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EDITORIAL

Effects of climate change on plant-pollinator interactions and its multitrophic consequences

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Abstract

There is wide consensus that climate change will seriously impact flowering plants and their pollinators. Shifts in flowering phenology and insect emergence as well as changes in the functional traits involved can cause alterations in plant-pollinator interactions, pollination success and plant reproductive output. Effects of rising temperatures, advanced snowmelt and altered precipitation patterns are expected to be particularly severe in alpine habitats due to the constrained season and upper range margins. Yet, our understanding of the magnitude and consequences of such changes in life history events and functional diversity in high elevation environments is incomplete.

This special issue collects novel insights into the effects of climate change on plant-pollinator interactions in individual plant species and on network structure of entire plant and pollinator communities in alpine ecosystems. Using simulated changes of earlier snowmelt, natural gradients of variation in temperature, precipitation and snowmelt, or a long-term monitoring approach, these studies illustrate how plant species, plant communities, and pollinators respond to variation in environmental conditions associated with scenarios of ongoing climate change.

The collection of papers presented here clearly demonstrates how spatial or temporal variation in the environmental climatic context affects flower abundances and plant community composition, and the consequences of these changes for pollinator visitation, pollination network structure, pollen transfer dynamics, or seed production. As changes in the availability of flowers, fruits, and seeds are likely to impact on other trophic levels, the time is ripe and pressing for a holistic multitrophic view of the effects of climate change on biotic interactions in alpine ecological communities.

Keywords Alpine environment · Biotic interaction · Environmental gradient · Pollen transfer · Pollination networks · Precipitation · Snowmelt · Temperature

In alpine habitats, contemporary species richness and diversity within and among plant communities is shaped by the fine-scaled mosaic of microclimatic niches (Körner 2003; Ohler et al. 2020; Scherrer and Körner 2009), yet they are subject to significant alterations in response to climate change. Climate change in the alpine zone will most detectably manifest as increased temperatures, causing reduced snow cover (Rumpf et al. 2022), and in altered precipitation patterns (Körner 2003), both increasing the length of the growing season for plants or shifting the timing of phenological events (Rammig et al. 2010; Inouye 2008, 2020). Tracking of microclimatic niches in alpine plants is mostly expressed as spatiotemporal variation in abundances as snowmelt timing fluctuates between topological microhabitats within the landscape (Scherrer and Körner 2011). At the highest elevations, increased temperatures may give rise to

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new habitats upon the melting of snowfields and glaciers, allowing for the new colonisation and upwards movement of alpine communities (Losapio et al. 2021; Walther et al. 2005). For lower elevation snow-free mountains, in contrast, there might be no such newly arising habitat available to migrate into, prohibiting spatial niche tracking (Easterling et al. 1997). Furthermore, plant species in the alpine zone appear vulnerable to competitive pressure from lowland species expanding their distributional ranges (Walther 2010). Therefore, the impact of climate change on plant communities is expected to intensify in alpine areas as compared to lowland areas.

Plant species exhibit diverse responses to climate change, resulting in a restructuring of communities as they shift into novel configurations (Alexander et al. 2018; Descombes et al. 2020; Molau 1997; Walther et al. 2002; Walther 2010). This reshuffling of species alters interactions both within and among trophic levels, which in turn can affect ecosystem functioning (Walther 2010; Blois et al. 2013). For example, asynchronous range shifts among species introduce novel community compositions though local extinction and colonization along latitudinal and altitudinal gradients (Pyke et al. 2016; Richman et al. 2020). Likewise, asynchronous shifts in phenological patterns among species have been demonstrated to impact plant community composition in alpine systems (CaraDonna et al. 2014; Hegland et al. 2009). Since plant communities, as primary producers, build the basis of trophic networks, any change in plant community composition can potentially impact higher trophic levels such as pollinators (Arrowsmith et al. 2023; Forrest 2015; Forrest and Thomson 2011; Memmott et al. 2007). Mismatches between plants and pollinators will lead to a decrease in pollinator visitation, pollen transfer and reproductive output of plant species that strongly depend on insect pollinators for reproduction (Kudo and Cooper 2019; Inouye 2020). Understanding how climate change impacts flowering plants, their pollinators and pollination is of paramount importance for conserving biodiversity and ecosystem functioning.

Existing research on the impacts of climate change on plant-pollinator interactions in alpine environments highlights the sensitivity of individual interactions at the species level, of bipartite networks at the community level, and it explores implications for evolutionary responses and ecological functioning at the ecosystem level (Fig. 1). These studies suggest that climate change can directly and

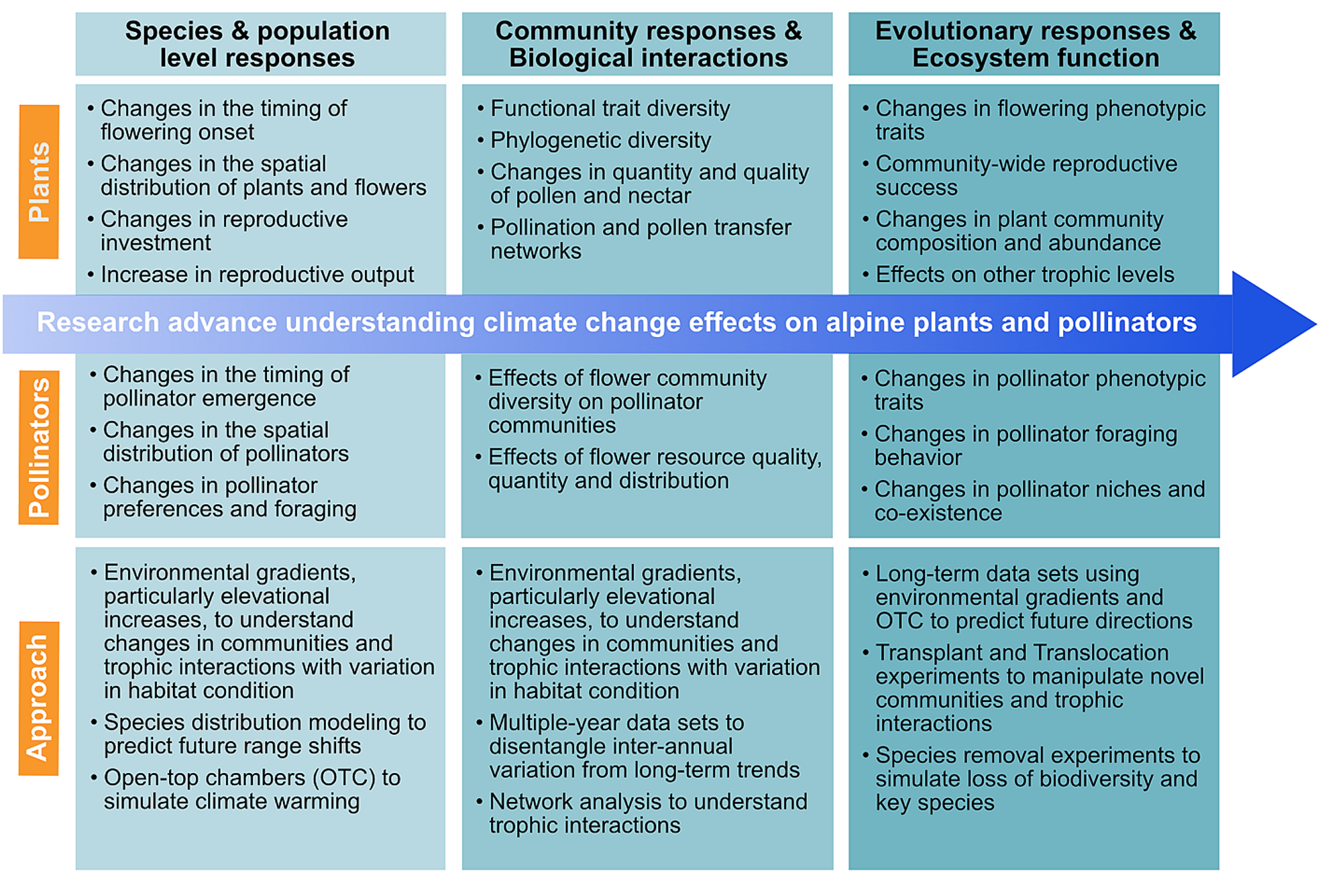

Fig. 1 Summary of levels and aspects of research that require further attention in studies on the effects of climate change on plants (top row), their pollinators (middle row) and the methodological approaches used (bottom row)

indirectly affect plants and pollinators, leading to modifications in the frequency and mode of interactions and potentially resulting in reduced pollination and plant reproductive success (reviewed in Inouye 2020). In the mid 1990s, the first open-top chamber experiments were established, significantly advancing our experimental methodology to directly test the effects of climate change on plant communities by simulating increased temperatures (Henry et al. 2022; Henry and Molau 1997). Early experiments in the context of pollination report changes in flowering phenology, insect visitation to flowers, and their resulting seed production (Alatalo and Totland 1997; Henry and Molau 1997; Totland and Eide 1999). Emerging long-term studies provide a further perspective of how pollinators respond to continuously changing plant community composition and subsequent changes in plant performance and reproductive investment (Alatalo et al. 2021; Klady et al. 2011; Pieper et al. 2011). About a decade later, snowmelt manipulation experiments allowed for experimental tests of the consequences of shifts in the growing season (Wipf and Rixen 2010) and are increasingly applied in a pollination ecological context (Kudo and Cooper 2019; Pardee et al. 2019). With advances in modelling approaches during the past decade, another line of research used species distribution models to investigate the possible consequences of temporal and spatial disruption of plants and pollinators, supporting the results of field experiments (Hoiss et al. 2015). Around the same time, the use of spatial transplants was suggested as a space-for-time substitution, involving targeted manipulations of single species colonisations/losses as well as shifts in entire communities (Morton and Rafferty 2017). While this approach has fostered some impactful insights into the consequences of climate-change induced species invasions on biotic interactions (Agrawal 2011; Rasmann et al. 2014; Descombes et al. 2020), it has seldom been applied in the context of pollination (but see Forrest and Thomson 2011; McCabe et al. 2022; Richman et al. 2020). To date, the most widely used approach remains the use of natural environmental gradients to study how communities and species interactions vary depending on contemporary habitat conditions, and to speculate about how they may respond to changes in those conditions over time (see references in this issue). In combination, the use of careful manipulation experiments and natural ecological gradients is a powerful approach to resolve species and community responses to ongoing climate change (Dunne et al. 2003).

This special issue highlights recent findings from diverse geographic regions (including the Rocky Mountains, Austrian and Swiss Alps, Norway, the Qinghai Tibetan Plateau, Southwest China, Taiwan, Japan and New Zealand) on the effects of climate-change on plant-pollinator interactions. The included studies range in focus from individual species to entire communities and from local to regional scales. Using experimental simulations, natural gradients and long-term monitoring data, these studies jointly advance our current understanding of the effects of climate change on flowering plant communities, their co-variation with flower visiting insect communities, and the consequences for pollination and reproductive success. Specifically, they expand on previous research documenting shifts in temporal and spatial patterns of flowering communities and insect visitation by providing a more mechanistic view of why and how these changes happen, as well as what consequences arise from them. Here, we briefly summarize the key findings of each contribution in this issue and synthesize their joint impact on the field.

Phenology is a key driver of interactions between plants and their pollinators, determining their temporal overlap, and plant pollination success and reproductive output. Rising temperatures, which advance snowmelt date and change precipitation patterns, can cause shifts in flowering phenology and insect emergence, altering plant-pollinator co-occurrences and temporal overlaps (Forrest and Thomson 2011; Inouye 2020). In this special issue, both Vassvik et al. (2024) and Rose-Pearson et al. (2024) investigated flowering phenology along snowmelt gradients in alpine Norway and the Rocky Mountains, respectively. Vassvik et al. (2024) intensively studied the small-scale spatial pattern of phenology among naturally variable snowmelt patches in the widespread herbaceous perennial *Ranunculus acris*, following up on some of the earliest and most influential studies in the field (Totland 1994; Totland and Eide 1999). In their setting, the quantity and quality of seed production depended on cumulative temperature and density of surrounding conspecific flowers and/or frequency of insect visitation, indicating the importance of interactive effects of changes in direct abiotic and indirect biotic factors for responses to snowmelt timing. Interestingly, pollen supplementation was particularly beneficial for reproduction under warmer temperatures, suggesting a shift in the limits to seed production from temperature to pollinators. The consequences of phenological shifts on pollinator interactions is expected to vary among species, but how pollination system and pollinator specificity influence the magnitude of effects is so far not well understood.

In a topologically heterogenous mountain landscape, Rose-Person et al. (2024) experimentally altered the timing of snowmelt and compared the community-wide patterns of phenology and insect visitation in advanced and control plots over the entire flowering season. Within control plots, topography, snowmelt, flowering phenology and flower abundance interactively predicted pollinator visitation rates, but this was interrupted in an unpredictable manner under earlier snowmelt conditions, even though overall insect visitation did not differ between treatments. This presumably is because late-flowering species disproportionally advanced their flowering, leading to a new composition and structure of the flowering community and resource availability for pollinators. Along the same lines, the study by Kudo et al. (2024) expanded the geographic scope of this topic, analysing an impressive data set including five geographic regions along a natural gradient of seasonality in temperature. They show that regional differences in temperature seasonality affect both community-wide flowering phenology and pollinator interactions. Furthermore, they suggest that flowering periods and their resilience to climatic fluctuations may be predicted from the dominant pollinator community, whereby fly-pollinated species without seasonality seem less affected than bee-pollinated plants with clear seasonality. Together, all three studies converge on the finding that responses of plant-pollinator interactions to climate change may be affected by both the abiotic environmental context and biotic factors such as co-flowering communities.

About two decades into major climate change research, long-term datasets are becoming increasingly available. These allow us to work with natural fluctuations in climatic conditions in order to identify the climatic factors responsible for variation in flowering and pollinator interactions and to predict future responses. In this special issue, Kudo et al. (2024) and Fang et al. (2024) used observations of inter-annual variation to estimate changes in plant and pollinator community patterns in response to temperature and precipitation. While Kudo et al. (2024)'s study focussed on variation in temperature and could show that it is a key driver of species phenology and abundance with subsequent effects on pollination networks, Fang et al. (2024) found that pollination networks were surprisingly stable across years. In their 10-year monitoring of plant-pollinator interactions in an alpine community in Southwestern China, higher temperatures led to decreased pollinator competition resulting in increased network specialisation, while less precipitation led to higher flower resource sharing among pollinators resulting in increased network nestedness. The results of these two studies imply that climate can directly impact pollination network features, but the magnitude of such effects may depend on the pollination system.

Variation in species' temporal and spatial responses to climatic changes induces altered community assemblage and consequently alters the composition and structure of functional flowering characters. Aguirre and Junker (2024) and Tu et al. (2024) both used spatial gradients to investigate how decreases in species phylogenetic and functional diversity in plant and pollinator communities subsequently changes their interaction network. First, Aguirre and Junker (2024) found in their analysis of 24 communities along an elevational gradient in the Austrian Alps that functional diversity of both plant and pollinators decreased with increasing elevation, altering network properties. However, the consequences differed somewhat: While decreases in flower and pollinator functional diversity increased network nestedness, the decrease in pollinator functional diversity additionally decreased functional complementarity and network modularity. Their findings suggest that losses in plant and pollinator functional diversity will cause changes in pollination networks and presumably affect pollination services, and that such effects are stronger for losses of pollinator than flower functional diversity. Tu et al. (2024) used a scenario of glacier retreat to understand how community composition and structure change along the successional recolonization of glacier forelands. Interestingly, although plant and pollinator diversity, and subsequently network diversity, increased from early successional stages, they were sharply reduced again in late successional stages, where few species are dominant within communities. Together, these two studies illustrate that altered flowering plant communities induce significant bottom-up changes in pollinator communities and rewire their interaction networks. Yet, how changes in pollination network structure affects pollination services and reproductive success is open for future research.

One important step forward towards understanding how altered pollination networks affect pollen transfer among species within the flowering community is made by Bi et al. (2024), who demonstrated that the environmental context of grazing pressure alters plant community composition, which in turn affects the structure of pollinator visitation and pollen transfer networks. Their study convincingly illustrates that flowering plants within communities are interconnected via complex pollen transfer networks, and further, that changes in the temporal or spatial occurrence of a single flowering species may not only affect its own pollinator interactions and pollination success, but also the success of other co-flowering species. On a positive note, these indirect plant-plant interactions were predominantly facilitative, meaning that plants promote each other's pollination and reproductive success even in species-rich communities as expected for stressful environments (Bertness and Callaway 1994). Therefore, lowland species establishment following climate warming may not necessarily threaten alpine species by competing for pollinators but could instead facilitate them when flower resources for pollinators are not limited.

The studies collected in this special issue jointly advance our current understanding of how plant and pollinator communities respond to changing environmental conditions associated with climate change scenarios (Fig. 1). Showing that reproductive success among established populations in individual species, and pollinator interactions within

Table 1 Current and future pressing questions to address to further understand climate-change-induced consequences for alpine plant-pollinator interactions, pollination and community changes across trophic levels

Level of Interaction	Questions
a. *Populations and species*	
	What factors determine variation in plant-pollinator interactions in response to climate change among populations and species?
	What factors determine differences among species in resilience and sensitivity to climate-change-induced interruption of historical plant-pollinator interactions?
	How do temporal, spatial or functional mismatches between plants and their pollinators affect the quantity and quality of pollination service and reproductive success?
	Which plant features allow for pollinator shifts that could buffer species against increased pollen limitation under declining historical pollinator interactions?
b. *Community-wide*	
	How do individual responses of species to changes in pollinator interactions translate to community-wide effects?
	What are the key climatic drivers causing changes in plant and pollinator communities and their interaction networks?
	How do pollen transport networks change upon altered quantity and quality of plant-pollinator visitation networks?
	What are the consequences of altered plant-pollinator networks for community-wide plant reproductive success?
	How do such climate-induced community-wide changes in plant-pollinator interactions compare across regions?
c. *Across trophic levels*	
	How do changes in the timing and mode of plant-pollinator interactions affect other flower interactions including florivores and microbes, and vice versa?
	How do alterations in the timing and magnitude of fruit and seed production as a consequence of changes in plant pollination affects frugivores and pre-/post-dispersal seed predators?
	Do demographic changes in plant species abundance or community composition as a consequence of changing seed production influence plant-herbivore interactions?

entire communities, can be surprisingly stable over changing abiotic conditions is a promising indicator for resilience in alpine pollination systems (Fang et al. 2024; Vassvik et al. 2024). However, effects of climate change on flowering characteristics such as flowering phenology may strongly depend on the life history and pollination mode of species and future research is needed to further predict which species are more sensitive and threatened than others (Kudo et al. 2024; Rose-Person et al. 2024). Alterations in species diversity and abundance within communities can impact community-wide plant-pollinator interactions and plant-plant interactions via changes in flowering onset and functional characteristics (Aguirre and Junker 2024; Bi et al. 2024; Tu et al. 2024; Kudo et al. 2024; Rose-Person et al. 2024). Yet, the consequences of individual species' responses in a community-wide and multitrophic context are not yet well researched. Present biodiversity research indicates that multitrophic consequences of community shifts in species richness or functional diversity, such as those found by Tu et al. (2024), Aguirre and Junker (2024) and Kudo et al. (2024), can be expected to initiate a sequence of bottom-up effects across trophic levels (Leal and Koski 2024; Walther 2010; Zhang et al. 2017). Thus, how these changes impact other trophic-levels associated with plant-pollinator interactions due to fruit and seed consumption or changing plant and pollinator population dynamics are urgent open questions (Table 1) to tackle for a full understanding of how biotic multitrophic interactions respond to future climate change in alpine ecosystems.

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Declarations

Competing interests The authors declare no competing interests.

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