

1
2 DR. EMILY K MEINEKE (Orcid ID : 0000-0002-5416-4233)

3
4
5 Article type : Primary Research Article

6
7
8 Phenological sensitivity to temperature mediates herbivory

9 Emily K. Meineke^{1*}, Charles C. Davis², T. Jonathan Davies^{3,4}

10

11 ¹ Department of Entomology and Nematology, University of California, Davis

12 ² Department of Organismic and Evolutionary Biology, Harvard University Herbaria

13 ³ Departments of Botany, Forest & Conservation Sciences, University of British Columbia,
14 Vancouver

15 ⁴ African Centre for DNA Barcoding, University of Johannesburg

16

17 *Emily K. Meineke, ekmeineke@ucdavis.edu, phone: (+1) 919-308-3267, One Shields Avenue,
18 Davis, CA 95616

19 **Running title:** Phenology drives herbivory

20 **Keywords:** phenology, climate change, warming, Anthropocene, global change, herbivore,
21 species interactions, insect

22 **Author contributions:** All authors conceived of the study. EKM collected data. EKM and TJD
23 contributed to statistical analyses. All authors wrote the paper.

24

25 **Abstract**

26 Species interactions drive ecosystem processes and are a major focus of global change research.

27 Among the most consequential interactions expected to shift with climate change are those

28 between insect herbivores and plants, both of which are highly sensitive to temperature. Insect

29 herbivores and their host plants display varying levels of synchrony that could be disrupted or

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/GCB.15600

This article is protected by copyright. All rights reserved

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

40

41

42

43 **Introduction**

44 Recent shifts in plant phenology capture the global fingerprint of climate change (Cleland et al.,
45 2007; Parmesan & Yohe, 2003; Root et al., 2003). Many plants flower, leaf-out, and fruit earlier
46 now than in the recent past due to anthropogenic climate warming (Rosenzweig et al., 2008).
47 These shifts may scale to affect myriad processes, from local food web dynamics (Walther,
48 2010) to global carbon cycling (Piao et al., 2007; Xia et al., 2014). Phenological tracking of
49 climate is typically assumed to benefit plants. For instance, plants that track early spring in warm
50 years may be able to take advantage of the extended growing season and increased access to
51 resources (Cleland et al., 2012; Springate & Kover, 2014), whereas observations indicate that
52 species that fail to track warming temperatures over time experience population declines (Willis
53 et al., 2008).

54 While changing plant phenology has been studied for decades (Schwartz, 2003), it
55 remains unclear how shifts in phenology induced by recent warming may modify ecological
56 relationships among closely interacting species, such as between plants and their associates. In
57 particular, there is concern that differential phenological sensitivities to warming might result in
58 phenological mismatches, in which the timing of cyclic life-history events that overlapped
59 historically become asynchronised (Parmesan, 2006; Visser et al., 2006) or that previously
60 adaptive asynchronies will be disrupted (Singer & Parmesan, 2010). A growing number of
61 observational studies have examined evidence for phenological mismatches (Edwards &
62 Richardson, 2004; Kharouba et al., 2018; Kharouba & Vellend, 2015; Post & Forchhammer,
63 2007), but long-term data to describe species interactions remain rare, and traditional statistical
64 models are underpowered to detect the subtle signal of shifting asynchrony against a background
65 of large inter-annual variability (Kharouba et al., 2018). Across biological systems, mixed

66 evidence indicates that lower trophic levels may have, on average, advanced their phenologies at
67 a faster pace than higher trophic levels (Thackeray et al., 2010). Yet there are numerous
68 examples in which phenology of associated species appear to be shifting similarly (Bartomeus et
69 al., 2011; Willmer, 2012).

70 Both insect and plant development are sensitive to temperature (Bale et al., 2002; Cleland
71 et al., 2007), though the specific cues plants and associated insects use to time life history events
72 may differ (Singer & Parmesan, 2010), and include photoperiod, chilling, ‘forcing’, and
73 precipitation (Hegland et al., 2009). For the vast majority of insect and plant species, the
74 combined and relative contributions of these cues have not been well characterized (Chuine &
75 Régnière, 2017). Iconic interactions, such as those between the oak-caterpillar-great tit, reveal
76 consequences of phenological change across trophic levels and provide an understanding of
77 mechanistic drivers within a few systems (e.g., Visser et al., 2006). However, it remains difficult
78 to generalize across diverse insect-plant associations (Forister et al., 2015; Visser & Gienapp,
79 2019). Therefore, there remains considerable debate as to the expected extent of phenological
80 mismatch between insect herbivores and their host plants under future climate projections, its
81 fitness consequences, and how to generalize across taxa (Gillespie et al., 2013; Liu et al., 2011;
82 Schwartzberg et al., 2014; Visser & Gienapp, 2019).

83 Here, we use the unique temporal record preserved in herbaria to compile an
84 unprecedented dataset on insect herbivory –as a measure of the strength of ecological
85 interactions– on commonly collected pressed vascular plants distributed widely across the
86 northeastern USA and France, two areas which have warmed more than the global average since
87 the acceleration of anthropogenic climate change (Intergovernmental Panel on Climate Change,
88 2015) (and see “Methods”). Herbaria capture a variety of plant-insect interactions spanning

89 space and time, yet have only recently emerged as a source for studying these symbioses
90 (Heberling & Isaac, 2017; Meineke, Davis, et al., 2018). Using this historical record,
91 encompassing 36 plant taxa and spanning 115 years, we evaluate how climate variation and
92 phenological sensitivity to shifting temperatures mediate herbivore interactions. Rather than
93 attempting to quantify changing synchrony of pairwise interactions, we assess the ecological
94 impact of shifting trophic interactions directly by analysing interannual variation in a readily
95 identifiable generalized form of herbivory damage, foliar chewing by mandibulate insect
96 herbivores. Chewing damage observed from fossilised plant leaves has been used to infer ancient
97 plant-herbivore interaction strengths, e.g., (Currano et al., 2008; Wilf et al., 2001); here, using
98 orders of magnitude more data, we evaluate how potential changes in trophic synchrony might
99 affect a key driver of plant fitness and evolution over deep time (Farrell et al., 1991; Futuyma &
100 Agrawal, 2009; Labandeira et al., 1994).

101 Plant phenology may mediate herbivory in myriad ways. We can envisage many
102 scenarios by which individual plant-herbivore interactions might be modified, for example,
103 through temperature mediated impacts on synchrony between early-season caterpillars and their
104 host trees (Forkner et al., 2008; Pureswaran et al., 2019; Schwartzberg et al., 2014; Visser &
105 Holleman, 2001). For other plants, herbivory may accumulate linearly or step-wise throughout
106 the growing season. Here, we consider the aggregate shifts in accumulated herbivore damage
107 through the growing season that may result from changes in synchrony. For example, with
108 climate change, plants that leaf out earlier in warm years may tend to experience an enemy-free
109 window at the start of the extended growing season. This enemy-free period would occur during
110 a vulnerable development time when plant leaves have yet to accumulate sufficient defenses
111 against herbivores—thus reducing herbivory and, potentially, the effect of herbivores on plant

112 fitness (Fig. 1a). However, if herbivores emerge concurrently or prior to plant leaf-out, herbivory
113 may remain constant or increase with extended growing seasons (Fig. 1b). Similarly, if novel
114 herbivores fill the niche of early-season feeders, plants that extend their growing seasons in
115 warmer years may experience increased herbivory relative to those same plants in cooler years
116 and other species with less phenologically sensitive responses to warming (Fig. 1c). While
117 obviously an oversimplification, these alternative scenarios clearly illustrate how herbivory may
118 be mediated by phenology of both plant and herbivore, and the uncertainties in making future
119 projections.

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

126

127 **Methods**

128 **Geographic extent**

129 We examined patterns of herbivory on herbarium specimens collected from the northeastern
130 USA (Massachusetts, Connecticut, and Rhode Island) and France over 115 years. Both regions
131 have seasonal climates in which the timing of leaf-out and flowering are strongly associated with
132 spring temperatures (Wolkovich et al., 2013). Importantly, georeferenced herbarium specimens
133 are also plentiful, span the time period from prior to anthropogenic warming in the 1970s until

134 the present day, and are extensively mobilized online (northeastern USA: Consortium of
135 Northeastern Herbaria [<http://portal.neherbaria.org/portal/>]; France: Muséum National D'histoire
136 Naturelle Herbarier
137 [https://science.mnhn.fr/institution/mnhn/collection/p/item/search/form?lang=en_US]).

138

139 **Climate data**

140 To describe long-term climates of our study regions, we extracted mean monthly temperatures
141 from PRISM for the northeastern USA [<http://prism.oregonstate.edu>] and minimum and
142 maximum daily temperatures from Berkeley Earth for France [<http://berkeleyearth.org/data/>]; the
143 latter were averaged to arrive at mean daily temperatures. While the northeastern USA
144 experiences higher mean temperatures in summer and lower mean temperatures in winter,
145 January and July are the coldest and warmest months, respectively, for both regions. We
146 calculated long-term mean average monthly temperature for January and July, alongside mean
147 annual temperatures from 1951 to 1980, after which the distortion of anthropogenic climate
148 warming becomes more pronounced. Temperatures were averaged by month and then by county
149 for the northeastern US, and by department for France. Mean average January temperatures were
150 $-3.18 \pm 2.70^{\circ}\text{C}$ in the northeastern USA, and $5.44 \pm 2.28^{\circ}\text{C}$ in France. Mean average July
151 temperatures were $21.47 \pm 1.18^{\circ}\text{C}$ in the northeastern USA and $18.64 \pm 1.54^{\circ}\text{C}$ in France. Thus,
152 despite France extending over a larger range of latitudes, the temperature variability across
153 counties in the northeastern USA and departments in France were similar. The average rate of
154 warming since 1960 is $2.87 \pm 0.23^{\circ}\text{C}/\text{century}$ in the northeastern USA and $2.77 \pm 0.22^{\circ}\text{C}/\text{century}$
155 in France, compared to a global average rate of 2.16 ± 0.11 (mean \pm standard deviation)
156 [<http://berkeleyearth.org/data/>].

157 **Species selection and herbarium specimen sampling**

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

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

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

196 *Specimens selected to assess effects of flowering sensitivity- France* We focused on species with
197 published flowering sensitivity estimates in Fitter & Fitter (Fitter & Fitter, 2002). To sample a
198 similar subset of the plant community across continents, we selected six focal species that were
199 congeners of the Northeastern USA species set, using the digital database of the Muséum
200 National D'histoire Naturelle Herbarier (MNHN), from the above list, assuming equivalent
201 sampling criteria. When multiple congeners were available, we selected the species with the best

202 coverage across space in recent years as collections were generally sparser towards the latter half
203 of the 20th century. We additionally sampled four more native species that fit similar criteria to
204 boost our overall sample size.

205 *Specimens selected to assess effects of leaf-out sensitivity- USA* We extracted the list of native
206 species with published leaf-out sensitivities to temperature in Polgar *et al.* (2014). To ensure
207 sufficient density of sampling of herbarium vouchers, this list was then filtered for species with
208 at least 10 herbarium specimens in each of the following time periods: 1900-1920, 1920-1940,
209 and 1940-1960. For each focal species, we estimated herbivory from 40 specimens collected
210 between 1900 and 1960 from Connecticut, Massachusetts, and Rhode Island, and on a minimum
211 of 10 and up to 20 species from 1960 to 2016 to capture the signature of recent climate change.

212 Unfortunately, we could not easily find equivalent data on leaf-out sensitivities for species well-
213 represented in the MNHN.

214

215 **Herbivory data collected from herbarium specimens**

216 We quantified herbivory on each herbarium voucher using a grid-based transect as described in
217 detail in recent publications (Meineke, Davis, et al., 2018; Meineke et al., 2019). Briefly, we
218 overlaid a grid with a total of 40 5 x 5-cm grid cells on each specimen. In five randomly selected
219 grid cells that were 40% or more covered in leaves, we scored the presence (1) or absence (0) of
220 herbivore chewing damage within each grid cell; a histogram of these data per species is
221 presented in Fig. S2. Chewing is the most common type of insect herbivore damage according to
222 field (Turcotte, Thomsen, et al., 2014) and herbarium studies (Meineke, Davis, et al., 2018;
223 Meineke et al., 2019) and may result from a wide range of mandibulate herbivores, including
224 Lepidoptera (caterpillars of butterflies and moths), Coleoptera (beetles), and Orthoptera

225 (grasshoppers). Our methods for quantifying herbivory are unlikely to capture insect outbreaks,
226 as heavy, and/or centralized damage tend to be avoided by collectors. Instead, our methods are
227 more likely to represent background herbivory that affects plants similarly from year to year.
228 Despite the lower intensity of this type of herbivory, it can have substantial effects on
229 photosynthesis (Zangerl et al., 2002). While there is anecdotal evidence that collectors might
230 preferentially select less damaged specimens (skewing total herbivory estimates low), we do not
231 see why the intensity of such selection would covary with temperature (see below), and previous
232 analyses on a larger sample of specimens suggests little evidence for a collector effect (Meineke
233 et al., 2019).

234

235 **Spatial, temporal, and trait-based covariates**

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

248 These time periods comfortably predate the recent anthropogenic signal of climate change (IPCC
249 2014).

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

263

264 **Modelling effects of phenology on herbivory**

265 We constructed hierarchical Bayesian regression models in Stan (Gelman et al., 2015) using the
266 *brms* package (Bürkner, 2017) in R (R Core Team, 2019) to explore the relationship between
267 herbivory and phenological sensitivity. Herbivory occurrences were modelled using a
268 hierarchical Bayesian regression fit with a zero-inflated binomial distribution. Initially, we
269 attempted to use a simple binomial error structure in our models, but the fit was poor and was

270 greatly improved by the inclusion of a zero-inflated error structure (Fig. S4). The model was
271 defined as:

272

273 *Grid cells with herbivory* ~ *overdispersed Binomial*(p_{ij} , n)

274

275 $\text{logit}(p_{ij}) = a + \beta_1 \text{phensens}_{ij} \times \beta_2 \text{mar}_{ij} + \beta_3 \text{latitude}_{ij} +$

276 $\beta_4 \text{longitude}_{ij} + \beta_5 \text{growthform}_j + \beta_6 \text{day}_{ij} +$

277 $\beta_7 \text{year}_{ij} + \beta_8 \text{firstphenday}_{ij} + u_j + u_{ij}$

278

279 Where *grid cells with herbivory* is the number of grid cells with chewing damage by mandibulate

280 herbivores p on specimen i from species j , and n is a constant representing the number of grid

281 cells examined on each specimen. We model $\text{logit}(p_{ij})$ as a function of a , the intercept, *phensens*,

282 the flowering or leaf-out sensitivity of species j depending on the specific model (see below),

283 *mar*, March mean temperature associated with specimen i of species j , *latitude*, the latitude

284 where specimen i of species j was collected, *longitude*, the longitude where specimen i of species

285 j was collected and u_i and u_{ij} , which are grouping factors (random effects) of phylogenetic

286 position and location (county-state, or Department, see below). We accounted for phylogenetic

287 relatedness among plant species using a correlation matrix inferred from the Zanne *et al.* (2014)

288 phylogeny described above. The contribution of phylogenetic effects in the fitted model were

289 estimated as the intra-class correlation (equivalent to Lynch's lambda (Lynch, 1991)) using the

290 "hypothesis" function in *brms*. We accounted for the effects of space by including location as a

291 group-level effect, specified as county-state combination for specimens collected in the USA or

292 the French 'department' for specimens collected in France. Models were fit with 2000 iterations

293 in four chains, with the initial 1000 iterations discarded after warm-up. For all models, we
294 assessed convergence (Rhat values equal to one) and model fit to the observed data using
295 posterior predictive checks in *brms*. We also calculated the variance explained using Bayesian R^2
296 as estimated in the “bayes_R2” function in *brms*.

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

311

312 **Results**

313 We recorded herbivory on a total of 1926 herbarium vouchers (Table S1). While the regions
314 captured by our herbarium sampling have significantly warmed on average, local temperatures
315 were also highly variable during the sampling period. The specimens used in our study,

316 therefore, captured a large amount of interannual temperature variability but did not experience
317 significant changes in March mean temperature over years (see Fig. S5; for all models, $p > 0.1$;
318 full statistics in Table S2).

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

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

339 Table 1a,c), but March temperature was not an important factor driving herbivory in France (Fig.
340 2b; Table 1b). Herbarium specimens collected at lower latitudes (areas associated with warmer
341 temperatures) also displayed more herbivore damage than those collected at higher latitudes
342 (Table 1), although credibility intervals tended to be large and, for French specimens,
343 substantially overlapped zero (Fig. 2b; Table 1b). We also observed evidence that herbivory was
344 greater on specimens collected in early years than on specimens collected in later years (Fig. 2),
345 but again credibility intervals tended to be large, and substantially overlapped zero in models
346 from USA specimens (Figs. 2a,c). Woody species showed marginally higher herbivory rates than
347 herbaceous species (Table 1a).

348

349 **Discussion**

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

362 costly tissue, that include higher frost risk (Chamberlain et al., 2019) and, as we show here,
363 heightened herbivore pressure.

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

380 Our findings align with other studies showing that phenological timing can affect
381 herbivory rates within species or genera (Mopper & Simberloff, 1995; Pearse, Baty, et al., 2015;
382 Pearse, Funk, et al., 2015; Pearse & Karban, 2013), and may have fitness consequences (Pearse,
383 Funk, et al., 2015). For example, valley oak (*Quercus lobata*) genotypes that leafed out early in
384 a given year also experienced higher herbivory rates in that year and reduced acorn production in

385 the following year (Pearse, Funk, et al., 2015). Our herbarium dataset provides the rare
386 opportunity to extend this framework to entire plant communities.

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

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

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

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

431 While models including flowering sensitivity included more plant species (n= 19), models
432 including leaf-out sensitivity (n=11) better captured the relationship between phenological timing
433 and herbivory, as would be expected given the direct biological relationship between leaf-out and
434 foliar insect feeding. Second, recapitulating earlier work (Meineke, Davis, et al., 2018; Meineke
435 et al., 2019), general herbivory trends match to expected patterns established in the literature on
436 plant-insect herbivore interaction strengths. For example, herbarium specimens collected later in
437 the growing season experienced more herbivory than those collected early (Meineke et al.,
438 2019), and specimens of woody species displayed greater herbivory than herbaceous species, a
439 pattern that has been widely established, e.g., (Turcotte, Davies, et al., 2014).

440 We observed a trend for increasing herbivory damage on phenologically sensitive species
441 in warmer years. With global temperatures rising, we might then expect to see increasing
442 herbivory through time (Meineke et al., 2019). It is notable, however, that in our Bayesian
443 regression, we find that, after accounting for co-variates (i.e., spring temperature and
444 phenological sensitivity), there is an overall trend toward lower herbivory intensity in recent
445 years. Other processes besides temperature change undoubtedly impact insect herbivory. Land
446 transformation (van Klink et al., 2020), succession (Jeffries et al., 2006), and pesticide use
447 (Wagner et al., 2021), among other drivers (Wagner, 2019), may affect insect herbivore
448 abundance and population dynamics over years. Recent studies have revealed evidence of
449 declines in insect abundance—the “insect apocalypse” (Goulson, 2019). Although there remains
450 some controversy surrounding these estimates (Wagner, 2019), a dramatic decline in herbivorous
451 insects—notably butterflies (Breed et al., 2013; van Strien et al., 2019; Wepprich et al., 2019),
452 which cause chewing damage in their larval phases—would obviously lead to predictions of
453 lower herbivory through time. Our results might thus inadvertently capture the ecological

454 signature of these recent biodiversity declines. Disentangling such confounding influences on
455 herbivory presents a major challenge for the future. Herbarium vouchers and biological
456 collections might contribute substantially to this effort, for example, via tracking changes in
457 plant defenses associated with herbivory (Small, 1985; Zangerl & Berenbaum, 2005) and
458 changing herbivore population dynamics through evidence of specialized damage that can be
459 attributed to particular herbivore taxa (Lees et al., 2011).

460

461 **Acknowledgements:** This project was supported by a Discovery Grant from The Natural
462 Sciences and Engineering Research Council of Canada (<http://www.nserc->
463 [crsng.gc.ca/index_eng.asp](http://www.nserc-crsng.gc.ca/index_eng.asp)) to TJD. This material is based upon work supported by the National
464 Science Foundation Postdoctoral Research Fellowship in Biology under grant no. (1611880) to
465 EKM. We thank the Harvard University Herbaria, University of British Columbia, and UC Davis
466 for institutional support.

467

468 **References**

- 469
- 470 Agrawal, A. A., Hastings, A. P., Johnson, M. T., Maron, J. L., & Salminen, J.-P. (2012). Insect
471 herbivores drive real-time ecological and evolutionary change in plant populations.
472 *Science*, 338(6103), 113–116. <https://doi.org/10.1126/science.1225977>
- 473 Aizen, M., & Patterson, W. (1995). Leaf Phenology and Herbivory Along a Temperature-
474 Gradient—A Spatial Test of the Phenological Window Hypothesis. *Journal of Vegetation*
475 *Science*, 6(4), 543–550. <https://doi.org/10.2307/3236353>
- 476 Ayres, M. P. (1993). Plant defense, herbivory, and climate change. In *Biotic interactions and*
477 *global change* (pp. 75–94). Sinauer Associates Inc., Sunderland, MA, USA.
- 478 Bale, J. S., Masters, G. J., Hodkinson, I. D., Awmack, C., Bezemer, T. M., Brown, V. K.,
479 Butterfield, J., Buse, A., Coulson, J. C., & Farrar, J. (2002). Herbivory in global climate
480 change research: Direct effects of rising temperature on insect herbivores. *Global Change*
481 *Biology*, 8(1), 1–16. <https://doi.org/10.1046/j.1365-2486.2002.00451.x>
- 482 Bartomeus, I., Ascher, J. S., Wagner, D., Danforth, B. N., Colla, S., Kornbluth, S., & Winfree, R.
483 (2011). Climate-associated phenological advances in bee pollinators and bee-pollinated
484 plants. *Proceedings of the National Academy of Sciences*, 108(51), 20645–20649.
485 <https://doi.org/10.1073/pnas.1115559108>
- 486 Bartomeus, I., Park, M. G., Gibbs, J., Danforth, B. N., Lakso, A. N., & Winfree, R. (2013).
487 Biodiversity ensures plant-pollinator phenological synchrony against climate change.
488 *Ecology Letters*, 16(11), 1331–1338. <https://doi.org/10.1111/ele.12170>
- 489 Breed, G. A., Stichter, S., & Crone, E. E. (2013). Climate-driven changes in northeastern US
490 butterfly communities. *Nature Climate Change*, 3(2), 142–145.
491 <https://doi.org/10.1038/nclimate1663>

- 492 Bürkner, P.-C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal*
493 *of Statistical Software*, 80(1), 1–28.
- 494 Chamberlain, C. J., Cook, B. I., García de Cortázar-Atauri, I., & Wolkovich, E. M. (2019).
495 Rethinking false spring risk. *Global Change Biology*, 25(7), 2209–2220.
- 496 Chuine, I., & Régnière, J. (2017). Process-Based Models of Phenology for Plants and Animals.
497 *Annual Review of Ecology, Evolution, and Systematics*, 48(1), 159–182.
498 <https://doi.org/10.1146/annurev-ecolsys-110316-022706>
- 499 Cleland, E. E., Allen, J. M., Crimmins, T. M., Dunne, J. A., Pau, S., Travers, S. E., Zavaleta, E.
500 S., & Wolkovich, E. M. (2012). Phenological tracking enables positive species responses
501 to climate change. *Ecology*, 93(8), 1765–1771. <https://doi.org/10.1890/11-1912.1>
- 502 Cleland, E. E., Chuine, I., Menzel, A., Mooney, H. A., & Schwartz, M. D. (2007). Shifting plant
503 phenology in response to global change. *Trends in Ecology & Evolution*, 22(7), 357–365.
504 <https://doi.org/10.1016/j.tree.2007.04.003>
- 505 Currano, E. D., Wilf, P., Wing, S. L., Labandeira, C. C., Lovelock, E. C., & Royer, D. L. (2008).
506 Sharply increased insect herbivory during the Paleocene-Eocene Thermal Maximum.
507 *Proceedings of the National Academy of Sciences*, 105(6), 1960–1964.
508 <https://doi.org/10.1073/pnas.0708646105>
- 509 Daru, B. H., Park, D. S., Primack, R. B., Willis, C. G., Barrington, D. S., Whitfeld, T. J., Seidler,
510 T. G., Sweeney, P. W., Foster, D. R., & Ellison, A. M. (2018). Widespread sampling
511 biases in herbaria revealed from large-scale digitization. *New Phytologist*, 217(2), 939–
512 955. <https://doi.org/10.1111/nph.14855>
- 513 Edwards, M., & Richardson, A. J. (2004). Impact of climate change on marine pelagic
514 phenology and trophic mismatch. *Nature*, 430(7002), 881–884.

515 Elzinga, J. A., Atlan, A., Biere, A., Gigord, L., Weis, A. E., & Bernasconi, G. (2007). Time after
516 time: Flowering phenology and biotic interactions. *Trends in Ecology & Evolution*, 22(8),
517 432–439. <https://doi.org/10.1016/j.tree.2007.05.006>

518 Ettinger, A. K., Gee, S., & Wolkovich, E. M. (2018). Phenological sequences: How early-season
519 events define those that follow. *American Journal of Botany*, 105(10), 1771–1780.
520 <https://doi.org/10.1002/ajb2.1174>

521 Farrell, B. D., Dussourd, D. E., & Mitter, C. (1991). Escalation of plant defense: Do latex and
522 resin canals spur plant diversification? *The American Naturalist*, 138(4), 881–900.

523 Feeny, P. (1970). Seasonal Changes in Oak Leaf Tannins and Nutrients as a Cause of Spring
524 Feeding by Winter Moth Caterpillars. *Ecology*, 51(4), 565–581.
525 <https://doi.org/10.2307/1934037>

526 Fitter, A. H., & Fitter, R. (2002). Rapid changes in flowering time in British plants. *Science*,
527 296(5573), 1689–1691. <https://doi.org/10.1126/science.1071617>

528 Forister, M. L., Novotny, V., Panorska, A. K., Baje, L., Basset, Y., Butterill, P. T., Cizek, L.,
529 Coley, P. D., Dem, F., & Diniz, I. R. (2015). The global distribution of diet breadth in
530 insect herbivores. *Proceedings of the National Academy of Sciences*, 112(2), 442–447.
531 <https://doi.org/10.1073/pnas.1423042112>

532 Forkner, R. E., Marquis, R. J., Lill, J. T., & Corff, J. L. (2008). Timing is everything?
533 Phenological synchrony and population variability in leaf-chewing herbivores of
534 Quercus. *Ecological Entomology*, 33(2), 276–285. [https://doi.org/10.1111/j.1365-
535 2311.2007.00976.x](https://doi.org/10.1111/j.1365-2311.2007.00976.x)

536 Fridley, J. D. (2012). Extended leaf phenology and the autumn niche in deciduous forest
537 invasions. *Nature*, 485(7398), 359–362. <https://doi.org/10.1038/nature11056>

- 538 Futuyma, D. J., & Agrawal, A. A. (2009). Macroevolution and the biological diversity of plants
539 and herbivores. *Proceedings of the National Academy of Sciences*, *106*(43), 18054–
540 18061. <https://doi.org/10.1073/pnas.0904106106>
- 541 García, M. B., & Ehrlén, J. (2002). Reproductive effort and herbivory timing in a perennial herb:
542 Fitness components at the individual and population levels. *American Journal of Botany*,
543 *89*(8), 1295–1302. <https://doi.org/10.3732/ajb.89.8.1295>
- 544 Gelman, A., Lee, D., & Guo, J. (2015). Stan: A probabilistic programming language for
545 Bayesian inference and optimization. *Journal of Educational and Behavioral Statistics*,
546 *40*(5), 530–543. <https://doi.org/10.3102/1076998615606113>
- 547 Gillespie, M. A., Jónsdóttir, I. S., Hodkinson, I. D., & Cooper, E. J. (2013). Aphid–willow
548 interactions in a high Arctic ecosystem: Responses to raised temperature and goose
549 disturbance. *Global Change Biology*, *19*(12), 3698–3708.
550 <https://doi.org/10.1111/gcb.12284>
- 551 Goulson, D. (2019). The insect apocalypse, and why it matters. *Current Biology*, *29*(19), R967–
552 R971. <https://doi.org/10.1016/j.cub.2019.06.069>
- 553 Hansen, B. B., Grøtan, V., Herfindal, I., & Lee, A. M. (2020). The Moran effect revisited:
554 Spatial population synchrony under global warming. *Ecography*, *43*(11), 1591–1602.
- 555 Havko, N. E., Das, M. R., McClain, A. M., Kapali, G., Sharkey, T. D., & Howe, G. A. (2020).
556 Insect herbivory antagonizes leaf cooling responses to elevated temperature in tomato.
557 *Proceedings of the National Academy of Sciences*, *117*(4), 2211–2217.
- 558 Heberling, J. M., & Isaac, B. L. (2017). Herbarium specimens as exaptations: New uses for old
559 collections. *American Journal of Botany*, *104*(7), 963–965.
560 <https://doi.org/10.3732/ajb.1700125>

- 561 Hegland, S. J., Nielsen, A., Lázaro, A., Bjerknes, A. L., & Totland, Ø. (2009). How does climate
562 warming affect plant-pollinator interactions? *Ecology Letters*, *12*(2), 184–195.
563 <https://doi.org/10.1111/j.1461-0248.2008.01269.x>
- 564 Hunter, A. F., & Elkinton, J. S. (2000). Effects of Synchrony with Host Plant on Populations of a
565 Spring-Feeding Lepidopteran. *Ecology*, *81*(5), 1248–1261. [https://doi.org/10.1890/0012-9658\(2000\)081\[1248:EOSWHP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[1248:EOSWHP]2.0.CO;2)
- 566
- 567 Hunter, M. D. (1992). A variable insect–plant interaction: The relationship between tree budburst
568 phenology and population levels of insect herbivores among trees. *Ecological*
569 *Entomology*, *17*(1), 91–95. <https://doi.org/10.1111/j.1365-2311.1992.tb01046.x>
- 570 Intergovernmental Panel on Climate Change (Ed.). (2015). *Climate change 2014: Synthesis*
571 *report*. Intergovernmental Panel on Climate Change.
- 572 Jeffries, J. M., Marquis, R. J., & Forkner, R. E. (2006). Forest age influences oak insect
573 herbivore community structure, richness, and density. *Ecological Applications*, *16*(3),
574 901–912.
- 575 Kharouba, H. M., Ehrlén, J., Gelman, A., Bolmgren, K., Allen, J. M., Travers, S. E., &
576 Wolkovich, E. M. (2018). Global shifts in the phenological synchrony of species
577 interactions over recent decades. *Proceedings of the National Academy of Sciences*,
578 *115*(20), 5211–5216. <https://doi.org/10.1073/pnas.1714511115>
- 579 Kharouba, H. M., & Vellend, M. (2015). Flowering time of butterfly nectar food plants is more
580 sensitive to temperature than the timing of butterfly adult flight. *Journal of Animal*
581 *Ecology*, *84*(5), 1311–1321. <https://doi.org/10.1111/1365-2656.12373>
- 582 Labandeira, C. C., Dilcher, D. L., Davis, D. R., & Wagner, D. L. (1994). Ninety-seven million
583 years of angiosperm-insect association: Paleobiological insights into the meaning of

584 coevolution. *Proceedings of the National Academy of Sciences*, 91(25), 12278–12282.
585 <https://doi.org/10.1073/pnas.91.25.12278>

586 Lees, D. C., Lack, H. W., Rougerie, R., Hernandez-Lopez, A., Raus, T., Avtzis, N. D., Augustin,
587 S., & Lopez-Vaamonde, C. (2011). Tracking origins of invasive herbivores through
588 herbaria and archival DNA: The case of the horse-chestnut leaf miner. *Frontiers in*
589 *Ecology and the Environment*, 9(6), 322–328. <https://doi.org/10.1890/100098>

590 Lemoine, N. P., Doublet, D., Salminen, J.-P., Burkepille, D. E., & Parker, J. D. (2017). Responses
591 of plant phenology, growth, defense, and reproduction to interactive effects of warming
592 and insect herbivory. *Ecology*, 98(7), 1817–1828. <https://doi.org/10.1002/ecy.1855>

593 Liu, Y., Reich, P. B., Li, G., & Sun, S. (2011). Shifting phenology and abundance under
594 experimental warming alters trophic relationships and plant reproductive capacity.
595 *Ecology*, 92(6), 1201–1207. <https://doi.org/10.1890/10-2060.1>

596 Lynch, M. (1991). Methods for the Analysis of Comparative Data in Evolutionary Biology.
597 *Evolution*, 45(5), 1065–1080. <https://doi.org/10.1111/j.1558-5646.1991.tb04375.x>

598 Meineke, E. K., Classen, A. T., Sanders, N. J., & Jonathan Davies, T. (2019). Herbarium
599 specimens reveal increasing herbivory over the past century. *Journal of Ecology*, 107(1),
600 105–117. <https://doi.org/10.1111/1365-2745.13057>

601 Meineke, E. K., Davies, T. J., Daru, B. H., & Davis, C. C. (2018). Biological collections for
602 understanding biodiversity in the Anthropocene. *Philosophical Transactions of the Royal*
603 *Society B: Biological Sciences*, 374(1763), 20170386.
604 <https://doi.org/10.1098/rstb.2017.0386>

- 605 Meineke, E. K., Davis, C. C., & Davies, T. J. (2018). The unrealized potential of herbaria for
606 global change biology. *Ecological Monographs*, 88(4), 505–525.
607 <https://doi.org/10.1002/ecm.1307>
- 608 Menzel, A., & Fabian, P. (1999). Growing season extended in Europe. *Nature*, 397(6721), 659.
609 <https://doi.org/10.1038/17709>
- 610 Meyer, C., Weigelt, P., & Kreft, H. (2016). Multidimensional biases, gaps and uncertainties in
611 global plant occurrence information. *Ecology Letters*, 19(8), 992–1006.
612 <https://doi.org/10.1111/ele.12624>
- 613 Mopper, S., & Simberloff, D. (1995). Differential Herbivory in an Oak Population—The Role of
614 Plant Phenology and Insect Performance. *Ecology*, 76(4), 1233–1241.
615 <https://doi.org/10.2307/1940930>
- 616 Nability, P. D., Zavala, J. A., & DeLucia, E. H. (2009). Indirect suppression of photosynthesis on
617 individual leaves by arthropod herbivory. *Annals of Botany*, 103(4), 655–663.
- 618 Park, D. S., & Davis, C. C. (2017). Implications and alternatives of assigning climate data to
619 geographical centroids. *Journal of Biogeography*, 44(10), 2188–2198.
620 <https://doi.org/10.1111/jbi.13029>
- 621 Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual*
622 *Review of Ecology, Evolution, and Systematics*, 37, 637–669.
623 <https://doi.org/10.1146/annurev.ecolsys.37.091305.110100>
- 624 Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts
625 across natural systems. *Nature*, 421(6918), 37–42. <https://doi.org/10.1038/nature01286>

626 Pearse, I. S., Baty, J. H., Herrmann, D., Sage, R., & Koenig, W. D. (2015). Leaf phenology
627 mediates provenance differences in herbivore populations on valley oaks in a common
628 garden. *Ecological Entomology*, *40*(5), 525–531. <https://doi.org/10.1111/een.12219>

629 Pearse, I. S., Funk, K. A., Kraft, T. S., & Koenig, W. D. (2015). Lagged effects of early-season
630 herbivores on valley oak fecundity. *Oecologia*, *178*(2), 361–368.
631 <https://doi.org/10.1007/s00442-014-3193-2>

632 Pearse, I. S., & Karban, R. (2013). Leaf drop affects herbivory in oaks. *Oecologia*, *173*(3), 925–
633 932. <https://doi.org/10.1007/s00442-013-2689-5>

634 Perez, T. M., Rodriguez, J., & Mason Heberling, J. (2020). Herbarium-based measurements
635 reliably estimate three functional traits. *American Journal of Botany*, *107*(10), 1457–
636 1464. <https://doi.org/10.1002/ajb2.1535>

637 Piao, S., Friedlingstein, P., Ciais, P., Viovy, N., & Demarty, J. (2007). Growing season extension
638 and its impact on terrestrial carbon cycle in the Northern Hemisphere over the past 2
639 decades. *Global Biogeochemical Cycles*, *21*(3). <https://doi.org/10.1029/2006GB002888>

640 Polgar, C., Gallinat, A., & Primack, R. B. (2014). Drivers of leaf-out phenology and their
641 implications for species invasions: Insights from Thoreau’s Concord. *New Phytologist*,
642 *202*(1), 106–115. <https://doi.org/10.1111/nph.12647>

643 Post, E., & Forchhammer, M. C. (2007). Climate change reduces reproductive success of an
644 Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal
645 Society B: Biological Sciences*, *363*(1501), 2367–2373.
646 <https://doi.org/10.1098/rstb.2007.2207>

- 647 Pureswaran, D. S., Neau, M., Marchand, M., De Grandpré, L., & Kneeshaw, D. (2019).
648 Phenological synchrony between eastern spruce budworm and its host trees increases
649 with warmer temperatures in the boreal forest. *Ecology and Evolution*, 9(1), 576–586.
- 650 R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation
651 for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- 652 Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., & Pounds, J. A. (2003).
653 Fingerprints of global warming on wild animals and plants. *Nature*, 421(6918), 57–60.
654 <https://doi.org/10.1038/nature01333>
- 655 Rosenthal, J. P., & Kotanen, P. M. (1994). Terrestrial plant tolerance to herbivory. *Trends in*
656 *Ecology & Evolution*, 9(4), 145–148. [https://doi.org/10.1016/0169-5347\(94\)90180-5](https://doi.org/10.1016/0169-5347(94)90180-5)
- 657 Rosenzweig, C., Karoly, D., Vicarelli, M., Neofotis, P., Wu, Q., Casassa, G., Menzel, A., Root,
658 T. L., Estrella, N., Seguin, B., Tryjanowski, P., Liu, C., Rawlins, S., & Imeson, A.
659 (2008). Attributing physical and biological impacts to anthropogenic climate change.
660 *Nature*, 453(7193), 353–357. <https://doi.org/10.1038/nature06937>
- 661 Schwartz, M. D. (2003). *Phenology: An integrative environmental science*. Kluwer Academic
662 Publishers.
- 663 Schwartzberg, E. G., Jamieson, M. A., Raffa, K. F., Reich, P. B., Montgomery, R. A., &
664 Lindroth, R. L. (2014). Simulated climate warming alters phenological synchrony
665 between an outbreak insect herbivore and host trees. *Oecologia*, 175(3), 1041–1049.
666 <https://doi.org/10.1007/s00442-014-2960-4>
- 667 Singer, M. C., & Parmesan, C. (2010). Phenological asynchrony between herbivorous insects
668 and their hosts: Signal of climate change or pre-existing adaptive strategy? *Philosophical*

669 *Transactions of the Royal Society B: Biological Sciences*, 365(1555), 3161–3176.
670 <https://doi.org/10.1098/rstb.2010.0144>

671 Small, E. (1985). Insect pests and the evolution of defensive glandular trichomes in alfalfa.
672 *Canadian Journal of Plant Science*, 65(3), 589–596. <https://doi.org/10.4141/cjps85-081>

673 Springate, D. A., & Kover, P. X. (2014). Plant responses to elevated temperatures: A field study
674 on phenological sensitivity and fitness responses to simulated climate warming. *Global*
675 *Change Biology*, 20(2), 456–465. <https://doi.org/10.1111/gcb.12430>

676 Thackeray, S. J., Sparks, T. H., Frederiksen, M., Burthe, S., Bacon, P. J., Bell, J. R., Botham, M.
677 S., Brereton, T. M., Bright, P. W., Carvalho, L., Clutton-Brock, T., Dawson, A.,
678 Edwards, M., Elliott, J. M., Harrington, R., Johns, D., Jones, I. D., Jones, J. T., Leech, D.
679 I., ... Wanless, S. (2010). Trophic level asynchrony in rates of phenological change for
680 marine, freshwater and terrestrial environments. *Global Change Biology*, 16(12), 3304–
681 3313. <https://doi.org/10.1111/j.1365-2486.2010.02165.x>

682 Turcotte, M. M., Davies, T. J., Thomsen, C. J., & Johnson, M. T. (2014). Macroecological and
683 macroevolutionary patterns of leaf herbivory across vascular plants. *Proceedings of the*
684 *Royal Society B: Biological Sciences*, 281(1787), 20140555.
685 <https://doi.org/10.1098/rspb.2014.0555>

686 Turcotte, M. M., Thomsen, C. J., Broadhead, G. T., Fine, P. V., Godfrey, R. M., Lamarre, G. P.,
687 Meyer, S. T., Richards, L. A., & Johnson, M. T. (2014). Percentage leaf herbivory across
688 vascular plant species: Ecological Archives E095-065. *Ecology*, 95(3), 788–788.
689 <https://doi.org/10.1890/13-1741.1>

- 690 van Klink, R., Bowler, D. E., Gongalsky, K. B., Swengel, A. B., Gentile, A., & Chase, J. M.
691 (2020). *Meta-analysis reveals declines in terrestrial but increases in freshwater insect*
692 *abundances*. 4.
- 693 van Strien, A. J., van Swaay, C. A., van Strien-van Liempt, W. T., Poot, M. J., & WallisDeVries,
694 M. F. (2019). Over a century of data reveal more than 80% decline in butterflies in the
695 Netherlands. *Biological Conservation*, 234, 116–122.
696 <https://doi.org/10.1016/j.biocon.2019.03.023>
- 697 Visser, M. E., & Gienapp, P. (2019). Evolutionary and demographic consequences of
698 phenological mismatches. *Nature Ecology & Evolution*, 3(6), 879–885.
699 <https://doi.org/10.1038/s41559-019-0880-8>
- 700 Visser, M. E., & Holleman, L. J. (2001). Warmer springs disrupt the synchrony of oak and
701 winter moth phenology. *Proceedings of the Royal Society of London. Series B: Biological*
702 *Sciences*, 268(1464), 289–294.
- 703 Visser, M. E., Holleman, L. J. M., & Gienapp, P. (2006). Shifts in caterpillar biomass phenology
704 due to climate change and its impact on the breeding biology of an insectivorous bird.
705 *Oecologia*, 147(1), 164–172. <https://doi.org/10.1007/s00442-005-0299-6>
- 706 Wagner, D. L. (2019). Insect declines in the Anthropocene. *Annual Review of Entomology*, 65,
707 457–480. <https://doi.org/10.1146/annurev-ento-011019-025151>
- 708 Wagner, D. L., Fox, R., Salcido, D. M., & Dyer, L. A. (2021). A window to the world of global
709 insect declines: Moth biodiversity trends are complex and heterogeneous. *Proceedings of*
710 *the National Academy of Sciences*, 118(2).

- 711 Walther, G.-R. (2010). Community and ecosystem responses to recent climate change.
712 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1549),
713 2019–2024. <https://doi.org/10.1098/rstb.2010.0021>
- 714 Wepprich, T., Adrion, J., Ries, L., Wiedmann, J., & Haddad, N. (2019). Butterfly abundance
715 declines over 20 years of systematic monitoring in Ohio, USA. *PLoS ONE*, 14(7),
716 613786. <https://doi.org/10.1371/journal.pone.0216270>
- 717 Wilf, P., Labandeira, C. C., Johnson, K. R., Coley, P. D., & Cutter, A. D. (2001). Insect
718 herbivory, plant defense, and early Cenozoic climate change. *Proceedings of the National
719 Academy of Sciences*, 98(11), 6221–6226. <https://doi.org/10.1073/pnas.111069498>
- 720 Willis, C. G., Ruhfel, B., Primack, R. B., Miller-Rushing, A. J., & Davis, C. C. (2008).
721 Phylogenetic patterns of species loss in Thoreau’s woods are driven by climate change.
722 *Proceedings of the National Academy of Sciences*, 105(44), 17029–17033.
723 <https://doi.org/10.1073/pnas.0806446105>
- 724 Willmer, P. (2012). Ecology: Pollinator–plant synchrony tested by climate change. *Current
725 Biology*, 22(4), R131–R132. <https://doi.org/10.1016/j.cub.2012.01.009>
- 726 Wolkovich, E. M., Cook, B. I., Allen, J. M., Crimmins, T. M., Betancourt, J. L., Travers, S. E.,
727 Pau, S., Regetz, J., Davies, T. J., Kraft, N. J. B., Ault, T. R., Bolmgren, K., Mazer, S. J.,
728 McCabe, G. J., McGill, B. J., Parmesan, C., Salamin, N., Schwartz, M. D., & Cleland, E.
729 E. (2012). Warming experiments underpredict plant phenological responses to climate
730 change. *Nature*, 485(7399), 494–497. <https://doi.org/10.1038/nature11014>
- 731 Wolkovich, E. M., Davies, T. J., Schaefer, H., Cleland, E. E., Cook, B. I., Travers, S. E., Willis,
732 C. G., & Davis, C. C. (2013). Temperature-dependent shifts in phenology contribute to

733 the success of exotic species with climate change. *American Journal of Botany*, 100(7),
734 1407–1421. <https://doi.org/10.3732/ajb.1200478>

735 Xia, J., Chen, J., Piao, S., Ciais, P., Luo, Y., & Wan, S. (2014). Terrestrial carbon cycle affected
736 by non-uniform climate warming. *Nature Geoscience*, 7(3), 173–180.
737 <https://doi.org/10.1038/ngeo2093>

738 Zangerl, A. R., & Berenbaum, M. R. (2005). Increase in toxicity of an invasive weed after
739 reassociation with its coevolved herbivore. *Proceedings of the National Academy of*
740 *Sciences*, 102(43), 15529–15532. <https://doi.org/10.1073/pnas.0507805102>

741 Zangerl, A. R., J. G. Hamilton, Miller, T. J., Crofts, A. R., Oxborough, K., Berenbaum, M. R., &
742 de Lucia, E. H. (2002). Impact of folivory on photosynthesis is greater than the sum of its
743 holes. *Proceedings of the National Academy of Sciences*, 99(2), 1088–1091.
744 <https://doi.org/10.1073/pnas.022647099>

745 Zanne, A. E., Tank, D. C., Cornwell, W. K., Eastman, J. M., Smith, S. A., FitzJohn, R. G.,
746 McGlenn, D. J., O'Meara, B. C., Moles, A. T., Reich, P. B., Royer, D. L., Soltis, D. E.,
747 Stevens, P. F., Westoby, M., Wright, I. J., Aarssen, L., Bertin, R. I., Calaminus, A.,
748 Govaerts, R., ... Beaulieu, J. M. (2014). Three keys to the radiation of angiosperms into
749 freezing environments. *Nature*, 506(7486), 89–92. <https://doi.org/10.1038/nature12872>

750
751

752 **Figure Captions**

753

754 **Fig. 1.** Conceptual diagram representing potential consequences of warming-induced

755 phenological shifts on insect damage to leaves. (A) Phenologically sensitive plant species

756 advance leaf-out in warmer years, but herbivores fail to advance. As a result, phenologically

757 sensitive plant species have an enemy-free window in warm years. Generally, we hold this as a

758 possibility because across diverse taxa, lower trophic levels often advance their phenology more

759 than higher trophic levels (Thackeray et al., 2010). (B) Highly sensitive plant species respond to

760 climate warming by leafing out early in the growing season and the herbivores that consume

761 them also emerge early (e.g., Visser et al., 2001). As a result, more sensitive plant species may

762 experience more herbivory in early springs because the time period in which they are exposed to

763 herbivores is lengthened, though effects on herbivory might be idiosyncratic among plant species

764 due to concurrent changes in predation or disease pressure on key herbivores, the length of time

765 it takes for plants to accumulate defenses, or other variables unaccounted for that shift in

766 response to climate change (Feeny, 1970; A. F. Hunter & Elkinton, 2000; M. D. Hunter, 1992).

767 (C) This scenario is the same as (B) but instead of herbivores that have historically attacked a

768 given plant species, novel herbivores are present in mandibulate life stages to eat plant species

769 that leaf out earlier in warmer years. Herbivory may be exacerbated if plants have no coevolved

770 defenses to the novel herbivore.

771

772 **Fig. 2.** Model estimates showing effects of time, space, and environmental variables on insect

773 damage to plants. Predicted effects of modelled variables on insect herbivory. The subset of

774 variables here displayed important effects on herbivory in at least one of the three models. Bold

775 lines represent 80% credibility intervals, and narrow lines represent 95% credibility intervals.

776 Shading indicates the interaction term between spring temperature and phenological sensitivity.

777 a-b include the effect of flowering sensitivity on the relationship between early spring
778 temperature and insect herbivore damage to plants (March mean temp. \times flowering sensitivity) in
779 (A) the northeastern United States and (B). congeneric species in France. (C) includes the effect
780 of leaf-out sensitivity on the relationship between early spring temperature and insect herbivore
781 damage to plants (March mean temp. \times leaf-out sensitivity) in the northeastern United
782 States. “FS” refers to flowering sensitivity to temperature, and “LS” refers to leaf-out sensitivity.

783

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

793

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

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

804

805 **Table**

806 **Table 1.** Bayesian models of insect chewing herbivory quantified on herbarium specimens.

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

814 *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

815

816 *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

817

818

819

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

Variable	β_{avg}	SE	2.5%	97.5%	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

820

821

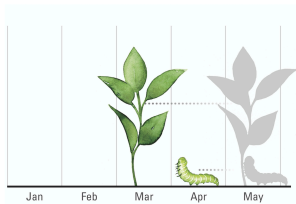
822

823

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

(a) Escape from herbivory:

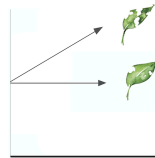
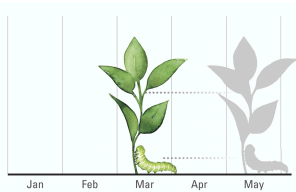
Phenologically sensitive plants
leaf out early, but herbivores
do not 'keep up'.



(b)

**Status quo or
extended season:**

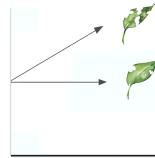
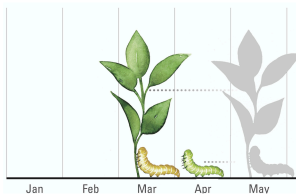
Phenologically sensitive plants
leaf-out early, and herbivores
also emerge early.



(c)

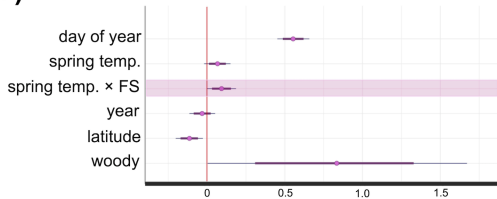
Novel interaction(s):

Phenologically sensitive plants
leaf out early, herbivores do not
'keep up', but novel herbivore(s)
are present.

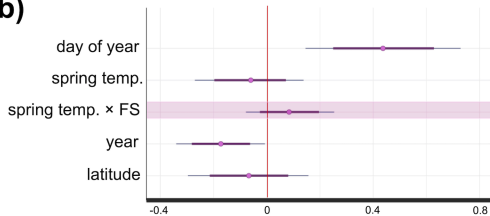




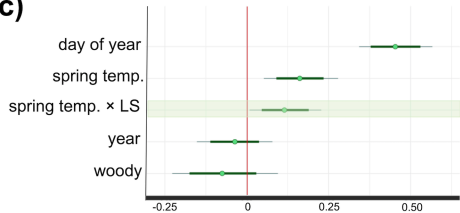
(a)



(b)

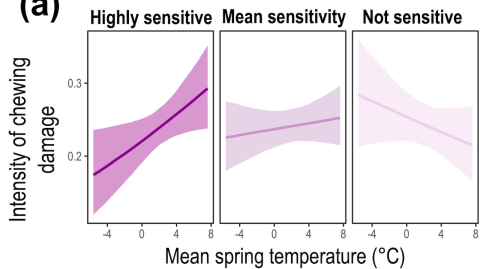


(c)

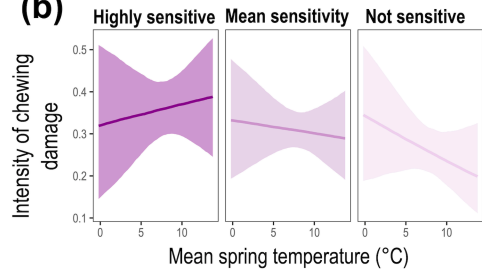




(a)



(b)



(c)

