A warming world and a fading buzz: The impact of climate change on pollinators

ABSTRACT

Insect pollinators are essential for the reproduction of over 80% of flowering plant species and contributeshugely to global crop production. Climate change resulting in rising temperature, increased drought, and more frequent extreme weather events can affect insect pollinators both directly and indirectly.The conservation of pollinators is crucial for maintaining the resilience of the ecosystem and food security at local and global scales. In this review we have compiled articles to have a better understanding of how climate change impacts pollinators by incorporating an up-to-date information on the available research. From the compiled information, we get to know that climate change can affect pollinators both directly and indirectly. The direct effects include changes in physiology and behaviour whereas the indirect effects result from altered interactions with food resources. By having a detailed idea about how severe the issues are and how interwoven they have become; the scientific community and beyond can adapting toand plan for improving resilience against the impacts of climate change.

Keywords: *ClimateChange, Insect Pollinators, Plant-PollinatorInteractions, Biodiversity conservation*

1. INTRODUCTION

The impact of climate change on insect pollinators is a significant concern in the context of global biodiversity conservation. Insect pollinators are responsible for the reproduction of over 80 per cent of flowering plant species (Ollerton *et al.*, 2011) and they contribute more than $300 billion annually to global crop production (IPBES, 2016). Climate change results in rising temperatures, increased drought, and more frequent extreme weather events (IPCC, 2007). This can impact insect pollinators both directly and indirectly.

The direct effects include changes in physiology and behaviour, such as increased developmental rates, metabolism, and activity levels up to certain temperature thresholds, beyond which injury or mortality may occur. Elevated temperatures can cause higher developmental rates and weight loss, resulting in depleted energy reserves and increased overwintering mortality. Climate change can also alter insect morphology and shift pollinator phenology. Additionally, instances of changes in pollinator abundance and geographic shifts in populations have also been observed.

Indirect effects are a result of altered interactions with food resources. Climate change affects plant physiology, morphology, phenology, abundance, and distribution, impacting pollinator food resources. Heat stress can hinder plant gametophyte development which reduces pollen availability. Increased temperatures and CO_2 levels can reduce leaf nitrogen content, thereby affecting larval host plants' quality. Changes in plant morphology, such as reduced floral size and altered volatile organic compounds, impact pollinator attraction and foraging behaviour. Shifts in plant phenology can lead to mismatches between plant and pollinator life cycles, reducing pollinator function and food supply.

2. DIRECT EFFECTS OF CLIMATE CHANGE ON INSECT POLLINATORS

2.1.Changes in Pollinator Physiology and Behaviour

Climate change results in variations in abiotic conditions such as warmer temperatures, drought, extreme weather events, and increasing variability in climate components. While insect pollinator physiology has been widely investigated under increasing temperatures, the impact of other climate change features on their physiology remains poorly understood. Experimental studies indicate that elevated temperatures generally contribute to higher developmental rates, metabolism, and activity levels in insect pollinators up to a certain threshold, beyond which injury or mortality may occur (Higgins *et al.*, 2014; Oyen *et al.*, 2016). Eating and foraging rates of insect pollinators increase with temperature (Willmer and Stone, 2004), but in the case of large-bodied pollinators like bumblebees, overheating may occurwhile flying at high temperatures (Dudley, 2000). Due to elevated metabolic rates under warmer overwintering temperatures, pollinators will often show higher developmental rates (Davidowitz *et al.*, 2004; O'Neill *et al.*, 2011; Radmacher and Strohm, 2010; Stephen, 1965), increased weight loss (Fründ*et al.*, 2013; Radmacher and Strohm, 2010; Slominski and Burkle, 2019; Stuhldreher *et al.*, 2014);which might result in depletion of energy reserves (CaraDonna *et al.*, 2018; Williams *et al.*, 2012). These alterations can also cause increased overwintering mortality (Bosch and Kemp, 2003, 2004; CaraDonna *et al.*, 2018; Sgolastra*et al.*, 2010; Slominski and Burkle, 2019; Stuhldreher *et al.*, 2014) and reduced size of the larval and adult (Davidowitz *et al.*, 2004; Radmacher and Strohm, 2010). On the other hand, some species, including solitary bees (*Megachile* spp.) and butterflies (*Papilio* spp.), have shown lower reductionor no loss of energy reserves (O'Neill *et al.*, 2011; Williams *et al.*, 2012) in response to warmer rearing or overwintering temperatures. Therefore, physiological and behavioural responses differ among species, with some pollinators demonstrating enhanced or lowered physiological rates under warmer temperatures.

2.2.Alterations in Insect Morphology and Other Traits

Rising temperatures due to climate change can affect the morphology and traits of insect pollinators. An observational study on the small carpenter bee, *Ceratinacalcarata*, revealed a decline in adult body size over 118 years of increasing temperatures (Kelemen and Rehan, 2021). High temperatures during experimental rearing of bumblebees have been shown to reduce their wing size and alter wing shape (Gerard *et al.*, 2018). Changes in body size and colour shifts have been recorded in a tropical bee species in response to precipitation gradients, with larger body sizes observed at drier sites (Suni and Dela Cruz, 2021).Altered climatic conditions may favour species with traits beneficial for resource acquisition. For example, in the Rocky Mountains, generalist short-tongued bumblebee species are replacing specialist long-tongued species, probably due to warming-induced reductions in flower availability (Miller-Struttmann *et al.*, 2015).

2.3.Shifts in Insect Pollinator Phenology

Phenology refers to the seasonal timing of life-cycle events. Changes in pollinator phenology are correlated with ambient temperature. Previous studies have reported earlier spring emergence in honey bees (Gordo and Sanz, 2006; Sparks *et al.*, 2010), native wild bees (Bartomeus*et al.*, 2011; Ovaskainen *et al.*, 2013) and butterflies (Forister and Shapiro, 2003; Gordo and Sanz, 2005, 2006)due to rising temperatures. In subtropical and tropical systems, where seasons are less pronounced, solitary bees may exhibit delayed spring emergence in response to warming, which may be due to inadequate winter chilling (CaraDonna *et al.*, 2018; Sgolastra*et al.*, 2010).

Some butterflies experience extended flight periods in warmer temperatures, which is linked to multi-voltinism (Altermatt, 2010; Roy and Sparks, 2000). Analyses of biodiversity databases and museum collections have documented reductions in the flight periods of insect pollinators over several decades, leading to mismatches with their host plants and decreased pollinator function (Burkle *et al.*, 2013; Duchenne *et al.*, 2020). However, it is difficult to attribute the causation of these patterns specifically to warmer temperatures.

It is apparent that phenological responses are primarily driven by temperature in temperate regions, while inadequate winter chilling or precipitation may play a more significant role at lower latitudes, likely influenced by regional drivers of seasonality (Cohen *et al.*, 2018).

2.4 Fluctuations in Insect Pollinator Abundance

While insect abundance losses have attracted attention in recent years, the precise effects of climate change on pollinator abundance are not as well understood compared to other factors such as land-use change and diseases. This information gap is partly due to the difficulties in estimating abundance changes over extended periods. However, a recent review of long-term data for sixty-six bumblebee species found that the frequency of abnormally hot days increases local extinction rates, reduces colonization and site occupancy, and lowers species richness within a region, regardless of land-use change (Soroye*et al.*, 2020).Changes in abundance can also represent species losses and increases. For instance, Hofmann *et al.* (2018) noticed an increase in warm-loving bee species and a decrease in cool-adapted bee species at the Munich Botanical Garden (Germany), a pesticide-free protected environment, between 1997 and 2017.

Bumble bees are experiencing shifts in their emergence times which can lead to mismatches between the timing of pollinator emergence and the availability of floral resources. There are distinct population trends between generalist and specialist species. Generalists may benefit from changing conditions, while specialists could become increasingly vulnerable as their specific floral resources decline.

2.5.Geographic Shifts in Insect Pollinator Populations

Shifts in species distributions have been observed owing to elevated temperatures from climate change. There is substantial evidence showing species moving to higher elevations and latitudes, especially for butterflies (Forister *et al.*, 2010; Hill *et al.*, 2002; Konvicka*et al.*, 2003; Mair *et al.*, 2012; Parmesan, 1996; Parmesan *et al.*, 1999; Pöyry *et al.*, 2009; White and Kerr, 2006) and bumblebees (Pyke *et al.*, 2016). However, some insect pollinators fail to keep pace with climate warming. For example, northern range shifts of eighty-one butterfly species in Canada did not match the rate of climate change (Bedford *et al.*, 2012), and both North American and European bumblebees showed range contractions by retreating from southern areas rather than shifting northward (Kerr *et al.*, 2015).Insect pollinators can benefit from climate change by expanding their geographic range. For example, some heat-adapted carpenter bees (*Xylocopa*) are observed to be expanding their distributions, and this expansion can be correlated with higher temperature in both winter and summer. This expansion can be possibly facilitated by decreased mortality in a critical phase in the life cycle of an insectSpecies inherently adapted to warmer climates, such as tropical or Mediterranean species, are more likely to thrive and expand their range as global temperatures rise.

This was noticed in the Indian native butterfly *Acraea terpsicore* has rapidly colonised new territories in Southeast Asia (Ghisbain*et al.*,2021).

3.DIRECT EFFECTS OFCLIMATE CHANGE ON PLANTS POLLINATED BY INSECTS

Climate change can significantly impact insect pollinators through altered interactions with their food resources. The indirect effects of climate change on pollinators due to the impact on their food resources may have a bigger influence on pollinators than the direct effects of climate change itself, as observed in some bumblebees (Ogilvie *et al.*, 2017). Atmospheric pollutants, including ozone (O_3), nitrogen oxides (NO_x), particulate matter (PM), and micro- and nanoplastics (MPs/NPs), significantly impact insect pollinators by altering the biosynthesis, emission, and perception of volatile organic compounds (VOCs) that mediate plant-pollinator interactions. Pollutants degrade floral scents, reducing the ability of pollinators to locate flowers. For instance, O_3 and NO_x can oxidize VOCs, shortening their atmospheric lifetime and altering their chemical composition, which diminishes the attractiveness of floral odors to pollinators like bees and butterflies. Additionally, pollutants can impair the olfactory systems of pollinators, affecting their ability to detect and respond to floral cues. Diesel exhaust and particulate matter can obstruct sensory receptors on insect antennae, further hindering their olfactory perception. These disruptions can lead to reduced pollinator visits, affecting plant reproduction and ecosystem services. The effects are particularly pronounced in specialized pollinators, which rely on specific floral scents, making them more vulnerable to environmental changes caused by air pollution(Pinto-Sevallos*et al.*, 2025). The impacts of climate change on plant biology aspects—specifically physiology, morphology, phenology, abundance, and distributions—that directly affect pollinator food resources are discussed hereunder.

3.1. Alterations in Plant Physiology and Development

Climate change can alter plant physiology and development, with substantial implications for pollinators. According to Snider and Ooserhuis (2011), heat stress can hinder the development of male and female gametophytes, limiting pollen availability for many insect pollinators. Heat stress can also diminish pollen tube germination, limit pollen tube growth, and modify anther and pistil tissue, thereby compromising reproductive success after insect pollination visits.

Physiological impacts on the quality of their larval host plants due to climate change can affect butterflies. Increased temperatures and CO_2 levels can reduce leaf nitrogen content for some species (Jeong *et al.*, 2018), while the resource allocation for defences can decrease as a result of drought stress (Gutbrodt*et al.*, 2011). The reduction in the quality of host plants led to a decreased body mass and increased duration of development for a tropical butterfly species (Kuczyk*et al.*, 2021).

3.2. Changes in Plant Morphology

The impact of climate change on floral features has already been documented. Hoover *et al.* (2012) demonstrated that due increase in temperature, elevated nitrogen levels, and increased CO_2levels, the nectar quality was affected and changes in nectar concentrationwere observed. Wilson Rankin *et al.* (2020) observeddecreased nectar and pollen protein quality due to reduced water availability. This decrease in pollen quality resulted in lower survival and productivity in bumblebees.

A meta-analysis by Kuppler and Kotowska (2021) reported that a continuous reduction in water availability led to decrease in floral size, among other features. Moreover, factors like increased CO_2, ozone, and temperature have been known to affect the volatile organic compounds (VOCs) emitted by plants (Yuan *et al.*, 2009). VOCs from various Mediterranean plants generally increased with temperature to a point and then decreased (Farré-Armengol*et al.* 2014).Both drought and CO_2influenced floral VOC emissions and composition, which in turn impacted pollinator attraction (Burkle and Runyon, 2016; Campbell *et al.*, 2019; Glenny *et al.*, 2018).

3.3.Shifts in Plant Phenology

A considerable change toward earlier dates for both first flowering and tree budburst was observed in a comprehensive analysis conducted by Parmesan and Yohe (2003).A study conducted with 385 plant species in Britain compared the average first day of flowering between the last decade and the previous four decades, also found that the average first day of flowering advanced by 4.5 days in the last decade (Fitter and Fitter, 2002).They also discovered that insect-pollinated species and annual species were more likely to flower earlier than wind-pollinated species and perennial species of the same genus.In another long-term study covering fifty-eight years for eleven plant species and twenty years for an additional thirteen species in the British Isles, Sparks *et al.* (2000) found that all flowering events were significantly related to temperature. They suggested that future temperature increases across the islands would continue to drive substantial changes in flowering events. Using observations initiated by Henry David Thoreau in 1852 and continuing until 2006, Miller-Rushing and Primack (2008) found that plants in the northeastern United States were flowering seven days earlier. They also noted that spring-flowering species were more responsive to temperatures in the preceding months than summer-blooming species.

The urban heat island effect, caused when cities experience significantly warmer temperatures compared to their surrounding rural areas due to factors such as increased energy use and the prevalence of impervious surfaces, can lead to extended growing seasons for plants, which may positively influence pollinators by extending the duration of plant-pollinator interactions through longer and warmer growing seasons. Furthermore, urban landscapes may provide floral resources during times when natural habitats have limited availability (Baldock, 2020).

3.4. Changes in Plant Food Resource Abundance/Quantity

Long-term observational studies suggest that increasing spring temperatures may contribute to reduced flower abundance (Inouye, 2008). Additionally, species that do not respond to temperature changes are more likely to have dropped in number over the past 150 years compared to species in which the flowering phenologies correlate with temperature. In an experiment by Hoover *et al.* (2012), climatic warming, elevated nitrogen levels, and increased CO_2 impacted the nectar concentration and overall nectar volume. Descamps *et al.* (2021) reported that when borage plants are grown at warmer temperatures (26°C), they had fewer and smaller flowers, with lower nectar volumecompared to flowers grown at cooler temperatures (21°C). Due to the reduction in the abundance of flowers and nectar,the visitation by bumblebeeswas decreased and it also affected their foraging behaviour.

Besides theeffects of climatic warming, CO_2 can have species-specific effects on the number of flowers and the amount of nectar produced. This was observed in the responses of butterfly-visited plants found in calcareous grasslands (e.g., Rusterholz and Erhardt, 1998). These studies indicate that modification in food resource quantity is often correlated with changes in floral quality.

4.INDIRECT EFFECTS OF CLIMATE CHANGE ON INSECT POLLINATORS

For plants and pollinators, climate-induced shifts in mutualistic interactions may be driven by the fact that pollinators often respond more to temperature in their development and activity. Climate change can directly affect the morphology, physiology, abundance, and distribution of plants which can indirectly result in disturbance in ecological relationships (Hegland *et al.*, 2009; Gérard *et al.*, 2020).

4.1. Trait Mismatches

From an observation of insect collections for over forty years, two alpine bumblebee species evolved shorter tongues which indicated a shift towards generalist foraging. During this period, the flowers on which they specially fed did not become shallower. This may be explained by the fact that since warmer summers can cause a reduction in available floral resources, the generalist foraging can have a selective advantage. This resulted in a mismatch between the long-tubed plants and the now shorter-tongued bumblebees (Miller-Struttmann *et al.*, 2015).

A study on the temperate-zone butterfly *Pieris napi*reported direct impacts of elevated temperatures on larvae, which resulted in faster development and lower adult body mass. They also showedthat due to the impact of temperature,the host-plant qualitywas reduced which indirectly resulted in larvae that fed on host plants (*Sinapisalba*, Brassicaceae) grown at higher temperatures exhibiting longer development times and reduced adult body mass (Bauerfeind and Fischer, 2013).

Additionally, in an experiment by Hoover *et al.* (2012), increased temperature, nitrogen, and CO_2cause changes in nectar quality. They also observed that bumblebees preferred nectar with higher sugar concentration. Therefore, plant traits modified by climate conditions could impact bee visitation, nectar consumption, and even survival.

4.2. Temporal Mismatches

Memmott *et al.*(2007) simulated global warming impacts on plant-pollinator networks and estimated that 17–80 % of pollinators, especially specialised feeders would experience reduced food supply.Burkle *et al.*(2013) compared historical data with contemporary sampling and observed that 50 % of bee species were lost from the system over 120 years. Moreover, the remaining bee species participated in fewer interactions with plant species, with over 20 per cent of these unique interactions lost due to temporal mismatches from shifts in the phenology of both bee and plant species, 17 per cent lost due to spatial mismatches or a combination of both (Burkle *et al.* 2013). A review of northeastern US bee museum collections over the past 140 years indicated that 56% of species exhibited changes in relative abundance, with declining species often having small phenological breadth (Bartomeus*et al.*, 2013). In a complementary study, Bartomeus*et al.* (2011) found that both bees and bee-pollinated plants had advanced their phenology by approximately ten days over the last 130 years, suggesting that some species may keep pace with shifts in their forage plants. Using forty years of data from a Russian boreal forest, Ovaskainen *et al.* (2013) demonstrated synchrony in the first appearance of bumblebees and early flowering plants. In contrast, Pyke *et al.* (2016) found earlier flowering phenology but unchanged bumblebee phenology over thirty-three years in high elevations, leading to decreased synchrony over time.

These differences across studies suggest that biogeographic regions may vary dramatically in temporal synchrony patterns, with elevation playing a key role in local plant and pollinator phenology. Experimental studies and those investigating focal plant and pollinator species have revealed greater variation in response to climate changes. Gillespie and Cooper (2021) found that delaying snowmelt in an Arctic community delayed plant flowering, reducing the overlap between floral availability and insect activity, though the composition of flowers and insect visitors was not significantly altered.

Research on field plant species showed that warmer temperatures advanced flowering for *Pulsatilla* plants earlier than their solitary bee (*Osmia* spp.) pollinators (Kehrberger and Holzschuh, 2019). Similarly, *Corydalis ambigua* plants often bloom before their bumblebee pollinators, with the mismatch increasing over time (Kudo and Ida, 2013). Cabbage white butterflies have been found foraging before their focal nectar plants bloom, largely due to increasing temperatures (Gordo and Sanz, 2005). However, experimental studies manipulating the onset of flowering for multiple plant species revealed few mismatches between plants and wild pollinators at flowering onset (Rafferty and Ives, 2011). These studies suggest that plasticity in wild pollinator response may reduce the potential for climate-induced temporal mismatches (Burkle *et al.*, 2013).

4.3. Spatial Mismatches

While substantial literature exists on temporal mismatches between plants and pollinators, concern about spatial mismatches due to climate change is growing but remains limited. Surveys by Pyke *et al.* (2016) found that most bumblebee species moved to higher altitudes from 1974 to 2007, whereas few plant species moved to higher latitudes, indicating reduced spatial synchrony.

A study modelling global climate change scenarios for a monophagous butterfly and its host plant indicated that all future scenarios—ranging from modest to maximum climate change—resulted in spatial mismatches, depending on the host plant's ability to occupy its projected niche (Schweiger *et al.*, 2008). Another modelling study focusing on 150 high-mountain plant species predicted an average range reduction of 44–50 per cent by the end of the 21st century, with Alpine species experiencing the highest range losses (Dullinger *et al.*, 2012).

These efforts highlight the potential for spatial mismatches, but there is still a lack of field-based studies compared to temporal mismatches, indicating a need for more research (Gérard *et al.*, 2020; Hegland *et al.*, 2009).

5. CONCLUSION

The diverse array of insect pollinators plays a crucial role in maintaining ecological balance and supporting global agriculture. While honey bees are widely recognized for their pollination services, the importance of other pollinators, including bumblebees, stingless bees, solitary bees, carpenter bees, butterflies, moths, and beetles, cannot be overlooked. Each of these insect groups contributes uniquely to the pollination of various wild and cultivated plant species, ensuring the successful reproduction and diversification of flowering plants.

The decline in pollinator populations due to climate change underscores the urgent need for comprehensive conservation efforts. Beyond focusing on honey bees and bumblebees, it is crucial to promote the use and conservation of solitary and native bee species, as well as non-bee pollinators. A diverse and resilient pollinator community is vital for sustaining agricultural productivity and ecological balance.

Future research can explore the potential effects of climate change on pollinators through changes in nesting habitat and resources. While significant progress has been made in understanding the impacts of climate change on plant food resources for pollinators, studies investigating the effects on nesting habitat remain limited. The quality and quantity of nesting habitats, such as the availability of mud, bare ground, stems, and other plant materials, could be influenced by climate change and related environmental shifts like wildfires and invasive species.Life-history traits are also likely to play a critical role in predicting the direct effects of climate change on nesting success for insect pollinators. In temperate areas with distinct seasons and winter snowpack, ground-nesting bees might be more protected from overwintering temperature changes than cavity or stem-nesting bees, which may be less insulated from temperature extremes.

One aspect of the effect of climate change on insect pollinators that has received relatively less attention is climate variability. Longer-term climate fluctuations beyond averages could trigger changes in insect pollinator emergence and life-cycle events. While great gains have been made in understanding the effects of climate change on pollinators, their food resources, and plant-pollinator interactions, there is still much unknown about the functional consequences for pollination and insect pollinators.

Therefore, advancing our understanding of the impacts of climate change on pollinators' nesting habitats and addressing the gaps in knowledge regarding climate variability are essential steps toward preserving and promoting a diverse and resilient pollinator community. This will ultimately support global agriculture and maintain ecological balance.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Authors hereby declare that NO generative AI technologies such as Large Language Models (Chat GPT, COPILOT etc.) and text-to-image generators have been used during the writing or editing of this manuscript.

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