



Adapting to change: bee pollinator signatures in anthropized environments

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Bees are essential pollinators for wild, ornamental, and agricultural plants, but human activities have disrupted their habitats, threatening their persistence. Although bees face numerous challenges in habitats heavily modified by human activities, certain species persist and thrive there. This review synthesizes recent literature on two types of traits that help bees survive in human-modified environments: preadaptive traits, which evolved before these environments existed, and adaptive traits, which have evolved in response to new conditions. This review highlights our limited understanding of adaptive traits and examines how trait combinations, including those influenced by epigenetics, contribute to bees' success in these altered habitats. Additionally, we discuss the promising use of genomic tools to reveal signatures of adaptation in these important pollinators.

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activities have significantly altered natural landscapes, transforming them into habitats that challenge the survival and efficiency of pollinator populations. Despite their essential role in ecosystem functioning, food security, and human well-being, anthropogenic activities are the primary driver of bee diversity loss [2]. Indeed, it is estimated that about 25% of bee species may be in decline worldwide [3]. One of the greatest challenges in the 21st century is determining to what extent bee pollinators will adapt to ongoing environmental changes [4] and whether these adaptations will occur fast enough to persist and support key ecosystem functions.

In this context, we discuss two types of traits that enhance species survival or reproductive success in a human-modified environment. First, we discuss traits that likely evolved in bees before becoming adaptive in anthropized environments and currently facilitate their persistence in these habitats (hereafter, 'preadaptive traits'). These traits can result from neutral or adaptive processes throughout their evolutionary history, functioning as exaptations. In contrast, traits can evolve in response to the unique selective pressures of these novel environments, and they can be the product of adaptive evolution (hereafter, 'adaptive traits'). While both types of traits are likely involved in the ability of bees to persist and thrive in human-modified environments, their evolutionary origin is different, and we argue that we know far less about adaptive than preadaptive traits (Figure 1). In this review, we summarize our current knowledge of the preadaptive traits that may enable bees to succeed in human-dominated environments and the limited evidence supporting adaptive processes in these settings. Additionally, we discuss traits associated with the management and domestication of pollinators and explore the role of epigenetic factors in adaptive processes. It is important to acknowledge that multiple traits are likely associated with bees' success in anthropized environments and that different ecological contexts may have a significant role in the ultimate evolutionary processes and outcomes leading to the combinations of these adaptive traits.



Introduction

Bees play a crucial role in nearly all terrestrial ecosystems, serving as vital providers of pollination services essential for the reproduction of wild plants, ornamental plants, and agricultural crops [1]. However, human

Preadaptive traits associated with human-modified habitats

Human activities have profoundly modified the vegetation structure and functioning of natural habitats, leading to habitat loss, fragmentation, and degradation. Two of

Figure 1

| | URBAN | AGRICULTURE |
|----------------|---|--|
| |  <i>Urban habitats</i> |  <i>Agricultural habitats</i> |
| Pre-Adaptation | Dietary generalism | Dietary generalism |
| | Flexibility in nesting requirements | Dietary specialization on crops |
| | High dispersal capacity | Ground nesting habits |
| | Larger brain sizes | Ability to detoxify pollutants |
| Adaptation | Stability of Heat Shock Proteins | Perception of chemical stimuli |
| | Pesticide detoxification | Perception of smell |
| | Cellular homeostasis | Pesticide detoxification |

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Summary of the traits associated with successful bee species in urban (in orange) and agricultural (in green) environments.

the most dominant types of human-modified environments are urban and agricultural landscapes, which currently cover over 55% of the terrestrial land surface [5]. For pollinators, urban environments can provide a mosaic of habitats with diverse floral resources and nesting substrates in human-made structures, but they also pose challenges to their health and persistence due to pollution, reduced underground nesting sites, and increased exposure to pests, pathogens, and pesticides [6]. In contrast, agricultural landscapes offer abundant floral resources during short blooming periods but are characterized by monocultures, habitat homogenization, alien species, and high levels of fertilizer and pesticide inputs [7].

Despite the challenges posed by human-modified environments, some bee species can persist and even thrive in these altered landscapes [8]. These ‘winner’ species, although the minority, typically possess pre-adaptive traits that confer advantages, allowing them to effectively exploit the environmental conditions of human-modified habitats (Figure 1). Biological traits associated with human-dominated landscapes include dietary generalism, flexibility in nesting requirements (or nesting substrates that are common in anthropized habitats), high dispersal capacity, and the ability to

detoxify pollutants. Sociality has also been hypothesized as a trait that confers resilience to environmental stressors because the social environment offers additional protection to the individuals within a colony [9]. Diet generalists are more likely to thrive in urban areas compared to specialists [6]. The flexibility in dietary requirements is a key trait due to the high but temporally and spatially variable plant diversity of urban habitats, often dominated by ornamental plants that have been extensively modified through artificial selection [10]. However, specialist bees can also thrive in human-modified environments if they specialize in plants that are cultivated as crops or ornamentals [11,12]. Another important preadaptive trait is large body size. Larger bees generally exhibit higher flight capacities, providing them with great dispersal abilities and, therefore, the potential to move through fragmented landscapes more effectively than smaller bees [13]. Higher dispersal capacities are advantageous for locating and utilizing scattered floral resources and nesting sites [14], as well as mediating high levels of gene flow among populations [15]. Dispersal abilities also enable bees to use higher-quality patches [16]. Nesting habits above ground can be desirable in urban landscapes [17], while ground nesting habitats may be more advantageous in agricultural settings [18], particularly in areas with mild tillage practices

[19]. An additional trait associated with the success of some bee species in anthropogenic environments is a big brain size relative to body size [20]. Recent evidence suggests that bigger brains offer bees enhanced behavioral plasticity to tolerate dynamic environments.

Two additional traits linked to bee resilience to anthropized environments are the ability to detoxify pollutants and tolerate heat stress. The P450 enzyme subfamily plays a critical role in the detoxification of xenobiotics, such as pesticides and herbicides that are commonly found in these environments. A recent comparative phylogenomic study across 75 bee species revealed that these gene families associated with chemical detoxification are highly conserved across lineages [21]. However, some groups, such as bees in the genus *Megachile*, entirely lack a few gene P450 subfamilies, making them >2500 times more susceptible to certain pesticides (e.g. neonicotinoids). Thus, the presence of more diverse P450 gene families likely facilitates bee adaptations to urban and agricultural habitats where pesticides are pervasive. Similarly, heat-tolerant species may be more resilient to the open environments characteristic of human-modified habitats. Indeed, heat-tolerant bees are abundant in urban areas where they experience higher ambient temperatures associated with greater impervious surfaces (a.k.a. the heat island effect) [17]. In contrast, less heat-tolerant species are less abundant in hotter areas within cities. Associations between heat tolerance traits and resilience to climate change have also been demonstrated for bumble bees (genus *Bombus*) [22]. Overall, these physiological traits have been associated with increased survival and reproductive success in human-modified environments.

Evidence of adaptive traits in human-modified environments

Urbanized habitats have already resulted in adaptive evolution in a wide variety of taxa [23]. Urbanization leads to the replacement of natural habitats by impervious surfaces and fragmented vegetation predominantly consisting of ornamental and exotic plant species. Organisms that inhabit these environments generally experience high levels of chemical and light pollution, high ambient temperatures due to the heat island effects, greater pressure from pathogens, and shifts in their foraging patterns. Several studies have demonstrated that bees show several ecological and physiological responses to these characteristics of urban environments [17,24–26]. Although evidence for bee adaptation in urban environments is scarce, it has been demonstrated in the common European bumble bee *Bombus lapidarius* [27]. Compared to rural populations, urban populations show signatures of adaptive change in genes associated with cellular stress (e.g. oxidoreductase activity), stability of Heat Shock Proteins (e.g. arginine-glutamic acid dipeptide repeats),

developmental processes (e.g. Wnt-11b-2-like genes), and detoxification (e.g. oxidoreductase activity). These gene functions were overrepresented among variants in the only genomic regions that showed significant differentiation between urban and rural populations despite panmixia. Overall, this case study exemplifies some possible adaptive mechanisms of bees in urban environments. While adaptive changes have been widely demonstrated in vertebrates, plants, and other insects in urban areas [23], the evidence for bees and other pollinators remains scarce.

In agricultural environments that are dominated by monocultures, evidence of ecological shifts in foraging behavior has been documented. Bees often visit flowers of a wide range of cultivated plants, which, although not their preferred host plants, are used to collect pollen and nectar resources during their bloom periods [28]. These behavioral shifts in foraging preferences raise the question of whether pollinators are adapting their sensory systems to better detect floral resources from cultivated plants. A recent study in the squash bee *Xenoglossa pruinosa* — specialist pollinators of *Cucurbita* plants — found evidence of signatures of positive selection on populations of this bee that exclusively inhabit agricultural areas [29]. Genomic regions with sensory functions (e.g. perception of chemical stimulus, odorant binding, perception of smell) were overrepresented among the genes under selection. Future studies should investigate the generality of these shifts in the sensory system of bees in response to human-modified environments. Another potentially important trait associated with adaptation to agricultural environments is the ability to detoxify xenobiotics [21]. While there is evidence of significant variation in the detoxification abilities and susceptibility of different groups of bees to xenobiotics, whether bees in agricultural areas are evolving increased resistance to pesticides commonly used in farming remains to be demonstrated. In *X. pruinosa* populations that exclusively inhabit agricultural areas, there is evidence of strong positive selection on one detoxification gene (UDP-glucuronosyltransferase) associated with pesticide resistance [29]. Although evidence for these adaptive changes is scarce across bees in agricultural environments, honey bee stocks are known to differ widely in their susceptibility to pesticides, suggesting that adaptive processes in these genes may be occurring among agricultural pollinators [30]. Indeed, heritable mutations on the cytochrome P450 monooxygenase proteins CYP9Q1 and CYP9Q3 have been associated with honey bee tolerance to the neonicotinoid insecticide clothianidin [31]. Detecting this type of adaptation highlights the potential for rapid evolutionary processes of bees in changing habitats, underscoring the capacity of some species to adjust to human-altered landscapes.

An important consideration in the context of adaptive processes to anthropized environments in bees is that

the rate and fixation of *de novo* mutations are influenced by effective population size, which varies significantly among species with different levels of social behavior [32]. Because of fewer reproductive individuals in social species, their effective population sizes are generally smaller than those of solitary species. This difference in the demographic parameters across species with different levels of sociality implies that adaptive processes resulting from natural selection may be more efficient among solitary species because the likelihood of genetic drift is smaller. Consequently, solitary bee species may be more likely to experience the rapid evolution of adaptive traits in human-dominated landscapes compared to social bee species. However, empirical studies testing these predictions are lacking.

Adaptations through domestication and management

At least 30 bee species are currently managed for bee products (e.g. honey, pollen, propolis) and/or pollination services worldwide [33]. These species have undergone varying degrees of management and domestication and thus likely exhibit signatures of adaptation to anthropized environments due to their close association with humans during their recent evolutionary history. As a result of the increasing demands for bee-pollinated crops in the past decades [34], more bee species are likely to be managed, commercialized, and introduced to novel environments for crop pollination services in the near future. Therefore, direct human selection of pollinators for management and domestication is likely an important mechanism of adaptation among bees.

The most heavily managed pollinator globally is the western honey bee *Apis mellifera*, which has been manipulated by humans for millennia and has served as a model species for bee genomics. Domestication generally leads to reductions in genetic diversity, the selection of desirable traits for management and production, and the accumulation of deleterious mutations that can reduce the population's fitness in the wild [35]. However, population genomics studies in honey bees have revealed that in some of their introduced ranges (e.g. the Americas), domestication and management have increased their genetic diversity as a result of admixture between different subspecies [36]. Still, through breeding practices, humans have selected for traits related to docility, honey production, and disease resistance among managed populations of *A. mellifera* [37,38]. Transcriptomic studies have revealed that domesticated honey bees exhibit changes in gene expression and genetic markers linked to these traits, highlighting the complex interplay between natural evolutionary processes and human-driven selection. Reductions in genetic diversity can make domesticated bees more vulnerable to diseases and environmental

changes. While low genetic diversity within a colony is known to reduce susceptibility to diseases in honey bees [39], no studies have explicitly investigated the effect of reductions in genetic diversity and pathogen susceptibility in managed bees.

One of the risks of the introduction of managed pollinators to novel environments is the potential for introgression of genetic information to native species. For example, the large-scale breeding, trading, and transport of the bumble bee *Bombus terrestris* for crop pollination have resulted in introgressed alleles from commercially bred subspecies into wild populations [40,41]. Even with low levels of introgression, maladaptive alleles can disrupt locally adapted gene complexes, thereby impairing the capacity of bee populations to cope with various environmental conditions in shifting environments. Therefore, the introgression of maladaptive genes could impact the survival of both managed species and their wild relatives. Another potential risk of the introduction of managed bees is related to transporting colonies across large spatial scales, a common practice among beekeepers [36]. This indiscriminate colony transportation not only poses numerous threats to native bee fauna but also risks eroding valuable local adaptations, such as genomic signatures linked to temperature, precipitation, and forest cover [37].

The utility of genomic tools to reveal signatures of adaptation

Genomic data provide a powerful tool for uncovering the genetic basis of traits that enable pollinators to persist and/or adapt to human-modified environments [42,43]. Specifically, comparative studies of gene families associated with hypothesized key biological preadaptive traits can help characterize their evolutionary patterns across the bee phylogeny (e.g. gene gains and losses) and their association with shifts in trait states [20]. These studies can also generate a predictive framework to identify bee lineages that may be more susceptible or tolerant to different stressors characteristic of anthropized habitats. For the identification of adaptive traits, genome-wide markers can be genotyped in bee populations sampled from human-dominated and natural habitats to detect outlier loci. This information can be used to link mutations with specific traits that confer fitness advantages in urban and agricultural landscapes [26,28].

With the advent of long-read sequencing technologies (e.g. PacBio, Nanopore) and the reduction in sequencing costs, the feasibility of using full genome sequence data to investigate evolutionary patterns of gene evolution and signatures of adaptation has increased exponentially. Collaborative efforts are accelerating the development of large publicly available genomic tools for this type of

study. Over 50 genomes have already been sequenced and assembled [29,44–47], and at least 100 others are under development through the Beename100 initiative (<https://www.beename100.org/>). Still, these genomes represent less than 1% of the total bee richness globally. The phylogenetic distribution of these available genomes is highly concentrated in one of the seven bee families (i.e. Apidae), currently representing over 80% of all the available genomes. This taxonomic bias currently limits the use of genome data for comparative studies across bee species that aim to identify preadaptive traits linked to resilience. By sequencing and analyzing the genomes of bee pollinators, it is possible to identify genes associated with ecological adaptation to human-modified environments. Reference genomes provide tools for studies to pinpoint specific genes and genetic variants that contribute to bees' ability to exploit anthropized environments [29,48].

The role of epigenetics

In addition to heritable traits as the raw material for micro- and macroevolutionary changes, the unique environmental factors of anthropized environments can have profound effects on basic biological processes such as cell differentiation and the development of organisms. These factors are expressed by epigenetic molecular mechanisms (EMMs) that include DNA methylation, histone modification, chromatin remodeling, and non-coding RNA regulation [49–51]. EMMs can cause short-term and long-term changes in gene expression [49]. The regulation of caste polyphenism in social insects is a fascinating example of how epigenetic information can be passed across cell divisions by EMMs [51,52].

Epigenetic responses can be triggered by various factors, such as diet, stress, toxins, and other chemical stressors, making insecticide resistance a subject of growing interest [50]. In honey bees, neonicotinoid pesticides can affect DNA methylation and cause changes in histone acetylation and deacetylation, which can be passed down to future generations (e.g. memory impairment). Sublethal effects of neonicotinoid exposure to honey bees include reduced fecundity and impaired immune response [50], which can also be passed on via maternal effects. Notably, studying bee epigenetics has sparked recent interest [50–52], but many epigenetic mechanisms remain insufficiently characterized and often rely on inferences based on a limited number of insect model species or even extrapolated from vertebrates. Understanding the role that natural environmental cues and human-induced stressors can play in EMMs is critical for assessing how to safeguard wild and managed pollinators.

Although epigenetic responses are often associated with negative consequences and responses to human-modified habitats, EMMs also influence how an organism

interacts with its environment and can be beneficial for survival in a changing world. Epigenetic modifications represent a potential mechanism for inheriting traits without alterations to the DNA sequence and can impact how pollinators respond to climate change. For example, the roles played by phenotypic plasticity, including epigenetic mechanisms, to acclimatization via non-genetic inheritance can offer bee populations protection against environmental shifts, enabling quick adaptive reactions to climate change [53]. However, there is little empirical evidence for acclimation capacity to heat tolerance among bees [54,55].

Gaps and future directions

Several knowledge gaps need to be addressed to advance our understanding of the relative importance of preadaptive and adaptive traits for the success of bees in human-modified habitats. Firstly, further investigation on species thriving in these environments is needed to characterize general patterns of adaptive traits associated with their success. For example, investigating evidence of selection on traits associated with heat tolerance and detoxification is necessary to demonstrate whether some bee species may be adapting to climate change and persistent exposure to pesticides. Other traits associated with resilience to pollutants and heavy metals on the evolutionary trajectories of bee populations are also critical and a major gap. Approaches using genome-wide scans for positive selection comparing populations in natural and human-dominated habitats are essential genomic tools to reveal ongoing adaptive processes in bees. Comparative genomic approaches should complement these studies to uncover the genetic basis of preadaptive traits associated with resilience. Explicitly investigating the genetic underpinning of traits adaptive to human-modified environments and mapping them onto a phylogenetic context provide a powerful approach to predicting 'winners' and 'losers' of anthropogenic change. Additionally, the population structure of managed bees and their wild relatives requires more detailed characterization. With the increasing use of managed bees for pollination services, detecting introgression, particularly maladaptive alleles, between managed and native bee populations is crucial. Currently, the role of epigenetic factors on the ability of bees to adapt to anthropized environments remains unexplored and is likely an important factor underlying the inheritance of traits without changes at the DNA level. One example of a currently unexplored avenue of research is whether changes in bee microbiomes are linked to their potential role in enhancing the detoxification of chemicals or digestion of diverse food sources in these environments, which are likely associated with epigenetic mechanisms. Focusing on these areas will help us gain a more comprehensive understanding of bee resilience and adaptation in human-dominated landscapes.

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

The authors declare no conflict of interest that may bias the content of this article.

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