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Review Article

Global warming and plant–pollinator mismatches

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The mutualism between plants and their pollinators provides globally important ecosystem services, but it is likely to be disrupted by global warming that can cause mismatches between both halves of this interaction. In this review, we summarise the available evidence on (i) spatial or (ii) phenological shifts of one or both of the actors of this mutualism. While the occurrence of future spatial mismatches is predominantly theoretical and based on predictive models, there is growing empirical evidence of phenological mismatches occurring at the present day. Mismatches may also occur when pollinators and their host plants are still found together. These mismatches can arise due to (iii) morphological modifications and (iv) disruptions to host attraction and foraging behaviours, and it is expected that these mismatches will lead to novel community assemblages. Overall plant–pollinator interactions seem to be resilient biological networks, particularly because generalist species can buffer these changes due to their plastic behaviour. However, we currently lack information on where and why spatial mismatches do occur and how they impact the fitness of plants and pollinators, in order to fully assess if adaptive evolutionary changes can keep pace with global warming predictions.

Introduction

The effects of a warming climate on species fitness and persistence are becoming more apparent, with an increasing number of studies demonstrating its multiple impacts on biodiversity year on year [1–3]. This global change can directly affect the fitness of species across their current ranges but it can also alter, perhaps more subtly, their ecological interactions [4]. In terrestrial ecosystems, one crucial ecological interaction is the pollination of plants by animals, an interaction largely dominated by insects [5], representing 9.5% of global food production [6]. Global warming has the potential to disrupt this mutualism, leading to potential mismatches (i.e. a failure to achieve an efficient interaction) hence putting plant and pollinator species at risk of extinction [7]. The number of studies demonstrating this effect is growing, and many different methods have been described to assess it empirically ([8], reviewed in [9]).

First, mismatches in plant–pollinator interactions can occur through reduced co-occurrence of the interacting partners in a shared habitat; this reduction may be temporal or spatial. These kinds of mismatches have received growing attention [10,11], particularly those of temporal mismatches between plants and pollinating insects [12]. These mismatches can be driven by a change in the flowering period of the plant [13] and/or the phenology of the pollinator [14], either of which can be advanced or delayed. The co-occurrence of plants and pollinators, essential for the interaction to occur, can also be spatially disrupted. The geographic overlap between interacting partners may decrease or increase under global warming [15–16] depending on the plasticity, adaptability and life-history traits of the species in question [17].

In addition to temporal or spatial mismatches, global warming also has the potential to impact plant–pollinator interactions that are mediated by physiological and/or morphological traits. The mechanical fit of the interaction can be affected, as pollination success can be dependent on morphological traits such as tongue length or overall body size in order to have access to plant resources, as well as plant morphology [18]. For example, increasing average temperatures have been shown to

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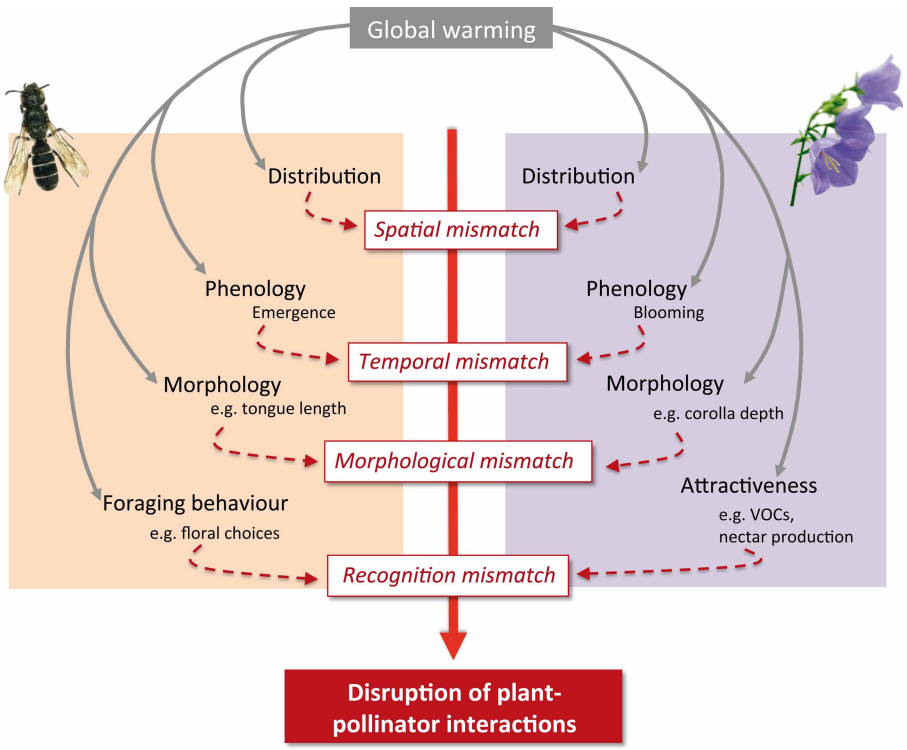

Figure 1. Potential impacts of global warming on plant-pollinator interactions.

Potential impacts of global warming on the distribution, phenology and morphology of plants (right panel) and pollinators (left panel) are shown. Besides global warming could also affect the foraging behaviour of pollinators as well as the attractiveness of plants. All these changes might result in as many mismatches (spatial, temporal, morphological and recognition mismatches), leading to the disruption of plant–pollinator interactions.

negatively affect body size in many organisms [19]. Moreover, temperature increases can impact the foraging behaviour of the pollinator [20], the attractiveness of the plant [21], as well as the quality and quantity of plant resources [22].

Here, we summarise the current knowledge about the effects of global warming in driving mismatches between plants and pollinators (Figure 1, Table 1). Though other climatic variables such as precipitation frequency, ozone (O_3) concentration or carbon dioxide (CO_2) concentration can also affect these interactions [23], we restrict our review to the impact of global warming as it is the most extensively studied. Within this framework, we first explore the way in which (i) spatial and (ii) temporal mismatches can affect plant–pollinator interactions before assessing the impact of (iii) morphological mismatches and (iv) modification of foraging behaviours and host attraction. Finally, we assess the likely ecological and evolutionary consequences, as well as factors that may buffer against the potential mismatches between plants and pollinators.

Table 1. Case studies about the impact of global warming on pollinators, plants and on their interactions. Reference numbers detailed in the bibliography section

Mismatch	Impact on pollinators	Impact on plants	Impact on the interaction
Spatial	[31–33]	[33,34]	/
Temporal	[15,25–27]	[26,49], reviewed in [13]	[25,27,28]
Morphological	[19,55]	[47,48,49,52]	[57]
Attraction and foraging behaviour	Reviewed in [77]	[65,67,69,70–72,78–83,86–88]	[48,88,94,95]

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Wrong time, wrong place: phenological and spatial mismatches

Global warming can have a strong impact on the activity pattern and life cycle development of organisms [9]. Many phenological shifts have already been reported at the species level for the insect emergence (e.g. [24,25]) or blooming time of flowering plants (e.g. [13]). Most of the studies showed a simultaneous advance in the phenology of pollinators and plants over the studied period in parallel with increasing average temperatures, but alternative patterns (i.e. simultaneous delays or opposite shifts) have also been described [25,26]. Mismatches between the emergence of bee species and the blooming of their main resources have been specifically recorded [26]. However, as far as we know, there is no study on the direct impact of these mismatches on pollinator individual fitness or population trends. In contrast, plants that flower earlier can miss part of the activity window of their main pollinators [27] and show a decrease in seed production [28]. Moreover, as these phenological shifts tend to be species specific for each species of the pollinator network, ecological communities are also disturbed. Duchenne et al. [25] recently demonstrated that non-random phenological shifts of European pollinators reduce the redundancy and the functional complementarity of their assemblages. Such a decrease in redundancy might alter the robustness of plant–pollinator networks to ongoing pollinators' extinctions [10]. Additionally, the decrease in functional complementarity can decrease the provision of pollination services [29] with fewer visits to a lower diversity of plants [30], probably resulting in a negative feedback for pollinators. These modifications in species community phenology can, therefore, potentially impact the performance of one of the most important ecosystem services for agriculture [26].

If a plant species and the insects that pollinate it occupy slightly different climatic niches, a warming climate has the potential to cause a spatial mismatch between the two if their distributions diverge. There are multiple examples of range shifts in pollinators that are probably driven by climate change (e.g. [31]), with the changes in bumblebees (*Bombus* spp.) particularly well documented. Bumblebees are cold-adapted species, and have shifted to more northern latitudes and to higher altitudes over the last 100 years [32,33]. Likewise, many plant species are also predicted to undergo similar changes [34]. However, there are few studies that have considered spatial changes in plant and pollinator communities at the same time or have observed this phenomenon in the field.

The situation is complicated further because pollination systems tend towards generalisation, with pollinators visiting multiple plant species and plant species being visited by multiple pollinator species [35]. Examples of individual plant species pollinated almost entirely by a single insect species that is, in turn, almost completely dependent on it for its own survival are the exception, rather than the rule (e.g. [36]). A simulation model incorporating different scenarios of species co-extinction and capacities for partner switches showed that projected plant extinctions under climate change are more likely to trigger animal co-extinctions than *vice versa*, with specialist pollinators being the most sensitive [37]. This contrasts with, for example, herbivory in butterflies (Lepidoptera) in which the majority of species are much more tightly bound to specific host plants [38]. A spatial divergence between the two is, therefore, more straightforward to model because a reduced area of overlap has clear negative fitness implications for the butterfly that cannot reproduce without its host plant [17,39]. Because pollinators may be generalised and therefore able to use different host plants across their range, and plants may also be variably dependent on pollination itself across their range [40], diverging spatial ranges will not necessarily have any fitness impacts on either group.

Examples of potential spatial mismatch come from models that predict the spatial distribution of plants and their pollinators separately under climate change scenarios, and then measure the extent to which these diverge (e.g. [41]). However, because these are predictions about the future, these models have necessarily not yet been verified. Where empirical observational studies have been conducted at a small spatial scale, though bumblebee pollinators moved to a higher altitudinal elevation over a 50-year period at a faster rate than flowering plants, the magnitude of this change was not great enough that they ceased to come into contact with the same suite of plant species [33]. Although, to date, climate-induced spatial mismatches between plants and pollinators have not been observed [9,11], marginal changes of a lower magnitude could occur which would reduce, but not eliminate, spatial co-occurrence. Studies that compare bee and plant interactions in the same region using a historic dataset and comparing it to the present day offer the opportunity to detect lost interactions and to attribute these to a lack of spatial or temporal co-occurrence. One such study [42] found that, of the lost interactions that were not caused by the extirpation of pollinator species, 41% were caused by a lack of spatial co-occurrence and 53% by a lack of temporal co-occurrence. However, because the environment in which this study was carried out has been highly fragmented between the two time periods it is unclear to what extent these changes can be attributed to climatic factors.

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Right time, right place but…

Morphological mismatches

The response of insect body size to global warming is generally consistent: It has largely been observed that it decreases at higher ambient temperatures, probably because of higher metabolic rate and accelerated development (i.e. following the temperature-size rule [19,43,44]). This decrease can subsequently impact the thermoregulatory activity of pollinators. For example, it has been shown that larger bees are better able to thermoregulate than smaller ones [45], even if hair colour and thickness also impact this ability [46]. The responses of flower size and plant height to global warming seem to be far less consistent and very species-specific. At higher temperatures than the optimum level for a species (which can additionally be different for vegetative or reproductive parts [47]), a decrease in flower diameter [48] or in plant height [49] can be observed, but there is no consensus that global warming will systematically affect plant morphology or resource accessibility [50,51] as the converse pattern has also been observed [52].

Floral morphology is partly linked to the natural selection exerted by pollinator morphology and *vice versa* [35,53]. If the degree of morphological matching is high, it potentially implies a strong reciprocal selection because any change to this matching could result in fitness impacts for either or both partners [53]. However, if the level of matching is low, it potentially implies a low reciprocal selection because of the high variability of the phenotypes involved in the interaction [53]. Nonetheless, in many plant–pollinator interactions, morphological matching requires precision and a consistent mechanistic fit between the two actors to ensure the contact between the sexual parts of the flower (i.e. pollen and stigma) and the body of the pollinator and therefore efficient pollination [54]. Floral morphology is thus linked to the pollinator taxa that they attract, notably because of the relationship between the length of nectar spurs, corolla tubes and the proboscis of the pollinator (e.g. [54,55]). The relationship between proboscis length and corolla depth has been investigated in various groups like euglossine and solitary bees [54] and butterflies [18]. In most of these studies, species with longer proboscises visit a wider range of flowers, and all of the studies highlighted a positive relationship between proboscis length and the depth at which nectar is produced.

As an example of a potential morphological mismatch, two bumblebee species have evolved shorter tongue lengths over the last 40 years while their associated flowers have not become shallower [57]. This tongue size matching is particularly crucial as it has been showed recently to be a strong driver of foraging efficiency in multi-species assemblages [58]. The overall size matching will also determine the efficiency of pollen transfer: smaller pollinators (with on average shorter tongues) can have lower pollination efficiency (e.g. [59] but see [60]) through reduced pollen delivery, therefore, having a lower single-visit pollen deposition rate and seed set while large- or middle-sized species are, most of the time, more likely to have greater contact with anthers and stigma and therefore have a greater pollination efficiency [61]. Most of the studies have focused on pollen deposition and the pattern is largely constant. However, with regards to pollen removal from anthers, results are less consistent and some of them indicate that pollen removal efficiency is independent from body size [62]. Indeed, many other morphological features from both partners are driving pollination efficiency, notably hair characteristics (e.g. size and density) [58,59] which can also be impacted by temperatures during development [60]. Overall, morphological mismatches between plants and pollinators are most likely to occur within plant species displaying specialised flower morphologies as their morphological fit with pollinators is most restricted [51].

Disruption to host attraction and foraging behaviours

Like most phytophagous insects, pollinators are known to rely on olfactory cues (specific volatile organic compounds [VOCs] in a specific ratio) to recognise host plants at a distance [63,64]. A modification in the composition or the perception of the VOCs can, therefore, lead to the breakdown of the recognition process. It has been shown that changes in ambient temperature can affect volatile emissions from flowers, altering the quality of the signal [65]. Warming not only increases rate and abundance of floral VOC emissions, but also changed the ratios among compounds that constituted the floral scents. This response of floral emissions to temperature differed among species and among different compounds within species [65]. Such species-specific modification of the volatile blend emitted may impair plant–pollinators interactions if pollinators become confused with a more fragrant atmosphere, or are no longer attracted to their host-plant floral cues. Moreover, visual stimuli displayed by plants also appear to play a major role in host selection [66]. Several studies have already shown that the stress of high temperatures affects both vegetative and floral morphological traits, and higher temperatures can reduce plant height [67], cause flower deformity (i.e. floral organ malformation; [68]), lead to lighter

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flower colours [69], reduce the number of flowers as well as flower size [70], advance the timing of the anthesis [71] and limit the production of floral resources [72].

Regarding the direct effect on pollinators, we only can speculate that higher temperatures might denature key proteins in olfaction (i.e. odorant-binding proteins and olfactory receptors [73]). It is already known that proteotoxic stressors (e.g. heat stress) can cause proteins to misfold and denature, resulting in a loss of biological function [74,75]. However, such heat denaturation of proteins involved in olfaction remains unlikely since they are particularly stable to thermal denaturation [76]. Exposure of pollinators to high temperatures may nevertheless induce serious damages such as denaturation of non-antennal proteins, disturbance of the nervous and endocrine systems, damage to DNA but also the alteration of the liquid-crystalline fluidity of the membrane, which could disrupt the whole organism and lead to death ([77], reviewed in [78]).

Elevated temperatures can also alter resource nutritional quality for pollinators as pollen appears to be particularly sensitive to heat (e.g. [79]). High temperatures can lead to a decrease in pollen viability, which is associated with changes in several metabolites [80]. For instance, heat stress can decrease the concentration of soluble carbohydrates [81] and proline [69] as well as alter the phospholipid content of pollen [82]. Moreover, plants may produce a repertoire of secondary metabolites in response to temperature rises [83]. Such increases in secondary metabolites as well as the accumulation of reactive oxygen species are likely to occur in pollen and may be detrimental to pollinators [84]. All these changes in pollen composition might decrease its suitability to pollinators, reducing their performance and health status [85,86]. Finally, these changes in pollen development and viability could also affect plant fitness as they could disrupt plant fertilisation and lead to a reduction in fruit and seed sets [87,88].

In addition, nectar chemical composition (i.e. sugar concentration) can also be affected by an increase in temperature, but to a lesser extent than pollen composition and nectar volume [79,89]. However, these modifications in nectar sugar concentration can compromise pollinator attractiveness and flower visitation rate [89], as bumblebees are able to discriminate between small differences in nectar concentration and prefer sugar concentrations higher than 40% [90]. In the same way, pollen quality can drive host selection and flower visitation [91,92]. Effects of global warming on pollen and nectar quality are, therefore, expected to affect pollinators as well as plant reproductive fitness.

Another cue that pollinators, especially bees, can use to recognise flowers is floral temperature. By using thermal detectors in their antennae and tarsi, bees can detect differences in overall flower temperature [93]. Previous studies have shown that bees prefer to collect warm nectar from flowers at low ambient temperatures [94]. However, this preference for warmer flowers may be context-dependent as shown by Australian stingless bees (*Trigona carbonaria*) that preferred warmer nectars at lower air temperatures (from 23 to 30°C), but changed their behaviour and selected ambient temperature nectar over warmer nectar when the air temperature reached 34°C [95]. While some plant species appear to modulate their temperature in a way consistent with bee preferences, other appear to lack a cooling mechanism, suggesting that they may be less attractive to bee pollinators under higher temperatures [96]. Regarding all these effects on sensory cues used by pollinators for host attraction, global warming is probably already disrupting the interactions between plants and pollinators since all these modifications might alter the attractiveness of flowers to pollinators and impact their foraging behaviour [89]. On the other hand, global warming may also alter foraging behaviour from the pollinator point of view. Learning abilities (i.e. association between floral traits and rewards [97]) of some pollinators such as bumblebees could be affected, therefore, impacting discrimination between sensory cues. This could impede the plasticity of pollinator behaviour (i.e. modification of their foraging behaviour as a response of altered floral traits) and threaten the plant–pollinator interactions.

Conclusions and perspectives

Mismatches in the interactions between plants and pollinators will lead to the emergence of new biological networks and communities (e.g. [98]). Though some communities will experience the loss of existing interactions, other communities could gain novel interactions [98,99]. Some communities could be more severely impacted. For example, stresses such as more frequent and intense heatwaves could predominantly impact summer-flowering communities through decreasing nectar production (particularly in Mediterranean regions where the temperatures are already very high) because the optimal temperature of nectar production is more likely to be exceeded. On the other hand, spring-flowering communities could be more severely impacted by phenological mismatches with their host plants that to date have been more frequently observed during the spring [100,101].

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A certain level of variation in matches and mismatches is thought to be common in networks subject to co-evolutionary dynamics [53]. Based on 'the most effective pollinator' principle [102], floral traits should evolve to attract and match with the most abundant and effective pollinators. We may expect, therefore, when plant–pollinator interactions are predominantly generalist in nature, pollinators will show plasticity and be able to adapt to changes. In contrast, specialised pollinators will show limited plasticity in their response and therefore be less resilient to climate warming ([103] but see [23]). Indeed, generalist species are mostly less affected or even favoured by changing communities while species with narrower niches tend to be at higher risk of extinction [16]. Under changing conditions, this core of generalist species could partly sustain the plant–pollinator network, buffering the effects of climate change. Plant–pollinator networks are expected to be more stable and resilient to changes than host–parasitoid networks because of their nested and dynamic structures which act as a buffer against perturbations or cascading effects of species loss [10,11]. However, as such networks may be disrupted at both spatial and temporal scales and synergistic effects of additional detrimental factors (e.g. agricultural changes, pesticides, resource availability [104]), there is the potential for the resilience of the plant–pollinator network to be substantially weakened [51]. Whereas pollinators can offset local limitation of floral resources or nesting sites through their flight ability, plant populations are more threatened at the local scale by the reduction in the abundance of effective pollinators and soil nutrients limitation [11]. However, even if plants are sessile, simulation models incorporating different scenarios of species extinction and abilities to switch from host plant or associated pollinators showed that under climate change, the impact of host plant extinction could have a higher chance of causing the co-extinction of their pollinators than the converse scenario, thus the more likely extinctions cascades would come from plants to pollinators [37].

As the pace of climate change is fast compared with the historical baseline, if species are to persist then species adaptation has to be equally fast, and the phenomenon of rapid evolution is known to be a crucial ecological process for species persistence [1]. The asynchrony resulting from spatial and/or temporal mismatches will be subject to selection and the ability of plants and pollinators to adapt remain unclear. To address this current knowledge gap, we need ambitious strategies for monitoring plants and their pollinators, not only to detect shifts in their temporal and spatial distribution (Table 1), but also in their phenotypic distribution [105]. So far only a limited pollinator diversity has been studied in these contexts; in detail, evidence for phenological mismatches as a result of microevolutionary responses has already been observed [106], thus a critical challenge is now to assess if the pace of adaptive evolutionary changes will be fast enough the track climate warming and prevent species extinctions [107]. Moreover, host shifts due to climate warming could also be observed, which could buffer the detrimental effects of changing conditions for pollinators [108]. Nevertheless, the last decade has seen much progress in the description and understanding of global warming and its impact on complex plant–pollinator networks even if responses in the field have been documented far less than responses under laboratory conditions. These advances should help us to mitigate the effects of global changes to sustain pollinator communities and pollination services.

Summary

- Global warming is a major threat for biodiversity, impacting both species and their interactions. A fundamental interaction in terrestrial ecosystems is the mutualism between pollinators and their host plants.
- Global warming can induce spatial and temporal mismatches when species fail to co-occur. While spatial mismatches are still poorly observed, there is growing evidence that temporal mismatches can reshape interactions within pollination networks.
- Mismatches can also occur between species that still co-occur. These can be due to morphological modifications, disruption to host attraction and foraging behaviours, as well as shifts in the quality of floral resources.
- Our understanding of the effects of global warming on this mutualism has advanced substantially and the resilience of plant–pollinator networks to changing conditions seems to be high. However, we still require field-realistic results based on ambitious datasets to assess to which extent the mismatches do occur.

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Competing Interests

The authors declare that there are no competing interests associated with the manuscript.

Author Contribution

M.G., M.V., T.W. and D.M. conceived the ideas. M.G. lead the writing of the manuscript. M.G., M.V., T.W. and D.M. were each responsible of the redaction of one or several sub-chapters.

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Abbreviations

VOCs, volatile organic compounds.

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