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3 **Title:** Distinct latitudinal patterns of shifting spring phenology across the Appalachian Trail
4 Corridor

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26 **Abstract**

27 Warming associated with climate change will likely continue to advance the onset of
28 spring phenology for many forest plants across the eastern United States. Understory forbs and
29 spring ephemerals which fix a disproportionate amount of carbon during spring may be
30 negatively affected by earlier canopy closure (i.e., phenological windows), however, information
31 on the spatial patterns of phenological change for these communities is still lacking. To assess
32 the potential for changes in spring phenological windows we synthesized observations from the
33 Appalachian Mountain Club's (AMC) Mountain Watch (MW) project, the National Phenology
34 Network (NPN), and AMC's iNaturalist projects between 2004 and 2022 ($n = 118,250$) across
35 the length of the Appalachian Trail (AT) Corridor (34°N - 46°N latitude). We used hierarchical
36 Bayesian modeling to examine the sensitivity of day of year of flowering and leaf-out for 11
37 understory species and 14 canopy tree species to mean spring temperature (April-June). We
38 conducted analyses across the AT Corridor, partitioned by regions of 4° latitude (South, Mid-
39 Atlantic, and North). Spring phenologies for both understory plants and canopy trees advanced
40 with warming (~ 6 days/ $^{\circ}\text{C}$ and ~ 3 days/ $^{\circ}\text{C}$, respectively). However, sensitivity of each group
41 varied by latitude, with phenology of trees and understory plants advancing to a greater degree in
42 the mid-Atlantic region (~ 10 days/ $^{\circ}\text{C}$) than the southern or northern regions (~ 5 days/ $^{\circ}\text{C}$). While
43 we find evidence that phenological windows remain stable in southern and mid-Atlantic portions
44 of the AT, we observed an expansion of the spring phenological window in the north where there
45 was greater understory temperature sensitivity compared to trees (~ 1.6 days/ $^{\circ}\text{C}$). Our analyses
46 indicate differential sensitivity of forest plant phenology to potential warming across a large
47 latitudinal gradient in the eastern United States. Further, evidence for a temperature-driven
48 expansion of the spring phenological window suggests a potential beneficial effect for understory
49 plants, although phenological mismatch with potential pollinators is possible. Using various
50 extensive citizen-science derived datasets allows us to synthesize regional- and continental-scale
51 data to explore spatial and temporal trends in spring phenology related to warming. Such data
52 can help to standardize approaches in phenological research and its application to forest climate
53 resiliency.

54

55 **Introduction**

56 *Spring phenology and changing climate*

57 Phenology represents the timing of critical life events for plants, both over their entire
58 lifespan and on an annual cycle (see Table 1 for definitions of important terms used throughout
59 this article; Cleland et al., 2007; Piao et al., 2019). The timing of events, such as flowering, bud-
60 break, fruiting, and leaf senescence, and the synchronicity between these events and important
61 climate and biotic interactions (pollination, seed dispersal, etc.) can dictate the performance (i.e.,
62 fitness) of plant individuals or even entire populations (Aerts et al., 2006). For example, spring
63 flowering timing of understory ephemerals in eastern North America is beneficial for plants

64 when synchronous with the peak activity of generalist insect pollinators, and when occurring
65 after late-season frosts (Neufeld and Young, 2003; Inouye, 2008; Rafferty and Ives, 2011;
66 Ettinger et al., 2018). In the former case, plant reproduction is enhanced through specific
67 flowering phenology, and in the latter, plant growth and survival are improved when flowering
68 avoids freezing temperatures. Phenological events are controlled tightly by physiological
69 mechanisms which rely on environmental cues like temperature and photoperiod (Neufeld and
70 Young, 2003; Gilliam, 2007; Wang et al., 2020; Moon et al., 2021).

71 In seasonal temperate forests, understory plants, which include spring ephemerals,
72 perennial forbs, shrubs, and tree seedlings, spend the majority of the growing season in low-light
73 conditions (Gilliam, 2007). To compensate, many of these species undergo bud break and leaf
74 expansion (referred to as leaf-out) prior to full canopy closure in the spring (Neufeld and Young,
75 2003; Lee and Ibanez, 2021a). In an environment with such high light-availability, understory
76 species can fix the majority of their annual carbon budget in this time period, in some cases up to
77 80-90% (Kudo et al., 2008; Augspurger and Salk, 2017; Heberling et al., 2018; Lee and Ibanez,
78 2021b). Thus, the brief period of time (referred to as the phenological window) between
79 understory leaf-out and canopy leaf-out is essential for understory plant performance (Heberling
80 et al., 2019).

81 Given the tight coupling of spring phenology and climate, warming caused by climate
82 change could alter the dynamics of the phenological window in several ways (Figure 1).
83 Importantly, current evidence suggests that different plant functional groups (understory
84 herbaceous plants and some shrubs *vs.* canopy trees) respond to different sets of environmental
85 cues, meaning that spring phenology of each could be altered asynchronously given accelerating
86 climate change and other global change drivers (Richardson and O’Keefe, 2009; Lee et al., 2022;
87 Alecrim et al., 2022; Miller et al., 2023). For instance, canopy trees may be more responsive to
88 air temperature (directly influenced by warming), while understory species may be relatively
89 more sensitive to soil temperature and snow depth (Zohner et al., 2016; Jánosi et al., 2020). In a
90 situation where canopy closure advances with air temperature increases at a greater rate than
91 understory leaf-out, understory species may suffer from lower photosynthetic rates leading to
92 reduced carbon gain, which may in turn have ecosystem-level consequences (Beard et al., 2019;
93 Heberling et al., 2019). Monitoring the phenological response of both forest canopy trees and

94 understory plants is essential for understanding the risks posed by climate change in these
95 systems.

96 *Contrasting patterns of phenological shifts*

97 Recent findings in eastern North America have illustrated greater advances of spring
98 phenology for canopy trees compared to spring-blooming understory herbaceous species over a
99 160-year period, leading to a potential future understory carbon budget loss of 12-26% from
100 increased shading (Heberling et al., 2019). Another study estimating spring phenology from
101 herbarium records came to similar conclusions for forests in eastern North America, although the
102 spring phenological window remained stable with warming in European and East Asian forests
103 (Lee et al., 2022). However, both Ge et al. (2015) and Alecrim et al., (2022) reached the opposite
104 conclusion, finding an expansion of the spring phenological window within forests in China and
105 the eastern United states, respectively, which, barring other phenological mismatches (i.e., with
106 pollinators), could be a net positive for understory species. Thus, based on conflicting evidence
107 there is no consensus on whether trees or understory plants are advancing their phenology more
108 strongly in response to climate change.

109 These recent conflicting findings may be the result of challenges stemming from the high
110 degree of environmental, geographic, genetic, and methodological variation encountered. For
111 example, higher-latitude regions are warming faster than others (particularly in spring and
112 winter), which could suggest greater magnitudes of phenological change over time in those
113 locations if species' phenologies are responding principally to temperature (Rice et al., 2018;
114 Montgomery et al., 2020). However, population-level intraspecific variation in phenological
115 temperature sensitivity may serve to blunt these responses (McDonough MacKenzie et al., 2018;
116 2019). Additionally, environmental variables both at a single site and across a wide geographic
117 range, such as precipitation, elevation, and edaphic factors, could also affect how species track a
118 changing climate (Du et al., 2020; Alecrim et al., 2022). This is particularly true given well-
119 established geographical patterns, such as Hopkins' Bioclimatic Law which hypothesizes a 4-day
120 shift in phenological events for every 1° latitude north, 5° longitude west, and 120 m increase in
121 elevation (Hopkins, 1920). Additionally, the diversity of phenological data used to estimate the
122 spring phenological window (i.e., wildflower leaf-out vs. flowering, herbaria records vs. direct

123 observation vs. experimental manipulation) could lead to different conclusions (Wolkovich et al.,
124 2012; Heberling et al., 2019; Alecrim et al., 2022; Lee et al., 2022). To help resolve these
125 discrepancies we need spatially and temporally extensive, multi-sourced phenological datasets
126 comprised of different functional groups that represent variation in climate and topography
127 across a large geographic area.

128 *Appalachian Trail Mega-transect and citizen science*

129 The Appalachian Trail (AT) Corridor and its surrounding 250,000 acres of federally
130 protected lands form the AT Mega-transect (Cohn, 2008). This corridor harbors rare, threatened,
131 and endangered species, encompasses important water resources, and shelters a high diversity of
132 wildlife (Cohn, 2008). The AT's north-south alignment across 14 states represents a lengthy
133 (12°) latitudinal gradient within the eastern United States and offers an ideal setting for collecting
134 relevant phenological data on a continental scale (Wang, 2020a; Wang, 2020b). Threats to the
135 environment of the AT—from encroaching development, acid rain and air pollution, invasive
136 species, polluted water, and climate change—represent threats to the health of everyone
137 downwind and downstream of the AT, roughly one-third of the U.S. population (McKinley et al.,
138 2019; Burns et al., 2020). Thus, the AT Corridor thus serves as an excellent monitoring nexus for
139 environmental conditions that directly affect more than 120 million Americans (McKinley et al.,
140 2019). The dense population and abundant recreational opportunities near and within the AT
141 Mega-transect also allow for ample community research engagement.

142 Community science, or citizen science, is the practice of engaging the community to
143 participate and collaborate in scientific research (Wandersman, 2003; Tebes, 2005; Cooper et al.,
144 2021). This method of data collection is a useful tool to expand spatial coverage of monitoring
145 projects that would be otherwise hindered by funding and resources. Additionally, community
146 scientists can help directly support conservation efforts, and build meaningful connections to
147 their community and natural environment (Bonney et al. 2016). With long-term phenology
148 monitoring supplemented with thousands of community scientist observations through platforms
149 like iNaturalist (Table 1), changes and shifts in phenological responses to warming can be
150 identified along the AT Corridor (Nugent, 2018; Soroye et al., 2022). Observing plant phenology

151 along the AT may allow us to better account for the high spatial and environmental variability
152 common in studies investigating shifting phenology with climate.

153 *Study questions*

154 Given the uncertainty around the direction and magnitude of changes to the spring
155 phenological window under a changing climate, as well as the need to understand the effects of
156 warming on forests within the AT Corridor, it is imperative that we use spatially extensive
157 phenological datasets. Using data from the Appalachian Mountain Club's (AMC) Mountain
158 Watch (MW) Project, National Phenology Network (NPN), and iNaturalist, we first determined
159 what climate or landscape factors are relevant drivers of spring phenology for our focal species
160 (14 canopy tree and 11 understory species). Using this information, we asked, (Q1) is spring
161 phenology of canopy trees and understory forbs and shrubs advancing with warming, (Q2) and if
162 so, are there differences in phenological sensitivity to temperature between these groups (i.e.,
163 causing a phenological mismatch)? We also asked (Q3) are there differences in the magnitude of
164 phenological shifts across the length of the AT corridor (~12° latitude) and by individual taxa?

165 **Methods**

166 *Study region*

167 Our study area includes all temperate broadleaf forests within HUC10 (U.S. Geological
168 Survey hydrological units, <https://irma.nps.gov/DataStore/Reference/Profile/2184124>)
169 watersheds that intersect the Appalachian Trail and surrounding Corridor. Temperate forests of
170 eastern North America are characterized by seasonality, with high light penetrating to the forest
171 floor in the shoulder seasons (early spring and late fall), and low light under closed tree canopy
172 during warmer months in the growing season (down to 1-5% canopy openness, Beeles et al.,
173 2022). Northern hardwood communities comprising sugar maple (*Acer saccharum*) and
174 American beech (*Fagus grandifolia*) dominate northern AT regions, while oak-hickory forests
175 (*Quercus sp.* and *Carya sp.*) are common along the southern AT within lower elevations
176 (Tourville et al., 2022; Janowiak et al., 2018). At higher elevations, evergreen montane spruce-fir
177 forests proliferate, although these do not display the same seasonality as lower-elevation
178 broadleaf forests. In the understory, herbaceous forbs, including spring ephemerals such as

179 *Dicentra sp. and Erythronium sp.*, shrubs such as *Viburnum sp.*, and tree seedlings of overhead
180 canopy species are common (Heberling et al., 2019; Tourville et al., 2022).

181 The AT is the longest footpath in the world (~2,190 miles), traveling through 14 U.S.
182 states from its southern terminus, Springer Mountain, Georgia, to its northern terminus, Katahdin
183 in Maine (see Figure 2). Over 3 million people visit the trail each year, making it an ideal
184 monitoring corridor for community science efforts, and where shifts in phenology can be
185 recorded over large geographic extents (Cohn, 2008). From Southern Appalachian grassy balds,
186 to the alpine zones of the Northeast, the AT is also home to diverse flora that may be influenced
187 by climate change. Higher latitudes in the Appalachians are warming and experiencing longer
188 growing seasons but elevational differences are mixed (Kimball et al., 2014; Janowiak et al.,
189 2018; Murray et al. 2021). While data from many other global montane sites have demonstrated
190 elevation-dependent warming (Pepin et al. 2022) this has not been the consistent pattern in the
191 northern Appalachians (Murray et al. 2021).

192 *Data collection*

193 In 2004, AMC began monitoring reproductive plant phenology events focused on
194 flowering for alpine species, and later expanded to include woodland species (trees, shrubs, and
195 forbs) and other phenophases such as leaf-out in northeastern mountains in the United States.
196 Initially designated the Mountain Watch (MW) project, this effort enlisted organizational staff,
197 partner organizations, and volunteers to gather phenology data on paper data sheets. The MW
198 Project has since evolved to utilize the National Phenology Network's (NPN) protocol and
199 currently collects data in two primary ways: through (i) the establishment of permanent plots in
200 the White Mountains of New Hampshire, and (ii) by using phone applications (apps) and
201 smartphones to enhance monitoring practices. In some cases, partner organizations have also set
202 up permanent plots and similarly evolved to use the NPN protocol. In recent years, monitoring
203 through community science has expanded from the Northeast to the entire AT Corridor using the
204 platform iNaturalist.

205 iNaturalist is a free smartphone app with currently 2.5 million active users and nearly 70
206 million observations (Barve et al., 2020; Callaghan et al., 2022). Users can upload photo
207 observations, provide a species ID, or receive one based on the program's algorithm or a

208 community of online naturalists. Observations are made research grade once there are two
209 corresponding species identifications. The iNaturalist geotagged images also reduce location
210 errors and eliminate the past challenge of inaccurate species ID from novice observers
211 (McDonough MacKenzie et al. 2017; McDonough MacKenzie et al. 2020). iNaturalist serves as
212 a supplement to permanent plots as NPN plots require consistent attention from skilled
213 naturalists while having limited spatial distribution. Importantly, iNaturalist observations can be
214 used to fill gaps between monitoring plots and expand spatial and temporal data coverage.
215 Researchers can also create projects on iNaturalist to capture observations of a specific species or
216 geographical range.

217 AMC's iNaturalist phenology projects incorporate NPN's protocol as observation fields
218 to identify the phenophase of a plant observation. Staff project curators and managers have the
219 task of adding observations of target species within the AT Corridor to the project if they have
220 not been uploaded to the project by the observer. AMC's iNaturalist project, *Flowers and Fauna*
221 *along the Appalachian Trail Corridor*, began in 2018 and with continued dedicated funding has
222 grown to now include >40,000 phenological observations (see Supplemental Figure S1). AMC's
223 ultimate goal is to establish a long-term dataset that can be expanded and analyzed year after
224 year to infer changes in plant phenological responses to changing climate along the full AT
225 Corridor.

226 *Data Preparation*

227 We synthesized and collated phenological observations from three sources: the AMC's
228 MW Project, the NPN online data portal, and the AMC's iNaturalist projects (>2 million
229 observations). Observations ranged from 2004 to the end of 2022 and represented multiple
230 phenophases (leaves, flowering, fruiting, senescence, etc.), and plant species (understory
231 woodland, canopy trees, and alpine species). As we were only interested in spring leaf and
232 flower phenology, we removed observations recorded of other phenophases and from other
233 seasons from the dataset. Additionally, we used only positive observations of phenology in
234 subsequent analysis (i.e., only records where the phenophase was actually observed). Since we
235 were only comparing spring phenology of understory and tree species in temperate broadleaf
236 forests, we removed alpine species observations from the dataset. Further, we removed

237 understory herbaceous species that either flower later in the growing season (i.e., after canopy
238 closure), or had fewer than 100 observations. We only kept tree species that had the potential to
239 maintain a dominant position in the forest canopy and had greater than 100 observations. We
240 used ArcPro v3.1 (ESRI, 2022) to create a watershed delineation buffer using USGS HUC10
241 watersheds around the AT. We included only records within our HUC10 AT buffer in our
242 analysis (in the eastern United States between approximately 34-46°N latitude).

243 All observations were highlighted for either day of year (DOY) of leaf-out (tree species
244 and understory species, DOY_{leaf}) or DOY of open flowering (understory species, DOY_{flower}),
245 consistent with previous studies comparing phenology across forest strata (Heberling et al., 2019;
246 Lee et al., 2022). NPN defines leaf-out as one or more individual leaves unfolded, meaning the
247 entire length of the leaf has emerged from the bud (NPN, 2023). Flowering is defined as when
248 one or more flowers are open so that reproductive parts are visible (NPN, 2023). Our approach
249 assumes that herbaceous species' flowering and leaf-out timing is tightly correlated for these
250 species (see Lee et al., 2022). Understory flowering may be a better choice of response over leaf-
251 out because intensity values, or ordinal categories for each phenophase (e.g., <5%, 5-25%, 25-
252 50%, 50-75%, 75-95%, >95%), are measured and associated with understory flowering but not
253 understory leaf-out. Like canopy tree DOY_{leaf} which also have associated intensity values,
254 DOY_{flower} can be viewed as a distribution. Understory plants with or without leaves as a binary
255 measure makes it difficult to truly assess true leaf-out timing.

256 We focused on common and ubiquitous species (found across the majority of the AT
257 Corridor, minimum >4° latitude) that flowered and leafed out at approximately the same time in
258 early spring. We subsequently removed observations where either leaf-out or flowering occurred
259 after DOY 200, as these were either likely in error or a second flowering which occurs in some
260 species under the right conditions. We also only included tree observations where budburst or
261 leaf expansion intensity values were 75-95%, indicating nearly total leaf-out. In total, after
262 accounting for observations that were excluded from our original search, we collected data for a
263 total of 25 species (14 tree species and 11 understory forb and shrub species) consisting of
264 118,250 individual observations across the entire AT Corridor (Figures 2, 3). In order to examine
265 latitudinal differences in spring phenology, observations were partitioned among three 4°

266 latitudinal bands: Southern AT (34-38°N), mid-Atlantic (38-42°N), and Northern AT (42-46°N)
267 (Figure 3).

268 Since all observations were geolocated (we only kept observations with < 250 m
269 accuracy error), we were able to extract potentially relevant landscape and climatological data
270 for each record. DAYMET 1 km gridded climate data were extracted for the year an individual
271 observation took place, which included mean, maximum, and minimum air temperatures (°C),
272 solar radiation (W/m²), snow water equivalent (SWE, mm), vapor pressure deficit (Vpd, kPa),
273 and total precipitation (mm) (Daymet: Daily Surface Weather Data on a 1-km Grid for North
274 America, Version 4 R1 <https://doi.org/10.3334/ORNLDAAAC/2129>). Daily values were extracted
275 for the entire year which the observation was recorded allowing us to calculate daily, monthly,
276 seasonal, and annual mean values for each climate variable. Accumulated growing degree days
277 (AGDD) were also derived from DAYMET temperature data using Equation 1 (Gavin et al.,
278 2008; Wason and Dovciak, 2017; Tourville et al., 2022):

$$279 \quad AGDD = \sum \left(\frac{T_{max} - T_{min}}{2} - T_{base} \right) \quad (1)$$

280 Where *AGDD* is the accumulated maximum value of growing degree days for spring only, T_{max}
281 and T_{min} are daily maximum and minimum temperatures, and T_{base} is a constant (4°C). Elevation
282 at each observation location was extracted from a national 10 m digital elevation model (DEM).

283 *Data Analysis*

284 In order to determine which candidate geographic and climate variables (Table 2)
285 influence spring phenology for both understory and canopy species and warranted inclusion in
286 subsequent models, a preliminary exploratory multiple regression analysis was undertaken using
287 DOY_{leaf} and DOY_{flower} as a response. Our main candidate variables included mean spring
288 temperature (April-June, AMJ), mean previous winter temperature (DJF), spring AGDD,
289 seasonal SWE (proxy for snow depth, DJF) latitude, and elevation (see Table 2 for all possible
290 candidate variables). Spring temperature was calculated as the average of the April, May, and
291 June daily temperatures for the year and the location associated with each phenology record.
292 April-June temperatures explained more variation in DOY than other spring windows (i.e.,
293 March-May, or individual months). All variables were scaled and centered and global models

294 with all candidate variables were examined. For both understory and canopy species,
295 standardized regression coefficients for mean spring temperature (negative interaction), elevation
296 and latitude (both positive interactions) were significant predictors of DOY (Supplemental
297 Figure S2). Regression models with spring temperature, latitude, and elevation explained more
298 or similar variation (marginal R^2) in DOY to more complex models, thus, we used these three
299 variables in subsequent modeling of changes to the spring phenological window (see below).

300 Using a hierarchical Bayesian approach, we modeled DOY of the observed phenological
301 event (leaf-out or flowering) for individual i of species j using a normal likelihood distribution
302 (see Lee et al., 2022):

$$303 \quad \text{DOY}_{i,j} \sim N(\mu_{i,j}, \sigma^2) \quad (2)$$

304 The mean, μ , was modeled with an intercept term (β_0), slope terms representing phenological
305 sensitivity to mean spring temperature (β_1), elevation (β_2), latitude (β_3), and species random
306 effects (α_j):

$$307 \quad \mu_{i,j} = \beta_0 + \beta_1 \times \text{SpringTemp} + \beta_2 \times \text{Elevation} + \beta_3 \times \text{Latitude} + \alpha_j \quad (3)$$

308 We used slightly informative priors to estimate parameters: $\beta_0, \beta_1, \beta_2, \beta_3, \alpha_j \sim N(0, 1E-3)$; $1/\sigma^2$
309 $\sim \text{Uniform}(0,100)$. Our models used 3,000 burn-in iterations, and three MCMC chains each
310 containing 10,000 iterations. Models were run separately for each stratum for the full AT (i.e.,
311 canopy vs. understory, addressing Q1 and Q2), and for each AT region (addressing Q3)
312 combination using the R2jags package (v0.7-1; Su and Yajima, 2022) in R v4.1.0 (R Core Team,
313 2023). Models for each individual species from both functional groups were also run. Parameter
314 values (means, variances, and covariances) were estimated from posterior distributions and are
315 considered significantly different if the 95% credible intervals (CIs) of their posterior
316 distributions do not overlap. Bayesian R^2 values were calculated to evaluate variance explained
317 by spring mean temperature on DOY (Gelman et al., 2019). Our parameter values were used to
318 model the direction and magnitude of change to spring phenological windows across the
319 landscape for each AT region in ArcPro v3.1. 1-km rasters of 30-year normal spring mean
320 temperature (DAYMET), elevation (DEM), and latitude were used as raster math inputs to
321 visualize changing phenological windows, but only for areas classified as temperate broadleaf
322 forest using the GAP/LANDFIRE National Terrestrial Ecosystems dataset (USGS, 2016).

323 For functional group modeling of DOY, we ultimately used 11 of the 14 tree species for
324 spring window calculations. The excluded species were still examined at a species level (see
325 Table 2). We felt this approach was appropriate because these species had relatively few
326 observations ($n < 500$; e.g., *Sorbus americana*). To test the assumption that understory species
327 flowering time is correlated with leaf-out timing, we re-ran all Bayesian models with DOY_{leaf} of
328 the understory as a response instead of DOY_{flower}. General patterns for broad functional groups
329 were not substantially different from one another (Supplemental Table S1).

330 Results

331 Q1 – Phenological patterns of understory and canopy species

332 Overall, spring phenology of both canopy trees and understory forest species tended to be
333 earlier when mean spring temperatures (April-June) were warmer across the entire AT Corridor.
334 On average, canopy trees advanced 3.8 days/°C of warming, while understory species as a whole
335 advanced 6.4 days/°C (Table 3). This was true whether looking at understory DOY_{flower} or
336 DOY_{leaf}, indicating that comparing understory flowering and canopy leaf-out timing was
337 appropriate as a proxy for understory leaf-out (Supplemental Table S1). Nine of the 11
338 understory species and six of the 14 canopy tree species significantly (95% CI non-overlapping
339 with zero) advanced their spring phenologies with warmer temperatures (Table 4). For
340 understory species, the spring ephemerals *Dicentra cucullaria* and *Erythronium americanum*
341 displayed the highest temperature sensitivity for flowering (> 6 days/°C), while *Clintonia*
342 *borealis*, *Viburnum lantanoides*, and *Trientalis borealis* were the least sensitive (< 3 days/°C,
343 Table 4). For canopy tree species with significant sensitivity values, *Fagus grandifolia*, *Acer*
344 *saccharum*, and *Quercus rubra* showed the most temperature sensitivity for leaf-out (> 4
345 days/°C), while *Acer rubrum* and *Betula alleghaniensis* were the least sensitive (< 3 days/°C,
346 Table 4). In general, later flowering or leaf-out occurred for individuals at higher elevations or
347 latitudes, consistent with previous studies and predictions under Hopkins' Bioclimatic law (Table
348 4).

349

350

351 *Q2 – Differences between functional groups*

352 Spring-flowering forest understory species responded more strongly to warmer
353 temperatures than did canopy trees when data were pooled across the entire length of the AT
354 Corridor – by approximately 1.6 days for every 1 °C increase in spring mean temperature (Table
355 3). In particular, the understory species *Dicentra cucullaria*, *Erythronium americanum*,
356 *Sanguinaria canadensis*, and our two *Trillium* species were much more sensitive to potential
357 temperature increases than most individual canopy tree species, with the exception of *Fagus*
358 *grandifolia* (Table 4). Greater understory sensitivity to temperature than canopy trees suggests an
359 expansion of the spring phenological window. Our models revealed that greater window
360 expansion was likely to occur at higher elevations and latitudes (Table 3).

361 *Q3 – Latitudinal patterns of phenology*

362 For southern and mid-Atlantic regions (34–38°N and 38–42°N, respectively), there were
363 no detectable differences between functional groups in responsiveness of spring phenology to
364 temperature (overlapping 95% CI). At northern latitudes (42–46°N), understory species as a
365 group advanced their spring phenologies more strongly than trees with respect to temperature, by
366 around 2.6 days/°C (Table 3, Figure 4). Both functional groups advanced their phenologies
367 nearly twice as much in the mid-Atlantic region (38–42°N) than either southern or northern AT
368 regions (Figure 4). Taken together, the phenological window likely experienced expansion to a
369 greater degree in northern latitudes, and in general, at higher elevations for all regions examined
370 (Figure 5). Spring windows expanded little or remained stable at mid- to southern latitudes
371 (Figure 5). We found that annual mean spring temperatures in our dataset increased for all
372 regions over the timespan analyzed (2004–2022), but only significantly at higher latitudes
373 (Figure 6), indicating greater warming at northern latitudes and more variation in temperature for
374 which plants can respond.

375 **Discussion**

376 Overall, we find regional disparities of plant spring phenological response to warming for
377 species within temperate deciduous forests of the eastern United States. Specifically, we
378 illustrate that spring phenology is advancing with temperature for both spring blooming forest
379 understory species and canopy trees in North America's eastern hardwood forest ecosystems

380 (addressing Q1). Spring phenology is also advancing to a greater degree at both higher latitudes
381 and elevations for most species examined. However, understory species' phenologies are
382 advancing at a greater rate than canopy tree leaf-out phenologies, but only significantly so at
383 northern latitudes (42–46°N) with no detectable difference between functional groups for lower
384 and middle latitudes (34–42°N, addressing Q2). Furthermore, both functional groups vary in
385 their phenological response to warmer temperatures across the latitudinal range, with understory
386 plants and canopy trees at middle latitudes advancing their spring phenologies more than those at
387 lower and higher latitudes (addressing Q3). Given that both functional groups were more
388 sensitive to temperature at middle latitudes (38–42°N) compared to low (34–38°N) and high
389 latitudes (42–46°N), other unmeasured factors may be at play influencing the temporal dynamics
390 of the spring phenological window. Since a high proportion of mid-Atlantic observations were
391 taken in urban areas (many near the New York City metropolitan area), one unexplored
392 possibility is that the temperature sensitivity of this region may be due to effects from land-use
393 (Luo et al., 2007; Zipper et al., 2016).

394 The phenological advance of both deciduous tree and spring-flowering understory plants
395 is supported by previous studies and suggests that rising spring temperatures could increase the
396 length of the growing season in temperate deciduous forests (Monahan et al. 2016; Melaas et al.,
397 2018; Seyednasrollah et al., 2020; Moon et al., 2021; Li et al., 2022). However, while our finding
398 that understory spring phenology is advancing faster than deciduous canopy trees under warmer
399 temperatures at northern latitudes (42–46°N) agrees with a recent study (Alecrim et al., 2022), it
400 is at odds with other studies conducted within the same region (Heberling et al., 2019; Lee et al.,
401 2022). The variation in canopy-understory phenology results across these studies may reflect
402 differences in methodological approaches, including the density of observations, and the study
403 species (see Alecrim et al., 2022; see below for possible explanations).

404 The observed differences in temperature sensitivity and potential changes to the spring
405 phenological window could be attributed to either disparities in changing environmental
406 conditions or differences in forest community composition across our latitudinal gradient.
407 Calculated mean spring temperatures (April–June) reveal warming trends for all regions
408 examined, however, only the northern AT experienced statistically significant warming between
409 2004–2022 (Figure 6). While the Mid-Atlantic region displayed greater temperature sensitivities

410 for both understory plants and canopy trees than other regions, only in the northern AT did we
411 find significantly different sensitivities between the two functional groups. It is possible that
412 consequences of greater warming in the north are altering plant responses to a changing climate
413 in ways at odds with conspecific southern populations (see below). Of course, disparate
414 community composition which encapsulate our study species across regions may also be driving
415 these patterns.

416 The northern AT region differs from lower latitudes in several other relevant ways. Most
417 notably, the northern AT is characterized by longer and colder winters, deeper snowpack, shorter
418 growing seasons, and is projected to warm faster than other regions over the course of this
419 century (US National Climate Assessment, 2018 (<https://nca2018.globalchange.gov/>), Janowiak
420 et al., 2018). These trends may be relevant in several ways. First, chilling requirements for
421 understory plants may still be met in the north despite recent warming (at least up to a certain
422 threshold not yet reached), meaning that these species will not suffer reduced performance and
423 could, at least in the short term, benefit from a longer spring window before canopy closure
424 (Zhang et al., 2007 Prevéy et al., 2017). Second, a decreasing snowpack, particularly in the
425 north, would decrease soil temperatures in the late winter period (Zhu et al., 2019; Zohner et al.,
426 2017), but would also allow for a greater time for herbaceous species to be uncovered by snow in
427 the spring, a critical time for growth (Marchin et al., 2015; Augspurger and Salk, 2017; Contosta
428 et al., 2017). While during the summer months understory temperatures are buffered (cooler) by
429 the canopy, this is not the case prior to canopy closure in the spring – suggesting that understory
430 species could be more directly influenced by surface air temperatures than has been previously
431 suggested (Richardson and O’Keefe; De Frenne et al., 2011; Jacques et al., 2015; De Frenne et
432 al., 2021). To resolve these various interacting factors, future work must measure relevant
433 climate covariates, such as snow cover and soil temperature, in locations that record phenology
434 of individual plants.

435 The temporal dynamics of spring phenology are hard to predict given the high variation
436 in published sensitivities (e.g., Heberling et al., 2019; Alecrim et al., 2022; Lee et al., 2022). We
437 argue that methodological differences between these disparate studies may be the root cause of
438 the observed discrepancies. First, the phenophase used to model functional group temperature
439 sensitivity (leaf-out vs. flowering) can influence the interpretation of the spring phenological

440 window. While we found that leaf-out and flowering timing were correlated in our study (and see
441 Heberling et al., 2019), appropriate ancillary data is required to successfully utilize each metric.
442 Namely, some kind of intensity value is needed to describe a distribution of these events, rather
443 than a presence/absence record (Buonaiuto et al., 2021). Without this information, it is difficult
444 to know the exact time of flowering or leaf-out. Second, a substantial amount of variation in both
445 temporal and spatial ranges examined could lead to the observed differences in reported results.
446 It would be difficult to compare the results of two phenological window studies examining
447 advancing phenology with an order of magnitude difference in the time record illustrated
448 (decadal vs. century timeframes), as the magnitude of warming is dissimilar (Ge et al., 2015;
449 Alecrim et al., 2022). Likewise, results from studies examining specimens at a local scale may
450 not be applicable to a regional-scale given the exponential growth of environmental variation
451 encountered, especially in the context of microclimates and climate refugia (Wielgolaski, 1999;
452 Wolkovich et al., 2021; Pastore et al., 2022). Third, the size and source of the dataset used may
453 be critical for phenological studies. Large phenology datasets, as is the case with our study, are
454 preferable to smaller ones for regional-scale studies; however, access to such rich data sources
455 are not always possible.

456 This study is unique in this area given our large sample size and use of citizen-science
457 derived iNaturalist data, which served to greatly expand the temporal and spatial variation
458 described in our study region (Supplemental Figure S1). We recommend that similar future
459 research engage with this efficacious resource. Further, while spring ephemerals and other
460 herbaceous species have been the focus of understory phenology patterns, tree seedlings have
461 largely been ignored in their phenological response to changing climate (Augspurger and
462 Bartlett, 2003; Lopez et al., 2008; Richardson and O’Keefe, 2009; but see Lee and Ibanez,
463 2021a). Seedlings represent the future composition of a forest, and any change in seedling
464 survival and growth related to shifting phenology is important to capture (Lee and Ibanez, 2021a;
465 2021b). We advocate for a stronger emphasis on observations of woody seedling species in the
466 understory moving forward.

467 Earlier flowering and leaf-out relative to canopy closure could serve to benefit plant
468 performance of understory forbs and shrubs through a number of mechanisms. Advanced leaf-
469 out and flowering could trigger an increase in photosynthate accumulation and storage (Keenan

470 et al., 2014; Teets et al., 2023). Greater access to resources could also provide a boost to both
471 vegetative growth and reproduction (Kudo et al., 2008; Heberling et al., 2019). Thus, assuming
472 understory plant fitness is not affected by other changes caused by shifting phenology or other
473 climate changes such as extreme precipitation or drought, an expansion of the phenological
474 window could make these species more resilient to a changing climate. This is especially true for
475 spring ephemeral species which almost entirely rely on high light availability in the spring.
476 Indeed, our results reveal that the most temperature sensitive species were ephemeral species
477 such as *Dicentra*, *Erythronium*, *Trillium*, and *Sanguinaria*.

478 Advancing understory spring leaf-out and flowering may also have negative impacts on
479 plant performance. First, earlier leaf-out could expose both spring ephemerals and trees to
480 unpredictable late frost (or “false spring”) events which can cause significant physical damage
481 and loss of fitness, particularly as climate change makes extreme frost events more common
482 (Augspurger, 2009; Marino et al., 2011, Casson et al. 2019). Leaf or leaf-bud loss to frost
483 represents a significant cost for deciduous trees, affecting growth, reproduction, canopy
484 expansion and nutrient reserves, as refoliation to compensate for damage demands extra
485 resources (Inouye, 2008; Augspurger, 2009; Pardee et al., 2019). Second, plant phenological
486 shifts relative to herbivores and pollinators may have a large effect on plant performance. For
487 instance, shifts in timing of herbivore emergence relative to plant phenology, as well as changes
488 in the frequency or severity of herbivore outbreaks could have major impacts on understory
489 shading and carbon budgets of trees and understory plants (Kudo et al., 2008; Weed et al., 2013).
490 Importantly, if plants and insects do not respond at the same rate to warming, mismatches
491 between flowers and flower-visitors could occur (Kudo and Ida, 2013; Petanidou et al., 2014;
492 Forrest, 2015; Kudo and Cooper, 2019). While not as relevant for wind-pollinated deciduous
493 trees, forest understory forbs are generally insect-pollinated, and given the short flowering period
494 of these species, phenological mismatches between these plants and their pollinators are possible
495 (Kudo and Ida, 2013; Kudo and Cooper, 2019).

496 *Conclusions*

497 Here, we find evidence that understory plants in eastern North America are advancing
498 their spring phenologies 1.6 days/°C faster than canopy trees near full leaf-out; in other words,

499 this functional group appears more sensitive to air temperature increases than trees. The
500 expansion of the spring phenological window could be a net positive for understory plant
501 performance under changing climate conditions; however, many other unexplored phenomena,
502 such as biotic interactions and climate-induced hydrologic variability, make forecasting changes
503 to forest communities challenging. We note distinct patterns of phenological sensitivity across a
504 latitudinal gradient, indicating that forest plant response to warming in eastern forests will not be
505 uniform across space. It is also difficult to determine how specific species will ultimately
506 respond to warming, or how long-term phenological dynamics will be altered (i.e., do threshold
507 responses to warming exist for these species?). We posit that more spatially diverse phenological
508 data, particularly from citizen-science driven efforts, can help inform research related to forest
509 resilience to climate change, and that future work would greatly benefit from a more
510 standardized approach.

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524 **Author Contributions**

525 JT conceived the research questions with input from GM and SN. JT planned and designed the
526 research and conducted all data analysis with input from GM and SN. JT wrote the manuscript,
527 and all authors contributed substantial revisions and edits.

528 **Conflict of Interest Statement**

529 The authors have no conflicts of interest to declare.

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779 **Tables**780 **Table 1:** Definitions of important terms used throughout the study.

Term	Definition
Phenology	Timing of recurring plant life stages and their relationships with weather and climate
Spring ephemeral	Perennial woodland wildflowers which develop aboveground early each spring, bloom, produce seed, and senesce during a brief window of time
Leaf-out	Leaf expansion following leaf budburst during spring months
Canopy closure	Full overlap of expanded tree canopy leaves which fully shades the forest understory
Spring phenological window	Brief period of high light conditions below the forest canopy starting with understory leaf-out and ending with full canopy closure
Phenological mismatch	Interacting species change the timing of regularly repeated phases in their life cycles at different rates
Hopkins' Bioclimatic Law	Hypothesized phenological pattern where a 4-day shift in phenology is predicted for a change of every 1° latitude north, 5° longitude west, and 120 m increase in elevation
Appalachian Trail Corridor (AT)	Lands immediately surrounding the Appalachian Trail that follow the Appalachian Mountain chain from Georgia to Maine (USA)
iNaturalist	An online platform that allows sharing of biodiversity observations and creates research-quality citizen science data
Appalachian Mountain Club (AMC)	An environmental non-profit organization dedicated to conservation, education, and recreation of lands within the AT Corridor
National Phenology Network (NPN)	An organization established in 2007 to collect, store, and share phenology data and information
Mountain Watch Project (MW)	An AMC project established in 2004 to monitor phenological change in high elevation environments within the AT Corridor
Phenophase	An observable stage in the annual life cycle of a plant that can be defined by a start and end point
Day of Year (DOY)	Julian date for which a particular phenophase is observed for an individual plant
Intensity values	Ordinal categories for a particular phenophase
Plant performance	Integrated measure of plant fitness which incorporates survival, growth, and reproductive success
Forest climate resilience	A measure of a forest's adaptability to a range of climate stresses which reflects the functional integrity of the ecosystem

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791 **Table 2:** Abbreviations, definitions, and the data source of independent variables (by category) used for exploratory analyses for
 792 predicting DOY of tree leaf-out and understory flowering across the AT Corridor. Elevation, latitude and longitude were derived from
 793 geolocation data of individual observations and regional 2 m digital elevation models (DEM). Climate values were extracted from
 794 DAYMET 1-km gridded datasets. AGDD was derived from extracted DAYMET temperature data.

Category	Variable	Abbreviation	Units	Description	Source
Geography	Elevation	Elev	m	altitude above sea level	AMC
	Latitude	Lat	°	degrees latitude	AMC
	Longitude	Long	°	degrees longitude	AMC
Climate	Spring maximum temperature (AMJ)	Spring Tmax	°C	maximum spring temperature for each observation year	DAYMET
	Spring minimum temperature (AMJ)	Spring Tmin	°C	minimum spring temperature for each observation year	DAYMET
	Spring mean temperature (AMJ)	Spring Tmean	°C	mean spring temperature for each observation year	DAYMET
	Accumulated solar radiation	SR	W/m ²	sum of incoming solar radiation for each observation year	DAYMET
	Maximum snow water equivalent (DJF)	SWE	mm	maximum snow water equivalent for observation winter	DAYMET
	Accumulated growing degree days	AGDD		sum of daily temperatures over plant growth threshold	DAYMET
	Spring mean vapor pressure deficit (AMJ)	VPD	Kpa	mean vapor pressure deficit of spring for observation year	DAYMET
	Total precipitation	PPT	mm	sum of accumulated precipitation for spring of observation year	DAYMET
Previous mean winter temperature (DJF)	Winter Tmean	°C	mean winter temperature for previous observation winter	DAYMET	

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806 **Table 3:** Posterior parameter (and 95% credible intervals, CI) estimates of DOY_{leaf} (canopy) and DOY_{flower} (understory) from
807 hierarchical Bayesian modeling for 8 species of understory plants and 11 species of canopy trees across the full AT and partitioned
808 between the three study regions, South (34-38°N), Mid-Atlantic (38-42°N), and North (42-46°N). DIC (deviance information
809 criterion) and Bayesian R^2 are included. Bolded parameter estimates include 95% CI not overlapping zero.

Full AT										
Region	Functional Group	n	DIC	R^2	Spring Mean Temperature (°C)	95% CI	Elevation (m)	95% CI	Latitude (°)	95% CI
Full AT	Understory	45293	200745	0.51	-6.12	-6.43, -5.82	30.80	28.83, 32.77	2.42	2.12, 2.72
Full AT	Canopy	72957	657608	0.23	-3.41	-3.77, -3.06	20.30	18.39, 22.31	3.87	3.58, 4.17
Region-specific										
South	Understory	10819	61861	0.30	-5.66	-7.65, -3.63	6.25	4.29, 8.21	-3.27	-5.03, 0.52
South	Canopy	35242	313516	0.19	-5.86	-6.49, -5.28	13.64	11.63, 15.58	3.80	3.09, 4.58
Mid-Atlantic	Understory	10834	64166	0.29	-11.45	-13.56, -9.35	-0.47	-2.42, 1.48	2.85	-0.17, 5.83
Mid-Atlantic	Canopy	13283	129899	0.17	-9.43	-11.38, -7.46	1.98	-0.09, 3.91	0.07	-2.16, 2.26
North	Understory	23640	179396	0.69	-6.35	-6.65, -6.06	37.83	35.87, 39.82	1.64	0.95, 2.33
North	Canopy	24432	197718	0.41	-3.68	-4.10, -3.25	22.15	20.22, 24.15	3.07	2.20, 3.93

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821 **Table 4:** Posterior parameter (and 95% credible intervals, CI) estimates of DOY_{leaf} (canopy) and DOY_{flower} (understory) from
822 hierarchical Bayesian modeling for individual canopy tree (gray shading) and understory plant species across the full AT Corridor.
823 DIC (deviance information criterion) is included. Bolded parameter estimates include 95% CI not overlapping zero.

Species	Common Name	Functional Group	n	DIC	Spring Mean Temperature (°C)	95% CI	Elevation (m)	95% CI	Latitude (°)	95% CI
Aquilegia canadensis	Red columbine	Understory	539	6398	-4.76	-5.92, -3.54	1.17	-2.61, 4.99	3.99	3.16, 4.77
Clintonia borealis	Blue-bead lily	Understory	5816	28739	-3.10	-4.06, -2.67	26.83	24.90, 28.79	4.31	3.58, 5.09
Cornus canadensis	Canada dogwood	Understory	5261	25607	-3.94	-4.87, -2.87	11.96	10.03, 13.91	4.59	2.26, 6.76
Dicentra cucullaria	Dutchman's breeches	Understory	571	7654	-6.02	-7.15, -4.98	5.56	7.87, 3.33	2.89	3.65, 2.09
Erythronium americanum	Trout lily	Understory	5891	12382	-6.43	-6.89, -6.07	3.10	1.13, 5.02	2.65	1.80, 3.49
Maianthemum canadense	Canada mayflower	Understory	6975	38522	-5.06	-6.34, -4.84	12.67	10.76, 14.62	0.19	-0.63, 1.01
Sanguinaria canadensis	Bloodroot	Understory	2434	3066	-5.27	-6.79, -4.75	-0.35	-2.31, 1.59	7.48	3.11, 11.74
Trientalis borealis	Starflower	Understory	535	2217	-0.42	-3.20, 2.67	3.42	1.45, 5.38	-5.47	-8.78, -2.20
Trillium erectum	Red trillium	Understory	6018	29870	-5.74	-7.94, -6.39	4.92	2.98, 6.85	1.17	0.44, 1.89
Trillium undulatum	Painted trillium	Understory	6152	22471	-4.36	-5.84, -3.42	14.33	12.38, 16.23	3.47	2.81, 4.13
Viburnum lantanoides	Hobblebush	Understory	5101	32503	-3.53	-4.68, -2.82	17.27	15.26, 19.28	7.63	6.46, 8.85
Acer pensylvanicum	Striped maple	Canopy	7901	63799	-3.72	-4.95, -2.49	12.01	10.00, 14.00	3.55	2.50, 4.59
Acer rubrum	Red maple	Canopy	26926	241645	-1.71	-2.25, -0.96	10.50	8.58, 12.54	4.86	4.33, 5.42
Acer saccharum	Sugar maple	Canopy	9422	84363	-4.02	-5.03, -3.10	-2.34	-4.24, -0.31	2.62	1.85, 3.47
Betula alleghaniensis	Yellow birch	Canopy	6069	49747	-2.61	-3.24, -1.47	14.53	12.63, 16.53	4.66	3.86, 5.48
Betula lenta	Sweet birch	Canopy	3548	32373	0.56	-0.94, 2.35	12.67	10.61, 14.58	7.71	6.68, 8.76
Betula papyifera*	Paper birch	Canopy	270	2347	-0.03	-6.12, 6.08	2.11	0.14, 4.02	-4.79	-11.69, 3.83
Fagus grandifolia	American beech	Canopy	8528	68346	-5.78	-6.36, -4.35	2.22	0.33, 4.14	0.74	-0.04, 1.52
Fraxinus americana	White ash	Canopy	790	7506	0.45	-3.37, 4.36	1.86	-0.09, 3.80	5.08	0.13, 10.13
Ostrya virginiana	Ironwood	Canopy	674	6324	-0.54	-4.40, 2.48	7.60	5.65, 9.62	9.42	5.25, 13.46
Prunus pensylvanica*	Pin cherry	Canopy	360	3208	-1.95	-9.82, 6.50	-1.69	-3.62, 0.31	-6.92	-22.07, 8.25
Prunus serotina	Black cherry	Canopy	2966	27533	0.80	-0.42, 2.13	6.41	4.51, 8.37	8.39	6.45, 10.32
Quercus rubra	Red oak	Canopy	4035	36833	-4.71	-6.34, -2.40	-0.69	-2.63, 1.26	0.15	-1.14, 1.43
Sorbus americana*	American mountain-ash	Canopy	418	3604	-2.31	-12.47, 8.96	-5.37	-7.30, -3.41	-5.88	-27.30, 17.22
Tilia americana	American basswood	Canopy	1050	9845	-0.90	-3.48, 1.32	2.00	0.04, 3.95	5.39	2.25, 8.58

824 *Species was modeled independently and not used in broad functional group modeling.

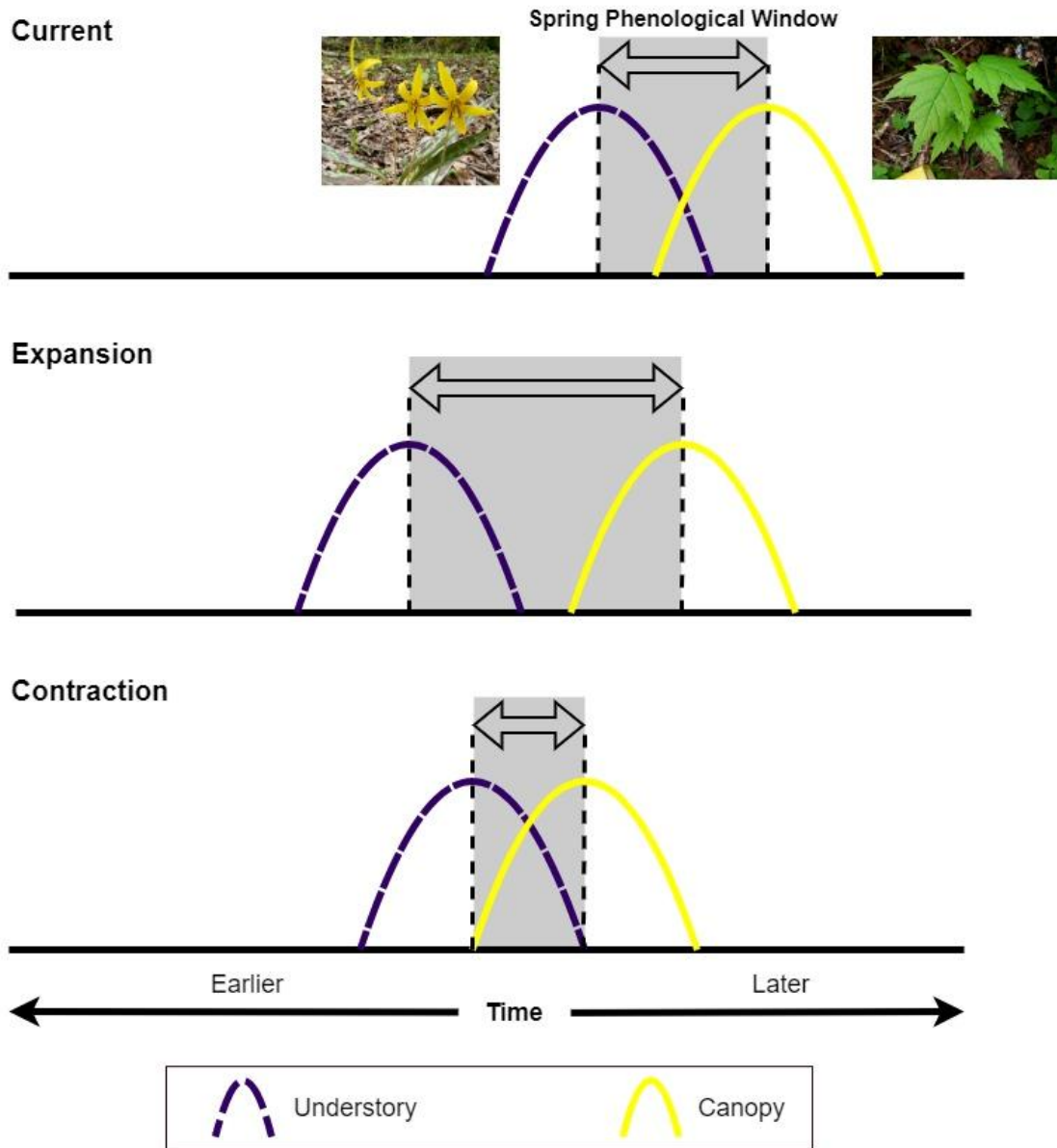
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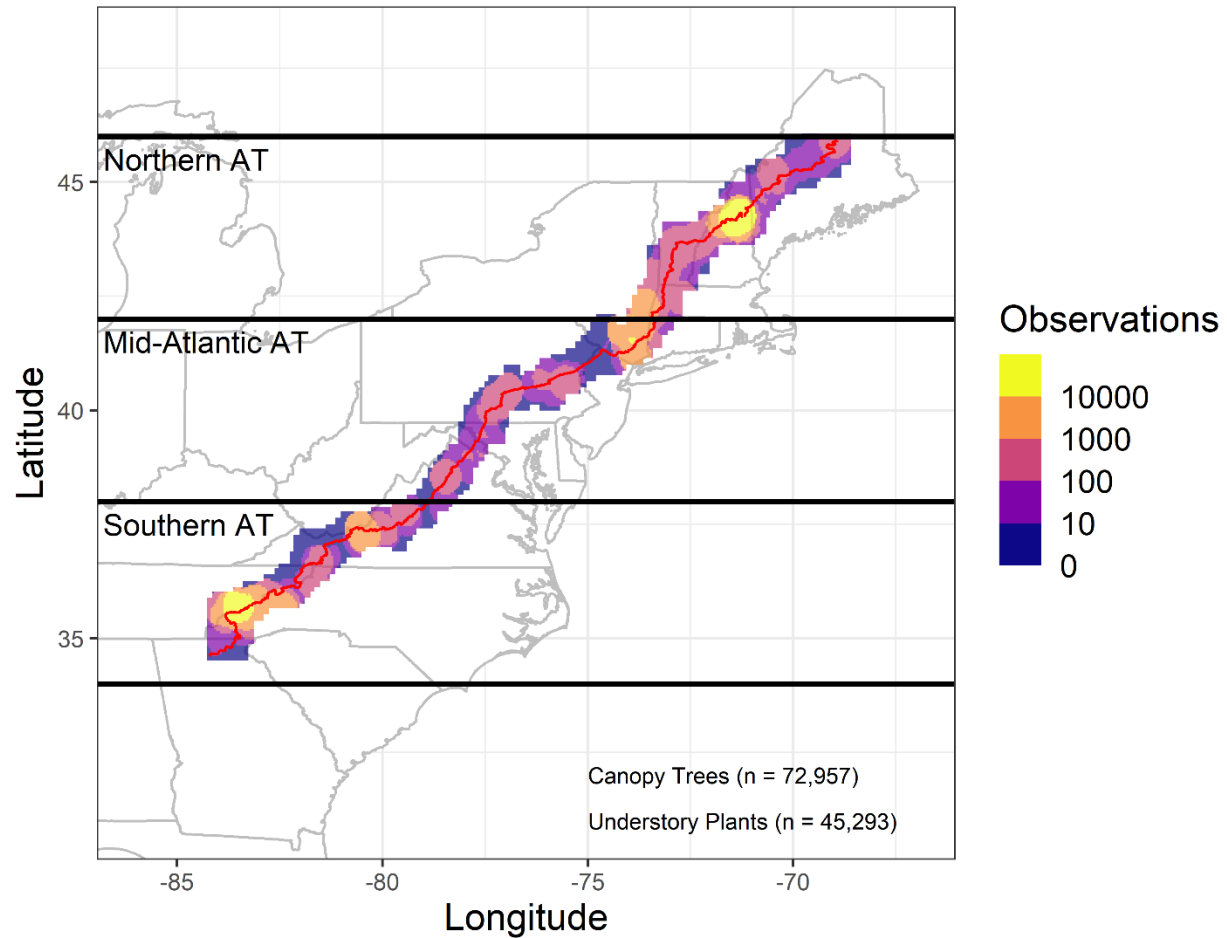
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829 **Figures**



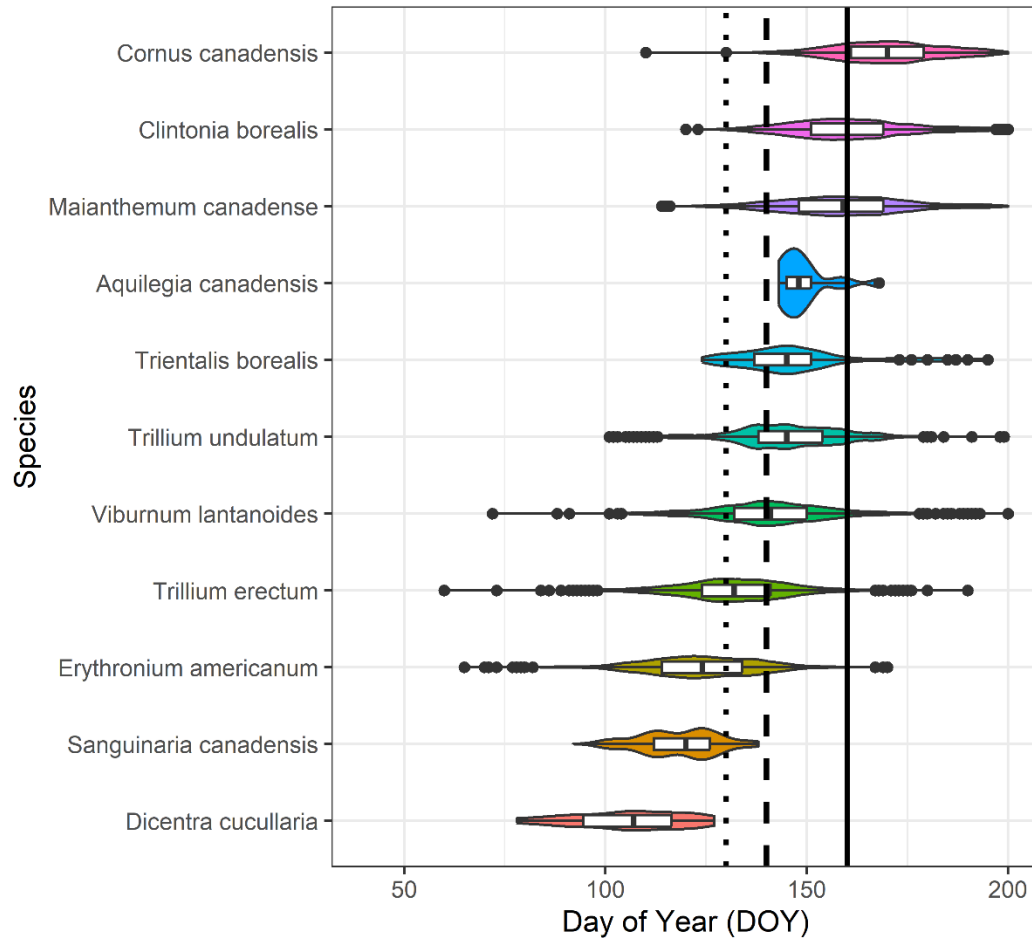
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831 **Figure 1:** Conceptual diagram depicting different scenarios for the shifting spring phenological
832 window under warming. Under the current scenario, both co-occurring understory (purple
833 dashed curve) and canopy (yellow solid curve) species advance their phenologies at the same
834 rate, keeping the window (shaded area) the same length through time. In an expansion scenario,
835 understory plants advance their phenologies faster than canopy trees, leading to a greater period
836 of high-light conditions for these species. Under the contraction scenario, canopy trees shift
837 faster than understory plants with warming, reducing the period of high-light conditions for
838 understory species and possibly leading to reduced annual carbon acquisition. Credit for all
839 photos: Jordon Tourville.



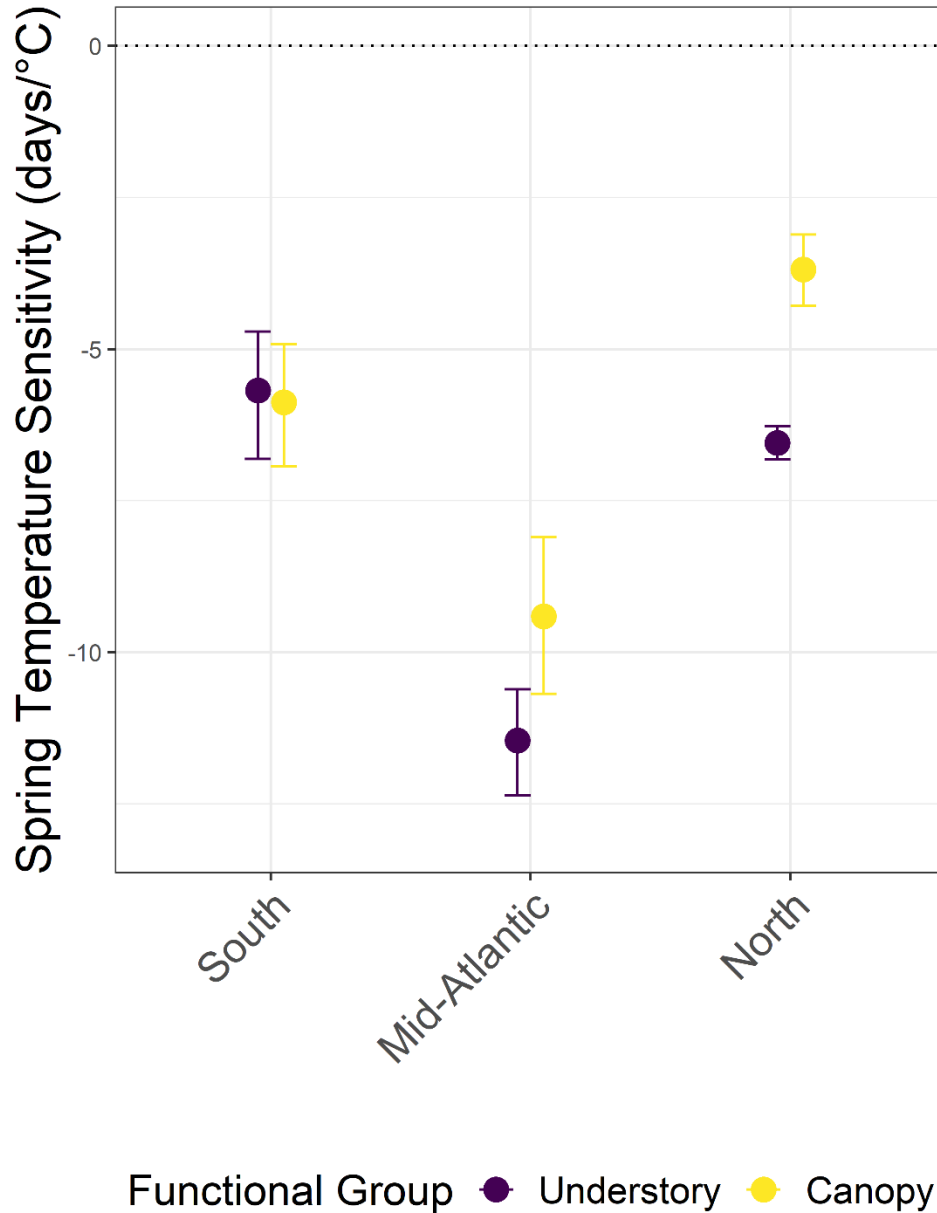
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841 **Figure 2:** Point density estimates of canopy tree and understory plant spring phenology
842 observations analyzed in this study across all HUC10 watersheds intersecting the AT between
843 2004-2022 (n = 118,250). The red line indicates the Appalachian Trail. Note that the scale is
844 logarithmic.



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846 **Figure 3:** Density and distribution of understory flowering observations for each of the 11
847 species examined in this study. The observations shown are only from the entire AT Corridor
848 (34-46° N latitude). The solid line displays the median canopy closure date (from observed
849 citizen-science data) between 2004-2022 for the northern AT (DOY = 160, June 9th), while the
850 dashed and dotted lines show median canopy closure date for the mid-Atlantic (DOY = 140, May
851 20th) and southern (DOY = 130, May 10th) AT regions, respectively. Asterisks (*) indicate
852 species definitively identified as spring ephemerals. Boxplots show median values for DOY_{flower}
853 (with 25% and 75% quantiles).

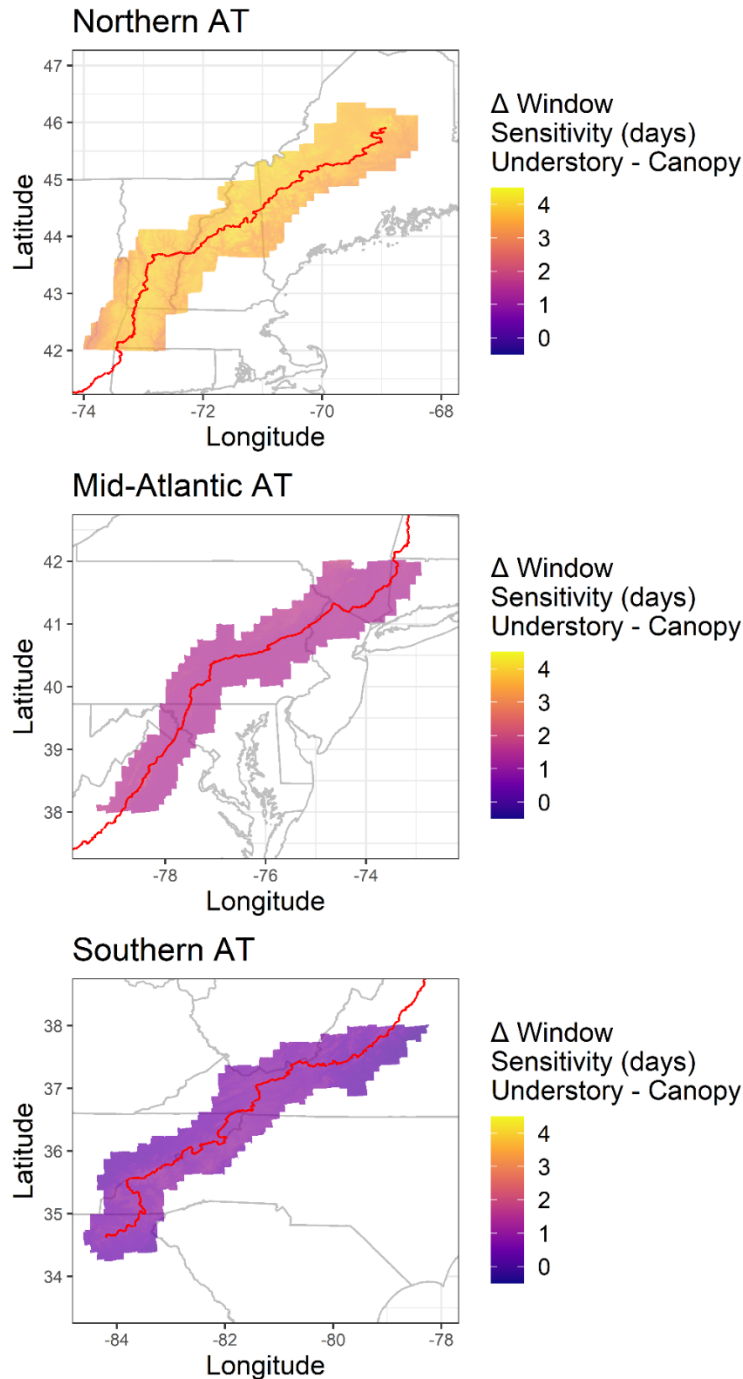


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855 **Figure 4:** Spring temperature sensitivity (number of days of phenology advance per 1°C of
856 warming) for both canopy trees and understory plants (as a whole), partitioned between our three
857 study regions (with 95% CI). Negative y-axis values indicate earlier phenology with warming.
858 The Northern region displays evidence for phenological window expansion, with a stable
859 window illustrated for the Southern region. Understory species also display greater temperature
860 sensitivity than canopy trees in the Mid-Atlantic region, although 95% CI overlap for both
861 functional groups.

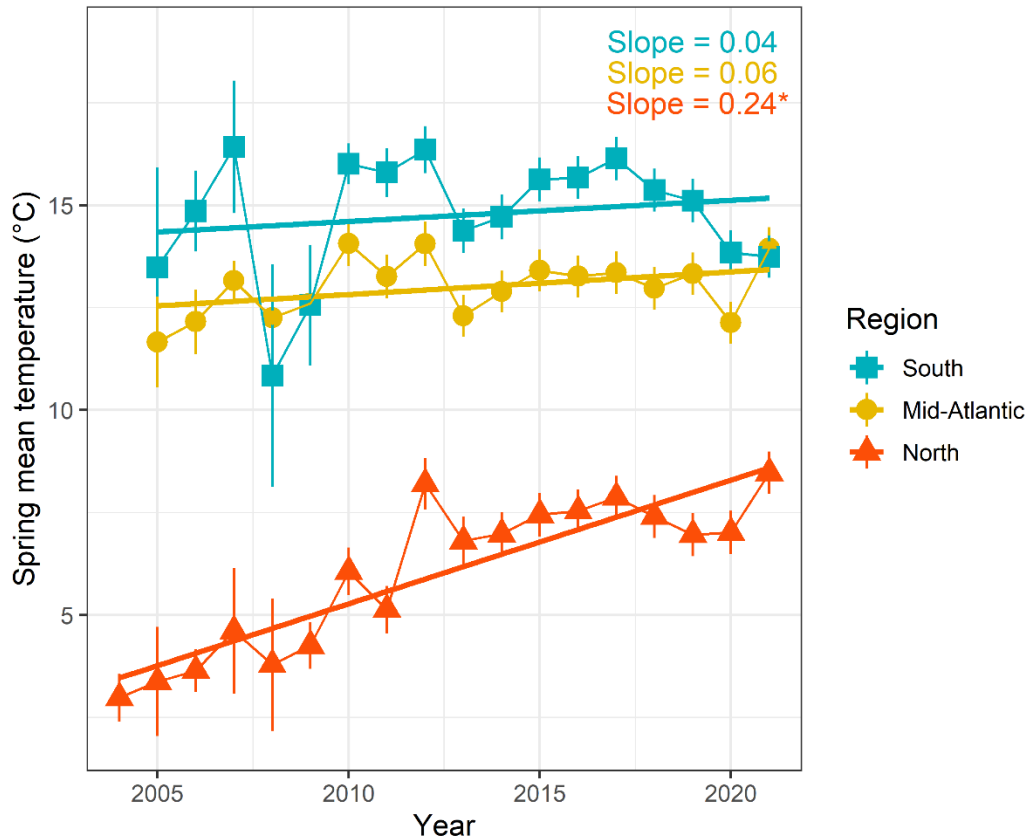
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865 **Figure 5:** Changes (Δ) in spring phenological windows between understory plants and canopy
866 trees, as influenced by temperature, elevation and latitude, in each study region along the AT
867 Corridor. Warmer colors indicate greater possible phenological window expansions whereas
868 cooler colors show smaller expansions, no differences, or contractions of the spring window.
869 Greater window expansions occur more commonly at higher elevations and latitudes, particularly
870 in the Northern region. Changes are more subtle in the Mid-Atlantic and Southern regions. The
871 red line indicates the AT.



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873 **Figure 6:** Annual spring (April-June) mean (\pm SE) temperatures between 2004-2022 across the
874 AT Corridor, partitioned between three latitudinal bands (South: 34-38°N, blue squares; Mid-
875 Atlantic: 38-42°N, orange circles; North: 42-46°N, red triangles). Linear fits display trends of
876 increasing temperature through time, although only the Northern region experienced significant
877 warming (see top-right for coefficient estimates and significance; * $p < 0.05$). Temperatures were
878 estimated from DAYMET daily measurements from all observation locations. Note that annual
879 spring mean temperatures were not recorded for the South and Mid-Atlantic regions in 2004 due
880 to poor data quality.