

PHENOLOGICAL MISMATCH: IMPLICATIONS FOR PLANT REPRODUCTIVE SUCCESS AND POPULATION INTERACTIONS UNDER THE ONGOING REGIONAL AND GLOBAL CLIMATE CHANGE

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ABSTRACT

Phenological mismatch occurs when there is a temporal asynchrony in periodically repeated life-cycle phases between two interacting species caused by climate change. We review literatures on phenological mismatch to affirm whether it has effects on plant reproductive success and population interaction, and to know whether the effects are becoming progressive under the ongoing climate change. Because of substantial variations in ecological responses to climate change among taxa, we stress the need to develop a benchmark to reflect, for example, how much a species should shift to match the change in its environment, caused by climate change. We further stress the need for quantification of shifts in phenology at functional levels in ecosystems, especially those with high species diversity, as this will provide a benchmark data that can compare with other ecosystems with similar environmental conditions. We hereby recommend researchers with long-term data set on phenology to link their data with those that may serve as a benchmark, because documentation of the occurrence of climate change-induced mismatch is crucial in assessing the impacts of climate change on the natural world.

Key words: Climate change, phenological mismatch, phenological shift, plant-pollinator interaction

1.0 INTRODUCTION

Understanding how species cope with vagaries of climate change is a fundamental concern of ecology. Rapid climate change in the past half-century (IPCC, 2013) has significantly modified vegetative phenology (Edwards and Richardson, 2004; Jiang, 2012). These spatiotemporal changes induced by climate change can lead to the phenology of interacting species becoming mismatched. Lengthening growing season and shift in plant development stages have been found in the globe (Hoffmann *et al.*, 2010; Linderholm, 2015). As pointed in benchmark article, “any differential impact of climatic variability on two species, such as predator and prey (or two areas, such as winter or summer ground), may affect the dynamics through a switch from matching to unmatching the environmental conditions” (Stenseth and Mysterud, 2002). Temporal mismatches can have impacts on a range of interactions including plant-pollinator relationships. In the worst case, temporal mismatches, where activity periods of interacting species either do not or only partially overlap can, in the case of plants and pollinators, have negative impacts on plants through reduced visitation by pollinators (Raffarty and Ives, 2011). This can lead to lower seed production (Kudo and Cooper, 2019) and ultimately a reduction in fitness. Pollinators may also suffer due to lack of floral resources reducing the amount of pollen and nectar availability and, in some cases, creating seasonal gaps in resource availability

(Timberlake *et al.*, 2019). Temporal mismatches may arise if the interacting organisms respond at different magnitudes, or in different directions to the same climatic cues, or different climatic cues altogether. Current evidence for temporal mismatches is mixed, especially in plant-pollinator interactions. Where phenological mismatch has been found, it is specific, often specialist, plant-pollinator interactions (Robbirt *et al.*, 2014). Trends in more generalist interactions were often less pronounced or more stable (Bartomeus *et al.*, 2013).

Most phenological shift observations come from temperate and boreal biomes where advancing biological springs and delayed biological winter arrivals are documented in response to increased temperatures (Menzel *et al.*, 2006). However, the impact of climate change on the reproductive phenology of tropical species is poorly understood (Morellato *et al.*, 2016; Sakai and Kitajima, 2019). Tropical species have been suggested to be more sensitive to climatic changes than temperate and boreal species, because they have evolved in areas with less seasonal environmental variation (Sheldon, 2019). One of the most intriguing and complex characteristics of reproductive phenology in tropical forests is high diversity within and among forests (Sakai, 2002).

2.0 CONCEPT OF PHENOLOGICAL MISMATCH

Phenological mismatch specifically describes asynchrony in the timing of biotic interactions and implies a deviation from average or evolved interactions. (Lee *et al.*, 2024). This typically (but not always) implies a negative fitness consequence for at least one of the interacting organisms.

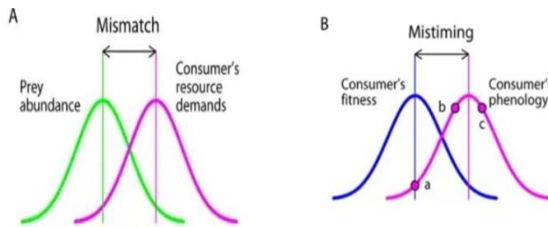


Figure 1: Distinction between phenological mismatch and timing

In Figure 1 above, Mismatch (A) occurs when the time in the annual cycle where resource demands of the consumer species are highest does not match with the period where this resource is most abundant. Mistiming (B) occurs when the phenology of either the individual (dots) or the population (vertical) deviates from the date at which fitness peaks, which will then lead to directional selection for either earlier (as depicted here) or later consumer phenology. Individual (a) is well-timed with the fitness optimum, while individuals (b) and (c) are too late and hence mistimed. Culled from: Visser and Gienapp (2019).

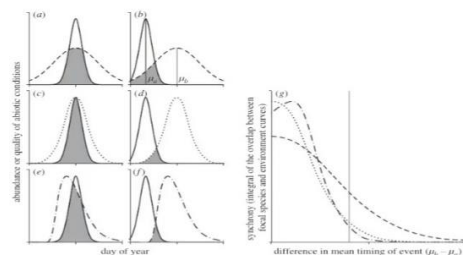


Figure 2: Deferring degrees and types of phenological mismatch

In Figure 2 (a-g) above, the left panel (a-f) illustrates how the synchrony (or degree of overlap between a focal species (solid line) and its environment (broken line) diminishes as the species' phenology advances. The distribution of suitable environmental conditions can be wide (a,b) or narrow (c,d). The distribution could also be asymmetrical (e,f). The curves could represent relationships between phenological phases of individuals or populations of the same or different species, e.g. flowering and pollinator activity, or predator and prey activity. The curves could also represent the relationship between an individual or population and appropriate abiotic conditions, e.g. leaf development and frost-free conditions, or tadpole development and water level. The right panel (g) illustrates how the synchrony between a species and its environment varies in response to increasing differences in the timing of activity of a species and its environment for the three cases shown in the left panel (a-f). Here, we represent synchrony as the area of overlap between the focal species and environment curves. The vertical line indicates the degree of synchrony when the focal species' phenology is advanced relative to its

environment (b,d,f). The dash and dot pattern in each curve in (g) matches the environmental curve (left panel) that it represents: dashed (a,b), dotted (c,d), and dot-dash (e,f). Culled from: Miller-Rushing *et al.* (2010).

Temporal mismatches can have impacts on a range of interactions including plant-pollinator relationships. In the worst case, temporal mismatches, where activity periods of interacting species either do not or only partially overlap can, in the case of plants and pollinators, have negative impacts on plants through reduced visitation by pollinators (Raffarty and Ives, 2011). This can lead to lower seed production (Kudo and Cooper, 2019) and ultimately a reduction in fitness. Pollinators may also suffer due to lack of floral resources reducing the amount of pollen and nectar availability and, in some cases, creating seasonal gaps in resource availability (Timberlake *et al.*, 2019). Temporal mismatches may arise if the interacting organisms respond at different magnitudes, or in different directions to the same climatic cues, or different climatic cues altogether. Current evidence for temporal mismatches is mixed, especially in plant-pollinator interactions. Where phenological mismatch has been found, it is specific, often specialist, plant-pollinator interactions (Robbirt *et al.*, 2014). Trends in more generalist interactions were often less pronounced or more stable (Bartomeus *et al.*, 2013).

A decoupling between the dates of key life-history events and resource availability may lead to strong negative consequences on species demography and population viability (Usui *et al.*, 2017). Current evidence for temporal mismatches is mixed, especially in plant-pollinator interactions. Where phenological mismatch has been found, it is specific, often specialist, plant-pollinator interactions (Robbirt *et al.*, 2014; Thomson, 2010). Trends in more generalist interactions were often less pronounced or more stable (Bartomeus *et al.*, 2013). 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). 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 (Inouye, 2020). Mismatches between the phenology of resource and consumer should affect demographic rates of the consumer due to reduced reproductive success or survival. They can also lead to selection on seasonal timing of the consumer because individuals that are better matched to the phenology of the resource will have a higher fitness than individuals that are less well matched.

3.0 PHENOLOGICAL MISMATCH UNDER CLIMATE CHANGE

Understanding how species cope with vagaries of climate change is a fundamental concern of ecology. Rapid climate change in the past half-century (IPCC, 2013) has significantly modified vegetative phenology (Jiang, 2012). Lengthening

growing season and shift in plant development stages have been found in the globe (Hoffmann *et al.*, 2010; Linderholm, 2015). These spatiotemporal changes induced by climate change can lead to the phenology of interacting species becoming mismatched. As pointed in benchmark article, “any differential impact of climatic variability on two species, such as predator and prey (or two areas, such as winter or summer ground), may affect the dynamics through a switch from matching to unmatching the environmental conditions” (Stenseth and Mysterud, 2002).

Plant species exhibit diverse responses to climate change, resulting in a restructuring of communities as they shift into novel configurations (Descombes *et al.*, 2020). This reshuffling of species alters interactions both within and among trophic levels, which in turn can affect ecosystem functioning (Blois *et al.*, 2013). The knowledge of how climate change impacts flowering plants, their pollinators, and pollination, is of paramount importance for conserving biodiversity and ecosystem functioning (Trunschke *et al.*, 2024). Phenological shifts are among the most widely studied biotic responses to climate change (Sandor *et al.*, 2021), and phenological advancement in response to climate have been shown for many taxonomic groups including plants (Renner and Zohner, 2018), arthropods (Robinet and Roques, 2010), amphibians (White and Uller, 2014), birds (Visser *et al.*, 2011), and mammals (Cherry *et al.*, 2013). Importantly, rates of advancement differ between taxa (Thackery *et al.*, 2010), potentially inducing or increasing so-called “phenological mismatch”, that is, disruption of synchronous interactions between ecologically coupled species.

Ecologically coupled species in the trophic interaction can either be mutualistic, or antagonistic, usually between consumers and their food source; the later disruption coined “trophic mismatch” (Renner and Zohner, 2018). However, changes in phenology can affect both antagonistic and mutualistic interactions (Sugar and Parmesan, 2010). Such changes can result in disruption of interactions through phenological mismatch; the partial or complete loss of temporal overlap between interaction species relative to historical, pre-climate change conditions. In antagonistic trophic interactions, mismatch will have positive fitness consequences for one of the species and negative impacts for the other, and trophic mismatch among herbivores and their food plants. In mutualistic interactions, mismatch will have negative consequences for both partners and should also be evolutionary unstable. Moreover, species in mutualistic relationships (plant-pollinators) appear more synchronized. In contrast, antagonistic interactions (i.e. consumer-resource) appear most likely to realize diverging phenologies (Beard *et al.*, 2019).

However, the effects of phenological shifts on the vital rates of populations are not well understood (Miller-Rushing *et al.*, 2010). There is inadequate understanding of how such effects will come about, how often they might occur, and how substantial their contribution to population dynamics will be.

This relatively short duration depending on genetic variation in relevant traits, strength of selection, and generation lengths, probably adds to the difficulty of detecting, and then attributing phenological mismatch to climatic change, which requires long-term data. Another challenge may be that mismatched interactions will benefit other mutualists or antagonists in an interaction network, depending on the degree of interdependence among partners, which is usually asymmetric (Benadi, *et al.*, 2014). Thus, phenological mismatch might occur when organisms that typically interact such as predator and prey or plant and pollinator are no longer active at the same time, or shift in phenology could alleviate existing mismatches and promote the expectation of newly available resources. Intimacy, seasonal duration, and degree of obligacy, and specificity are characteristics of mutualism that may determine the likelihood of phenological disruption (Rafferty *et al.*, 2014). In many cases, food sources tend to advance at faster rates than their consumers (Both *et al.*, 2006). When trophic mismatches result in insufficient food available during the prime period of offspring growth, this can have drastic effects on growth and survival of the offspring, thereby impacting the consumer’s fitness (Lameris *et al.*, 2018) and potentially resulting in population declines (Reed *et al.*, 2013).

Climate change has been shown to have impacts on species over both space and time (Bellard *et al.*, 2012). For crops and the insects that pollinate them, these impacts can include where and when they occur, with evidence indicating a trend of poleward (latitudinal) and uphill (altitudinal) spatial shifts in both plants and animals (Chen *et al.*, 2011). Climate change also influences phenology, or the timing of key life-history events, causing events such as insect first flight date and flowering plant budburst, to occur increasingly early in the year (Bartomeus *et al.*, 2011). These spatiotemporal changes induced by climate change can lead to the phenology of interacting species becoming mismatched. In the worst case, temporal mismatches, where activity periods of interacting species either do not or only partially overlap can, in the case of plants and pollinators, have negative impacts on plants through reduced visitation by pollinators (Raffarty and Ives, 2011). This can lead to lower seed production (Kudo and Cooper, 2019) and ultimately a reduction in fitness. Pollinators may also suffer due to lack of floral resources reducing the amount of pollen and nectar availability and, in some cases, creating seasonal gaps in resource availability (Timberlake *et al.*, 2019).

4.0 PHENOLOGICAL SHIFTS IN TROPICAL AND TEMPERATE REGIONS

Most phenological shift observations come from temperate and boreal biomes where advancing biological springs and delayed biological winter arrivals are documented in response to increased temperatures (Menzel *et al.*, 2006). However, the impact of climate change on the reproductive phenology of tropical species is poorly understood (Morellato *et al.*, 2016). One of the most intriguing and complex characteristics of reproductive phenology in tropical forests is high diversity

within and among forests (Sakai, 2002). Tropical species have been suggested to be more sensitive to climatic changes than temperate and boreal species, because they have evolved in areas with less seasonal environmental variation (Sheldon, 2019). Tropical species have been suggested to be more sensitive to climatic changes than temperate and boreal species because they have evolved in areas with less seasonal environmental variation (Sheldon, 2019). Tropical ecosystems contain comparatively higher plant diversity and functional diversity compared to other terrestrial ecosystems. As a result of the higher taxonomic diversity, phenological patterns in the tropics are also more diverse than in the temperate regions (Corlett and Lanfrankie, 1998). This has made the correct identification and tracking individuals' phenological events in tropical studies more challenging (Abernethy *et al.*, 2018). Moreover, studies have shown that rainfall changes may be a more important environmental cue for plant phenology in the tropics, compared to temperature changes that tend to be the main cue of temperate phenological responses (Morellato *et al.*, 2000). The influence of rainfall on plant phenology in the tropics is also complicated by supra-annual events such as the El Nino Southern Oscillation and will hence be challenging to interpret without especially long-term datasets (Sheldon, 2019).

In addition, there are comparatively less resources allocated towards long-term scientific programmes in tropical countries, thus creating difficulty in sustaining and preserving long-term data` (Abernethy *et al.*, 2018). Incorporation of modelling in forecasting and predicting impacts of changing climate on the ecosystem has, hitherto, largely centered on predicting the effects of warming temperatures on temperate species phenology. Thus, the absence of predictive models that captures the mechanistic relationships between climatic factors and reproductive phenology in the tropics, has put a huge limit to the expected progress in tropical phenological studies.

Within the tropics, the effects of a warming planet on species phenology are more likely to be driven by changes in the seasonal precipitation cycle rather than temperature. Consequently, the application of phenological paradigms based mostly on studies in temperate regions to tropical systems can result in incomplete predictions, for example, of phenological responses to climate change in the tropics (Davis *et al.*, 2022). Given regional differences in climate change, and the disparities in projected climate changes between the temperate regions and the tropics, it is likely that phenological shifts will not be uniform across the globe and that conclusions drawn from the temperate terrestrial and marine systems might not always apply to other regions, particularly so in the tropics. Unlike a clear period of biological dormancy, such as that enforced by low winter temperatures at high northern altitude, which make phenology distinct, phenological cycles in the tropics are often less distinct. This means that continuous monitoring in the tropical regions may be more critical and sophisticated statistical tools for interpretation will be required.

5.0 SUMMARY AND CONCLUSION

Studies on phenological mismatch have focused more on specialist plant-pollinator interactions, with paucity of research on trends in more generalist interactions (i.e. generalist flowers-pollinators and generalist plants-herbivores interactions). Moreover, phenological mismatch and mechanisms in the tropics, characterized by high species diversity, remains unclear. More attentions have been focused on temperate regions, apparently because clear annual cycles in plant phenology predominate in the region. Presumably, regular rhythm in temperature and day length and existence of winter, which limits all biological activities, impose such patterns. Given the regional differences in plant community structures and the disparity in projected climate change impacts between the temperate and tropical regions, we hereby stress the need to develop a unified benchmark to reflect how much a species should shift to match the change in its environment, caused by climate change. Also, we need to understand how much a species should shift to alleviate existing mismatches and promote the expectation of newly available resources. To this effect, quantification of phenology along functional levels based on, for example, phenological functional traits will provide a benchmark data that can compare with other ecosystems with similar environmental conditions, thus help in making generalization. Thus, we recommend researchers with long-term data set on phenology should link their data with those that may serve as a benchmark, because documentation of the occurrence of climate change-induced mismatch is crucial in assessing the impacts of climate change on the natural world.

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