The Conservation of Native Honey Bees Is Crucial

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Highlights

The western honey bee, *Apis mellifera*, is globally the most prominent pollinator used for pollination services in crops and is often known only as a domesticated species managed by beekeepers.

Recent studies suggest that the presence of large numbers of introduced managed colonies can threaten wild bee populations. Therefore, proposals to exclude *A. mellifera* colonies from protected areas have arisen.

The diversity of honey bee subspecies in Europe, Africa, and western Asia as a threatened component of the native fauna is underappreciated.

In Europe, wild honey bee populations are endangered, due to lack of nesting sites and hybridization between and the transfer of pathogens and parasites from managed to wild populations.

Natural areas, especially protected areas, are critical for the conservation of the wild populations of the western honey bee in its native range.

Abstract

Recent studies have emphasized the role of the western honey bee, *Apis* mellifera, as a managed agricultural species worldwide, but also as a potential threat to endangered wild pollinators. This has resulted in the suggestion that honey bees should be regulated in natural areas to conserve wild pollinators. We argue that this perspective fails to appreciate the multifaceted nature of honey bees as native or introduced species with either managed or wild colonies. Wild populations of *A. mellifera* are currently imperiled, and natural areas are critical for the conservation of local subspecies and genotypes. We propose that a differentiation between managed and wild populations is required and encourage integrated conservation planning for all endangered wild bees, including *A. mellifera*.

Keywords

Apis mellifera; beekeeping; human-mediated hybridization; pollination; protected areas; subspecies and genotypes

Emerging Perspective of Honey Bee Regulation

The current widespread decline of insect pollinators [1] could negatively affect human well-being and food production, as many crops rely on animal pollination for the quantity and quality of their yield [2]. To meet the demand for pollination services in crops, it is common practice to introduce managed pollinators, in particular colonies of the western honey bee (*Apis* mellifera) [3]. Conversely, as agricultural landscapes adversely affect honey bee survival through, for instance, pesticide exposure and limited flower availability 1., 2., 4., 5., beekeepers often keep managed colonies, at least temporally, far from agriculture, even in protected areas [6]. Recent studies have shown that the introduction of large numbers of managed colonies into protected areas can have detrimental effects on wild bee populations 7., 8., 9., 10., 11., 12., 13.. There is evidence for competition between introduced managed honey bees and native wild bee pollinators in the context of floral resource limitation 14., 15., 16., 17.. Pathogen spillover from managed to wild bee pollinators reduces pollinator health 18., 19.. Pests introduced with managed honey bees transfer to and reproduce on native *Bombus impatiens*, and honey bee viruses and diseases generally have a high propensity for spillover into other bee populations [20] and vice versa [21]. Therefore, proposals to regulate honey bees in protected areas to facilitate wild bee conservation have been made 6., 9., 11., 12., 17., 22.. While the detrimental effects of managed honey bees on other wild bee populations should be considered in conservation planning, we aim to present an alternative viewpoint based on the fact that *A. mellifera* is a natural component of the fauna of Africa, Europe, and western Asia. By evaluating: (i) the natural history of honey bees and human-mediated hybridization issues; (ii) the threats to local subspecies of *A. mellifera* in Europe and Africa; (iii) the current imperiled status of wild populations in their native range; and (iv) the role of natural areas for the conservation of wild populations, we highlight the urgent need for integrated conservation planning for all endangered bees, including the wild populations of the western honey bee.

What Are Honey Bees?

The western honey bee (*A. mellifera* L.) is a native species of Africa, Europe, and western Asia (Figure 1, Key Figure). The species split into four evolutionary branches that represent a huge diversity of 31 subspecies (also called geographic races) 23., 24., 25., which vary in terms of molecular characteristics, behavior, chemistry, and morphology 23., 26.. During the last glacial period, the European population of *A. mellifera* retreated southwards into four refuges: the Iberian Peninsula, the Italian Peninsula, the Balkan Peninsula, and the Middle East. Geographic barriers such as the Alps, Pyrenees, and Balkan Mountains contributed to reproductive isolation of the populations [23]. When the European glaciers retreated, the populations re-expanded northwards (Box 1). The African populations were not affected by glaciation and evolved independently.

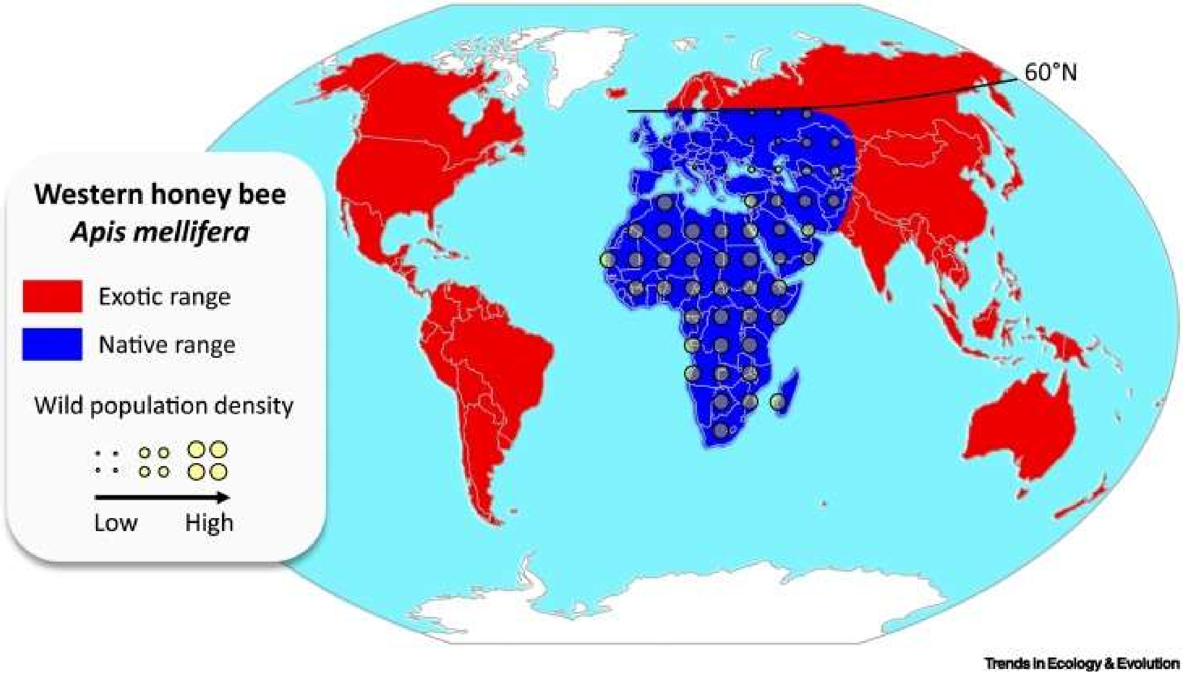

Figure 1. Key Figure. Worldwide, the Western Honey Bee *Apis* mellifera Exhibits a Multifaceted Nature as Both Native and Exotic, Managed or Wild Species. In Europe, the native range of *A. mellifera* is limited at 60°N, corresponding to the native range of plant species such as *Corylus* sp. and *Tilia* sp. [23]. The eastern limits of the native range include the Middle East, Kyrgyzstan, western China, and parts of Kazakhstan 23., 24., 25.. The density of wild honey bee colonies is higher in Africa than in Europe. Humans have introduced the species throughout the rest of the world.

Box 1

Human-Mediated Hybridization as a Threat to Wild Populations of the Western Honey Bee across Europe and Africa

After the last glacial period, the so-called O evolutionary branch of the European population *Apis* mellifera caucasica expanded from the Caucasus to the north (*A. m. pomonella*) and to the west (*A. m. anatoliaca*), while the C branch (A. m. *ligustica*, *A. m. carnica*, A. m. *cecropia*) spread from the Balkan and Italian Peninsulas to the northeastern coasts of the Mediterranean Sea and Central Europe and the M branch (*A. m. mellifera*, *A. m. iberiensis*) moved from the Iberian Peninsula into Western, Northern, and northeastern Europe [23] (Figure I). The African population was less affected by glacial events and evolved independently through the A branch (*A. m. scutellata*, *A. m. adansonii*, *A. m. capensis*).

For decades in Europe, large-scale commercially oriented beekeepers practiced the selection of honey bee colonies (e.g., long-distance translocation of subspecies, queen rearing) for yield improvement and docility 23., 33.. Even if not systematic among all beekeepers and regions (e.g., in some Central and Eastern European countries traditional beekeeping remains widespread), the support for nonnative subspecies and human-mediated hybridization has led to an important anthropogenic disturbance in the spatial distribution of evolutionary branches and subspecies in Western Europe (Figure I). However, introgressive human-mediated hybridization could have negatively affected locally adapted populations of wild honey bees with a loss of fitness-related characters. Cross-fostering of colonies from different European localities revealed that western honey bee colonies of local origin survived longer, indicating that genotype–environment interactions can affect colony fitness [67].

Whereas treatment against *Varroa* mites may have hindered the natural evolution of parasite resistance/tolerance in managed colonies, their hybridization with wild colonies is likely to lead to the transfer of susceptible phenotypes to wild populations, thereby increasing the risk of extinction in the wild. Conversely, the presence of wild honey bees that are subject to natural selection could have a positive effect on the resistance and resilience of managed introduced populations through transfer of adaptive characters [68]. Wild populations are important reservoirs of local adaptations that ultimately determine the survival of honey bees in the wild [69]. For instance, in Africa (and North America), it seems that the wild populations actually mitigate the effects of *Varroa* mites, allowing colonies to build resistance [31].

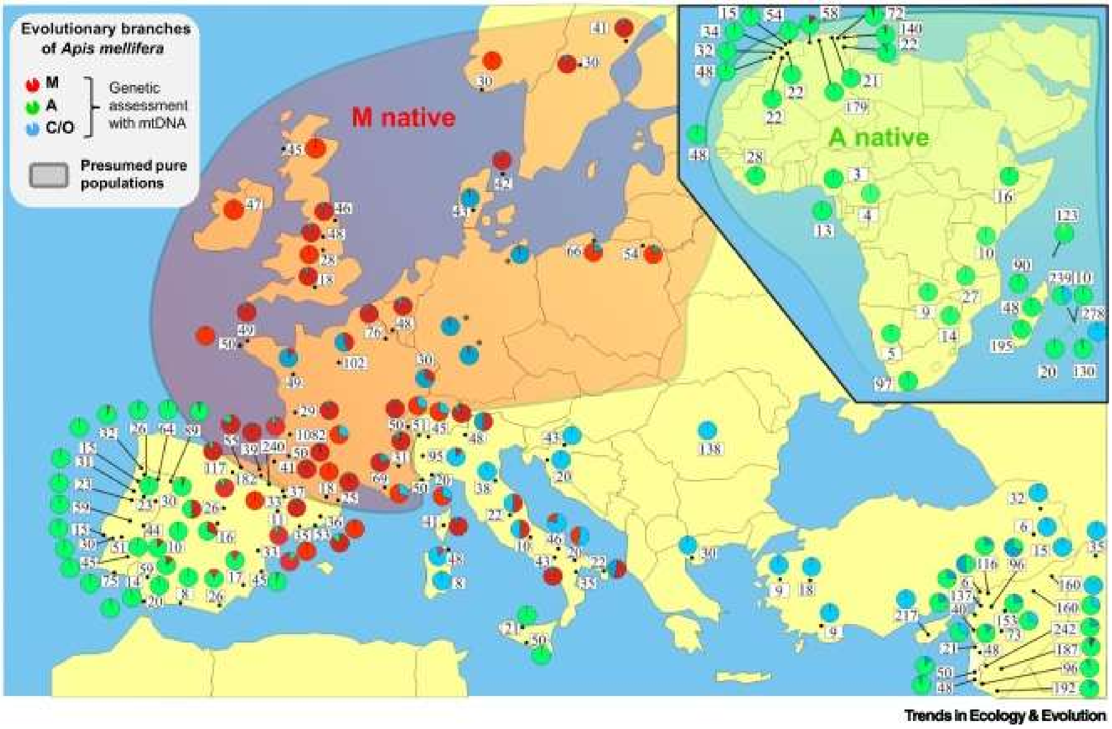

Figure I. Current Human-Mediated Introgression of Western Honey Bee Populations in Europe and Africa.

In its native range, the populations of *Apis* mellifera are represented by different evolutionary branches; namely, the M branch (in red), the A branch (in green), and, in blue, the C and O branches that are not distinguishable using mitochondrial DNA (mtDNA) analysis. This mtDNA molecular approach estimates the introgression rate of multiple haplotypes (pie charts) in a population (i.e., the number of colonies, shown by number). A large-scale synthesis of published mtDNA data (black points show the sampling sites) shows evidence of human-mediated introgression at the lineage level in many European regions. For instance, in Belgium, Denmark, France, Germany, Poland, Sweden, and the UK where pure M populations are presumed (highlighted areas), sampled populations reveal frequent introgression of the combined C and O branches. Although no mtDNA data are available to assess the introgression rate in Germany, it is well established that the managed honey bee populations are highly hybridized in this region, through the deliberate replacement and use by beekeepers of *A. m. carnica* since the 1950s 70., 71.. Evidence of human-mediated introgression also occurs in the Maghreb and the Indian Ocean islands (Republic of Mauritius, Rodrigues Island, and La Réunion) where the presumed pure A populations face introgressions of other lineages. In some regions where naturally evolved lineages overlap, such as in Spain, Italy, Eastern Europe, and the Middle East, human-mediated introgression is intertwined with natural hybridization. Details on the synthesis method and the complete list of references are available in Section S1 in the supplemental information online. The size of the map of Africa was reduced since fewer data are available from this region.

A. mellifera is particularly well known as a honey producer, but also as an important pollinator of many crops 3., 27. and wild plants 27., 28.. Therefore, the single species *A. mellifera* is often referred to as ‘the honey bee’, although there are at least eight other honey bee species in the genus *Apis* [29]. Many studies consider ‘managed pollinator’ as synonymous with ‘honey bees’, although most honey bee species are not managed 30., 31.. For instance, the giant honey bee *Apis dorsata*, the dwarf honey bee *Apis florea*, and the Bornean honey bee *Apis koschevnikovi* exist only as wild populations. Although *A. mellifera* has been introduced worldwide and is managed for honey production and crop pollination (Figure 1) [31], it is clear that the western honey bee cannot be defined as a domesticated species *per se*: managed colonies can swarm or abscond to establish wild colonies and beekeeping management has never entailed complete control over mating and reproduction [32]. Here, we define as ‘wild’ all honey bee colonies that live without human management interventions, regardless of potential past human-mediated hybridization.

Wild Western Honey Bees in Natural Areas

The western honey bee exhibits a multifaceted nature as a native or exotic, managed or wild species (Figure 1). However, arguments for restricting the presence of honey bee colonies in protected areas to facilitate the conservation of other wild bees 6., 9., 11., 12., 17., 22. apply only to the exotic and/or managed case. Little attention has been paid to colonies of *A. mellifera* living in the wild [33]. Honey bee health issues [1] have primarily been discussed in terms of their impact on beekeeping and crop pollination [2], while wild populations are often not considered or, in Europe, are considered extinct [6]. Nonetheless, some studies show that wild colonies of *A. mellifera* still exist in their native European range. For instance, a density of 0.1 wild colonies per km^2 was recorded in northern Poland [34], and similar densities were estimated in German woodlands (0.13 wild colonies per km^2) [35]. Wild colonies were also reported to colonize the forests of the Southern Urals [36] and indirect surveys of colony densities using genetic markers suggest that wild colonies occur in France [37], Ireland, and Italy [38]. However, it is unclear whether the survival and reproductive rate of wild colonies allows the maintenance of stable, self-sustaining populations or whether the occurrence of wild colonies in Europe depends on the recurring emigration of swarms from managed apiaries. The available density estimates in Europe 34., 35. are quite low compared with the reported density of wild honey bee colonies living in a comparable mixed landscape within its exotic range, in the temperate forests of New York State (1.0 wild colonies per km^2) 39., 40., or in relation to estimated wild colony densities within the native range in Africa (up to 10.2 wild colonies per km^2) [38].

The wild colony densities are likely to be primarily limited by the general scarcity of nesting sites (similar to other wild bees) in human-dominated landscapes (e.g., cities, croplands, managed forests). Tree-related cavities were the primary nesting sites of the wild colonies of *A. mellifera* in post-glacial Europe [41], and today old rural avenues and remnants of near-natural forests still provide suitable cavities that are regularly colonized by wild colonies 33., 34. (Figure 2A). The promotion of tree-related microhabitats as refuges for wild colonies in natural areas 34., 35. would therefore potentially foster the growth of wild, locally adapted western honey bee populations [42], thereby benefitting both *A. mellifera* and the beekeeping sector. However, insufficient data are available and there is an urgent need for census and monitoring programs to assess wild colony densities, life-history parameters (survival, reproductive rates), and the factors that drive their population dynamics.

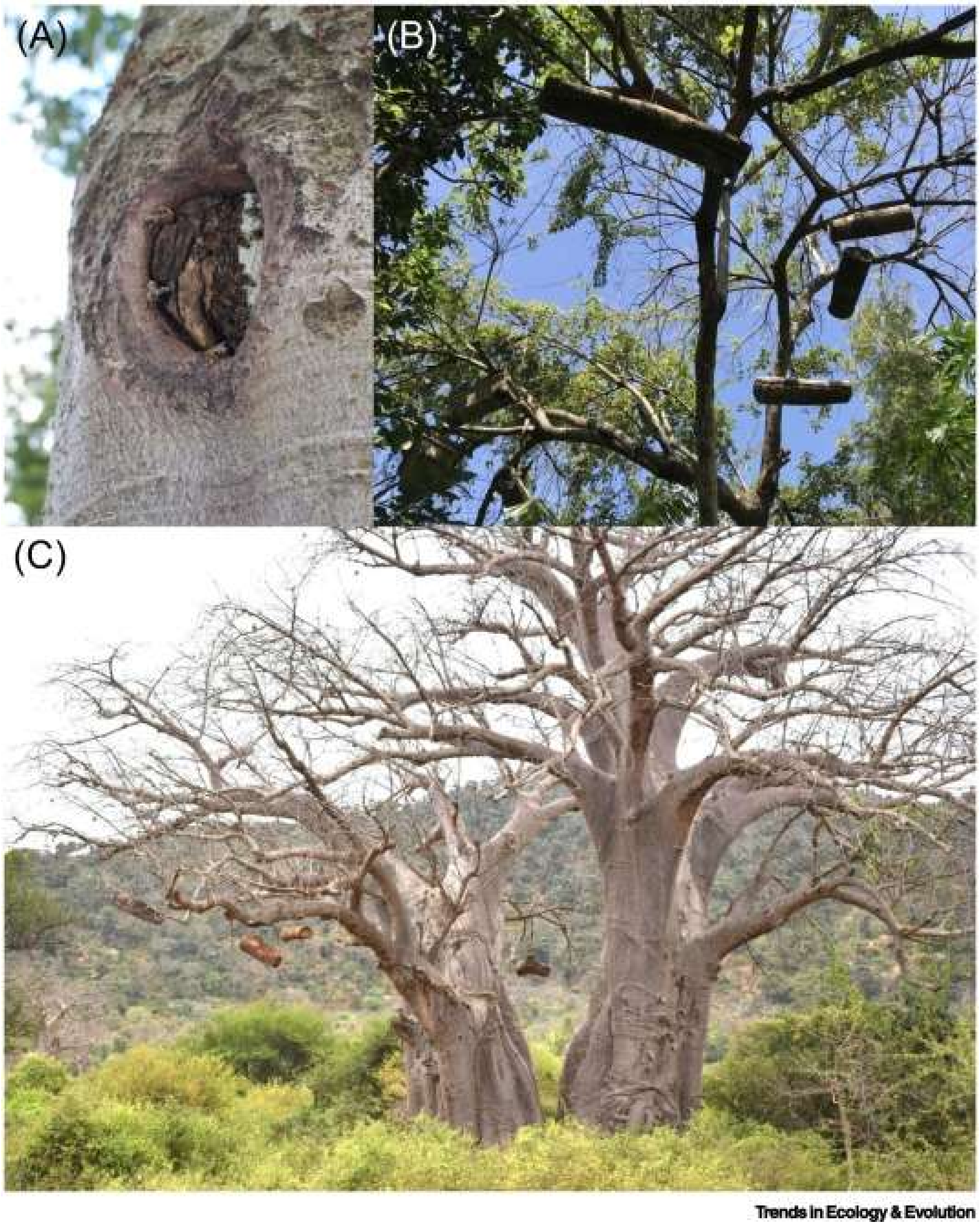

Figure 2. Wild Western Honey Bees in Natural Areas within Their Native Range.

The wild populations of *Apis* mellifera are endangered in most parts of Europe; however, wild colonies still exist in protected areas such as in the biosphere reserve of the Swabian Alb, Germany (A), where they regularly nest in old woodpecker cavities in beech trees (*Fagus sylvatica*) (P.L. Kohl and B. Rutschmann). In Africa, the density of wild colonies is much higher than in Europe and is supported by the supply of additional nesting sites: traditional beehives mounted in trees. In traditional beekeeping performed in natural areas – for instance, (B) at the border of Arusha National Park, Tanzania (I. Steffan-Dewenter) and (C) in the lowlands of Mt Kilimanjaro, Tanzania (H.K. Njovu) – beekeepers use local genotypes exclusively and do not control the reproduction of local populations or treat colonies against diseases.

In Africa, more than 90% of *A. mellifera* colonies are wild [43]. African populations are poorly characterized but include at least 14 subspecies with significant diversity in individual morphology [44] and pheromonal characteristics [26]. Moreover, beekeeping in many

African countries is practiced using traditional methods [43] and is an integral part of cultural heritage and forest conservation strategies [45]. Traditional beekeeping is characterized by no human influence on breed selection and rearing 43., 45.. A substantial part of beekeeping in Africa involves the use of traditional beehives, which are often hung on branches of scattered trees located in the natural woodlands or forests (Figure 2B,C). Besides its medicinal use [46] and economic importance to rural communities [43], honey is connected to some longstanding traditions and cultural values in many African countries. For instance, honey is used as a bride price and an important ingredient in an alcoholic beverage known as 'tej' in Ethiopia [47] and was used as offerings in ancient Egypt [48]. In some other countries such as South Africa, honey bee colonies are also conventionally managed for pollination services in crops [49].

Wild Western Honey Bees Are Endangered

Current evidence for the impact of introduced managed honey bee colonies on wild bee populations 7., 8., 9., 10., 11., 12., 13., 14., 15., 16., 17., 18., 19., 20. is limited and restricted to *Apis*–non-*Apis* interactions. However, introduced managed honey bees can also have a critical impact on wild populations of native honey bees [50]. Coexistence with managed apiaries exposes wild honey bee populations to bee pests and pathogens 21., 51.. For instance, the introduction of the ectoparasitic *Varroa destructor* mite caused a drastic decline of wild populations of *A. mellifera* in Europe [31], resulting in beekeepers treating their colonies using various acaricides [51]. The human-mediated dissemination of pests and pathogens could have reduced the population size of wild western honey bees almost to extinction in Europe [50], imperiling their survival in the native European range [36]. Moreover, coexistence with managed apiaries exposes wild honey bee populations to introgressive hybridization (see below) 38., 52..

Across its native range, honey bee populations have significantly higher genetic diversity in Africa than in Europe 52., 53.. The genetic diversity of the African subspecies combined with large numbers of wild colonies should result in higher resilience and resistance to changing environments [31] and to new pathogens 33., 43., 54.. Another major difference between African and European populations is that, in Africa, current beekeeping is still mostly based on trapping wild swarms and does not involve selective breeding [45], whereas in Europe breeding has altered the population structure 43., 50.. The wild populations of the western honey bee in Africa represent a highly valuable genetic resource that should be preserved, as they represent a source of genetic material for managed honey bee populations in the future.

The Human-Mediated Hybridization Challenge

The conservation of wild honey bee populations has received little attention. Historically, human-mediated hybridization has been considered the key conservation challenge. Until the mid-19th century, beekeeping comprised trapping swarms and robbing honey, while modern beekeeping is based on the use of standardized hives (e.g., Dadant and Langstroth) that allow year-round intensive management of large numbers of hives per beekeeper, hive movement over long distances (e.g., pollination services, global trade), pest and pathogen treatment, and partial control over reproduction (e.g., swarming control, queen rearing). Both queen selection and large-scale movements have led to human-mediated hybridization 23., 33.. A synthesis of published data on the genetic origin of *A. mellifera* sampled across Europe and Africa revealed that the post-glacial distribution of evolutionary branches has been anthropogenically disturbed with the introgression of nonlocal subspecies (Box 1). This suggests that a substantial proportion of the *A. mellifera* population throughout Europe is now artificially hybridized, leading to concerns of loss of biological diversity and the possible extinction of subspecies from previous distribution ranges. Nevertheless, biogeographical post-glacial differentiation remains visible (Box 1), suggesting that locally adapted subspecies are still present for future conservation. Over the past decades, conservation efforts have not addressed the protection of human-mediated hybrids [55]. For instance, the International Union for Conservation of Nature (IUCN) Red List guidelines exclude the consideration of hybrids, and all populations of *A. mellifera* are considered hybrids 56., 57.. However, in the absence of human activity, regionally adapted hybridized populations can be an important source of variability from an evolutionary perspective [58].

Concluding Remarks

We argue for the redirection of attention from managed honey bees to the neglected conservation of wild honey bees. Both wild *A. mellifera* and other wild bee populations are endangered in their native ranges due to widespread habitat loss. Further, they can be affected by managed pollinator species due to pathogen transmission and resource competition 1., 20.. The wild populations of *A. mellifera* are threatened by an additional factor, human-mediated hybridization associated with managed colonies. We therefore recommend conservation planning initiatives for all endangered wild bees including wild colonies of *A. mellifera*. As a starting point, a revision of the IUCN Red List of bees 56., 57., 59. should be initiated to pinpoint the current risk of extinction of wild western honey bee populations in Europe. This first step would help to mitigate conflict between conservationists and beekeepers by demonstrating their shared interests and to support the idea that inclusive solutions could be found for sustainable environmental management [60].

The local indigenous interactions between *A. mellifera* and the other wild bees in Africa, Europe, and western Asia present conservation challenges different from those where *A. mellifera* is exotic (e.g., eastern Asia, North and South America, Australasia). In the exotic range, traditional approaches to environmental management prevent the establishment of conservation programs for an exotic species. In cases where honey bees are indigenous, the conservation of the web of interactions between all wild bee populations (including honey bees) needs to be managed through the regulation of beekeeping, to mitigate the risks of interspecific pest transmission and the impact of apiaries on wild honey bee colonies.

In practice, how is the species *A. mellifera* to be conserved? In protected forest areas, the conservation of arboreal cavities could foster the colonization of wild honey bee colonies and thus promote the conservation of local subspecies (Box 2). In many European countries and regions, commercial beekeepers have placed little value on the local subspecies that are near extinction. However, recent initiatives by beekeeping associations and national policies aim to rescue and conserve such local subspecies 61., 62., 63., 64.. For instance, several conservation programs for the dark honey bee *A. m. mellifera* have been started in Western Europe[i,ii] 37., 65.. Here, traditional, small-scale beekeepers can play an important role in the conservation of local subspecies of *A. mellifera*. This requires the local reproduction of colonies or use of traditional techniques to catch and breed wild swarms from local populations instead of introducing nonnative (commercial) subspecies [66]. Moreover, education programs for local hobby beekeepers should teach beekeeping practices that allow natural selection and the use of local bees [32].

Box 2

How to Conserve the Western Honey Bee in Its Native Range

Natural areas are critical for the conservation of wild western honey bee populations. Particularly valuable are large forest areas without (or with extensive) management that foster the availability of senescent trees with cavities for colony nesting (Figure I). We recommend a step-by-step approach to conduct honey bee conservation programs, including:

• large-scale monitoring of wild western honey bee populations in large protected forest areas in Europe,
• genetic assessment of populations to identify those with low levels of introgression for protection 37., 65.,
• assessment of remaining natural areas with respect to their potential to provide the habitat requirements of wild honey bees – for instance, via the census of senescent trees with large cavities,
• management concepts to exclude risks of human-mediated hybridization and pest transmission from managed colonies, based on honey bee mating range 65., 72., and a supplemental buffer area with bee-friendly practices to minimize direct risks of pesticides and mass-flowering disturbances.

For the African populations, a similar approach should be considered in mixed landscapes, while a simple approach should be adopted for natural areas and agroforestry where current risks of human-mediated hybridization are lower (Figure I).

Several conservation programs of the dark European honey bee *Apis mellifera* – one subspecies of the M evolutionary branch – have started throughout Europe following this approach 37., 65.. The establishment of these conservation programs is critical for the preservation of regional genetic diversity and variability of honey bee populations in Europe. Moreover, conservation programs could maintain a reservoir of resistance against diseases and pests that can provide various honey bee strains and traits for beekeeping. Beekeepers can take advantage of the presence and conservation of wild colonies in the areas surrounding their activities and thus increase the long-term resilience of their managed colonies. Raised awareness of the risks associated with declining wild honey bee populations and the related loss of adaptive characteristics will encourage and support traditional beekeeping that uses specific management techniques and local subspecies.

Figure I. Proposed Conservation Planning for the Western Honey Bee in Its Native Range.

We propose a generic step-by-step approach to conduct honey bee conservation programs across (A) Europe and (B) Africa. After large-scale monitoring of wild western honey bee populations in large protected areas (in red) in mixed landscapes, we recommend a genetic assessment analysis to identify and protect populations with low levels of human-mediated hybridization. In cases where genetic analyses identify a sufficiently high level of a local subspecies genotype in a population proposed for conservation [e.g., up to 90% in the case of artificially hybridized populations, as found in France, Germany, and the UK (orange dots)], a census of available tree cavities can be undertaken and measures to increase nesting sites that support wild colonies implemented. Management interventions are applied to exclude risks of human-mediated hybridization and pest transmission from managed colonies (purple beehives) in a radius of 4–6 km surrounding the protected area (in green), where bee-friendly practices are needed to mitigate direct risks of pesticides and flower scarcity. While no beehives should be placed inside the protected core area to minimize human-mediated disturbance (black line), small-scale beekeeping should be allowed in the buffered bee-friendly area (in green) if the local subspecies genotype is used. This concept could help to protect wild colonies from the impacts of managed beehives and promote the use of local subspecies by beekeepers (so-called conservation beehives). In the case of African populations, in agroforestry and natural areas no spatial separation is necessary, as traditional beekeeping (white beehives) does not entail human-mediated hybridization.

Conservation programs for the western honey bee need to consider various pressures including human-mediated habitat loss, introgression of hybrids, transmission of pests and disease from managed colonies, and agricultural management that exposes bees to pesticides and leads to reduced diversity and abundance of floral resources (Box 2). The establishment of such conservation programs is critical to the preservation of the regional genetic diversity and variability of honey bee populations in Europe and Africa (Box 2). We conclude that in the context of ongoing global change, increased efforts to protect wild populations of honey bees – *A. mellifera* across its native range as well as other honey bee species in Asia – are essential to maintain the genetic diversity and ecological functions of this fascinating genus of social insect.

Outstanding Questions

What is the population status of wild honey bees across their native range? Insufficient field data are available on the density, dynamics, and genetic structure of wild populations of the western honey bee in Europe, as well as in Africa, and there are no long-term monitoring programs.

How do wild western honey bees respond to global environmental changes? There is an urgent need to study the ecology of wild western honey bees to determine factors that drive their population dynamics.

Are African populations of the western honey bee more resilient to global environmental change? Little is known about the African populations of *A. mellifera*, but the high genetic diversity of African subspecies along with the large numbers of wild colonies is likely to result in higher resilience and resistance to a changing environment.

How does human-mediated introgression and hybridization affect resistance to parasites, pathogens, and diseases in European populations of western honey bees? Beekeeping activities could cause the loss of resistance traits in wild populations.

Does the presence of wild western honey bee colonies positively affect managed populations and beekeeping activities? Wild honey bees could have a positive effect on the fitness of managed populations through the introgression of beneficial traits for local adaptation.

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Resources

[i]www.sicamm.org

[ii]www.fedcan.org

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