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RESEARCH ARTICLE

Snowmelt timing alters the phenology but not the performance of an understory spring ephemeral plant

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Abstract

1. Spatial and temporal variation in fine-scale environmental conditions can influence local population abundance and structure ecological communities. In temperate deciduous forests, some herbaceous plant species, including some spring ephemerals, locally cluster around the bases of canopy trees. Despite the conspicuousness of this pattern, no experimental tests have been conducted to discriminate among hypothesized mechanisms.
2. We tested whether earlier spring snowmelt in rings around the base of deciduous trees ('thaw circles') was responsible for improved plant performance and greater local abundance via advanced spring phenology and longer growing seasons (the time between emergence and either senescence or canopy closure). Individuals of Dutchman's breeches (*Dicentra cucullaria*), a common spring ephemeral plant, were transplanted into a fully factorial field experiment of manipulated snowmelt timing (early vs. late) and tree proximity (near vs. far) in a temperate deciduous forest (Québec, Canada). Spring phenology and plant performance (peak leaf-bearing stem abundance and total leaf area) were tracked for 2 years.
3. Advanced spring emergence with early snowmelt, in both naturally occurring thaw circles and where snow was experimentally removed, lengthened growing seasons by 10%–19%, a meaningful extension for spring-flowering herbs with a short window of activity. Surprisingly, Dutchman's breeches transplanted near trees experienced lengthened growing seasons as well, even after accounting for snowmelt timing and stem abundance. However, leaf area and stem abundance increased only with close tree proximity, with no effects of snowmelt timing on these aspects of performance.
4. *Synthesis*. Growing season length was disconnected from Dutchman's breeches' performance, with early snowmelt likely not the proximate cause of greater local abundance of this spring ephemeral herb around the base of deciduous trees. Instead, other factors associated with tree proximity, including edaphic conditions and microclimate buffering, may play a primary role in Dutchman's breeches' local distribution. Experimental manipulation of fine-scale environmental conditions

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and resource availability will prove increasingly informative for understanding population dynamics and community structuring in an era of rapid global change.

KEYWORDS
Dutchman's breeches, fine-scale environmental heterogeneity, microclimate, phenology, plant performance, temperate deciduous forest, understory spring ephemeral plants

1 | INTRODUCTION

Spatial and temporal heterogeneity in environmental conditions (e.g. topography, climate) and resources (e.g. water, light) influence species distributions and community structure (Cottenie, 2005; Stein et al., 2014). Though heterogeneity occurs across scales, recent research has increasingly focused on fine-scale environmental heterogeneity (e.g. microclimate; De Frenne et al., 2021; Lembrechts & Lenoir, 2020) to better link the conditions that individual organisms experience to their behaviour, ontogeny, physiology and phenology. However, the fine-scale distribution of organisms is often driven by multiple environmental factors simultaneously, making experimental manipulation of potential drivers essential for elucidating mechanisms underlying local species distributions.

For sessile organisms like plants, local environmental conditions and resource availability are particularly important for survival, growth and reproduction (Silvertown, 2004). Plant resources are not distributed evenly across space (e.g. Canham et al., 1994; Kleb & Wilson, 1997) nor are they continuously available through time (e.g. Cain et al., 1999). Spatial heterogeneity in resources and microclimate influences local plant species distributions in many ecosystems (Conti et al., 2017; Niittynen et al., 2020). Variation in resource availability through time is also important for local species distributions, contributing to temporal resource partitioning (Bratton, 1976; Stratton et al., 2000). However, since plants can only utilize temporally fluctuating resources if they are active while resources are available, understanding the drivers and implications of variable plant phenology is critical for determining local survival and performance (Forrest & Miller-Rushing, 2010).

Plant phenology—the timing of biological events like emergence and flowering—can vary with fine-scale environmental heterogeneity. Phenology is often advanced with topographic exposure (Jackson, 1966), earlier snowmelt (Billings & Bliss, 1959; Price & Waser, 1998) and warmer local temperatures (Reed et al., 2019; Stuble et al., 2021). However, shifted phenology does not always correspond to improved performance (Iler et al., 2021; Jerome et al., 2021; Zettlemoyer et al., 2024). For example, while earlier phenology can extend growing seasons (Gunderson et al., 2012), plants may experience early-season frost damage (Inouye, 2000; Richardson et al., 2018) or late-season drought-induced mortality (Iler et al., 2019), with some species only advancing rather than extending periods of activity (Rosa et al., 2015).

In temperate deciduous forest understories, resources and environmental conditions vary over fine spatial and temporal scales (Beatty, 2014; Givnish, 1982; Whigham, 2004). Abiotic factors like the timing and magnitude of light availability can affect community richness and flowering (Burton et al., 2014; Willems et al., 2021). Species occurrence and population sizes often vary with fine-scale topoedaphic conditions (Beatty, 1984; Catella et al., 2019; Struik & Curtis, 1962), such as the conspicuous clustering of some species near the bases of canopy trees. Greater population sizes of evergreen [e.g. *Anemone acutiloba* (DC.) G. Lawson] and deciduous spring ephemeral species (e.g. *Claytonia caroliniana* Michx.) have been observed nearer to than further from trees (Beck & Givnish, 2021; Bratton, 1976; Vellend et al., 2017). Increased fitness and performance near trees have also been observed for the spring ephemeral *Erythronium americanum* Ker Gawl. (Collins et al., 1984). Despite its apparent importance for local species distributions and community structuring, drivers of this pattern remain poorly understood.

Several hypotheses have been advanced to explain the greater local abundance and performance of certain understory species near tree trunks. Thin, leached soils adjacent to trees may exclude tall, deep-rooting herbs, increasing the performance of shallowly rooting species (Beck & Givnish, 2021; Bratton, 1976; Levia & Frost, 2003). Alternatively, nutrient-rich stemflow or high rates of nitrogen mineralization may enrich soils around trees (Andersson, 1991; Boerner & Koslowsky, 1989; Crozier & Boerner, 1984) potentially creating favourable microsites for nitrogen-demanding species like spring ephemerals (Muller, 1978; Neufeld & Young, 2014). Trees may also influence understory microclimates, shifting the timing of resource availability. Snow-free zones or 'thaw circles', can form around trees in spring prior to snowmelt in evergreen, deciduous and mixed temperate forests (Brooke et al., 1970; Veblen et al., 1977; Vellend et al., 2017). For deciduous trees, this often occurs when incident sunlight radiates from tree boles and raises local air temperatures, melting the snow around the base of trees (Geiger, 1965). Early snowmelt may shift the phenology of adjacent understory plants, with earlier emergence lengthening growing seasons by 1 week or more (an increase of ~25% for some species) and potentially contributing to improved performance and greater local abundance (Vellend et al., 2017). However, these hypothesized relationships among thaw circle formation, understory plant phenology and performance have not been experimentally tested. For spring ephemerals in particular, whose narrow window of photosynthetic activity is bounded by spring snowmelt and canopy closure (Givnish, 1987; Neufeld & Young, 2014), even marginal changes in the timing, amount or length of resource availability could have outsized effects on population performance (Lapointe, 2001).

In this study, we tested whether thaw circles around the base of deciduous trees influenced the phenology and performance of the spring ephemeral Dutchman's breeches [*Dicentra cucullaria* (L.) Bernh.], one of several species that cluster around tree trunks

(Bratton, 1976). To isolate the effects of thaw circle formation from other potential mechanisms, we experimentally planted Dutchman's breeches in a fully factorial design of manipulated snowmelt timing (early vs. late) and canopy tree proximity (near vs. far). We asked two questions: (1) How does the timing of emergence and the duration of the growing season vary with snowmelt timing and proximity to canopy trees? (2) How do variable snowmelt timing and tree proximity affect performance? We expected that early snowmelt would advance spring emergence, which in turn would contribute to longer growing seasons for Dutchman's breeches regardless of proximity to canopy trees. We expected this to cascade to performance, with greater abundance and leaf area for experimental plants that experienced early snowmelt both near and far from trees.

2 | MATERIALS AND METHODS

2.1 | Study system

We conducted our study on the east-facing slope of Mont St-Joseph in Mont-Mégantic National Park within the Eastern Townships of Québec, Canada (Figure 1; Vellend et al., 2021). The annual climate is cool, with 30-year (1981–2010) average temperatures ranging from −11.3°C in January to 17.5°C in July (Notre-Dame-des-Bois station #7025670; Government of Québec, 2024). Annual precipitation over the same period averaged 1367 mm, with ~70% falling as rain (Government of Québec, 2024). The park is mostly forested and underlain by humo-ferric and ferro-humic shallow podzols (Marcotte & Grandtner, 1974). Our study site (~220 × 220 m) was located within a deciduous forest dominated by sugar maple (*Acer saccharum* Marsh.) at ~740 m above sea level.

Among several understory spring ephemerals at the site, Dutchman's breeches was chosen because of its propensity to cluster around canopy tree bases (Bratton, 1976) and its relatively low local abundance, minimizing any confusion between experimental and naturally occurring plants. This species primarily occurs in mesic deciduous forests across eastern and central North America, with some populations in the northwestern United States (Stern, 1961). Foliage leaves (i.e. not the minute scale leaves found below-ground) are the only vegetative above-ground plant part, emerging annually from subterranean tuberous leaf bases (Walton & Hufford, 1994). As such, the number and size of foliage leaves provide an estimate of total above-ground vegetation plant size and thus performance. Dutchman's breeches' foliage leaves emerge prior to canopy closure in the spring and last 4–7 weeks (often towards the shorter end at our relatively northern location), during which time mature individuals flower for ~1–2 weeks (Neufeld & Young, 2014; Schemske et al., 1978). For simplicity, given how plants appear in the field, we refer to foliage leaves as 'leaf-bearing stems'. Below-ground, one individual consists of several parts (described in Walton & Hufford, 1994). The 'leaf base zone' typically includes three large tuberous leaf bases and renewal buds for the next year's growth in one coherent structure; below the leaf base zone are numerous (>10) small tuberous leaf bases, which readily detach from the large leaf base zone upon excavation. Flowers are primarily bee pollinated,

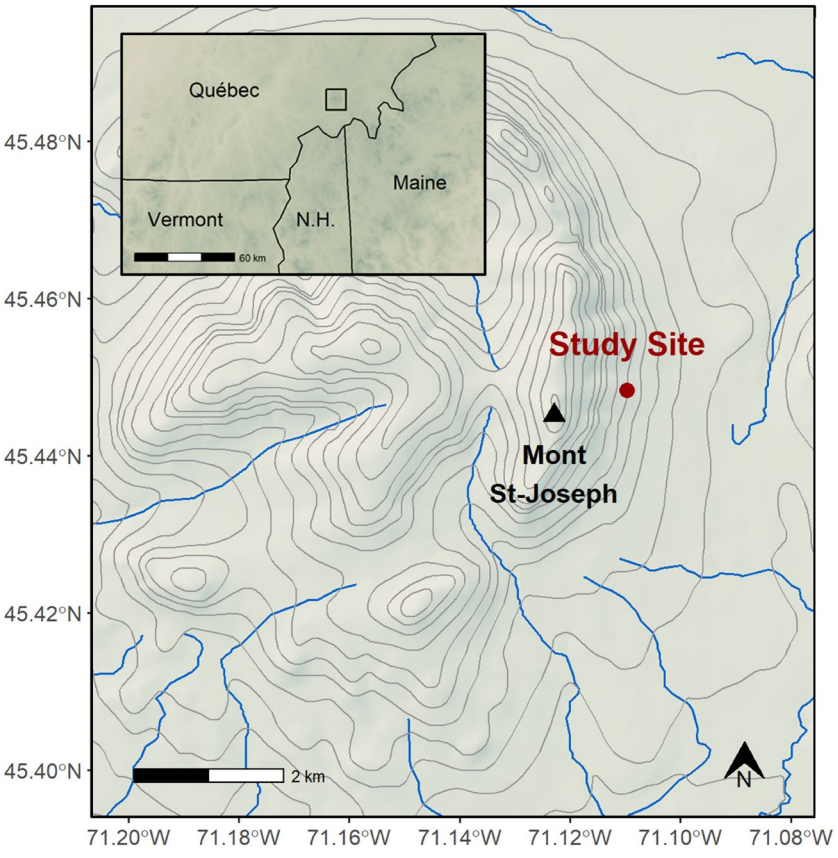


FIGURE 1 Study site location on the east-facing slope of Mont St-Joseph in Mont-Mégantic National Park (Québec, Canada).

and individuals are obligately outcrossing (Macior, 1970; Schemske et al., 1978). Seeds are ant-dispersed (Berg, 1969; Stern, 1961), but individuals may also spread vegetatively via plagiotropic rhizomes (Walton & Hufford, 1994).

2.2 | Study design and data collection

To test the effects of snowmelt timing and tree proximity on Dutchman's breeches phenology and performance, we selected 80 mature sugar maple trees (i.e. with crowns in the upper forest canopy) that had no other large tree trunks within 2 m. Within a relatively homogenous area of forest dominated by sugar maple (over several hectares), we expanded out from the first tree until 80 trees were found that met our criteria. These trees were randomly assigned to two treatments: early snowmelt (i.e. naturally occurring thaw circles) and late snowmelt (i.e. snow addition to thaw circles to delay snowmelt). Within the area encompassing these 80 trees, we then placed 80 'far' plots 2–5 m away from a focal tree. We first chose a random cardinal direction (°) and distance (between 2 and 5 m) from the focal tree and repeated this as necessary until a location was found that was not on a large rock or fallen log, and >2 m from any other trees with a >10 cm diameter at breast height (DBH), well outside of naturally occurring thaw circles. These plots were randomly assigned to one of two treatments: early snowmelt (i.e. snow removal to match snowmelt timing of nearby thaw circles) and late snowmelt (i.e. naturally later snowmelt). For plots far from trees with early snowmelt, all snow in a 0.5-m radius around transplants (~1.3 m^2) was removed, concurrent with the formation of naturally occurring thaw circles around adjacent canopy trees. At the same time, snow was added to thaw circles in the late snowmelt, near tree plots. Snow depth was manipulated and measured weekly beginning in February of both years until the entire site was snow-free each spring.

In each plot ($n = 160$), we established three 10 × 10 cm subplots separated by ~10 cm, within which we planted either (1) one leaf base zone (hereafter, large size class), (2) ten small tuberous leaf bases (hereafter, small size class) or (3) no individuals. Treatments were randomly assigned to subplots. Large and small size classes are physiologically and developmentally distinct plant parts (see above) and were planted in separate subplots because of potential differences in their phenology and performance (Austen et al., 2017; Sercu et al., 2021). In plots near trees, individuals were planted within ~30 cm of the tree trunk on the southwest side of the canopy sugar maple stem to reduce shading from the focal tree trunk. Subplots without planted individuals served as controls to monitor naturally occurring individuals. Despite low abundance in our control plots [Dutchman's breeches present in six (2.8%) and 11 (6.9%) control plots in 2018 and 2019, respectively; Table S1], naturally occurring individuals tended to occur more often in plots near trees (Table S2). However, the difference in abundance between experimentally planted near vs. far plots exceeded that in controls (Appendix S1). As such, we treated individuals in planted plots as those that were experimentally added, acknowledging that some may be naturally occurring. Planted Dutchman's breeches were excavated from adjacent forest stands outside of the study area in 2017, planted in experimental plots the following day and monitored in spring 2018 and 2019.

Temperature loggers (HOBO U23 Pro v2) were installed in a subset of randomly chosen plots in each treatment combination in 2018 ($n = 3$ in early-far, 3 in early-near, 2 in late-far and 2 in late-near) to track the potential influence of treatments on microclimate (i.e. air temperature; °C). Loggers were shielded from solar radiation and positioned at the soil surface. Slope (°) was measured using a clinometer, both surrounding the plot over ~5 m (hereafter, macroslope) and within the plot over ~1 m (hereafter, microslope), and, for plots planted near trees, the DBH (cm) was recorded for the adjacent canopy tree (Table S2).

For each planted subplot, we quantified several aspects of plant phenology and performance in 2018 and 2019: (1) the timing of emergence (i.e. the day of year of the first observed individual); (2) the length of the growing season, which we define as the time between emergence and either (a) the date on which the last individual was observed (hereafter, senescence) or (b) canopy closure; (3) the maximum number of leaf-bearing stems; and (4) the total leaf area (cm^2), which was estimated non-destructively for each leaf using leaf length and width measurements and a locally derived allometric equation (Figure S1). The day of year (DOY) of canopy closure (75% leaf out) in 2018 (149.5) and 2019 (161) was estimated using nearby phenological cameras established for a separate study (Gamhewa, 2023). The abundance and area of leaves capture total above-ground vegetative plant size, consistent with other measures of plant performance (e.g. biomass, percent cover; Cleland et al., 2012; León-Sánchez et al., 2018) as intermediaries between an individual's phenotype and fitness (Arnold, 1983).

Plots were visited at least 15 times in both 2018 and 2019 to manipulate snowmelt early in the spring and to assess phenology and performance during the growing season. The interval between census dates varied seasonally and between years due to logistical constraints, but visits occurred at 2–7 day intervals during peak activity (April–June). In each census, emerged stems with leaves in each subplot were assigned to one of four phenophases: fully expanded, yellowing, partially wilted and fully wilted. Leaf area was estimated once for each subplot in 2018 (31 May or 2 June) and 2019 (12 June) during or close to maximum stem abundance.

2.3 | Data analyses

We fit several models to determine how phenology, growing season length and performance varied between treatments and across local environmental conditions. In addition to snowmelt timing (early vs. late) and tree proximity (near vs. far) as primary foci, we included additional predictors over which phenology and performance may vary, including initial plant size class (small vs. large), microslope (°) and macroslope (°). Given that the tails of phenological distributions (i.e. 'firsts' and 'lasts') are sensitive to population size (Miller-Rushing et al., 2008; Primack et al., 2023), we also included peak stem abundance as a predictor of emergence and senescence (see below). In

all models, we used early snowmelt, near trees and small individuals as the reference levels for our categorical predictors; microslope, macroslope and stem abundance were *z*-transformed to allow comparison between coefficient estimates. In addition, we fit separate models just for plots planted near trees to determine how growing season length and performance varied with adjacent tree size (DBH) which may influence thaw circle area (Veblen et al., 1977). Separate models were fit for 2018 and 2019 in all cases because of differences in the onset of spring (Figure S3) and to isolate potential cumulative treatment effects in the second year of the experiment.

2.3.1 | Phenology

To determine drivers of variation in growing season length, we first fit interval-censored, proportional odds Bayesian regression models to estimate the timing of emergence and senescence in each planted subplot. Interval-censored models account for uncertainty in the timing of phenological events by including both the DOY on which an event was observed and either the previous or subsequent census date (for emergence and senescence, respectively) as bounds within which the event occurred. Bayesian models were fit with the icenReg package (Anderson-Bergman, 2017) and included weakly informative priors [$N(0, 100)$], four Markov chain Monte Carlo chains with 1000 runs each (after 2000 runs for burn-in), a thinning interval of five and a Weibull baseline parametric distribution for the response variable. Convergence was assessed by trace plots, and significant predictors (see above) of either emergence or senescence were those for which 95% credible intervals did not overlap zero. The posterior median DOY of emergence and senescence was estimated for each subplot. Subplots with no emergence were not included (2018: $n=11$ and 13 subplots planted with small and large individuals, respectively; 2019: $n=35$ and 31).

We then quantified growing season length using the estimated DOY of emergence and either (a) the estimated DOY of senescence or (b) canopy closure, depending on which occurred first. To determine drivers of variation in growing season length ($\alpha=0.05$), we fit a generalized linear model with a Gaussian distribution with all the above predictors except peak abundance. Peak abundance was not included here because it was already accounted for in our estimates of emergence and senescence, and it was not the focus of our analysis (which, instead, was snowmelt timing and tree proximity). Finally, we combined subplots within plots planted near trees to determine the effect of tree DBH on growing season length across all individuals in small and large size classes.

2.3.2 | Performance

Generalized linear models were next fit to identify important predictors ($\alpha=0.05$) of peak stem abundance and leaf area. Peak stem abundance, the maximum number of censused stems with fully expanded leaves, was treated as a count variable and included all plots (i.e. including those with no emergence; $n=160$ subplots planted with small and large individuals in each year). Because of overdispersed model residuals (Appendix S1), models were fit with a negative binomial distribution using the MASS package (Venables & Ripley, 2002). We then regressed peak stem abundance summed across subplots planted with individuals in small and large size classes over tree DBH for plots near trees.

Leaf area was defined as the total estimated area of all leaves within subplots regardless of phenophase (i.e. fully expanded through senescing leaves). Only plots with measured leaf area were included for analysis (2018: $n=140$ and 143 subplots planted with small and large individuals, respectively; 2019: $n=102$ and 99). Data for leaf area, as a continuous response variable, were positively skewed in both years (Figure S2), so our generalized linear models were fit with a gamma distribution and log link. Finally, we regressed the total leaf area from both subplots across tree DBH for plots planted near trees.

All data analyses and visualization were done in *R* (R Core Team, 2023) using the above packages and ggplot2, ggpubr, ggspatial, raster, terra and tidyterra (Dunnington, 2022; Hernangómez, 2023; Hijmans, 2023a, 2023b; Kassambara, 2023; Wickham, 2016).

3 | RESULTS

Snow manipulation successfully shifted the timing of snowmelt in both 2018 and 2019, with early and late snowmelt treatments tracking one another regardless of tree proximity (Figure S3). However, earlier snowmelt did not necessarily mean consistently warmer microclimate temperatures. In the subset of plots with temperature loggers, plots near trees accumulated more growing degree days throughout the growing season in 2018 than plots far from trees regardless of snowmelt timing (Figure S4).

3.1 | Dutchman's breeches' phenology

Early snowmelt prompted earlier emergence for planted Dutchman's breeches in both 2018 (95% credible interval = 0.52–1.26) and 2019 (0.78–1.74; Table S4). This led to growing seasons that were ~2 days longer with early snowmelt in 2018 and ~4.3 days longer in 2019 (Figure 2), corresponding to 10%–19% longer growing seasons in naturally occurring thaw circles and where snowmelt was experimentally removed. Emergence also occurred earlier near versus far from trees in 2018 (0.14–0.94; Table S4) while plants senesced later near trees in 2019 (−1.42 to −0.41; Table S5), which together contributed to growing seasons that were 1.4–3.3 days longer near trees regardless of snowmelt timing (Figure 2). Growing seasons did not vary with tree DBH for plots close to trees (Table 1) but emergence tended to occur earlier and senescence later in subplots with greater stem abundance, supporting the notion that phenology estimates across groups of individuals are sensitive to population size (Tables S4 and S5). Subplots planted with larger individuals also experienced growing seasons that were 15% longer than those with small individuals in 2019 (Figure 2).

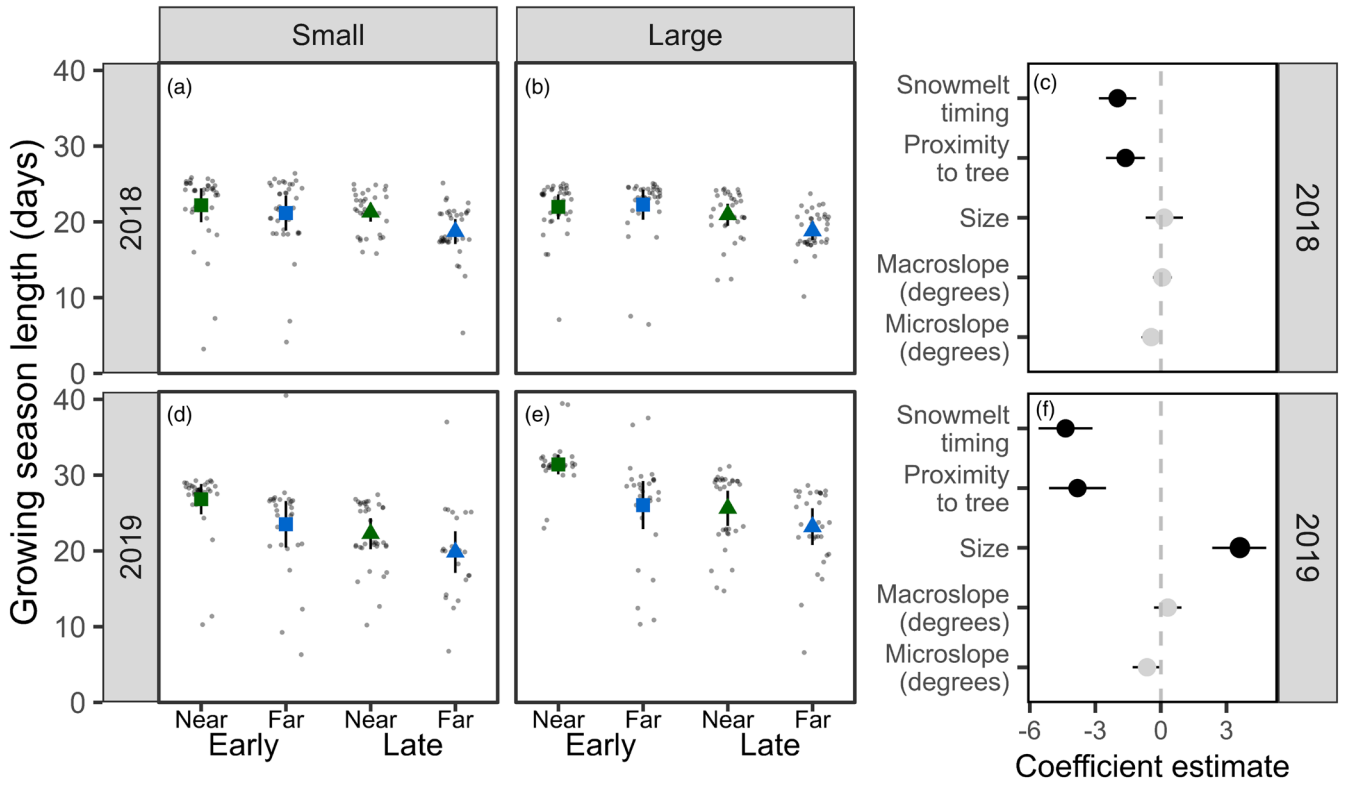


FIGURE 2 Growing season length (days) for experimentally planted small and large Dutchman's breeches. Mean (±3 SE) growing season lengths are shown for small (a, d) and large (b, e) individuals measured in 2018 (a, b) and 2019 (d, e) across treatments of snowmelt timing (early vs. late; squares and triangles, respectively) and tree proximity (near vs. far; green and blue, respectively). Coefficient estimates and 95% confidence intervals of potential predictors of growing season length are shown for 2018 (c) and 2019 (f). Grey coefficient estimates are not different from zero ($\alpha = 0.05$). Early snowmelt, near trees and small individuals are the references for the three categorical predictors.

TABLE 1 Simple linear regression models of Dutchman's breeches phenology and performance over tree diameter at breast height (DBH) for experimental plants near trees in a temperate deciduous forest in Mont-Mégantic National Park (Québec, Canada).

Response variable	Year	Estimate ± SE	*F*-statistic (degrees of freedom)	*p*	R^2_{adj}
Growing season length (days)	2018	−0.01 ± 0.04	0.02 (1, 72)	0.90	−0.014
	2019	0.02 ± 0.05	0.19 (1, 72)	0.66	−0.011
Peak stem abundance	2018	0.10 ± 0.05	4.76 (1, 77)	0.032	0.046
	2019	0.26 ± 0.09	7.51 (1, 77)	0.0076	0.077
Leaf area (cm^2)	2018	0.09 ± 0.10	0.94 (1, 76)	0.34	−0.001
	2019	0.23 ± 0.16	2.09 (1, 68)	0.15	0.015

Note: All response variables were considered across subplots planted with small and large individuals.

3.2 | Dutchman's breeches' performance

Despite its consistent influence on phenology, snowmelt timing did not affect performance. Instead, peak stem abundance was markedly lower further from trees in both 2018 (20% fewer stems) and 2019 (51% fewer stems) regardless of snowmelt timing (Figure 3). Fewer large individuals were planted than small individuals, and this difference persisted (Figure 3). Peak stem abundance did not vary with macro- or microslope, but for those plots near trees, increased with canopy tree DBH in both 2018 and 2019 (Table 1; Figure S5).

Total leaf area was 35% and 44% lower far from trees than near trees in 2018 and 2019, respectively (Figure 4). Total leaf area was greater in subplots with initially large individuals than in subplots with small individuals in both years (Figure 4). Leaf area also declined in plots with greater microslope in both 2018 and 2019 (Figure 4), but did not vary with macroslope or, for plots near trees, stem DBH (Table 1).

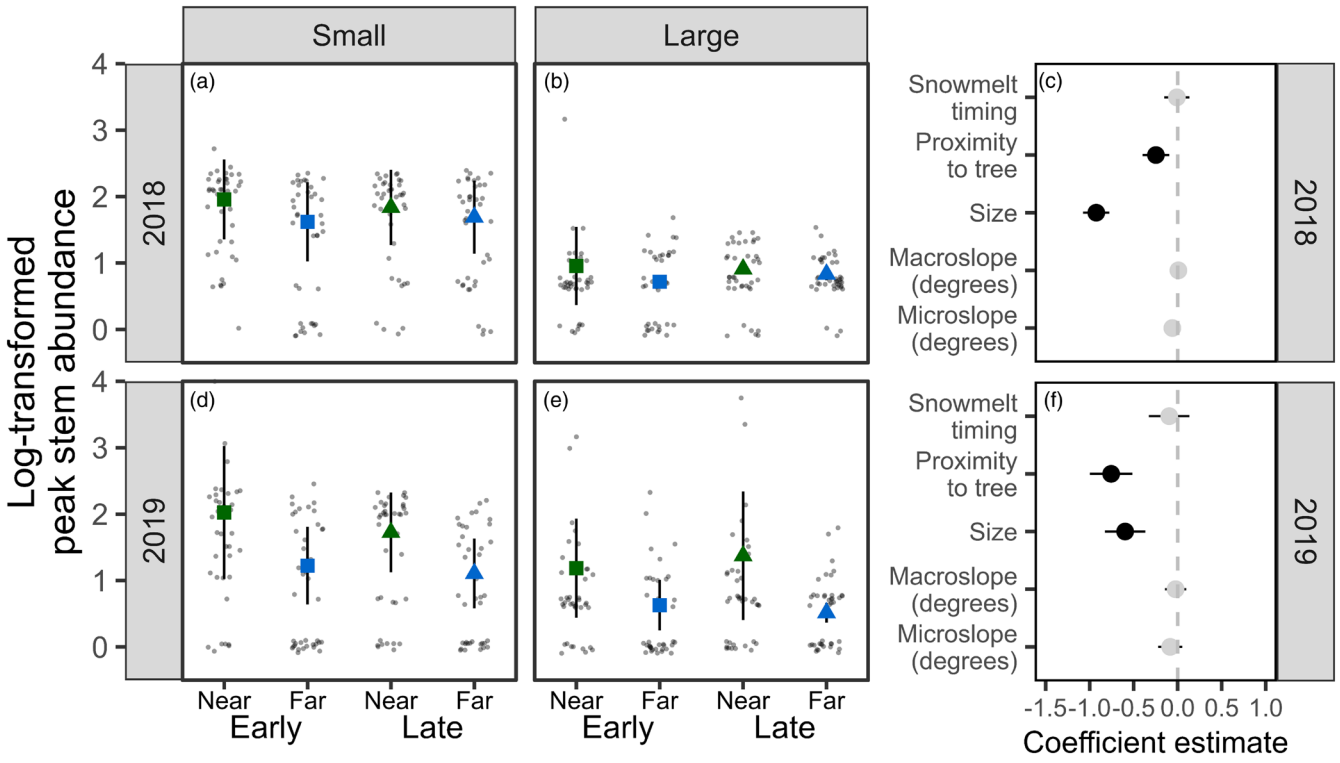


FIGURE 3 Peak abundance for experimentally planted small and large Dutchman's breeches [logarithm-transformed (base 10) for presentation]. Mean peak abundance (±3 SE) is shown for small (a, d) and large (b, e) individuals measured in 2018 (a, b) and 2019 (d, e) across treatments of snowmelt timing (early vs. late; squares and triangles, respectively) and tree proximity (near vs. far; green and blue, respectively). Coefficient estimates and 95% confidence intervals for potential predictors of peak abundance are shown following generalized linear regression modelling of peak abundance in 2018 (c) and 2019 (f). Grey coefficient estimates are not different from zero ($\alpha = 0.05$). Early snowmelt, near trees and small individuals are the references for the three categorical predictors.

4 | DISCUSSION

Early snowmelt—whether experimentally induced or naturally occurring in thaw circles—provided longer growing seasons for Dutchman's breeches transplants (research question 1). However, these extended growing seasons did not alter performance (research question 2). Instead, peak stem abundance and leaf area were greater near canopy trees where, regardless of snowmelt timing, growing seasons were also longer. Stem abundance increased with increasing diameter of the adjacent tree, while growing season length did not, suggesting this species' greater performance and natural local clustering near canopy trees is independent of phenology. Shifts in performance and phenology were typically greater in 2019 than in 2018, either because of cumulative effects over two growing seasons (i.e. greater resource acquisition in subplots with more leaf-bearing stems and leaf area) or year-to-year differences in the onset of spring. Together, these results clearly implicate factors other than early snowmelt and thaw circle formation in the locally high abundance of Dutchman's breeches and likely other understory herbaceous plant species, around the bases of temperate deciduous canopy trees.

4.1 | Early snowmelt does not improve performance

The failure of earlier emergence and extended growing seasons in early snowmelt treatments to confer performance advantages was unexpected. Spring ephemerals rely on the high-light forest understory environment prior to canopy leaf out for carbon assimilation (Heberling, Cassidy, et al., 2019; Rothstein & Zak, 2001) and the importance of the length of this spring window has received considerable attention in the context of anthropogenic climate change (Jacques et al., 2015; Lee, Alecrim, et al., 2024). However, if extended growing seasons result primarily from earlier emergence rather than later senescence, exposure to colder temperatures or severe frost early in the spring may reduce spring ephemeral performance (Augspurger & Salk, 2017) and, though not the direct focus of this study, survival (Tessier, 2022). We observed frost damage to some individuals in 2019, but these were not concentrated in particular treatments, and our experiment was not designed to test the effects of temperature on performance. Regardless, our results indicate that extending the growing season via early snowmelt by up to ~4 days was not enough to improve performance during our

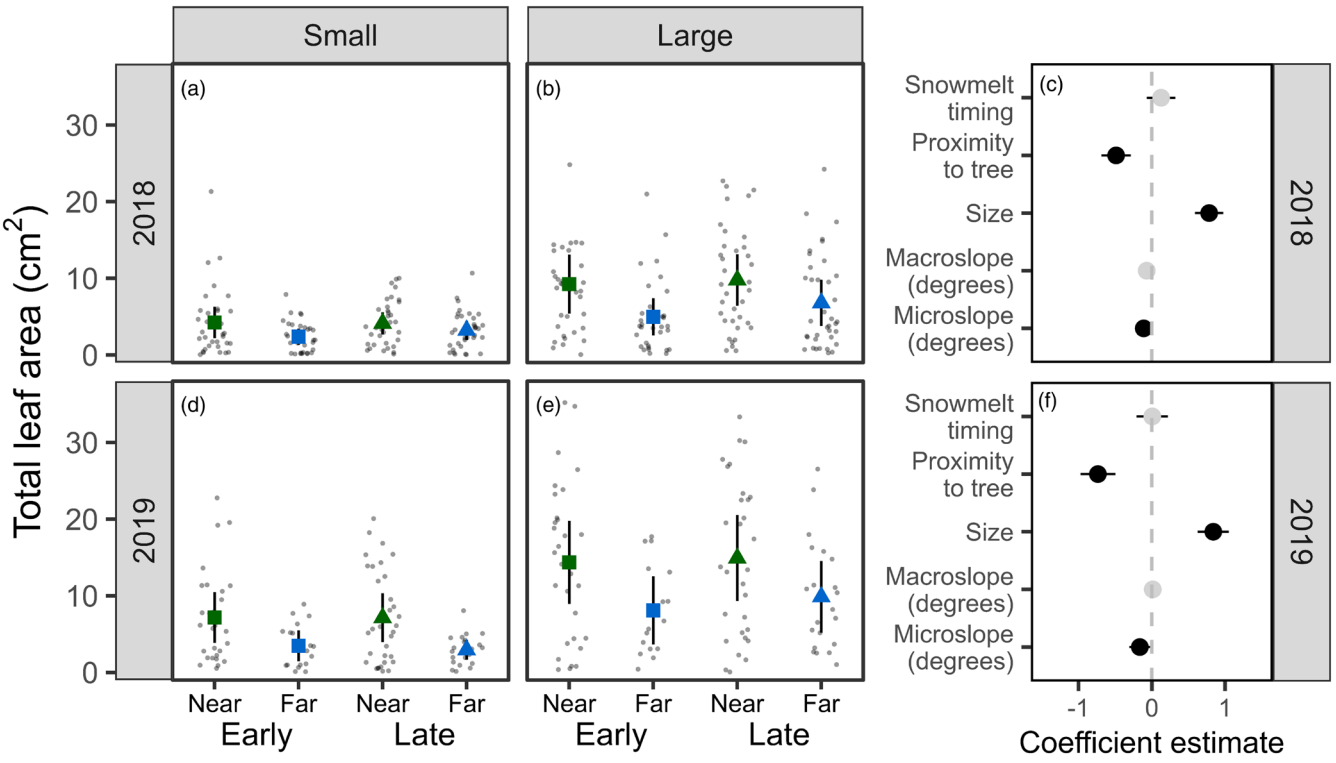


FIGURE 4 Total leaf area (cm^2) of experimentally planted small and large individuals of Dutchman's breeches. Mean leaf area (±3 SE) is shown for subplots of small (a, d) and large (b, e) individuals measured in 2018 (a, b) and 2019 (d, e) across treatments of snowmelt timing (early vs. late; squares and triangles, respectively) and tree proximity (near vs. far; green and blue, respectively). Coefficient estimates and 95% confidence intervals for potential predictors of total leaf area are shown following generalized linear regression modelling for 2018 (c) and 2019 (f). Grey coefficient estimates are not different from zero ($\alpha = 0.05$). Early snowmelt, near trees and small individuals are the references for the three categorical predictors.

two-year study. This, coupled with the snowmelt-independent influence of tree proximity on both growing season length and plant performance, illustrates how microsite suitability depends simultaneously on both the quality and quantity of resources *and* buffering from suboptimal environmental conditions.

Several alternative mechanisms to explain the local clustering of some understory plant species around trees warrant further investigation. Stemflow during precipitation events influences soil moisture and nutrient availability at the base of canopy trees (Levia & Frost, 2003). For example, white oak (*Quercus alba*) stemflow appears to locally enrich soils through ion leaching from tree bark, which in turn positively correlates with the abundance of several understory species across seasonal photosynthetic guilds (Crozier & Boerner, 1984). However, plant-available nutrients may bypass upper soil horizons via root-induced preferential flow (i.e. funnelling of water and nutrients along tree roots; Johnson & Lehmann, 2006), potentially rendering nutrients unavailable for shallowly rooted herbaceous individuals. Thinner soils adjacent to tree trunks might similarly influence local plant distributions, potentially precluding the establishment of species with relatively large, deep root systems (Beck & Givnish, 2021). This soil-depth hypothesis is consistent with Bratton's (1976) observation that some understory species reach greater abundance near both trees and boulders. Further, it allows for the possibility that this phenomenon is independent of phenology, which appears to be the case.

Alternatively, microclimate buffering near trees in spring—independent of snowmelt timing—has largely been ignored as a potential factor influencing local species distributions. Although we had only a small number of temperature loggers, accumulated growing degree days in 2018 were noticeably greater near trees regardless of snowmelt timing (Figure S4). Solar irradiance that contributes to thaw circle formation in late winter may similarly increase post-snowmelt temperatures close to tree trunks. Warming can improve individual growth and reproduction for certain species (De Frenne et al., 2011; Jacques et al., 2015), and tree trunk temperatures can warm to ~25°C above ambient air temperatures in spring (Webster et al., 2016). This is consistent with the observed longer growing seasons for Dutchman's breeches near trees in our experiment, even after accounting for snowmelt timing and peak abundance. Given several interrelated factors distinguishing microsites near vs. far from trees, field experiments (e.g. redirecting stemflow or manipulating nutrients or temperature) like the one presented here are necessary to disentangle the various potential proximate and ultimate causes of understory species associations with trees. Regardless of the mechanisms, the increased abundance of spring ephemerals near tree trunks is likely to influence community- and

ecosystem-level processes since spring ephemerals themselves alter local soil nutrient dynamics (Anderson, 2014; Muller, 2014).

4.2 | Implications beyond leaf area and abundance

While leaf area and stem abundance are useful measures of plant performance, fine-scale variation in growing conditions and spring phenology may have consequences for other aspects of performance and fitness not measured here. For example, phenological asynchrony across plant subpopulations (e.g. between those inside and outside thaw circles) could lead to temporal reproductive isolation (Rivest et al., 2023), reducing gene flow and possibly seed set. Dutchman's breeches also rely on invertebrates for pollination and seed dispersal (bees and ants, respectively; Macior, 1970; Schemske et al., 1978; Stern, 1961). Phenological mismatch between plants and their pollinators may be amplified with earlier snowmelt (Kudo & Cooper, 2019; but see Sevenello et al., 2020) and have outsized negative effects for obligately outcrossing species like Dutchman's breeches. While we did not quantify plant fitness, others have found reduced reproduction with warming and early snowmelt in some perennial plant populations (Zettlemoyer et al., 2024). However, greater leaf area (and thus potential resource acquisition) for individuals near tree bases coupled with this species' ability to spread vegetatively (Walton & Hufford, 1994) may minimize any adverse effects of reduced gene flow, flowering and seed set. Determining the fitness consequences of varied phenology and microsite location for this and other species is an important next step.

Intensive study of a single species in an experimental field setting was critical for isolating the effects of one potential driver of its local distribution. A key challenge to predicting consequences of global change is understanding how complex fine-scale spatial and temporal environmental heterogeneity interacts with broad-scale gradients to influence species performance and abundance (Denney et al., 2020). For example, the importance of phenological escape for spring ephemerals, and thus the potential effects of shifted phenology, varies with latitude in eastern deciduous forests (Alecrim et al., 2023; Lee, Yancy, & Heberling, 2024). Additionally, ephemerality (the extent to which a species' above-ground activity only occurs prior to spring canopy closure) can vary across a species range (Yancy et al., 2024), suggesting environmental drivers of fine-scale abundance and fitness may vary among populations of the same species. Dutchman's breeches is one of the many spring ephemeral species that contribute to the considerable diversity of temperate forest understories (Gilliam, 2007) and provide cultural ecosystem services (e.g. aesthetic beauty of areas with greater wildflower abundance) (Graves et al., 2017). These species may experience shifts in the onset, quality and length of the spring growing season with climate change, depending on how the timing of tree canopy closure also responds to warming (Heberling, McDonough MacKenzie, et al., 2019; Lee et al., 2022).

5 | CONCLUSIONS

Our study highlights the importance of linking fine-scale environmental variability, phenology and performance for determining the drivers of local species distributions. Extended growing seasons, either naturally or via anthropogenic climate change, do not guarantee improved performance, even for spring ephemeral species like Dutchman's breeches with a short period of above-ground activity. Continued research conducted at the scale at which organisms experience and respond to their environment will be important for elucidating mechanisms of species distributions, local occurrence and thus whole community assembly. Insights such as these are crucial for understanding the natural history of ecologically and culturally significant species, which in turn are needed to anticipate their responses to global change.

AUTHOR CONTRIBUTIONS

David A. Watts, Amanda B. Young and Mark Vellend designed the study and performed the research. Nathan G. Kiel and Mark Vellend analysed the data. Nathan G. Kiel and Mark Vellend wrote the manuscript with contributions from David A. Watts and Amanda B. Young.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data are available with the Environmental Data Initiative: https://doi.org/10.6073/pasta/0aac8d39cd71bc6991eb73df408ad279 (Kiel et al., 2025).

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SUPPORTING INFORMATION

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

Table S1: Stem abundance of naturally occurring Dutchman's breeches populations in a temperate deciduous forest in Mont-Mégantic National Park (Québec, Canada).

Table S2: Mean difference in abundance of naturally occurring Dutchman's breeches populations in a temperate deciduous forest in Mont-Mégantic National Park (Québec, Canada).

Table S3: Abiotic factors measured for all plots (macro- and microslope; °) or just those plots close to trees (tree diameter at breast height; cm) in a temperate deciduous forest in Mont-Mégantic National Park (Québec, Canada).

Table S4: 95% credible intervals for predictors in the interval-censored Bayesian regression model for the start of the growing season (i.e., plant emergence; DOY) of experimentally planted Dutchman's breeches.

Table S5: 95% credible intervals for predictors in the interval-censored Bayesian regression model for end of growing season (i.e., plant senescence; DOY) of experimentally planted Dutchman's breeches.

Figure S1: Allometric relationship between Dutchman's breeches leaf area (cm^2) and the product of leaf length and width (cm^2).

Figure S2: Histograms of subplot leaf area (cm^2) of Dutchman's breeches in a temperate deciduous forest in Mont-Mégantic National Park (Québec, Canada) in both (a) 2018 and (b) 2019.

Figure S3: Snow cover (%) (±3 SE) throughout late winter and spring in 2018 (a) and 2019 (b) in each treatment combination of manipulated microsite location (near vs. far from tree trunks; green and blue, respectively) and snowmelt timing (early vs. late; light and dark shading, respectively) in a temperate deciduous forest in Mont-Mégantic National Park (Québec, Canada).

Figure S4: Accumulated growing degree days (°C) at the soil surface (measured with HOBO U23 Pro v2 temperature loggers) throughout spring 2018 in each treatment combination of manipulated microsite location (near vs. far from tree trunks; green and blue, respectively) and snowmelt timing (early vs. late; light and dark shading, respectively) in a temperate deciduous forest in Mont-Mégantic National Park (Québec, Canada).

Figure S5: Peak stem abundance of Dutchman's breeches plots (combined subplots planted with small and large individuals) planted near trees over variable tree size [diameter at breast height (cm)] in 2018 (a) and 2019 (b) within a temperate deciduous forest in Mont-Mégantic National Park (Québec, Canada).

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