



The Diversity Decline in Wild and Managed Honey Bee Populations Urges for an Integrated Conservation Approach

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OPEN ACCESS

Edited by:

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Specialty section:

This article was submitted to
Conservation and Restoration
Ecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: 31 August 2021

Accepted: 24 January 2022

Published: 03 March 2022

Citation:

Panziera D, Requier F,
Chantawannakul P, Pirk CWW and
Blacquière T (2022) The Diversity
Decline in Wild and Managed Honey
Bee Populations Urges for an
Integrated Conservation Approach.
Front. Ecol. Evol. 10:767950.
doi: 10.3389/fevo.2022.767950

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Many parts of the globe experience severe losses and fragmentation of habitats, affecting the self-sustainability of pollinator populations. A number of bee species coexist as wild and managed populations. Using honey bees as an example, we argue that several management practices in beekeeping threaten genetic diversity in both wild and managed populations, and drive population decline. Large-scale movement of hive stocks, introductions into new areas, breeding programs and trading of queens contribute to reducing genetic diversity, as recent research demonstrated for wild and managed honey bees within a few decades. Examples of the effects of domestication in other organisms show losses of both genetic diversity and fitness functions. Cases of natural selection and feralization resulted in maintenance of a higher genetic diversity, including in a *Varroa destructor* surviving population of honey bees. To protect the genetic diversity of honey bee populations, exchange between regions should be avoided. The proposed solution to selectively breed all local subspecies for a use in beekeeping would reduce the genetic diversity of each, and not address the value of the genetic diversity present in hybridized populations. The protection of *Apis mellifera*'s, *Apis cerana*'s and *Apis koschevnikovi*'s genetic diversities could be based on natural selection. In beekeeping, it implies to not selectively breed but to leave the choice of the next generation of queens to the colonies, as in nature. Wild populations surrounded by beekeeping activity could be preserved by allowing Darwinian beekeeping in a buffer zone between the wild and regular beekeeping area.

Keywords: honey bees, selective breeding, natural selection, biodiversity, genetic variation

INTRODUCTION

While the demand for crop pollination services increases worldwide (Aizen et al., 2008), many populations of wild and managed bee species are reported to be in decline due to several drivers such as parasites, pesticides and habitat loss (Potts et al., 2010; Kleijn et al., 2015). Although some stingless bee, bumble bee, mason bee and leafcutter bee species are managed for pollination, we

restrict the discussion to the honey bee species that are managed for pollination and hive products, *Apis mellifera*, *Apis cerana* and *Apis koschevnikovi*. These species have a double status, being both managed and wild-living (Pirk et al., 2016, 2017; Requier et al., 2019). In the latter category we include “feral” colonies –which can be native to the area or not–, once managed but reverted to a wild-living condition. Because honey bee queens mate indifferently with drones from both managed and wild-living colonies, the two groups are interconnected and beekeeping practices can have an impact on the whole population. Specifically, this double status imposes a serious threat for the genetic diversity of honey bees (Espregueira Themudo et al., 2020; Tanasković et al., 2021), potentially compromising the ability to cope with the existing and oncoming stresses. We propose an integrated approach to protect the genetic diversity of both managed and wild populations of honey bees.

STATUS AND THREATS ON WILD-LIVING AND MANAGED HONEY BEE POPULATIONS

Honey bees, i.e., the *Apis* genus of the *Apidea* family (Hymenoptera), include 11 species: 10 native to South-eastern Asia (of which five managed ones), and one native to Africa, Middle-East, Central Asia and Europe (*Apis mellifera*). *Apis mellifera* is represented by 31 subspecies (reviewed in Fontana et al., 2018; Fontana, 2019), of which 15 are native to Europe, 11 in Africa and 5 in the Middle-East and central Asia. In Europe, not many colonies still live in the wild. Jaffé et al. (2010) showed that in Europe, in most cases, all the mating drones originated from nearby managed colonies, with only a small share of the drones coming from unidentified (likely non-managed) colonies in Ireland and Italy. Nevertheless, recent evidence shows that wild-living populations of *Apis mellifera* are still present in Europe (Oleksa et al., 2013; Kohl and Rutschmann, 2018; Requier et al., 2020; Bila Dubaić et al., 2021; Kevill et al., 2021; Rutschmann et al., 2022). Densities of 0.1 wild colonies per km² have been reported in German forests where *Apis mellifera* uses tree cavities as nesting sites (Kohl and Rutschmann, 2018). Accordingly, Requier et al. (2020) estimated that more than 80,000 wild-living honey bee colonies could currently persist in European forests, representing 2% of the current managed honey bee population in Europe. Eleven subspecies of *A. mellifera* are endemic to Africa, of which some are in decline (Hepburn and Radloff, 1998). In Africa, traditional beekeeping practices are dominantly used and the densities of wild colonies are much higher than in Europe (Moritz et al., 2007). Jaffé et al. (2010) showed that in South Africa as well as in Sudan, in contrast to the situation in Europe, many of the mating drones –often the entirety– were from the wild.

South-eastern Asia represents the only geographical area where five cavity nesting honey bee species originally coexist and are managed or semi-managed (*A. cerana*, *A. indica*, *A. koschevnikovi*, *A. nigrocinta* and *A. nuluensis*) along with five open nesting wild species (*A. andreniformis*, *A. breviligula*, *A. dorsata*, *A. florea*, *A. laboriosa*) (Arias and Sheppard, 2005;

Lo et al., 2010; Chantawannakul et al., 2018). *A. cerana* has a wider habitat range than *A. koschevnikovi*, which is limited to the tropical evergreen forests of the Malay peninsula, Borneo and Sumatra (Hepburn and Radloff, 2011). *A. cerana*, *A. indica* and *A. koschevnikovi* are still managed in a traditional way, using straw baskets, clay pots, cavities of tree trunks, and are not subjected to large breeding efforts (Chantawannakul et al., 2004, 2018). *A. cerana* comprises several subspecies such as *A. cerana cerana* in Vietnam and China and *A. cerana japonica* in Japan. Several subspecies of *A. mellifera* (*A. m. ligustica*, *A. m. carpatica*, *A. m. caucasia*, *A. m. mellifera*, *A. m. carnica*) were introduced in Asia at independent events and locations and are now widespread across the continent (Chantawannakul et al., 2018).

Similarly, *Apis mellifera* has been introduced to the Americas, Australia and Oceania by settlers (Crane, 1999), where it is widely used for pollination of crops and has spread in the wild as feral colonies and populations (e.g., Seeley, 2007; Seeley et al., 2015). In South America, the African subspecies *A. m. scutellata* has also been introduced and hybridized with the European subspecies. These hybrids, called “Africanized honey bees” have widely expanded their range up to the Southern part of North America (Winston, 1992).

Apis cerana has recently invaded the north of Australia (Gloag et al., 2016), while *Apis florea* has reached and spread in Africa (Ruttner, 1992). *Apis florea* has been introduced in Sudan and may be expected to spread (Bezabih et al., 2014). Although competition with native *A. mellifera* subspecies cannot be excluded, it seems limited (El Shafie et al., 2002). These introduction events also gave rise to the exchange and spill-over of foreign pathogens and parasites between honey bee species and between Asia and the other continents. Since the introduction of *A. mellifera* in parts of Asia where it did not previously occur, higher prevalence of bee pathogens and parasites has been reported in the native honey bee species (Forsgren et al., 2015; Chanpanitkitchote et al., 2018). Similarly, host-switch events of several diseases and parasites such as *Varroa* spp. (Roberts et al., 2015; Traynor et al., 2020), *Nosema ceranae* and *Tropilaelaps mercedesae* (Chantawannakul et al., 2018), from native honey bee species to *A. mellifera* have been observed. Such examples are a reminder that importing honey bee nukes and queens, or any others species, to non-native areas can cause disease transfers between introduced and native species.

Several threats to honey bees are common worldwide, such as habitat loss, large-scale agriculture, use of pesticides and a number of parasites and diseases. *Varroa destructor*, an ectoparasitic mite that has spread to all continents with the exception of Australia (present however in New Zealand) is generally considered the greatest threat to honey bee health (Traynor et al., 2020). Although *V. destructor* has spread across Africa too, little damage was reported. This might be explained by a greater ability of large honey bee populations, of which a significant proportion consists of wild-living colonies, to quickly adapt to the new parasite through natural selection (Moritz et al., 2007; Pirk et al., 2016, 2017). Beekeeping in America and Australia is highly industrialized and large scale, with –apart from a small contribution of side-line beekeepers– a low number of queen breeders taking care of the genetic make-up of most bee

colonies. It is important however to note that, in parallel, feral populations are present and numerous in South America and Australia. In Europe, several subspecies are under threat due to loss of genetic diversity as a result of admixture (previously isolated populations interbreeding) (Jensen et al., 2005; Ellis et al., 2018; Espregueira Themudo et al., 2020; Henriques et al., 2021; Tanasković et al., 2021). Additionally and as we will see below, migratory beekeeping, queen trade, breeding and selection for specific traits may ultimately reduce the fitness of managed and wild populations.

THE DOUBLE STATUS OF HONEY BEES AS MANAGED AND WILD SPECIES AFFECTS THEIR GENETIC DIVERSITY

The worldwide introduction of *Apis mellifera* subspecies outside of their native ranges has led to biological invasions (e.g., Africanized honey bees in the Americas). Moreover, the wide use of migratory beekeeping, queen trade and breeding beyond the native ranges led to many events of human-mediated hybridization (De la Rúa et al., 2009; Requier et al., 2019). While admixture can increase genetic diversity in the immediate term (Harpur et al., 2012; Oldroyd, 2012), it may also lead to large scale homogenization and the subsequent decrease of genetic diversity driving the loss of local adaptations (De la Rúa et al., 2013; Espregueira Themudo et al., 2020). Some of these changes, sometimes intentional for managed stocks, can have significant repercussions for the fitness of wild local populations as wild queens and managed drones mate together (Neumann and Blacquièrre, 2017).

When analyzing genomes of individuals from museum collections and extant populations, Espregueira Themudo et al. (2020) saw a decrease in genetic diversity (lower nucleotide diversity) in the two main lineages of Western Europe (lineages C and M) accompanied by signs of positive selection within the major royal jelly protein gene family. The authors argue that this observed decrease, initiated during the last century, is possibly caused by an artificial selection pressure focused on queen's performance combined with a lower density of colonies, in a more fragmented habitat dominated by managed apiaries.

Targeted selection may greatly affect the genetic diversity of honey bee species and induce adverse side-effects. Although honey bees are not (yet) domesticated, we will in the next paragraph take examples from domesticated species in order to give a broader perspective of the effects of decreasing genetic diversity.

DOMESTICATION VERSUS NATURAL SELECTION: IMPACTS ON GENETIC DIVERSITY IN HONEY BEES

The impact of domestication on species is an important topic in evolution. For instance, Fages et al. (2019) tracked the genetic diversity of the horse along its 5000 years of domestication.

Despite some loss of variation due to selection for desired traits of horses, breeding was only local and the total variation remained stable for millennia. This strongly changed when ~200 years ago the horse became a fashionable animal for the rich and noble, and breeding and selection reached a global scale. Since then, most of the variation has been lost, up to a level where several deleterious variants in the genome appeared, which cannot be repaired due to genetic linkage, and because wild horses are since a long time fully extinct. In honey bees, we see that domestication/selective breeding leads to diversity loss, which can translate into the loss of local adaptations (Kovačić et al., 2020). As in other species, this process may be accelerated by breeding becoming a large scale and well-organized activity aided by the implementation of modern molecular biology tools.

In the heavily domesticated cattle (*Bos taurus*) the level of domestication (and the level of contact with humans) was found to strongly correlate negatively with brain size: in dairy cattle a loss of brain volume of 30% had occurred in comparison with cattle's most recent ancestor (auroch, *Bos primigenius*), while in bullfighting cattle the loss was limited to 15% (Balcarcel et al., 2021). The loss of essential functions like brain power in cattle might in the case of the honey bee translate into loss of hive wisdom: limitation of the flexibility of task division, and limitations to reach homeostasis (Oldroyd and Fewell, 2007).

Mattila and Seeley (2014) showed that, since only a subset of the patriline within a colony perform scouting tasks, polyandrous *A. mellifera* colonies, being genetically more diverse, are far better in exploiting changing resources than monandrous colonies with a limited genetic diversity. Moreover, patriline are not represented equally in performing other tasks (Robinson and Page, 1988), highlighting the risks of targeted selection for specific traits, through which crucial traits might be lost. A comparison between artificially made "normal" (i.e., 15 drones) polyandrous and hyper-polyandrous colonies (30 and 60 drones) demonstrated a better performance of hyper polyandrous colonies (Delaplane et al., 2015). Finally, a recent study highlighted the role of hyper polyandry in capturing rare specialist allele combinations, further increasing the colony's fitness (Delaplane et al., 2021).

In domesticated chickens, there has been selection against brooding (an anti-fitness change in the Darwinian sense) and by following selective sweeps occurring during the feralization of an admixed domestic population on an Island, Johnsson et al. (2016) demonstrated that feralization targeted different alleles than domestication did, especially alleles that correlate with reproductive output and sexual selection, thus the loss on fitness traits and reproduction was substantial.

Espregueira Themudo et al. (2020) showed that the genetic diversity of European honey bees had been reduced within a few decades, possibly by selection and breeding for specific traits, and by abandoning the local stock. While it is difficult to obtain reliable estimates of the proportion of beekeepers actively using artificial selection, surveys reporting voluntary replacements and purchase of queens point to high numbers in Europe (Gray et al., 2020; Bieńkowska et al., 2021). Selection and breeding aiming for varroa resistance traits might cause the loss of additional genetic information. It is thus striking to

see that, in the honey bees of Arnot Forest, natural selection over a few decades did not cause a high loss of nuclear DNA variation, even after a severe bottleneck resulting in the loss of many matriline (Mikheyev et al., 2015). According to these examples, it seems honey bee domestication attempts decrease the genetic diversity and fitness values conversely to natural selection.

CONSERVING THE GENETIC DIVERSITY OF WILD AND MANAGED HONEY BEE POPULATIONS

Conservation of native honey bees is needed to preserve their genetic diversity, both for wild and managed populations (Alaux et al., 2019; Requier et al., 2019). In the case of equally abundant wild and managed colonies in the population, an integrated conservation approach for both populations could be applied. In Europe, however, wild populations of honey bees are usually intensively surrounded by managed populations with which they hybridize and are thus under the same human-mediated pressure on their genetic diversity (De la Rúa et al., 2009). Avenues for protection and conservation of the wild and native populations of honey bees in Europe have been proposed by Requier et al. (2019). In order to protect all genetic diversity of European subspecies and populations of honey bees, such an approach should be applied even where no wild colonies are reported, and beekeepers should allow the formation of new feral colonies through swarming. While swarming represents a loss from the beekeeper's perspective and can sometimes be problematic when swarms settle in dense urban areas (see Bila Dubaić et al., 2021), it could help increase the sizes and resilience of the reportedly alarmingly small wild populations of honey bees in Europe (Moritz et al., 2007; Seeley, 2019; Requier et al., 2020). Nevertheless, many beekeepers tend to abandon their original local bee stocks or often allow input of genetic material from distant areas (Meixner et al., 2010). Had the genetic diversity of managed honey bees been increased through admixture before (Harpur et al., 2012; Oldroyd, 2012), the consequent homogenization might ultimately drive the loss of local adaptations (De la Rúa et al., 2013). Recent studies showed that, since the 2nd half of the 20th century, the genetic diversity of several European honey bee populations has significantly decreased in their native range (Espregueira Themudo et al., 2020; Tanasković et al., 2021). How can this initiated and speedy loss be stopped?

Several authors have proposed to conserve honey bee subspecies and their genetic diversity through "utilization" (Uzunov et al., 2017). The promoted idea is that breeding local populations or subspecies to become more suitable for beekeepers would guaranty the adoption and thus the conservation of these genetically "improved" bees. This approach would require independent breeding programs for each (local) subspecies/ecotype. However, would this domestication really conserve genetic diversity? Selective breeding reduces genetic diversity by definition since some alleles and thus traits are increased in frequency at the cost of others, and the chosen targets

in general do not result in an increased fitness. For example, most selective breeding programs select for a lower swarming tendency, which implicates selection against reproduction of the colonies in an evolutionary sense, decreasing fitness (Seeley, 2017). Most selection programs select for gentleness. Yet, recent research showed that gentleness favored the entrance of foreign worker bees and their *V. destructor* mites into the colonies, leading to an increased infestation rate and a lower fitness (Kulhanek et al., 2021). Using the approach of selective breeding of local subspecies and populations would lead to a large number of "improved" sub-species or local populations, all with a decreased genetic diversity and an impoverished fitness. As pointed out by Requier et al. (2019), although some hybridized locally adapted populations would be worth conserving, most existing breeding programs as well as conservation efforts fixate on subspecies perceived as "pure" (Büchler et al., 2010).

Several breeding programs currently aim to select colonies resistant to varroa. As *Varroa destructor* is the main present threat for apiculture and the European honey bee, selection and breeding programs have started since its arrival in many places (see e.g., Le Conte et al., 2020). Some of these select on specific traits, some on the outcome of combinations of traits (for instance mite population growth), and a few just on survival of the colonies (natural selection). Apart from the natural selection approach, such programs will invariably result in an important decrease of genetic variation. In addition, one should keep in mind that, although it may seem to be the case now, *V. destructor* is not the ultimate nor final threat to the western honey bee. Even when selection is on survival, beekeepers sometimes use only the "best" colonies/queens to produce the next generation, which narrows the genetic input and contrasts with natural selection, through which all vital colonies contribute to the next generation. Furthermore, by choosing only the "best" queens (mated with the "best" drone lines), one does only select the bees and prevents coevolution with their parasites and symbionts (Neumann and Blacquièrre, 2017; Blacquièrre and Panziera, 2018; Grindrod and Martin, 2021).

TOWARD AN INTEGRATED CONSERVATION APPROACH OF THE GENETIC DIVERSITY IN HONEY BEES

The genetic variation present in local populations is of value, whether of pure or hybridized nature, and part of it may help adapting to local conditions. Since natural exchange of genes between colonies is restricted to within ~10 km areas, the concept of locality is of a rather small scale (Moritz et al., 2007; Jaffé et al., 2010). The integrated conservation approach of honey bee diversity we suggest is based on these aspects and considers two fundamental points: (i) First of all, we recommend to leave reproduction to the colony: it may choose the queens to rear, which will mate with the most vital drones in the environment. This would prevent leaving only the few "best" chosen queens and drone lines to produce the next generation. Note that in natural selection, survival of the fittest

(Darwin et al., 1858) is not achieved by only survival of the best fitting but by a step-by-step elimination of the least fitting through lower reproductive success. Using this approach in beekeeping would avoid reducing diversity excessively. (ii) If wild populations of honey bees share an area with colonies managed by beekeepers, they will mate together and be affected by the narrower genes/alleles pool. As proposed by Requier et al. (2019), isolation zones should be created to protect these wild honey bees, in which colonies managed with Darwinian beekeeping methods could coexist (Blacqui re et al., 2019; Seeley, 2019). Moreover, the safeguard of wild-living populations of honey bees could be directly promoted by the conservation of natural nesting sites such as tree cavities (Oleksa et al., 2013; Kohl and Rutschmann, 2018; Requier et al., 2019). Thus, conservation plans of unmanaged forests and old trees present in hedgerows or isolated would promote the conservation of wild-living honey bees (Requier et al., 2020), as well as the conservation of semi-natural habitats (Rutschmann et al., 2022). While much focus has been on providing beekeepers with bees that are deemed desirable from a human perspective, a shift toward a situation in which natural selection is allowed to act

would help to preserve a genetic diversity that will be crucial for the conservation of honey bee species and the long-term sustainability of beekeeping.

AUTHOR CONTRIBUTIONS

DP, FR, PC, CP, and TB conceived the idea. DP and TB wrote the first draft of the manuscript with substantive input from FR, PC, and CP. All authors contributed to the revisions and approved the final manuscript.

FUNDING

DP was supported by Biointeractions and Plant Health (part of Wageningen University and Research) internal fund. FR received funding from the French Biodiversity Agency (OFB 21.0894). PC was supported by the Ricola foundation and the Chiang Mai University fund. CP received funding from the National Research Foundation of South Africa.

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