Long-term effects of phenological mismatches on plant competition across forest biomes

A literature review of asymmetrical plant competition in temperate and boreal forests

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Abstract

Climate change is expected to influence the phenophases of plants. For deciduous temperate and boreal understorey vegetation, the spring season is quite relevant as the majority of carbon assimilation is performed during this season. Lately, early and false springs have caused the overstorey species to leaf out at an earlier time than expected. This has direct and indirect impacts on the understorey vegetation due to changes in light conditions. Phenological mismatch within asymmetrical plant competition is expected to be intensified, as overstorey plants experience a prolonged growth season while the understorey vegetation experiences a decreased light window. This thesis explores, through a literature review of published papers, the influence of light conditions on the understorey vegetation of deciduous temperate and boreal forests within North America, Asia and Europe.

This thesis analysed 28 papers, of which temperate forest species were mentioned in 25 papers, 2 investigated boreal forests and 1 paper investigated a transition zone between a mixed-deciduous forest and a boreal forest. The results indicate that some species like *Acer saccharum* seedlings*, Quercus rubra* seedlings*, Viola pubescens* and *Tiarella cordifolia* may be able to adapt to future shadier conditions while other species like *Aesculus glabra* and *Allium tricoccum* may be unable to adapt in time. Some studies have already observed that light conditions have an impact beyond phenological response in understorey vegetation species. Carbon gain and resource allocation seemed to be impacted by the decrease in light window for tree seedlings and herbaceous species. This could potentially impact the species´ fitness to the environment. Management measures such as gap cutting and thinning the stand could increase the brightness to the understorey layer, promoting shade-intolerant species.

Keywords: Phenological mismatch, boreal, temperate, forest, asymmetrical plant competition

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1. Background

Climate change has now been impacting seasonal weather conditions for several decades, causing imbalances in ecosystems. One example of its impact is the change in timing of abiotic factors which trigger vegetation phenology. Phenology is the study of repeated biotic events of a species. For plants, these are seasonal or annual events triggered by biotic or abiotic factors (Saxena & Rao 2020). Plants align their phenological stages, also known as phenophases, with seasonal changes in abiotic conditions such as temperature and light, which are linked with seasonality. During winter, some species of plants from boreal and temperate forests enter a state of dormancy (Basler & Korner 2014). The decrease in temperatures and day-length in autumn induces the dormancy (Basler & Korner 2014). The different stages of dormancy can be influence by a few variables like genetic factors and environmental conditions (Basler & Korner 2014). During dormancy, plants stop their growth during as well as winter buds are formed (Basler & Korner 2014).

In temperate and boreal regions, deciduous species tend to be more active in spring and summer (Lee et al. 2024). Sensitivity to environmental cues is species dependent. There exists a large variety of understorey species, which can range from evergreen species to spring ephemerals, summer greens and winter greens (Lee et al. 2024). Due to this biodiversity richness, there exists a large variety of phenological strategies that understorey plants have developed (Lee et al. 2024). Herbaceous and woody species tend to have different sensitivity to environmental cues (Lee et al. 2022). Trees seems to be more responsive to environmental temperatures in comparison to herbaceous species (Lee et al. 2022).

The interaction between overstorey vegetation and the understorey vegetation is complex. Nevertheless, failure to correctly align their phenology to the seasons may result in plants being damaged by frost or not making full use of the available season to assimilate carbon and optimize their growth (Lee et al. 2024). Lately, trees have been experiencing a prolonged growth season due to early and false springs and warmer autumns (Allstadt et al. 2015; Lee & Ibáñez 2021a). These changes in canopy trees' phenophases impact understorey vegetation´s biotic and abiotic conditions. Understorey plants tend to have a variety of requirements as some species may require a brief period of intense early spring light while others are more shade tolerant. Day or night length and temperature are the main drivers of changes in phenophases in most temperate and boreal trees (Saxena & Rao 2020). Changing temperature patterns could lead to phenological mismatches if the understorey vegetation does not adjust to overstorey species' phenological changes.

Phenological mismatch (also known as phenological asynchrony) refers to divergence between the phenophases of two or more interacting species (Renner

& Zohner 2018). This phenomenon has been observed across several different interacting species and in several different environments, such as trophic mismatch between birds' egg laying period and insect abundance or asynchrony between insects egg hatching dates and the phenophases of the plants which are their food source (Renner & Zohner 2018).

One type of interaction impacted by phenological mismatches is plant competition. Asymmetrical competition happens when larger plants have a competitive advantage to acquire resources over smaller plants (Anten & Bastiaans 2016). One example is how trees have an advantageous access to light in comparison to understorey plants due to a height difference. Figure 1 is an example of this type of interaction between species. Spring and autumn are important seasons when it comes to plant phenology and competition in deciduous forests. The photo was taken during spring, and it shows the light conditions still being favourable for the understorey layer, as the leaves of the trees are not fully developed yet. Leaf out and leaf senescence change abiotic factors like light conditions and leaf litter in the understorey layer.

Figure 1. An example of asymmetrical competition in spring as trees begin their bud break period. The understorey layer still has bright light conditions, allowing for a diverse understorey vegetation with several flowers. Photo taken by the author in 2024 at park Alnarp, Sweden. The region has the characteristics of a temperate biome, and it is managed.

Spring is a crucial season for shade-intolerant species, as there is a short window of bright light in the understorey layer prior to tree canopy closure (Greco et al. 2019). Additionally, plants are still prone to frost damage or loss in productivity during this season if they do not correctly align their phenophases with seasonal weather and shading from the tree canopy (Allstadt et al. 2015).

Big changes in tree phenology may result in the understorey vegetation being unable to adapt, causing impacts due to asymmetrical competition between the overstorey and understorey vegetation. According to Lee & Ibáñez (2021), many understorey plant species acquire 50%-80% of their carbon during the weeks at the beginning of the growing season when intense light still reaches the understorey vegetation. Furthermore, understorey species are varied and compose about 80% of the flora of deciduous forests around the world (Lee et al. 2022). If shade-intolerant understorey species are unable to shift their growth period to match the overstorey plants' phenological shifts, it could lead to a decrease in biodiversity. This could be due to a decrease in species abundance, further mismatches between herbivores and pollinators, unsuccessful reproduction and development, etc.

Beyond herbaceous species, tree seedlings may also be affected by the light conditions in the understorey layer. Natural regeneration of trees within deciduous forests may be impacted by an extended overstorey leafy season. Lee & Ibáñez (2021) highlighted that mismatches between tree canopy leaf out and seedlings' phenophases could harm plant performance, impact tree recruitment and potentially change the forest structure.

Climate change is an ongoing threat which will continue to impact forests in coming decades. Its direct impact on woody species is estimated to be an average of 3–8 days advance in leaf out times per 1°C increase (Renner & Zohner 2018). One way in which the understorey vegetation may cope is through phenological escape, which occurs when the understorey species adapt their phenophases to accommodate to the earlier tree canopy closure (Lee & Ibáñez 2021b). However, not all of the understorey species are able to change their phenophases. This could lead to potential carryover effects, which is when an event in the history of an individual plant's life has an impact on their present behaviour (O'Connor et al. 2014). Within the context of phenological mismatches, the understorey vegetation´s response to a change in seasonal light availability may impact future seasons or years. An understanding of phenological mismatches' impacts on future seasons and years may help to develop climate-resilient management plans.

1.1 Aim

This study addresses how phenological mismatches between the spring leafing phenology of trees and understorey species lead to long-term effects on the understorey vegetation of deciduous forests in boreal and temperate regions.

The goal of this study is to conduct a literature review to understand the carryover effects caused by phenological mismatches resulting from plant asymmetrical competition in deciduous temperate and boreal forests. This study aims to gather data from published papers to analyse patterns of long-term effects recognized in boreal and temperate forests to gain insight into the expected consequences for plants across different forest layers and ecosystems. The hypothesis is that phenological mismatches where plants compete asymmetrically will have long-term effects on understorey species composition, decrease carbon assimilation of seedlings and understorey species, compromise regeneration, and potentially facilitate invasive species.

2. Methodology

2.1 Data collection

A literature review was conducted to gain insight into how carryover effects of phenological mismatches under asymmetrical plant competition are playing out in Asia, Europe and North America. This methodology provided access to huge amounts of data in a short time from different regions. Data collection was carried in the spring semester of 2025. Web of Science was the selected database to find the literature used in this study. The search terms consisted of ((“phenological mismatch*” OR "phenological asynchrony" OR irrad* OR "phenological synchrony" OR "asymmetrical competition" OR "plant competition" OR "phenological escape" OR light* OR shad* OR PAR OR radiation) AND phenolog* AND leaf* AND (overstor* OR understor* OR tree OR shrub OR canopy OR forest*)) NOT insect* NOT defoliator* NOT crop* NOT satellite* NOT tropic*. This search yielded a total of 1,253 results which were refined to 1,088 papers by limiting the document types to articles, review articles and dissertations/theses. Then an export record containing author, title, source and abstract of the1,088 papers was downloaded from Web of Science as an Excel sheet.

The selection criteria consisted of two main factors. The papers needed to cover asymmetrical plant competition of deciduous forest systems in spring and come from the temperate or boreal forest biome. This step was to manually analyse the 1,088 papers initially selected using the METAGEAR package (Lajeunesse 2016) in R version 4.2.3 (R Core Team, 2023) to ensure that they are relevant for this research. METAGEAR includes functions to aid data retrieval and systematic review, including title and abstract screening. The Excel sheet obtained from Web of Science was uploaded to R and analysed using code obtained from Lajeunesse (2022). To optimize the research, the keywords "phenology," "spring," "understory," "understorey," "leaf," "canopy" and "light" were inserted into the code. However, a paper would not automatically be excluded if those words were not present as there could be synonyms or different spellings not accounted for.

Paper selection was conducted by firstly observing the title. If the title lacked terminology which made the paper obviously off topic for this specific research, then the abstract would be read. If a paper did not contain an abstract, it was automatically excluded from the search. This step resulted in 314 papers being suitable for this study only based on title and abstract.

The next step was to further refine papers relevant to this study from the 314 selected studies. At this stage, the papers’ aims and discussion sections were briefly read to see if they fulfilled the criteria set out in Table 1. The criteria in Table 1 are a guide to assess which papers were useful to be processed to better understand the long-term effects of phenological mismatches in asymmetrical plant competition. Appendix 1 contains a comprehensive table of the papers selected for this analysis and their respective DOIs.

Table 1. Criteria for article selection

Must be about species present in either boreal or temperate (or both) deciduous forest ecosystems
Focus must be on the spring leaf out phenology and its impact on light conditions
Must be about asymmetrical competition or the adaptation capability of understorey species
Studies which investigate climate change consequences that impact tree phenology beyond temperature change (e.g. fire, drought, flood) were not considered
Studies regarding agricultural crops, fruit orchards and urban areas were not considered

2.2 Data processing

The data analysis had two steps. The first step was a qualitative analysis to understand the context of the results as well the recognized long-term effects. Generally, this data was found in the discussion and conclusions sections of the selected papers, however some papers may already explain this in their results sections. The second step was to turn the qualitative data into quantitative data. Excel for Microsoft 365 MSO (Version 2504 Build 16.0.18730.20030) was used for calculations and figures. Some information regarding the years, species composition, and study sites of the papers was analysed to understand the diversity in the available data as well the transferability potential of the results. Still, the focus of the results was on the long-term effects and what consequences have been recognized as well as how often they appear across different studies.

3. Results

A total of 28 studies were selected from the Web of Science search. The selected studies were quite recent; all were published between 2000 and 2024. The studies focused on forests and species located in the Northern Hemisphere. Figure 2 illustrates the distribution of the continents studied by the different papers. All the papers investigated the understorey vegetation's responses to changes in light conditions. Of these papers, only 2 focused on boreal forests while 25 focused on temperate forests. Kwit et al. (2010) investigates a transition zone between a mixed-deciduous and a boreal forests, with a mixture between evergreen species and deciduous species.

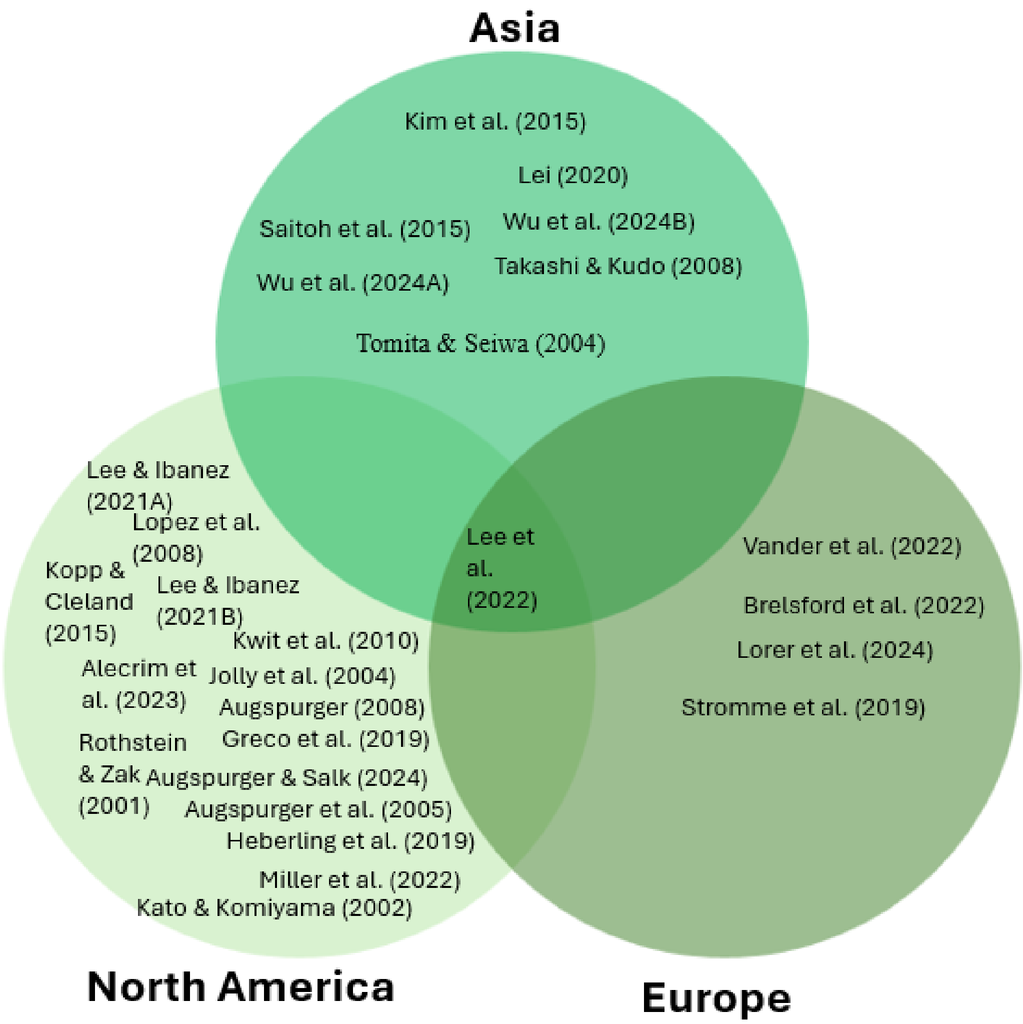

Figure 2. The studies´ continents of data collection.

Lee et al. (2022) suggests that deciduous forests in North America are more prone to phenological mismatch than in Asia or Europe. Their data shows that the overstorey plants are more sensitive to climate change in relation to leaf out period in North America (Lee et al. 2022). The study theorises that the likely explanation is that North America experiences a higher interannual variability in weather compared to Asia and Europe, increasing selective pressure (Lee et al. 2022). Their simulation, however, showed that it is expected that around the years 2081-2100 the light window in Europe will suffer little change and Asian forests will have a longer light window while North America will have a shorter light window (Lee et al. 2022).

Thus, what can be expected for the understory to respond to these proposed changes in light windows? Spring ephemerals in the understorey layer showed similar responses across all three continents (Lee et al. 2022). Lee et al. (2022) commented that their results showed that understorey vegetation of Asian and European forests were as sensitive as their overstorey layer. In North America, the understorey vegetation was a bit more sensitive in the North than in the South (Lee et al. 2022). Their computer simulation for 2081-2100 expects that phenological escape for Asian and European herbaceous species will be successful while North American species will likely suffer from population and fitness declines (Lee et al. 2022).

3.1 Analysis of long-term effects

The published research could be categorized into three different groups in relation to their findings about long-term effects (Figure 2). The first category is the papers which recognized effects through empirical data, historical data or conducting computer simulations of consequences such as decrease in carbon gain or earlier fruiting which have a long-term impact. The second category is papers which found no evidence of long-term impacts. The third category is papers inconclusive about long-term impacts, in which researchers believe there is a possibility, but data was insufficient for conclusive results. Of the selected papers, 55% did observe long-term effects, 26% did not (or did not mention) long-term effects and 19% had inconclusive results (Figure 3).

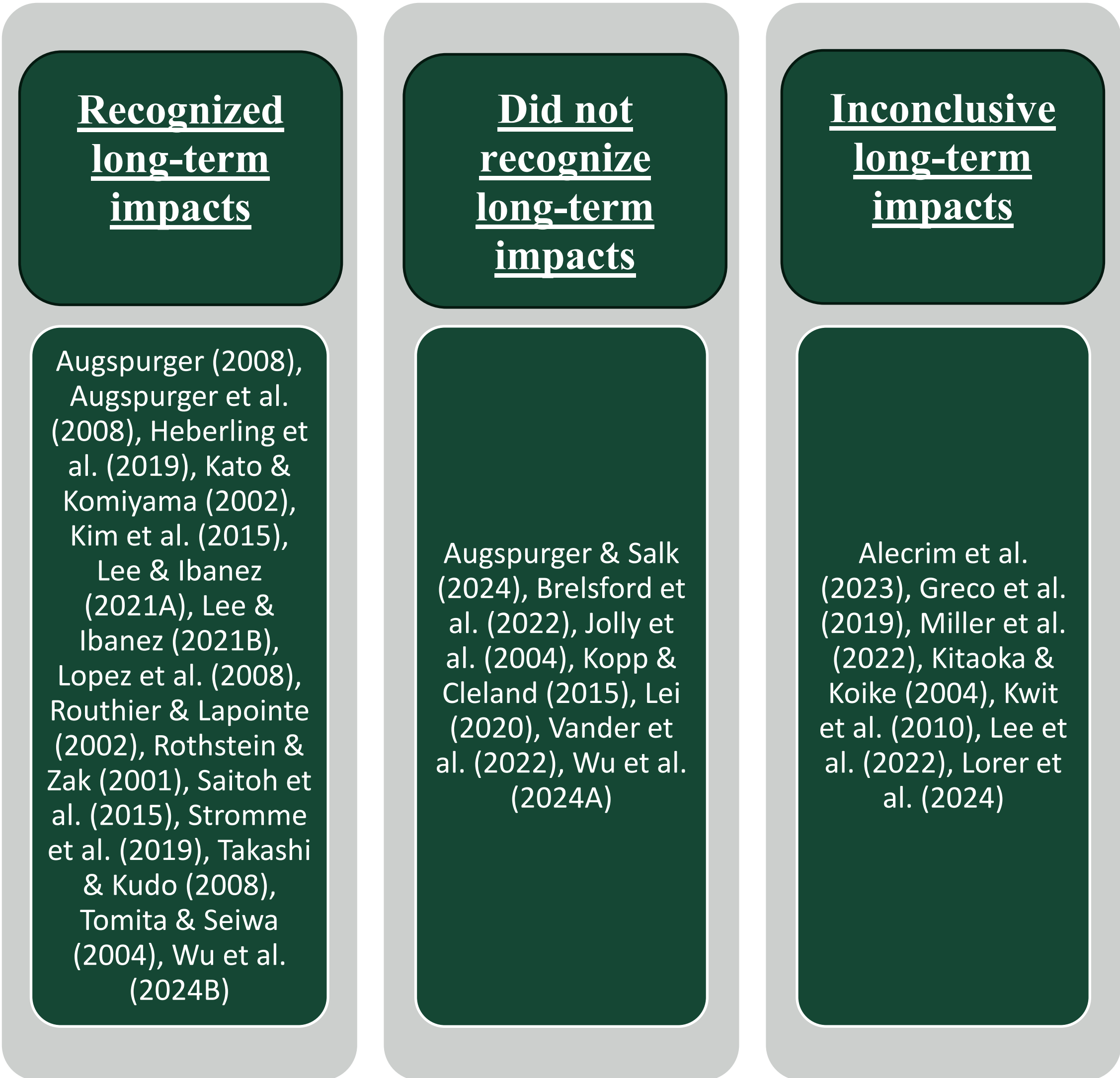

Figure 3. Comprehensive categorization of the studies based on their findings. In the first category are studies which recognize the long-term impacts of phenological mismatch through historical data, computer simulations, literature reviews and experiments. In the second column are studies which utilized the same research methods of the previous category without finding convincing evidence of consequences of phenological mismatches. In the third category are studies were the researchers mention possibilities of long-term effects without certainty because it either was not the focus of the study or they do not have enough data to confirm their suggestions.

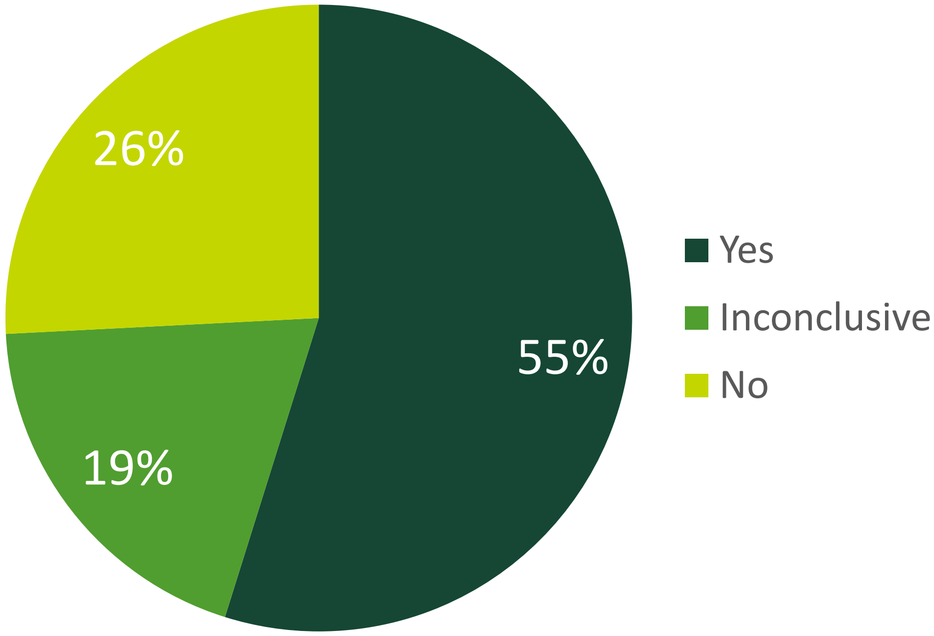

Figure 4. Distribution of papers' findings of long-term effects among the categories shown in Figure 3.

3.2 Carbon assimilation

Spring is a critical season for carbon assimilation by plants. Many understorey plants will store carbon assimilated during the spring in their roots as a reserve for next year´s growth (Routhier & Lapointe 2002). In extreme cases, insufficient carbon assimilation could kill a plant due to carbon starvation (Lee & Ibáñez 2021b). Therefore, an impact on a plant's carbon assimilation capacity could harm next year´s growth and development. The increase in light exposure for overstorey vegetation leads to an increase in carbon metabolic activity for these plants while there is a decrease in the carbon budget for the understorey layer (Saitoh et al. 2015). In the long term, boreal and temperate forests could have a thriving overstorey layer while having an underdeveloped understorey layer.

Heberling et al. (2019) found that the carbon assimilation of understorey plants became compromised with an earlier tree canopy closure through historical data of temperate wildflower species and the creation of a model in R heir results predict that wildflowers in the United States had a higher carbon assimilation by 4.0–8.7% a hundred years prior in comparison to the present (Heberling et al. 2019). This was due to a decrease of 6.5 days in the light window for the understorey layer within the century (Heberling et al. 2019). If by 2080 there is an increase of 2.5–4.5°C in temperatures in the United States, the simulation showed an expected decrease of 5.7–12.6% in the understorey layer's carbon budget

(Heberling et al. 2019). If species are unable to adapt, this could decrease plant growth and reproduction success.

Saitoh et al. (2015) also used a model to analyse the carbon budget of a Japanese forest in the case of a phenological mismatch of light conditions between the deciduous overstorey vegetation and the evergreen understorey vegetation of a temperate forest. The results show a decrease in gross primary production and net primary production of the understorey vegetation (Saitoh et al. 2015). Thus, there was a decrease in their contribution to the ecosystem´s carbon budget (Saitoh et al. 2015).

Nevertheless, species showing phenological escape were observed to have successfully assimilated more than half of their yearly carbon gain in this period (Lee & Ibanez 2021b). Kwit et al. (2010) explain that a species' capacity for phenological escape is correlated with its carbon assimilation and carbon budget processes. Their study showed that if seedlings of *Acer saccharum* leaf out 6 days earlier, they could gain 200% more carbon (Kwit et al. 2010). However, this plasticity potential in leafout timing is highly species specific and depends on variables like leaf structure and nutrient allocation properties which determine how well seedlings adapt their photosynthetic properties (Kwit et al. 2010).

Lee & Ibáñez (2021b) found that seedling development and survival depends on spring light since it is extremely important for carbon assimilation potential. They observed that seedlings of *Acer saccharum* assimilated 84.3% of their annual foliar carbon during the spring, while the same figure was only 53.5% for *Quercus rubra* seedlings (Lee & Ibáñez 2021b). Understanding the implications for seedlings' carbon gain is relevant to understand forest regeneration (Lee & Ibáñez 2021b). Their study showed a strong correlation between seedling leafout timing and carbon assimilation potential (Lee & Ibáñez 2021b). These results suggest that plant adaptation relies on carbon assimilation potential. Future recruitment of species which are unable to phenologically escape could be compromised (Lee & Ibáñez 2021b).

3.3 Phenological responses of understorey vegetation

Phenological plasticity to changes in environmental conditions are highly dependent upon the species studied. An example would be the difference between adaptation potential between *Aesculus glabra* and *Acer saccharum*. Augspurger (2008) comments on the potential of cascading effects if seedlings are deprived of sufficient light. An example of cascade effects was found in *Aesculus glabra,* which showed earlier leaf senescence in combination with a reduced growth season in spring, resulting in high mortality (Augspurger 2008). Phenological escape may be the determining factor for recruitment survival in species like *Acer saccharum* (Lee & Ibanez 2021a). Lopez et al. (2008) reinforces this idea with their data, which showed that a shorter light window for the understorey layer led to higher mortality and decreased growth for *Aesculus glabra* and *Acer saccharum* seedlings.

However, even if species seemed to adapt to the new shade conditions in spring, some impacts may appear at later phenophases (Kim et al. 2015). For instance, species like *Erythronium japonicum* adapted their leaf out resource allocation to shadier conditions (Kim et al. 2015). However, these species also experienced an earlier leaf senescence period (Kim et al. 2015). This could indicate that their adaptation to early tree canopy closure may not be sustainable in the long term.

Not all studies seemed to have found data which shows that phenological mismatch will be a problem for understorey plants. For instance, Alecrim et al. (2023) found that understorey herbs showed plasticity to adjust within a short time span, but the long-term effects were not as clear. Shade-tolerant species seem to adapt well to shorter light windows (Kopp & Cleland 2015). The longer overstorey growing season proved to not be so important since the understorey vegetation was able to make similar adjustments (Augspurger & Salk 2024). Strømme et al. (2019) also mentions that the increased growth season had a positive impact of growth on young *Populus tremula* trees. In relation to saplings, Augspurger & Salk (2024) comment that their results showed that changes in light availability were not as significant as expected for most studied species. Moreover, other seasons may also have a significant role in phenology of understorey species. Vander et al. (2022) argue that for some genera like *Corylus*, summer and autumn have a greater impact on seedling development than spring has. Their reasoning is that "plant height and height increment" are correlated with timing of bud formation and leaf senescence rather than leafout timing (Vander et al. 2022).

3.4 Biomass gain and resource allocation

Light conditions' impact on the resource allocation of understory plants is important as light conditions change, and plants will need to adapt. Rothstein & Zak (2001) compared the respiration adaptation capacity of *Allium tricoccum, Viola pubescens* and *Tiarella cordifolia* to different light conditions in relation to biomass gain. *Allium tricoccum* was the most shade intolerant of the three species (Rothstein & Zak 2001). Although it presented a similar respiration level to *Viola pubescens* in spring, it had a significant biomass loss when faced with shadier conditions (Rothstein & Zak 2001). This could indicate that a decrease in light availability to the understorey layer could potentially lead to compromised development and growth of spring ephemerals.

However, the species *Viola pubescens* and *Tiarella cordifolia* were able to adapt to shadier conditions by reducing respiration during summer (shaded conditions) while increasing photosynthesis in spring and autumn (brighter conditions, leading to an overall positive carbon balance (Rothstein & Zak 2001). A positive carbon balance meant that these species were able to effectively gain biomass in shadier conditions (Rothstein & Zak 2001). These species have different light requirements; *Tiarella cordifolia* is more shade tolerant than *Viola pubescens* (Rothstein & Zak 2001). Still, in comparison to *Allium tricoccum,* both species seemed to successfully adapt to shadier conditions while maintaining a sustainable biomass gain (Rothstein & Zak 2001). This could indicate that some species are able to cope with the changes in their environment and should suffer minimal impact of phenological mismatch.

Kato & Komiyama (2002) claim that light conditions during spring are a major variable predicting mass gain. Their study observed a significant gain in dry mass of understorey woody species in conditions where direct light reached the understorey layer, resulting in reproductive success and survival (Kato & Komiyama 2002). Takashi & Kudo (2008) states that in their experiment, spring ephemerals allocating their carbon for reproduction was dependent on the light conditions. In shaded conditions, the understorey focused their carbon translocation on the leaves and stems to provide enough resources for flowering and fruiting (Takashi & Kudo 2008). Vegetative reproduction seemed to mainly occur in high light conditions prior to tree canopy closure, and this process restricted the level of carbon that plants would allocate for leaves and stems (Takashi & Kudo 2008).

Plants which did not produce flowers did not have a notable difference in resource allocation from different years (Kim et al. 2015). Understorey plants which produce flowers seem to prioritize carbon allocation to above-ground growth (Kim et al. 2015). Kim et al. (2015) compared resource allocation for reproductive strategy in *Erythronium japonicum.* This species showed a decrease in flower size under shadier conditions in comparison to higher-light conditions (Kim et al. 2015). Another example of adaptation is *Sasa kurilensis,* which adapts its leaves to the light conditions (Wu et al. 2024a). Within low-light conditions, S*asa kurilensis* leaves had a smaller leaf area than in higher light conditions (Wu et al. 2024a). Leaf area is an important factor for respiration and photosynthesis. This led to less carbon content as well lower leaf dry mass content in shaded conditions (Wu et al. 2024a).

Shade tolerance is a characteristic dependent on species. Tree genera like *Quercus* have been shown to tolerate 15% of full light understory conditions (Wu et al. 2024b). Still, tolerating shade does not mean that those conditions are ideal for the species. Wu et al. (2024b) that *Quercus mongolica* seedling were able to accumulate a higher biomass in their roots and branches in 40% of full light conditions in comparison to 20% of full light. This indicates that even species which are able to withstand the phenological mismatch may not develop as well as in brighter conditions.

3.5 Biodiversity

Many of the papers also explain the possible consequences of phenological mismatches from an ecological standpoint. Miller et al. (2023) argues that a loss of understorey layer´s biodiversity could impact the carbon cycle, influence the regeneration of the overstorey layer and change nutrient availability for different species. Alecrim et al. (2023) highlight that factors such as browsing and pollination are affected by phenological mismatches within asymmetrical plant competition, which may reinforce the decrease in fitness of some understorey species.

However, a change in light conditions through management should be planned and monitored. Light conditions have the potential to indirectly impact understory conditions (Tomita & Seiwa 2004). Although shaded forests such as beech forests tended to have less understory variation, an increase in understory biodiversity could lead to a decrease in seedling survival due to an increased plant competition. The genus *Sasa* is an important understory species for Asian temperate forest systems, as it was mentioned by Tomita & Seiwa (2004) and Wu et al. (2024a). Yet, in Tomita & Seiwa´s (2004) study the dense *Sasa* population decreased light conditions (as this is an evergreen species that shades shorter plants), decreasing the survival rates for beech seedlings. Furthermore, it also encouraged animal foraging in the region, which leads to fewer seeds and beech seedlings (Tomita & Seiwa 2004).

4. Discussion

The aim of this paper was to gain a better understanding of the possible long-term effects of phenological mismatches under asymmetrical plant competition. The number of papers selected for this literature review was low, but it covered a large scope of topics from three continents. The main issue revealed by this review is the impact that a lack of light availability has on carbon assimilation for seedlings and other understorey vegetation when the overstorey growing season is extended. The initial hypothesis can be partially accepted, as it is not possible to expect that all species will suffer long-term impacts of phenological mismatch nor that all species will have phenological mismatches. However, species like *Allium tricoccum, Aesculus glabra, Erythronium japonicum* have shown consequences like decrease in biomass gain and early leaf senescence. On a long-term basis, this could lead to decrease in fitness.

Not all papers found a significant result of long-term effects of phenological mismatches. Yet, they might be helpful to analyse the gaps in research of papers which found long-term effects. One argument from many papers in this category is that the understorey vegetation response to light and temperature conditions is non-linear, making reliable outcome predictions complex (Augspurger & Salk 2024, Kopp & Cleland 2015). Still, papers which did not observe long-term effects consist of less than a half of the number of papers investigated in comparison with papers that mentioned long-term effects.

Managing of biodiversity under phenological mismatches in asymmetrical competition will depend on forest type as well as goals. To promote the development of species impacted by this type of phenological mismatch, it is necessary to increase light reaching the understory vegetation. If the focus is to increase understorey biodiversity, one management strategy could be the creation of gaps. This procedure would leave space for light to reach the forest floor, mitigating the impacts of the extended growing season of trees on the light conditions of the understorey layer. Another possible measure is to ensure that the overstorey canopy is not too dense. The density of canopy can be managed through thinning regimes, which will increase light availability to the understorey vegetation.

The chosen methodology for this paper allowed for data from different continents (Europe, Asia and North America) to be taken into consideration. There seems to be a gap in research when it comes to comparing phenological mismatches across different continents. From all the analysed papers, only Lee et al. (2022) compared the long-term impacts from different Asia, North America and Europe. As climate change is a global issue, it could be relevant to understand similarities of the same forest type in different continents. This joint effort could promote greater collaboration between institutions which aim to promote climate resilient forests.

There was a variation in methodologies used by the selected papers. This could be a positive feature as it could decrease the impact of systematic error or biases present in the studies. Many studies like Lee et al. (2022) regarding phenological mismatches across forest layers have a longitudinal design and observe repeated patterns, compare between seasons or generate models for what will happen in the future. However, models are not perfect and there could be confounding variables unaccounted for.

This study only accounts for light and temperature. Yet, there are other variables which could have a great influence on the understorey vegetation. For example, Lee & Ibanez (2021b) explain that water regimes were significant for carbon assimilation in seedlings. Strømme et al. (2019) comments that delayed bud break could be a carryover effect from insufficient low temperatures during previous seasons. During spring, temperature and light conditions are highly correlated with each other and it can be difficult to isolate the impact of only one of these variables.

A disproportionate number of studies investigated temperate forests in comparison to relatively few studying boreal forests. Therefore, the results found in this research cannot be considered representative for all deciduous boreal forests. One reason for the low number of papers could be due to publication bias, as there may be fewer negative effects on this forest type. However, deciduous boreal species such as *Larix, Betula* and *Populus* are incredibly important for biodiversity and understanding how climate change is impacting species interactions, making phenological research relevant to develop efficient management strategies. Considering how important the spring season is for understorey species, more research in this area should investigate the carryover effects of phenological mismatch in asymmetrical plant competition in boreal ecosystems. A greater focus on deciduous boreal forest systems would help obtain more conclusive results on this forest type.

5. Conclusion

Long-term effects of phenological mismatches on asymmetrical plant competition are nuanced. A majority of the studies used in this literature review suggest that long-term effects are expected. Surprisingly, there was not a strong focus on how biodiversity is going to be affected. Many studies commented on the impact of light availability to the understorey layer on carbon assimilation and biomass gain, which happens during the spring. It is expected that during the upcoming years, there will be a decrease in understory carbon assimilation as well as a lower biomass gain due to a shortened spring light window. However, this paper only analysed in depth 28 studies and thus more research with a larger sample size would help to build more conclusive results. Management strategies such as the creation of gaps could help mitigate the impacts of phenological asynchrony on asymmetrical plant competition as it would promote heterogeneity in light conditions for the understorey layer. These results mainly reflect what could be expected to happen in deciduous temperate forest systems. Future research is needed on deciduous boreal forest systems to be able to obtain conclusive results in that forest type.

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Appendices

Appendix 1

Table 2. Selected studies for analysing long-term effects of phenological mismatches

Study	DOI	Continent	Forest type
Alecrim et al. (2023)	10.1111/1365-2745.14023	North America	Temperate
Augspurger (2008)	10.1007/s00442-008-1000-7	North America	Temperate
Augspurger et al. (2005)	10.1111/j.1365-2435.2005.01027.x	North America	Temperate
Augspurger & Salk (2024)	10.1371/journal.pone.0306023	North America	Temperate
Brelsford et al. (2022)	10.1111/ppl.13723	Europe	Boreal
Greco et al. (2019)	10.1139/cjb-2019-0083	North America	Temperate
Heberling et al. (2019)	10.1111/ele.13224	North America	Temperate
Jolly et al. (2004)	10.1093/treephys/24.9.1069	North America	Temperate
Kato & Komiyama (2002)	10.1046/j.1440-1703.2002.00529.x	North America	Temperate
Kim et al. (2015)	10.1007/s12374-014-0545-8	Asia	Temperate
Kopp & Cleland (2015)	10.1371/journal.pone.0139029	North America	Temperate
Kwit et al. (2010)	10.1139/X09-196	North America	Boreal
Lee et al. (2022)	10.1038/s41467-022-34936-9	Asia, Europe, North America	Temperate
Lee & Ibanez (2021A)	10.1111/gcb.15678	North America	Temperate

Lee & Ibanez (2021B)	10.1111/1365-2435.13821	North America	Temperate
Lei (2020)	10.1007/s11258-020-01023-2	Asia	Temperate
Lopez et al. (2008)	10.3732/ajb.0800104	North America	Temperate
Lorer et al. (2024)	10.1111/nph.19425	Europe	Temperate
Miller et al. (2023)	10.1111/1365-2745.14021	North America	Temperate
Routhier & Lapointe (2002)	10.3732/ajb.89.3.500	North America	Temperate
Rothstein & Zak (2001)	10.1046/j.0269-8463.2001.00584.x	North America	Temperate
Saitoh et al. (2015)	10.1007/s11284-014-1229-z	Asia	Temperate
Strømme et al. (2019)	10.1016/j.plaphy.2018.08.029	Europe	Boreal
Takashi & Kudo (2008)	10.1093/aob/mcm296	Asia	Temperate
Tomita & Seiwa (2004)	https://doi.org/10.1111/j.1654-1103.2004.tb02275.x	Asia	Temperate
Vander et al. (2022)	10.3390/f13050654	Europe	Temperate
Wu et al. (2024A)	10.3390/plants13050719	Asia	Temperate
Wu et al. (2024B)	10.1016/j.fecs.2024.100185	Asia	Temperate

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