northeastern USA and 2.77± 0.22°C/ century in France, compared to a global average rate of 2.16 ± 0.11 (mean± standard deviation) [http://berkeleyearth.org/data/].

Species selection and herbarium specimen sampling

Species were selected first based on the availability of previously published phenological sensitivity metrics. We refer to two metrics of phenological sensitivity, flowering sensitivity and leaf-out sensitivity. We use the general term “phenological sensitivity” to refer to the extent to which a particular life event (e.g., for plants, budbreak, leaf-out, flowering, fruiting) responds to temperature from year to year (e.g., days change in phenology per °C warming). When a species is more phenologically sensitive, the timing of flowering and/or leaf-out advances more in response to warmer temperatures from year-to-year relative to co-occurring species exposed to the same cues. We use the specific terms “flowering sensitivity” and “leaf-out sensitivity” to refer to how much these respective events advance in years when temperatures are warmer. Data on flowering sensitivity were extracted from Wolkovich *et al*. (2012) and leaf-out sensitivity from Polgar *et al*. (2014; Appendix S1).

While flowering is not a direct measure of a phenological stage that affects leaf-feeding insects, for many species flowering and leaf-out are closely associated, and flowering sensitivity and leaf-out sensitivity are thus correlated (albeit sometimes weakly) (Ettinger et al., 2018). This is the case in our dataset, although sample size of species with both flowering and leaf-out sensitivities was too low to draw strong statistical inference (Fig. S1). Although we recognize the limitations of using flowering sensitivity as a proxy, we include models for both flowering and leaf-out because vastly more data are available for the former, and flowering sensitivity data are available for a wider breadth of taxa. In addition to the covariates listed above, we included growth form (woody or herbaceous) in the USA model (all but two species sampled from France were herbaceous).

Specimens selected to assess effects of flowering sensitivity- Northeastern USA Herbarium specimens were obtained from collections at the Harvard University Herbaria (HUH) and the University of Connecticut (UCONN). Because we were interested in exploring the relationship between phenological change and herbivory, we first queried these collections to extract the list of native species for which estimates of phenological sensitivity were available, which we extracted from the meta-analysis of Wolkovich *et al*. (2012). To ensure sufficient density of sampling of herbarium vouchers, this list was then filtered for species with at least 15 herbarium specimens in each of the following time periods: 1900- 1920, 1920- 1940, and 1940- 1960 – this threshold was selected to maximize the trade-off between the diversity of included species against the depth of sampling per species. To reduce phylogenetic bias (see also Statistical Methods below), we then randomly selected an even balance of rosids and asterids (the two main plant clades within the eudicots) from our filtered list; we aimed for ten species from each group, but only nine asterids met our criteria. For each focal species, we estimated herbivory (see below) across 40 specimens collected between 1900 and 1960 from Connecticut, Massachusetts, and Rhode Island, and from a minimum of 15 and up to 40 species from 1960 to 2016, across which herbarium specimens were typically sparser, to capture the signature of recent climate change.

Specimens selected to assess effects of flowering sensitivity- France We focused on species with published flowering sensitivity estimates in Fitter & Fitter (Fitter & Fitter, 2002). To sample a similar subset of the plant community across continents, we selected six focal species that were congeners of the Northeastern USA species set, using the digital database of the Muséum National D'histoire Naturelle Herbier (MNHN), from the above list, assuming equivalent sampling criteria. When multiple congeners were available, we selected the species with the best coverage across space in recent years as collections were generally sparser towards the latter half of the 20th century. We additionally sampled four more native species that fit similar criteria to boost our overall sample size.

Specimens selected to assess effects of leaf-out sensitivity- USA We extracted the list of native species with published leaf-out sensitivities to temperature in Polgar *et al*. (2014). To ensure sufficient density of sampling of herbarium vouchers, this list was then filtered for species with at least 10 herbarium specimens in each of the following time periods: 1900-1920, 1920-1940, and 1940-1960. For each focal species, we estimated herbivory from 40 specimens collected between 1900 and 1960 from Connecticut, Massachusetts, and Rhode Island, and on a minimum of 10 and up to 20 species from 1960 to 2016 to capture the signature of recent climate change. Unfortunately, we could not easily find equivalent data on leaf-out sensitivities for species well-represented in the MNHN.

Herbivory data collected from herbarium specimens

We quantified herbivory on each herbarium voucher using a grid-based transect as described in detail in recent publications (Meineke, Davis, et al., 2018; Meineke et al., 2019). Briefly, we overlaid a grid with a total of 40 5 x 5-cm grid cells on each specimen. In five randomly selected grid cells that were 40% or more covered in leaves, we scored the presence (1) or absence (0) of herbivore chewing damage within each grid cell; a histogram of these data per species is presented in Fig. S2. Chewing is the most common type of insect herbivore damage according to field (Turcotte, Thomsen, et al., 2014) and herbarium studies (Meineke, Davis, et al., 2018; Meineke et al., 2019) and may result from a wide range of mandibulate herbivores, including Lepidoptera (caterpillars of butterflies and moths), Coleoptera (beetles), and Orthoptera (grasshoppers). Our methods for quantifying herbivory are unlikely to capture insect outbreaks, as heavy, and/or centralized damage tend to be avoided by collectors. Instead, our methods are more likely to represent background herbivory that affects plants similarly from year to year. Despite the lower intensity of this type of herbivory, it can have substantial effects on photosynthesis (Zangerl et al., 2002). While there is anecdotal evidence that collectors might preferentially select less damaged specimens (skewing total herbivory estimates low), we do not see why the intensity of such selection would covary with temperature (see below), and previous analyses on a larger sample of specimens suggests little evidence for a collector effect (Meineke et al., 2019).

Spatial, temporal, and trait-based covariates

We associated each herbarium specimen with spatial and temporal data from voucher labels. Specifically, we recorded the latitude, longitude, day of year, and the year when a specimen was collected. For specimens collected in the northeastern USA, we recorded the latitude and longitude of the centroid of the county where the specimen was collected in the absence of more specific location data. We additionally included species data on phylogenetic position, growth form (woody or herbaceous), and the mean date of first flower. We used the phylogeny from Zanne *et al*. (2014) and extracted data on species' growth form from the BIEN Database [http://bien.nceas.ucsb.edu/bien/]. The mean date of first flower allowed us to differentiate between early and late season plant species. For species in the northeastern USA, we used the average flowering date from 1888 to 1902 according to data collected by Alfred Hosmer[20,21] (Table S1). For species from France, mean first flower date was similarly calculated as the average first flower date recorded by Fitter and Fitter (Fitter & Fitter, 2002) from 1954 to 1970.

These time periods comfortably predate the recent anthropogenic signal of climate change (IPCC 2014).

Climate substantially affects herbivory and phenology. We therefore recorded spring temperatures in the year specimens were collected. For northeastern USA we extracted mean daily temperature data from the PRISM Climate Group gridded data [http://prism.oregonstate.edu], and calculated county-level means for each month in each year (Park & Davis, 2017). We used mean March temperatures to represent the onset of spring because it is the first month in the northeastern USA where mean daily temperatures exceed freezing (Fig. S3), when a subset insect and plant species are likely to begin accumulating degree days. Analogous data associated for French specimens were extracted from the Berkeley Earth Gridded Monthly Land Temperature Data [http://berkeleyearth.org/data/]. Specifically, we extracted minimum and maximum daily temperatures, and averaged them to calculate mean monthly temperatures in each year. To describe the regional temperature variation captured by the herbarium specimens, we built simple linear models of year specimens were collected against March mean temperature.

Modelling effects of phenology on herbivory

We constructed hierarchical Bayesian regression models in Stan (Gelman et al., 2015) using the *brms* package (Bürkner, 2017) in R (R Core Team, 2019) to explore the relationship between herbivory and phenological sensitivity. Herbivory occurrences were modelled using a hierarchical Bayesian regression fit with a zero-inflated binomial distribution. Initially, we attempted to use a simple binomial error structure in our models, but the fit was poor and was greatly improved by the inclusion of a zero-inflated error structure (Fig. S4). The model was defined as:

$$Grid\ cells\ with\ herbivory \sim overdispersed\ Binomial(p_{ij}, n)$$

$$logit(p_{ij}) = a + \beta_1 phensens_{ij} \times \beta_2 mar_{ij} + \beta_3 latitude_{ij} +$$
$$\beta_4 longitude_{ij} + \beta_5 growthform_j + \beta_6 day_{ij} +$$
$$\beta_7 year_{ij} + \beta firstphenday_{ij} + u_j + \mathrm{u}_{\mathrm{ij}}$$

Where *grid cells with herbivory* is the number of grid cells with chewing damage by mandibulate herbivores p on specimen i from species j, and n is a constant representing the number of grid cells examined on each specimen. We model $logit(p_{ij})$ as a function of a, the intercept, *phensens*, the flowering or leaf-out sensitivity of species j depending on the specific model (see below), *mar*, March mean temperature associated with specimen i of species j, *latitude*, the latitude where specimen i of species j was collected, *longitude*, the longitude where specimen i of species j was collected and u_i and u_{ij}, which are grouping factors (random effects) of phylogenetic position and location (county-state, or Department, see below). We accounted for phylogenetic relatedness among plant species using a correlation matrix inferred from the Zanne *et al*. (2014) phylogeny described above. The contribution of phylogenetic effects in the fitted model were estimated as the intra-class correlation (equivalent to Lynch's lambda (Lynch, 1991)) using the "hypothesis" function in *brms*. We accounted for the effects of space by including location as a group-level effect, specified as county-state combination for specimens collected in the USA or the French 'department' for specimens collected in France. Models were fit with 2000 iterations in four chains, with the initial 1000 iterations discarded after warm-up. For all models, we assessed convergence (Rhat values equal to one) and model fit to the observed data using posterior predictive checks in *brms*. We also calculated the variance explained using Bayesian R^2 as estimated in the "bayes_R2" function in *brms*.

We present two sets of models, the first exploring the relationship between flowering sensitivity, temperature, and herbivory, and the second exploring the relationship between leaf-out sensitivity, temperature, and herbivory. In each model, the interaction term between phenological sensitivity (flowering or leaf-out) and temperature indicates the extent to which the effects of early spring temperatures on herbivory are related to phenological sensitivity. All continuous predictors were scaled and centered on zero to allow comparison of effect sizes within models. Tests of model robustness are described in Appendix S2. First, we fit two separate models for congeneric species in the USA and France, both of which included the interaction term between March mean temperature and flowering sensitivity. To assess the interaction of phenological sensitivity and spring temperature on herbivory more directly, we constructed an additional model for the set of species for which leaf-out sensitivity data were available from the USA only (for details, see above), including the interaction between March mean temperature and leaf-out sensitivity. All species in this model are woody and we thus did not include growth form as a predictor.

Results

We recorded herbivory on at total of 1926 herbarium vouchers (Table S1). While the regions captured by our herbarium sampling have significantly warmed on average, local temperatures were also highly variable during the sampling period. The specimens used in our study, therefore, captured a large amount of interannual temperature variability but did not experience significant changes in March mean temperature over years (see Fig. S5; for all models, $p > 0.1$; full statistics in Table S2).

In all models, day of year had the strongest effect on herbivory—specimens collected on dates that were later in the growing season accumulated more herbivory (Fig. 2; Fig. S6; Table 1; β ranged from 0.45- 0.55, 95% CI [0.15, 0.73]). Species that showed greater phenological sensitivity to temperature also experienced more herbivory in warmer years (Figs. 2-4; Table 1; for all models, β ranged from 0.08- 0.12). The model that included leaf-out sensitivities showed a stronger interactive effect with temperature on herbivory than models including flowering sensitivities, though all interactive effects between phenological sensitivity and temperature followed the same trend (Table 1; Fig. 3). For example, with all other variables held constant, for species whose leaf-out timing was highly sensitive responses to interannual temperature, such as the high-bush blueberry *Vaccinium corymbosum*, the predicted intensity of herbivory approximately doubled with a 5° C increase in March mean temperature. This 'increase' references interannual variation in temperature, not change in mean temperature over time driven by climate change (see below). In contrast, for species whose leaf-out was less sensitive to temperature, such as the gray birch *Betula populifolia*, March mean temperature had little or no predicted effect on herbivory. In models that included the interactive effects of phenological sensitivity and temperature, Bayesian R^2 values varied from 0.17 to 0.20 (Table 1). We did not find strong evidence for effects of phylogenetic relatedness in any models (Table S3).

Main effects of March mean temperature, after accounting for the interaction between temperature and phenological sensitivity, varied by continent (Fig. 2). In the USA, herbarium specimens from years with higher March temperatures also displayed more herbivory (Fig. 2a,c;

Table 1a,c), but March temperature was not an important factor driving herbivory in France (Fig. 2b; Table 1b). Herbarium specimens collected at lower latitudes (areas associated with warmer temperatures) also displayed more herbivore damage than those collected at higher latitudes (Table 1), although credibility intervals tended to be large and, for French specimens, substantially overlapped zero (Fig. 2b; Table 1b). We also observed evidence that herbivory was greater on specimens collected in early years than on specimens collected in later years (Fig. 2), but again credibility intervals tended to be large, and substantially overlapped zero in models from USA specimens (Figs. 2a,c). Woody species showed marginally higher herbivory rates than herbaceous species (Table 1a).

Discussion

Insect herbivore damage presents an important selection pressure on plants, and precipitated an evolutionary arms race that has driven speciation across the insect and plant tree of life. Here, using herbarium specimens collected on two continents over 100+ years from 36 plant species, we reveal that early season plants and plants demonstrating greater phenological sensitivity to temperature experience more herbivory in warm than cool years, while later season, less sensitive co-occurring plants do not. Our results indicate that as plant phenology shifts with global climate warming, so might herbivory pressure. While there is some evidence to suggest that plant species that have adjusted their phenologies to better track shifting temperatures have fared better under recent warming trends (Willis et al., 2008), our data indicate there may also be a penalty for leafing out early in warm years. The aggregate effects of climate warming on plant fitness likely reflect complex trade-offs between the benefits of leafing out early (e.g., longer growing season and time for resource accumulation) and the costs of increased exposure of costly tissue, that include higher frost risk (Chamberlain et al., 2019) and, as we show here, heightened herbivore pressure.

We found that plants that were sensitive to climate accumulated more herbivory in warm years, while co-occurring, less sensitive species did not. Thus, phenological tracking may extend the window of opportunity for insect herbivores. If specialist insect herbivores of sensitive plants were insensitive to climate, we would have predicted sensitive plants might have been able to escape herbivory in warm years. We find the opposite to be true. This could be because phenologically sensitive plants and their insect herbivores are shifting timing of leaf-out and emergence, respectively, in synchrony. In warm years, more sensitive plants may also be more synchronized with each other and with early season herbivores (Hansen et al., 2020; Pearse, Funk, et al., 2015). However, it is also possible that either generalist herbivores or a diversity of opportunistic herbivores dominate the insect herbivore community—which might be relatively common in temperate latitudes (Forister et al., 2015)—such that temporal escape from one herbivore increases exposure to another. Similar 'diversity' effects have been shown to moderate impacts of temporal asynchrony between plants and pollinators (Bartomeus et al., 2013); however, to the best of our knowledge, this has not been explored for the strength of changing plant-herbivore interactions. In both scenarios, earlier plant phenology simply extends the window of opportunity for insect herbivores.

Our findings align with other studies showing that phenological timing can affect herbivory rates within species or genera (Mopper & Simberloff, 1995; Pearse, Baty, et al., 2015; Pearse, Funk, et al., 2015; Pearse & Karban, 2013), and may have fitness consequences (Pearse, Funk, et al., 2015). For example, valley oak (*Quercus lobata*) genotypes that leafed out early in a given year also experienced higher herbivory rates in that year and reduced acorn production in the following year (Pearse, Funk, et al., 2015). Our herbarium dataset provides the rare opportunity to extend this framework to entire plant communities.

We suggest that increased herbivory could reflect an underappreciated fitness cost to phenological tracking as the climate warms, beyond the more widely recognized costs associated with phenological asynchrony, e.g., (Schwartzberg et al., 2014). Even small amounts of herbivory can have large effects on photosynthesis that extend beyond the areas of leaves that are actually damaged (Zangerl et al., 2002), suggesting that fitness costs might be larger than assumed from the observed extent of damage on a given leaf. In addition, climate warming may have complex and interactive effects on plant defense pathways that exacerbate photosynthetic losses induced by herbivores (Havko et al., 2020). However, the cost surface landscape is likely complex, and variable across taxa and locations. For example, mandibulate chewing herbivory has variable effects on photosynthesis across taxa, which can be mediated by the amount of leaf area lost (direct effects) and indirect, non-linear effects, related to losses that rely on the extent of vascular damage, defense-induced down-regulation, and autotoxicity (Nabity et al., 2009). In addition, some plants have evolved tolerance to insect herbivory (Rosenthal & Kotanen, 1994). Nevertheless, herbivory still represent an important contemporary selective pressure (Agrawal et al., 2012), and eco-evolutionary feedbacks between insect herbivory and plant phenology have been well established (Aizen & Patterson, 1995; Ayres, 1993; Schwartzberg et al., 2014). Thus, as the climate continues to warm, shifts in herbivory may present a selective pressure moderating or driving future shifts in phenology (Elzinga et al., 2007; Lemoine et al., 2017). This moderating effect of herbivores on plants might also help explain some of the large variation in plant phenological sensitivities, i.e., while most plants are advancing phenological events with recent warming, others show muted responses or even demonstrate phenological delays

(Wolkovich et al., 2012). While our study does not capture the net fitness effects of phenological shifts on plants, our results suggest that any fitness gains from climate tracking are unlikely to have been achieved through escaping insect herbivores.

The temporal snapshot of the growing season provided by herbarium specimens does not allow us to definitively assess whether phenologically sensitive plants experience more total herbivory throughout the season in warmer years or if the window of herbivory simply moves to earlier in the growing season. There is evidence, however, that entire growing seasons are being extended as spring phenology events are shifting earlier and autumn events later (Fridley, 2012; Menzel & Fabian, 1999). It is probable, therefore, that the total time between leaf-out and senescence has also lengthened for phenologically sensitive species, resulting in higher total herbivory, and even leaf damage in late season might reduce plant performance in subsequent years for long-lived species (García & Ehrlén, 2002). Nonetheless, it is also possible that the additional days for photosynthesis in warmer years for more sensitive species compensates for the cost of increased exposure to herbivory.

Herbarium specimens are now established as a critical form of ecological data (Heberling & Isaac, 2017; Meineke, Davies, et al., 2018; Meineke, Davis, et al., 2018). However, herbarium data, like all data, are subject to potential biases (Daru et al., 2018; Meyer et al., 2016). Recent work has shown that herbarium specimens can provide reliable measures of plant functional traits, including specific leaf area, leaf thickness, and wood specific gravity (Perez et al., 2020). Our study provides novel evidence that herbarium specimens can also provide useful estimates of changing herbivory within species across time and space. First, the signal between phenological sensitivity and herbivory is stronger when estimated on leaf-out—which is a more direct measurement of phenology relevant to insect herbivores that eat leaves—than flowering.

While models including flowering sensitivity included more plant species (n= 19), models including leaf-out sensitivity (n=11) better captured the relationship between phenological timing and herbivory, as would be expected given the direct biological relationship between leaf-out and foliar insect feeding. Second, recapitulating earlier work (Meineke, Davis, et al., 2018; Meineke et al., 2019), general herbivory trends match to expected patterns established in the literature on plant-insect herbivore interaction strengths. For example, herbarium specimens collected later in the growing season experienced more herbivory than those collected early (Meineke et al., 2019), and specimens of woody species displayed greater herbivory than herbaceous species, a pattern that has been widely established, e.g., (Turcotte, Davies, et al., 2014).

We observed a trend for increasing herbivory damage on phenologically sensitive species in warmer years. With global temperatures rising, we might then expect to see increasing herbivory through time (Meineke et al., 2019). It is notable, however, that in our Bayesian regression, we find that, after accounting for co-variates (i.e., spring temperature and phenological sensitivity), there is an overall trend toward lower herbivory intensity in recent years. Other processes besides temperature change undoubtedly impact insect herbivory. Land transformation (van Klink et al., 2020), succession (Jeffries et al., 2006), and pesticide use (Wagner et al., 2021), among other drivers (Wagner, 2019), may affect insect herbivore abundance and population dynamics over years. Recent studies have revealed evidence of declines in insect abundance—the “insect apocalypse” (Goulson, 2019). Although there remains some controversy surrounding these estimates (Wagner, 2019), a dramatic decline in herbivorous insects—notably butterflies (Breed et al., 2013; van Strien et al., 2019; Wepprich et al., 2019), which cause chewing damage in their larval phases—would obviously lead to predictions of lower herbivory through time. Our results might thus inadvertently capture the ecological signature of these recent biodiversity declines. Disentangling such confounding influences on herbivory presents a major challenge for the future. Herbarium vouchers and biological collections might contribute substantially to this effort, for example, via tracking changes in plant defenses associated with herbivory (Small, 1985; Zangerl & Berenbaum, 2005) and changing herbivore population dynamics through evidence of specialized damage that can be attributed to particular herbivore taxa (Lees et al., 2011).

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Figure Captions

Fig. 1. Conceptual diagram representing potential consequences of warming-induced phenological shifts on insect damage to leaves. *(A)* Phenologically sensitive plant species advance leaf-out in warmer years, but herbivores fail to advance. As a result, phenologically sensitive plant species have an enemy-free window in warm years. Generally, we hold this as a possibility because across diverse taxa, lower trophic levels often advance their phenology more than higher trophic levels (Thackeray et al., 2010). *(B)* Highly sensitive plant species respond to climate warming by leafing out early in the growing season and the herbivores that consume them also emerge early (e.g., Visser et al., 2001). As a result, more sensitive plant species may experience more herbivory in early springs because the time period in which they are exposed to herbivores is lengthened, though effects on herbivory might be idiosyncratic among plant species due to concurrent changes in predation or disease pressure on key herbivores, the length of time it takes for plants to accumulate defenses, or other variables unaccounted for that shift in response to climate change (Feeny, 1970; A. F. Hunter & Elkinton, 2000; M. D. Hunter, 1992). *(C)* This scenario is the same as *(B)* but instead of herbivores that have historically attacked a given plant species, novel herbivores are present in mandibulate life stages to eat plant species that leaf out earlier in warmer years. Herbivory may be exacerbated if plants have no coevolved defenses to the novel herbivore.

Fig. 2. Model estimates showing effects of time, space, and environmental variables on insect damage to plants. Predicted effects of modelled variables on insect herbivory. The subset of variables here displayed important effects on herbivory in at least one of the three models. Bold lines represent 80% credibility intervals, and narrow lines represent 95% credibility intervals. Shading indicates the interaction term between spring temperature and phenological sensitivity.

a-b include the effect of flowering sensitivity on the relationship between early spring temperature and insect herbivore damage to plants (March mean temp. × flowering sensitivity) in ***(A)*** the northeastern United States and ***(B)***. congeneric species in France. ***(C)*** includes the effect of leaf-out sensitivity on the relationship between early spring temperature and insect herbivore damage to plants (March mean temp. × leaf-out sensitivity) in the northeastern United States. "FS" refers to flowering sensitivity to temperature, and "LS" refers to leaf-out sensitivity.

Fig. 3. Plants with high phenological sensitivity to temperature experience elevated insect herbivore damage in warm springs. *(A,B)* Effect of flowering sensitivity on the relationship between early spring temperature and insect herbivore damage to plants in a, the northeastern United States and b. congeneric species in France. *(C)* Effect of leaf-out sensitivity on the relationship between early spring temperature and insect herbivore damage to plants in the northeastern United States. Predictions are evaluated at mean+ standard deviation ("Highly sensitive"), mean sensitivity, and mean− standard deviation ("Not sensitive"). Intensity of chewing damage represents the predicted mean proportion of grid squares per specimen with mandibulate herbivore damage.

Fig. 4. Relationships between the March mean temperature the year when a specimen was collected and herbivory for *(A)* the dataset used in the March temp. × flowering sensitivity model from the northeastern USA, *(B)* the dataset used in the March temp. × flowering sensitivity model from France, and c, the dataset used in the March temp. × leaf-out sensitivity model from the northeastern USA. Note that the March temperature ranges on the x-axis vary between the USA *(A, C)* and France *(B)*. Regression lines are for simple linear models of number of grid cells

with chewing damage against March mean temperature, and do not represent model fits from the full Bayesian analyses. Grey areas represent 95% confidence intervals around the mean. Data points represent discrete values between zero and six, but are jittered so that all data points (herbarium specimens) are visible.

Table

Table 1. Bayesian models of insect chewing herbivory quantified on herbarium specimens. Predictors include: day of year, March mean temperature, year, plant species flowering sensitivity, plant species mean first flower or leaf date, latitude, longitude, growth form (woody or herbaceous), and the interactive effect of March mean temperature and flowering or leaf-out sensitivity on. For each parameter, β_{avg} is the estimated average effect on insect chewing herbivory. Values of each variable were scaled prior to analysis, and thus, β_{avg} can be directly compared across model predictors. The effective sample size (the effective number of independent samples in the posterior distribution) is indicated by n_{eff}.

a. Flowering sensitivity model – United States (Bayesian $R^2 = 0.19$)

Variable	β_{avg}	**SE**	**2.5%**	**97.5%**	n_{eff}
Intercept	-1.05	0.62	-2.32	0.22	3076
Day of year	0.55	0.05	0.45	0.66	9333
March temp.	0.07	0.04	-0.01	0.15	3026
Year	-0.03	0.04	-0.11	0.06	9175
Flowering sensitivity	0.12	0.27	-0.42	0.65	3173
First flower date	0.12	0.31	-0.50	0.73	3803
Latitude	-0.11	0.05	-0.21	-0.02	8654
Longitude	0.03	0.05	-0.06	0.12	6585
Growth form (woody)	0.82	0.41	-0.01	1.62	7161
March temp. × Flowering sensitivity	0.09	0.05	0.00	0.19	8695

b. Flowering sensitivity model – France (Bayesian $R^2 = 0.20$)

Variable	β_{avg}	**SE**	**2.5%**	**97.5%**	n_{eff}
Intercept	-0.39	0.36	-1.09	0.27	1790
Day of year	0.44	0.15	0.15	0.73	4249
March temp.	-0.06	0.10	-0.27	0.14	3201

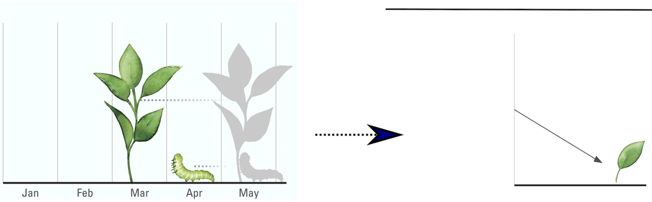
Year	-0.17	0.09	-0.34	-0.01	4434
Flowering sensitivity	-0.07	0.46	-1.02	0.86	1601
First flower date	-0.23	0.45	-1.11	0.66	1742
Latitude	-0.07	0.11	-0.30	0.16	2491
Longitude	0.04	0.12	-0.19	0.26	2357
March temp. × Flowering sensitivity	0.08	0.09	-0.08	0.25	4959

c. Leaf-out sensitivity model – United States (Bayesian R^2= 0.17)

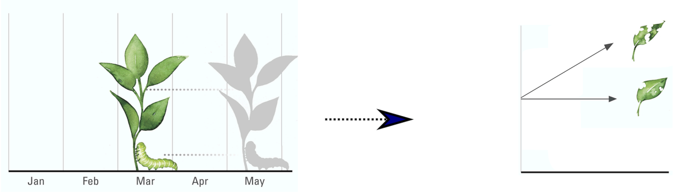
Variable	β_{avg}	**SE**	**2.5%**	**97.5%**	$\mathbf{n_{eff}}$
Intercept	-0.38	0.35	-1.00	0.28	1409
Day of year	0.45	0.06	0.34	0.57	3781
March temp.	0.16	0.06	0.05	0.28	2996
Year	-0.04	0.06	-0.15	0.08	3587
Leaf-out sensitivity	0.07	0.20	-0.35	0.46	1471
First leaf date	-0.19	0.21	-0.65	0.23	1326
Latitude	-0.07	0.08	-0.23	0.10	1809
Longitude	-0.11	0.08	-0.27	0.03	1873
March temp. × Leaf-out sensitivity	0.12	0.06	0.01	0.23	4095

Predicted effect of spring temperature (**x-axis**) on insect herbivory damage to plants (**y-axis**)

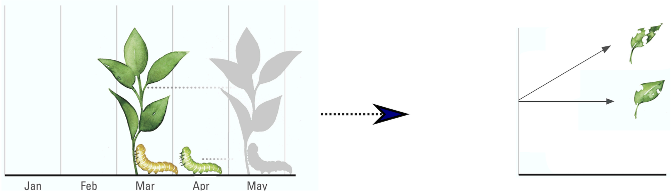
(a) Escape from herbivory: Phenologically sensitive plants leaf out early, but herbivores do not ‘keep up’.

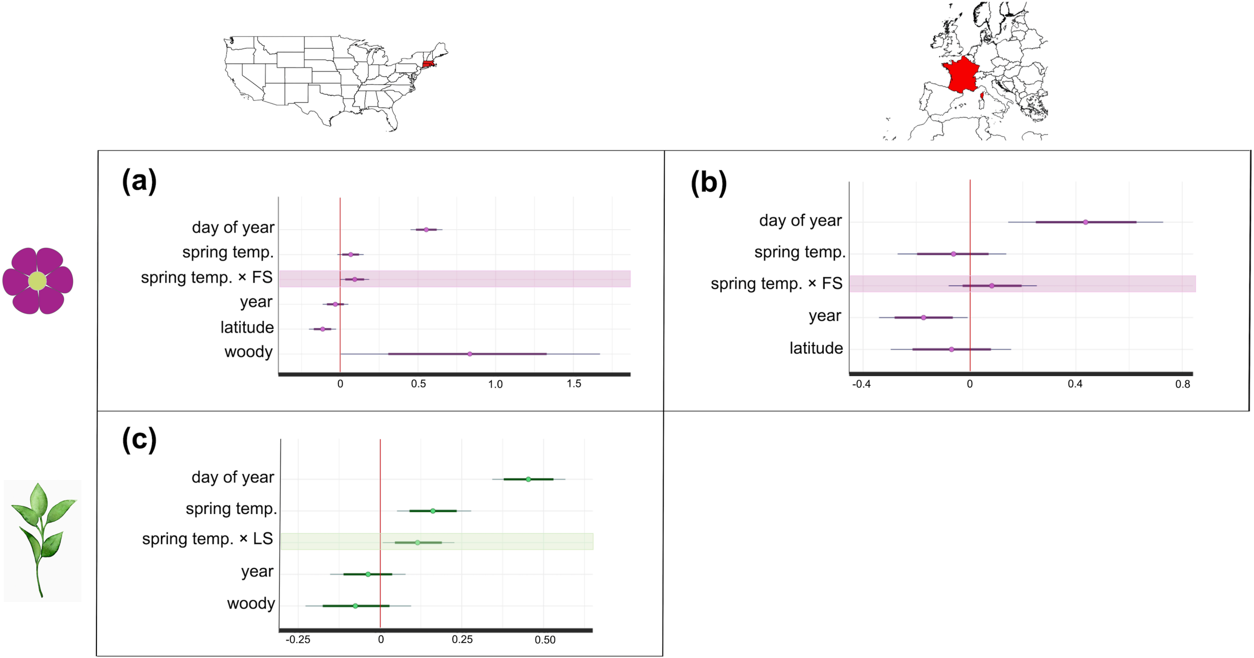


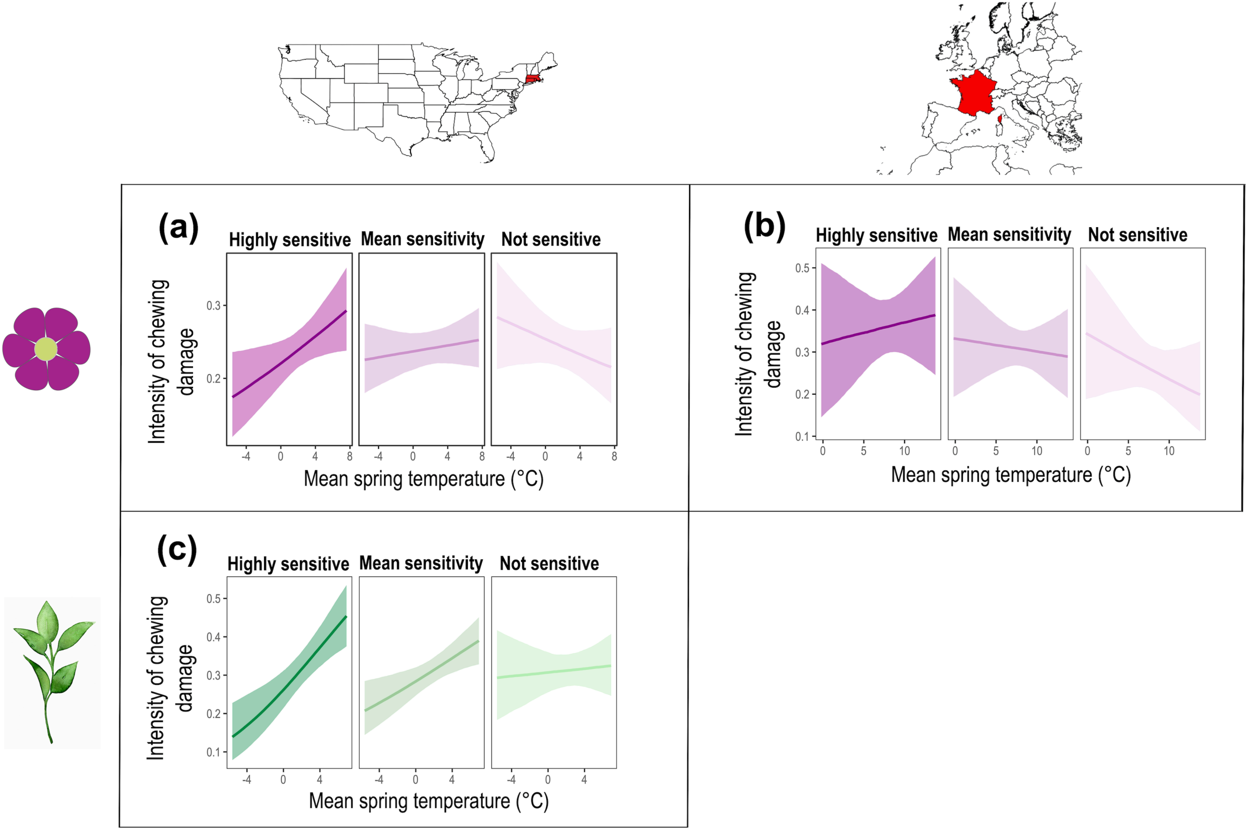
(b) Status quo or extended season: Phenologically sensitive plants leaf-out early, and herbivores also emerge early.

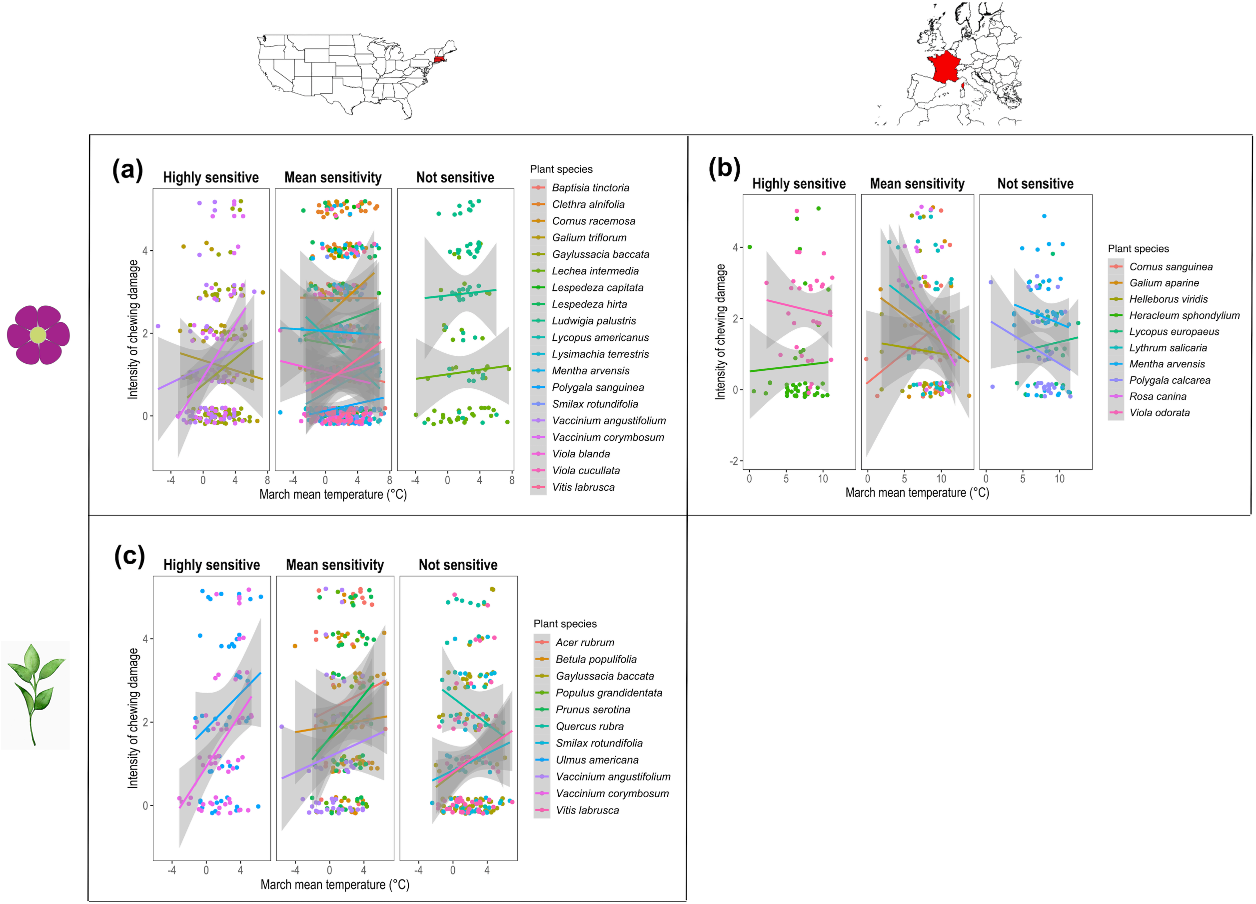


(c) Novel interaction(s): Phenologically sensitive plants leaf out early, herbivores do not ‘keep up’, but novel herbivore(s) are present.




(a)
day of year
spring temp.
spring temp. × FS
year
latitude
woody
0
0.5
1.0
1.5
(b)
day of year
spring temp.
spring temp. × FS
year
latitude
-0.4
0
0.4
0.8
(c)
day of year
spring temp.
spring temp. × LS
year
woody
-0.25
0
0.25
0.50


(a)
Highly sensitive
Mean sensitivity
Not sensitive
Intensity of chewing damage
0.2
0.3
-4
0
4
8
Mean spring temperature (°C)
(b)
Highly sensitive
Mean sensitivity
Not sensitive
Intensity of chewing damage
0.1
0.2
0.3
0.4
0.5
0
5
10
Mean spring temperature (°C)
(c)
Highly sensitive
Mean sensitivity
Not sensitive
Intensity of chewing damage
0.1
0.2
0.3
0.4
0.5
-4
0
4
Mean spring temperature (°C)


(a)
Highly sensitive
Mean sensitivity
Not sensitive
Intensity of chewing damage
0
2
4
-4
0
4
8
March mean temperature (°C)
Plant species
Baptisia tinctoria
Clethra alnifolia
Cornus racemosa
Galium triflorum
Gaylussacia baccata
Lechea intermedia
Lespedeza capitata
Lespedeza hirta
Ludwigia palustris
Lycopus americanus
Lysimachia terrestris
Mentha arvensis
Polygala sanguinea
Smilax rotundifolia
Vaccinium angustifolium
Vaccinium corymbosum
Viola blanda
Viola cucullata
Vitis labrusca
(b)
Highly sensitive
Mean sensitivity
Not sensitive
Intensity of chewing damage
-2
0
2
4
0
5
10
March mean temperature (°C)
Plant species
Cornus sanguinea
Galium aparine
Helleborus viridis
Heracleum sphondylium
Lycopus europaeus
Lythrum salicaria
Mentha arvensis
Polygala calcarea
Rosa canina
Viola odorata
(c)
Highly sensitive
Mean sensitivity
Not sensitive
Intensity of chewing damage
0
2
4
-4
0
4
March mean temperature (°C)
Plant species
Acer rubrum
Betula populifolia
Gaylussacia baccata
Populus grandidentata
Prunus serotina
Quercus rubra
Smilax rotundifolia
Ulmus americana
Vaccinium angustifolium
Vaccinium corymbosum
Vitis labrusca