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Photoperiod–Temperature Interactions in a Changing Climate: A Review of Plant Phenological Responses

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ABSTRACT

Aim: Climate change is reshaping plant phenology and species distributions, especially in temperate and boreal ecosystems, where advances in spring events have already extended the growing season. While temperature has been the primary focus of many studies, the role of photoperiod—a stable, latitude-dependent cue—remains underexplored. This review aims to assess the combined effect of both photoperiod and temperature on plant responses to climate change.

Location: Northern hemisphere.

Taxon: Spermatophytes.

Methods: In this review, we synthesise evidence from 68 studies covering 344 taxa to evaluate how photoperiod interacts with rising temperatures to influence plant phenology.

Results: Key life cycle events such as bud burst, flowering and senescence are shown to be shaped by complex photoperiod–temperature interactions. Spring phenology seems to be the most affected by this interaction, with long photoperiods counterbalancing insufficient winter chilling in many species. Moreover, photoperiod constraints may limit the adaptive potential of certain species, particularly in high-latitude regions, and act as a barrier to range expansion under climate warming.

Conclusions: Understanding temperature–photoperiod interactions is essential for predicting species responses, guiding conservation strategies and improving ecosystem management in a changing climate. For example, this interaction might affect the choice of suitable plant material for assisted colonisation.

1 | Introduction

Global mean temperatures are projected to rise by up to 4.5°C by 2100, with even greater warming expected at northern latitudes (Collins et al. 2013; IPCC 2023). This climate change is affecting key plant traits, including phenology, nutrient uptake, plant defence mechanisms and interactions with mutualists, antagonists and competitors (Toby Kiers et al. 2010; Becklin et al. 2016; Steinbauer et al. 2018). Phenological shifts—such as earlier flowering—although varying widely across species, have been shown in many taxa, with ~70% of plants advancing their phenology in the past decades (Menzel et al. 2006; Amano et al. 2010; Wolkovich et al. 2012; Parmesan and Hanley 2015; Park and Talbot 2018). This extension in growing seasons, due to earlier springs and delayed autumns, could enhance forest productivity (Keenan et al. 2014), yet these benefits may be counteracted by mid-summer heat stress and drought (Stinziano and Way 2014), as well as by changed snowfall (Bokhorst et al. 2016). Such changes in flowering and fruiting have significant implications for agriculture, forestry, and carbon cycling (Menzel 2002; Piao et al. 2008). For instance, European spring events advanced by 2.5 days per decade between 1971 and 2000, potentially affecting ecological interactions (Menzel et al. 2006). Shifts in phenology have been one of the strongest and most consistent responses to climate change and are likely to play an important role in

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mediating population dynamics within and beyond species' ranges (Zettlemoyer and Peterson 2021). Shifts in species distributions towards higher latitudes and elevations are reshaping community assemblages, potentially leading to speciation events, extinction and species turnover (Parmesan and Yohe 2003; Gottfried et al. 2012; Alcala and Vuilleumier 2014; Rogora et al. 2018; Porro et al. 2022), eventually leading to reduced plant fitness (Nicotra et al. 2010).

Beside rising temperature, photoperiod, a consistent latitudinal cue, plays a particularly crucial role in temperate and polar zone plant phenology (Körner and Basler 2010). Unlike temperature, which fluctuates unpredictably, photoperiod follows a stable annual cycle dictated by Earth's axial tilt (Jackson 2009). Near the equator, photoperiod remains constant at 12 h, whereas at higher latitudes, day length varies significantly throughout the year. This seasonal predictability allows plants to anticipate environmental changes, with photoperiod perception occurring in leaves and regulated by the circadian clock (Jackson 2009; Singh and Mas 2018). As a critical seasonal cue, photoperiod regulates flowering, dormancy and growth cessation (Heide 1993a; Partanen et al. 1998; Basler and Körner 2012) and may ultimately limit species' ability to shift poleward in response to climate change (Way and Montgomery 2015).

This interaction may strongly affect the outcome of climate change on impacted species and ecosystems, especially on cold-adapted high-latitude ones (Hänninen and Tanino 2011; Saikkonen et al. 2012). While temperature is often seen as the primary driver of early-season phenology, photoperiod constraints may limit species' adaptation to warming (Ettinger et al. 2021). Understanding the interactions between photoperiod and temperature, alongside their genetic and ecological foundations, is crucial for predicting how plants will respond to climate change. While longer growing seasons can enhance plant growth and productivity (Oleksyn et al. 1992; Richardson et al. 2009), photoperiod mismatches may constrain these benefits (Way and Montgomery 2015).

In this review, we examined how the interaction between photoperiod and temperature influences plant phenology under climate change. Our goal was to synthesise current evidence of this interaction and identify knowledge gaps by addressing the following questions:

1. Given that photoperiod provides a stable seasonal cue while temperature varies under global warming, do phenological shifts arise from the altered relationship between these two drivers?
2. If such shifts occur, are they more pronounced in spring (budburst) or autumn (senescence) phenophases?
3. Do responses differ across taxonomic groups, growth forms or habitat types in terms of the combined effects of photoperiod and temperature?

By addressing these questions, we aim to highlight key patterns in plant phenological responses to shifting climatic and photoperiodic regimes, which may affect plant range shifts, and to suggest future directions for research on the temporal and spatial consequences of these interactions.

2 | Methods

To answer the above-mentioned questions, we searched relevant articles using the following queries in Scopus and Web of Science: photoperiod AND climate change, AND plants, AND migration, AND latitude. The search included all publication years up to September 2024 and was limited to English-language journal articles. We also considered other articles found through cross-referencing, to ensure comprehensive coverage of relevant research. Given the extensiveness and heterogeneity of the studies found, and the complexity of the photoperiod–climate interaction, we focused exclusively on temperature as a direct and consistent proxy for climate change in relation to plant phenology, excluding other climate-related variables, such as precipitation, snowfall or drought, to ensure more clarity and comparability among studies. We excluded papers that focused solely on molecular pathways and mechanisms, physiological aspects or methodological papers, as well as studies addressing light quality rather than daylength. We also excluded papers that did not investigate any phenological phases. Since only two papers focused on the Southern Hemisphere, we excluded them as well and only considered data regarding the Northern Hemisphere. After this search, we analysed review, descriptive and experimental papers covering at least one taxon, one phenological phase (budburst, flowering or senescence) and considering both temperature and photoperiod.

From each article, we extracted information about the response of each phenological phase(s) considered, categorising the different phenophases into three response categories: photoperiod control, temperature control and photoperiod–temperature interaction. To identify differences in response at the life form level, the response categories were separately assessed for herbs, shrubs and trees. Finally, we investigated taxonomical patterns in the response categories at the family level. Only families represented by at least five records were included in the analyses (19 out of 70 families).

3 | Results

Starting from 141 papers, after applying the abovementioned criteria, we included 68 articles in our review, covering 344 taxa and 70 families. A total of 497 records were compiled across three phenological phases (budburst, flowering, senescence), of which trees accounted for 277 observations, shrubs for 114 and herbs for 106 (Supporting Information S1). Across the 68 studies reviewed, temperature emerged as the dominant driver of plant phenology (52%), while photoperiod (21%) and photoperiod–temperature interactions (27%) showed variable influence depending on the phenophase and life form.

3.1 | Budburst

The combined effects of temperature and photoperiod on budburst were investigated across 209 records, with trees being by far the most represented group ($n = 196$), followed by shrubs ($n = 12$). Herbs were excluded from the analysis of bud burst, given that only one record for this group was found. Overall, budburst appeared to be primarily temperature-driven, with half of the records showing a dominant temperature control, and only a small percentage relying solely on photoperiodic control (Figure 1A). For this phenological phase, a clear interaction between photoperiod and temperature emerged, especially on trees, which showed the greatest variability in response, with almost half of the cases controlled by temperature and 38% exhibiting a temperature–photoperiod interaction, while only 15% were predominantly photoperiod-driven. Shrubs, in contrast, were more clearly governed by temperature, with only a minority showing an interaction or a pure photoperiodic response.

3.2 | Flowering

A total of 103 records investigated the regulation of flowering, with herbs being the most represented growth form ($n=79$), followed by shrubs ($n=16$) and trees ($n=8$). Across all forms, temperature was again the most frequent driver, although the proportion of photoperiod-controlled responses was noticeably higher than for budburst (Figure 1B).

Herbaceous species showed an equal distribution between temperature and photoperiod control, suggesting that both cues play a comparable role in the timing of flowering, whereas photoperiod–temperature interactions accounted for only 15% of studied cases. In shrubs and trees, temperature remained the dominant factor, with photoperiodic regulation being comparatively rare, and interaction emerging only in a small percentage of cases in shrubs.

3.3 | Senescence

Sixty-one records investigated autumnal phenological events, of which trees were the most represented life form ($n=40$),

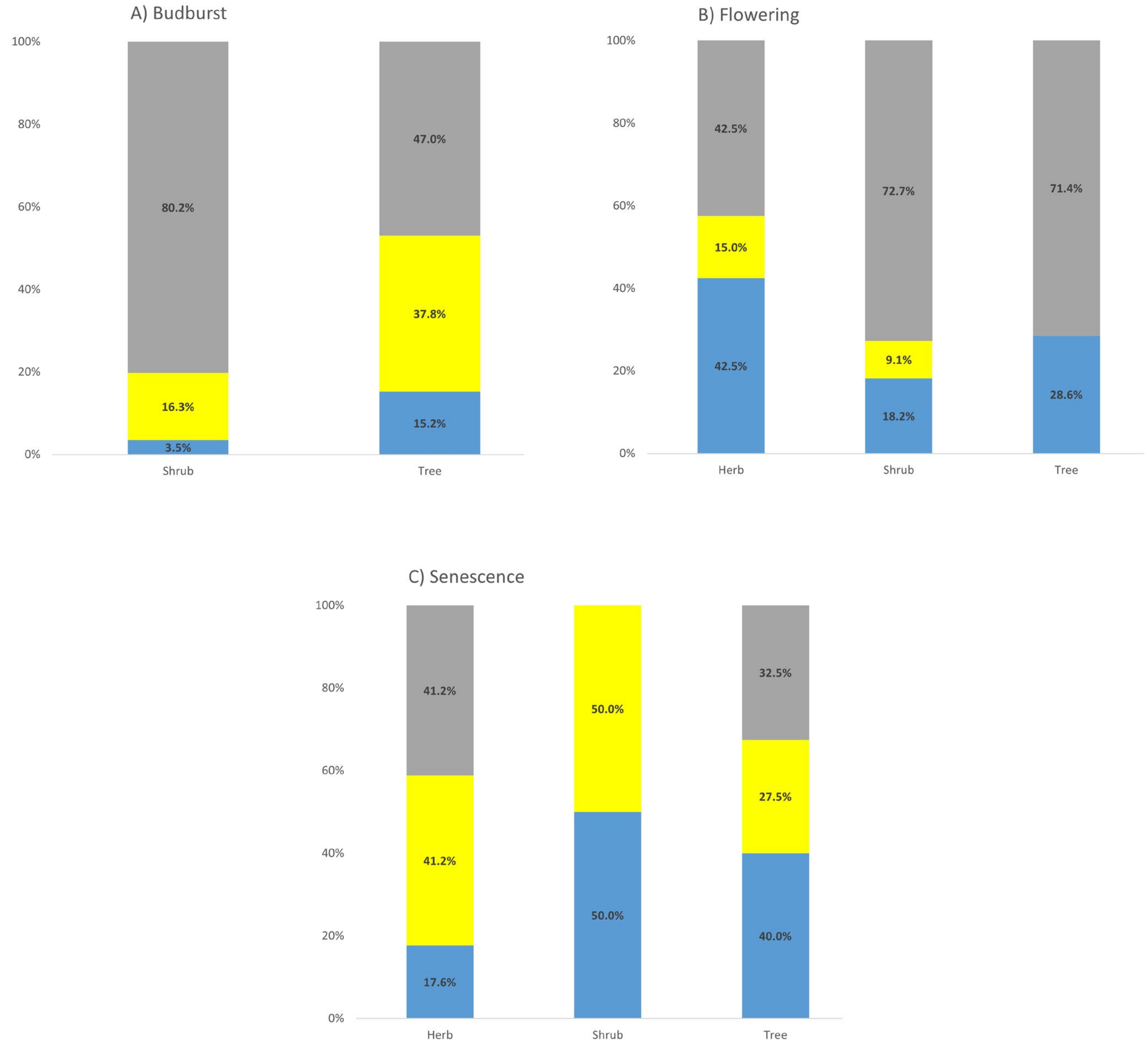

FIGURE 1 | Relative role of temperature (grey), photoperiod (yellow) and their interaction (blue) on budburst (A), flowering (B) and senescence (C) across different life forms.

followed by herbs ($n = 17$) and shrubs ($n = 4$). Across all life forms, the contribution of photoperiod was more pronounced than for spring phenophases (Figure 1C): a third of all cases were primarily photoperiod-controlled, a third reflected an interaction with temperature, and another third were temperature-driven.

Trees showed a relatively balanced distribution between photoperiod and temperature control, while 27.5% exhibited interactive effects. In herbs, temperature and interaction effects were equally represented, whereas pure photoperiodic control accounted for only a minority of cases. Shrubs, though represented by only four records, showed combined or photoperiodic control (50% each) and no exclusively temperature-driven cases. These results suggest that photoperiod becomes increasingly important in controlling the end of the growing season, especially in woody species where senescence must precede dormancy induction.

3.4 | Taxonomy

In total, the dataset included 70 plant families, but a limited number were particularly well represented. *Rosaceae* (56 records), *Betulaceae* (48), *Fagaceae* (43), *Salicaceae* (37), *Pinaceae* (32), *Sapindaceae* (26), *Poaceae* (19) and *Fabaceae* (17) together accounted for more than 65% of all records (315 out of 476) encompassing many dominant temperate taxa and key model species commonly used in phenological research. Across all taxa, temperature control predominated, followed by photoperiod–temperature interactions and exclusively photoperiodic regulation. However, this general pattern masked strong family-level contrasts. In fact, marked taxonomic differences emerged in the relative influence of temperature, photoperiod, and their interaction on plant phenology (Figure 2).

Among woody lineages, *Betulaceae*, *Fagaceae*, *Juglandaceae* and *Pinaceae* showed the most pronounced evidence of interactive effects (over 40% of records), reflecting the high degree of photoperiodic regulation typical of temperate and boreal trees such as *Fagus sylvatica*, *Quercus robur* and *Abies alba*. However, while temperature was also a dominant factor for Betulaceae, photoperiod exerted a strong influence in the other families.

Salicaceae, including *Populus* and *Salix*, showed an uneven distribution among temperature (51.4%), photoperiod (27.0%) and interactive control (21.6%).

In contrast, several taxa showed no evidence of photoperiodic regulation, indicating a predominantly temperature-driven phenological strategy. *Brassicaceae*, *Ericaceae*, *Hydrangeaceae* and *Ulmaceae* all lack records of photoperiod control, with phenological timing instead governed by temperature alone or by temperature–photoperiod interactions.

Herbaceous-dominated families such as *Asteraceae* and *Poaceae*, exhibited primarily temperature-driven control, with minor contributions from photoperiodic sensitivity.

Other families exhibit a relatively even distribution among photoperiodic, temperature and interactive controls, indicating flexible or transitional phenological strategies. *Hamamelidaceae*, for instance, show a nearly uniform representation across the three categories, suggesting mixed control mechanisms possibly linked to its wide temperate distribution and early-flowering habit. Similarly, *Juglandaceae* and *Cornaceae* display comparable proportions, reflecting an intermediate response where neither cue predominates, and phenological timing likely adjusts to local climatic conditions.

Families containing both woody and herbaceous representatives, such as *Rosaceae* and *Sapindaceae*, were predominantly temperature-driven (75.0% and 52.0%, respectively) but still retained measurable photoperiodic or interactive components. For *Rosaceae*, in particular, the high number of records (56) strengthens the results concerning their low photoperiod sensitivity.

4 | Discussion

Phenology, the study of life cycle events in plants, is affected by key ecological factors, like temperature, precipitation, light availability, etc. and is a key indicator signal of plant response to climate change due to its integration of long-term climatic signals (Chuine 2010; Ranjitkar 2013; Svystun and Jönsson 2022). In the context of global warming, interactions between different environmental cues are crucial to shaping plant species phenology, range shifts and evolutionary

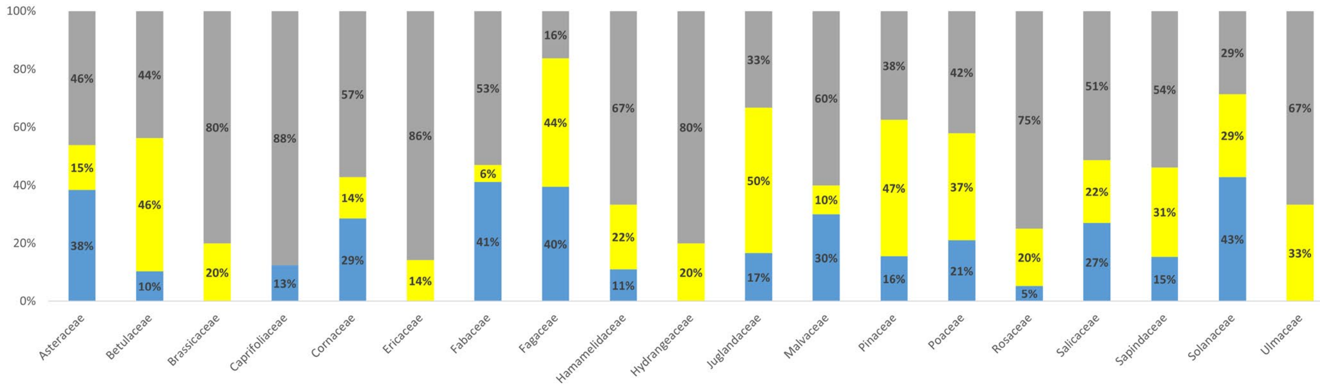

FIGURE 2 | Relative influence of temperature, photoperiod and their interaction on phenology across plant families (nomenclature according to the ICN).

dynamics. Among the several possible interactions on plant response to climate change, the one between photoperiod (a stable cue) and temperature (rising under global warming) is often overlooked in the literature (Saikkonen et al. 2012; Singh et al. 2017), with only spring phenophases in arboreal species being sufficiently investigated.

Sensitivity to photoperiod varies across species and ecotypes (Howe et al. 1995; Partanen 2005; Sanz-Pérez et al. 2009; Gauzere et al. 2017); some taxa are strictly regulated by daylength, while others rely more on temperature cues (Heide and Prestrud 2005; Tanino et al. 2010).

In this review, we analyse phenological data from 68 articles and 344 taxa, to investigate the combined role of photoperiod and temperature on plant phenology and the consequences that might arise under a change scenario.

4.1 | Budburst

Our results reinforce that, although air temperature is the dominant driver of budburst timing, photoperiod may act as a modulatory factor, fine-tuning thermal sensitivity in species from temperate and boreal zones, as suggested by the relatively high frequency of combined responses that we found. The interaction between temperature and day length is particularly relevant in trees, accounting for over a third of studied records.

In seasonally cold climates, temperate and boreal trees synchronise their annual growth cycles with environmental cues, entering dormancy in autumn and resuming growth in spring. This synchronisation ensures survival through harsh winters and optimal resource use during the growing season (Singh et al. 2017). Species that rely more on temperature cues than photoperiod to resume growth may gain a competitive advantage in warming climates (Ettinger et al. 2021).

However, early-season species that initiate growth too soon face a heightened risk of frost damage, reinforcing the importance of photoperiodic constraints in preventing premature budburst against unpredictable frost events (Kramer 1936; Withrow 1959; Sakai and Larcher 1987; Ettinger et al. 2021).

Interestingly, our results show how even within temperate deciduous tree families occupying similar geographic ranges, such as *Betulaceae* and *Fagaceae*, contrasting strategies in the regulation of budburst are evident. In Betulaceae, species such as *Betula pendula* show a stronger response to spring temperature forcing, reflecting an opportunistic strategy that maximises early-season carbon gain under favourable thermal conditions (Häkkinen et al. 1998). In contrast, members of the *Fagaceae*, particularly *Fagus sylvatica*, display a pronounced photoperiodic control of budburst (Heide 1993b; Basler and Körner 2012; Vitasse and Basler 2013; Laube et al. 2014), which functions as a conservative mechanism to prevent frost damage in unpredictable springs (Vitasse et al. 2009; Davi et al. 2011). These differences likely reflect divergent adaptive strategies to similar climatic conditions: temperature-sensitive taxa adopt a 'risk-prone' approach, advancing growth to exploit early warmth, whereas photoperiod-sensitive taxa follow a 'risk-avoidant' strategy, relying on daylength cues to ensure phenological stability.

Bud dormancy consists of two main phases: Endodormancy, an internally regulated state in which growth is suppressed, and ecodormancy, imposed by external unfavourable conditions (Lang et al. 1987; Chuine et al. 2016; Lundell et al. 2020).

The release of endodormancy requires sufficient accumulation of chilling (prolonged exposure to low temperatures), whereas ecodormancy is terminated once forcing temperatures—a period of sustained warmth—are met (Caffarra and Donnelly 2011; Caffarra et al. 2011; Basler and Körner 2012; Fu et al. 2012). Photoperiod alone cannot break dormancy, but it provides a stable and reliable cue that interacts with temperature to regulate the transition between dormancy and active growth (Espinosa-Ruiz et al. 2004; Rinne et al. 2011; Way and Montgomery 2015).

Chilling requirements vary among different taxa. For instance, the *Populus* genus requires prolonged cold exposure to break dormancy, whereas *Betula* spp. and *Picea glauca* can resume growth even with less chilling requirements (Myking and Heide 1995).

The role of photoperiod also depends on the species, with taxa such as *Ulmus* spp., *Aesculus hippocastanum* and *Picea abies* exhibiting weak photoperiodic control, relying instead on chilling and forcing temperatures (Ghelardini et al. 2010; Basler and Körner 2012; Vitasse and Basler 2013; Laube et al. 2014).

In some cases, however, long photoperiods can compensate for insufficient chilling, facilitating budburst despite mild winters (Wareing 1953; Heide 1993a, 1993b). *Ulmus* populations also display a latitudinal cline in photoperiodic response, with northern ecotypes more sensitive to daylength than southern ones (Håbjørg 1978; Ghelardini et al. 2010).

Species from oceanic climates often depend more on photoperiodic cues due to high variability in spring temperature (Körner and Basler 2010), while invasive species with lower chilling requirements and greater phenological plasticity—such as members of *Pinus* and *Rosaceae*—may gain a competitive advantage under climate change, being less constrained by photoperiod and capable of extending their growing season (Hulme 2011; Wolkovich and Cleland 2011; Richardson and Rejmánek 2011; Laube et al. 2014).

Photoperiod can therefore interact with temperature cues to regulate budburst, sometimes compensating for insufficient chilling by promoting dormancy release when daylength reaches a critical threshold, thereby ensuring timely spring growth, even when chilling requirements are not met (Laube et al. 2014).

The interplay between chilling, forcing and photoperiod is therefore a strong driver of spring phenology, especially in woody plants (Heide 1993a; Körner and Basler 2010; Polgar and Primack 2011; Basler and Körner 2012; Laube et al. 2014; Flynn and Wolkovich 2018). Insufficient chilling or restrictive photoperiod thresholds may delay budburst despite higher temperatures (Heide 1993a; Basler and Körner 2012; Laube et al. 2014).

This trade-off explains why, despite global warming, budburst has advanced less than expected—a likely consequence of reduced winter chilling and delayed dormancy induction during warmer autumns (Murray et al. 1989; Yu et al. 2010; Heide 2003; Laube et al. 2014; Malyshev 2020).

Finally, intraspecific variation in the relative influence of temperature and photoperiod further complicates predictions. Genotypes from harsher climates tend to show reduced plasticity compared to those from milder environments (Vitasse 2013), suggesting that populations locally adapted to narrow photoperiodic regimes may be less able to track changing conditions. This reinforces the need to account for genotypic variation in chilling and photoperiodic responses when forecasting phenological shifts or planning assisted migration strategies.

4.2 | Flowering

Similarly to budburst, photoperiodic regulation of flowering also varies widely among plant species. Unlike budburst, temperature and photoperiod generally act independently in determining flowering time, with a clear interaction only emerging in a minority of cases (Figure 1B).

A strong temperature control of flowering emerges in species studied by Geissler et al. (2023) (see Supporting Information S1), who confirmed a strong correlation between rising temperatures and earlier flowering, with a flowering advancement of 2.26 days per 1°C increase in annual temperature and of 2.93 days per 1°C increase in spring temperature.

When it comes to photoperiod regulation, plants can show an obligate photoperiodic response, where flowering occurs only under specific daylengths, or a facultative response, where photoperiod enhances but does not strictly determine flowering (Jackson 2009). For example, short-day plants (SDPs) flower under decreasing daylength, while long-day plants (LDPs) require extended photoperiods; exceptions exist, such as *Xanthium strumarium*, an SDP capable of flowering under long days, and some *Lolium* cultivars, LDPs that bloom even under short days (Thomas and Vince-Prue 1997).

The critical daylength (CDL) is not fixed but depends on plant age and environmental conditions; for instance, a case in which an interaction between thermal and photoperiodic conditions emerges is represented by *Hyoscyamus niger*, which exhibits shorter CDL under cooler night temperatures (Jackson 2009).

Long-term observations conducted by Zeng et al. (2024) indicate that flowering shifts under climate change differ among photoperiodic groups: short day species (e.g., *Glycine*, *Phaseolus*, *Desmodium*) by ~1.4 days per decade; day-neutral species (e.g., *Geum*) have advanced their flowering time by 0.9 days per decade, and long day species (e.g., *Calibrochoa*, *Pisum*, *Trifolium*) have only shown slight delays (~0.2 days per decade).

Precise flowering timing is particularly crucial for reproductive success in arctic and alpine environments, where the growing season is short (~8–12 weeks). The pattern in flowering reflects shorter life cycles and the need to synchronise reproduction with seasonal windows of suitable conditions. Entomophilous species must align flowering with pollinator activity, while anemophilous species tend to flower immediately after snowmelt, responding primarily to temperature cues rather than daylength (Heide 2001; Keller and Körner 2003). Recent studies have shown that warming temperatures are advancing the emergence and main flight periods of bumblebees (Pawlikowski et al. 2020), while altering snowpack and thermal conditions in alpine habitats are disrupting bumblebee community composition and phenology (Miller-Struttmann et al. 2022). This phenological mismatch could reduce pollination success in species whose flowering remains constrained by daylength. Plant-pollinator interactions may, in particular, be influenced by herbaceous plant species losing pace with climate change, leading to biotic mismatches (Rauschkolb et al. 2024).

Experimental studies in alpine snowbeds show that late snowmelt reduces the heat requirement for flowering in species such as *Salix herbacea*, allowing them to bloom under cooler conditions (Carbognani et al. 2016). However, photoperiod becomes limiting once daylength exceeds species-specific thresholds, reinforcing flowering synchrony (Carbognani et al. 2016; Inouye 2008; Kawai and Kudo 2018).

Under climate change scenarios, alpine species that rely heavily on photoperiod may struggle to adjust to earlier snowmelt, while nonphotoperiod-sensitive species, which respond primarily to temperature, may initiate flowering earlier but face an increased risk of frost damage (Wadgymar et al. 2018).

A slight interaction between photoperiod and temperature emerges in the flowering time of herbaceous species, with both cues contributing to variable degrees depending on the species (Figure 1A). In contrast, no such interaction emerges in the tree taxa analysed in our study. For this life form, temperature acts as the primary cue for flowering time, while photoperiod accounts for fewer than one-third of the cases. For instance, long-day deciduous trees like *Acer* and *Fraxinus* initiate flowering primarily in response to increasing daylength. Conversely, early-spring flowering trees, like *Salix* and *Betula*, rely more on temperature cues to initiate flowering.

In general, photoperiod-sensitive species, particularly long-lived trees and late-successional plants, regulate flowering to prevent premature responses to transient warming (Körner and Basler 2010; Zeng et al. 2024) and late-flowering species are more influenced by photoperiod than early-flowering ones (Schaber and Badeck 2003).

Overall, while photoperiod can modulate flowering timing, its interaction with temperature is less pronounced than in budburst, and flowering phenology is largely constrained by species-specific genetic programs.

4.3 | Senescence

The impact of the different drivers of autumn senescence has mostly been studied in trees, with our results confirming that autumn leaf senescence in temperate and boreal deciduous arboreal species is primarily triggered by photoperiod, which signals growth cessation, bud formation and the onset of dormancy as winter approaches (Cooke et al. 2012; Olsen et al. 1997; Ruttink et al. 2007). This process allows nutrient reallocation from leaves to storage organs, avoiding the need for frost-hardy foliage and ensuring survival (Chabot and Hicks 1982; Chapin III et al. 1990). As senescence progresses, chloroplast degradation reduces photosynthetic efficiency (Gan and Amasino 1997; Keskitalo et al. 2005), representing a trade-off between carbon gain and nutrient conservation: early senescence limits photosynthesis, while delayed senescence increases frost risk and can impair xylem function (Wirtz 2000; Fracheboud et al. 2009).

Although short photoperiods dictate the onset of senescence, our results indicate a relevant role in the interaction between day length and temperature, which modulates the rate and progression of this phenophase (Jiang et al. 2022; Rohde et al. 2011). For example, studies on *Betula* show that moderately warm temperatures (15°C–18°C) can accelerate dormancy establishment even under short-day conditions (Junttila et al. 2003). Similarly, chlorophyll degradation rates vary with latitude: Northern populations of *Populus tremula* enter senescence later but degrade chlorophyll more rapidly, balancing carbon acquisition and nutrient remobilisation (Fracheboud et al. 2009). In contrast, species like *Larix decidua* and *Quercus robur* maintain photoperiod-driven timing of senescence, though thermal or drought stress can advance leaf fall, shortening the effective growing season (Keskitalo et al. 2005).

Photoperiod-sensitive genera such as *Populus* and *Fagus* exhibit strong genetic control over bud set and growth cessation, with northern ecotypes responding more sharply to decreasing daylength than southern ones (Heide 1974; Espinosa-Ruiz et al. 2004; Fracheboud et al. 2009; Singh et al. 2017). This variability influences species' responses to climate warming: while growing seasons are generally lengthening, photoperiod remains the dominant cue for autumn phenology, and temperature primarily affects the speed of leaf senescence (Keskitalo et al. 2005; Junttila 2007; Fracheboud et al. 2009).

Contrary to results in arboreal species, our data set indicates that temperature is the primary driver of senescence in many herbaceous species, like *Agropyron cristatum*, *Festuca ovina* and *Poa alpina*, although it is important to underline how herbaceous species are underrepresented in our database, when it comes to this phenophase (17 records in herbs against 40 in trees).

By contrast, a few species exhibit strict photoperiodic control, including *Carex przewalskii*, *Oxyria digyna* and *Stipa sareptana*. In these plants, daylength serves as the dominant cue, regulating developmental transitions independently of temperature fluctuations.

A significant portion of herbaceous species, however, demonstrates interaction between photoperiod and temperature, highlighting the complexity of environmental regulation. *Elymus nutans*, *Koeleria cristata*, *Leymus secalinus* and *Medicago sativa* rely on both cues, with photoperiod setting a temporal window and temperature modulating the rate or magnitude of developmental processes (Supporting Information S1). These taxa may be particularly responsive to climate change, as shifts in temperature or daylength could differentially affect growth and reproduction depending on the balance of these cues.

Overall, the interaction between photoperiod and temperature in autumn senescence is less pronounced than in budburst, but it remains ecologically relevant: Photoperiod triggers the process (particularly in temperate deciduous trees) while temperature modulates its rate, influencing carbon allocation, nutrient cycling and plant resilience under changing climates.

4.4 | Taxonomy

Our comparative analysis revealed clear taxonomic differences in phenological control, reflecting variation in life form, ecological strategy and evolutionary history. Across all families, temperature regulation dominated (51%), while photoperiod–temperature interactions and pure photoperiodic control accounted for 29% and 20%, respectively. These contrasts indicate that phenological strategies are not randomly distributed among lineages but reflect adaptive trade-offs between environmental predictability and life-history traits.

Families dominated by herbaceous or evergreen taxa, such as *Brassicaceae* and *Ericaceae*, were largely temperature-driven, suggesting adaptive advantages in thermally variable environments where rapid responses to transient warmth favour early growth and reproduction. Similarly, *Hydrangeaceae* and *Ulmaceae*, composed mainly of woody deciduous species, showed strong thermal dependence, indicating reliance on temperature thresholds for dormancy release and spring reactivation rather than on genetically constrained photoperiodic cues. The lack of photoperiodic control in *Ericaceae* and *Ulmaceae* suggests a more opportunistic phenological strategy, prioritising flexibility over strict seasonal synchronisation—an advantage in temperate or subalpine climates where temperature provides a more reliable signal of seasonal progression.

In contrast, woody lineages with broad geographic distributions, such as *Betulaceae* and *Fagaceae*, displayed a pronounced integration of photoperiod and temperature cues, consistent with the need to coordinate growth cycles across wide latitudinal gradients. Despite overlapping habitat ranges, these families exhibit opposing cue hierarchies: Betulaceae respond predominantly to temperature, while *Fagaceae* are more photoperiod-sensitive. This divergence likely reflects distinct risk-management strategies, with temperature-sensitive species adopting a 'risk-prone' approach to maximise early carbon gain, and photoperiod-sensitive taxa following a 'risk-avoidant' strategy to prevent frost damage—potentially facilitating their coexistence through ecological niche differentiation.

Other lineages showed distinctive patterns. *Salicaceae* combined both cues, supporting the idea that temperate deciduous trees coordinate growth onset and cessation through dual regulation under variable spring and autumn conditions. Rosaceae were predominantly temperature-dependent, consistent with their ecological diversity and prevalence in open habitats where temperature is a reliable predictor of seasonal change. *Fabaceae* exhibited high variability, ranging from temperature-driven to photoperiod-sensitive responses, reflecting their broad latitudinal distribution and diversity of growth forms. *Poaceae* and *Asteraceae* were largely temperature-controlled, in line with their short life cycles and high phenological plasticity. Conversely, *Solanaceae* showed the strongest photoperiodic regulation (42.9%), in agreement with the circadian and photoreceptor-mediated control of flowering and growth described in both wild and cultivated representatives of the family (Müller et al. 2016).

Taken together, these results reveal a clear functional gradient:

- Woody taxa from temperate and boreal zones (e.g., *Fagaceae*, *Betulaceae*, *Pinaceae*) exhibit strong photoperiod–temperature coupling.
- Herbaceous families rely primarily on temperature cues, maximising growth and reproduction under favourable thermal conditions.
- Photoperiodic regulation is most prevalent among long-lived species with marked seasonal dormancy, emphasising its role in determining the onset and cessation of growth cycles.

Overall, these taxonomic contrasts support the view that photoperiod sensitivity predominates in long-lived woody species, while temperature dependence characterises short-lived herbs (Saikkonen et al. 2012; Zohner et al. 2016; Flynn and Wolkovich 2018). This divergence reflects evolutionary adaptations linked to lifespan, growth form and latitude, which ultimately shape each lineage's capacity to track or buffer ongoing climate warming. Photoperiod-sensitive taxa may maintain phenological stability under rising temperatures, whereas thermally responsive species exhibit greater plasticity but face increased risks of frost exposure and seasonal mismatch.

4.5 | Research Gaps and Future Directions

Our review highlights that the effects of photoperiod–climate interactions on plant responses to climate change remain insufficiently explored. Many studies investigating climate change impacts on plants have used fixed photoperiods, limiting the ability to fully assess their role in phenological responses (e.g., Oleksyn et al. 1992). Experimental manipulations of photoperiod are challenging, particularly in the field, requiring complex setups or reciprocal transplanting across latitudes, which is logistically and legally demanding (movement of living material across borders), especially for tree species. Seedlings or twig cuttings facilitate experimental manipulations and transportation. Twig cuttings, specifically, are vastly used in manipulative studies, as they have been shown to precisely mirror the phenology of donor trees because dormancy release is controlled at the bud level and not influenced by hormonal signals from other parts of a tree, such as the stem or the roots (Zohner et al. 2016). However, these approaches introduce additional variability: Phenological responses differ with life stage (e.g., juvenile cuttings are more sensitive to photoperiod than adults, as observed in *Prunus avium* by Besford et al. 1996), collection time and whether experiments are conducted in situ or ex situ (Zohner et al. 2016; Taulavuori et al. 2017). Such methodological differences likely contribute to the often-equivocal results found in the literature, even when considering the same species (See Supporting Information S1).

Furthermore, research on this topic to date has focused largely on trees, likely because of their importance in forestry, with budburst predominantly studied in arboreal species and flowering in herbaceous ones, limiting our ability to draw general conclusions across different life forms. Experimental data on other phenophases, as well as on shrubs, herbs and cold-adapted species, remains scarce. This highlights the need for targeted studies addressing understudied taxa and phenophases to understand the broader ecological consequences of photoperiod–temperature interactions.

Additionally, understanding interactions between photoperiod constraints and other abiotic and biotic factors—such as water and nutrient availability, competition, pollination and soil microbiomes—will be crucial for predicting future species and ecosystem dynamics.

Standardised, coordinated research networks, such as the Global Observation Research Initiative in Alpine Environments (GLORIA), the International Long-term Ecological Research (ILTER) or the International Tundra Experiment (ITEX), could improve comparability, replicability, and generality of findings across species, life forms and phenophases.

5 | Implication Under Climate Warming

Climate change is reshaping plant distributions, exposing species to environmental conditions that may exceed their physiological limits. While gene flow and local adaptation can buffer these effects, the current rate of warming often outpaces the natural migratory capacity of many taxa, especially long-lived ones like trees (Ward and Kelly 2004; Loarie et al. 2009; Kremer et al. 2014). As global temperatures rise, suitable habitats shift poleward and upward (Parmesan 2006; Pauli et al. 2012), but many populations may fail to track these changes if their phenotypic plasticity is limited (Aitken et al. 2008; Anderson et al. 2012; Shaw and Etterson 2012; Burrows et al. 2014; Franks et al. 2014).

However, range shifts are constrained not only by temperature but also by photoperiodic regimes, which change predictably with latitude. As species migrate northward in the northern hemisphere, they encounter longer summer days and greater seasonal variation in daylength, potentially decoupling thermal cues from photoperiodic regulation (Huffeldt 2020). Misalignment between thermal and photoperiodic cues can create ‘photic barriers’, limiting northward expansion and altering ecological interactions such as pollination and competition (Settele et al. 2016; Huffeldt 2020, 2021; Tougeron 2021), though the influence of photoperiod on latitudinal shifts in species distributions varies greatly between taxa (Saikkonen et al. 2012; Huffeldt 2020, 2021; Tougeron 2021). Therefore, while warming facilitates the poleward expansion of thermophilus taxa (Parmesan 2006), adaptation to nonclimatic factors—particularly photoperiod, soil and biotic interactions—can strongly limit the establishment and persistence of other taxa (Alberto et al. 2013; Corlett and Westcott 2013; Bjorkman et al. 2017). Thus, photoperiod emerges as a key determinant of migration capacity (Tomiolo and Ward 2018). This is particularly true for trees, where natural migration is often temporally decoupled from climate change because dispersal and selection processes are too slow to achieve rapid adaptation (Savolainen et al. 2007; Petit et al. 2008).

As shown by our results, species differ widely in their photoperiodic sensitivity. In a climate change context, species less constrained by photoperiodic control may gain a competitive advantage under global warming, as they can respond more directly to temperature increases, extend their growing season, and thus achieve greater carbon gain and competitive dominance (Zohner and Renner 2014; Zohner et al. 2016; Ettinger et al. 2021). This is, for example, the case of most *Rosaceae*, which have been shown to respond to temperature, independently of the photoperiodic regimes (Heide and Prestrud 2005) and *Rhododendron arboreum*, a species with reduced photoperiod sensitivity and lower chilling requirements (Ranjitkar 2013). Conversely, species with strong photoperiodic regulation, like *Fagus sylvatica*, may struggle to adjust to new latitudes where critical daylength thresholds no longer coincide with local climatic conditions, potentially reducing their range or requiring assisted colonisation (sensu IUCN/SSC 2013) to preserve ecosystem stability.

Moreover, intraspecific variation in photoperiod sensitivity can be substantial, especially in species with broad latitudinal ranges, leading to local ecotypes that differ in their photoperiodic thresholds and seasonal timing. These dynamics have critical implications for assisted migration, increasingly adopted in forest management and conservation (McLachlan et al. 2007; Aitken et al. 2008; Leech et al. 2011). Successful translocation requires selecting genotypes adapted not only to the target climate but also to its photoperiodic regime, since maladaptation to daylength can severely impair survival and growth. Such differentiation has direct implications for this type of conservation strategy, as the success of translocated material depends not only on thermal adaptation but also on matching photoperiodic regimes. For instance, in *Pinus sylvestris*, core range populations (54°–57° N) exhibit greater photoperiodic plasticity than northern ones (57°–67° N), which rely on earlier and sharper declines in daylength to trigger growth cessation (Giertych 1981; Oleksyn and Giertych 1984).

Photoperiod also acts as a selective filter for non-native species. Although alien taxa may benefit from reduced biotic pressures (Aitken et al. 2008; Van der Putten et al. 2010), their expansion may be limited by photoperiod mismatches. *Ambrosia artemisiifolia*, for example, requires specific photoperiod–temperature combinations for flowering, which currently restrict its spread in northern Europe despite suitable temperatures (Deen et al. 1998; Scalone et al. 2016). Nevertheless, repeated introductions and high genetic diversity may allow gradual adaptation of northern genotypes (Dlugosch and Parker 2008; Chun et al. 2011).

6 | Conclusions

Our analysis indicates that photoperiod–temperature interactions exert variable influences depending on phenological phase and life form. Spring phenology, particularly budburst, is most strongly affected, especially in trees, where photoperiod can often compensate for a lack of chilling requirements under warming scenarios. Flowering, predominantly studied in herbaceous species, appears to be genetically regulated and less sensitive to these interactions, often relying primarily on either temperature or photoperiod. Leaf senescence, by contrast, is largely photoperiod-driven, particularly in trees, whereas temperature mainly affects the rate of photosynthetic apparatus degradation and progression towards the end of the growing season.

Herbaceous and short-lived taxa generally relied on temperature as their main cue, reflecting adaptive advantages in environments with high thermal variability. In contrast, long-lived woody species exhibited stronger photoperiodic regulation or combined cue integration, strategies that promote stability but may constrain flexibility under rapid climate warming. Such differences highlight that phenological sensitivity is not uniform across lineages but is shaped by evolutionary trade-offs between plasticity and predictability.

In the context of climate change, as warming shifts climatic niches poleward, species that are primarily temperature-driven may expand their ranges more rapidly but risk mismatches with photoperiodic constraints, frost events or pollinator activity. Conversely, photoperiod-sensitive species may maintain phenological stability but exhibit reduced competitiveness in longer and warmer growing seasons. Understanding these contrasting strategies is therefore essential for predicting range shifts, community reassembly and species competitiveness under future climates. Furthermore, this knowledge is critical for guiding assisted migration and restoration strategies, where selecting genotypes or species with appropriate photothermal sensitivities will determine the success of translocations.

In summary, plant phenology represents a finely tuned balance between temperature-driven flexibility and photoperiodic stability. Recognising how these cues interact across species and life forms is fundamental for forecasting ecological responses to global change and for developing adaptive management strategies that sustain biodiversity and ecosystem function in an increasingly unpredictable climate.

Author Contributions

Martina Tarascio and Thomas Abeli conceived the idea for the review, conducted the literature search and wrote the manuscript. Lisa Brancaleoni, Anna Cazzavillan, Maurizio Cutini and Renato Gerdol contributed by suggesting additional relevant literature, reviewing the manuscript and providing input for minor revisions and improvements. All authors read and approved the final version of the manuscript.

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Disclosure

Statement on Inclusion: Our study was a global review and was based on published data. As such, the inclusion of local coauthors was not required.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data used in this work comes from the reviewed literature. All reviewed articles and species information are available in Supporting Information S1.

References

Aitken, S. N., S. Yeaman, J. A. Holliday, T. Wang, and S. Curtis-McLane. 2008. "Adaptation, Migration or Extirpation: Climate Change Outcomes for Tree Populations." *Evolutionary Applications* 1, no. 1: 95–111. https://doi.org/10.1111/j.1752-4571.2007.00013.x.

Alberto, F. J., S. N. Aitken, R. Alía, et al. 2013. "Potential for Evolutionary Responses to Climate Change–Evidence From Tree Populations." *Global Change Biology* 19, no. 6: 1645–1661. https://doi.org/10.1111/gcb.12181.

Alcala, N., and S. Vuilleumier. 2014. "Turnover and Accumulation of Genetic Diversity Across Large Time-Scale Cycles of Isolation and Connection of Populations." *Proceedings of the Royal Society B: Biological Sciences* 281, no. 1794: 20141369. https://doi.org/10.1098/rspb.2014.1369.

Amano, T., R. J. Smithers, T. H. Sparks, and W. J. Sutherland. 2010. "A 250-Year Index of First Flowering Dates and its Response to Temperature Changes." *Proceedings of the Royal Society B: Biological Sciences* 277, no. 1693: 2451–2457.

Anderson, J. T., A. M. Panetta, and T. Mitchell-Olds. 2012. "Evolutionary and Ecological Responses to Anthropogenic Climate Change: Update on Anthropogenic Climate Change." *Plant Physiology* 160, no. 4: 1728–1740. https://doi.org/10.1104/pp.112.206219.

Basler, D., and C. Körner. 2012. "Photoperiod Sensitivity of Bud Burst in 14 Temperate Forest Tree Species." *Agricultural and Forest Meteorology* 165: 73–81. https://doi.org/10.1016/j.agrformet.2012.06.001.

Becklin, K. M., J. T. Anderson, L. M. Gerhart, S. M. Wadgymar, C. A. Wessinger, and J. K. Ward. 2016. "Examining Plant Physiological Responses to Climate Change Through an Evolutionary Lens." *Plant Physiology* 172, no. 2: 635–649. https://doi.org/10.1104/pp.16.00793.

Besford, R. T., P. Hand, C. M. Richardson, and S. D. Peppitt. 1996. "Photoperiod Effect on Bud Burst in *Prunus* Is Phase Dependent: Significance for Early Photosynthetic Development." *Tree Physiology* 16, no. 5: 491–496. https://doi.org/10.1093/treephys/16.5.491.

Bjorkman, A. D., M. Vellend, E. R. Frei, and G. H. Henry. 2017. "Climate Adaptation is not Enough: Warming Does not Facilitate Success of Southern Tundra Plant Populations in the High Arctic." *Global Change Biology* 23, no. 4: 1540–1551.

Bokhorst, S., S. H. Pedersen, L. Brucker, et al. 2016. "Changing Arctic Snow Cover: A Review of Recent Developments and Assessment of Future Needs for Observations, Modelling, and Impacts." *Ambio* 45: 516–537. https://doi.org/10.1007/s13280-016-0770-0.

Burrows, M. T., D. S. Schoeman, A. J. Richardson, et al. 2014. "Geographical Limits to Species-Range Shifts Are Suggested by Climate Velocity." *Nature* 507, no. 7493: 492–495. https://doi.org/10.1038/nature12976.

Caffarra, A., and A. Donnelly. 2011. "The Ecological Significance of Phenology in Four Different Tree Species: Effects of Light and Temperature on Bud Burst." *International Journal of Biometeorology* 55: 711–721. https://doi.org/10.1007/s00484-010-0386-1.

Caffarra, A., A. Donnelly, and I. Chuine. 2011. "Modelling the Timing of *Betula pubescens* Budburst. II. Integrating Complex Effects of Photoperiod Into Process-Based Models." *Climate Research* 46, no. 2: 159–170. https://doi.org/10.3354/cr00983.

Carbognani, M., G. Bernareggi, F. Perucco, M. Tomaselli, and A. Petraglia. 2016. "Micro-Climatic Controls and Warming Effects on Flowering Time in Alpine Snowbeds." *Oecologia* 182: 573–585. https://doi.org/10.1007/s00442-016-3669-3.

Chabot, B. F., and D. J. Hicks. 1982. "The Ecology of Leaf Life Spans." *Annual Review of Ecology and Systematics* 13: 229–259. https://www.jstor.org/stable/2097068.

Chapin, F. S., III, E. D. Schulze, and H. A. Mooney. 1990. "The Ecology and Economics of Storage in Plants." *Annual Review of Ecology and Systematics* 21: 423–447. https://www.jstor.org/stable/2097032.

Chuine, I. 2010. "Why Does Phenology Drive Species Distribution?" *Philosophical Transactions of the Royal Society, B: Biological Sciences* 365, no. 1555: 3149–3160. https://doi.org/10.1098/rstb.2010.0142.

Chuine, I., M. Bonhomme, J. M. Legave, et al. 2016. "Can Phenological Models Predict Tree Phenology Accurately in the Future? The Unrevealed Hurdle of Endodormancy Break." *Global Change Biology* 22, no. 10: 3444–3460. https://doi.org/10.1111/gcb.13383.

Chun, Y. J., V. Le Corre, and F. Bretagnolle. 2011. "Adaptive Divergence for a Fitness-Related Trait Among Invasive *Ambrosia artemisiifolia* Populations in France." *Molecular Ecology* 20, no. 7: 1378–1388. https://doi.org/10.1111/j.1365-294X.2011.05013.x.

Collins, M., R. Knutti, J. Arblaster, et al. 2013. "Chapter 12 - Long-Term Climate Change: Projections, Commitments and Irreversibility." In *Climate Change 2013: The Physical Science Basis. IPCC Working Group I Contribution to AR5*. Cambridge University Press. http://www.climatechange2013.org/images/report/WG1AR5_Chapter12_FINAL.pdf.

Cooke, J. E., M. E. Eriksson, and O. Junttila. 2012. "The Dynamic Nature of Bud Dormancy in Trees: Environmental Control and Molecular Mechanisms." *Plant, Cell & Environment* 35, no. 10: 1707–1728. https://doi.org/10.1111/j.1365-3040.2012.02552.x.

Corlett, R. T., and D. A. Westcott. 2013. "Will Plant Movements Keep Up With Climate Change?" *Trends in Ecology & Evolution* 28, no. 8: 482–488. https://doi.org/10.1016/j.tree.2013.04.003.

Davi, H., M. Gillmann, T. Ibanez, et al. 2011. "Diversity of Leaf Unfolding Dynamics Among Tree Species: New Insights From a Study Along an Altitudinal Gradient." *Agricultural and Forest Meteorology* 151, no. 12: 1504–1513. https://doi.org/10.1016/j.agrformet.2011.06.008.

Deen, W., T. Hunt, and C. J. Swanton. 1998. "Influence of Temperature, Photoperiod, and Irradiance on the Phenological Development of Common Ragweed (*Ambrosia artemisiifolia*)." *Weed Science* 46, no. 5: 555–560. https://doi.org/10.1017/S0043174500091098.

Dlugosch, K. M., and I. M. Parker. 2008. "Founding Events in Species Invasions: Genetic Variation, Adaptive Evolution, and the Role of

Multiple Introductions." *Molecular Ecology* 17, no. 1: 431–449. https://doi.org/10.1111/j.1365-294X.2007.03538.x.

Espinosa-Ruiz, A., S. Saxena, J. Schmidt, et al. 2004. "Differential Stage-Specific Regulation of Cyclin-Dependent Kinases During Cambial Dormancy in Hybrid Aspen." *Plant Journal* 38, no. 4: 603–615. https://doi.org/10.1111/j.1365-313X.2004.02070.x.

Ettinger, A. K., D. M. Buonaiuto, C. J. Chamberlain, I. Morales-Castilla, and E. M. Wolkovich. 2021. "Spatial and Temporal Shifts in Photoperiod With Climate Change." *New Phytologist* 230, no. 2: 462–474. https://doi.org/10.1111/nph.17172.

Flynn, D. F. B., and E. M. Wolkovich. 2018. "Temperature and Photoperiod Drive Spring Phenology Across All Species in a Temperate Forest Community." *New Phytologist* 219, no. 4: 1353–1362. https://doi.org/10.1111/nph.15232.

Fracheboud, Y., V. Luquez, L. Bjorken, A. Sjodin, H. Tuominen, and S. Jansson. 2009. "The Control of Autumn Senescence in European Aspen." *Plant Physiology* 149, no. 4: 1982–1991.

Franks, S. J., J. J. Weber, and S. N. Aitken. 2014. "Evolutionary and Plastic Responses to Climate Change in Terrestrial Plant Populations." *Evolutionary Applications* 7, no. 1: 123–139. https://doi.org/10.1111/eva.12112.

Fu, Y. H., M. Campioli, G. Deckmyn, and I. A. Janssens. 2012. "The Impact of Winter and Spring Temperatures on Temperate Tree Budburst Dates: Results From an Experimental Climate Manipulation." *PLoS One* 7: e47324. https://doi.org/10.1371/journal.pone.0047324.

Gan, S., and R. M. Amasino. 1997. "Making Sense of Senescence (Molecular Genetic Regulation and Manipulation of Leaf Senescence)." *Plant Physiology* 113, no. 2: 313–319. https://doi.org/10.1104/pp.113.2.313.

Gauzere, J., S. Delzon, H. Davi, M. Bonhomme, I. G. de Cortazar-Atauri, and I. Chuine. 2017. "Integrating Interactive Effects of Chilling and Photoperiod in Phenological Process-Based Models. A Case Study With Two European Tree Species: *Fagus sylvatica* and *Quercus petraea*." *Agricultural and Forest Meteorology* 244: 9–20. https://doi.org/10.1016/j.agrformet.2017.05.011.

Geissler, C., A. Davidson, and R. A. Niesenbaum. 2023. "The Influence of Climate Warming on Flowering Phenology in Relation to Historical Annual and Seasonal Temperatures and Plant Functional Traits." *PeerJ* 11: e15188. https://doi.org/10.7717/peerj.15188.

Ghelardini, L., A. Santini, S. Black-Samuelsson, T. Myking, and M. Falusi. 2010. "Bud Dormancy Release in Elm (*Ulmus* spp.) Clones—A Case Study of Photoperiod and Temperature Responses." *Tree Physiology* 30, no. 2: 264–274. https://doi.org/10.1093/treephys/tpp110.

Giertych, M. 1981. "Summary of Results on Scots Pine (*Pinus sylvestris* L.) Height Growth in IUFRO Provenance Experiments."

Gottfried, M., H. Pauli, A. Futschik, et al. 2012. "Continent-Wide Response of Mountain Vegetation to Climate Change." *Nature Climate Change* 2, no. 2: 111–115. https://doi.org/10.1038/nclimate1329.

Håbjørg, A. 1978. "Photoperiodic Ecotypes in Scandinavian Trees and Shrubs." *Meld Nor Landbrukshøgsk* 57, no. 33: 1–20.

Häkkinen, R., T. Linkosalo, and P. Hari. 1998. "Effects of Dormancy and Environmental Factors on Timing of Bud Burst in *Betula pendula*." *Tree Physiology* 18, no. 10: 707–712. https://doi.org/10.1093/treephys/18.10.707.

Hänninen, H., and K. Tanino. 2011. "Tree Seasonality in a Warming Climate." *Trends in Plant Science* 16, no. 8: 412–416. https://doi.org/10.1016/j.tplants.2011.05.001.

Heide, O. M. 1974. "Growth and Dormancy in Norway Spruce Ecotypes (*Picea abies*) I. Interaction of Photoperiod and Temperature." *Physiologia Plantarum* 30, no. 1: 1–12. https://doi.org/10.1111/j.1399-3054.1974.tb04983.x.

Heide, O. M. 1993a. "Daylength and Thermal Time Responses of Budburst During Dormancy Release in Some Northern Deciduous Trees." *Physiologia Plantarum* 88, no. 4: 531–540. https://doi.org/10.1111/j.1399-3054.1993.tb01368.x.

Heide, O. M. 1993b. "Dormancy Release in Beech Buds (*Fagus sylvatica*) Requires Both Chilling and Long Days." *Physiologia Plantarum* 89, no. 1: 187–191. https://doi.org/10.1111/j.1399-3054.1993.tb01804.x.

Heide, O. M. 2001. "Photoperiodic Control of Dormancy in *Sedum telephium* and Some Other Herbaceous Perennial Plants." *Physiologia Plantarum* 113, no. 3: 332–337. https://doi.org/10.1034/j.1399-3054.2001.1130305.x.

Heide, O. M. 2003. "High Autumn Temperature Delays Spring Bud Burst in Boreal Trees, Counterbalancing the Effect of Climatic Warming." *Tree Physiology* 23, no. 13: 931–936. https://doi.org/10.1093/treephys/23.13.931.

Heide, O. M., and A. K. Prestrud. 2005. "Low Temperature, but Not Photoperiod, Controls Growth Cessation and Dormancy Induction and Release in Apple and Pear." *Tree Physiology* 25, no. 1: 109–114. https://doi.org/10.1093/treephys/25.1.109.

Howe, G. T., W. P. Hackett, G. R. Furnier, and R. E. Klevorn. 1995. "Photoperiodic Responses of a Northern and Southern Ecotype of Black Cottonwood." *Physiologia Plantarum* 93, no. 4: 695–708. https://doi.org/10.1034/j.1399-3054.1995.930417.x.

Huffeldt, N. P. 2020. "Photic Barriers to Poleward Range-Shifts." *Trends in Ecology & Evolution* 35, no. 8: 652–655. https://doi.org/10.1016/j.tree.2020.04.011.

Huffeldt, N. P. 2021. "Importance of Photic Constraints Depends on the Population." *Trends in Ecology & Evolution* 36, no. 6: 480–481. https://doi.org/10.1016/j.tree.2021.03.008.

Hulme, M. 2011. "Reducing the Future to Climate: A Story of Climate Determinism and Reductionism." *Osiris* 26, no. 1: 245–266.

Inouye, D. W. 2008. "Effects of Climate Change on Phenology, Frost Damage, and Floral Abundance of Montane Wildflowers." *Ecology* 89, no. 2: 353–362. https://doi.org/10.1890/06-2128.1.

IPCC. 2023. *Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by Core Writing Team, H. Lee, and J. Romero. IPCC.

IUCN/SSC. 2013. "Guidelines for Reintroductions and Other Conservation."

Jackson, S. D. 2009. "Plant Responses to Photoperiod." *New Phytologist* 181, no. 3: 517–531. https://doi.org/10.1111/j.1469-8137.2008.02681.x.

Jiang, N., M. Shen, P. Ciais, et al. 2022. "Warming Does Not Delay the Start of Autumnal Leaf Coloration but Slows Its Progress Rate." *Global Ecology and Biogeography* 31, no. 11: 2297–2313. https://doi.org/10.1111/geb.13581.

Junttila, O. 2007. "Regulation of Annual Shoot Growth Cycle in Northern Tree Species." In *Physiology of Northern Plants Under Changing Environment*, edited by E. Taulavuori and K. Taulavuori, 177–210. Research Signpost.

Junttila, O., J. Nilsen, and B. Igeland. 2003. "Effect of Temperature on the Induction of Bud Dormancy in Ecotypes of *Betula pubescens* and *Betula pendula*." *Scandinavian Journal of Forest Research* 18, no. 3: 208–217. https://doi.org/10.1080/02827581.2003.9728291.

Kawai, Y., and G. Kudo. 2018. "Variations in Ramet Performance and the Dynamics of an Alpine Evergreen Herb, *Gentiana nipponica*, in Different Snowmelt Conditions." *American Journal of Botany* 105, no. 11: 1813–1823. https://doi.org/10.1002/ajb2.1186.

Keenan, T. F., J. Gray, M. A. Friedl, et al. 2014. "Net Carbon Uptake Has Increased Through Warming-Induced Changes in Temperate Forest

Phenology." *Nature Climate Change* 4, no. 7: 598–604. https://doi.org/10.1038/nclimate2253.

Keller, F., and C. Körner. 2003. "The Role of Photoperiodism in Alpine Plant Development." *Arctic, Antarctic, and Alpine Research* 35, no. 3: 361–368. https://doi.org/10.1657/1523-0430(2003)035[0361:TROPIA]2.0.CO;2.

Keskitalo, J., G. Bergquist, P. Gardeström, and S. Jansson. 2005. "A Cellular Timetable of Autumn Senescence." *Plant Physiology* 139, no. 4: 1635–1648. https://doi.org/10.1104/pp.105.066845.

Körner, C., and D. Basler. 2010. "Phenology Under Global Warming." *Science* 327, no. 5972: 1461–1462. https://doi.org/10.1126/science.1186473.

Kramer, P. J. 1936. "Effect of Variation in Length of Day on Growth and Dormancy of Trees." *Plant Physiology* 11, no. 1: 127–137.

Kremer, A., B. M. Potts, and S. Delzon. 2014. "Genetic Divergence in Forest Trees: Understanding the Consequences of Climate Change." *Functional Ecology* 28, no. 1: 22–36. https://doi.org/10.1111/1365-2435.12169.

Lang, G. A., J. D. Early, G. C. Martin, and R. L. Darnell. 1987. "Endo-, Para-, and Ecodormancy: Physiological Terminology and Classification for Dormancy Research."

Laube, J., T. H. Sparks, N. Estrella, J. Höfler, D. P. Ankerst, and A. Menzel. 2014. "Chilling Outweighs Photoperiod in Preventing Precocious Spring Development." *Global Change Biology* 20, no. 1: 170–182. https://doi.org/10.1111/gcb.12360.

Leech, S. M., P. L. Almuedo, and G. O'Neill. 2011. "Assisted Migration: Adapting Forest Management to a Changing Climate." *Journal of Ecosystems and Management* 12, no. 3: 18–34. https://doi.org/10.22230/jem.2011v12n3a91.

Loarie, S. R., P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field, and D. D. Ackerly. 2009. "The Velocity of Climate Change." *Nature* 462, no. 7276: 1052–1055. https://doi.org/10.1038/nature08649.

Lundell, R., H. Hänninen, T. Saarinen, H. Åström, and R. Zhang. 2020. "Beyond Rest and Quiescence (Endodormancy and Ecodormancy): A Novel Model for Quantifying Plant–Environment Interaction in Bud Dormancy Release." *Plant, Cell & Environment* 43, no. 1: 40–54. https://doi.org/10.1111/pce.13650.

Malyshev, A. V. 2020. "Warming Events Advance or Delay Spring Phenology by Affecting Bud Dormancy Depth in Trees." *Frontiers in Plant Science* 11: 856. https://doi.org/10.3389/fpls.2020.00856.

McLachlan, J. S., J. J. Hellmann, and M. W. Schwartz. 2007. "A Framework for Debate of Assisted Migration in an Era of Climate Change." *Conservation Biology* 21, no. 2: 297–302. https://www.jstor.org/stable/4620812.

Menzel, A. 2002. "Phenology: Its Importance to the Global Change Community." *Climatic Change* 54, no. 4: 379–385. https://doi.org/10.1023/A:1016125215496.

Menzel, A., T. H. Sparks, N. Estrella, et al. 2006. "European Phenological Response to Climate Change Matches the Warming Pattern." *Global Change Biology* 12, no. 10: 1969–1976. https://doi.org/10.1111/j.1365-2486.2006.01193.x.

Miller-Struttmann, N., Z. Miller, and C. Galen. 2022. "Climate Driven Disruption of Transitional Alpine Bumble Bee Communities." *Global Change Biology* 28, no. 21: 6165–6179. https://doi.org/10.1111/gcb.16348.

Müller, N. A., C. L. Wijnen, A. Srinivasan, et al. 2016. "Domestication Selected for Deceleration of the Circadian Clock in Cultivated Tomato." *Nature Genetics* 48, no. 1: 89–93. https://doi.org/10.1038/ng.3447.

Murray, M. B., M. G. R. Cannell, and R. I. Smith. 1989. "Date of Budburst of Fifteen Tree Species in Britain Following Climatic Warming." *Journal of Applied Ecology* 26: 693–700. https://www.jstor.org/stable/2404093.

Myking, T., and O. M. Heide. 1995. "Dormancy Release and Chilling Requirement of Buds of Latitudinal Ecotypes of *Betula pendula* and *B. pubescens*." *Tree Physiology* 15, no. 11: 697–704. https://doi.org/10.1093/treephys/15.11.697.

Nicotra, A. B., O. K. Atkin, S. P. Bonser, et al. 2010. "Plant Phenotypic Plasticity in a Changing Climate." *Trends in Plant Science* 15, no. 12: 684–692. https://doi.org/10.1016/j.tplants.2010.09.008.

Oleksyn, J., and M. Giertych. 1984. "Results of a 70 Years Old Scots Pine (*Pinus sylvestris* L.) Provenance Experiment in Puławy, Poland."

Oleksyn, J., M. G. Tjoelker, and P. B. Reich. 1992. "Growth and Biomass Partitioning of Populations of European *Pinus sylvestris* L. Under Simulated 50 and 60 N Daylengths: Evidence for Photoperiodic Ecotypes." *New Phytologist* 120, no. 4: 561–574. https://doi.org/10.1111/j.1469-8137.1992.tb01806.x.

Olsen, J. E., O. Junttila, and T. Moritz. 1997. "Long-Day Induced Bud Break in *Salix pentandra* Is Associated With Transiently Elevated Levels of GA1 and Gradual Increase in Indole-3-Acetic Acid." *Plant and Cell Physiology* 38, no. 5: 536–540. https://doi.org/10.1093/oxfordjournals.pcp.a029202.

Park, A., and C. Talbot. 2018. "Information Underload: Ecological Complexity, Incomplete Knowledge, and Data Deficits Create Challenges for the Assisted Migration of Forest Trees." *Bioscience* 68, no. 4: 251–263. https://doi.org/10.1093/biosci/biy001.

Parmesan, C. 2006. "Ecological and Evolutionary Responses to Recent Climate Change." *Annual Review of Ecology, Evolution, and Systematics* 37, no. 1: 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100.

Parmesan, C., and M. E. Hanley. 2015. "Plants and Climate Change: Complexities and Surprises." *Annals of Botany* 116, no. 6: 849–864. https://doi.org/10.1093/aob/mcv169.

Parmesan, C., and G. Yohe. 2003. "A Globally Coherent Fingerprint of Climate Change Impacts Across Natural Systems." *Nature* 421, no. 6918: 37–42. https://doi.org/10.1038/nature01286.

Partanen, J. 2005. "Height Growth Onset and Cessation in Norway Spruce (*Picea abies*), Scots Pine (*Pinus sylvestris*) and Silver Birch (*Betula pendula*)." *New Research on Forest Ecosystems*: 163–181.

Partanen, J., V. Koski, and H. Hänninen. 1998. "Effects of Photoperiod and Temperature on the Timing of Bud Burst in Norway Spruce (*Picea abies*)." *Tree Physiology* 18, no. 12: 811–816. https://doi.org/10.1093/treephys/18.12.811.

Pauli, H., M. Gottfried, S. Dullinger, et al. 2012. "Recent Plant Diversity Changes on Europe's Mountain Summits." *Science* 336, no. 6079: 353–355. https://doi.org/10.1126/science.1219033.

Pawlikowski, T., T. H. Sparks, P. Olszewski, K. Pawlikowski, L. Rutkowski, and R. Jakubowski. 2020. "Rising Temperatures Advance the Main Flight Period of *Bombus bumblebees* in Agricultural Landscapes of the Central European Plain." *Apidologie* 51, no. 4: 652–663. https://doi.org/10.1007/s13592-020-00750-9.

Petit, R. J., F. S. Hu, and C. W. Dick. 2008. "Forests of the Past: A Window to Future Changes." *Science* 320, no. 5882: 1450–1452. https://doi.org/10.1126/science.1155457.

Piao, S., P. Ciais, P. Friedlingstein, et al. 2008. "Net Carbon Dioxide Losses of Northern Ecosystems in Response to Autumn Warming." *Nature* 451, no. 7174: 49–52. https://doi.org/10.1038/nature06444.

Polgar, C. A., and R. B. Primack. 2011. "Leaf-Out Phenology of Temperate Woody Plants: From Trees to Ecosystems." *New Phytologist* 191, no. 4: 926–941. https://doi.org/10.1111/j.1469-8137.2011.03803.x.

Porro, F., S. Orsenigo, T. Abeli, et al. 2022. "Richer, Greener, and More Thermophilous?—A First Overview of Global Warming Induced Changes in the Italian Alpine Plant Communities Within the New GLORIA Italia NETWORK." *Plant Biosystems - An International*

Journal Dealing with all Aspects of Plant Biology 156, no. 1: 307–311. https://doi.org/10.1080/11263504.2021.1992527.

Ranjitkar, S. 2013. "Effect of Elevation and Latitude on Spring Phenology of Rhododendron at Kanchenjunga Conservation Area, East Nepal." *International Journal of Applied Sciences and Biotechnology* 1, no. 4: 253–257. https://doi.org/10.3126/ijasbt.v1i4.9154.

Rauschkolb, R., S. F. Bucher, I. Hensen, et al. 2024. "Spatial Variability in Herbaceous Plant Phenology Is Mostly Explained by Variability in Temperature but Also by Photoperiod and Functional Traits." *International Journal of Biometeorology* 68: 761–775. https://doi.org/10.1007/s00484-024-02621-9.

Richardson, A. D., D. Y. Hollinger, D. B. Dail, J. T. Lee, J. W. Munger, and J. O'keefe. 2009. "Influence of Spring Phenology on Seasonal and Annual Carbon Balance in Two Contrasting New England Forests." *Tree Physiology* 29, no. 3: 321–331. https://doi.org/10.1093/treephys/tpn040.

Richardson, D. M., and M. Rejmánek. 2011. "Trees and Shrubs as Invasive Alien Species–a Global Review." *Diversity and Distributions* 17, no. 5: 788–809. https://doi.org/10.1111/j.1472-4642.2011.00782.x.

Rinne, P. L., A. Welling, J. Vahala, et al. 2011. "Chilling of Dormant Buds Hyperinduces FLOWERING LOCUS T and Recruits GA-Inducible 1, 3-β-Glucanases to Reopen Signal Conduits and Release Dormancy in *Populus*." *Plant Cell* 23, no. 1: 130–146. https://doi.org/10.1105/tpc.110.081307.

Rogora, M., L. Frate, M. L. Carranza, et al. 2018. "Assessment of Climate Change Effects on Mountain Ecosystems Through a Cross-Site Analysis in the Alps and Apennines." *Science of the Total Environment* 624: 1429–1442. https://doi.org/10.1016/j.scitotenv.2017.12.155.

Rohde, A., C. Bastien, and W. Boerjan. 2011. "Temperature Signals Contribute to the Timing of Photoperiodic Growth Cessation and Bud Set in Poplar." *Tree Physiology* 31, no. 5: 472–482. https://doi.org/10.1093/treephys/tpr038.

Ruttink, T., M. Arend, K. Morreel, et al. 2007. "A Molecular Timetable for Apical Bud Formation and Dormancy Induction in Poplar." *Plant Cell* 19, no. 8: 2370–2390. https://doi.org/10.1105/tpc.107.052811.

Saikkonen, K., K. Taulavuori, T. Hyvönen, et al. 2012. "Climate Change-Driven Species' Range Shifts Filtered by Photoperiodism." *Nature Climate Change* 2, no. 4: 239–242. https://doi.org/10.1038/nclimate1430.

Sakai, A., and W. Larcher. 1987. "Low Temperature and Frost as Environmental Factors." In *Frost Survival of Plants: Responses and Adaptation to Freezing Stress*, 1–20. Springer Berlin Heidelberg.

Sanz-Pérez, V., P. Castro-Díez, and F. Valladares. 2009. "Differential and Interactive Effects of Temperature and Photoperiod on Budburst and Carbon Reserves in Two Co-Occurring Mediterranean Oaks." *Plant Biology* 11, no. 2: 142–151. https://doi.org/10.1111/j.1438-8677.2008.00119.x.

Savolainen, O., T. Pyhäjärvi, and T. Knürr. 2007. "Gene Flow and Local Adaptation in Trees." *Annual Review of Ecology, Evolution, and Systematics* 38, no. 1: 595–619.

Scalone, R., A. Lemke, E. Štefanić, A. K. Kolseth, S. Rašić, and L. Andersson. 2016. "Phenological Variation in *Ambrosia artemisiifolia* L. Facilitates Near Future Establishment at Northern Latitudes." *PLoS One* 11, no. 11: e0166510. https://doi.org/10.1371/journal.pone.0166510.

Schaber, J., and F. W. Badeck. 2003. "Physiology-Based Phenology Models for Forest Tree Species in Germany." *International Journal of Biometeorology* 47: 193–201. https://doi.org/10.1007/s00484-003-0171-5.

Settele, J., J. Bishop, and S. G. Potts. 2016. "Climate Change Impacts on Pollination." *Nature Plants* 2, no. 7: 1–3. https://doi.org/10.1038/nplants.2016.92.

Shaw, R. G., and J. R. Etterson. 2012. "Rapid Climate Change and the Rate of Adaptation: Insight From Experimental Quantitative Genetics." *New Phytologist* 195, no. 4: 752–765. https://doi.org/10.1111/j.1469-8137.2012.04230.x.

Singh, M., and P. Mas. 2018. "A Functional Connection Between the Circadian Clock and Hormonal Timing in Arabidopsis." *Genes* 9, no. 12: 567. https://doi.org/10.3390/genes9120567.

Singh, R. K., T. Svystun, B. AlDahmash, A. M. Jönsson, and R. P. Bhalerao. 2017. "Photoperiod- and Temperature-Mediated Control of Phenology in Trees–a Molecular Perspective." *New Phytologist* 213, no. 2: 511–524. https://doi.org/10.1111/nph.14346.

Steinbauer, M. J., J. A. Grytnes, G. Jurasinski, et al. 2018. "Accelerated Increase in Plant Species Richness on Mountain Summits Is Linked to Warming." *Nature* 556, no. 7700: 231–234. https://doi.org/10.1038/s41586-018-0005-6.

Stinziano, J. R., and D. A. Way. 2014. "Combined Effects of Rising [CO_2] and Temperature on Boreal Forests: Growth, Physiology and Limitations." *Botany* 92, no. 6: 425–436. https://doi.org/10.1139/cjb-2013-0314.

Svystun, T., and A. M. Jönsson. 2022. "Exploring Populus Phenological Response to Climate Change Using Observational Data and Ecosystem Modelling." *Agricultural and Forest Meteorology* 314: 108766. https://doi.org/10.1016/j.agrformet.2021.108766.

Tanino, K. K., L. Kalcsits, S. Silim, E. Kendall, and G. R. Gray. 2010. "Temperature-Driven Plasticity in Growth Cessation and Dormancy Development in Deciduous Woody Plants: A Working Hypothesis Suggesting How Molecular and Cellular Function Is Affected by Temperature During Dormancy Induction." *Plant Molecular Biology* 73: 49–65. https://doi.org/10.1007/s11103-010-9610-y.

Taulavuori, K., E. Taulavuori, K. Saravesi, et al. 2017. "Competitive Success of Southern Populations of *Betula pendula* and *Sorbus aucuparia* Under Simulated Southern Climate Experiment in the Subarctic." *Ecology and Evolution* 7, no. 12: 4507–4517. https://doi.org/10.1002/ece3.3026.

Thomas, B., and D. Vince-Prue. 1997. "Photoperiodic Control of Flower Initiation: Some General Principles." In *Photoperiodism in Plants*, 3–28. Elsevier.

Toby Kiers, E., T. M. Palmer, A. R. Ives, J. F. Bruno, and J. L. Bronstein. 2010. "Mutualisms in a Changing World: An Evolutionary Perspective." *Ecology Letters* 13, no. 12: 1459–1474.

Tomiolo, S., and D. Ward. 2018. "Species Migrations and Range Shifts: A Synthesis of Causes and Consequences." *Perspectives in Plant Ecology, Evolution and Systematics* 33: 62–77. https://doi.org/10.1016/j.ppees.2018.06.001.

Tougeron, K. 2021. "How Constraining Are Photic Barriers to Poleward Range-Shifts?" *Trends in Ecology & Evolution* 36, no. 6: 478–479. https://doi.org/10.1016/j.tree.2021.02.008.

Van der Putten, W. H., M. Macel, and M. E. Visser. 2010. "Predicting Species Distribution and Abundance Responses to Climate Change: Why It Is Essential to Include Biotic Interactions Across Trophic Levels." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 365, no. 1549: 2025–2034. https://doi.org/10.1098/rstb.2010.0037.

Vitasse, Y. 2013. "Ontogenic Changes Rather Than Difference in Temperature Cause Understory Trees to Leaf out Earlier." *New Phytologist* 198, no. 1: 149–155. https://doi.org/10.1111/nph.12130.

Vitasse, Y., and D. Basler. 2013. "What Role for Photoperiod in the Bud Burst Phenology of European Beech." *European Journal of Forest Research* 132: 1–8. https://doi.org/10.1007/s10342-012-0661-2.

Vitasse, Y., S. Delzon, E. Dufrêne, et al. 2009. "Leaf Phenology Sensitivity to Temperature in European Trees: Do Within-Species Populations Exhibit Similar Responses?" *Agricultural and Forest Meteorology* 149, no. 5: 735–744. https://doi.org/10.1016/j.agrformet.2008.10.019.

Wadgymar, S. M., J. E. Ogilvie, D. W. Inouye, A. E. Weis, and J. T. Anderson. 2018. "Phenological Responses to Multiple Environmental Drivers Under Climate Change: Insights From a Long-Term Observational Study and a Manipulative Field Experiment." *New Phytologist* 218, no. 2: 517–529. https://doi.org/10.1111/nph.15029.

Ward, J. K., and J. K. Kelly. 2004. "Scaling Up Evolutionary Responses to Elevated CO_2: Lessons From Arabidopsis." *Ecology Letters* 7, no. 5: 427–440. https://doi.org/10.1111/j.1461-0248.2004.00589.x.

Wareing, P. F. 1953. "Growth Studies in Woody Species V. Photoperiodism in Dormant Buds of *Fagus sylvatica* L." *Physiologia Plantarum* 6, no. 4: 692–706. https://doi.org/10.1111/j.1399-3054.1953.tb08442.x.

Way, D. A., and R. A. Montgomery. 2015. "Photoperiod Constraints on Tree Phenology, Performance and Migration in a Warming World." *Plant, Cell & Environment* 38, no. 9: 1725–1736. https://doi.org/10.1111/pce.12431.

Wirtz, K. W. 2000. "Simulating the Dynamics of Leaf Physiology and Morphology With an Extended Optimality Approach." *Annals of Botany* 86, no. 4: 753–764. https://doi.org/10.1006/anbo.2000.1230.

Withrow, R. B. 1959. "Photoperiodism and Related Phenomena in Plants and Animals." Proceedings of the Conference on Photoperiodism. Committee on Photobiology of the National Academy of Sciences National Research Council, National Science Foundation.

Wolkovich, E. M., and E. E. Cleland. 2011. "The Phenology of Plant Invasions: A Community Ecology Perspective." *Frontiers in Ecology and the Environment* 9, no. 5: 287–294. https://doi.org/10.1890/100033.

Wolkovich, E. M., B. I. Cook, J. M. Allen, et al. 2012. "Warming Experiments Underpredict Plant Phenological Responses to Climate Change." *Nature* 485, no. 7399: 494–497. https://doi.org/10.1038/nature11014.

Yu, H., E. Luedeling, and J. Xu. 2010. "Winter and Spring Warming Result in Delayed Spring Phenology on the Tibetan Plateau." *Proceedings of the National Academy of Sciences* 107, no. 51: 22151–22156. https://doi.org/10.1038/hdy.2009.134.

Zeng, K., A. T. Sentinella, C. Armitage, and A. T. Moles. 2024. "Species That Require Long-Day Conditions to Flower Are Not Advancing Their Flowering Phenology as Fast as Species Without Photoperiod Requirements." *Annals of Botany* 135, no. 1–2: 113–124. https://doi.org/10.1093/aob/mcae121.

Zettlemoyer, M. A., and M. L. Peterson. 2021. "Does Phenological Plasticity Help or Hinder Range Shifts Under Climate Change?" *Frontiers in Ecology and Evolution* 9: 689192. https://doi.org/10.3389/fevo.2021.689192.

Zohner, C. M., B. M. Benito, J. C. Svenning, and S. S. Renner. 2016. "Day Length Unlikely to Constrain Climate-Driven Shifts in Leaf-Out Times of Northern Woody Plants." *Nature Climate Change* 6, no. 12: 1120–1123. https://doi.org/10.1038/nclimate3138.

Zohner, C. M., and S. S. Renner. 2014. "Common Garden Comparison of the Leaf-Out Phenology of Woody Species From Different Native Climates, Combined With Herbarium Records, Forecasts Long-Term Change." *Ecology Letters* 17, no. 8: 1016–1025. https://doi.org/10.1111/ele.12308.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** jbi70113-sup-0001-DataS1.xlsx.