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REVIEW ARTICLE

The effects of climate change on boreal plant-pollinator interactions are largely neglected by science

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ABSTRACT

The boreal forest, one of the world's largest terrestrial biomes, is currently experiencing rapid climate-driven changes. This review synthesizes the limited research available on climate-change impacts on boreal plant-pollinator systems, revealing several knowledge gaps and shedding light on the vulnerabilities of boreal ecosystems. Using four complementary Web of Science searches, we found 5198 articles, of which only 11 were relevant. Our findings reveal that research on boreal plant-pollinator interactions is limited to date, as is our understanding of the insect fauna and pollination systems in the boreal region. Existing research often focuses on conspicuous plants, neglecting many other ecologically significant species. In addition, current studies often lack detailed data on pollinator species, which restricts our capacity to assess the vulnerability of specific plant-pollinator interactions to climate change. For example, most articles use plant reproductive success as a proxy for pollinator effectiveness without considering pollinator identity. This approach successfully assesses overall plant fitness, but overlooks changes to pollinator communities, such as those resulting from thermophilization, that may be relevant to projecting climate-change impacts. Moreover, pollinator taxon seems to affect the responses of plant reproduction to warming, with fly-pollinated plants appearing to be more resilient to temperature changes than bee-pollinated plants. Future research should prioritize foundational plant species and key pollinators, including flies, which are crucial to boreal pollination ecology. Understanding species-specific responses to warming is equally important for identifying which species and interactions may be most vulnerable to climate change. Studies should also examine the role of forest microclimates, as they may buffer boreal regions during broader climatic shifts, helping to mitigate the impacts of warming on these ecosystems. Addressing these gaps is essential for predicting climate impacts on boreal biodiversity and for informing conservation strategies that support biodiversity and benefit human communities reliant on boreal ecosystem services.

Introduction

The boreal biome is the largest contiguous forested region of the world, occupying a circumpolar belt nestled between the temperate and arctic or alpine biomes (Tuhkanen, 1984). This vast expanse is characterized by a dominance of coniferous trees, which provide the foundation for diverse ecosystems (Kuuluvainen, 2009). Recent assessments, such as the Arctic Climate Impact Assessment (ACIA, 2005) warn that climate change may profoundly alter the function and structure of boreal forests, more than in many other of the Earth's biomes (Venäläinen et al., 2020; Rao et al., 2023). While global temperatures have increased by on average 1.1 °C above those of the late 19th century (IPCC, 2023), they are increasing approximately twice as fast in some boreal regions (SMHI, 2023). This has placed the boreal biome at higher risk of climate change-related impacts compared to other areas, where harmful consequences for biodiversity (Gauthier et al., 2015) and ecosystems (Ito et al., 2020) have already been reported, highlighting the need for continued research and development of adaptive strategies.

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The extensive and rapid changes to the climate system are expected to affect fauna and flora by a variety of abiotic and biotic means and interactions. For instance, temperature rise can cause an earlier onset of spring and later arrival of autumn weather conditions, thus lengthening the vegetation period (Hayhoe et al., 2007). The vegetation period in the boreal biome is short, and species must have reliable environmental cues to ensure the suitable timing of their phenological adaptations. Many species, for example, use temperature or snowmelt as a phenological cue for leafing, flowering, or the cessation of hibernation. However, the snowmelt date is already being affected by climate change in boreal forests (Mellander et al., 2007; Kirtman et al., 2013). Although warmer weather during spring may have some positive effects such as reduced risks of frost damage to vegetation (Park et al., 2021), environmental changes that alter phenological cues to an already limited growing season may ultimately have detrimental effects that outweigh positive aspects of a longer vegetation period.

In response to increasing temperatures, many species are shifting their distributions to higher elevations and latitudes, *i.e.*, northwards in the northern hemisphere and southwards in the southern, in order to track the changing climate (Taheri et al., 2021). As a result of these distribution shifts, some species are colonizing new areas whilst others, which fail to adapt to the novel conditions or species interactions, may go extinct. Evidence of such distributional shifts is increasingly being reported in diverse biotic groups (Pecl et al., 2017) and geographical regions (Chen et al., 2011), and are more conspicuous and happen faster at higher latitudes (Virkkala & Lehikoinen, 2014). If the available climatic conditions in the new areas are not suitable for a distribution shift, the net result can also be a reduction in a species distribution area. Additionally, as a result of climate change, species can change their local abundance by shifting their positions along environmental niche gradients, *i.e.*, without colonization or extinction events, but rather by being pushed or pulled from their environmental optima (Antão et al., 2022).

Species that interact with each other may react differently to environmental change depending on their adaptive capabilities and phenotypic plasticity, potentially leading to a phenological mismatch (Visser & Gienapp, 2019). These spatial and temporal mismatches represent distinct dimensions of climate change-driven disruptions in ecological interactions. Spatial mismatch takes place when species shift their distributions due to environmental change in a way that prevents them from interacting (*e.g.*, Schweiger et al., 2008). On the other hand, temporal mismatch occurs when there is a discrepancy in the timing of key events in the life cycles of interacting species (Visser & Gienapp, 2019). This can manifest as changes in the timing of migration, reproduction, or flowering, and disrupt inter-species synchrony. Both spatial and temporal mismatches can disrupt the coexistence of interacting species and thus compromise their biotic relationship and their survival. This disruption can lead to considerable top-down or bottom-up consequences for plant and animal communities that ultimately affect ecosystem functioning (Beard et al., 2019), especially since ecosystem functioning depends largely on species interactions rather than on biodiversity *per se* (Stanworth et al., 2024).

Pollination is a particularly sensitive ecosystem function and service that can be affected by spatial and temporal mismatches (Kudo & Ida, 2013). When the synchrony between flowering and pollinator phenology is altered, both plant and pollinator fitness may be compromised (Kudo & Cooper, 2019). Spring emergence of some bees and bumblebees has been reported to advance by approximately 10 days over the past 130 years in North America (Bartomeus et al., 2011), and by 5 days during the past 20 years in Sweden (Blasi et al., 2023). Similarly, warmer springs have advanced the flowering time by 0.49 days per decade in Sweden (Auffret, 2021) and 2.4 days $\cdot$ $°C^{-1}$ in north-central North America (Calinger et al., 2013), although plant responses to warming and changes in precipitation seem to be species-specific (Rice et al., 2021). Despite both pollinators and plants having accelerated their timing of emergence and flowering, it is when these responses take place to differing degrees that mismatch takes place.

There is limited evidence of phenological mismatches in mutualistic relationships, which is possibly a result of strong selection on mutualists to have co-adapted phenological strategies (Renner & Zohner, 2018; Milberg & Palm, 2024). Phenological mismatches in pollination interactions are still rather unexplored, as is our understanding of their demographic implications (Hegland et al., 2009). Moreover, conflicting insights into the presence and impacts of phenological mismatch arise from literature. For instance, research on multi-species plant-pollinator assemblages suggest that the overall structure of pollination networks is probably resistant to the extent of climatic change that has occurred thus far (Hegland et al., 2009). However, research conducted in the temperate forests of Illinois (USA) reveals a degradation in both the structure and function of plant-pollinator networks over time (Burkle et al., 2013). Although such before-and-after studies can provide valuable insights, they often face inherent challenges due to multiple often correlated factors changing simultaneously. For this reason, their findings should be interpreted with caution. Nevertheless, this work indicates that at least some pollination networks may already be degrading under current climatic stressors, with the resilience of other networks likely to erode when placed under additional climatic strain. Similarly, Kudo and Ida (2013) observed that when spring came early in a cold-temperate forest in Japan, seed production of an understory plant species was reduced due to phenological mismatch with pollinators.

Species that hold specific interactions or depend upon each other for survival, like many plants and pollinators, are especially vulnerable to disturbances and local extinction (Weiner et al., 2014). Projected plant extinctions under climate change are more likely to trigger animal pollinator co-extinctions than vice versa (Schleuning et al., 2016). Since specialization in mutualistic interactions seems to increase with latitude (Schleuning et al., 2012), the rapidly warming boreal regions, which already exhibit low diversity in both plants and pollinators (Esseen et al., 1997), are especially at risk of experiencing shifts in species composition that disrupt plant-pollinator interactions (Memmott et al., 2007; Antão et al., 2022). As a consequence, species may compensate for lost ecological interactions by forming new interactions with species they previously did not interact with, typically because these species did not overlap in space or time. This process is known as interaction rewiring (CaraDonna et al., 2017). For instance, a plant species may establish new mutualistic relationships with other pollinator species that have shifted their geographical range or phenology due to climate change (Zoller et al., 2023). Interaction rewiring can, therefore, act as a buffer against the detrimental effects of ecological mismatches, helping to preserve ecological processes like pollination during environmental shifts (Burkle & Alarcón, 2011). However, the success of rewiring depends on the availability of suitable new partners, the flexibility of species to adapt to these novel interactions, and the resilience of the overall network structure (Bascompte & Jordano, 2007). While interaction rewiring offers a mechanism of ecological resilience, not all species or networks are equally capable of rewiring, and the long-term sustainability of these new interactions remains unknown (Valdovinos et al., 2018). For an overview on the potential mechanisms through which climate change may affect boreal plant-pollinator systems, see Fig. 1.

Here we conducted a literature review to address the effects of climate change on plant-pollinator interactions in boreal forests. We specifically asked how climate change affects plant-pollinator interactions in these forests, with an emphasis on the consequences of changing interactions for individuals, species and communities. We synthesized existing literature on the impacts of climate change on plant-pollinator interactions in the boreal biome, focusing on alterations in temperature and precipitation. Our efforts included an examination of the observed and projected effects of climate change, with an emphasis to identify potential consequences for pollinators and ecosystem functioning and the ability of pollinators to cope with phenological shifts and potential mismatches. Through these efforts we establish a baseline of

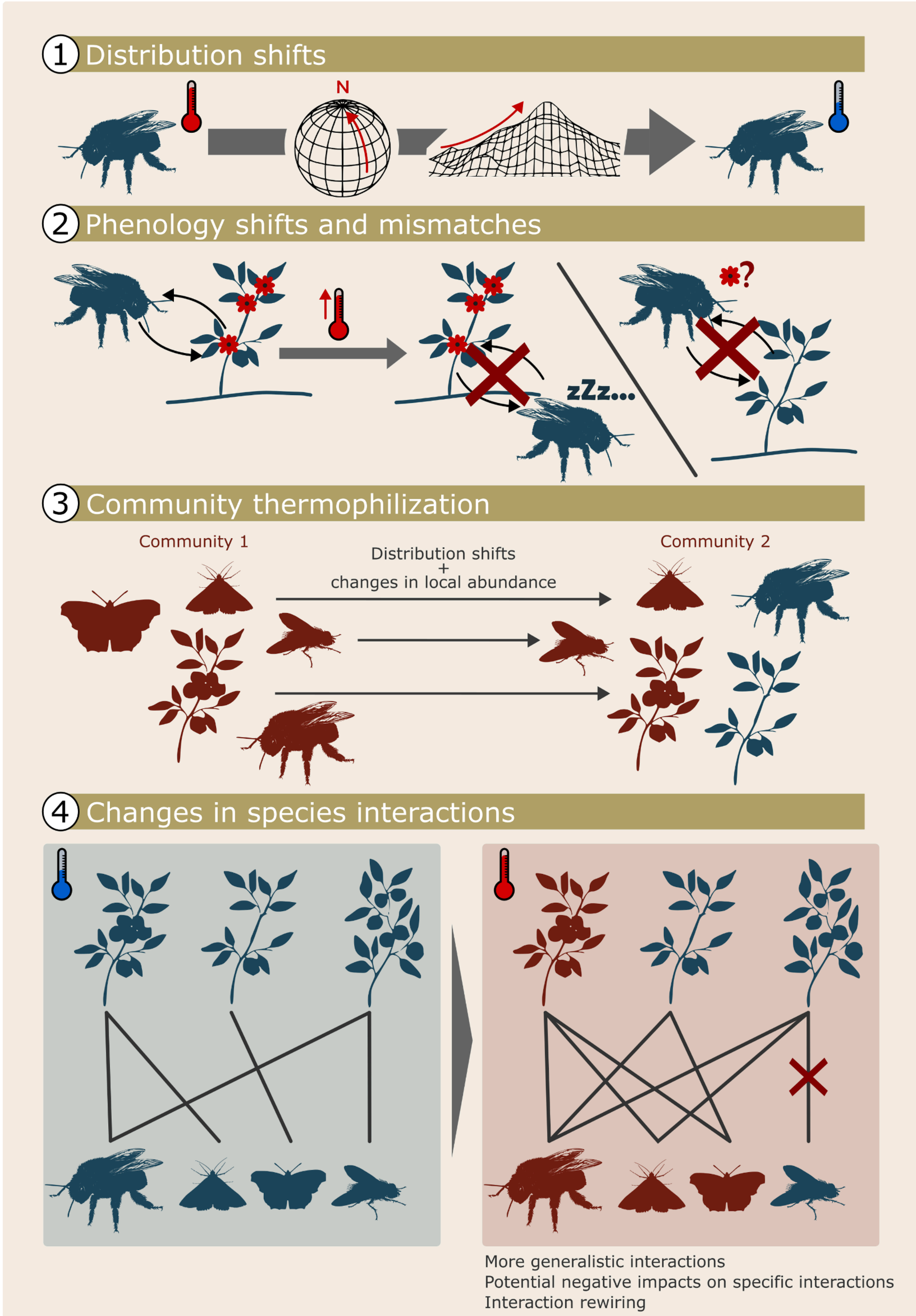

Fig. 1. Overview of the possible mechanisms through which climate change may affect boreal plant-pollinator systems. Organisms depicted in red represent warm-adapted species, and blue ones represent cold-adapted species. In response to warming, cold-adapted plant and pollinator species may shift their distribution ranges towards cooler, more suitable areas (1), or fail to do so and reduce their local abundance or become locally extinct. Moreover, in response to warming, species may alter their phenology (2). Both changes in distribution ranges and phenology may lead to interaction mismatches when plant-pollinator partners fail to adapt at the same spatial or temporal scale. Moreover, warm-adapted species will benefit from warming compared to cold-adapted species, and together with species shifting their distribution from warmer areas will produce the thermophilization of species communities (3). Warmer temperatures benefit more generalistic interactions (4), and may negatively impact specific interactions. In addition, the arrival of new species from warmer areas and potential local species loss may rewire plant-pollinator interactions.

information that can serve as a starting point for future research and conservation strategies.

Materials and methods

Literature search and criteria

We carried out four distinct searches in the Web of Science (WoS) search engine in November 2023. All search queries (see i–vii in Fig. 2) included a section on (i) climate change, (ii) forest categories, and (iii) regions for inclusions and, (iv) exclusion (*e.g.*, tropical forests). In addition, depending on the focus of the search, additional sections were added, concerning either (v) pollinators or (vi) understory vegetation, including the common and scientific name of the most common species, or both (v) and (vi). For the four searches, we included all databases available to the Swedish University of Agricultural Sciences through WoS, namely: the Web of Science Core Collection, BIOSIS Citation Index, Current Contents Connect, CABI: CAB Abstracts®, Data Citation Index, Derwent Innovations Index, KCI-Korean Journal Database, MEDLINE®, ProQuest™ Dissertations & Theses Citation Index, SciELO Citation Index and Zoological Record. Results from the Preprint Citation Index were excluded. Only works written in English were considered.

The main search involved elements i-vi, and thereby included both pollinators and understory vegetation. To make sure that other relevant studies involving pollinators were not overlooked, a second search was conducted including only pollinators (*i.e.*, elements i–v). For these two search queries, Web of Science results were refined to select only peer-reviewed scientific articles. Additionally, we conducted a search of review articles involving only understory vegetation in boreal forests. For this, two separate searches were conducted, using the same i–iv + vi elements. For one of the searches, review articles were filtered from the results by refining the Web of Science search using the built-in 'review articles' feature. For the last search, a new section (vii) specifying keywords such as "review" and "meta-analysis" was included in the search query.

Article deduplication and inclusion criteria

We utilized the R package 'synthesisr' (Westgate & Grames, 2020) to eliminate duplicates from each of the four searches in the literature review. Initially, duplicates were identified by exact title matches. Subsequently, we applied optimal string alignment distance calculations to all titles transformed to lowercase and disregarding punctuation marks to identify additional potential duplicates. These were manually reviewed and removed as needed. Afterwards, we calculated the overlap between the results found in our four searches and identified further duplicates across the entire pool of articles collected from all searches by repeating the same process.

The first search (plants and pollinators together) yielded 550 results, 543 after removing all duplicates. All of these articles overlapped with those found in the second search (only pollinators), which yielded 583 articles, 576 after removing duplicates. Therefore, by including this second search, we found 33 new articles that did not appear in the first search. Then, the search that also included reviews on understory vegetation through the Web of Science filtering options returned 843 articles, and the search that included reviews and meta-analyses returned 4447 articles; which reduced to 4351 after removing duplicates. After pooling the articles of all searches and removing duplicates, 5198 unique articles remained. Screening of these articles took place in three steps: firstly, the titles of the articles were screened, and articles non-related to natural sciences, as well as conference communications, books or book chapters, and works in languages other than English, were removed. This reduced the number of articles to 4529. Then, abstracts were screened and we excluded studies outside the geographical range of the boreal biome (*i.e.*, outside of the countries mentioned in Fig. 2, section iii in the search query), research unrelated to forests, research on forest pests and silviculture, and articles focusing only on trees or soil. At this stage, 172 articles remained. The final step involved a detailed examination of the remaining articles to ensure they aligned with our specific focus. We established three key inclusion criteria for this review. First, articles should consider the impacts of climate change, as understanding these effects is essential for assessing shifts in ecosystem dynamics. Second, each study should focus on forest understory vegetation, as this component includes the vast majority of non-wind pollinated plant species in the boreal forest and is crucial for supporting both pollinators and overall forest health. Finally, the research needed to explicitly mention pollinators in their study system, either in relation to understory vegetation or in connection to climate change. By applying these criteria, we refined our article selection to ensure a comprehensive and relevant collection of studies that addressed the intersections of climate change, pollinators, and understory vegetation within boreal forest ecosystems.

The screening of the search query results yielded a total of eight articles. Additionally, three more articles that were not found through our search queries but we nevertheless considered relevant were included, bringing the final count to 11 articles. For a visual representation of the screening process, refer to Fig. 2, which presents the PRISMA diagram of our literature review.

Results

Out of the 5198 reviewed articles, only 11 fulfilled our search criteria (Table 1). This in itself highlights the lack of research on the impacts of climate change on boreal plant-pollinator interactions. These articles were sourced from the different Web of Science queries, which demonstrate the effectiveness of our complementary search approach. Yet, none of these articles tackled our research question in its entirety. Studies on plant-pollinator networks and their change over time or in different climatic conditions were missing, and the effect of climate change on the interactions between plants and pollinators at the species level was not addressed. Conversely, our selected studies mainly assessed how changes in climate affected plant reproductive success as well as plant and pollinator phenology. Although this may hint at some of the expected impacts of climate change, the studies were not very informative about the broader and more complex effects of climate change on plant-pollinator interactions. Moreover, the studies also often fail to document pollinator species identities and their specific interactions with plants, overlooking crucial insights into species-specific responses to climate change. In addition, they rarely incorporate detailed temperature measurements or consider the potential buffering effects of forest microclimates on pollinator activity, further limiting our ability to predict climate change impacts accurately.

Overview of the selected studies

Climate change was addressed in various ways across the reviewed articles. Among the 11 studies, eight quantified its tangible impacts through time series analyses spanning periods ranging from two to 41 years, including assessments during extreme events (Barrett & Helenurm, 1987; Helenurm & Barrett, 1987; Kudo et al., 2004; Nishikawa, 2009; Kudo & Ida, 2013; Boulanger-Lapointe et al., 2017; Kudo & Cooper, 2019; Sevenello et al., 2020). One study utilized altitudinal gradients as a proxy for warming (Olsen et al., 2022), while another focused on species at their distribution limits compared to other locations (Blinova, 2002). Lastly, one study examined both an altitudinal gradient and the upper elevation range limit of two plant species (Rivest & Vellend, 2018).

We divided the 11 studies that fulfilled our search criteria into three different groups of climate-related studies: Studies of the effect of pollinator and flowering phenology on plant reproduction ($n = 6$), the effect of biotic or abiotic factors on plant reproduction ($n = 4$), and studies exploring the different reproductive systems of understory

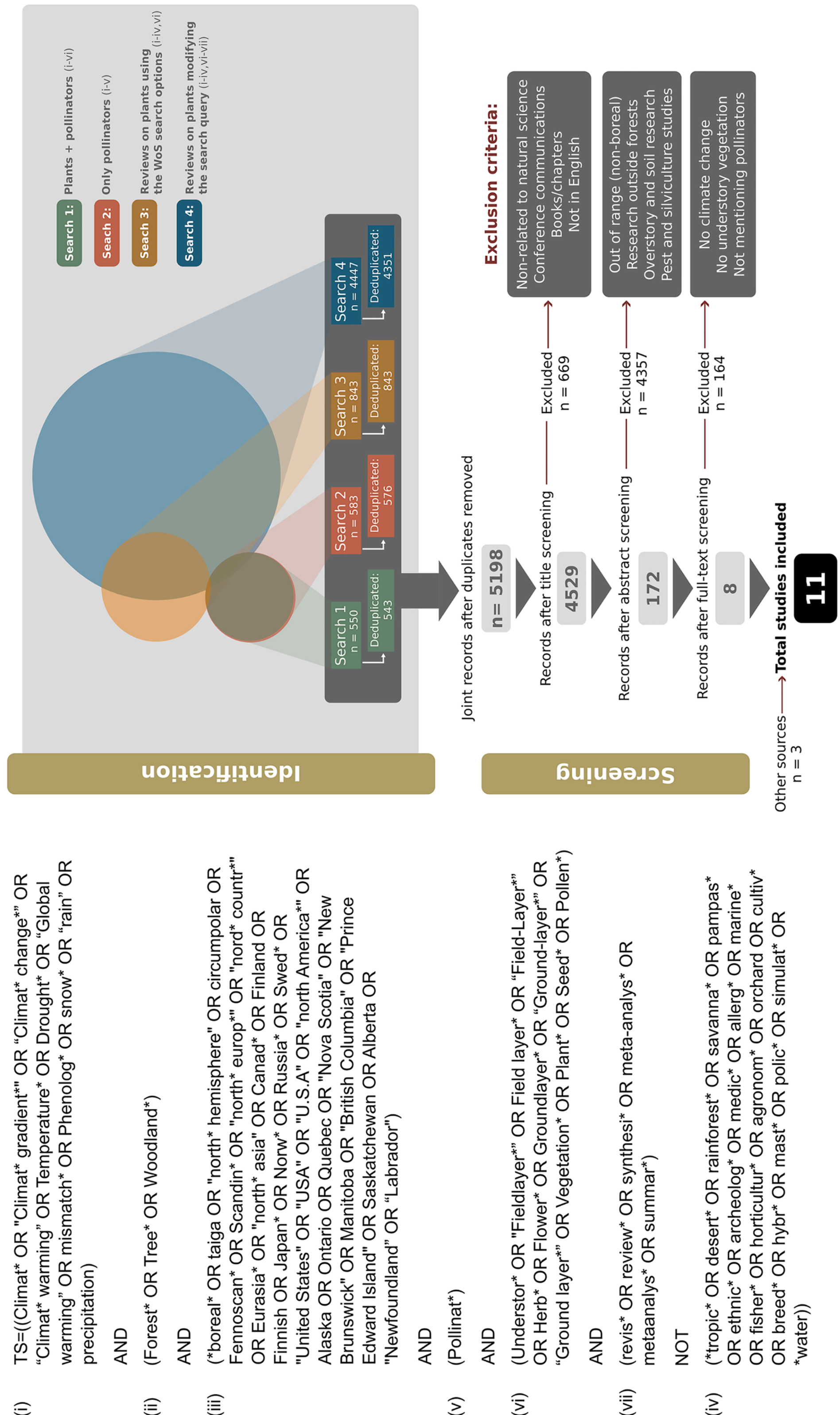

Fig. 2. Search query and PRISMA diagram for the four literature searches conducted. Different combinations of the elements i-vii were used in each search. See text for details.

flowering vegetation ($n = 1$).

Phenology studies focused either on both plants and their pollinators (Kudo et al., 2004; Nishikawa, 2009; Kudo & Ida, 2013; Kudo & Cooper, 2019; Sevenello et al., 2020) or exclusively on plants (Helenurm & Barrett, 1987). When both plants and pollinators were considered, the temporal overlap between flowering phenology and pollinator activity was assessed. Phenological mismatch was reported in two studies from Japan (Kudo & Ida, 2013; Kudo & Cooper, 2019), which both focused on

Table 1
Summary of the articles that fulfilled the search criteria of the literature review addressing the effects of climate change on plant reproduction or pollinators in boreal forests.

Study	Location	Response variable	Pollinator measurement	Pollinator proxy	Detection of pollen limitation	Climate change approach	Climate (change) effect
Blinova (2002)	Murmansk region in NW Russia	Plant seed set, seed size	No	Hand-pollination	Yes	Species northern distribution limit	Warmer years reduce frost damage
Barrett & Helenurm (1987)	Central New Brunswick	Plant seed set	Recorded but not related to climate change	Direct observation and sampling. Exclusion	Yes, in 8/12 plants	Compare different years with an extended winter	Insect visitation only occurs when temperatures are high enough.
Helenurm & Barrett (1987)	Central New Brunswick	Flowering and fruiting phenology	No, but see Barrett & Helenurm (1987)	–		Compare different years with an extended winter	See Barrett & Helenurm (1987)
Boulanger-Lapointe et al. (2017)	NW Finnish Lapland	Abundance of flowers and fruits	No	Anecdotal observation		Time-series observation (41 years)	Warmer winters did not significantly influence plant reproductive success
Nishikawa (2009)	Sapporo, Northern Japan	Plant seed set	Recorded, but not related to climate change	Direct observation and hand pollination	Yes, with inter-annual variation	Compare different seasons with different snowmelt date	Temperature affects pollinator availability, which affects seed set
Sevenello et al. (2020)	Québec, Canada	Plant and pollinator phenology	Yes	Trapping (pan traps)		Time-series over 6 years	Temperature is a good predictor of the phenology of some plants/ bees, but this cannot be generalized
Rivest & Vellend (2018)	Québec, Canada	Plant seed set	No	Hand-pollination	Yes	Altitudinal gradient, upper elevational range limit of species distribution	Different plant species pollinated by different pollinators may respond differently to altitudinal gradients (= temperature)
Kudo & Cooper (2019)	N Japan	Plant seed set	Yes	Transects Hand-pollination	Yes, varying in different years	Time-series observation (19 years)	Early snowmelt increased the risk of phenological mismatch
Kudo et al. (2004)	N Japan	Plant seed set	No	Fruit and seed set		Extremely warm year vs. normal years	Very warm spring decreased seed set of bumblebee-pollinated plants, but not of fly-pollinated plants
Kudo & Ida (2013)	N Japan	Flowering and bee phenology Seed set	Yes	Hand-pollination Seed set	Yes	Time-series observation (10–14 years)	Phenological mismatch caused by different responses of plants/ pollinators to temperature/ snowmelt
Olsen et al. (2022)	Norway	Plant seed set and seed weight	No Pollinators were excluded or reduced, but never measured	Seed set Pollinator exclusion		Altitudinal gradient	Negative effect of pollinator exclusion on plant seed set was less pronounced in forests compared to alpine sites. V. *myrtillus* is relatively robust to changes in the pollinator community in a warmer climate.

the spring ephemeral *Corydalis ambigua* Cham. & Schltdl. and its interplay with canopy closure and pollinator emergence and activity. Most of the studies that exclusively addressed factors influencing plant reproduction mainly focused on abiotic factors, namely differences in climate (Blinova, 2002; Boulanger-Lapointe et al., 2017; Rivest & Vellend, 2018). The biotic factors related to plant reproduction, studied within the context of climate change impacts, included herbivory by insects and rodents (Boulanger-Lapointe et al., 2017) or ungulates (Rivest & Vellend, 2018), as well as pollinator availability (Olsen et al., 2022). Finally, a single study explored the different reproductive systems of 12 boreal understory plants (Table 2, Barrett and Helenurm (1987)). Of these plant species, six depended exclusively on insects for pollination, four species were weakly autogamous, one was strongly autogamous and one appeared to be apomictic.

Species studied

Collectively, the 11 articles studied 23 different plant species across 11 families. Most of the species studied were from the families Liliaceae and Ranunculaceae, encompassing four species each, Melanthiaceae and Ericaceae, with three species each, and Orchidaceae, represented by two species (Table 2). Most of these plants are common with large natural distributions: 13 have a north-American distribution, five have a Eurasian distribution and five are circumpolar, or at least are present in both North America and Eurasia. Although pollination was mentioned in all these 11 articles, pollinators were only recorded in six studies, and very seldom at the species level. Barrett and Helenurm (1987), despite collecting a total of 552 insects comprising 103 taxa, limit their species-level identification to bumblebee (four species), with all others taxa identified to the level of family (*i.e.*, “Syrphidae”, “Staphylinidae”), epifamily (*i.e.*, “solitary bees”) or even order (*i.e.*, “flies”). Two studies (Kudo & Ida, 2013; Kudo & Cooper, 2019) consider only bumblebees at the genus level, although they state that 90 % of the bumblebees visiting their study plant are *Bombus hypocrita* Pérez 1905, citing their previous work. Blinova (2002) records hoverflies at the genus level, and Sevenello et al. (2020) bees at the genus level. Finally, Nishikawa (2009) identifies flies and bees at genus level, with some exceptions (*Apis mellifera* L. and *Bombus hypocrita*).

Table 2
List of plant species and their distributions studied in the selected articles relevant to the review on the impact of climate change on plant-pollinator interactions in boreal forests.

Species	Distribution	References
Adonis ramosa	Eastern Eurasia	Kudo et al. (2004)
Anemone acutiloba	Eastern North America	Sevenello et al. (2020)
Anemone americana	Eastern North America	Sevenello et al. (2020)
Anemone flaccida	Eastern Eurasia	Kudo et al. (2004)
Aralia nudicaulis	Northern North America	Helenurm & Barrett (1987); Barrett & Helenurm (1987)
Chimaphila umbellata	Circumpolar	Helenurm & Barrett (1987); Barrett & Helenurm (1987)
Clintonia borealis	Eastern North America	Helenurm & Barrett (1987); Barrett & Helenurm (1987)
Cornus canadensis	North America, except south and east Asia	Helenurm and Barrett (1987); Barrett and Helenurm (1987)
Corydalis ambigua	Eastern Eurasia	Kudo et al. (2004); Kudo & Cooper (2019)
Cypripedium acaule	Eastern North America	Helenurm and Barrett (1987); Barrett and Helenurm (1987)
Cypripedium calceolus	Euroasia	Blinova (2002)
Erythonium americanum	Central-eastern North America	Rivest & Vellend (2018)
Gagea lutea	Eurasia	Nishikawa (2009); Kudo et al. (2004)
Linnaea borealis	Circumpolar	Helenurm & Barrett (1987); Barrett & Helenurm (1987)
Maianthemum canadense	North America, except southern part	Helenurm & Barrett (1987); Barrett & Helenurm (1987)
Medeola virginiana	Eastern North America	Helenurm & Barrett (1987); Barrett & Helenurm (1987)
Orthilia secunda (as *Pyrola secunda*)	Circumpolar	Helenurm & Barrett (1987); Barrett & Helenurm (1987)
Oxalis montana	Eastern North America	Helenurm & Barrett (1987); Barrett & Helenurm (1987)
Trientalis borealis	Eastern and North America	Helenurm & Barrett (1987); Barrett & Helenurm (1987)
Trillium erectum	east-central North America	Rivest & Vellend (2018)
Trillium grandiflorum	Eastern North America	Sevenello et al. (2020)
Trillium undulatum	Eastern North America	Helenurm & Barrett (1987); Barrett & Helenurm (1987)
Vaccinium myrtillus	Circumpolar, except NE North America	Boulanger-Lapointe et al. (2017); Olsen et al. (2022)

Discussion

Our synthesis of the available literature exposes significant knowledge gaps and taxonomic biases, providing only limited and indirect answers to questions regarding climate change effects on boreal plant-pollinator networks. Overall, the state of knowledge in this area is characterized by a scarcity of comprehensive studies, and often focuses on widely distributed plant species, neglecting many other ecologically significant but less prevalent species of both plants and insects. Moreover, there is a notable absence of studies specifically addressing plant-pollinator interactions in the context of climate change. The limited understanding of insect fauna and pollination systems in the boreal region highlights the need for further investigation, and below we identify some potential paths for advancing boreal pollination research. These trajectories include new methodologies to record pollinator diversity and activity, as well as the integration of temperature measurements providing high spatial and temporal resolution. Such approaches will enhance our understanding and ability to predict the effects of climate change on plant-pollinator interaction dynamics.

Pollinator effectiveness under climate change

Climate change is expected to alter pollinator effectiveness and change plant reproductive success, which can be measured directly or indirectly. Out of the nine studies that addressed plant reproductive success, six conducted pollen supplementation experiments by hand-pollinating flowers and comparing their seed set to natural open pollination (Barrett & Helenurm, 1987; Blinova, 2002; Nishikawa, 2009; Kudo & Ida, 2013; Rivest & Vellend, 2018; Kudo & Cooper, 2019). Hand-pollination is a common method in pollination studies in which pollen is manually transferred from the anthers of a flower to the stigma of the same or another flower (Wurz et al., 2021). When hand-pollinated plants yield a higher seed set than the control, it is usually considered as evidence that pollinators did not carry pollen up to the plant's reproductive capacity, thus indicating pollen limitation. These articles measured pollen limitation in relation to climate change directly through long-time series observations or indirectly through proxies such as a species' distribution limits, altitudinal gradients or comparing years with different snowmelt date.

Pollen limitation is reported in all the hand-pollinating experiments ($n = 6$). Pollen supplementation produced a higher percentage of pollinated flowers, and bigger seed capsules (Blinova, 2002), as well as a consistently higher seed set (Kudo & Ida, 2013). However, pollen limitation varied between years (Nishikawa, 2009; Kudo & Cooper, 2019). In fact, long time series data may be needed in order to effectively characterize populations as pollination-limited (Thomson, 2019). Moreover, pollen limitation is widespread across flowering plants in different climatic regions (Rosenheim et al., 2014). Rivest and Vellend (2018) suggest that the extent of pollen limitation may depend on the plant's reproductive strategy and pollinator type (see section "The importance of taxonomic and functional pollinator identity").

One of the most frequent explanations for the lack of pollinator effectiveness is that temperature limits pollinator activity or their population sizes (Motten et al., 1981; Mahoro, 2002; Thomson, 2010; Kudo & Ida, 2013; Mola et al., 2021). This is consistent with the results we found from the boreal studies, in which all six articles reporting pollen limitation alluded to the lack of pollinators or their low activity as the cause for pollen limitation. For instance, Barrett and Helenurm (1987), report that bumblebees were the only major pollinators of some understory plants in New Brunswick (Canada), and the only flower visitors during cold days. Despite extensive sampling efforts, they did not observe any pollinators for *Medeola virginiana* L. (Liliaceae) nor *Cypripedium acaule* Aiton (Orchidaceae) in 3 years. Of the latter species, pollinia were removed only in 26 out of 236 flowers, indicating the general lack of pollinators in the area. Similarly, despite not reporting pollen limitation, Boulanger-Lapointe et al. (2017) found a higher plant reproductive success in a boreal forest than in an alpine site, presumably because of higher pollinator activity, which may be low in Alpine areas due to even lower temperatures

If pollen limitation in boreal forests is driven by low pollinator activity, rising temperatures derived from climate change could potentially boost insect activity and thereby mitigate such limitation. In fact, in the explored literature, pollen limitation varied inter-annually depending on climatic conditions. However, warmer temperatures do not always result in higher insect activity, but rather in phenological mismatch, at least in early spring. Kudo and Cooper (2019) and Kudo and Ida (2013) found that in years of early snowmelt, *Corydalis ambigua* flowers before its pollinators emerge from hibernation, which limits seed production. Similarly, Nishikawa (2009) reports that the seed set of *Gagea lutea* is affected by pollinator availability. In a year with early snowmelt, seed-set was limited by insufficient pollinators owing to low temperature in early spring. Finally, Rivest and Vellend (2018) show different responses in pollen limitation and reproductive success in two plants at their altitudinal distribution limit, based on their different pollinator groups and responses to abiotic stress. These findings reinforce the complexity of warming impacts, and merit further investigation.

Plant reproductive success was used as the response variable when studying the effect of climate change in all but two of our selected articles, which exclusively focused on flowering, fruiting and pollinator phenology (Helenurm & Barrett, 1987; Sevenello et al., 2020). In these two articles, plant seed set was used as a proxy for pollinator effectiveness. This is an effective approach to assessing overall plant fitness, but it is blind to recording many potential underlying changes to biodiversity that may be relevant to projecting climate change related impacts. With changes in phenology and distribution shifts caused by climate change, or even re-shuffling of species within their environmental niches (Antão et al., 2022), there could be changes in the structure of plant and pollinator communities, leading to potentially new interactions (de Manincor et al., 2023) and the permanent loss of others (Memmott et al., 2007). For instance, if mismatches occur, or if a particular pollinator becomes locally extinct, its role may be taken over by other pollinators through interaction rewiring, especially as warming can promote more generalized foraging (de Manincor et al., 2023) and colonization by pollinator species from warmer climates (Ghisbain et al., 2021). In such cases, differences may not be observed in plant reproductive success despite changes in species interaction networks. Focusing only on seed set and other plant reproduction proxies neglects how the pollinator community composition may be changing and whether conservation measures towards any pollinator species should be taken to avoid its decline and subsequent possible extinction. For example, given the microclimatic buffering in forests (Díaz-Calafat et al., 2023), forest management could target the thermal requirements of specific species.

Imbalance and bias in studied species

Plant species

The 11 studies found by our searches included 23 unique plant species. Among these, there was a dominance of species from the families Liliaceae, Melanthiaceae and Ranunculaceae, all with large conspicuous flowers. A majority of these plant species have large geographical distributions, *e.g.*, covering half of North America, or even being circumpolar. In contrast, only a few species with a narrower geographic range were studied. These results are consistent with the findings of a recent meta-analysis that claims that plant ecology studies are clearly biased towards conspicuous species with broad distributions, while rare or ecologically important species are often neglected (Adamo et al., 2021).

As the need for the understanding of processes on boreal plant-pollinator systems under climate change is urgent and spans many species and regions, we suggest that future research prioritizes those species that are key to ecosystem function, processes and services. Boreal understory vegetation is commonly dominated by few ericaceous species that due to their importance for ecosystem processes are considered foundation species (Hedwall et al., 2019). Among the selected studies, only two focus on one of these foundation species: *Vaccinium myrtillus*. Although the general impacts of climate change on boreal foundation plant species have been partially addressed in the literature (*e.g.*, Kreyling et al., 2012; Puchalka et al., 2022), this research does not usually assess changes in plant reproduction over time, but rather focuses on changes in their distribution and cover (see however, Langvall & Ottosson Löfvenius, 2021). Most of these foundational species are clonal and therefore changes to their cover are not necessarily related to changes in patterns of sexual reproduction or their pollinators. Future studies on the impact of climate change thus should include analyses of both sexual and vegetative reproduction of foundation plants, and hence provide a more holistic understanding of their responses to environmental change.

Furthermore, while many studies focused on plant species' responses at their northern distribution limits, investigating their southern boundaries would provide unique insights into how organisms cope with rising temperatures and changing habitats. Populations at the southern limits of a species' distribution often face greater environmental stressors than in the north, at least in the northern hemisphere, which makes them particularly vulnerable to climate-induced changes (Rao et al., 2023). Therefore, incorporating research at species' southern distribution limits is essential for securing comprehensive climate change impact assessments and conservation strategies.

Pollinator species

Pollinators were only studied directly in less than half of the articles reviewed, and their species identities were rarely documented. The lack of information on pollinator species is probably related to the fact that the insect fauna of the boreal forest is much less well known than the flora (Kevan et al., 1993). Kevan et al. (1993) reviewed the pollination systems of the boreal forests and revealed knowledge gaps on pollination strategies and interactions that are unfortunately still largely unexplored. Similarly, data on the impacts of climate change on the insects of the forested ecosystems of northeastern North America is limited (Rodenhouse et al., 2009). The paucity of relevant knowledge is similar in boreal Europe, where although the flower visitation habits of many insect groups are known, their contribution to the pollination of understory forest vegetation has not been adequately investigated (Kevan et al., 1993). Bees, being considered one of the most efficient and important pollinators worldwide, including bumblebees, which are especially adapted to the low temperatures in northern latitudes, remain understudied in northern Europe (Leclercq et al., 2023). This suggests that other less charismatic pollinators such as flies, which historically have received less attention than bees, are likely even more understudied. Flies are more abundant flower visitors than bees and other pollinators at higher latitudes (Elberling & Olesen, 1999) and elevations (McCabe et al., 2019), and seem to be ample flower visitors under cold conditions in which other pollinators are inactive or show low activity (Kearns, 2001). In fact, Kudo et al. (2004) observed that seed production did not decrease in fly-pollinated plants in an early flowering year, when it drastically decreased for bee-pollinated plants. Despite flies being reported as generally less efficient than other pollinators when assessing pollen deposition after single flower visits, their higher flower visitation rates may result in comparatively higher pollen deposition, and therefore, be more effective at resultant pollination than what is provided by non-fly pollinators (Kearns, 2001). However, despite being of high potential relevance to successful pollination in northern latitudes (Elberling & Olesen, 1999; Rivest & Vellend, 2018), there is very little knowledge about the role of flies in the pollination of boreal plants.

Pollinators and plant-pollinator interactions can be difficult and time-consuming to record in some cold ecosystems, primarily due to the insects' low activity at low temperatures (Beattie, 1971). However, recent technological advancements have sparked new approaches that efficiently record insect data and their interactions with flora, overcoming these challenges with relatively little effort. For instance, high resolution cameras equipped with motion sensors can be used to capture images or videos of insects visiting flowers (Pegoraro et al., 2020). Through image analysis and machine learning algorithms, researchers can accurately identify and quantify different insect species (Valan et al., 2019; Spiesman et al., 2021), offering a non-invasive and efficient way to monitor pollinator populations. Additionally, flower environmental DNA (eDNA) can be used to detect the presence of pollinators (Thomsen & Sigsgaard, 2019). By sequencing the eDNA traces that insects leave on flowers when visiting them, researchers can identify the species that have visited those flowers, providing valuable insights into plant-pollinator interactions and insect diversity without the need for direct observation. Although some methodological developments remain, we encourage the use of these new approaches in order to better monitor boreal insect pollinator communities and their changes over time.

The importance of taxonomic and functional pollinator identity

Different pollinator species modulate their phenology or activity in diverse ways depending on their specific requirements, which may lead to different pollinators being more efficient in particular scenarios. For instance, Rivest and Vellend (2018) found that elevation differently affects the seed set of two understory plant species from temperate/boreal forests, *Erythonium americanum* Ker Gawl. (Liliaceae) and *Trillium erectum* L. (Melanthiaceae). On the one hand, *E. americanum* shows a consistent decrease in seed set with elevation, but no pollen limitation. Contrastingly, *T. erectum* shows pollen limitation at its elevation range limit, although seed set decreases only slightly with elevation. These two plant species are visited by different groups of pollinators. Namely, *E. americanum* is visited by Hymenoptera and Coleoptera, and *T. erectum* is visited by Diptera. It is possible that bumblebees, one of the groups of pollinators of *E. americanum*, were more reliable at higher altitudes than the pollinators of *T. erectum* (flies), although pollen limitation has also been observed in other *Erythonium* species at its upper elevation range limit in years when visitation by bumblebees was low (Theobald et al., 2016). Similarly, Kudo et al. (2004) find that the effects of an exceptionally warm spring on plant reproductive success depends on the type of pollinators, with apparently negative effects for plants pollinated by bees, but with no effects for fly-pollinated species. This suggests that flies, for which the responses to climate change are still largely unknown, may be more resistant to warming in boreal systems than other pollinators such as bees. In fact, muscoid flies have become more common in subarctic pollinator networks. This change comes amid a significant turnover in pollinator species and rewiring of plant–pollinator interactions, in which only 7% of the interactions remained the same as those of a century ago (Zoller et al., 2023).

By not recording pollinators and their interactions with specific plant species, we risk overlooking crucial insights into species-specific responses to climate change. Understanding these dynamics is pivotal for assessing the resilience of different species to environmental shifts and predict its effects on both plants and pollinators. Without such data, efforts to mitigate the impacts of climate change on pollinator communities and the ecosystems they support may be compromised, hindering effective conservation strategies and exacerbating biodiversity loss.

Response and matching traits mediate spatial and temporal mismatches in the occurrence and abundance of species, as well as the formation of novel ecological interactions and secondary extinctions, respectively (Schleuning et al., 2020). While response traits refer to characteristics that influence how an individual responds to its abiotic and biotic environment (Pacifici et al., 2017), matching traits influence species compatibility and their likelihood of interaction, such as those related to morphology, physiology, or chemistry (Balazs et al., 2020; Garibaldi et al., 2015). The only response trait considered in the articles evaluated in this review was phenology. However, no other traits related to warming, such as thermal tolerance, drought resistance, or physiological acclimation capacities or matching traits, were evaluated.

A plant's or animal's physiological capacity to survive and reproduce under specific temperature conditions, or physiological processes that govern a species' phenology, such as the timing of blooming or insect emergence from hibernation, depends largely on its response traits.

However, the ability of species to cope with climate change will depend not only on their individual response traits but also on how well their matching traits align with those of other species in their community (Schleuning et al., 2020). Species that are unable to synchronize their life cycles or physical traits with their ecological partners will face higher risks of population decline, range shifts, or extinctions, further contributing to biodiversity loss and ecosystem disruption in the face of climate change.

Hence, both response and mathcing traits are crucial to predict the likelihood of plant-pollinator interaction mismatches and the potential for cascading impacts, such as secondary extinctions and reduced plant reproductive success under climate change. Incorporating a broader range of response traits in future studies would provide a more comprehensive understanding of species resilience to climate change (Pacifici et al., 2017).

Forest disturbance regimes and plant-pollinator interactions

In addition to the direct effects of alterations in temperature and precipitation on plant-pollinator interactions that we reviewed, climate change is also likely to cause significant changes in the boreal forest disturbance regimes (Seidl et al., 2017) resulting in new light regimes (De Frenne, 2024). The frequency and severity of extreme weather events, disturbances such as fire, and insect outbreaks are expected to increase (de Groot et al., 2013; Price et al., 2013; Pureswaran et al., 2015), affecting forest growth, regeneration, and consequently, the populations and community dynamics of boreal plants and pollinators.

Droughts can reduce the availability of water for both plants and pollinators, leading to lower plant reproductive success and declines in pollinator populations (Rering et al., 2020). Droughts and other extreme weather conditions can cause stress in plants, leading to reduced flowering, lower nectar production, and poor-quality pollen (Descamps et al., 2021). This reduces food availability for pollinators (Phillips et al., 2018) and may lead to declines in pollinator health and reproduction. Drought-stressed plants may also alter their flowering times (Roth et al., 2023), potentially desynchronizing with pollinator activity periods (Crimmins et al., 2010).

An increase in fire frequency and intensity can result in the loss of mature trees, shrubs, and understory plants that provide essential food (nectar and pollen) and nesting habitats for pollinators. While fire can enhance habitat for some generalist pollinators by creating open spaces and abundant flowering plants (Taylor & Catling, 2011), high fire frequency may decrease pollinator numbers (Carbone et al., 2019). Following a fire, the regrowth of vegetation may favor early-successional plants, which often benefit certain pollinator species (Taki et al., 2013), but can also cause declines in other species that depend on the pre-fire flora. Moreover, the timing of post-fire flowering may shift as plant species regenerate at different rates (Ne'eman et al., 2000). This can cause temporal mismatches between the availability of floral resources and the activity periods of pollinators, leading to reduced pollination success and potential population declines in both plants and pollinators.

Insect outbreaks often result in large-scale tree mortality, particularly among coniferous species (Jaime et al., 2024). While these trees are not directly involved in pollination systems, their loss can lead to changes in understory vegetation (Runyon et al., 2020). The death of large numbers of trees can open up the forest canopy, leading to increased light availability. This shift may promote the growth of herbaceous plants and shrubs, temporarily increasing floral resources for pollinators (Rozendaal & Kobe, 2016). Lastly, insect outbreaks affecting understory vegetation can make plants allocate more resources to defence mechanisms rather than to floral resources (Haas & Lortie, 2020), which could have significant implications for pollinators.

The role of temperature for plants and pollinators

Given that temperature and its variation serves as a primary factor influencing pollinator activity (Williams, 1961) and spring phenology in temperate and boreal ecosystems (Kramer et al., 2000), it is reasonable to assume that temperature exerts control over pollinator community composition directly (Geppert et al., 2023) or indirectly (McCombs

Box 1
Future research directions

Given the findings of this review, we propose several avenues for future research aimed at understanding the intersection between climate change, boreal forest understory vegetation and pollinators:

Collect baseline data on plant-pollinator interactions

Establish baseline data on current plant-pollinator interactions to facilitate future comparisons. This can involve documenting visitation rates, pollinator diversity, and pollinator foraging behavior to assess the impact of climate change over time. Currently, we lack sufficient data to assess whether interaction rewiring is taking place in plant-pollinator interactions in boreal forests. Historical plant-pollinator interaction data could be obtained by identifying pollen grains in museum insect collections. This approach can offer valuable insights into past interactions, allowing comparison with current dynamics and ultimately enable the prediction of future trends under climate change.

Moreover, long-term monitoring programs to track changes in plant-pollinator interactions over time could be established. These studies can yield valuable insights into how gradual climate changes and extreme weather events impact these relationships. Additionally, monitoring both plant and pollinator populations will help identify shifts in community composition and potential cascading effects within ecosystems. To enhance the effectiveness of these studies, innovative methodologies such as citizen science, eDNA or camera traps in combination with machine learning can be used to gather data on pollinator activity and their interactions with boreal flora.

Functional traits and adaptations

Examine the functional traits of key plant and pollinator species that could mediate their responses to climate change. This includes investigating traits such as thermal tolerance, drought resistance, physiological acclimation capacities, and the ability to shift phenology in response to temperature changes.

Moreover, functional traits are a useful tool to study species-specific responses to warming. Understanding how individual plant and pollinator species respond to climate change will help identify which species are most vulnerable or resilient to climate change impacts, and where conservation efforts should be prioritized.

Multi-trophic interactions

Explore the interactions between plants, pollinators, and other trophic levels (*e.g.*, herbivores, predators) to understand how changes in one group can affect others. For example, if populations of herbivores increase in response to longer growing seasons, plants may allocate more resources to defense mechanisms rather than to floral structures, which could have significant implications for pollinators.

Microclimate effects

Study the role of forest microclimates in mitigating the impacts of climate warming on plant-pollinator interactions. This can include studies on how variation in light and novel light regimes, humidity, and temperature within the forest understory influence both plant and pollinator species distributions, pollinator activity, and their interactions.

Foundational plants

Prioritize research on foundational plant species that play critical roles in boreal ecosystems. Understanding their interactions with pollinators and responses to climate change is essential for maintaining ecosystem function.

Collaborative research efforts

Foster collaborations among researchers, conservationists, and land managers to enhance data collection and knowledge sharing. This can help build a comprehensive understanding of boreal forest ecosystems, their pollinators and their interactions.

et al., 2022), especially in areas where it constrains plant reproduction. Forests buffer macroclimatic temperatures (De Frenne et al., 2013), which results in the creation of a diverse array of microclimatic conditions within the forest ecosystem (Díaz-Calafat et al., 2023), offering potential climatic refugia to the species hosted there (Greiser et al., 2020). These microclimatic conditions can drive the responses of understory plants (Zellweger et al., 2020) and insects (Greiser et al., 2022) to warming, and therefore the buffering effect of forests may represent a natural regulating mechanism against the negative effects of climate warming. Moreover, the microclimate buffering capacity of boreal forests is expected to increase as a result of climate change by the end of this century (De Lombaerde et al., 2022), thus increasing also the importance of microclimate buffering in this biome. This effect is however highly uncertain considering the predicted increases in disturbances that may result in disruptions of the canopy cover (see above). Only two of our selected articles used (altitudinal) temperature gradients as a proxy for climate change and none of the articles considered microclimate in their analyses, despite its capacity to affect pollinator availability (Beattie, 1971). The accumulating evidence of the importance that tree layer density and tree species composition has on understory temperatures, and the observed impact of climate change on plants (Sanczuk et al., 2023), highlights the need to take the micro-climate into account in studies of plant-pollinator interactions (see Box 1). Hence, we also suggest that efforts be made to understand the potential for forest understory microclimates to mitigate the impact of climate change on plant-pollinator networks in boreal forests.

Conclusions

Our assessment of the published scientific literature focusing on how climate change affects pollinator plant interactions in boreal forests consistently revealed a pattern of pollen limitation in boreal understory plants, often attributed to a reduced pollinator activity in low temperature conditions. However, the lack of detailed information on pollinator species and their interactions presents challenges in assessing the resilience of these interactions to climate change. We propose a set of future research directions to address these gaps (see Box 1). Species-specific responses to climate change emphasize the complexity of the dynamics between plants and pollinators, and also merit further research. Specifically, we see a need for further research into foundational plant species with clear links to ecosystem functioning as well as key pollinators (such as flies), which are important in the boreal biome. The scarcity of data on boreal pollinators underscores the need not only for innovative methodologies to study these ecosystems effectively, but also for increased attention and research efforts, as this area remains understudied compared to other regions. Furthermore, the impacts of climate change on boreal plants, pollinators and their interactions should be considered from the perspective of forest microclimate, which may mitigate the impacts of climate warming on plant-pollinator interactions through the buffering of understory temperatures.

CRediT authorship contribution statement

Joan Díaz-Calafat: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Conceptualization. **Adam Felton:** Writing – review & editing, Methodology, Conceptualization. **Erik Öckinger:** Writing – review & editing, Methodology, Conceptualization. **Pieter De Frenne:** Writing – review & editing, Methodology, Conceptualization. **Sara A.O. Cousins:** Writing – review & editing, Methodology, Conceptualization. **Per-Ola Hedwall:** Writing – review & editing, Supervision, Methodology, Conceptualization.

Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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