



Multifactorial drivers and synergistic mechanisms underlying global bee decline: Ecological, agricultural, and human health consequences

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Abstract

Animal pollination is a foundational ecosystem service that sustains global biodiversity, agricultural productivity, and human nutrition, with bees representing the most ecologically and economically significant pollinator group. Mounting evidence over the past three decades documents widespread and accelerating declines in both wild and managed bee populations across multiple continents. This review synthesizes current knowledge on the ecological roles of bees, global and regional patterns of decline, species-specific vulnerabilities, and the interacting drivers underlying the pollinator crisis. The global bee decline cannot be attributed to a single stressor but instead arises from synergistic interactions among pesticides, habitat loss and fragmentation, climate change, pathogens, and emerging mechanisms such as gut microbiome disruption. Evidence indicates that these stressors often operate multiplicatively rather than additively, amplifying physiological impairment, reducing reproductive success, and destabilizing populations at landscape scales. Although managed honey bee colony numbers appear stable in some regions, this stability masks substantial losses in wild bees and feral honey bee populations, which provide irreplaceable ecological functions and functional diversity. The review further highlights geographic inequities in data availability and conservation capacity, with biodiversity-rich tropical regions facing the most significant knowledge gaps. The consequences of pollinator decline extend beyond crop yields to ecosystem stability, food security, nutritional health, and economic resilience, particularly in low-income nations that are disproportionately dependent on pollinator-mediated agriculture. While limited examples of evolutionary and behavioral adaptation—such as *Varroa*-resistant honey bee populations—offer cautious optimism, these adaptive responses remain insufficient to counteract intensifying environmental pressures. Effective mitigation therefore requires integrated strategies that simultaneously reduce pesticide exposure, restore and reconnect semi-natural habitats, manage pathogen spillover, and incorporate climate resilience into conservation planning. Addressing pollinator decline is not solely a biodiversity imperative but a prerequisite for sustaining ecosystem function, agricultural systems, and human well-being in a rapidly changing world.

Keywords: Pollinator crisis, bees, pesticides, pathogens, *Varroa* mite, habitat loss, habitat fragmentation, climate change, synergistic stressors, agricultural productivity, conservation planning

Introduction

Animal pollination represents one of the most critical ecosystem services underpinning global biodiversity and agricultural productivity. Among pollinating taxa, bees (order Hymenoptera) stand as the most ecologically and economically significant group, facilitating reproduction in approximately 87% of flowering plant species and contributing directly to the production of 75% of leading global food crops [1, 2]. The ecological value of these interactions extends far beyond simple food production, as plant-pollinator networks form the foundational architecture of terrestrial ecosystems, supporting complex food webs and maintaining genetic diversity across plant populations. Current estimates suggest that 5-8% of global agricultural production, equivalent to \$235-577 billion annually, depends directly on animal pollinators, with bees accounting for the majority of this service [3, 4].

However, over the past three decades, mounting evidence has documented alarming declines in both wild and managed bee populations across multiple geographic regions. The phenomenon, increasingly recognized as the 'pollinator crisis,' has emerged as a defining conservation challenge of the 21st century. Regional assessments have confirmed substantial pollinator declines in northwestern Europe and North America, with preliminary evidence suggesting similar trends in South America, Asia, and other regions, though comprehensive data remain limited outside

well-studied areas [3, 5]. A landmark 2021 study analyzing over a century of global biodiversity data revealed that bee species richness declined by approximately 25% between 2006-2015 [39] compared to pre-1990 levels, with declines accelerating markedly after the 1990s [6]. More recent regional analyses confirm that these trends continue unabated. In western North America, once-common species such as the western bumble bee (*Bombus occidentalis*) have experienced precipitous population collapses, with projections suggesting additional declines of 51-97% by the 2050s under current trajectories [7].

Previous reviews of the pollinator crisis have addressed individual stressors in depth — particularly neonicotinoid pesticides [8], habitat loss [5], climate change, and pathogen pressure [9] — or have focused on specific taxonomic groups or geographic regions. However, three critical analytical gaps remain unaddressed in the existing literature. First, no comprehensive review has systematically examined the evidence for synergistic rather than merely additive interactions among these stressors, and the profound conservation implications that follow from this distinction. Second, the consequences of pollinator decline have been framed predominantly in ecological and economic terms, without adequate integration of the rapidly accumulating evidence on direct human health outcomes. Third, existing reviews have not sufficiently articulated the geographic inequity dimension of the crisis — the disproportionate

concentration of both pollinator loss and its consequences in low-income, biodiversity-rich nations that bear the greatest burden while possessing the least adaptive capacity.

To develop these arguments, this review synthesises current scientific understanding of the pollinator crisis with particular emphasis on bees as the taxonomic group of greatest ecological and economic significance. While other pollinating taxa — including butterflies, flies, beetles, and vertebrate pollinators — make significant contributions, the critical ecological and economic importance of bees justifies their central position in this analysis. The scope of this review encompasses both wild and managed bee species, with a taxonomic focus on major pollinating groups including honey bees (*Apis* spp.), bumble bees (*Bombus* spp.), stingless bees, and solitary bees (including Megachilidae, Halictidae, and Andrenidae). The review examines the evidence for population declines across geographic regions and taxa, analyses the proximate and ultimate drivers of these declines with specific attention to their synergistic interactions, evaluates the cascading consequences for agricultural productivity, food security, human health, and ecosystem stability, and identifies the critical knowledge gaps that constrain evidence-based conservation in precisely those regions where the need is most acute.

Geographically, the current review draws primarily on studies from North America, Europe, and emerging research from Asia and South America, while highlighting regions where data remain critically insufficient. Temporally, the present analysis emphasizes trends documented over the past three decades (1990-present), with particular attention to accelerating changes observed since 2010.

The Ecological Role of Bees

1. Pollination Biology: Mechanisms and Functional Diversity

Pollination occurs when bees transfer pollen grains—containing male gametes—from the anthers of one flower to the stigma of another flower (or to the same flower), thereby enabling fertilization and subsequent seed production. Bees are uniquely effective pollinators because their morphology and behavior are specialized for pollen collection and transfer^[10]. Unlike many other flower-visiting insects that primarily consume nectar, bees actively collect pollen as a protein source for their larvae, resulting in frequent and direct contact with plant reproductive structures. Their branched body hairs enhance pollen adherence, while behavioral traits such as flower constancy—the tendency to repeatedly visit flowers of the same species during a foraging bout, often with individual foragers visiting hundreds to thousands of flowers in succession—increase conspecific pollen transfer and reproductive efficiency^[11].

Certain taxa, particularly bumble bees and many solitary species, are capable of performing buzz pollination (floral sonication), a specialized behavior that facilitates pollen release from poricidal anthers in numerous wild plants and economically important crops. Although this ability is not universal across all bee groups, such functional diversity in pollination strategies enhances the reproductive success of a broad spectrum of flowering plants. Importantly, pollination effectiveness varies among bee taxa and body sizes, and diverse bee assemblages provide more stable and complementary pollination services than any single species alone. This functional complementarity underpins the

resilience of plant–pollinator networks in both natural and agricultural systems^[12, 13].

2. Diversity of Bee Species and Their Specialized Roles

Bees (Insecta: Hymenoptera: Apoidea: Anthophila) constitute one of the most diverse groups of pollinators, with approximately 20,000 described species distributed across seven families: Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae, Melittidae, and Stenotritidae^[14]. This remarkable taxonomic and functional diversity translates into extraordinary variation in body size (from 2 mm to over 40 mm), nesting behavior, social organization, phenology, and floral specialization — attributes that collectively determine the structure and stability of pollination networks^[15]. Recent empirical evidence demonstrates that maintaining high bee species richness is essential for sustaining pollination services across temporal scales^[16].

Managed honey bees (*Apis* spp.), particularly the Western honey bee (*Apis mellifera*), dominate global agricultural pollination services due to their large colony sizes, generalist foraging behavior, and ease of transport. However, they represent only a small fraction of global bee biodiversity and cannot substitute for the full functional breadth of wild pollinator communities. Bumble bees (*Bombus* spp.) are especially important in temperate and high-elevation ecosystems and for crops that require buzz pollination. Stingless bees (tribe Meliponini) dominate many tropical systems, whereas solitary bees—comprising approximately 90% of described bee species—include numerous specialists that are essential for maintaining plant reproductive success in both natural and semi-natural habitats^[11, 17].

The ecological and agricultural stability of pollination systems therefore depends not on a single managed species but on diverse pollinator assemblages that collectively buffer environmental variability and sustain plant reproduction across spatial and temporal scales^[18].

3. Ecological Roles and Ecosystem Services Beyond Food Production

In wild ecosystems, bees pollinate an estimated 87% of flowering plant species, thereby maintaining plant genetic diversity, supporting recruitment, and structuring plant community composition^[1, 19]. These plant–pollinator interactions constitute a foundational component of terrestrial food webs, as the fruits and seeds produced through bee-mediated pollination provide essential resources for granivorous and frugivorous insects, birds, and mammals. Recent ecological research indicates that the loss of pollination services can trigger cascading trophic effects across entire ecosystems: reduced seed production diminishes food availability for seed consumers, while decreased fruit production affects frugivore populations and, consequently, predators at higher trophic levels^[3].

Beyond their direct contributions to crop yields, bees play fundamental roles in sustaining ecosystem structure and function. By facilitating outcrossing and promoting gene flow among plant populations, they maintain heterozygosity, reduce inbreeding depression, and enhance adaptive potential under environmental change. In fragmented landscapes, the loss of pollinator connectivity can accelerate genetic erosion in plant communities, compounding biodiversity decline and reducing ecosystem resilience^[20, 21].

Bees also influence ecosystem processes through their nesting activities. In systems dominated by ground-nesting species, nest excavation modifies soil structure, enhances aeration, and affects nutrient cycling. These activities create microhabitats that benefit soil-dwelling organisms and can improve local plant productivity by enhancing root growth conditions. Additionally, the organic materials incorporated into nests—including pollen, nectar, plant resins, and leaf fragments—contribute to localized nutrient enrichment [1, 3, 20, 21].

Moreover, bee communities serve as sensitive bioindicators of environmental quality, reflecting landscape heterogeneity, floral resource availability, and levels of chemical exposure. Declines in bee diversity and abundance therefore often signal broader environmental degradation affecting multiple taxa. Conservation of bee diversity is thus inseparable from the preservation of ecosystem resilience, plant diversity, and long-term ecological stability [13].

Evidence of Bee Population Decline

1. Global Patterns and Temporal Trends

The accumulation of occurrence data spanning more than a century has enabled the first comprehensive assessments of global bee population trends, revealing widespread and accelerating declines across multiple taxonomic groups and geographic regions. Analysis of over 6.8 million occurrence records from the Global Biodiversity Information Facility (GBIF) demonstrates that the number of bee species being recorded has decreased steeply since the 1990s, with approximately 25% fewer species documented between 2006 and 2015 compared to pre-1990 levels [6]. This decline represents a profound shift from historical patterns — the diversity of collected bee species in the 2010s was approximately half that observed in the 1950s, indicating not merely localized extirpations but widespread range contractions and genuine species losses [6]. While these patterns must be interpreted cautiously given potential biases in data collection intensity, taxonomic expertise availability, and reporting effort across time periods, the consistency and magnitude of observed declines across independent datasets suggest that genuine biological changes are occurring.

Bumble bees have experienced especially precipitous population collapses — relative abundances of several North American species have declined by up to 96% over recent decades, with formerly abundant species now occupying drastically reduced portions of their historical ranges [2]. Recent modeling studies project that these declines will intensify: between 38-76% of European bumble bee species currently classified as 'Least Concern' on the IUCN Red List are expected to lose at least 30% of their ecologically suitable habitat by 2061-2080 under various climate and land use scenarios [22]. Even under the most optimistic projections, bumble bee populations are anticipated to continue declining across nearly half of the regions in their current range. For managed honey bee populations, trends are more complex and geographically heterogeneous. While acute colony losses remain alarmingly high — United States beekeepers reported losses of 48.2% of colonies from April 2022 [23] to April 2023, with a 12-year average annual mortality rate of approximately 40% — nevertheless, total colony numbers have remained relatively stable in North America owing to intensive management interventions including colony splitting, queen replacement, and package bee purchases [23, 24].

Critically, the apparent stability or even growth in managed honey bee populations globally masks severe declines in wild bee populations, including feral honey bee colonies. The population trends of wild western honey bees (*Apis mellifera*) have been neglected by conservationists because the species has been considered to consist of managed colonies only. New data suggest that wild honey bee colonies make up one sixth to one fifth of the overall European honey bee population, with wild colonies currently representing demographic sinks in six of seven assessed countries and an estimated population decline of 56% per decade — meeting IUCN criteria for classification as 'Endangered' [25, 26]. This distinction between managed and wild populations is crucial, as wild bees provide irreplaceable ecological services that managed colonies cannot fully substitute, including specialized pollination of native flora, maintenance of plant-pollinator network stability, and resilience to environmental disturbances that disproportionately affect large-scale commercial operations. Compounding this concern, accumulating evidence suggests that high-density managed honey bee populations may themselves contribute to wild bee suppression through several interacting mechanisms — meaning that the expansion of managed apiculture used to compensate for pollination deficits may inadvertently accelerate the very wild bee declines it is intended to offset. Floral resource competition represents the most extensively documented mechanism: in landscapes with high managed colony densities, honey bees monopolise nectar and pollen resources, reducing foraging success and reproductive output for wild bee species foraging within overlapping ranges. Mallinger *et al.* (2017) [27], in a meta-analysis of 19 studies across multiple continents, found that honey bee presence was associated with significantly reduced wild bee abundance and species richness, with effects most pronounced in resource-limited landscapes where floral diversity and availability were already constrained by agricultural intensification [27]. Lindström *et al.* (2016) [28] corroborated these findings in a Swedish landscape study, demonstrating that proximity to managed apiaries negatively predicted wild bee abundance independently of habitat quality. Pathogen spillover represents an equally serious but less visible mechanism of suppression [28]. Managed honey bee colonies harbour elevated loads of pathogens — including *Nosema ceranae*, deformed wing virus, and trypanosomatid parasites — that can be transmitted to wild bees via shared floral resources, with foraging bees depositing infectious particles on flower surfaces that are subsequently contacted by wild bee visitors [29]. Spillover transmission has been documented for multiple bumble bee species and has been implicated in population-level declines in wild *Bombus* populations following the introduction of commercially reared colonies into previously naive regions. These findings carry a direct and uncomfortable implication for conservation policy: recommendations to expand managed honey bee populations as a solution to pollination deficits must be evaluated against the evidence that doing so in ecologically sensitive or resource-limited landscapes may suppress wild pollinator communities, reducing the very functional diversity and resilience that managed colonies cannot replicate.

2. Regional Variations in Decline Patterns

North America: North America exhibits some of the most extensively documented bee declines, with particularly severe impacts in western and southern regions (Figure 1). Species distribution modeling of major bee and butterfly families reveals declining species richness throughout western North America over the past century, contrasting with disproportionate increases in eastern regions^[30]. Wild bee declines in North America appear particularly acute for formerly common generalist species, challenging earlier assumptions that widespread, ecologically flexible taxa would be buffered against environmental change. The once-abundant western bumble bee (*Bombus occidentalis*) has undergone a 57% decline in occurrence across its historical range between 1998 and 2020, driven primarily by increasing summer temperatures, drought conditions, and neonicotinoid pesticide exposure^[7]. Future projections suggest this species will experience additional declines of 51-97% by the 2050s depending on climate scenario, with some degree of decline projected across all modeled warming scenarios. California — which produces over half of the United States' fresh produce and depends heavily on pollination services — experienced its largest recorded managed colony loss rate in recent years, with weighted average winter losses of 82.95% from 2022 to 2023^[23, 24].

Europe: European wild bee populations face severe and multifaceted threats, with recent comprehensive assessments revealing the full scale of the conservation crisis. The most recent IUCN European Red List assessment documents that 172 of 1,928 evaluated wild bee species — approximately 9% of the regional fauna — are now threatened with extinction, representing a dramatic increase from 77 species (4%) classified as threatened in 2014^[31]. This substantial increase reflects both genuine population declines and improved knowledge, as the proportion of Data Deficient species decreased from 57% to 14% over the same period, enabling more comprehensive threat assessments. According to the most recent available trend data, 7.7% of species exhibit declining population trends, while 12.6% remain stable and only 0.7% are increasing — alarmingly, trends for the remaining 79% remain unknown^[32]. Bumble bees face particularly dire prospects, with 25.8% of European species classified as threatened. The common buff-tailed bumble bee (*Bombus terrestris*), currently widespread across temperate Europe, is projected to see its southern distribution limit retreat from the Sahara Desert to the Loire Valley in central France by 2080 as warming temperatures exceed thermal tolerance limits^[22]. The EU has identified pollinator decline as one of the largest threats to European nature, human wellbeing, and food security, noting that one in three bee, butterfly, and hoverfly species are disappearing, prompting the 2023^[89] 'New Deal for Pollinators' initiative aimed at reversing declines by 2030^[33].

Asia: The situation in Asia presents a complex and often contrasting picture, with managed bee populations showing increases in some countries while native wild bee populations face severe pressures. Managed honey bee populations have increased substantially in major honey-producing nations — particularly China and India — driven by commercial beekeeping expansion to meet domestic and international honey demand. However, these increases in

managed colonies coincide with mounting evidence of wild bee declines (Figure 1), particularly in regions undergoing rapid agricultural intensification^[34]. In western Nepal, comprehensive surveys of traditional beekeepers managing the native *Apis cerana cerana* revealed that 76% of beekeepers reported declines in honey bee populations, while 86% and 78% reported decreases in honey yield and number of occupied hives, respectively^[34]. Quantitative data confirmed these perceptions — honey yield per hive fell by 50% between 2012 and 2022, while the number of occupied hives decreased by 44%. Beekeepers identified climate change and declining flower abundance as the primary drivers of these declines, raising concerns for regional food and economic security given that honey sales contribute 16% of total household income and *A. cerana* provides critical pollination services for local crops. Climate suitability modeling suggests divergent future trajectories across the Asian continent — approximately 18 species may experience expanded suitable habitat (averaging 99% increases), while 27 species face projected declines of 47% in high-suitability areas by 2070 under severe climate scenarios^[35].

Other Regions: Beyond Asia, data on bee population trends in South America, Africa, and Oceania remain limited compared to northern temperate regions, though available evidence suggests similar patterns of decline. Continental-scale analyses of GBIF occurrence records indicate sustained decreases in bee species richness in Africa since the 1990s, while Asian declines appear to have commenced two to three decades earlier^[22]. Australia faces a particularly concerning trajectory, with models predicting increased climate suitability for only 9 bee species (averaging 16.3% gains) compared to 97 species experiencing declines by mid-century. The scarcity of long-term monitoring data in tropical and subtropical regions — which harbor the greatest bee diversity globally — represents a critical knowledge gap limiting our ability to assess the true global extent of pollinator decline and develop effective regional conservation strategies^[22].

3. Species-Specific Declines and Conservation Status

While broad taxonomic and geographic patterns reveal concerning trends, examination of individual species trajectories provides critical insight into the mechanisms driving bee decline and identifies taxa requiring urgent conservation intervention. Species-level analyses reveal that decline is not uniform across functional groups — social bees, specialist pollinators, and species with restricted ranges face disproportionate extinction risks compared to solitary generalists with broad geographic distributions. Nevertheless, mounting evidence challenges the assumption that common, widespread species are immune to decline, with several formerly abundant taxa now experiencing rapid population collapses.

Bumble bees represent the most extensively studied group of declining wild bees, with conservation assessments identifying multiple species as imperiled. The rusty patched bumble bee (*Bombus affinis*) was historically one of the most common bumble bee species in eastern North America but experienced a relative abundance decline of up to 95% and an estimated 87% contraction of its geographic range since the late 1990s, leading to its listing under the U.S. Endangered Species Act in 2017 — the first bumble bee

species in the continental United States to receive such protection [36, 37, 38]. Similarly, the western bumble bee has contracted from extensive portions of its former range across western North America, with climate change and pesticide exposure identified as proximate drivers [7]. In Europe, the Mediterranean species *Andrena transitoria* — formerly common across a range extending from Sicily to Ukraine and into Central Asia — has declined by 30% over the past decade due to agricultural intensification, with local extinctions documented in several countries [32, 35]. European populations of the buff-tailed bumble bee face projected extirpations from southern portions of their range, with suitable habitat shifting northward beyond the dispersal capacity of most populations.

Wild honey bee populations, often overlooked in conservation assessments that focus on managed colonies, face severe demographic challenges. Recent recognition that substantial populations of feral *A. mellifera* persist in Europe has prompted formal conservation evaluation, revealing that these wild populations function as demographic sinks with colony survival rates insufficient for population maintenance [25, 26]. The 56% per decade population decline observed across six European countries meets IUCN Red List criteria for 'Endangered' status, highlighting that managed apiculture practices alone cannot ensure the persistence of self-sustaining wild populations.

Critical data limitations constrain our understanding of species-specific decline patterns, particularly for regions outside Europe and North America and for taxonomic groups receiving less research attention than bumble bees and honey bees. The European bee fauna exemplifies this challenge — despite comprising nearly 2,000 species, population trends remain unknown for 79% of taxa, severely limiting conservation prioritization and resource allocation [32]. For tropical and subtropical regions harboring peak bee diversity, baseline surveys remain incomplete, *let alone* the time-series data necessary to detect population trends. This geographic and taxonomic bias in monitoring effort creates a compounding knowledge deficit — the regions and taxa most likely experiencing severe declines are precisely those for which evidence remains most limited, potentially masking the true global magnitude of the pollinator crisis and delaying conservation interventions until populations have crossed irreversible thresholds.

4. Drivers of Bee Population Decline

The decline of bee populations documented across multiple continents reflects not a single catastrophic stressor but rather a complex network of interacting drivers that operate across multiple spatial and temporal scales. While habitat loss, pesticides, climate change, and pathogens each pose significant independent threats to bee populations (Figure 2), mounting evidence suggests that synergistic interactions among these stressors amplify their individual effects, creating conditions where bees face compounding challenges that exceed the sum of individual threats [39]. Understanding these drivers and their interactions is essential for developing effective conservation strategies capable of reversing current decline trajectories.

1. Pesticides and Agrochemicals

Synthetic pesticides—particularly systemic insecticides—represent one of the most intensively studied drivers of bee decline. Among these, neonicotinoids have received

sustained scientific scrutiny because of their widespread prophylactic use and well-documented effects on bee behavior, reproduction, and survival [40]. Applied primarily as seed coatings across millions of hectares worldwide, these compounds are absorbed into plant tissues, including nectar and pollen, resulting in chronic exposure for foraging bees. Woodcock *et al.* (2016) [41], in an 18-year longitudinal study of 62 wild bee species across English agricultural landscapes, provided the first population-level evidence directly linking neonicotinoid use to wild bee declines [41]. Evidence for pesticide-driven bee decline now spans laboratory, semi-field, and large-scale field investigations. At the organismal level, sublethal exposure impairs navigation, foraging efficiency, immune function, and reproductive success. At the colony level, exposure reduces brood development and long-term stability [42]. Most compelling, however, are population-scale analyses demonstrating ecological consequences beyond individual species. A comprehensive assessment of pesticide effects on wild bee communities found that increasing neonicotinoid and pyrethroid use was associated with widespread occupancy declines across hundreds of North American bee species, representing the first evidence that pesticide impacts extend beyond focal taxa to depress entire assemblages [40]. This conclusion was based on 178,589 observations spanning 1,081 species over a 20-year period (1995–2015), a dataset sufficiently large to detect community-level patterns that smaller studies cannot resolve.

Importantly, pesticide effects rarely occur in isolation. A growing body of evidence indicates that fungicides—often assumed to pose minimal risk to pollinators—can amplify insecticide toxicity under field-realistic conditions. Experimental and semi-field studies demonstrate that co-exposure to commonly applied fungicides and neonicotinoids increases worker mortality and can exacerbate *Varroa destructor* infestation beyond the effects of either stressor alone. Such findings expose a key limitation of conventional risk assessment frameworks, which typically evaluate active ingredients individually rather than under the mixture conditions characteristic of real agricultural landscapes [43, 44].

Environmental persistence further broadens exposure pathways. Only a fraction of applied systemic insecticides is taken up by crops; the remainder accumulates in soils and disperses into adjacent habitats through dust drift and water movement. Field studies consistently detect residues in non-crop wildflowers growing near treated fields, demonstrating that bees are exposed beyond the flowering period of treated crops and across broader landscapes than regulatory models often assume [45]. Consequently, conservation areas and restored habitats embedded within agricultural matrices are not insulated from chemical exposure.

Regulatory responses vary internationally, with some jurisdictions restricting or banning outdoor uses of key neonicotinoids, while others continue widespread application. However, a central concern extends beyond individual compounds to the broader issue of chemical substitution. As restrictions have tightened in certain regions, newer insecticides—including sulfoximines and butenolides—have entered markets as replacements. Although chemically distinct, these compounds act through similar neurotoxic mechanisms and have been shown to impair bee reproduction, flight performance, and behavior

under realistic exposure conditions^[44, 46]. This pattern exemplifies what environmental scientists call “regrettable substitution,” wherein one harmful chemical class is replaced by functionally analogous compounds without materially reducing ecological risk.

Collectively, the evidence indicates that pesticide impacts on bees operate across multiple biological levels—from sublethal physiological impairment to population-scale declines—and interact with other stressors, including pathogens and habitat loss. Landscape-scale analyses further suggest that pesticide hazards reduce wild bee abundance and diversity independently of surrounding habitat composition, implying that habitat restoration alone is unlikely to offset chemical pressures in intensively managed systems^[40].

The policy implications extend beyond restricting individual compounds. Risk assessment frameworks must account for mixture toxicity, chronic sublethal exposure, and mechanism-based evaluation of new insecticides prior to widespread adoption. Without such structural reform, reductions in one pesticide class may be offset by the introduction of another with comparable ecological consequences. Integrated Pest Management (IPM) approaches, which apply targeted treatments only when pest populations exceed economically significant thresholds, have achieved up to 95% reductions in total insecticide applications while maintaining or enhancing crop yields through the conservation of wild pollinators and natural pest control agents^[47].

2. Habitat Loss and Fragmentation

Habitat loss and fragmentation driven by agricultural intensification and urban expansion represent foundational drivers of pollinator decline. These processes eliminate or degrade the floral and nesting resources essential for bee survival and reproduction. Agricultural intensification—the process of increasing productivity through monoculture cropping, mechanization, and agrochemical inputs—has fundamentally transformed landscapes globally, converting species-rich grasslands, prairies, hedgerows, and meadows into homogeneous crop fields that provide ephemeral floral resources during brief bloom periods but offer negligible forage or nesting opportunities during the remainder of the year. This landscape simplification reduces both the abundance and diversity of flowering plants, removing the temporal continuity of floral resources that bees require to sustain colonies from early spring through late autumn. High-intensification agricultural landscapes host only half the bee species diversity of low-intensification landscapes, reflecting the direct relationship between landscape heterogeneity and pollinator community richness^[48].

The mechanisms through which habitat loss affects bees operate at multiple spatial scales and impact multiple life stages. At local scales (within 100–500 meters), bees require diverse floral resources providing continuous nectar and pollen availability throughout their active season, as well as suitable nesting substrates. Approximately 70% of bee species nest underground in bare or sparsely vegetated soil, while cavity-nesting species require dead wood, hollow stems, or other pre-existing cavities^[5]. At landscape scales (1–2 kilometers), bees depend on networks of habitat patches that provide complementary resources, with different plant communities flowering in succession and multiple nesting sites distributed across foraging ranges.

Agricultural intensification eliminates both local and landscape-scale resources simultaneously—modern farming practices remove hedgerows, fill wetlands, plow grasslands, apply herbicides that eliminate flowering “weeds,” and compact soil that ground-nesting bees require for burrow excavation^[2].

Knauer *et al.* (2025)^[49], in a meta-analysis synthesising bee assemblage data from 681 crop fields across three continents, provided robust evidence that local pesticide hazards and declining proportions of semi-natural habitat independently and additively reduce wild bee populations in agricultural systems^[49]. Notably, these two stressors together suppressed not only wild bee abundance and species richness, but also functional diversity and phylogenetic diversity—indicating that the damage extends beyond population size to the deeper ecological structure of bee communities. Critically, this study found that semi-natural habitat availability did not buffer against pesticide effects—both drivers independently and additively reduce wild bee abundance and species richness, while pesticide exposure additionally reduces functional and phylogenetic diversity in agricultural systems^[49]. The additive rather than synergistic nature of these effects suggests that conservation interventions must simultaneously address both stressors rather than focusing exclusively on either habitat restoration or pesticide reduction. For habitat restoration specifically, recent research indicates that current policy guidelines substantially underestimate the land area required to support wild bee communities. Pindar & Raine (2023)^[50] demonstrate that safeguarding wild bee assemblages in Canadian landscapes requires 11.6–16.7% habitat cover from diverse habitat types—including tallgrass woodlands and wetlands—representing 2.6–3.7 times the coverage recommended in existing conservation policies^[50]. Habitat fragmentation compounds the effects of habitat loss by isolating remaining habitat patches and reducing connectivity. In fragmented landscapes, social and solitary bees preferentially visit large, nearby patches over small, isolated ones, reflecting energy optimization—travel between isolated patches increases energetic costs while reducing resource acquisition, ultimately compromising colony growth and reproductive success^[2]. For social species, isolation from native habitats imposes disproportionate costs because of their need for abundant resources to support large colonies, while solitary species with smaller individual resource requirements demonstrate greater tolerance to patch isolation. Specialist bees (oligolectic species restricted to single plant families) face heightened extinction risk in fragmented landscapes because their required host plants occur at lower densities and may disappear entirely from small habitat fragments. De Sousa *et al.* [2022]^[51] documented that six decades of agricultural expansion and intensification in the Brazilian Cerrado—which drove habitat fragmentation and loss—reduced orchid bee species richness and abundance at landscape scales, with effects expected to intensify given the particular vulnerability of orchids to fragmentation^[51].

3. Climate Change

Climate change has emerged as a pervasive and accelerating threat to bee populations, operating through multiple distinct but interconnected mechanisms including direct thermal stress, disruption of phenological synchrony between bees and flowering plants, alteration of geographic ranges,

reduction in floral resource quality, and increased frequency of extreme weather events. Unlike habitat loss or pesticide exposure, which operate primarily at local to regional scales, climate change represents a global-scale stressor that interacts with and amplifies other decline drivers. The most direct effect of warming temperatures is thermal stress, as rising heat pushes cold-adapted species beyond their physiological tolerance limits, particularly bumble bees, which evolved in cold temperate and alpine environments. Rahimi & Jung [2024]^[35], modelling climate suitability for 1,365 bee species under severe warming scenarios (SSP585), revealed that approximately 65% of species face potential reductions in climatically suitable habitat by 2070, with Africa and Europe experiencing the most pronounced negative effects^[35].

Perhaps the most ecologically significant impact of climate change involves disruption of phenological synchrony—the temporal matching of life history events between interacting species. Warming temperatures advance spring phenology for both plants and bees, but critically, the two groups often shift at different rates. Wyver *et al.* [2023]^[52], in a comprehensive 40-year analysis of 88 wild bee species in Great Britain, revealed that bee emergence dates advanced by an average of 4.0 days per decade in response to rising spring temperatures, a rate that lags significantly behind plant phenological shifts—UK plants are advancing flowering dates by an average of 5.4 days per decade^[52]. While this 1.4-day-per-decade differential may appear modest, even small temporal mismatches between bee emergence and peak flower availability can severely constrain bee nutrition and population growth, particularly for specialist species dependent on specific plant taxa. Stemkovski *et al.* [2020]^[53] found that bee phenology is less sensitive than flower phenology to climatic variation, indicating a growing potential for reduced synchrony between bees and their floral resources as warming continues^[53].

Elevated atmospheric CO₂ concentrations, while stimulating plant growth, reduce protein content in pollen, threatening bee nutrition particularly during larval development. At this stage, adequate protein intake determines adult body size, immune function, and long-term survival. Ziska *et al.* [2016]^[54] demonstrated that rising CO₂ has measurably reduced pollen protein concentration in goldenrod—a critical late-season food source for North American bees—with pollen protein content declining by approximately one third since 1960^[54]. Changing precipitation patterns alter flowering phenology independently of temperature effects: drought conditions can trigger early flowering or reproductive failure in moisture-stressed plants, while excessive rainfall can delay flowering or physically damage flowers, reducing nectar and pollen availability. Extreme weather events increasingly disrupt bee populations directly—flooding events during critical foraging periods can force colony relocation or result in brood mortality if nests are inundated, while the increasing frequency and severity of wildfires eliminate both nesting habitat and floral resources across vast landscapes, with recovery timescales extending years to decades depending on fire intensity and regional climate.

4. Pathogens and Parasites

Among biotic stressors, the ectoparasitic mite *Varroa destructor* has emerged as the most consequential threat to

managed honey bees globally. Originally associated with Asian honey bee species, *Varroa* shifted hosts to the Western honey bee (*Apis mellifera*) in the twentieth century and has since spread to nearly all regions where managed colonies are maintained. Its impact arises not only from direct parasitism but also from its role as an efficient vector and amplifier of viral pathogens, most notably Deformed Wing Virus (DWV). Abban *et al.* [2024], in a comprehensive survey of symptomatic honey bee colonies across the United States from 2015 to 2022^[23, 82], reported a mean national infestation level of 8.21%, with 85.14% of sampled colonies harboring detectable mite populations^[55]. Infestation levels exceeded the 4% critical damage threshold during eight of twelve calendar months. Substantial geographic variation was observed, with the Upper Midwest exhibiting the highest infestation rates (13.9%) and the West the lowest (5.1%), reflecting differences in climate, management practices, and potentially the genetic background of bee populations^[55].

By feeding on developing and adult bees, *Varroa* compromises host physiology and immune function while facilitating viral replication. In unmanaged systems, DWV typically persists at low titers; however, mite-mediated transmission dramatically elevates viral loads, transforming a largely asymptomatic infection into a virulent epidemic capable of collapsing entire colonies. Wilfert *et al.* [2016]^[56] demonstrated through phylogeographic analysis that DWV spread globally from a common source within European honey bee populations, driven by the novel transmission pathway provided by *Varroa*^[56]. The synergistic interaction between mite and virus establishes a self-reinforcing cycle: mite feeding suppresses immune responses, increasing susceptibility to viral infection, while viral replication inflicts additional physiological damage that intensifies mite impacts. At the colony level, this cascade manifests as progressive weakening, reduced adult populations, overwintering failure, and eventual collapse.

Although research has focused primarily on managed honey bees, pathogen pressure is not confined to apiaries. High densities of managed colonies can elevate pathogen prevalence in surrounding landscapes, increasing spillover risk to wild bee communities through shared floral resources. Molecular surveys across multiple regions have detected honey bee-associated viruses, including DWV, in bumble bees and solitary species. In several instances, viral replication—rather than passive contamination—has been confirmed in wild hosts, indicating active infection^[57].

Managed honey bee colonies are routinely transported across large geographic distances for crop pollination, facilitating pathogen dissemination among regions that would otherwise remain epidemiologically isolated. Combined with high colony densities in agricultural landscapes, this movement can generate persistent reservoirs of infection that amplify disease risk for wild pollinators already experiencing habitat loss and chemical exposure.

Disease impacts rarely operate independently. Experimental and field studies increasingly document interactions between pathogens and other stressors. Sublethal pesticide exposure impairs immune function, elevating viral replication rates and reducing host survival^[42]. Nutritional stress associated with habitat degradation similarly weakens immune defenses and exacerbates parasite burdens.

Pathogen virulence is therefore context-dependent and frequently intensified under environmental stress.

Beyond managed systems, the long-term consequences for wild bee populations remain insufficiently quantified but potentially severe. Unlike honey bees, most wild bees lack large perennial colonies capable of buffering individual mortality; thus, even modest pathogen-induced mortality may translate more directly into population decline.

Collectively, the *Varroa*–DWV complex exemplifies how anthropogenic drivers—including species translocation, intensive management, and environmental stress—can restructure disease dynamics at landscape and global scales. Addressing pollinator decline therefore requires not only improved parasite control within apiaries but also coordinated strategies to reduce pathogen spillover and mitigate interacting stressors across managed and wild pollinator communities.

The microsporidian pathogen *Nosema ceranae* represents an additional significant threat to honey bee health. This parasite causes nosemosis, a midgut epithelial infection characterized by energetic depletion, reduced lifespan, and impaired colony performance^[55]. Abban *et al.* [2024] reported infection intensities ranging from low detectable levels to 16.8 million spores per bee across symptomatic colonies and identified a significant positive correlation between *Varroa* infestation levels and *Nosema* spore counts, suggesting synergistic pathology^[55].

Colonies co-infected with *V. destructor* and *N. ceranae* exhibit more severe symptoms and higher mortality than colonies infected with either pathogen alone, likely reflecting compounded immune suppression and nutritional stress. More broadly, the introduction of pathogen complexes—including *Nosema bombi* and the intestinal protozoan *Crithidia bombi*—into North American wild bumble bee populations through global trade in commercial greenhouse pollination has been implicated in dramatic population declines of several previously common species since the 1990s^[55, 57].

5. Gut Microbiome Disruption as an Emerging Mechanism

An increasingly recognized dimension of pathogen-related bee decline involves disruption of the gut microbiome in bees—the structured community of symbiotic bacteria essential for immune regulation, nutrient metabolism, and pathogen defense. In honey bees and bumble bees, the microbiome is dominated by a relatively small set of core taxa, including *Snodgrassella alvi*, *Gilliamella apicola*, and *Lactobacillus* spp., whose composition is closely linked to host immune competence^[58]. Dysbiosis—the disruption of this microbial community—compromises these protective functions and increases susceptibility to infection at both individual and colony levels.

Multiple anthropogenic stressors induce microbiome dysbiosis, with pesticide exposure among the most extensively documented drivers. Sublethal neonicotinoid exposure alters gut bacterial composition, reducing beneficial core taxa and promoting proliferation of opportunistic pathogens such as *Serratia marcescens* [59–62]. Glyphosate—the most widely applied herbicide globally—illustrates a related but distinct mechanism. Although not classified as an insecticide and therefore often excluded from pollinator risk assessments, glyphosate inhibits the enzyme 5-enolpyruvylshikimate-3-phosphate

synthase (EPSPS) in susceptible gut bacteria, disrupting microbiome structure and reducing host survival following pathogen challenge^[59, 61]. Given its pervasive presence in agricultural landscapes, this microbiome-mediated pathway represents a largely unaccounted dimension of pollinator risk.

Antibiotic use in managed apiculture constitutes a second source of disruption. Treatments such as oxytetracycline and tylosin, applied to control American foulbrood (*Paenibacillus larvae*), significantly reduce gut microbial diversity and are associated with increased susceptibility to opportunistic infections and reduced immune gene expression^[62]. Consequently, interventions intended to suppress one pathogen may inadvertently compromise microbiome-dependent defenses against others, contributing to chronic disease vulnerability.

Diet quality provides a third pathway linking agricultural intensification to microbiome instability. Bees foraging in species-poor, monoculture-dominated landscapes consume nutritionally restricted pollen diets that reduce microbiome diversity and immune resilience^[63, 64]. In contrast, access to diverse floral resources supports more stable microbial communities and enhances resistance to chemical and biological stressors. This relationship offers a mechanistic explanation for the well-established association between landscape floral diversity and pollinator health that extends beyond nutritional sufficiency alone.

Taken together, these findings position gut microbiome disruption as a mechanistic bridge linking pesticides, agricultural simplification, and management practices to immunosuppression and heightened disease susceptibility. Because conventional colony health assessments typically focus on pathogen loads and adult population metrics rather than microbial composition, microbiome-mediated declines may remain undetected. Consequently, recovery of microbial stability may lag behind reductions in external stressors, with important implications for evaluating conservation outcomes.

6. Evolutionary and Adaptive Responses

The preceding sections emphasize interacting stressors driving bee decline; however, this framing requires an important qualification: some bee populations exhibit measurable evolutionary and behavioural resilience. Recognizing adaptive capacity does not diminish the severity of current declines—most populations show no evidence of compensatory adaptation—but it introduces necessary nuance to conservation strategy and identifies areas where cautious optimism is warranted.

The most well-documented example involves resistance to *Varroa destructor* in honey bees. Although most managed and wild populations remain highly susceptible and dependent on chemical control, a small number of geographically isolated populations have evolved heritable resistance through natural selection. The untreated Gotland population in Sweden has persisted despite chronic mite pressure, with research identifying enhanced grooming behaviour, elevated hygienic response, and suppressed mite reproduction as key resistance mechanisms^[65, 66]. Similarly, feral colonies in the Arnot Forest (New York State) have survived for decades without treatment, independently evolving comparable resistance traits^[67]. These cases demonstrate that natural selection can produce mite-resistant genotypes within ecologically relevant timescales, providing

a foundation for breeding programmes aimed at reducing chemical dependency.

Pesticide tolerance represents a second adaptive axis, though its conservation value is more limited. Some chronically exposed bee populations exhibit upregulated detoxification enzymes, particularly cytochrome P450s, conferring partial tolerance to neonicotinoids^[68, 69]. However, detoxification is energetically costly and may reduce reproductive output, immune function, or foraging efficiency under field conditions. Moreover, evidence of adaptive responses is concentrated in honey bees; most wild bee species have smaller population sizes, lower genetic diversity, and longer generation times, which constrain evolutionary responses in the taxa facing the greatest extinction risk.

Behavioural and phenological plasticity in response to climate change constitutes a third dimension of resilience. In Great Britain, wild bee emergence dates have advanced by approximately four days per decade in response to warming temperatures^[52], indicating measurable phenological adjustment. However, plant phenology has shifted more rapidly in many systems, suggesting that plasticity may be insufficient to prevent climate-driven mismatches. Some bumble bees have expanded into higher elevations and latitudes; however, such range shifts are constrained by habitat availability and landscape fragmentation.

Collectively, these findings indicate that bees are not passive recipients of environmental change; evolutionary and plastic responses are occurring. Nevertheless, the pace, taxonomic breadth, and demographic impact of these adaptations remain modest relative to the scale of stressor intensification. Isolated cases of natural resistance, though encouraging, have not prevented widespread declines and cannot substitute for systemic reductions in pesticide use, pathogen pressure, and habitat loss. The appropriate conservation conclusion is therefore not complacency but integration: identified resistance traits—particularly *Varroa*-resistant genotypes—should be incorporated into breeding and management programmes alongside broader efforts to reduce environmental stressors.

7. Synergistic Effects and Multiple Stressor Interactions

While the preceding sections have necessarily examined individual drivers of bee decline separately, the mechanisms producing population-level declines are defined above all by synergistic interactions where combined stressors generate effects exceeding the sum of their independent impacts. These synergies operate through multiple pathways: physiological interactions where one stressor compromises tolerance to another, behavioral interactions where impairment in one domain — such as the navigational impairment associated with sublethal neonicotinoid exposure — exacerbates vulnerability to other stressors, and ecological interactions where landscape-scale conditions mediate organism-level responses. Recognition of these synergistic effects fundamentally transforms our understanding of the pollinator crisis: bees may tolerate individual stressors at environmentally realistic levels, yet the same exposures become lethal or severely detrimental when experienced simultaneously.

The interaction between pesticides and fungicides exemplifies chemical synergies that amplify toxicity. Iwasa *et al.* [2004]^[69] demonstrated that fungicides —

traditionally considered benign to pollinators — potentiate neonicotinoid toxicity by inhibiting cytochrome P450 detoxification enzymes, with demethylation inhibitor fungicides capable of increasing neonicotinoid lethality to bees by orders of magnitude under laboratory conditions^[69]. Sanchez-Bayo & Goka [2014]^[70], in a comprehensive risk assessment of pesticide residues in bee-collected pollen, confirmed that the synergism of ergosterol-inhibiting fungicides with neonicotinoid insecticides results in substantially elevated real-world risks, despite the individually low prevalence of each compound in pollen^[70]. Shepherd *et al.* [2024]^[44] subsequently confirmed that this synergy operates at the colony level, showing that commercially used fungicide formulations at label rates interact with field-realistic neonicotinoid concentrations to increase worker bee mortality and *Varroa destructor* infestation levels compared to either chemical alone^[44]. This pesticide-fungicide synergy has profound practical implications — bees foraging in agricultural landscapes encounter complex mixtures of agrochemicals, and safety assessments evaluating single active ingredients in isolation may substantially underestimate real-world risks. Perhaps most significantly, neonicotinoid contamination extends far beyond treated fields and far beyond the crop flowering period — a finding with profound implications for how bee exposure is assessed and regulated. In Canadian agricultural landscapes, Tsvetkov *et al.* [2017]^[71] found that neonicotinoids were detected predominantly not on treated corn itself but on pollen collected from non-crop plants — willows, clovers, and wildflowers — growing near crop fields^[71]. This means that bees are exposed to neonicotinoids throughout the entire growing season, not only during the brief window of crop bloom that most risk assessments and regulatory frameworks assume. Botias *et al.* [2015]^[39] further demonstrated that the majority of neonicotinoids returning to hives in bee-collected pollen derived not from the treated crop itself but from contaminated wildflowers growing in surrounding field margins, confirming that the window of exposure extends well beyond crop flowering periods^[72]. Climate change interacts synergistically with virtually every other stressor driving bee decline. Extended active foraging seasons resulting from warmer autumns and earlier springs disrupt honey bee colony age structure and facilitate *Varroa* mite movement between colonies on foraging workers, accelerating parasite and virus transmission both within and between apiaries^[73]. Thermal stress reduces bee immune function, increasing susceptibility to pathogens and pesticide exposure^[2, 5]. Phenological mismatches between bee emergence and flower availability create nutritional stress precisely when colonies face maximum energetic demands during spring buildup, reducing resilience to subsequent stressors encountered during the foraging season^[53]. Drought conditions force bees to forage over greater distances to locate floral resources, increasing energetic costs, the probability of pesticide exposure, and predation risk, while reducing time available for colony maintenance behaviors. Most consequentially, habitat loss and fragmentation interact with climate change to create landscapes where suitable microhabitats become increasingly isolated and inaccessible. In such degraded landscapes, bees face a double disadvantage — they lack the diverse floral resources needed to buffer phenological mismatches, and

they lack the habitat connectivity required for range shifts that would otherwise allow them to track shifting climate conditions.

The interaction between habitat quality and pesticide exposure demonstrates how landscape context mediates organism-level responses to toxins. Initially, researchers hypothesized that semi-natural habitat might buffer bees against pesticide effects by providing alternative foraging resources and reducing exposure. However, Knauer *et al.* [2025]^[49], in their meta-analysis of 681 crop fields across three continents, conclusively refuted this hypothesis, finding strictly additive rather than interactive effects — pesticide hazards reduced bee populations independently of landscape composition, while habitat loss independently depressed populations — both operating additively with no buffering interaction between them^[49]. This finding suggests that even habitat restoration alone is unlikely to rescue bee populations in pesticide-intensive landscapes, and that pesticide reduction alone is unlikely to compensate fully for habitat loss. Only integrated approaches addressing multiple stressors simultaneously offer realistic prospects for population recovery. The synergistic framework also explains why common, generalist bee species — previously assumed to be buffered against decline by their ecological flexibility — now experience rapid population declines: while individual stressors might remain within tolerable ranges, their combination creates conditions exceeding even generalists' adaptive capacity.

Consequences of Bee Population Decline

The cascading effects of pollinator decline extend far beyond the immediate loss of individual bee species, manifesting as tangible threats to agricultural productivity, economic stability, ecosystem integrity, and ultimately human health and food security. This section draws on quantitative evidence to demonstrate that the pollinator crisis represents not a distant environmental concern but an ongoing global health and economic emergency — one with disproportionate impacts on the world's most vulnerable populations.

1. Agricultural Impacts and Crop Yield Reductions

Current pollinator deficits are already producing measurable reductions in crop yields globally, with direct field measurements revealing that insufficient pollinator visitation now limits agricultural productivity across 28–61% of crop systems worldwide. This phenomenon — known as *pollinator limitation* — affects blueberries, coffee, and apples most frequently, with yield gaps directly attributable to inadequate pollination services rather than other agricultural constraints^[74, 75]. An analysis of the CropPol database — drawing on 198,360 plant–pollinator interactions and 2,083 yield measurements from 32 crop species grown across 120 study systems in 27 countries — confirms that increasing pollinator visitation in low-visitation fields to levels observed in the best-performing 10% of fields could close 63% of current yield gaps^[74, 75]. This finding demonstrates that pollination services represent a critical but frequently suboptimal component of agricultural production, with substantial unrealised potential even within existing farming systems. In agricultural regions where smallholder farmers depend heavily on pollinator-mediated crops—including much of South and Southeast Asia, sub-Saharan Africa, and parts of Latin

America—pollinator decline poses direct threats to rural livelihoods and economic stability.

Quantitative assessments of current pollinator-attributable yield losses reveal substantial impacts across major crop categories. Smith *et al.* [2022]^[76], in a modelling study published in *Environmental Health Perspectives*, estimated that insufficient pollination currently results in losses of approximately 4.7% of global fruit production, 3.2% of vegetables, and 4.7% of nuts — deficits that occur independently of geographic location, climate, or other landscape characteristics^[76]. These seemingly modest percentage losses translate into massive absolute quantities of foregone food production given the scale of global agriculture. Moreover, these impacts demonstrate striking geographic inequity — low-income countries experience far more severe yield gaps, with estimated losses reaching 26% of total vegetable production and 8% of nut production in these regions, compared to global averages of 3.2% and 4.7% respectively^[76]. This disparity reflects multiple factors including lower managed pollinator availability, reduced wild bee populations due to agricultural intensification, and climate change impacts that disproportionately affect tropical and subtropical regions where wild bee diversity naturally peaks.

Crop-specific analyses reveal that certain high-value agricultural products face particularly acute pollination limitations. Tropical export crops including cocoa, mango, watermelon, and coffee face the highest projected risks from combined agricultural land use and climate change impacts on pollinator abundance, with localised risks predicted to increase most rapidly in sub-Saharan Africa, northern South America, and Southeast Asia^[77]. Beyond direct yield reductions, pollination quality affects multiple dimensions of crop marketability — inadequate pollination produces fruits with asymmetric shapes, reduced size, lower seed set, decreased sugar content, and shorter shelf life, all of which reduce market value even when total biomass production appears adequate^[2].

Aizen *et al.* [2008]^[78], in a widely cited study, demonstrated that crops with greater pollinator dependence exhibit not only lower mean yields but also reduced yield stability over time — yield variability increases with pollinator dependence, meaning these crops experience greater year-to-year fluctuations that threaten farmer livelihoods and food supply chains^[78]. This reduced stability stems from the inherent variability in wild pollinator abundance and activity across seasons and years, as determined by weather conditions, floral resource availability, and pathogen prevalence. Critically, Garibaldi *et al.* [2011]^[79] found that for pollinator-dependent crops specifically, the lower rate of yield growth relative to non-dependent crops has driven compensatory expansion of cultivated area — a pattern consistent with the broader global trend documented by FAO data showing that cultivated area increased by 33% and crop yield by 57% over the past 50 years, with area expansion serving as the primary mechanism for meeting growing production demand where yield growth has stalled^[79]. This strategy further degrades pollinator habitat, accelerating the very decline it was intended to offset.

2. Economic Implications and Market Disruptions

The economic ramifications of pollinator decline extend throughout agricultural value chains and global trade

networks, generating costs that far exceed direct production losses. However, accurately characterising these costs requires careful distinction between scenarios of partial pollinator loss — reflecting current and near-term trajectories — and complete pollinator collapse, a hypothetical worst-case condition that, while analytically useful for bounding potential impacts, does not represent a likely near-term outcome and should not be conflated with present economic reality.

The most directly policy-relevant estimates derive from partial-loss scenarios calibrated to observed and projected decline rates. A European assessment by Feuerbacher *et al.* [2025]^[80] estimated that wild pollinator loss in Europe alone — modelled on realistic near-term trajectories rather than complete collapse — could reduce crop yields by approximately 8%, trigger modest cropland expansion, and diminish net exports, resulting in a global annual welfare decline of €34 billion projected for the year 2030^[80]. Critically, even this comparatively conservative estimate assumes continuation of current decline rates without significant policy intervention, meaning it likely underestimates outcomes under accelerating loss scenarios while remaining more credible as a near-term policy benchmark than complete-collapse projections. These economic impacts would be felt most acutely by consumers in EU member states with comparatively weaker biodiversity policy implementation, illustrating how policy choices regarding pollinator conservation generate direct and near-term economic consequences.

Smith *et al.* [2022]^[76] provide perhaps the most grounded economic assessment, estimating current — not projected — pollinator-attributable losses of approximately 4.7% of global fruit production, 3.2% of vegetables, and 4.7% of nuts^[76]. These losses are already occurring under present conditions of partial pollinator decline, and their economic translation into price increases, reduced market access, and foregone agricultural income represents a measurable present-day cost rather than a modelled future scenario. The geographic inequity of these losses is particularly pronounced — low-income countries experience estimated losses reaching 26% of total vegetable production and 8% of nut production, compared to global averages of 3.2% and 4.7% respectively, reflecting lower managed pollinator availability, reduced wild bee populations due to agricultural intensification, and disproportionate climate change impacts in tropical and subtropical regions.

Complete-collapse modelling, while inherently hypothetical, nonetheless provides analytically valuable upper bounds for economic risk assessment and for evaluating the cost-effectiveness of conservation investment. Feuerbacher *et al.* [2025]^[80], modelling a complete global pollinator collapse, projects a 30% average increase in crop prices, producing an estimated global welfare loss of \$729 billion — equivalent to 0.9% of global GDP and 15.6% of total agricultural production value dedicated to human food consumption in 2020^[80]. This figure should be interpreted strictly as a theoretical ceiling on potential economic damage under the most extreme scenario, not as a forecast. Its primary utility is in demonstrating that even very substantial conservation investments — costing orders of magnitude less than \$729 billion — would be economically justified on a pure cost-benefit basis if they meaningfully reduce the probability of approaching collapse-level pollinator losses. Taken at face value as a description of current or near-term risk, however,

this figure overstates economic reality and risks undermining the credibility of more conservative but better-grounded estimates.

The disproportionate economic vulnerability of low and lower-middle income countries represents perhaps the most concerning and robust finding across both partial and complete-loss scenarios, since it is consistent regardless of the modelling assumptions used. Annual economic losses from pollinator decline in Honduras reach 12% of agricultural GDP, 17% in Nigeria, and 31% in Nepal — percentages that substantially exceed production losses of 3%, 15%, and 19% respectively in these same countries^[76]. This discrepancy between production and economic losses reflects the outsized role of pollinator-dependent crops as high-value export commodities in these nations, including coffee, cocoa, cashews, and specialty fruits. In Nepal, honey sales account for 16% of total household income among traditional beekeeping communities, and native honey bees provide critical pollination services for regional crops, meaning that pollinator decline simultaneously threatens both direct income streams and broader agricultural productivity^[34]. The concentration of economic risk in already-vulnerable nations creates conditions where even partial pollinator losses could trigger rural livelihood collapse, accelerate urban migration, and intensify food insecurity precisely where adaptive capacity remains most limited.

International trade dynamics amplify economic impacts beyond producing regions regardless of which loss scenario is considered. Approximately 17% of global crop production value depends on pollination services, yet pollinator-dependent crops constitute 28% of global agricultural trade, reflecting their strong international demand and comparatively high tradability^[80]. Consequently, pollinator losses in producing countries cascade through global supply chains, affecting food availability and prices in importing nations far from the sites of actual bee decline. Murphy *et al.* [2022]^[4] demonstrated that countries classified as Heavily Indebted Poor Countries face compounding vulnerabilities — they simultaneously experience high rates of pollinator-dependent crop production, lack the economic resources to invest in pollinator conservation, and possess limited capacity to absorb economic shocks from crop price volatility^[4]. Furthermore, nations with the highest pesticide use per hectare of cropland — which correlates strongly with pollinator decline — frequently export significant quantities of pollinator-dependent crops, generating a self-defeating dynamic in which production practices undermine the ecological foundation supporting their own agricultural economies^[4]. The convergence of trade exposure, geographic inequity, and ecologically self-undermining production systems means that the economic consequences of pollinator decline cannot be addressed by any single nation acting alone — effective responses will require coordinated international policy action across both producing and importing regions.

3. Human Health and Food Security Consequences

Smith *et al.* [2022]^[76], in the first modelling study to quantify the human health toll of insufficient wild pollinators, estimated that current pollinator deficits are associated with approximately 427,000 excess deaths annually^[76]. These deaths are attributable to reduced

consumption of fruits, vegetables, and nuts, with a consequent rise in diet-related non-communicable diseases — including cardiovascular disease, stroke, diabetes, and certain cancers [76]. This estimate was derived using a comparative risk assessment framework applied sequentially across pollinator yield gap data, global agricultural trade modeling, country-level dietary intake projections, and established epidemiological risk coefficients for diet-disease relationships — a multi-step causal chain in which uncertainties compound across stages. The finding that pollinator decline is currently causing hundreds of thousands of deaths per year — rather than representing a distant future threat — compels an urgent reappraisal of the importance of conservation action.

Micronutrient deficiencies represent an equally critical but often overlooked dimension of the pollinator-health relationship. Pollinator-dependent crops provide disproportionately high contributions to human micronutrient intake. Animal pollination is estimated to account for up to 40% of the total dietary nutrient supply to humanity [81]. The contribution is particularly pronounced for specific micronutrients — more than 40% of global vitamin A, lycopene, and β -cryptoxanthin supply derives from crops that require animal pollination, meaning that these nutrients are structurally dependent on pollinator availability in ways that staple crops cannot compensate for. Eilers *et al.* further estimated that 58% of calcium and 29% of iron in the global food supply come from pollinator-dependent crops, with 9% and 6% of those totals respectively attributed to the direct contribution of pollination services rather than other cultivation factors [81]. Smith *et al.* [2015] [82], modelling the effects of complete pollinator removal, projected that 71 million people in low-income countries would become newly deficient in vitamin A, while an additional 2.2 billion people already consuming below adequate levels would experience further declines in vitamin A intake [82]. Uwingabire & Gallai [2024] [83] subsequently projected that partial pollinator loss scenarios would reduce global vitamin A availability by approximately 8%. The impacts would be geographically concentrated — in the most severely affected regions, up to 50% of plant-derived vitamin A production depends on pollination services. These regions span tropical and subtropical Asia, parts of the Middle East, and sections of Latin America and Oceania, precisely the areas where vitamin A deficiency already constitutes a significant public health burden [83].

Chaplin-Kramer *et al.* [2014] [84] mapped the geographic overlap between pollinator-dependent micronutrient production and existing patterns of nutritional deficiency — and the finding is stark. Regions already identified by WHO as having high prevalence of vitamin A deficiency are three times more likely than other regions to depend on pollinators for more than 30% of their vitamin A production [84]. The same pattern holds for iron: regions with high iron-deficiency anaemia prevalence are disproportionately concentrated in areas where more than 15% of iron production depends on pollination services. The implication is unambiguous — the populations most nutritionally dependent on pollinators are precisely those already most nutritionally insecure. Vitamin A deficiency alone causes 800,000 deaths annually, primarily among women and children; it doubles the mortality risk from several childhood diseases and quadruples the rate of

maternal mortality during childbirth relative to vitamin A-sufficient populations [85]. Iron deficiency causes preventable iron-deficiency anaemia, increased susceptibility to infection, and cognitive impairment, collectively affecting hundreds of millions globally [85]. The micronutrient contribution of pollinator-dependent crops cannot be readily replaced by staple crops — grains provide inadequate levels of vitamins A, C, E, and various carotenoids regardless of quantity consumed [81].

Economic access to nutritious food represents the critical mechanism linking pollinator decline to human health outcomes. When pollinator losses reduce fruit, vegetable, and nut production, prices for these commodities increase while availability decreases, rendering nutritionally adequate diets economically inaccessible to low-income populations. Uwingabire & Gallai [2024] [83] project that complete pollinator collapse scenarios would produce crop price increases averaging 187%, with pollinator-dependent foods becoming effectively inaccessible for precisely those populations whose diets already contain insufficient quantities of these protective foods [83]. Even partial pollinator losses that reduce yields by 3–5% translate into price increases sufficient to exclude substantial portions of global populations from accessing recommended dietary intake levels, particularly in developing countries where food expenditures constitute large fractions of household budgets. This economic mechanism explains how relatively modest production declines generate disproportionate health impacts: the most vulnerable populations experience effective exclusion from nutritious food markets rather than merely reduced consumption. Taken together, the mortality burden, micronutrient deficiency risk, and economic exclusion dynamics described in this section establish that the health consequences of pollinator decline are not a future projection but a present and measurable global health emergency — one that falls with greatest force on populations least equipped to respond.

4. Ecosystem Disruption and Biodiversity Loss

Beyond agricultural and human health impacts, pollinator decline triggers cascading ecological effects that destabilise entire ecosystems and threaten wild plant biodiversity. Ollerton *et al.* [2011] [1] estimated that approximately 87% of flowering plant species depend on animal pollinators for reproduction — meaning that the decline of bees, the dominant functional group within animal pollinator communities, directly compromises reproductive success for the vast majority of terrestrial plant communities [1]. Reduced pollination translates into decreased fruit and seed production for wild plants, limiting food availability for granivorous (seed-eating) and frugivorous (fruit-eating) insects, birds, and mammals that depend on these resources. These trophic cascade effects propagate through food webs — diminished seed production reduces populations of seed-eating species, which in turn affect their predators at higher trophic levels, potentially restructuring entire community assemblages [2,3].

Plant-pollinator network stability depends critically on maintaining diverse pollinator assemblages, as different bee species provide temporally and functionally complementary services. Winfree *et al.* [2022], analysing pollination of multiple crop species by wild bees across several years, demonstrated that the number of wild bee species required to maintain minimum effective pollination levels increases

steeply with the timescale examined — 2–3 times more bee species are needed to sustain pollination over a full growing season compared to a single day, and twice as many species are needed over six years compared to a single year, reflecting temporal turnover in species composition and activity^[16]. The loss of bee diversity therefore reduces the temporal consistency of pollination services even when overall pollinator abundance remains unchanged, making plant populations vulnerable to reproductive failure during periods when the remaining bee species are inactive or scarce. For specialist plant-pollinator mutualisms — particularly orchids and other plants with highly specialised floral structures — the loss of their specific pollinator species severely compromises reproductive success and, over time, may precipitate local extinction, as these plants cannot be effectively pollinated by alternative visitors. Genetic consequences of reduced pollination extend beyond immediate reproductive failure. When pollinator scarcity reduces outcrossing rates, plant populations experience increased inbreeding, reduced heterozygosity, and loss of genetic diversity — changes that compromise adaptive capacity and increase vulnerability to diseases, pests, and environmental stressors^[3]. In fragmented landscapes where pollinator-mediated gene flow between plant populations is already constrained by distance, further pollinator losses can isolate populations genetically, triggering inbreeding depression and reduced fitness that may ultimately contribute to local extinctions. These genetic effects operate on long timescales, meaning that the full consequences of current pollinator losses may not manifest for decades as plant populations gradually decline through interacting demographic and genetic processes. Plant-pollinator network stability becomes increasingly compromised as pollinator losses create structural weak points, raising the probability that perturbations will trigger cascading extinctions affecting multiple interacting species simultaneously^[86]. The ecological consequences described in this section — operating across timescales ranging from seasonal reproductive cycles to multi-decadal genetic erosion — are particularly difficult to reverse once set in motion, underscoring the importance of preventive conservation action before network thresholds are breached.

Knowledge Gaps and Future Research Directions

Despite substantial progress in documenting pollinator declines and identifying their proximate drivers, critical knowledge gaps persist that constrain our capacity to develop evidence-based conservation strategies, accurately predict future trajectories, and implement effective interventions at appropriate scales. These gaps reflect both fundamental limitations in our baseline biological knowledge of most pollinator taxa and methodological challenges in quantifying complex ecological processes under real-world conditions. Addressing these deficiencies represents an urgent research priority, as conservation decisions made with incomplete information risk misdirecting limited resources toward ineffective interventions and failing to halt ongoing declines. This section identifies the most pressing knowledge gaps across geographic and taxonomic domains, and proposes research directions necessary to advance pollinator science toward actionable conservation outcomes.

The most fundamental knowledge gap involves the profound geographic inequality in pollinator research effort,

with studies overwhelmingly concentrated in North America and Europe while tropical and subtropical regions — which harbour peak pollinator diversity — remain critically understudied. This geographic bias generates systematic distortions in our understanding of global pollinator decline. Tropical regions harbour the majority of flowering plant and pollinator species, and evidence indicates that agricultural intensification and climate change produce particularly severe pollinator reductions in these systems; yet baseline occurrence data for most tropical pollinator species remain insufficient to parameterise even rudimentary distribution models^[77]. Millard *et al.* [2023]^[87], drawing on a dataset of 2,673 sites and 3,080 insect pollinator species, demonstrated that the interactive combination of agriculture and climate change is associated with large reductions in insect pollinators globally, while simultaneously highlighting that limited occurrence data in the tropics fundamentally restricts assessment of these effects^[87]. Watteyn *et al.* [2025]^[88] provided a striking illustration of how knowledge gaps compound to constrain conservation planning: for Neotropical vanilla orchids, only 11 of 63 species had sufficient occurrence records to model, and only four were confirmed as animal-pollinated — revealing how data scarcity forecloses even basic assessment of extinction risk in biodiverse tropical systems^[88].

Taxonomic biases compound geographic inequalities. Research effort focuses disproportionately on economically important managed species — particularly honey bees and commercially reared bumble bees — while solitary bees, stingless bees, and non-bee pollinators including flies, butterflies, beetles, and vertebrate pollinators receive far less attention despite their critical ecological roles. Whipple *et al.* [2023]^[89], in a systematic review published in *iScience*, identified only 119 relevant studies documenting bumble bee and butterfly responses to climate change, with the bee literature particularly limited compared to that on butterflies^[89]. For wild bee species specifically, Nieto *et al.* [2014]^[32], in the European Red List of Bees, found that population trend data remain unavailable for 79% of European species — the best-studied regional fauna globally — severely constraining conservation prioritisation even where monitoring infrastructure exists^[32]. The situation deteriorates dramatically in biodiversity-rich developing nations — regions that harbour exceptional pollinator diversity yet possess minimal monitoring capacity — creating conditions where extinction or extirpation of pollinators could irreversibly diminish biodiversity and ecosystem services before scientific documentation even occurs.

Addressing these geographic and taxonomic biases — particularly in currently understudied regions — requires substantial investment in baseline biodiversity surveys, taxonomic capacity-building, standardised long-term monitoring infrastructure, and integration of traditional ecological knowledge. Each of these represents an urgent priority for global bee conservation efforts.

The United States Geological Survey's 2025^[90]–2035 Pollinator Science Strategy exemplifies the kind of sustained institutional commitment required, acknowledging that despite progress from 2015–2025, a broad array of knowledge gaps must be addressed to enable successful conservation programme delivery^[90]. Among the most pressing priorities are establishing standardised monitoring protocols applicable across diverse ecosystems and taxa,

and building regional taxonomic expertise through dedicated training programmes. These efforts should be complemented by the development of open-access data repositories that aggregate occurrence records from multiple sources, and by community science initiatives that expand data collection capacity beyond professional researchers — both of which are essential for generating the temporal depth and geographic breadth of data that conservation modelling requires. Research funding should be explicitly directed toward underrepresented regions and taxa rather than continuing to concentrate resources in already well-studied systems. Furthermore, integrating the traditional ecological knowledge held by Indigenous communities and local beekeeping practitioners — who possess multigenerational observations of pollinator population dynamics — could substantially enhance understanding in data-deficient regions, provided that such partnerships are pursued in ways that respect intellectual property rights and ensure equitable collaboration. Without resolving the geographic and taxonomic inequities in pollinator knowledge, evidence-based conservation will remain structurally impossible in precisely those regions where the need is greatest.

Conclusion

The evidence discussed in this review demonstrates that global bee populations face a severe and accelerating crisis, driven by the synergistic interaction of habitat destruction, pesticide contamination, climate change, and pathogen emergence. This decline is not a hypothetical future scenario but a measurable present reality — bee species richness has fallen by approximately 25% since the 1990s, formerly abundant species occupy substantially reduced portions of their historical ranges, and managed honey bee colonies experience annual mortality rates approaching 40–50% in some regions despite intensive management interventions. The cascading consequences extend far beyond ecological concerns, manifesting as tangible threats to human health, economic stability, and food security. Modeling-based estimates indicate that current pollinator deficits are associated with approximately 427,000 excess deaths annually through reduced dietary availability of fruits, vegetables, and nuts^[76], while economic modelling projects welfare losses exceeding \$700 billion under complete pollinator collapse scenarios^[80]. These impacts fall disproportionately on the world's most vulnerable populations — low-income countries experience both the highest rates of pollinator-dependent crop production and the greatest economic and nutritional vulnerability to reductions in pollination services.

The drivers of bee decline operate through complex, synergistic pathways that defy simple solutions. Neonicotinoid insecticides and other systemic pesticides compromise pollinator survival, reproduction, navigation, and immune function at concentrations routinely encountered in agricultural landscapes, with fungicides potentiating toxicity through inhibition of detoxification enzymes. Agricultural intensification has eliminated the diverse floral resources and nesting substrates that bees require. It has transformed heterogeneous landscapes into monocultures that provide ephemeral food availability during brief bloom periods but offer negligible forage or nesting support throughout the remainder of the year. Climate change disrupts the delicate phenological

synchrony between bees and flowering plants, with mismatches of even a few days producing nutritional stress during critical developmental stages, while simultaneously imposing direct thermal stress that exceeds physiological tolerance limits for cold-adapted species. Pathogens and parasites — particularly the *Varroa destructor* mite and associated viruses — have triggered catastrophic colony losses in honey bees while spillover from commercial operations threatens wild bee populations. Critically, these stressors do not operate in isolation — the finding that pesticide effects and habitat loss each independently depress bee populations, with no buffering of one stressor by remediation of the other, demonstrates that conservation strategies addressing only one driver while ignoring others cannot succeed. Only comprehensive, integrated approaches that simultaneously reduce pesticide exposure, restore habitat, support climate adaptation, and manage disease can reverse current decline trajectories. Conservation strategies that protect and enhance bee populations consequently yield co-benefits for general biodiversity conservation, as habitats that support diverse bee assemblages typically harbor rich communities of butterflies, hoverflies, other beneficial insects, and vertebrate wildlife.

Encouragingly, evidence-based conservation strategies capable of arresting and reversing bee decline exist and are being successfully implemented in multiple contexts. Regulatory restrictions on neonicotinoid use — exemplified by the European Union's comprehensive outdoor ban and closure of emergency exemption loopholes — demonstrate that science-based policy can reduce landscape-scale pesticide exposure when sustained policy commitment is maintained in the face of competing economic pressures. Agricultural practice modifications including Integrated Pest Management have achieved up to 95% reductions in insecticide applications while maintaining or enhancing yields through conservation of wild pollinators and natural pest control agents, challenging the assumption that intensive pesticide use is essential for food security. Habitat restoration interventions — from hedgerow establishment in intensive agricultural landscapes to turfgrass conversion in urban parks — have produced measurable increases in pollinator abundance, diversity, and reproductive success, with strategic spatial planning capable of identifying configurations in which biodiversity conservation and agricultural productivity are complementary rather than competing objectives. Community-based conservation initiatives including pollinator gardens, roadside restoration, and corporate-supported habitat creation have engaged millions of participants and protected thousands of hectares, demonstrating that collective action by non-professionals can generate meaningful landscape-scale conservation outcomes. These successes provide templates for scaling effective interventions globally, though realising this potential requires substantial increases in funding, technical capacity, and institutional commitment.

The urgency of the pollinator crisis demands immediate and sustained attention. The economic costs projected under continued decline scenarios are sufficient to justify substantial conservation investments purely on cost-benefit grounds, independent of ethical or ecological considerations. Reversing current pollinator decline trajectories requires comprehensive, evidence-based conservation strategies that address multiple stressors simultaneously while accommodating the economic realities

of agricultural production and land management. The complexity of the crisis demands equally multifaceted solutions — yet the evidence reviewed here also demonstrates that such solutions are achievable. Regulatory reform, agricultural innovation, habitat restoration, and public engagement have each produced demonstrable gains where implemented with adequate commitment and resources. What remains is to scale these successes to match

the scale of the challenge: to treat pollinator conservation not as a peripheral environmental concern but as a foundational investment in the ecological systems that sustain human health, food security, and the biological diversity on which all terrestrial life ultimately depends.

Captions for the Figures

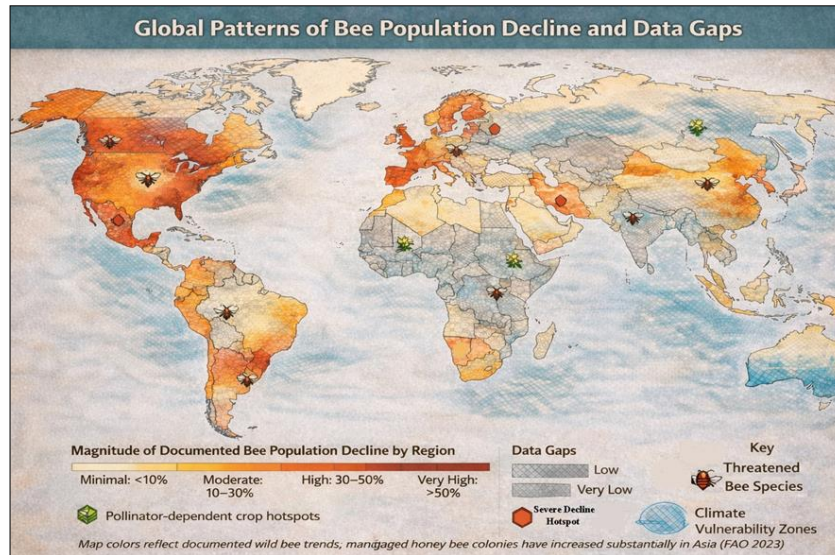


Fig 1: Global patterns of documented wild bee population decline and associated data gaps

Color gradients represent the magnitude of documented wild bee population decline by region, ranging from minimal (<10%, pale cream) to moderate (10–30%, orange), high (30–50%, dark orange), and very high (>50%, deep red-brown). Cross-hatched overlays indicate regions with low (light hatching) or very low (dense hatching) monitoring data availability, reflecting pronounced geographic inequities in pollinator research effort that disproportionately affect tropical and subtropical biodiversity hotspots. Severe decline hotspots, identified through regional assessments and occurrence record analyses, are shown with

hexagonal markers. Bee icons indicate the approximate distributions of threatened bee species of conservation concern, while green diamond markers denote pollinator-dependent crop production hotspots where agricultural pollination services are at critical risk. In the figure, the map colors reflect documented trends in wild bee populations. In contrast, managed honey bee colony numbers have increased substantially in parts of Asia (FAO, 2023), underscoring the critical distinction between managed apiculture metrics and the conservation status of wild pollinator communities.

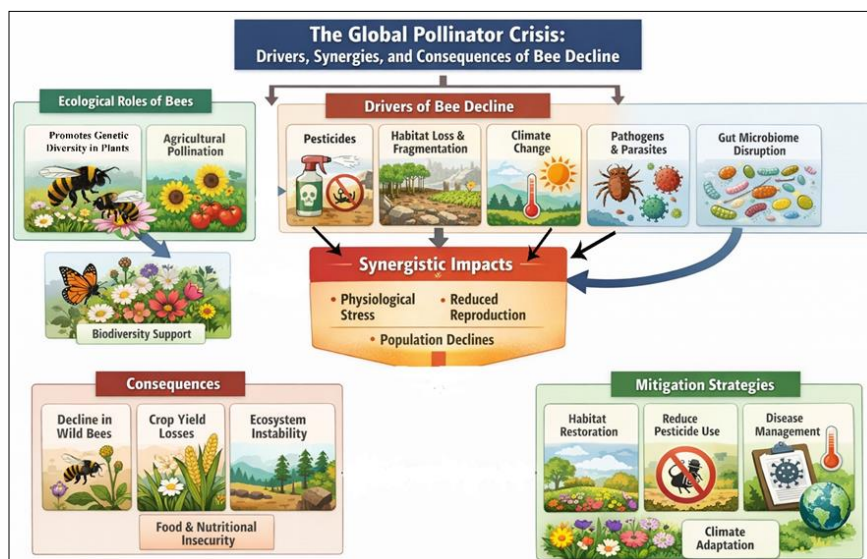


Figure 2: Conceptual framework illustrating the multifactorial drivers, synergistic mechanisms, and cascading consequences of the global pollinator crisis, with corresponding mitigation strategies

Bees perform foundational ecological roles (left panel), including agricultural pollination, the promotion of genetic diversity in plant populations, and broader biodiversity support through the maintenance of plant–pollinator networks. These services are simultaneously threatened by five principal drivers of decline (upper center): pesticide exposure (particularly systemic neonicotinoids and synergistic fungicide co-exposures); habitat loss and fragmentation driven by agricultural intensification; climate change (including thermal stress and phenological disruption); pathogen and parasite pressure (notably *Varroa destructor* and associated viral complexes); and gut microbiome disruption as an emerging mechanistic pathway.

Critically, these stressors do not operate independently but converge through synergistic interactions (center), producing compounding physiological stress, reduced reproductive success, and accelerating population declines that exceed the sum of their individual effects. The downstream consequences (lower left) manifest across ecological and societal dimensions, including declines in wild bee populations, crop yield losses, food and nutritional insecurity, and broader ecosystem instability resulting from disruption of plant–pollinator networks and trophic cascade effects.

Effective mitigation (lower right) requires integrated, multi-pronged strategies—including habitat restoration and connectivity enhancement, reduction and regulation of pesticide use, disease and parasite management, and climate adaptation planning—that address multiple stressors simultaneously. This framework reflects the conclusion that single-driver interventions are insufficient to reverse current decline trajectories

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