PHENOLOGICAL ESCAPE AND ITS IMPORTANCE FOR UNDERSTORY PLANT SPECIES IN TEMPERATE FORESTS

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Understory forest plants are often limited by shade from the canopy above them. Many such species therefore make use of a shade avoidance strategy referred to as "phenological escape" to access ephemeral light availability during periods when the canopy above them is open (e.g., in early spring). In this primer, we review past literature on phenological escape and related topics. We discuss (1) the physiological importance of this shade avoidance strategy, (2) the effects that climate change may have on species performance via changes in phenological escape, (3) the potential for climate change to result in phenological mismatch related to shade avoidance, and (4) the potential avenues of future research in this area of study. Phenological escape is an important strategy used by spring-active plant species ranging from spring ephemeral wildflowers to deciduous tree seedlings, allowing them to assimilate 50%–100% of their annual carbon budgets before the canopy closes above them. Access to spring light, and thus success of this shade avoidance strategy, is projected to change in response to climate change. Change in access to light, and therefore change in spring performance, likely depends on functional group (woody vs. nonwoody plants), continent, and other geographic and environmental drivers.

Keywords: phenology, carbon gain, spring, fall, spring ephemeral wildflower, deciduous, phenological mismatch, understory biodiversity.

Introduction

Forests can seem like static natural cathedrals, but these ecosystems are constantly changing—year to year and season to season. Seasonal change is perhaps best exemplified in temperate deciduous forests, which are governed so much by differences in environmental conditions that we use terms associated with plant life cycles such as "growing season" and "[leaf] fall" interchangeably with "summer" and "autumn." Importantly, the timing of these seasonal life history events, which is generally referred to as phenology (see "Glossary"), varies over years in response to interannual variation in the environmental conditions that cue it.

This variation in phenology has many important effects on individual-, population-, and community-level plant performances, largely through overlap in resource availability and activity periods with other plants and animals (here and throughout, we define activity period as the duration of all aboveground activity, particularly photosynthesis in green tissues, but including flowering, fruiting, and activity of nonplants, such as flower visitation by pollinators). For the former, plants are often adapted such that their activity overlaps strongly with the availability of critical resources while often avoiding activity during particularly stressful periods. Deciduous species, for example, are primarily active in spring and summer, when they can minimize frost damage and optimize access to soil nutrient pools, liquid water, and temperatures suitable for maintaining active photosynthesis. Initiating activity too early can lead to damage from frost that stunts growth and reduces reproductive success (Vitasse et al. 2014; Augspurger and Salk 2017), whereas waiting too long in spring to initiate the growing season can lead to suboptimal carbon assimilation as a result of a competitive disadvantage for limiting resources (Kwit et al. 2010; Lee and Ibáñez 2021*b*). Mismatch between plants and critical resources can thus play a large role in governing ecological processes ranging from intraspecific demography to interspecific coexistence (Visser and Gienapp 2019).

Phenological mismatch (see "Glossary") specifically describes asynchrony in the timing of biotic interactions and implies a deviation from average or evolved interactions. This typically (but not always) implies a negative fitness consequence for at least one of the interacting organisms. As reviewed by Renner and Zohner (2018), David Cushing (1990) initially used this term to describe a lack of synchrony in activity between Arctic cod larvae and their planktonic food source. Since then, it has been

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used to describe phenological asynchrony between predator and prey (Damien and Tougeron 2019), between producer and consumer (Kharouba and Wolkovich 2020), between plants and pollinators (Kudo and Ida 2013; Gérard et al. 2020), and between competitors (Nakazawa and Doi 2012; Stenseth et al. 2015; Visser and Gienapp 2019; Labonté et al. 2023). However, studies of plant phenological mismatch have focused predominantly on plant interactions with animals as either consumers or pollinators. Plant-plant mismatch is often studied only in the context of indirect competition for pollinators (e.g., Anderson and Schelfhout 1980; Labonté et al. 2023).

Over the past decade, several studies have begun to highlight the ways in which direct plant-plant interactions (primarily reproduction and competition) are affected by phenological asynchrony. For example, a mismatch between male and female individuals of dioecious species could affect reproductive success under increased asynchrony (Forrest 2014; Yang et al. 2022). Furthermore, high variability in phenology within populations of wind-pollinated plants has been directly linked to reduced reproductive success (Koenig et al. 2012), suggesting that flowering phenology in such species is subject to strong stabilizing selection. These case studies provide initial evidence that seed set and fruit production can be directly affected by asynchrony between plants, irrespective of plant-pollinator interactions.

Several reviews have previously described in great detail various types of phenological mismatch and how they affect plant communities (Wolkovich and Cleland 2011; Visser and Gienapp 2019). In this primer, we focus on evidence for a specific type of niche partitioning that is absent from previous reviews on phenological mismatch but that has been recently implicated as likely to be negatively affected by future climate change. This ecological strategy, called phenological escape (see "Glossary"; Jacques et al. 2015; Heberling et al. 2019*b*; Lee and Ibáñez 2021*a*, 2021*b*), refers to understory plants avoiding shade to gain access to light by emerging earlier than canopy trees in temperate deciduous forests. That is, by occupying a different temporal niche than canopy trees, understory plants escape summer shady periods to improve their photosynthetic performance. Understory plants emerge and/or leaf out up to several weeks before nearby canopy trees so as to assimilate 50%–100% of their annual carbon budgets in early spring prior to being shaded out (Kwit et al. 2010; Heberling et al. 2019*a*; Lee and Ibáñez 2021*b*), and access to this ephemeral resource is strongly implicated as affecting various metrics of plant performance, such as growth, survival, and reproductive success (Kudo et al. 2008; Kwit et al. 2010; Heberling et al. 2019*b*; Lee and Ibáñez 2021*a*, 2021*b*). Access to spring light is projected to change because of differences in phenological sensitivity (see "Glossary") to various environmental forcing cues between understory plants and co-occurring canopy trees (Heberling et al. 2019*b*; Lee and Ibáñez 2021*a*; Lee et al. 2022), suggesting that it is a prime candidate for current and future phenological mismatches. Here, we describe (i) the physiological importance of access to early spring light for understory plant species, (ii) the causes of shifts in canopy and understory phenology and the consequences to access to light, and (iii) the ecological implications for changing phenological escape as a case study in phenological mismatch, particularly within the context of projected climate change.

Physiological Importance of Access to Spring Light Availability

Ecosystems are often defined by the resource limitations that shape plant communities, with mean temperature, temperature variability, and water availability being the predominant drivers. In that sense, temperate deciduous forests are defined by their seasonality and the broad range of environmental conditions that they are exposed to over the course of a given year. Different types of deciduous forests exist (e.g., the dry-season deciduous forests in Central and South America), but deciduous species in temperate forests are most often cold deciduous, meaning that they senesce their leaves at the end of summer and remain dormant through a cold, wet winter.

Understory herbaceous plant species are extremely biodiverse in temperate forests, with one recent paper estimating that they comprise around 80% of the total plant biodiversity in North American temperate forests (Spicer et al. 2020). To this point, some temperate North American forests have been shown to have up to 10 times more species in the herbaceous understory layer than in the canopy (Gilliam 2007). Understory plants vary widely in their phenological strategies. These diverse strategies provide an important aspect of niche differences across species that presumably promote coexistence and high diversity of herbaceous species on the forest floor (Gilliam 2007). A striking feature of the herbaceous layer in many deciduous forests is that one encounters different species from month to month, making a single midseason survey far from a complete inventory of all species present. Ranging from plants active for only a few weeks to

Glossary

Phenological escape. A shade avoidance strategy employed by understory plant species that involves emerging from dormancy during open-canopy periods of high light availability. This term has commonly been applied to understory plants that are active in spring but could also be applied to fall-active species that maintain photosynthetic activity after the canopy reopens.

Phenological mismatch. Asynchrony in the timing of biotic interactions, especially referring to the discordance of peak activity between two interacting species or organisms. This term is particularly common in climate change ecology, where it is used to imply a deviation from average or evolved interactions as a result of changes in the environmental drivers that cue species-level activity.

Phenological syndrome. As defined by Kudo et al. (2008), a phenological syndrome is a set of species characteristics that co-occur. More generally, phenological syndromes are analogous to phenological functional groups and used to categorize species as, for example, evergreen, spring active, spring ephemeral, summer green, or fall blooming.

Phenology. The timing of repeated life history events. For deciduous plant species, this term often refers to the annual timing of budburst, leaf expansion, leaf coloring, leaf senescence, flowering, and fruiting.

Phenological sensitivity. Also referred to as a reaction norm, it is the change in expressed phenology either over time or over a gradient of some environmental driver that cues the phenological event. Sensitivity is often calculated as the change in either average or peak phenology per change in time or temperature.

evergreen plants that maintain green aboveground tissue year round, understory plants are often categorized into phenological syndromes (see "Glossary") that include groups such as spring ephemeral (leaves die back before tree canopy leaves flush), summer green (maintain green leaves through summer), wintergreen (leaves produced in fall or winter), and evergreen (leaves last longer than 1 yr; Uemura 1994; Neufeld and Young 2014). It is important to note that while these discrete groupings are useful, there is considerable diversity within phenological syndromes across a complex continuum of leaf strategies and phenological traits, including, for example, some species that produce overwintering rosettes or multiple leaf flushes. Of particular importance to phenological escape are winter-deciduous species that leaf out in early spring, when access to direct sunlight is high and risk of damage from frost is reduced. This group includes species that are active aboveground only specifically during this period (spring ephemerals; sensu Yancy et al. 2024) as well as species that maintain their aboveground activity later into the growing season (including spring-active wildflowers and seedlings and saplings of many temperate deciduous tree species). Most spring ephemerals are perennial and store carbon in belowground rooting structures during dormancy (Lubbers and Lechowicz 1989; Lapointe and Lerat 2006). However, there is at least one exception to this, which is the annual spring ephemeral *Floerkea proserpinacoides* (McKenna and Houle 2000).

For temperate deciduous plants, especially trees, budburst and leaf expansion are primarily cued by three environmental drivers (Richardson et al. 2006; Ettinger et al. 2020; Buonaiuto and Wolkovich 2021): spring temperature forcing (the accumulation of warm temperature exposure above some critical threshold), winter chilling (sometimes referred to as vernalization effects; the accumulation of cold temperature below a critical threshold while in dormancy), and photoperiod (daylength). Additionally, many spring-active and spring ephemeral wildflower species have shallow roots and rhizomes that are sensitive to soil moisture and temperature, which is less variable than air temperature. In high-latitude or high-elevation montane systems, understory emergence and flowering phenology may instead be correlated primarily with the timing of snowmelt and the associated increase in temperatures that normally accompany it (e.g., Anderson et al. 2012). Importantly, however, deciduous forest canopies are rare in these systems, so there may be less ephemeral light available for understory wildflowers to utilize. The role of soil moisture on plant phenology is not well established for temperate deciduous forests, especially in the mesic forests that harbor much of the herbaceous diversity in temperate forests.

Spring temperature forcing is an important signal for two primary reasons. First, accumulation of warm temperatures signals a reduction in risk from late-winter and early-spring frost events, which can greatly reduce the survival and reproductive performance of deciduous plant species active during this period (Inouye 2008; Augspurger 2009; Vitasse et al. 2014; Gezon et al. 2016; Park et al. 2021). Second, photosynthetic rates scale nonlinearly with temperature (Caemmerer 2000), and accumulation of spring forcing temperatures signals to plants that conditions are sufficient to photosynthesize at or near peak efficiency: too cold and photosynthesis is inhibited by lack of energy and inaccessible soil water (Ensminger et al. 2008), but too warm and net carbon gain becomes inhibited by disproportionately elevated respiration rates relative to concurrent increases in photosynthetic rates (Caemmerer 2000; Lee and Ibáñez 2021*b*).

In addition to temperature, photosynthetic carbon assimilation in temperate deciduous forests is often also inhibited by insufficient access to light. Understory light levels can decrease by up to three orders of magnitude once canopy trees expand their leaves (fig. 1; Augspurger et al. 2005; Jacques et al. 2015; Lee and Ibáñez 2021*b*). In contrast to understory conditions, however, canopy trees are rarely light limited throughout the growing season and can therefore afford to be relatively conservative with their foliar phenology, prioritizing avoidance of frost damage (Seiwa 1999). Their conservative strategy means that they delay their leaf expansion several weeks after environmental conditions are initially suitable, providing a window of opportunity for understory plant species to exploit elevated understory light levels (Neufeld and Young 2014; Augspurger and Salk 2017).

By leafing out before the canopy closes, spring-active understory plant species are able to assimilate between 50% and 100% of their annual aboveground carbon budget in as little as 3–4 wk (Kwit et al. 2010; Heberling et al. 2019*a*; Lee and Ibáñez 2021*b*). This is especially true for spring ephemeral wildflowers (Heberling et al. 2019*a*), which are characterized by completion of aboveground activity prior to canopy leaf out (Yancy et al. 2024). This group always assimilates 100% of its aboveground carbon budget in early spring and is therefore expected to be highly sensitive to interannual variation in the duration of spring light windows (fig. 2; Neufeld and Young 2014; Heberling et al. 2019*b*; Lee et al. 2022). Still, spring-active understory plants have been shown to strongly rely on this period of time regardless of their growing season length. For example, temperate tree seedlings that have 7–8-mo-long growing seasons still assimilate 50%–80% of their annual carbon budgets within an early light availability window that is only 2–3 wk long (Kwit et al. 2010; Lee and Ibáñez 2021*b*). Additionally, even understory herbaceous species that retain leaves well into summer (summer greens; fig. 2) rely on this early-spring high light window for photosynthesis (e.g., *Arisaema triphyllum* [Jack-in-the-pulpit] assimilates >40% of annual carbon through spring photosynthesis; Heberling et al. 2019*a*).

Spring-active deciduous plants are often adapted to maintain extremely high photosynthetic rates during this early period of high light availability (Sparling 1967; Taylor and Pearcy 1976; Lapointe 2001). For example, Kudo et al. (2008) used high photosynthetic rates to define a spring-blooming phenological syndrome, further noting that access to spring light was directly and positively correlated with fruiting success in understory wildflower species. Elevated photosynthetic efficiency was also recorded for the spring ephemeral *Claytonia virginica* (Virginia spring beauty; Heberling et al. 2019*a*), with maximum photosynthetic rates that were substantially higher than observed rates for spring-active (but not ephemeral) wildflower species. Importantly, spring ephemeral wildflowers tend to be shade avoiders as opposed to shade tolerators (sensu Rothstein and Zak 2001) and thus show limited ability to acclimate to shady conditions (Eickmeier and Schussler 1993). Instead, these species senesce their leaves as the canopy closes above them.

In contrast, species that employ phenological escape while also maintaining leaves later into the growing season often demonstrate the capacity to maintain high photosynthetic rates in early spring before downregulating their photosynthetic machinery in

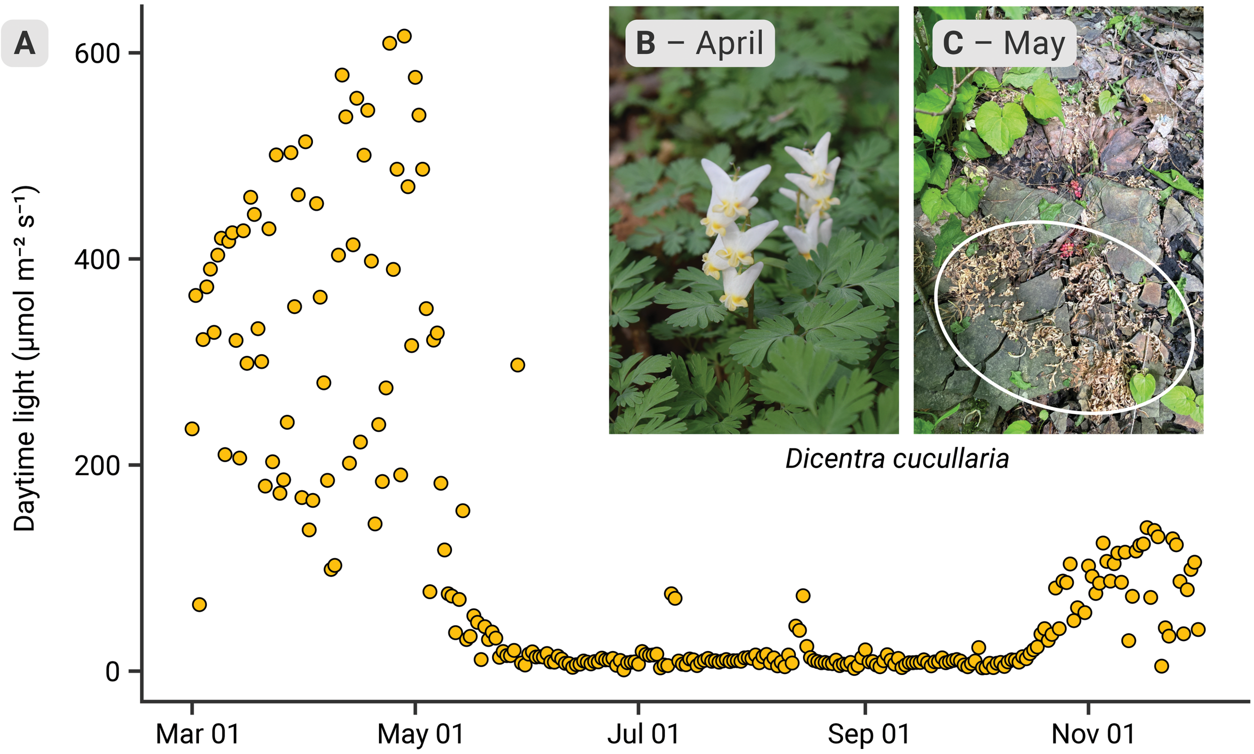

Fig. 1 Points in *A* represent average daily daytime light levels (μmol m^{-2} s^{-1}) at a site in southeast Michigan (data from Lee and Ibáñez 2021*b*). Spring ephemeral wildflowers, such as *Dicentra cucullaria* (Dutchman's breeches), are active in early spring (*B*) to make use of available understory light before senescing (*C*) once the canopy begins to close. The senescent plant in *C* is indicated with the circle. Average daytime light levels decrease by up to three orders of magnitude following canopy leaf out and closure.

the shady part of the growing season. This has been demonstrated broadly in nonephemeral herbaceous wildflower species (Ida and Kudo 2008; Heberling et al. 2019*a*) but more commonly studied in spring-active woody plant species. For example, Lee and Ibáñez (2021*a*) recorded a pronounced shift to more shade-tolerant photosynthetic rates (e.g., lower maxima coupled with lower light compensation points to better efficiency in low light conditions) for temperate deciduous tree seedlings, with reductions in overall capacity associated with corresponding reductions in respiration demand. Similar acclimation has been demonstrated in other tree seedlings (Augspurger et al. 2005; Kwit et al. 2010; Peltier and Ibáñez 2015), saplings and understory trees (Gill et al. 1998; Augspurger et al. 2005), and shrubs (Gill et al. 1998; Xu et al. 2007; Martinez and Fridley 2018), suggesting that seasonal regulation of photosynthesis is an important adaptation for deciduous understory species in general and woody understory species in particular (Valladares and Niinemets 2008).

So far in this primer, we have focused on evidence for how access to spring light affects photosynthetic carbon assimilation, but it is important to also address how changes in spring carbon assimilation translate to individual plant performance and population-level demography. Although this is a growing area of research with a limited number of studies, there are studies that both directly and indirectly relate phenological escape to individual metrics of plant performance. The main direct evidence comes from Lee and Ibáñez (2021*a*), who directly related tree seedling phenology and access to spring light to photosynthetic carbon assimilation and individual-based metrics of growth and survival. Specifically, they found that earlier seedling leaf expansion (and thus greater access to spring light) was significantly positively correlated with both spring and annual carbon accumulation. Carbon accumulation was, in turn, then positively correlated with annual growth and probability of survival.

To our knowledge, only one study has mechanistically linked wildflower performance to spring carbon assimilation. Lapointe (1998) demonstrated that spring-active *Trillium erectum* was able to successfully reproduce solely from carbohydrates assimilated during spring photosynthesis without relying on carbon stored in belowground tissue. Although this study did not include variation in spring light availability as an experimental treatment, other studies have directly linked phenological escape to wildflower carbon assimilation in spring (Heberling et al. 2019*a*). Another study related leaf-level gas exchange to wildflower phenology and reproductive performance (Jacques et al. 2015) but did not compute individual aboveground carbon budgets as part of the analysis. Other studies found important relationships between spring shade avoidance and wildflower reproductive success (Kudo et al. 2008) even within species (albeit without direct measurement or estimation of carbon gain; Routhier and Lapointe 2002), thereby supporting the hypothesis that phenological escape is important for maintaining natural populations of spring wildflowers. Furthermore, Routhier and Lapointe

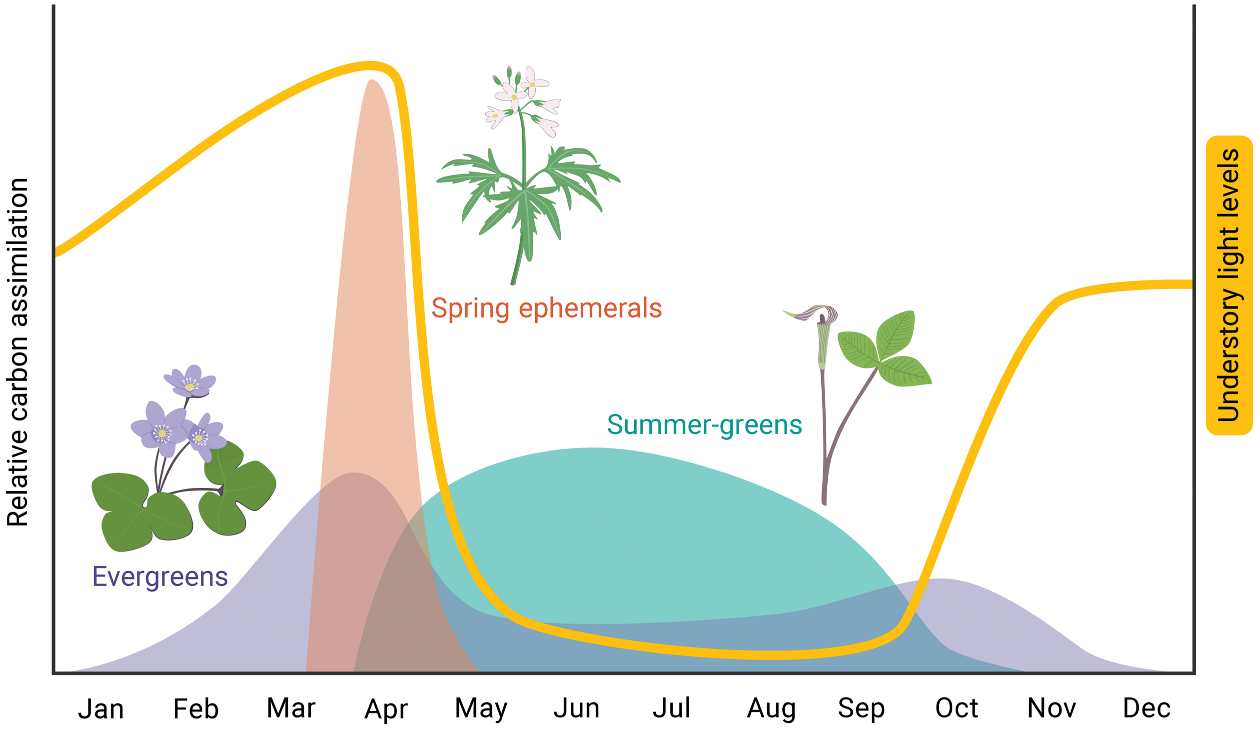

Fig. 2 Conceptual figure illustrating differences in seasonal distributions of photosynthetic activity (carbon assimilation) for temperate herbs with differing phenological syndromes (evergreens [purple], spring ephemerals [pink], summer greens [blue]) relative to understory light levels (line). The shape and magnitude of these conceptual photosynthetic activity curves may vary within and among species. For example, summer-green species vary in their relative proportion of early-spring photosynthetic gain that occurs before overstory tree canopy closure.

(2002) hypothesized that a latitudinal difference in the duration between understory emergence and tree leaf out, where the window duration increased with latitude, may explain the relative geographic distribution of species with the spring ephemeral strategy. That is, the authors predicted that longer spring light windows in the north could be at least partially responsible for spring wildflower southern range limits.

Most recently, Yancy et al. (2024) found important biogeographic and environmental drivers of spring ephemeral wildflower distributions across eastern North America. Results from their work suggest that phenological escape dynamics can also affect species distributions and long-term population persistence across the landscape. Specifically, "true" spring ephemeral wildflowers (those that completed 100% of their aboveground activity prior to canopy closure) were found to be most abundant at central latitudes in eastern North American forests. This pattern of reduced ephemeral abundance in the northern and southern regions of the temperate forest biome is likely indicative of a combination of drivers. More frequent and severe frost events could reduce spring wildflower success in the north and at higher elevations, while earlier canopy closure and longer tree growing seasons in the south could restrict the ability for understory plants to avoid canopy shade (Yancy et al. 2024). Furthermore, northern distributions of many species are likely to be affected by the history of glaciation in North America and by species-level dispersal rates following glacier recession (Vellend et al. 2003). Still, the results from Yancy et al. (2024) suggest that up to one in every five understory wildflower species in eastern North America is categorized as spring ephemeral (and therefore as strongly reliant on phenological escape) in at least part of its range.

In sum, phenological escape provides a mechanism by which a wide variety of spring-active deciduous plant species obtain enough energy to grow, survive, and reproduce. Species ranging from deciduous tree seedlings to spring ephemeral wildflowers rely on elevated access to light in early spring to assimilate 50%–100% of their annual carbon budgets. There is both direct and indirect evidence that their capacity to do so determines individual performance metrics such as growth, probability of survival, and reproductive success. Recent evidence further suggests that a wide diversity of understory wildflowers in North America relies on phenological escape, especially at central latitudes. In the next section, we discuss how access to spring light is expected to change as a direct result of climate change.

Climate Change Effects on Phenological Escape

Shifts in plant phenology are some of the most common and intuitive signals of climate change, with some phenology datasets dating back several centuries (e.g., Aono 2015). We now have decades of research showing that the start of season phenology of Northern Hemisphere temperate tree species is shifting earlier (Menzel and Fabian 1999; Parmesan and Yohe 2003; Menzel et al. 2006; Piao et al. 2019) and that these shifts correlate strongly with warmer spring temperatures (Menzel et al. 2006; Ettinger et al. 2020). Climate change is therefore altering the initiation (and sometimes the duration) of growing seasons for temperate tree species (Linderholm 2006; Song et al. 2009), at least as recorded for mature canopy trees. Until recently, however, the responsiveness of understory plant phenology to environmental variation was largely unstudied. That is, as illustrated in figure 3, temperate forest canopies were closing earlier in the year, but it was unknown whether deciduous understory species were shifting at the same rate.

Recently, several studies have sought to address this gap in the literature using different types of data and for different groups of understory species. The first of these studies was conducted by Heberling et al. (2019*b*) using historical observations dating back ~170 yr. The authors of this paper compared the phenological sensitivity of a suite of spring-blooming wildflower species to that of co-occurring canopy tree species in the state of Massachusetts. By using comparisons to more recent datasets, the authors found that wildflower species were less sensitive to changes in temperature than tree species, resulting in a 7-d reduction in access to spring light for wildflower species from 1852 to 2018. Furthermore, using an extreme climate change projection for the year 2080, they predicted that wildflower access to spring light will decrease by a further 8 d over the next ~60 yr.

These initial findings have received mixed support from subsequent studies. Lee et al. (2022) used herbarium specimens instead of observational data while also expanding the spatial extent of study to include data from across all of eastern North America (as opposed to just one location in Massachusetts) as well as temperate deciduous forests in Europe and Asia. While these authors found support for diminishing spring light windows for wildflowers in North America, they instead found neutral to positive change in spring light window length for wildflowers on the other two continents, suggesting that climate change will not be as dire for spring ephemeral wildflowers outside of North America. A second study using the North American subset of the Lee et al. (2022) herbarium data (Miller et al. 2022) binned observations to look for differences in phenological sensitivity in wildflowers and canopy trees associated with latitudinal and environmental gradients. They found that past and future changes in phenological escape depended on whether they were considering warm, cool, or intermediate parts of species' ranges; wildflowers experienced the previously described reductions in access to early spring light in the northern, cooler parts of their range but fared better in the warm and intermediate regions.

Likewise, Alecrim et al. (2023) conducted an analysis highly similar to the Miller et al. (2022) analysis but using community science observational data instead of data sourced from herbarium collections. These authors used tree and wildflower phenology data sourced from the National Phenology Network (https://www.usanpn.org/) spanning the eastern United States and separated the data into latitudinal bins while looking for biogeographic gradients in phenological sensitivity. Contrary to the results from the other three papers, Alecrim et al. (2023) found that wildflower species

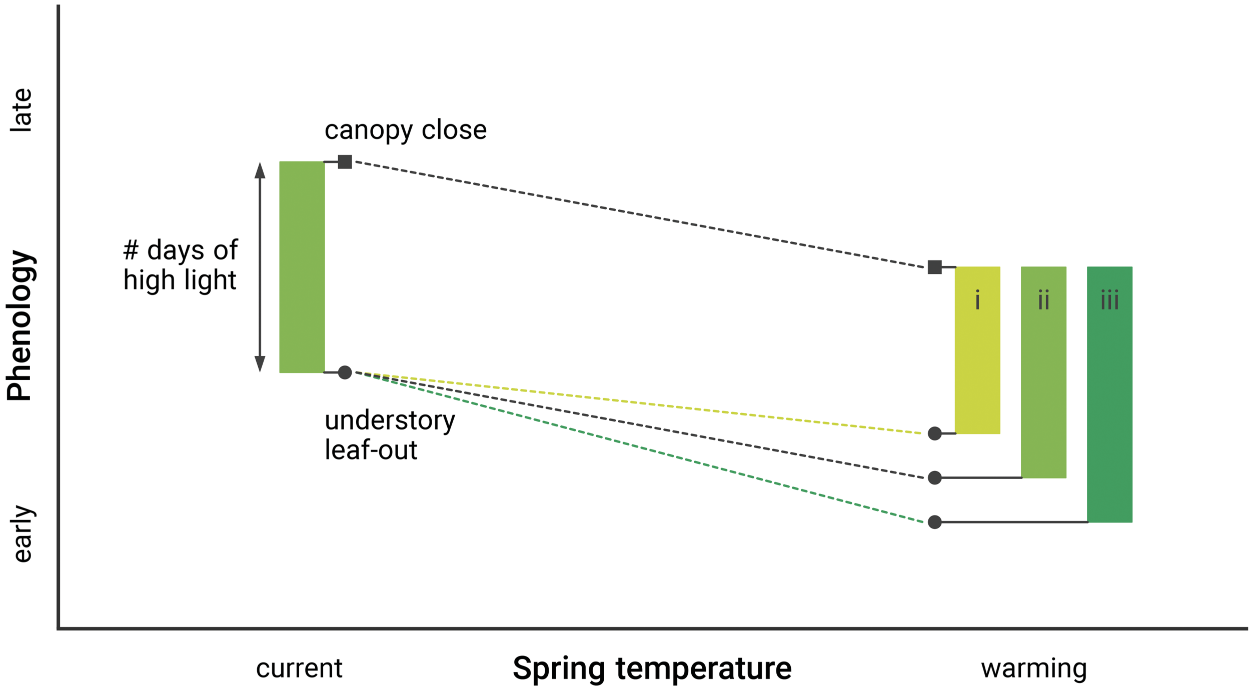

Fig. 3 Spring-active understory plants emerge from dormancy before the canopy closes in late spring, allowing them to make use of early-season high light availability (duration represented by the height of the bar on the left of the figure). Timing of canopy closure (squares) and understory leaf-out phenology (points) are both moving earlier as spring temperatures warm, but duration of spring light access might decrease (i), stay the same (ii), or lengthen (iii), depending on whether understory phenological sensitivity is weaker than, equal to, or stronger than the sensitivity of co-occurring canopy trees, respectively. This figure is adapted with permission from Lee and Ibáñez (2021*a*).

were overall more sensitive to spring temperature than co-occurring tree species, resulting in projected increased access to spring light under warmer temperatures (a result also echoed by research done in the Appalachian Trail corridor; Tourville et al. 2023). Interestingly, although the authors found more extreme differences in phenological sensitivity between wildflowers and trees in northern regions (somewhat echoing the results of Miller et al. 2022), they instead found that wildflowers were more sensitive than co-occurring canopy trees, suggesting that the understory plants will gain access to light under climate change conditions.

Last, authors from some of these studies came together to conduct an in-depth comparison of the Miller et al. (2022) and Alecrim et al. (2023) papers to determine whether the dramatically different results could be reconciled in a comparative analysis. Although Lee et al. (2024) were unable to fully reconcile the differences between the two reports, they concluded that differences in species selection and spatiotemporal study extents were at least partially responsible for the differences between these two studies. Lee et al. (2024) found strong similarities in phenological sensitivity of individual species—species that were present in both the herbarium and the community science datasets had similar sensitivities across both datasets. However, while this echoes a recent study suggesting strong similarities in phenological sensitivity when comparing herbarium and community science datasets (Ramirez-Parada et al. 2022), Lee et al. (2024) found that the inferred changes in mismatch (i.e., whether understory plants were predicted to gain or lose access to spring light) differed consistently across the two datasets. This finding suggests that the inferences we make about biological interactions depend strongly on the type and scope of data used and that researchers in this area should consider this issue as they design and implement their experiments and models.

Climate change implications for phenological escape of other groups of understory plant species (other than spring ephemeral wildflowers) are less studied, but existing evidence suggests that woody plant species may fare relatively better under warming springs. In addition to the wildflowers discussed previously, Miller et al. (2022) also examined phenological sensitivity of various native and invasive shrub species using herbarium data. Shrubs were found to be relatively more sensitive than wildflowers and approximately as sensitive as trees to variation in spring temperatures, suggesting that they may be able to maintain access to light moving forward. Furthermore, another study found spring leaf-out phenology of temperate tree seedlings to be more sensitive to spring temperature than conspecific co-occurring canopy trees. Lee and Ibáñez (2021*a*), building on other work showing the importance of phenological escape for seedling carbon budgets (Lee and Ibáñez 2021*b*), found that climate change is projected to lead to increased spring light windows for juvenile trees in the North American Great Lakes region. This, too, suggests that woody understory plant species may be better situated to maintain (or even increase) access to spring light than herbaceous wildflowers.

An important caveat to the results discussed in the previous paragraph is that much of the work investigating phenological escape has been observational, relying on herbarium collections (Lee et al. 2022; Miller et al. 2022), historical observations (Heberling et al. 2019*b*), or community science datasets (Alecrim et al. 2023; Tourville et al. 2023). While some experimental studies do exist (Lee and Ibáñez 2021*a*, 2021*b*), they have been limited in scope to only a few species studied at the site level. More experimental studies are likely needed to better evaluate and predict how phenological escape might change over time.

Ecological Implications of Reduced Phenological Escape

In the previous sections, we presented evidence in the literature showing (i) the importance of access to spring light for the carbon budgets of spring-active understory plant species and (ii) how climate change could alter access to spring light because of differences in phenological sensitivity to spring temperatures. However, so far these dynamics have all been described in terms of individual-level performance metrics. For example, access to spring light determines survival and reproductive success of spring wildflowers (Lapointe 1998; Routhier and Lapointe 2002; Ida and Kudo 2008; Kudo et al. 2008; Neufeld and Young 2014). In woody plants, such as deciduous tree seedlings, access to spring light is directly tied to annual growth and probability of survival (Lee and Ibáñez 2021*a*, 2021*b*). The question remains: how do changes in phenological escape and individual plant performance scale up to affect population- and community-level ecological dynamics?

This is a question that in large part remains unanswered. A recent meta-analysis that investigated how phenological shifts affect demography found very few studies that directly and mechanistically linked the two topics, at least for plants (Iler et al. 2021). The authors found many studies that linked phenology shifts to individual metrics of performance (reproductive success, growth, survival, etc.; see "Climate Change Effects on Phenological Escape" above for examples), but only a few studies then went the extra step of determining how changes in individual performance affect population-level dynamics. For example, one study that did specifically investigate this relationship in montane wildflowers found that earlier phenology linked to warmer springs reduced survival because of increased risk of drought (and, to a lesser extent, increased frost damage; Iler et al. 2019). This reduction in survival was then mechanistically linked to reductions in population growth rates (finite rate of increase [λ]; Caswell 2008), meaning that reduced survival directly and negatively influenced the population's ability to persist in the study location.

Overall, though, studies that directly link plant phenology shifts with changes in demographic rates remain rare despite the commonly held assumption that changes in individual performance associated with the former will translate directly into changes in the latter (Iler et al. 2021). This assumption should be questioned and explicitly tested, however, because the extent to which individual performance affects population-level dynamics depends on the species and the system. For example, although seed set has been shown to be negatively affected by shifts in phenology (Ida and Kudo 2008; Kudo et al. 2008) and posited as a potential consequence of reductions in spring light availability for spring ephemeral wildflowers (Heberling et al. 2019*a*; Lee et al. 2022), reductions in fruit production and seed set will have only negative consequences for population-level performance if a species is seed limited at a given location (e.g., Lundgren et al. 2015). Similarly, it is theorized that growth and survival limitations will play larger roles in shaping long-lived plant demography (such as for woody or perennial species) while fluctuation in reproductive success and germination will more strongly shape short-lived plant species (Franco and Silvertown 2004). It is therefore important that future studies of phenological escape (and shifts in phenology more broadly) work to apply their results to trends in demography and to explore how and whether changes in access to light manifest in changes to population persistence.

Beyond plant demography, changes in phenological escape may also indirectly affect other organisms that interact with understory plant species. One example of this is the potential disruption of plant-pollinator interactions. Previous research provides evidence for disruption in general plant-pollinator interactions due to shifting activity periods (Kudo et al. 2008; Kudo and Ida 2013). That is, flowering phenology and pollinator phenology can have different (or even opposite) sensitivities to environmental variation, leading to decreased overlap in activity with climate change.

It is also possible for phenological escape to further disrupt these interactions by increasing the amount of time that wildflowers spend in shade, even if plants and pollinators would otherwise overlap in activity periods. For example, bumble bees (genus *Bombus*) are often some of the earliest pollinators to emerge in spring and rely heavily on spring ephemeral wildflowers and other early-flowering plants for nectar resources (Timberlake et al. 2019). This can be especially true for queens of some species because they are first to emerge in order to initiate their hive before the rest of the colony becomes active later in spring (Timberlake et al. 2019; Mola et al. 2021). Bee activity has also been shown to decrease with increasing canopy closure within a growing season (Proctor et al. 2012; Williams and Winfree 2013; Hanula et al. 2015) and to be generally lower in mature closed-canopy forests (Hilmers et al. 2018). Thus, diminishing spring light window duration could disrupt wildflower-pollinator interactions regardless of the level of phenological overlap that already exists between the two groups. That is, even if flowering phenology and pollinator activity are shifting earlier in spring at the same rate, earlier understory shading may reduce pollinator activity in the forest interior, thereby leading to reduced reproductive success (Kudo et al. 2008).

Potential Avenues for Future Research

Climate change–driven shifts in phenological escape and plant-plant interactions more broadly are relatively new ideas that deserve further exploration. In addition to a need for more evidence as to how changes in individual performance translate to population-level demographic performance (see “Ecological Implications of Reduced Phenological Escape”), there are several areas that we want to highlight here that represent persisting knowledge gaps related to phenological escape and could prove to be fruitful avenues of future research (table 1).

Management Strategies for Mitigating Reduced Phenological Escape

Despite the need for a better understanding of how overstory-understory phenological mismatch affects understory plant population- and community-level dynamics, reduced access to spring light is likely to have negative effects on growth, survival, recruitment, and reproduction. As such, an important question arises: is it possible to manage native systems so that negative effects on population persistence are avoided or mitigated? To date, we are unaware of any studies that have addressed management strategies pertaining to this specific mismatch, although there have been proposed strategies for addressing plant-pollinator mismatch by manipulating phenology in various ways. Olliff-Yang et al. (2020) proposed management strategies aimed at extending phenology in plant and pollinator populations so that there is increased overlap in their periods of activity (and thus increased pollination success). For example, one of their proposed management strategies is to better utilize natural variation in microclimate across the landscape; managers would focus on conserving or planting pollinator resources in areas where microclimatic conditions favor extended flowering or where pollinator activity periods are particularly long (Olliff-Yang et al. 2020). While extending phenology may not work well for mitigating mismatch in phenological escape (frost and shade barriers may prevent plants from gaining meaningful access to resources if phenology is extended earlier or later), a similar strategy might be employed of planting or conserving spring wildflowers in areas where canopy closure is particularly delayed. Additionally, forest management practices such as canopy thinning could be a useful strategy for providing more light to the understory. It will likewise be important to gain a better understanding of how natural canopy thinning (e.g., from large disturbance events or pest outbreaks) might affect phenological escape. Still, the efficacy of these strategies remains untested and will require future work to evaluate.

Increasing Representation of Understory Diversity

To date, studies of phenological escape have been greatly limited in biodiversity of the focal species. Existing evidence suggests a wide range in phenological sensitivity among both understory and canopy species (Richardson et al. 2006; Ge et al. 2015; Lee et al. 2022; Willems et al. 2022), meaning that shifts in phenological escape are likely to be dependent on which species are interacting with each other and, for stand-level trends, community composition. Recently, nearly 20% of understory wildflower species were shown to demonstrate at least some degree of spring ephemerality in eastern North American deciduous forests (Yancy et al. 2024), suggesting that phenological escape is important beyond the few dozen wildflower species so far studied across North American, Asian, and European temperate forests (e.g., Lee et al. 2022). Phenological escape has also been shown to be important for woody plant species (Lee and Ibáñez 2021*a*, 2021*b*; Miller et al. 2022) and summer-green herbaceous wildflowers (Heberling et al. 2019*a*), which remain generally unstudied outside of a handful of species. Relatively few studies have quantified annual carbon gain patterns across species (Heberling et al. 2019*a*). More research is needed on the summer-green phenological syndrome and the relative functional importance of spring and summer photosynthesis in these diverse species. These phenological syndromes may also shift within species depending on other factors, such as age (Dion et al. 2016). Last, most existing studies of phenological escape are limited to temperate deciduous forests in the Northern Hemisphere, so expanding research to Southern Hemisphere forests (though less commonly winter deciduous) will be an

Table 1

Questions Related to Phenological Escape and the Current Strength of Evidence Present in the Literature

Question related to phenological escape	Evidence from previous research
Are overstory and understory plants sensitive to environmental conditions with respect to their phenology?	There is strong evidence that plants are sensitive to environmental conditions—especially spring warming, winter chilling, and daylength. In temperate systems, warmer springs are largely driving earlier phenology.
Do understory plants employ shade avoidance behavior?	There is strong evidence that many understory species (ranging from spring ephemeral wildflowers to deciduous tree seedlings) engage in phenological shade avoidance. However, this evidence is so far limited to temperate deciduous forests in the Northern Hemisphere. Furthermore, plants may change their phenological strategy and other life history strategies as they age (Cavender-Bares and Bazzaz 2000; Dion et al. 2016). More information is needed on whether phenological escape is important in temperate forests in other regions of the world and across other forest types, including forests with evergreen tree species or different seasonality.
Will climate change cause changes in duration of phenological escape?	There is strong evidence that climate change is affecting the duration of spring light availability periods as a result of trees and understory plants having different sensitivities to environmental conditions (especially spring warming). However, studies differ in whether they predict that access to seasonal light availability is increasing or decreasing. These signals seem to be dependent on continent, variation across latitudes, and type of data used in estimating sensitivity. Furthermore, several other global change factors have been shown to affect plant phenology, and future research will be required to determine how changes in such factors affect phenological escape.
Is it possible to manage for changes in access to spring light to conserve species that rely on phenological escape?	More research is needed to investigate how management strategies, such as canopy thinning, affect the performance of understory species that rely on phenological escape.
Will projected changes in access to ephemeral light be consistent across all understory plant species that rely on phenological escape?	There is mixed evidence to support this point. On one hand, multiple studies have found that spring-active understory wildflower species have similar sensitivities to spring temperature and, therefore, that they should experience similar phenological mismatch under climate change. On the other hand, however, the number of species investigated is relatively low and generally constrained to spring-active wildflower species. Future research will be needed to explicitly evaluate whether and how changes in understory light availability affect underrepresented groups, such as shrubs, as well as unrepresented species within otherwise well-represented groups. More information is also needed on how phylogenetic relatedness affects phenological sensitivity and phenological escape.
Is phenological escape as important in autumn as it is in spring?	While some studies have investigated the importance of fall phenological escape in woody plant species, little research to date has specifically quantified the importance of fall phenological escape in herbaceous plant species. Furthermore, the woody plant studies that exist have generally found that fall phenological escape is far less important for carbon assimilation than that in spring (but see Fridley 2012). Still, more information is needed on both these points.
Will changes in phenological escape be consistent across species' ranges?	Recent evidence suggests that shifts in phenological escape will differ across southern, central, and northern sections of species' ranges (at least in eastern North America). The exact differences varied depending on the study, suggesting that further work (and especially experimental work) is needed on this topic. Furthermore, there is ample evidence that phenological sensitivity in general depends somewhat on local patterns of adaptation to historical climates, suggesting that there will be spatially explicit differences in how plants respond to climate change.
Will changes in phenological escape be consistent across long time periods?	The answer to this question is uncertain and will depend on whether shifts to earlier phenology are linear or whether they start to saturate at some point, as has been predicted repeatedly throughout the phenological literature, although seldom supported. Such saturation in phenological sensitivity would likely create inconsistencies relative to the current projections of changes in phenological escape.

Note. This table lists questions related to phenological escape and the current strength of evidence present in the literature (or alternatively that there is insufficient evidence available) to answer each question. Several of these questions are discussed in detail as avenues for future research. For evidence present in the literature, see the main text for representative citations.

important next step in understanding the global importance of access to spring light.

Application in Non-, Semi-, or Drought-Deciduous and Nontemperate Forests

Another important limitation of phenological escape research has been that all studies to date have focused on the temperate deciduous forest biome. However, seasonally ephemeral wildflowers are found in diverse ecosystems, including not only temperate deciduous forests but also other systems like prairies and evergreen forests (Kindscher and Wells 1995; Sawada et al. 1997; Bowers 2005; Neufeld and Young 2014), suggesting that seasonal variation in light availability could still be important even without a fully deciduous, tree-dominated canopy. For example, light availability has been shown to shape prairie communities (Hautier et al. 2009; Borer et al. 2014), meaning that variation in seasonally ephemeral light availability may be important to shorter-stature species in these communities as well. Furthermore, other types of forest communities may comprise different versions of phenological escape than the ones described so far for spring-active species in winter-deciduous forests. The phenomenon can be found in spring-flowering annuals in deserts (Bowers 2005), though rather than escaping shade from tree canopy closure as in temperate deciduous forests, these species presumably take advantage of short periods of suitable soil moisture and temperature. Drought-deciduous forests, as well as forests where leaf senescence occurs cyclically within a species but is only loosely coordinated among species (e.g., Daubenmire 1972; Wright and van Schaik 1994), could provide additional examples of phenological escape dynamics. Not only could these dynamics add to explanations of species' persistence and community-level interactions, but data collected in these systems would contribute important information about how Southern Hemisphere and/or tropical forests differ in terms of the processes that drive them.

Phenological Escape in Fall

Although we spent most of this primer discussing phenological escape at the beginning of the growing season, understory light availability can also be elevated at the end of the growing season when trees senesce their leaves and the canopy reopens. To date, there have been a few studies that have explored the importance of late-season phenological escape in fall-active species, and the studies that exist have contributed conflicting results. For example, both Gill et al. (1998) and Lee and Ibáñez (2021*a*) researched the importance of fall phenological escape for carbon assimilation of woody plants, but both papers concluded that fall photosynthesis contributed relatively little to net annual carbon assimilation and, in the latter case, individual metrics of performance (tree seedling growth and survival). In contrast, fall phenological escape (often also called "extended leaf phenology"; Smith 2013) has been shown to be important for carbon assimilation in woody shrub species (e.g., some nonnative species in eastern North America are reported to assimilate nearly 20% of annual carbon in fall; Fridley 2012) and in some spring-active herbaceous wildflower species that have growing seasons that persist beyond the tree canopy (e.g., *Asarum canadense* [Canadian wild ginger] is reported to assimilate nearly 20% of annual carbon after canopy tree leaf fall; Heberling et al. 2019*a*). Further research is warranted for exploring the importance of fall phenological escape in these and other functional groups (particularly fall-blooming, summergreen wildflower species that are not active in the spring light window).

Potential Interactions with Other Anthropogenic and Geospatial Drivers

From the handful of cited studies that specifically quantified shifts in phenological escape, most of them focus solely on phenological sensitivity to temperature (Heberling et al. 2019*b*; Miller et al. 2022; Alecrim et al. 2023), although some included other drivers such as elevation (Lee et al. 2022) and vernalization effects (Lee and Ibáñez 2021*a*). There are still many other drivers that are linked to spring phenology shifts and could thus affect shifts in the duration of phenological escape across variation in environmental conditions both over time (in response to anthropogenic climate change) and over space (geospatial patterns). For example, nitrogen fertilization can delay flowering phenology in some herbaceous species (e.g., Yin et al. 2016), meaning that increasing nitrogen fertilization associated with anthropogenic change could impact wildflower sensitivities and access to early spring light. Furthermore, because spring ephemeral wildflowers often overwinter belowground in shallow rooting structures, their phenology may be relatively more cued by soil temperature and soil moisture (Neufeld and Young 2014) than by air temperature (which is generally what tree phenology responds to). Last, spring phenology depends on factors associated with spatial location, such as photoperiod (Ettinger et al. 2020), and a recent study found that there is substantial variation in phenological sensitivity for wildflower flowering across space, even when environmental drivers are comprehensively accounted for (Willems et al. 2022). Thus, we recommend that researchers explore how other drivers linked to environmental variation across space and time affect phenological escape dynamics.

Conclusions

Phenological escape, although not well defined until recently, is an important ecological driver of understory plant performance in systems where understory light availability is seasonal and ephemeral. Access to elevated understory light levels in spring (and, to a lesser extent, fall) has been consistently found to account for between 50% and 100% of the annual aboveground carbon budgets for a wide range of species ranging from spring ephemeral wildflowers to woody tree seedlings and shrubs. Spring carbon assimilation has been directly and indirectly linked to individual-level performance metrics such as growth, survival, and reproductive success, meaning that access to spring light is likely to have a strong role in demographic processes (although this largely remains untested in practice). Climate change is expected to alter access to spring light for many species and thus has the capacity to dramatically affect temperate plant species through changes in phenological escape. Still, unanswered questions remain, particularly concerning whether and how phenological escape affects understory plant performance for species that do not rely on spring light (such as those in drought- or mixed-deciduous forests and those that instead rely on access to fall light). Filling these knowledge gaps is an important next step toward understanding how climate change shapes plant performance and plant communities.

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Literature Cited

Alecrim EF, RD Sargent, JRK Forrest 2023 Higher-latitude spring-flowering herbs advance their phenology more than trees with warming temperatures. J Ecol 111:156–169. https://doi.org/10.1111/1365-2745.14023.

Anderson JT, DW Inouye, AM McKinney, RI Colautti, T Mitchell-Olds 2012 Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. Proc R Soc B 279:3843–3852. https://doi.org/10.1098/rspb.2012.1051.

Anderson RC, S Schelfhout 1980 Phenological patterns among tallgrass prairie plants and their implications for pollinator competition. Am Midl Nat 104:253–263. https://doi.org/10.2307/2424864.

Aono Y 2015 Cherry blossom phenological data since the seventeenth century for Edo (Tokyo), Japan, and their application to estimation of March temperatures. Int J Biometeorol 59:427–434. https://doi.org/10.1007/s00484-014-0854-0.

Augspurger CK 2009 Spring 2007 warmth and frost: phenology, damage and refoliation in a temperate deciduous forest. Funct Ecol 23:1031–1039. https://doi.org/10.1111/j.1365-2435.2009.01587.x.

Augspurger CK, JM Cheeseman, CF Salk 2005 Light gains and physiological capacity of understorey woody plants during phenological avoidance of canopy shade. Funct Ecol 19:537–546. https://doi.org/10.1111/j.1365-2435.2005.01027.x.

Augspurger CK, CF Salk 2017 Constraints of cold and shade on the phenology of spring ephemeral herb species. J Ecol 105:246–254. https://doi.org/10.1111/1365-2745.12651.

Borer ET, EW Seabloom, DS Gruner, WS Harpole, H Hillebrand, EM Lind, PB Adler, et al 2014 Herbivores and nutrients control grassland plant diversity via light limitation. Nature 508:517–520. https://doi.org/10.1038/nature13144.

Bowers JE 2005 El Niño and displays of spring-flowering annuals in the Mojave and Sonoran Deserts. J Torrey Bot Soc 132:38–49. https://doi.org/10.3159/1095-5674(2005)132[38:ENADOS]2.0.CO;2.

Buonaiuto DM, EM Wolkovich 2021 Differences between flower and leaf phenological responses to environmental variation drive shifts in spring phenological sequences of temperate woody plants. J Ecol 109:2922–2933. https://doi.org/10.1111/1365-2745.13708.

Caemmerer SV 2000 Biochemical models of leaf photosynthesis. Vol 2. Techniques in plant sciences. CSIRO, Collingwood, Australia.

Caswell H 2008 Matrix population models: construction, analysis, and interpretation. 2nd ed. Sinauer, Sunderland, MA.

Cavender-Bares J, FA Bazzaz 2000 Changes in drought response strategies with ontogeny in *Quercus rubra*: implications for scaling from seedlings to mature trees. Oecologia 124:8–18. https://doi.org/10.1007/PL00008865.

Cushing DH 1990 Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Pages 249–293 *in* JHS Blaxter, AJ Southward, eds. Advances in marine biology. Vol 26. Academic Press, London. https://doi.org/10.1016/S0065-2881(08)60202-3.

Damien M, K Tougeron 2019 Prey-predator phenological mismatch under climate change. Curr Opin Insect Sci 35:60–68. https://doi.org/10.1016/j.cois.2019.07.002.

Daubenmire R 1972 Phenology and other characteristics of tropical semi-deciduous forest in north-western Costa Rica. J Ecol 60:147–170. https://doi.org/10.2307/2258048.

Dion P, J Brisson, B Fontaine, L Lapointe 2016 Light acclimation strategies change from summer green to spring ephemeral as wild-leek plants age. Am J Bot 103:963–970. https://doi.org/10.3732/ajb.1500503.

Eickmeier WG, EE Schussler 1993 Responses of the spring ephemeral *Claytonia virginica* L. to light and nutrient manipulations and implications for the "vernal-dam" hypothesis. Bull Torrey Bot Club 120:157–165. https://doi.org/10.2307/2996945.

Ensminger I, L Schmidt, J Lloyd 2008 Soil temperature and intermittent frost modulate the rate of recovery of photosynthesis in Scots pine under simulated spring conditions. New Phytol 177:428–442. https://doi.org/10.1111/j.1469-8137.2007.02273.x.

Ettinger AK, CJ Chamberlain, I Morales-Castilla, DM Buonaiuto, DFB Flynn, T Savas, JA Samaha, EM Wolkovich 2020 Winter temperatures predominate in spring phenological responses to warming. Nat Clim Change 10:1137–1142. https://doi.org/10.1038/s41558-020-00917-3.

Forrest JRK 2014 Plant size, sexual selection, and the evolution of protandry in dioecious plants. Am Nat 184:338–351. https://doi.org/10.1086/677295.

Franco M, J Silvertown 2004 A comparative demography of plants based upon elasticities of vital rates. Ecology 85:531–538. https://doi.org/10.1890/02-0651.

Fridley JD 2012 Extended leaf phenology and the autumn niche in deciduous forest invasions. Nature 485:359–362. https://doi.org/10.1038/nature11056.

Ge Q, H Wang, T Rutishauser, J Dai 2015 Phenological response to climate change in China: a meta-analysis. Glob Change Biol 21:265–274. https://doi.org/10.1111/gcb.12648.

Gérard M, M Vanderplanck, T Wood, D Michez 2020 Global warming and plant-pollinator mismatches. Emerg Top Life Sci 4:77–86. https://doi.org/10.1042/ETLS20190139.

Gezon ZJ, DW Inouye, RE Irwin 2016 Phenological change in a spring ephemeral: implications for pollination and plant reproduction. Glob Change Biol 22:1779–1793. https://doi.org/10.1111/gcb.13209.

Gill DS, JS Amthor, FH Bormann 1998 Leaf phenology, photosynthesis, and the persistence of saplings and shrubs in a mature northern hardwood forest. Tree Physiol 18:281–289. https://doi.org/10.1093/treephys/18.5.281.

Gilliam FS 2007 The ecological significance of the herbaceous layer in temperate forest ecosystems. BioScience 57:845–858. https://doi.org/10.1641/B571007.

Hanula JL, S Horn, JJ O'Brien 2015 Have changing forests conditions contributed to pollinator decline in the southeastern United States? For Ecol Manag 348:142–152. https://doi.org/10.1016/j.foreco.2015.03.044.

Hautier Y, PA Niklaus, A Hector 2009 Competition for light causes plant biodiversity loss after eutrophication. Science 324:636–638. https://doi.org/10.1126/science.1169640.

Heberling JM, ST Cassidy, JD Fridley, S Kalisz 2019*a* Carbon gain phenologies of spring-flowering perennials in a deciduous forest indicate a novel niche for a widespread invader. New Phytol 221:778–788. https://doi.org/10.1111/nph.15404.

Heberling JM, C McDonough MacKenzie, JD Fridley, S Kalisz, RB Primack 2019*b* Phenological mismatch with trees reduces wildflower carbon budgets. Ecol Lett 22:616–623. https://doi.org/10.1111/ele.13224.

Hilmers T, N Friess, C Bässler, M Heurich, R Brandl, H Pretzsch, R Seidl, J Müller 2018 Biodiversity along temperate forest succession. J Appl Ecol 55:2756–2766. https://doi.org/10.1111/1365-2664.13238.

Ida TY, G Kudo 2008 Timing of canopy closure influences carbon translocation and seed production of an understorey herb, *Trillium apetalon* (Trilliaceae). Ann Bot 101:435–446. https://doi.org/10.1093/aob/mcm296.

Iler AM, PJ CaraDonna, JRK Forrest, E Post 2021 Demographic consequences of phenological shifts in response to climate change. Annu Rev Ecol Evol Syst 52:221–245. https://doi.org/10.1146/annurev-ecolsys-011921-032939.

Iler AM, A Compagnoni, DW Inouye, JL Williams, PJ CaraDonna, A Anderson, TEX Miller 2019 Reproductive losses due to climate change-induced earlier flowering are not the primary threat to plant population viability in a perennial herb. J Ecol 107:1931–1943. https://doi.org/10.1111/1365-2745.13146.

Inouye DW 2008 Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. Ecology 89:353–362.

Jacques MH, L Lapointe, K Rice, RA Montgomery, A Stefanski, PB Reich 2015 Responses of two understory herbs, *Maianthemum canadense* and *Eurybia macrophylla*, to experimental forest warming: early emergence is the key to enhanced reproductive output. Am J Bot 102:1610–1624. https://doi.org/10.3732/ajb.1500046.

Kharouba HM, EM Wolkovich 2020 Disconnects between ecological theory and data in phenological mismatch research. Nat Clim Change 10:406–415. https://doi.org/10.1038/s41558-020-0752-x.

Kindscher K, PV Wells 1995 Prairie plant guilds: a multivariate analysis of prairie species based on ecological and morphological traits. Vegetatio 117:29–50. https://doi.org/10.1007/BF00033257.

Koenig WD, KA Funk, TS Kraft, WJ Carmen, BC Barringer, JMH Knops 2012 Stabilizing selection for within-season flowering phenology confirms pollen limitation in a wind-pollinated tree: phenology and acorn production in *Quercus lobata*. J Ecol 100:758–763. https://doi.org/10.1111/j.1365-2745.2011.01941.x.

Kudo G, TY Ida 2013 Early onset of spring increases the phenological mismatch between plants and pollinators. Ecology 94:2311–2320. https://doi.org/10.1890/12-2003.1.

Kudo G, TY Ida, T Tani 2008 Linkages between phenology, pollination, photosynthesis, and reproduction in deciduous forest understory plants. Ecology 89:321–331.

Kwit MC, LS Rigg, D Goldblum 2010 Sugar maple seedling carbon assimilation at the northern limit of its range: the importance of seasonal light. Can J For Res 40:385–393. https://doi.org/10.1139/X09-196.

Labonté A, LS Monticelli, M Turpin, E Felten, E Laurent, A Matejicek, L Biju-Duval, et al 2023 Individual flowering phenology shapes plant-pollinator interactions across ecological scales affecting plant reproduction. Ecol Evol 13:e9707. https://doi.org/10.1002/ece3.9707.

Lapointe L 1998 Fruit development in *Trillium*: dependence on stem carbohydrate reserves. Plant Physiol 117:183–188. https://doi.org/10.1104/pp.117.1.183.

——— 2001 How phenology influences physiology in deciduous forest spring ephemerals. Physiol Plant 113:151–157. https://doi.org/10.1034/j.1399-3054.2001.1130201.x.

Lapointe L, S Lerat 2006 Annual growth of the spring ephemeral *Erythronium americanum* as a function of temperature and mycorrhizal status. Can J Bot 84:39–48. https://doi.org/10.1139/b05-140.

Lee BR, EF Alecrim, JRK Forrest, JM Heberling, RB Primack, RD Sargent 2024 Phenological mismatch between trees and wildflowers: reconciling divergent findings in two recent analyses. J Ecol 113:1–16. https://doi.org/10.1111/1365-2745.14317.

Lee BR, I Ibáñez 2021*a* Improved phenological escape can help temperate tree seedlings maintain demographic performance under climate change conditions. Glob Change Biol 27:3883–3897. https://doi.org/10.1111/gcb.15678.

——— 2021*b* Spring phenological escape is critical for the survival of temperate tree seedlings. Funct Ecol 35:1848–1861. https://doi.org/10.1111/1365-2435.13821.

Lee BR, TK Miller, C Rosche, Y Yang, JM Heberling, SE Kuebbing, RB Primack 2022 Wildflower phenological escape differs by continent and spring temperature. Nat Commun 13:7157. https://doi.org/10.1038/s41467-022-34936-9.

Linderholm HW 2006 Growing season changes in the last century. Agric For Meteorol 137:1–14. https://doi.org/10.1016/j.agrformet.2006.03.006.

Lubbers AE, MJ Lechowicz 1989 Effects of leaf removal on reproductions vs. belowground storage in *Trillium grandiflorum*. Ecology 70:85–96. https://doi.org/10.2307/1938415.

Lundgren R, A Lázaro, Ø Totland 2015 Effects of experimentally simulated pollinator decline on recruitment in two European herbs. J Ecol 103:328–337. https://doi.org/10.1111/1365-2745.12374.

Martinez KA, JD Fridley 2018 Acclimation of leaf traits in seasonal light environments: are non-native species more plastic? J Ecol 106:2019–2030. https://doi.org/10.1111/1365-2745.12952.

McKenna MF, G Houle 2000 Why are annual plants rarely spring ephemerals? New Phytol 148:295–302. https://doi.org/10.1046/j.1469-8137.2000.00756.x.

Menzel A, P Fabian 1999 Growing season extended in Europe. Nature 397:659. https://doi.org/10.1038/17709.

Menzel A, TH Sparks, N Estrella, E Koch, A Aaasa, R Ahas, K Alm-Kübler, et al 2006 European phenological response to climate change matches the warming pattern. Glob Change Biol 12:1969–1976. https://doi.org/10.1111/j.1365-2486.2006.01193.x.

Miller TK, JM Heberling, SE Kuebbing, RB Primack 2022 Warming temperatures are linked to phenological mismatch among native and non-native forest plants. J Ecol 111:356–371. https://doi.org/10.1111/1365-2745.14021.

Mola JM, LL Richardson, G Spyreas, DN Zaya, IS Pearse 2021 Long-term surveys support declines in early season forest plants used by bumblebees. J Appl Ecol 58:1431–1441. https://doi.org/10.1111/1365-2664.13886.

Nakazawa T, H Doi 2012 A perspective on match/mismatch of phenology in community contexts. Oikos 121:489–495. https://doi.org/10.1111/j.1600-0706.2011.20171.x.

Neufeld HS, DR Young 2014 Ecophysiology of the herbaceous layer in temperate deciduous forests. Pages 35–95 *in* FS Gilliam, ed. The herbaceous layer in forests of eastern North America. Oxford University Press, New York. https://doi.org/10.1093/acprof:osobl/9780199837656.003.0003.

Olliff-Yang RL, T Gardali, DD Ackerly 2020 Mismatch managed? phenological phase extension as a strategy to manage phenological asynchrony in plant-animal mutualisms. Restor Ecol 28:498–505. https://doi.org/10.1111/rec.13130.

Park IW, T Ramirez-Parada, SJ Mazer 2021 Advancing frost dates have reduced frost risk among most North American angiosperms since 1980. Glob Change Biol 27:165–176. https://doi.org/10.1111/gcb.15380.

Parmesan C, G Yohe 2003 A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42. https://doi.org/10.1038/nature01286.

Peltier DMP, I Ibáñez 2015 Patterns and variability in seedling carbon assimilation: implications for tree recruitment under climate change. Tree Physiol 35:71–85. https://doi.org/10.1093/treephys/tpu103.

Piao S, Q Liu, A Chen, IA Janssens, Y Fu, J Dai, L Liu, X Lian, M Shen, X Zhu 2019 Plant phenology and global climate change: current progresses and challenges. Glob Change Biol 25:1922–1940. https://doi.org/10.1111/gcb.14619.

Proctor E, E Nol, D Burke, WJ Crins 2012 Responses of insect pollinators and understory plants to silviculture in northern hardwood forests. Biodivers Conserv 21:1703–1740. https://doi.org/10.1007/s10531-012-0272-8.

Ramirez-Parada TH, IW Park, SJ Mazer 2022 Herbarium specimens provide reliable estimates of phenological responses to climate at unparalleled taxonomic and spatiotemporal scales. Ecography 2022: e06173. https://doi.org/10.1111/ecog.06173.

Renner SS, CM Zohner 2018 Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. Annu Rev Ecol Evol Syst 49:165–182. https://doi.org/10.1146/annurev-ecolsys-110617-062535.

Richardson AD, AS Bailey, EG Denny, CW Martin, J O'Keefe 2006 Phenology of a northern hardwood forest canopy. Glob Change Biol 12:1174–1188. https://doi.org/10.1111/j.1365-2486.2006.01164.x.

Rothstein DE, DR Zak 2001 Photosynthetic adaptation and acclimation to exploit seasonal periods of direct irradiance in three temperate, deciduous-forest herbs. Funct Ecol 15:722–731. https://doi.org/10.1046/j.0269-8463.2001.00584.x.

Routhier MC, L Lapointe 2002 Impact of tree leaf phenology on growth rates and reproduction in the spring flowering species *Trillium erectum* (Liliaceae). Am J Bot 89:500–505. https://doi.org/10.3732/ajb.89.3.500.

Sawada S, S Chida, Y Sawaguchi, N Nagasawa 1997 Dry matter production, population structure and environmental conditions of the spring ephemeral *Erythronium japonicum* growing in various habitats differing in sunlight exposure in cool temperate Japan. Ecol Res 12:89–99. https://doi.org/10.1007/BF02523614.

Seiwa K 1999 Changes in leaf phenology are dependent on tree height in *Acer mono*, a deciduous broad-leaved tree. Ann Bot 83:355–361. https://doi.org/10.1006/anbo.1998.0831.

Smith LM 2013 Extended leaf phenology in deciduous forest invaders: mechanisms of impact on native communities. J Veg Sci 24:979–987. https://doi.org/10.1111/jvs.12087.

Song Y, HW Linderholm, D Chen, A Walther 2009 Trends of the thermal growing season in China, 1951–2007. Int J Climatol 30:33–43. https://doi.org/10.1002/joc.1868.

Sparling JH 1967 Assimilation rates of some woodland herbs in Ontario. Bot Gaz 128:160–168. https://doi.org/10.1086/336393.

Spicer ME, H Mellor, WP Carson 2020 Seeing beyond the trees: a comparison of tropical and temperate plant growth forms and their vertical distribution. Ecology 101:e02974. https://doi.org/10.1002/ecy.2974.

Stenseth NC, JM Durant, MS Fowler, E Matthysen, F Adriaensen, N Jonzén, K-S Chan, et al 2015 Testing for effects of climate change on competitive relationships and coexistence between two bird species. Proc R Soc B 282:20141958. https://doi.org/10.1098/rspb.2014.1958.

Taylor RJ, RW Pearcy 1976 Seasonal patterns of the CO_2 exchange characteristics of understory plants from a deciduous forest. Can J Bot 54:1094–1103. https://doi.org/10.1139/b76-117.

Timberlake TP, IP Vaughan, J Memmott 2019 Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. J Appl Ecol 56:1585–1596. https://doi.org/10.1111/1365-2664.13403.

Tourville J, G Murray, S Nelson 2023 Distinct latitudinal patterns of shifting spring phenology across the Appalachian Trail corridor. bioRxiv, https://doi.org/10.1101/2023.12.11.571108.

Uemura S 1994 Patterns of leaf phenology in forest understory. Can J Bot 72:409–414. https://doi.org/10.1139/b94-055.

Valladares F, Ü Niinemets 2008 Shade tolerance, a key plant feature of complex nature and consequences. Annu Rev Ecol Evol Syst 39:237–257. https://doi.org/10.1146/annurev.ecolsys.39.110707.173506.

Vellend M, JA Myers, S Gardescu, PL Marks 2003 Dispersal of *Trillium* seeds by deer: implications for long-distance migration of forest herbs. Ecology 84:1067–1072. https://doi.org/10.1890/0012-9658(2003)084[1067:DOTSBD]2.0.CO;2.

Visser ME, P Gienapp 2019 Evolutionary and demographic consequences of phenological mismatches. Nat Ecol Evol 3:879–885. https://doi.org/10.1038/s41559-019-0880-8.

Vitasse Y, A Lenz, G Hoch, C Körner 2014 Earlier leaf-out rather than difference in freezing resistance puts juvenile trees at greater risk of damage than adult trees. J Ecol 102:981–988. https://doi.org/10.1111/1365-2745.12251.

Willems FM, JF Scheepens, O Bossdorf 2022 Forest wildflowers bloom earlier as Europe warms: lessons from herbaria and spatial modelling. New Phytol 235:52–65. https://doi.org/10.1111/nph.18124.

Williams NM, R Winfree 2013 Local habitat characteristics but not landscape urbanization drive pollinator visitation and native plant pollination in forest remnants. Biol Conserv 160:10–18. https://doi.org/10.1016/j.biocon.2012.12.035.

Wolkovich EM, EE Cleland 2011 The phenology of plant invasions: a community ecology perspective. Front Ecol Environ 9:287–294. https://doi.org/10.1890/100033.

Wright SJ, CP van Schaik 1994 Light and the phenology of tropical trees. Am Nat 143:192–199. https://doi.org/10.1086/285600.

Xu C-Y, KL Griffin, WSF Schuster 2007 Leaf phenology and seasonal variation of photosynthesis of invasive *Berberis thunbergii* (Japanese barberry) and two co-occurring native understory shrubs in a northeastern United States deciduous forest. Oecologia 154:11–21. https://doi.org/10.1007/s00442-007-0807-y.

Yancy AJ, BR Lee, SE Kuebbing, HS Neufeld, ME Spicer, JM Heberling 2024 Evaluating the definition and distribution of spring ephemeral wildflowers in eastern North America. Am J Bot 111:e16323. https://doi.org/10.1002/ajb2.16323.

Yang Y, JM Heberling, RB Primack, BR Lee 2022 Herbarium specimens may provide biased flowering phenology estimates for dioecious species. Int J Plant Sci 183:777–783. https://doi.org/10.1086/722294.

Yin T-F, L-L Zheng, G-M Cao, M-H Song, F-H Yu 2016 Species-specific phenological responses to long-term nitrogen fertilization in an alpine meadow. J Plant Ecol 10:301–309. https://doi.org/10.1093/jpe/rtw026.