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The Future of Insect Mutualisms Under Global Warming

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ABSTRACT: Mutualisms, defined as interspecies interactions with reciprocal benefits, face unprecedented threats under global warming. Insects, integral to numerous mutualistic relationships, will be confronted with multidimensional challenges to their metabolic processes, phenology, and behavior due to rising temperatures. This dynamic stands to alter the delicate balance between costs and benefits within mutualistic partnerships. Through a comprehensive review, this paper explores the future of insect mutualisms under global warming, revealing context-dependent effects and their potential outcomes, which extend from insect diversity to ecosystem services. The review further identifies gaps in existing literature, which are necessary to resolve in order to make more nuanced conservation strategies and safeguard the future of our natural systems.

KEYWORDS: Animal Sciences, Earth and Environmental Sciences, Ecology, Environmental Effects on Ecosystems, Entomology, Mutualism, Plant, Fungi.

Introduction

Our planet's climate is undergoing drastic changes, which have become a significant global concern in recent years. Of those changes, global warming—an increase in earth's global average temperature—is a persistent threat, impacting multiple aspects of our planet's environment.[1] All sources of greenhouse gas, from industrial activities to agricultural practices, absorb and radiate the heat from the sun. Hence, contributing to the overall issue of global warming.[2] The consequences are profound and present substantial threats to global environments. The increase in average global temperature is changing the phenologies of several species: natural events like flowering, migration, and hibernation occurring at different times.[3] The complex changes brought by global warming are multifaceted, small effects all contribute to the larger ecosystem, leading to the disruption of ecological relationships, of which insects are bearing the effects.

Insects are ectotherms, whose body temperature and movement velocity fluctuate in response to changes in external temperature.[4,5] Unlike endothermic organisms (e.g., mammals and birds), ectotherms are unable to maintain a constant internal body temperature, making them highly sensitive and vulnerable to temperature change.[5,6] The average temperature increase in their geographic range can impact fundamental metabolic processes, affecting the geographic distribution, organism phenology, growth,[7] behaviour[8-9] and physiology[10,11] of ectotherms.[12] Moreover, having an increased average temperature would challenge the maximum physical threshold of certain ectotherms during high temperature seasons. This may shorten the organism's overall lifespan or even be lethal.[11,13] However, predicting the future of insects under the influence of global warming is a challenging task. Simply examining individual organisms or a single species doesn't provide a comprehensive understanding of the existential threats to many insect species because insects are highly interconnected with their surroundings and rely on the support from other organisms to survive. Therefore, it is important to examine one of the most delicate relationships of insects with other organisms in nature—mutualism.

Mutualism is the relationship between organisms where they engage in reciprocal exchanges that benefit both parties within this relationship.[13,14] Under high environmental pressure and competition, organisms aim to minimize costs while achieving a balance between cost and benefits, so some may evolve to take part in mutualism. Insects, found in nearly every corner of the globe, support the fundamental functioning of a diverse array of species, thereby establishing a rich variety of mutualistic relationships. These interactions span various domains of life, with insects engaging in mutualistic partnerships with other insects, fungi, and plants. The reciprocal benefits that emerge from these relationships range from the provision of vital nutritional support and the transportation of other organisms to the sharing of essential energy resources and protection.[15,16]

This paper will delve into the intriguing world of insect mutualistic relationships, focusing on some of the common examples, including interactions between insects, insects and fungi, and insects and plants. Furthermore, we will explore the potential consequences of global warming on these intricate partnerships. By examining the potential impacts of rising temperatures, I aim to offer insights into the changes in these mutualistic relationships under global warming, specifically the effects brought by elevated average temperature.

Mutualisms

This section introduces the concept of mutualism, discussing the three types of insect mutualisms: insect-insect, insect-fungi and insect-plant. This background information is necessary to demonstrate fundamental concepts. It is important to understand the myriad of reciprocal benefits between insects and other organisms in a mutualism before considering how insect mutualisms could change under global warming.

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Insect-Insect Mutualisms:

Mutualistic interactions among insects are characterized by mutual advantages, contributing to the survival, fitness, and overall success of the population. These benefits mainly focus on the provision of food, protection and transportation[15] where the interacting individual or population usually trade one for another.[17] Such mutualistic relationships result in optimal energy use and fitness, sometimes leading to the evolutionary loss of high-investment traits in one species or the other.[16] Through collaboration, Insect-insect mutualisms can enhance the population growth of both parties as more energy can be imputed on reproduction instead of resource acquisition.[15,16]

The interaction between ants and homopterans is one of the most extensively studied relationships among insect-insect mutualisms, primarily due to its prevalence around the world, across a wide range of microhabitats.[8,13,18,19] This relationship serves as a typical example of insect-insect mutualism, where approximately 40% of aphid species are tended by ants.[20] Aphids supply ants with honeydew as a valuable food source, and, in return, ants offer protection against potential predators and competitors.[8,18,21] Ants serve the role of guardians that attend and protect the aphids from their natural enemies, thus increasing aphid survival rates and helping aphids to avoid competition with other herbivorous insects, allowing them to allocate more resources to improving colony longevity.[8,18–21] In return, aphids excrete honeydew from their intake of cell sap from plant's phloem, while ants try to enhance excretion rates and feeding activities in aphids through tactile stimuli. The act of consuming the honeydew by ants can also effectively reduce microhabitat contamination which may encourage the growth of bacteria or fungi and affect the health of aphids.[18]

Even though the relationship between ants and aphids is a type of mutualism, mutual benefits are not always in balance. In some cases, ant attendance negatively affects aphid growth and reproduction.[13,18] This occurs when more reliant aphid species evolve to accommodate the demand of ants, adjusting their resource allocation from growth and reproduction to honeydew secretion under ants' care. Their feeding habits and honeydew composition change (e.g., increase in amino acid concentration), even at the cost of their own growth and reproduction.[13] As aphid colonies grow and honeydew-supplied carbohydrates become less limiting, there may be an increase in the incentives for ants to view aphids as prey rather than mutualistic partners; in the extreme case, ants reduce aphid population in the absence of predators.[18,20]

Despite the potential negative impacts, the removal of ants from aphid colonies depending on this mutualistic relationship can trigger aphids to escape, affecting feeding and reproductive rates and experience a higher extinction rate due to predation pressure;[18] This emphasizes the significance of ant-aphid mutualism in providing protection against predators. Not only with homopterans, ants also gain sugar from some caterpillars in return for their protection service.[16,22] Such flexibility demonstrated in this example suggests the dynamism present in longstanding mutualisms, which will be important under the impact of global warming.

Though mutualism between ants with other sugar providers is common, there are other more specialized forms of transportation-based mutualism among insects. The carriers enable the riders to access otherwise distant or inaccessible resources, enhancing their survival and reproductive prospects. In exchange, the riders contribute to the carriers' well-being by acting as a protective shield, deterring parasites or predators that could harm their transporters.[15] Southern pine beetle, for example, provides long-distance transport for predaceous mites, *Dendrolaelaps neodisetus*, in return for their service to remove parasites.[23]

This background information about insect-insect mutualism reveals the complexity of two different insect populations or individuals interacting together. Insect mutualisms rely heavily on environmental contexts to find a balance between cost and benefit of both parties. When mutualism faces the ramifications of global warming, the change in temperature and other environmental factors will affect both individuals and interspecific interactions altogether, resulting in complex outcomes of insect-insect mutualism. These are explored in greater detail later.

Insect-Fungi Mutualisms:

Insect-fungi mutualism occurs when insects[24,25] engage in reciprocal interactions with one or more species of fungi. This can be both ectosymbiotic or endosymbiotic, yielding a range of benefits: nutrition, protection, and dispersal.[14] The fungi engaged in these relationships exhibit diverse abilities, such as the degradation of plant tissue, support nest structure, and the production of antimicrobial compounds.[14] In most insect-fungi mutualisms, fungi concentrate limiting nutrients, break down essential food sources and detoxify certain substances.[14] In return, insects protect them against competition (e.g., microorganisms, other fungi species), by actively farming the fungi (could even incorporate fungi as part of their nest) or dispersing fungal spores passively through life cycles, thereby facilitating fungal reproduction.[14] In more interdependent mutualism relationships, fungi provide essential nutritional support for insects in their early stage of development.[26]

Some insects lack the ability to independently digest complex plant polymers such as cellulose, so they depend on fungi to enzymatically break down these compounds into more digestible forms.[14,24] This process can be either ectosymbiotic or endosymbiotic. As observed in termites, faunal enzymes ingested from fungi cultures can remain active within an insect's digestive tract, facilitating the breakdown of cellulose.[24] There are also less complicated farming practices like the Brazilian stingless bee *Scaptotrigona depilis* with the fungus Monascus. The bees only provide basic substrates for the fungi to grow on brood cells, and then the larvae will cut and ingest the growing mycelia to increase their survival rate.[26] Ambrosia beetles (*Scolytidae and Platypodidae*) farm ambrosia fungi on wood as their main food source, so they support its reproduction by developing a specialized cuticle that secretes lipids for fungal nourishment.[14,27]

Leaf-cutter ants form a mutualism with certain fungi for the limiting nitrogen, crucial for their growth and development.[28]

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These ants act collectively to gather fresh leaf cuttings with only a low level of nitrogen content, mixing them with saliva[28] and depositing them near the refuse dump, where the fungi grow. Each leaf-cutter ant colony exclusively supports one species of fungus, where the leaf-cutter ants actively cultivate and protect the fungi. In the absence of ants, the fungus would be left alone to face the invasion and competition with foreign fungi or bacteria.[28] However, some ants are able to engage in a secondary mutualism with *Actinobacteria*, producers of antibiotics that safeguard their fungus gardens against potential competitors.[25]

To expand the fungal culture, ants consume mature fungal tissue rich in proteolytic enzymes and then redistribute these enzymes by defecating at a garden chamber site of newly implanted inoculum. The rapid growth of the new inoculum will be supported by the optimum temperature and humidity in the nest, ensuring the continuity of this mutualism.[20,24] In return, fungi can serve as a component of their nest or shelter[14] and provide ants with the opportunity to consume specific fungal tissues[15] that contain a higher concentration of nitrogen, benefiting their growth. Impressively, these ants exhibit dietary flexibility by foraging in a diverse array of plant families.[20] The nutrient enrichment facilitated by leaf-cutter ant colonies significantly enhances fine root production and overall plant diversity in the vicinity of their refuse piles, underscoring the profound ecological implications of this mutualistic association.[25]

Other than farming, many species of insects choose to engage in the passive dispersal of fungi spores while getting direct provision of nutrients from fungi, crucial for their early larval development. The non-social beetle *D. bucculenta* engages in such a mutualism where the adult females lay eggs into bamboo culms and disperse the spores of the yeast *Wickerhamomyces anomalus* from their ovipositor-associated mycangium into the chamber.[29] This allows a consistent presence of white fungal layers providing essential nutrients for larval growth and development. In the mutualistic relationship between *Penicillium* and *Bactrocera dorsalis* fruit flies, the fungus benefits from the fruit flies' oviposition behavior that creates openings for fungal entry, while the fungi enhance the fitness of the flies by supplying vital nutrients essential for their maturation.[30]

In rare cases, the mutualistic partnership can involve more than two organisms. *Dendroctonus ponderosae*, a species of bark beetle, engage in mutualistic partnerships with two distinct fungi, each occupying different temperature ranges to reduce competition. These beetles consume spore layers produced by these fungi as a source of nutrients and carry the fungal spores within specialized structures, facilitating active dispersal.[31] Sometimes, the nutrient provision can come from insects. The large phytophagous weevils secrete a thick waxy layer on their backs to support the growth of fungi for the purpose of disguise and chemical protection, thus decreasing the predation level of these weevils.[32]

Insect-fungi mutualisms are more interdependent than insect-insect mutualisms. Their interactions are both affected by and are affecting their natural environment—some even support essential ecosystem services. Their interdependentness will be further discussed in later sections under the context of elevated average temperatures and the potential consequences for insect-fungi mutualisms in the future.

Insect-Plant Mutualisms:

Insect-plant mutualisms occur globally across a wide range of ecosystems. They are defined as any reciprocal benefit between an insect and a plant, including pollination, protection and seed dispersal.[22] Insect-plant mutualisms support a number of critically important ecosystem functions, which may be under threat due to global warming.

Pollination is one such critical mutualism for ecosystem function, providing necessary sexual reproduction for the growth of plants and sustaining their diversity.[10,15] This relationship is a general form of mutualism where no specific insect is bonded with a specific plant; it benefits a range of different species.[22] In pollination, insects tend to gain food benefits such as nectar as a source of carbohydrates and protein,[33] while plants gain the benefit of sexual reproduction.[22] For example, when nectarivore insects collect or consume the food source provided by the flower, they pick up pollen that is then transferred from an anther to the stigma of a different flower as it continues a search for food, thus helping the plants to achieve sexual reproduction.[33] The primary objective of the insect is to maximize its nutrient acquisition from the floral food source for survival and reproduction,[10,34] while the plant seeks to minimize the resource cost but still maintain a high-quality visitation by insects to ensure effective pollination.[33]

Insects including bees,[12,22,35] flies and butterflies are considered polyphilic, meaning they participate in multi-taxa mutualisms simultaneously.[15] Some other species are oligophilic or even monophilic, interacting with more specific species of plant such as the relationship between the Joshua tree and yucca moths.[7] Despite their differences, being a pollinator provides pivotal significance in the provision of indispensable ecosystem services. These services encompass not only the propagation of plants but also the enhancement of genetic diversity, increased agricultural yields, and the maintenance of biodiversity within ecosystems.[36]

Many plants provide extrafloral nectaries (EFN), nectar secreted from various locations outside the flower itself,[22] which offer similar nutrient value to that found in floral nectar. For certain ant species, EFNs are able to enhance the individual ant's growth rate and foster the prosperity of the entire colony.[33] This supplementary food source holds appeal for a range of insects and often leads to the formation of protective mutualisms,[16] often with ants playing a prominent role as plant guardians.[17] Ants do this by attacking competitors or herbivores that may damage the plan.[22] The protection benefit can also be gained indirectly by plants while ants are protecting aphids; they chase away other herbivores that may compete for resources with aphids.[37] However, this protective behavior of insect mutualists, in chasing away herbivores that could harm the plant, is initiated with a self-serving motive; their aim is to maintain the plant's health to maximize EFN production, ultimately ensuring the mutualists receive the maximum pos-

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sible nutrient benefit. Consequently, this protective conduct of plant defenders may bring negative effects, particularly during the flowering phase. In certain cases, mutualists like ants may negatively affect pollination as their metapleural glands secrete chemicals that may disrupt pollen's reproductive function unintendedly, ultimately reducing the reproductive success of their plant partners.[33]

Besides nectars, many insects seek nutrients from seeds, which are rich in fats and proteins, leading to seed dispersal for plants.[22] Insect dispersers are crucial for one's persistence in its species in nature.[38] Examples of this mutualistic interaction have been observed with hornets dispersing *S. tuberosa* seeds. The hornets exhibit behavior that involves biting the diaspores, carrying them to a new location, and later abandoning them. The seeds are then gathered by foraging ants and taken to their nest, thus facilitating long-distance seed dispersal in this species;[39] over 80 plant families have been documented to rely on ant-mediated seed dispersal.[22] To safeguard plant vital reproductive tissue from being consumed by insects during this dispersal process, many plants dependent on insect-mediated seed dispersal have developed a nutrient-rich outgrowth from the durable seed coat known as an elaiosome. This adaptation effectively transforms the original seed consumers into elaiosome consumers, redirecting the insects' focus towards this nutritious appendage and, in the process, aids in the dispersal of seeds.[20]

Insect-mediated seed dispersal confers several advantages to plant populations. It mitigates the problem of seed accumulation around parent plants, reducing intraspecific competition and enhancing gene flow.[38] Furthermore, plants benefit from insect dispersal by experiencing a reduction in seed predation, where those seeds are placed in fertile microhabitats instead of being consumed. The practice of ants placing seeds within their nests has been observed in certain species. This allows plants to access nutrients from the nest walls, as these ants transport debris into their nests as a source of fertilizer.[15]

Significant similarities between the three types of mutualism reveals the fundamental basis of insect forming mutualism relationships—the exchange of benefits. Since the two species often demand different types of benefit from each other, it is hard to directly quantify and compare the balance of such reciprocal benefit. Maintaining an equilibrium serves as a crucial factor influencing the stability of these relationships, particularly when considering the impact of global warming. The next section explores the possible futures of insect-based mutualisms.

■ Insect Mutualism Under Global Warming

Mutualism is built on the basis of reciprocal benefits, but global warming threatens the balance of reciprocal benefits by changing the environmental conditions of insects. Whether the effect towards insects under increased average temperature is positive or negative, the changes in species and populations cascade into the broader ecological system and the mutualism may be disrupted. As the quantity or quality of benefits being exchanged is altered, organisms may abandon their mutualism.[17] The impact of global warming can manifest differently among species and populations due to their distinct physical and chemical characteristics. The local weather change will also contribute to the different outcomes.[40] The changes are highly dependent on ecological context and the dependency of a certain species on that mutualism; species that occupy a smaller ecological niche will be more impacted than generalist species.[17]

In the case of insects and their mutualistic partners, a spectrum of outcomes is possible, ranging from individual deaths and subsequent population collapse caused by extreme high temperatures[41] to populations thriving under more suitable conditions created by global warming [Figure 1].[42] Many species will fall somewhere in the middle of this spectrum, potentially adjusting their behavior and phenology to better cope with the changing environment. Since the effect of increased average temperature differs between different species, the changes in the interaction between mutualistic partners[4] would result in complex consequences in mutualisms, which are difficult to predict. Any alteration to the mutualism, whether positive or negative, in one partner's response to global warming is likely to have an impact on the mutualistic relationship. Particularly when such changes result in a decrease in benefit provision, this may cause sudden changes to the mutualism and the ecosystem network;[17] to the extreme, mutualism relationships can be disintegrated. Therefore, it is of utmost importance to comprehend the potential effects of global warming on insects and their mutualistic interactions, given their pivotal role in ecosystem functioning and their substantial economic significance to human society.

Temperature Effects on Insects:

Insects, as ectothermic organisms, are susceptible to average temperature increases, primarily affecting their basal metabolic processes. Elevated temperatures increase the metabolic rate and respiration of insects, a response that can exceed their optimum rate up to a critical thermal maximum.[43] The accelerated metabolic rate affects enzymatic activity and disrupts metabolic compensation, thereby potentially inducing adverse consequences for insect physiology.[6] However, recovery, after an insect is exposed to their critical thermal maximum, can occur in some individuals when the temperature becomes more moderate.[40] Extreme high temperature events can have far-reaching effects throughout an insect's life cycle, ultimately influencing population dynamics. Elevated temperatures experienced during crucial developmental stages, such as the egg, larval, or pupal phases, can result in reduced adult survival and fertility.[40] Furthermore, these negative effects can extend to subsequent generations, leading to diminished survival rates.[40] In sum, negative effects can cascade from individual deaths and population collapse to the loss of entire species.

Global warming causes injuries in insects and will reduce both the population and the benefit provided. This would discourage any mutualistic partner's cooperation with the insects, weakening the mutualism. For example, a decrease in the overall abundance of aphids would directly reduce the production of honeydew,[5] hence limiting the growth and reproduction of ants. In addition to impacting survival and reproductive success, temperature changes can also have effects on the body size of insects.

In general, exposure to high temperatures across developmental stages can increase metabolic and development rates,[40] causing overall reduced growth or change of behavioral responses. Slower growth may create a negative feedback loop under global warming, where a smaller body size minimizes heat retention.[42] For insects that provide protection benefits through physical strength, such an effect will directly reduce their protection provisioning within a mutualism. In the case of aphids and mealybugs,[5] the effect of physical injury and changes in the aphids' or mealybugs' nutrition intake can alter the nutrient composition of their honeydew.[8] This may change the behavior of consumer ants,[8] as the reduction of nutritional benefit weakens the mutualism, in which ants may resort to hunting their partner aphids for food when honeydew production declines.[18]

The varied negative responses to temperature changes among insect species underscore the complexity of temperature's effect towards insects, but the ultimate aim for these insects is to inhabit an area with a suitable temperature range for survival and reproduction.[9] On the other hand, an increase in average temperature will bring warmer temperatures in winter and nighttime which may positively affect the survival of some insects,[40] an example of favorable conditions caused by elevated temperature. Some aphids and mealybugs have been shown to benefit from increased temperatures when conditions match for optimal growth and reproduction.[21,42] Simultaneously, such global change could decrease potential predators of a party in the mutualism as higher trophic levels face higher survival pressure from environmental changes.[17]

Under the condition of elevated temperature, insects may exhibit adaptive behavioral responses as a means of coping with the heightened metabolic demands. Alternatively, they may opt for an increased frequency of foraging in their surrounding environment or intensify their interactions with mutualistic partners to secure their nutrient intake. This behavioral adjustment is not only energy-efficient for the insects but also influences their mutualistic partners, potentially altering the dynamics of the mutualism relationships they participate in.

In the typical case of ants, these insects may reduce their foraging activities or choose to forage during cooler hours of the day to mitigate the challenges posed by environmentally high temperatures.[8] This behavioral adjustment is driven by an energy-saving strategy aimed to reduce the metabolic costs associated with movement under thermally demanding conditions. Temperature variations geographically can lead to an increase or decrease in the abundance of foraging ant populations, with different areas experiencing distinct responses to these temperature shifts.[9,44] This can also lead to a reduction in the aggressiveness of ants, hence reducing the level of protection to their mutualistic partners.[21] This change in activity patterns can have profound implications on the duration and frequency of interactions between mutualistic partners, potentially leading to mismatches in ecological synchrony.

Behavior change can also lead to a potential decrease in protection or care provided to their partners. The decrease in the tending behavior of ants towards aphids, observed under conditions of elevated temperature, highlights a trend where insects may invest less in mutualistic activities, leading to a potential breakdown in the mutualism between partners.[8] This reduction in protective behaviors has cascading effects, making colonies more vulnerable to natural enemies and disrupting the delicate balance that exists in mutualistic relationships. To the extreme, the absence of protection benefits provided would negatively affect the population of insects being protected; hence having the entire mutualism collapse.[18]

Temperature Effects on Plants:

Similar to insects, plants as organisms also have different ranges of optimum temperatures between different species and throughout their developmental stages.[45] The increase in overall temperature will affect seed germination, photosynthesis, respiration and other living processes to a different extent. Elevated temperature at different stages of plant development will cause various extents of injuries. Chronic heat injuries may result in the inactivation of enzymes or the inhibition of protein production to sustain normal metabolic processes, causing permanent effects on the plant.[45]

Temperature increase under global warming, along with rising carbon dioxide levels, is predicted to lead to an increase in plant biomass.[46] Though plant biomass increases, the availability of minerals and nutrients does not, leading to potential effects on primary consumers. For organisms involved in direct mutualism with plants, the decrease in nutrient value of plant nectar and pollen will impact insect growth and behavior as the food benefit becomes less attractive. This will likely lead to a decrease in the strength of mutualism as the plant can no longer fulfil the nutritional needs of the insects. In return, insects will use the time and energy for plant protection to forage for more nutritional food or find a substitute to replace this mutualism relationship.

Furthermore, insects that rely on plants to sustain their mutualism with other organisms would also be affected. Take the leaf-cutter ants as an example, the decline in leaf quality due to altered nutrient content may directly impact the nutrition benefit provided by ants towards the fungi, hence reducing the nutrient benefit in return to the ants, changing their foraging and feeding behavior, potentially leading to a reduction in their population size and overall impact on the ecosystem.

Temperature Effects on Fungi:

The elevating temperature around the world is likely to create a suitable environment for many fungi species to have faster mycelium growth, but their spore production decreases accordingly.[47] The effect on insect-fungi mutualisms largely depends on the specific species of fungi in that specific mutualism, and how susceptible it can be during growth and reproduction. For instance, the bark beetle *Dendroctonus ponderosae* has two mutualistic fungi that emerge at different temperature ranges, due to temperature effects on their sporulation in pupal chambers.[31] As the average temperature increases, the warm-adapted fungus will dominate the mutualism and

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outcompete the cold-adapted fungus, potentially reducing the bark beetle's total mutualistic partners down to one.

Looking at plant-fungi mutualisms, we can predict that changes in temperature may disrupt the balance of these interactions, affecting insect-fungi relationships similarly. Plant-fungi mutualisms are also susceptible to temperature variations, which can have cascading effects on insects relying on these interactions. Temperature directly affects arbuscular mycorrhizal fungi (AMF) growth and temperatures outside the optimum range will reduce the growth.[48] AMF, in turn, can alleviate the negative effects of temperature stress on millet growth and physiological parameters, including mycorrhizal colonization rate and soil aggregation.[49] The imbalance in the provision of benefits within these mutualistic interactions, triggered by temperature fluctuations, may lead to a collapse of the mutualism, affecting not only the plants and fungi but also the insects dependent on these associations.

More research targeting species-specific insect-fungi mutualism under elevated temperature is needed for a comprehensive understanding of the trend of insect-fungi mutualism in the future. Current research could only inform predictions for the effects on individual parties, which may be inaccurate compared to the complex real-life situation.

Phenological Mismatch:

The presence of global warming has brought an elevation of average temperature and changes in climate patterns. Environmental conditions such as temperature, rain and snow melt are important cues for organisms to proceed in their life cycles. Such characteristics are shared among insects, plants and fungi. As species rely on distinct environmental cues to undergo significant life history events, phenological mismatch arises.[40,50] This can lead to an overall negative impact on mutualistic relationships involving insects, plants, and fungi. The mismatch may result in a failure to form mutualistic partnerships, discouraging the cooperation between species. Moreover, the mismatch may encourage species to seek out new mutualistic partners; some species may be greatly affected by the loss or gain of a new mutualistic partner, leading to cascading effects on the entire ecosystem.

Various aspects of the impact of phenological mismatch are discernible when examining the perspective of plants, where flowering phenology relies on temperature cues while their pollinators may rely on other environmental cues.[50] The temporal adjustments in the flowering period can substantially diminish the visitation rate of pollinators, thereby exerting effects on plant reproductive success due to the reduction in pollination quality and having the ensuing effects on seed development.[35] Global warming-induced change in snowmelt timings instigate premature blooming in plants.[50] Nevertheless, this climatic shift results in relatively lower belowground temperatures, consequently retarding the emergence of bees. This decelerated bee emergence, in turn, contributes to a reduction in seed production, as their pollination behavior is compromised.[50] Even a few days of mismatch can be significant in disrupting this mutualistic relationship.[50] When elevated average temperature introduces a replacement of a cold-adapted insect species by a warm-adapted insect species in an area, this can disrupt the synchrony of insect-plant mutualism. The difference in species and living environment will result in different phenological cues, leaving seeds without a disperser,[38] impacting the survival and distribution of plant species involved in this mutualism.

In cases where elevated temperatures induce earlier arrivals of aphids on host plants before ants become active, the immediate protective association between aphids and ants is compromised.[8] Consequently, aphids are left susceptible to predation, resulting in a rapid decline in their population before the arrival of their protectors. The small abundance of aphids directly results in a reduced capacity to provide substantial nutritional benefits to the ants. This diminished nutritional provisioning prompts the ant protectors to perceive the association as insufficiently rewarding. Therefore, the two parties fail to establish a mutualism and the disruption of this mutualistic interaction has deleterious repercussions, exerting negative influences on the growth and reproductive capacities of both aphids and ants.

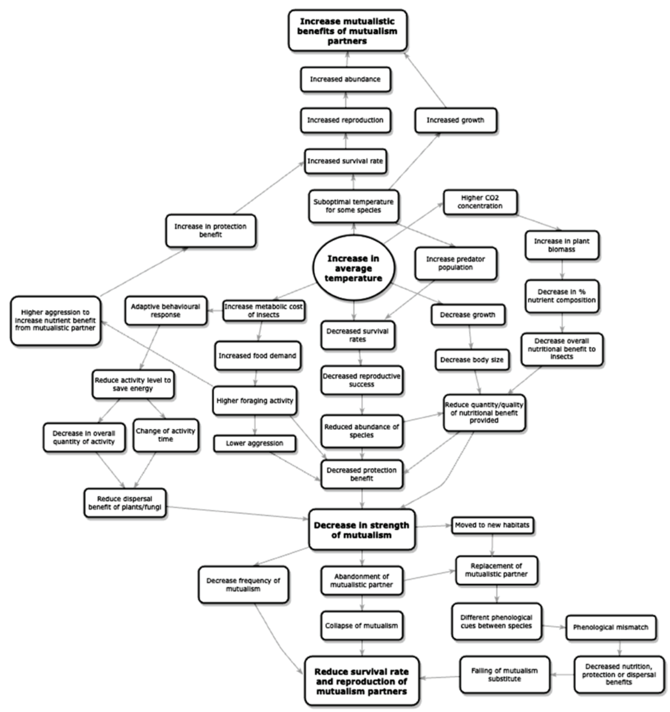

Figure 1: A directed acyclical graph showing the mechanisms by which the strength of insect mutualisms may increase or decrease under global warming. While most scenarios result in a decreased survival and reproduction for one of the partners in a mutualism, there are instances where warming temperatures could facilitate an increase in benefits between partners, thereby strengthening the mutualism.

Discussion

The complexity of ecological interactions is evident as multiple effects from elevated average temperature can be present within a single mutualism relationship. My review and synthesis demonstrate the impossibility of creating a generalized prediction for all mutualisms under future global warming. Although there is no single outcome for mutualism, I have highlighted the critical mechanisms and traits that will determine their future status. Further, there is no consensus in the literature; contradictory experimental results observed in some studies could be attributed to the diverse array of variables at play, ranging from the type of temperature change (average increase or extreme high-temperature events) to the specific species involved and their mutualistic partner. In rare instances, experiments have demonstrated that certain species can adapt to temperature changes, or conversely, abandon their weakly-formed mutualism altogether, further contributing to context-dependent outcomes for the future of mutualisms under global warming. It is essential to recognize that the impacts of temperature on mutualistic relationships extend beyond a simple cause-and-effect relationship, requiring a comprehensive understanding of the various factors influencing these intricate ecological dynamics.

To gain a clearer understanding of the future of mutualisms under global warming, researchers should explore the context-dependent nature of these interactions by considering factors such as potential new mutualisms driven by local community diversity, the influence of environmental stressors beyond temperature alone, and ecosystem integrity (e.g., continued availability of food and habitat) under global warming. Conducting experiments that simulate both gradual increases in average temperature and extreme high-temperature events will provide a more comprehensive understanding of the range of responses exhibited by different species. Special attention should be given to the identification of specific mechanisms underlying observed effects, including the potential interplay of both positive and negative impacts within a given mutualism. Additionally, considering temporal dynamics, such as phenological mismatches and evolutionary adaptations, will contribute valuable insights. Collaborative, interdisciplinary studies that integrate knowledge from ecology, physiology, and climatology will be instrumental in researching temperature-induced changes in mutualistic relationships. By addressing these recommendations, researchers can pave the way for a more holistic comprehension of the impacts of climate change on ecological dynamics and foster informed conservation strategies for preserving the delicate balance of mutualistic interactions in our changing world.

Conclusion

In conclusion, the mutualistic relationships involving insects, plants, and fungi are undeniably sensitive to increases in average temperature. The analysis of how the temperature increase due to global warming affects various aspects of these insects and their mutualism interactions reveals a complex interplay of both positive and negative consequences [Figure 1]. However, it is crucial to recognize that the scenarios described in this paper focus on the individual factor of average temperature increase and may not fully capture the complex reality of ecological systems. With temperature itself, there are many other changes to consider, including the magnitude and rate of temperature relative to the life cycle, and evolutionary timescales for adaptation of different species. Interacting variables, such as habitat availability, pollution, carbon dioxide concentration and other aspects of climate change beyond just temperature can contribute to the overall effect.

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