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CLIMATE CHANGE IMPACTS ON HONEYBEE SPREAD AND ACTIVITY: A SCIENTIFIC REVIEW

Mahmoud Abbas Ali*[a], Islam M. Abdellah[b], and Mohamed R. Eletmany*[c]

[a] Plant Protection Department, Faculty of Agriculture, South Valley University, Qena, Egypt 83523

[b] Department of Chemistry, Faculty of Science, Aswan University, Aswan, Egypt 81528

[c] Department of Chemistry, Faculty of Science, South Valley University, Qena, Egypt 83523

* **Corresponding author:** Mohamed R. Eletmany, Chemistry Department, South Valley University, Qena, Egypt 83523. *Email:* mrmoham2@ncsu.edu

Abstract:

Climate change poses multiple threats to honeybee health through mechanisms including higher temperatures, shifting seasons, extreme weather, reduced forage, and increased disease. This review synthesizes the current literature on how various climate factors interact to impact honeybee biology, immunity, distribution, and floral resources. Rising temperatures accelerate colony metabolism, limit foraging time, and increase pesticide toxicity. Altered precipitation patterns and increased frequency of floods and droughts restrict nutrition availability. Range shifts decouple bees from viable habitats and forage. Climate warming also amplifies parasites, pathogens, and diseases. Models predict steep future declines in managed and wild bee populations across regions without intervention. Protecting bees will require targeted conservation, sustainable agriculture, and reducing greenhouse gas emissions.

Introduction

Honeybees (*Apis mellifera*) play a vital role as pollinators for numerous wild plants and agricultural crops. As a managed species transported across the globe by beekeepers, honeybees pollinate $15 billion worth of food crops in the United States alone [1]. Worldwide, nearly 90% of wild flowering plant species depend on animal pollination, along with more than 75% of leading global food crops [2]. This enormous contribution to terrestrial biodiversity and food production depends on healthy bee populations. However, honeybees face intensifying pressure from multiple environmental stressors, including climate change [3].

Rising global temperatures, shifting rainfall patterns, and increased frequency of extreme weather events all impact honeybee colonies. Bees are sensitive to temperature and precipitation changes because their biology directly depends on the availability of flowering plants and stable weather conditions for foraging [4]. Even subtle changes in climate can desynchronize bee emergence and flower blooming periods, limit bees' foraging time, increase pesticide exposures, facilitate the spread of pathogens, and cause large-scale shifts in floral resources [5]. These impacts are compounded by other threats like Varroa mite parasitism, pesticide exposure, and habitat loss [6].

Understanding how climate change interacts with other stressors to affect honeybee health can help guide conservation efforts. Detailed projections suggest declines in honeybee populations across much of North America, Europe, and South America over the coming decades if greenhouse gas emissions continue unabated [5]. However, habitat protection, climate change mitigation, and management practices like suppressing mites and providing supplemental forage can help limit climate impacts on bees [7, 8]. This review synthesizes current research on mechanisms by which climate change influences honeybee biology, behavior, immunity, distribution, and interactions with other species. Elucidating these complex relationships is key to sustaining honeybee communities, the wild plants they pollinate, and the critical ecosystem services they provide.

1 Impacts of Warming Temperatures

2 Higher temperatures speed up bees' metabolic rates, limiting foraging time.

Rising global temperatures as a result of climate change pose a significant threat to honeybees by speeding up their metabolic rates and limiting critical foraging time. Honeybees are ectothermic, meaning their internal body temperature mirrors that of their external environment [8]. Higher ambient temperatures accelerate bees' metabolism, heart rate, and movement, depleting their energy stores more rapidly [9]. This energetic stress constrains the amount of time bees can spend foraging outside the hive for pollen and nectar before returning to rest and refuel [10]. Here is one paragraph integrating the quantitative climate impact data on bees. Models estimate that just 1°C of warming could lead to 50% bumblebee range contractions in North America and Europe [5], while further warming of 0.7°C may triple extinction risks for endangered native bees [5]; similarly, simulations suggest 30-50% honeybee colony losses in the Upper Midwest of the U.S. by mid-century due to reduced floral resources [7], and under a high emissions scenario, half of bumble bee species in North America and Europe face potential population declines of 40% or more in 50 years [11]. Moreover, a 2°C temperature rise could cause over 20% migratory honeybee habitat losses in North America [12], while historic flooding events have instantly wiped out up to 90% of hives [13] and single heavy rains can lead to 25-50% colony starvation and losses by preventing bee foraging [14]. Together, these quantitative models and historical data highlight the alarming vulnerability of both commercial and wild bees to intensifying climate change impacts.

Reduced foraging activity has well-documented detrimental effects on individual bee and colony health. Bees forced to shorten foraging trips bring back less pollen to sustain developing brood and less nectar to make honey stores for winter [15]. Maturing larvae and adults depend on steady pollen nutrition. Inadequate pollen intake slows growth, weakens immunity, and shortens the lifespan of individual bees [16]. At the colony level, smaller worker populations, limited food reserves, and poor health leave hives more vulnerable to collapse, especially when faced with additional stressors like parasitic mites or pesticide exposure [17].

Climate warming further strains bees by desynchronizing colony build-up and flower blooming. In temperate regions, rising spring temperatures now often cause plants to bloom weeks earlier than in the past, before managed colonies reach optimal numbers from overwintering losses [18]. This mismatch means fewer viable floral resources precisely when bees' metabolic needs peak in early spring [5]. Late season heat waves also prematurely dry up many flower species, causing abrupt nutritional deficits [8].

Consequences of warming on honeybees jeopardize pollination services required to maintain wild plant communities and sustain crop yields. Up to 35% of food crops globally benefit from insect pollination, along with 87.5% of flowering plants [2]. Declining bee populations and foraging rates translate directly into reduced fruit and seed production for many pollinator-dependent crops like apples, cherries, squash, and almonds [19]. Farmers may face lower yields, smaller fruit size, and more misshapen produce without adequate bee visitation. Supplementing commercial honeybee hives provides temporary relief, but climate impacts on large-scale migratory operations limit availability and drive-up pollination rental costs for growers [15]. Additional research quantifying temperature thresholds for bees and identifying heat-resilient genetic stock can help guide strategies to safeguard essential pollinators in a warming world.

3 warmer winters increase honeybee susceptibility to Varroa mites

Rising winter temperatures driven by climate change allow greater survival and reproduction of Varroa mites, increasing parasitism of honeybees. Varroa is a devastating external parasite that feeds on the hemolymph of adult and pupal bees. Mite populations typically decline in winter but explode exponentially in spring and summer [20]. However, warmer winters enable more mites to persist over the cold season. Early spring buildup and higher infestation rates in summer result.

Higher overwintering mite loads correlate directly with weakened bee health and colony losses. Bees exhibit physical damage, reduced body weight, and wing deformities. Colonies often collapse prior to peak mite infestation in fall due to cumulative summer reproduction [21]. For example, UK winters warming by 1-2°C was associated with 5-10 times greater Varroa levels in spring [20].

Inadequate cold to naturally suppress mites also drives up chemical control costs for beekeepers. Reliance on miticides like tau-fluvalinate and coumaphos increases pesticide residues in hives while facilitating mite resistance [22]. However, selective breeding shows promise for increasing honeybee grooming behaviors and hygienic traits to better withstand Varroa parasitism even under warmer winters [23].

Varroa acts as a vector for many other bee viruses as well, exacerbating risks. Deformed wing virus, Israeli acute paralysis virus, and other pathogens replicate more rapidly in bees parasitized by Varroa [21]. Warmer overwinter conditions likewise enable greater viral loads within colonies. Altogether, climate change could increase overwinter losses of unmanaged honeybee colonies by up to 50% if mite impacts go unchecked [12].

The consequences for agriculture could be severe, as over 75% of global crop production relies on animal pollination services [2]. Sustaining resilient honeybee populations will require expanded mite monitoring and control programs. However, transitioning away from traditional miticides toward integrated pest management and breeding resistant stock can help limit mite impacts under increasingly mild winters.

4 Disrupted Synchrony: Earlier Spring Unaligns Bee Emergence and Flower Blooming

Climate change has caused an earlier spring onset of warming across temperate regions, advancing flower bloom schedules faster than bee emergence schedules can adapt. This mismatch in phenology deprives crucial early-season forage for bees, impacting colony buildup, health, and reproduction [24]. Flowering plants respond directly to temperature and spring immediately, while bees remain constrained by winter diapause and colony development rates [25]. Even small timing shifts of a few weeks can create significant nutritional deficits that combine with other stressors to affect bee populations.

For example, flower bloom advanced by over 2 weeks across central Massachusetts while bee emergence time held constant, resulting in pronounced phenological mismatch [26]. Apple trees in New York reached full bloom 3-4 weeks before adequate managed bee colonies were present in orchards for pollination [27]. Solitary bees also suffered starvation and losses when floral resources appeared before nest establishment [24].

Starvation, smaller colony sizes, and impaired development without early nutrition stress both commercial hives and wild bees. Queens produce fewer eggs without sufficient spring pollen, limiting colony growth and foraging capacity all season [28]. Forced to forage further or on alternative plants, bees show weakened immunity and reduced hygienic behaviors [3]. Declining bee populations also lower pollination redundancy, increasing crop yield risks.

Nearly 75% of leading global crops depend on insect pollination for fruit set and quality [2]. Strategies like ensuring floral strips with sequential blooming species or supplemental feeding may help provide bridging resources until bee forage is naturally abundant. However, mitigating climate change remains critical to realigning bee and flower phenology at scales beyond farmlands to sustain diverse pollinator populations.

5 Changes in Precipitation Patterns

5.1 Heavy rainfall prevents bees from foraging.

Increased precipitation variability as a result of climate change poses significant foraging challenges for honeybees. Prolonged heavy rainfall events prevent bees from flying out to collect pollen and nectar. Honeybees do not forage in rain because they cannot regulate their flight body temperature in cool, wet conditions [29]. Bees that become chilled and soaked are likely to die, creating selective pressure to avoid exiting the colony during rains. This evolutionary adaptation that once ensured colony survival now puts bees at risk from more extreme rainfall.

Modern honeybee colonies can withstand 1-2 days without foraging before food stores are critically depleted [30]. However, contemporary climate models project dramatic increases in the frequency and severity of heavy rainfall in many regions [31]. Back-to-back downpours of more than 2 inches per day increasingly force colonies to go upwards of a week without adequate nutrition [7]. Developing brood suffers immediate setbacks, while food reserves dwindle. Colonies already weakened by pesticide exposures or mite infestations often cannot recover once intense rains subside [17].

Several studies have directly linked multi-day heavy rainfall events to massive regional honeybee colony losses. For example, unusual late spring deluges in the Yucatan peninsula decimated over 50% of managed hives by preventing flight for 5-7 days during critical early season foraging [14]. Similarly, a week-long rainy period in Ontario, Canada correlated with 25% colony loss due to starvation when bees could not leave hives [32]. Honey stores and pollen supplies collected the previous season only last so long when new influx is halted.

These rain-induced nutritional deficits intersect with seasonal variations in flower availability. Torrential downpours in early spring and late fall are especially damaging, as fewer flowers are in bloom compared to summer [7]. Extreme rainfall compounded by fewer food options prevents colonies from building up strength after winter or storing adequate honey for overwintering. More exposed and isolated hives face exacerbated risks, indicating landscape factors like forage quality and diversity mediate the impacts of precipitation extremes [33].

Lost honey production and pollination services from rainfall-limited bee foraging stand to directly impact crop yields and farmer livelihoods. Nearly 75% of leading global crops benefit from pollinators [2]. Prolonged rains reduce bee movement among flowers, resulting in lower fruit set, decreased seed production, and stunted growth in crops like almonds, apples, blueberries, cucumbers, and onions [19]. Supplementing with commercial hives provides only partial compensation when inclement weather restricts even managed bees. Overall, climate models forecast increasing precipitation variability in important agricultural regions, highlighting the need for habitat conservation and climate adaptation strategies to lessen the consequences of rain events for bees and the crops they pollinate.

6 Flooding can destroy hives and nesting sites.

Increased frequency and severity of flooding driven by climate change poses direct threats to managed honeybee colonies and wild native bee populations by destroying hives and underground nesting sites. Intense storms and rainfall overwhelm landscapes, causing widespread flooding that can fully submerge hives and burrows for days or weeks [7]. Bees become trapped, drown, or are swept away by floodwaters along with their brood and food stores. The direct mortality and loss of established colonies decimates local bee populations relied upon as crop pollinators [34].

For managed hives, beekeepers suffer costly inventory losses and business disruptions from flood events. A single commercial apiary may contain hundreds of wooden hive boxes stacked in rows. Floods knock over and sweep away these vulnerabilities hives, especially in low-lying, river floodplain areas with fertile foraging habitat that attract beekeepers [35]. Historic inland and coastal flooding has wiped out up to 90% of hives in affected apiaries within hours [13]. Even in cases where hives remain physically intact, interior conditions deteriorate rapidly. Drowning adult bees cannot ventilate hives, feed larvae, or preserve food stores. Colonies require long rebuilding periods to recover former population sizes.

Wild, unmanaged bees face even greater exposure in underground burrows in the soil. 70% of native bee species nest in self-dug holes or small tunnels [36]. Intense precipitation saturates and inundates the soil, causing nests to flood. Entire local solitary bee populations can be extinguished if late-stage larvae and pupae submerge [37]. Declines in native pollinators intensify dependence on resilient managed honeybees, but frequent hive destruction impairs their compensatory capacity [34].

Reduced pollinator populations hinder crop yields for farmers. Nearly 75% of globally important crop plants rely on animal pollination for fruit production, seed set, and quality [2]. With fewer active bee colonies available after flooding, inadequate pollination lowers yields, decreases fruit sizes, and causes plant defects across crops like apples, blueberries, cucumbers, alfalfa, and soybeans [19]. Supplementing with commercial hives from non-flooded areas provides only partial buffering. Overall, climate models forecast increasing regional flood risks across agricultural watersheds and coastal areas due to more extreme precipitation and sea level rise [38]. Safeguarding bees to sustain crop pollination services will require reducing flood exposure through improved landscape and apiary site selection.

7 Drought limits floral resources that honeybees depend on:

Increasing frequency and severity of drought conditions driven by climate change threatens honeybee nutrition by limiting availability of flowering plants. Honeybees rely on nectar and pollen from blooming flowers as their sole food sources [29]. However, water stress during extended drought substantially reduces floral abundance and diversity across bee foraging landscapes [39]. With fewer viable plant species in bloom, colonies face inadequate access to the carbohydrates, proteins, lipids, vitamins, and minerals required to stimulate brood-rearing, produce honey stores, and maintain immunity [40]. These drought-induced nutritional deficits intersect with other stressors like parasites and pesticides to impair individual and colony-level bee health.

Multiple studies have directly linked drought intensity to decreasing floral cover. For example, sites experiencing extreme drought exhibited 65% lower flower density compared to average rainfall sites [41]. Similarly, flower species richness declined by over 50% during extreme versus moderate drought years in South African grasslands [42]. Even brief 1-2 week dry periods significantly reduce subsequent flower blooms of moisture-sensitive wildflower species that bees preferentially forage on [43]. Overall, climate projections forecast increasing aridity and reduced growing season precipitation across many important bee habitats and agricultural areas [44].

Drought-limited floral resources force honeybee colonies to compensate by flying longer distances to find sparse or alternative nourishment. However, further-flung foraging expends more energy while bringing back less total pollen and nectar. Colonies reared on drought-constrained forage produce fewer and smaller bees with lowered protein stores [45]. Reduced colony buildup and weakened immunity results in higher overwintering losses, leaving fewer resilient pollinators come spring [33].

Drought stress on floral resources reduces bee visitation, limiting pollination, yield, and quality for crops like almonds, apples, cherries, onions, squash, and berries [19]. Direct irrigation can mitigate impacts on crop flowers. However, sustaining resilient bee populations ultimately requires reducing drought frequency through climate mitigation and increasing floral diversity at broader scales through habitat restoration.

8 Effects on Pesticide Exposure

9 Hotter temperatures increase pesticide toxicity for bees.

Rising global temperatures as a result of climate change threaten honeybees by increasing the toxicity of pesticides bees encounter during foraging. Higher ambient temperatures have been experimentally shown to amplify the lethality of numerous chemical pesticides and fungicides for bees [46]. This occurs because heat speeds up bees' metabolic rates, while also increasing the bioavailability and reactivity of many pesticide compounds [47]. Even sublethal doses become hazardous when combined with additional energetic stress from heat. Compromised navigation, immunity, and colony growth can result from interactive pesticide-temperature effects.

Multiple studies demonstrate a direct link between increasing temperature and pesticide toxicity. For example, honeybees exposed to the common neonicotinoid insecticide imidacloprid experienced 10% greater mortality at 41°C versus 25°C ambient temperature [46]. The miticide tau-fluvalinate became four times more toxic at 34°C compared to 15°C [47]. Higher temperatures also increase pesticide toxicity in wild native bee species, including bumble bees [48]. Overall, field realistic temperature increases of just a few degrees Celsius make the difference between normal survival and widespread bee deaths after pesticide encounters.

Elevated pesticide toxicity under hot conditions becomes further exacerbated as climate warming alters typical bee foraging behavior and flower availability. Hot weather prompts bees to gather more water, leading to increased contact with tainted water sources near agricultural areas [8]. Higher temperatures also cause many mass flowering crops to transition more rapidly from bloom to post-bloom stages, depriving bees of quality forage [25]. Bees searching further afield are exposed to more pesticide-treated areas.

With bee populations already in decline, increased pesticide lethality under rising temperatures poses risks to the pollination services bees provide. Nearly 75% of leading global food crops benefit from animal pollination [2]. Pesticide exposure reduces bee foraging, learning, and navigation, resulting in less effective crop pollination even at sublethal levels [49]. Declining bee populations also lower pollination redundancy. Additional research quantifying the synergistic risks from heat and pesticides can help improve guidelines for agricultural chemical use under climate change. Reducing overall pesticide inputs by adopting sustainable practices remains key to ensuring food security.

10 Altered flowering schedules lead to more pesticide exposure.

Shifting flowering schedules driven by climate change led to greater pesticide exposure for bees foraging in agricultural areas. Rising temperatures are causing many plant species to bloom earlier in spring and transition more quickly through flowering stages [25]. However, crop planting schedules and pesticide spray regimens remain tied to the calendar rather than plant phenology. This mismatch results in flowering crops attracting more bee visitation after pesticide application, compared to historical synchrony between bloom period and chemical use [50]. More overlap means increased toxicity risk for bees gathering pollen and nectar.

Several regional analyses have quantified flower stage acceleration and linked earlier blooming to higher pesticide residues in bee colonies. Across Massachusetts, typical apple flowering advanced by 8 days over a century, while initial pesticide sprays held constant, increasing risk of exposure (Koh et al., 2016). Apple bloom accelerated by 4 weeks in New York was associated with 5-fold higher in-hive pesticides versus historical levels [50]. Oilseed rape blooming 23 days earlier in the UK corresponded to increased neonicotinoid contamination in pollen loads [50].

Further climate-induced changes may amplify exposure beyond bloom timing shifts. Higher temperatures drive faster pest insect development, prompting increased chemical applications [51]. More variable weather causes more frequent supplemental or preventative calendar sprays regardless of crop growth stage. Overall, estimates project a doubling of total bee exposure time to agricultural pesticides across US regions under climate change scenarios [52].

Elevated pesticide contact reduces colony health, foraging activity, and pollination services. Bees exposed during blooms show impaired navigation, flower handling, and learning [49]. Reduced populations and bee fitness lower crop pollination, yield, and quality. However, bee-safe application practices like night spraying or soil-targeted inputs can mitigate risks. Modeling optimal crop-specific spray schedules based on new climate-driven flowering phenology will be key to protecting bees in agricultural landscapes.

11 Extreme weather events spread pesticides from agricultural areas.

More frequent and intense storms, floods, and wind events driven by climate change spread agricultural pesticides into new areas, expanding bee exposure. Heavy rains wash pesticide residues from croplands into adjacent woodlands and prairie fragments [53]. Floodwaters contaminated with farm chemicals infiltrate wetlands many miles away [54]. High winds carry spray drift of pesticides hundreds of meters from application sites [34]. These climate extremes transport neurotoxic insecticides, fungicides, and herbicides into novel environments where they contact wild native bees and contaminate new foraging resources for managed bees.

Multiple regional analyses have linked extreme weather to increased pesticide presence in habitats bees occupy. For example, major flooding in Iowa spread agricultural pesticides up to 60 times higher concentrations into prairie strips and conservation reserve areas [55]. Runoff from blueberry fields after extreme rainfall in Quebec was found to fatally contaminate streams and riparian flowers foraging bees visited [56]. Following hurricanes, neonicotinoid residues were detected in pollen samples from previously isolated apiaries [57].

Honeybees and wild native bees lack mechanisms to evolve tolerance to synthetic pesticides infiltrating their ranges so suddenly [58]. Bees collecting contaminated pollen experience impaired learning, orientation, and immunity, reducing colony health and pollination services [49]. Solitary native bees face extinction of local populations after foraging from flowers laden with agricultural pesticides. Supplementing managed hives provides only partial buffering when pesticide infiltration is widespread across floral landscapes. However, enhancing natural habitat buffers along agricultural fields can help limit dispersal of chemicals during extreme weather. Overall, reducing reliance on pesticides via sustainable farming methods remains vital to protecting bees from intensifying climate instability.

12 Range Shifts

13 Climate change causes range shifts in bees and their floral resources

Climate warming is causing shifts in the geographic distributions of both honeybees and the wild flowering plants they rely on for forage. As temperatures rise, the habitable ranges for bees and flowers move poleward in latitude and upward in elevation to track suitable climate conditions [11]. However, plants and pollinators are responding at differing rates, resulting in spatial mismatch and disruption of plant-pollinator mutualisms [59]. Honeybees in particular may struggle to locate quality foraging resources in their new ranges without intentional management intervention.

Warming-driven range shifts have already been documented extensively. Over a century, the average latitude of bumble bee species across Europe and North America moved nearly 200 miles northward [11]. Half of plant species tracked similar poleward shifts, but the other half shifted very little or even contracted equatorward [60]. Mountainous areas exhibited altitudinal shifts, with plant and bee ranges moving upslope. Asynchrony is likely to increase as climate change accelerates the translocation of species.

Spatial mismatches create nutritional deficits, competition pressure, and decreased reproduction that threaten honeybee health and survival [61]. Colonies require a consistent, diverse mix of pollen and nectar. In new ranges lacking familiar forage, they show reduced colony growth, increased susceptibility to disease, and lower overwintering success [33]. Solitary bees also decline without essential host plants. Supplementing honeybee hives with protein does not compensate for lack of phytochemical diversity.

These nutritional limitations intersect with other climate impacts like increased pesticide exposure in agricultural areas colonized by shifting bees. Altogether, climate-driven range shifts may decrease honeybee populations up to 50% in historically suitable North American and European habitats by 2100 [5]. Sustaining bees and crop yields will require boosting floral diversity and modifying beekeeping practices to track range shifts. Additional modeling work can pinpoint which species and regions face the greatest asynchrony threats.

14 Migratory Beekeeping at a Crossroads: Navigating Uncertain Climate-Driven Range Shifts

Commercial migratory beekeeping practices in major agricultural regions face challenges tracking the shifting geographic ranges of honeybees driven by climate change. Controlled transport of managed hives follows fixed seasonal routes to provide crop pollination services and produce honey [62]. However, warming temperatures are pushing the habitable zones for bees poleward and upward faster than current migratory patterns can likely adjust [11]. Failure to keep pace with range shifts may reduce honeybee health and pollination services. The migration was also reported in *Apis floria* especially in hot areas [63].

Seasonal transhumance beekeeping routes evolved to take advantage of stable historical climates and flowering phenology. But anthropogenic climate change disrupts the synchrony. As warming accelerates range shifts, established migratory routes no longer optimally overlap with viable bee forage across seasons [5]. Colonies forced to overwinter in suboptimal southern climates or forage in altered northern ecologies exhibit decreased health and survivorship [33].

Rapid innovation in migratory practices could potentially realign bee translocation with new climate conditions. However, financial costs, logistical barriers, and policy restrictions on interstate movement may delay adaptation [64]. Stationary commercial operations focused on crop pollination face parallel challenges, as local forage conditions change around them. Altogether, the beekeeping industry estimates Managed colonies transported long distances already suffer more disease and colony loss [62]. Inadequate floral resources in new regions exacerbated by climate mismatch further reduce colony resilience.

Growers may face shortages of managed hives for rent and decreased pollination services from weakened colonies. Careful planning and coordination across sectors can modify beekeeping practices to better align with accelerating climate shifts and sustain food production [65].

15 **Impacts on Bee Health and Immunity**

16 Temperature extremes and malnutrition weaken Honeybee immunity

Increasing climate variability exposes honeybees to more frequent temperature extremes and nutritional stress that combine to weaken bee immune systems. Bees already function near their thermal limits [8]. Intense heat or cold events force colonies to devote more resources regulating hive temperature rather than to individual immunity [66]. Simultaneously, extreme weather limits foraging opportunities, resulting in inadequate or poor quality nutrition. Malnourishment impairs individual bee immunocompetence and further depresses colony-level defenses against pathogens [16]. These intersecting climate impacts leave colonies more susceptible to disease outbreaks.

Several controlled studies have directly demonstrated decreased immunocompetence in bees exposed to thermal stress and pollen shortages. Bees fed poor diets exhibited 60% lower expression of genes involved in pathogen defense compared to well-fed bees [67]. Short-term heat stress reduced production of antimicrobial peptides by bees subsequently infected with Nosema ceranae [68]. Combined nutritional deprivation and thermal extremes caused the greatest hindrance to mounting immune responses.

Colony-level immunosuppression occurs when individual bees cannot produce sufficient antimicrobial peptides and detoxification enzymes. Impaired social immunity enables more rapid spread of pathogens between nestmates [69]. Colonies stressed by inadequate nutrition and extreme temperatures also exhibit poor hygienic behaviors to remove diseased brood [70]. Reduced sanitation provides reservoirs sustaining viral, bacterial, and fungal infections within the hive.

With honeybee colonies already in global decline, interactions between worsening climate factors and immunity present significant concerns for agriculture. Up to 75% of leading global food crops benefit from pollination by healthy bee populations [2]. Growers may face production-limiting shortages if increasingly frequent weather extremes continue to facilitate bee disease outbreaks. Sustaining robust pollinator-dependent crops will require habitat conservation to provide diverse bee forage across seasons and selective breeding to enhance immune expression.

17 Enhanced Vulnerability of Honeybees to Parasites, Pathogens, and Diseases Under Warming Conditions:

Rising global temperatures as a result of climate change are increasing the vulnerability of honeybees to harmful parasites, pathogens, and diseases. Higher temperatures directly accelerate the replication cycles of many bee infections [71]. Warmer conditions also weaken bee immune defenses, creating favorable conditions for outbreaks. In addition, hotter weather enables ranges expansions for exotic parasites and pathogens into new regions. These compounding factors are facilitating bee disease emergence and transmission, highlighting the urgency of developing mitigation strategies.

The parasitic Varroa destructor mite poses one of the greatest threats amplified by climate change. Varroa populations can double in as little as 10 days at peak summer temperatures [4]. Bees expend crucial resources attempting to regulate hive temperatures against overheating. Colonies stressed by heat and mites exhibit reduced hygienic behaviors, further accelerating mite growth [70]. Higher temperatures also increase viral titers associated with Varroa, leading to more infections.

Climate warming similarly expands occurrence of fungal and bacterial diseases. Nosema ceranae fungal loads increase at warmer temperatures, while heat-stressed bees show weakened immune defenses [72]. Higher temperatures are implicated in historic expansions of European Foulbrood, enabling these bacteria to emerge as a global honeybee killer [73]. Ranges for Chronic Bee Paralysis Virus and Israeli Acute Paralysis Virus shifted poleward as temperatures warmed [74].

Invasions of the Tropilaelaps mite and Africanized honeybees via climate-driven range expansion present additional threats to managed European honeybees. Reduced winter cold limits act historically contained these tropical parasites and aggressive bee subspecies [4]. But warming enables their spread into temperate regions, posing risks of novel disease transmission.

With honeybee colonies already in decline, increased disease susceptibility due to climate change poses significant concerns for pollination services. Nearly 75% of global crops depend on animal pollination for fruit set, yield, and quality [2]. Sustaining resilient, healthy bee populations will require expanded disease monitoring and prevention programs, selective breeding efforts, and climate mitigation to slow the conditions promoting epidemics.

18 Conclusions

19 How multiple climate factors combine to threaten bee diversity:

The cumulative impacts of climate change via multiple interacting stressors present significant threats to managed honeybee colonies and wild native bee abundance and diversity. Higher temperatures, shifting precipitation patterns, increased frequency of extreme weather, and range shifts combine to weaken bee health through mechanisms such as altered phenology, reduced foraging, worsened disease impacts, and pesticide exposure [5]. These climate factors also facilitate migration of non-native parasites and pathogens into new regions, furthering jeopardizing bee communities. Overall, models project steep future declines in populations of both generalist honeybees and specialist native bees across much of North America, Europe, and South America without targeted conservation efforts.

Estimates suggest a single magnitude of 1°C warming in the continental US and Europe could extirpate up to 49% of bumble bee species, while only 2°C warming may lead to range losses of up to 36% for honeybees [5]. Combining these temperature impacts with increased frequency of extreme rainfall, heatwaves, or drought based on climate projections drastically increases extinction risks for bees in a given region. Declining bee populations directly translate into reduced pollination services, as over 75% of global crops benefit from insect pollination [2].

However, habitat restoration, pesticide restrictions, and climate change mitigation initiatives can offset some detrimental impacts on bees. Planting diverse floral strips promotes bee nutrition and buffers weather variability [75]. Organic farming methods eliminate pesticide risks. Reducing the pace of continued emissions avoids the most severe climate disruption scenarios. A multifaceted approach across sectors will be necessary to sustain pollinators in a rapidly changing climate.

20 Models projecting future declines in bee populations without intervention

Predictive models forecast steep regional declines in managed honeybee colonies and wild native bee abundance across North America, Europe, and South America over the coming decades if climate change continues unabated. Models incorporate known climate impacts like warming temperatures, increased pesticide exposures, and reduced forage resources to estimate future bee population trajectories [5]. Simulations consistently show unsustainable colony losses between now and 2100 in the absence of targeted conservation efforts.

For example, models suggest average honeybee colony losses approaching 50% in the Upper Midwest region of the U.S. by mid-century due solely to climate-driven reductions in floral resources [7]. Under a high emissions scenario, half of bumble bee species in Europe and North America may experience range contractions and population collapses within 50 years [11]. Even slight additional warming could triple extinction risks for specialist native bees already in decline [5].

These projected losses raise significant food security concerns, as over 75% of leading global crops depend on animal pollination services for optimal yield and quality [2]. However, simulations indicate habitat restoration, chemical use restrictions, reduced greenhouse gas emissions, and other interventions could prevent the worst case declines. Targeted modeling enables identification of vulnerable species and regions to prioritize conservation attention.

Sustaining resilient bee populations amidst intensifying climate pressures will require proactive policies informed by ecological models to limit future declines. Failing to act risks widespread pollinator extinctions and subsequent crop production losses. But collaborative mitigation strategies can safeguard essential pollination services.

21 Protecting bees requiring habitat conservation and climate change mitigation:

Safeguarding managed honeybee colonies and wild native bee populations from intensifying climate change impacts will require coordinated efforts in habitat conservation and climate change mitigation. Protecting diverse floral resources and nesting sites enables bees to withstand temperature extremes, shifting seasons, heavy rains, and drought [76]. Reducing the pace of continued warming avoids exceeding bees' physiological limits. Combining sustainable land management with greenhouse gas emissions reductions is key to ensuring viable bee populations.

Targeted habitat restoration around farms and across broader landscapes provides bees with supplemental nutrition and shelters them from exposure to pesticides, parasites, and extreme weather [77]. Planting wildflower field margins and creating linear bee habitats along roads diversifies foraging options. Protecting woodlands, grasslands, and diverse natural areas preserves nesting sites and food sources. Organic farming eliminates pesticide toxicity risks on both crops and adjacent flowers bees utilize.

However, curbing the magnitude of climate warming through policy remains essential to facilitating bee adaptation. The Paris Agreement's goal of limiting global temperature rise to 1.5°C may reduce range contractions for some bumble bees by 66% versus 2°C warming [78]. Phasing out greenhouse gas emissions from fossil fuel burning avoids creating conditions that exceed bees' resilience limits.

Sustained crop pollination services and conservation of wild bee diversity ultimately depend on simultaneous efforts across scales to provide habitat refugia in the context of an equilibrating climate system [79]. Holistic initiatives accounting for land, energy, and ecological factors offer the best chance of preserving abundant and diverse bee populations in the future [80-106].

22 Recommendations

- Increase floral diversity in farms, roadsides, and natural areas to improve bee forage.
- Transition to organic methods and sustainable pest management to reduce toxicity risks.
- Selectively breed bees for resilience to higher temperatures, drought, and diseases.
- Adjust beekeeping practices and transportation to track shifting floral ranges.
- Expanded funding for research quantifying climate threshold impacts on bees.

23 Future Research:

- Identify temperature, pesticide, and nutritional interaction effects on bee immunity.
- Elucidate how shifting seasons impact colony development and health.
- Model future changes in bee geographic distributions and floral resource availability.
- Quantify economic costs of climate impacts on pollination services.
- Develop regional climate adaptation strategies for apiaries and wild bee habitats.

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25 Competing interests

The authors declare that there are no competing interests.

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