Apidologie (2025) 56:67
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https://doi.org/10.1007/s13592-025-01193-w

Review article

Living in harmony with nature: the key to resilience of honeybees (*Apis mellifera*) in Africa

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Received 10 January 2025 – Revised 28 May 2025 – Accepted 10 June 2025

Abstract – Managed honeybees play a crucial role in enhancing agricultural crop production and plant biodiversity conservation and ensuring food security. However, beekeepers, especially those in the Northern Hemisphere, are experiencing high honeybee colony losses, mainly due to the ectoparasitic mite *Varroa destructor*. This could threaten our future food security. The presence of *V. destructor* has also been reported in Africa; however, honeybees are less affected by the mite. Moreover, local beekeepers do not consider the mite as a threat to their colonies, and colonies survive without mites' treatment. Mite-resistant honeybee populations have also been reported in various parts of Europe, but they are limited in number and confined to specific regions. Therefore, understanding why mite-resilient honeybee populations are flourishing in many African countries is crucial for developing effective management strategies to improve honeybee health worldwide. Hence, this review synthesizes existing knowledge about the factors and traits that allow mite-resilient honeybee populations in Africa to flourish and aims to translate the insights gained from Africa into more effective approaches for managing the impact of *V. destructor* worldwide. The results suggest that African-derived honeybees are resilient to a broad set of threats including *V. destructor* because they live in harmony with nature. Resilience is attributed to a more bee-friendly environment, to better balanced colony densities, to beekeepers' management practices, and to the bee's behavioural adaptation and physiological and genetic traits. Nature-based beekeeping practices that allow natural selection to operate and maintain the genetic diversity of local honeybee subspecies are the key to their resilience against *V. destructor*.

African honeybees / Genetic diversity / Natural selection / Resilience / *Varroa destructor*

1. INTRODUCTION

Managed honeybees (*Apis mellifera*) play a crucial role in enhancing crop production (Garratt et al. 2014), plant biodiversity conservation (Bradbear 2009), stabilizing ecosystem (Sabbahi 2022), and supporting food and nutrition security (Dafar 2018). However, there is clear evidence of high honeybee colony losses, especially in the Northern Hemisphere, potentially threatening our future food and nutrition security (VanEngelsdorp et al. 2012). These losses are attributed to several interacting biotic and abiotic factors including honeybee diseases and pests, nutritional stress caused by habitat losses, and improper pesticide use (VanEngelsdorp et al. 2012; Naug 2009). Of the biotic threats, the ectoparasitic mite *Varroa destructor* and the viruses it vectors, such as the deformed wing virus (DWV), are the primary drivers of colony losses (VanEngelsdorp et al. 2012; Martin et al. 2012).

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Communicated by Klaus Hartfelder.

Published online: 07 July 2025

European and American beekeepers have relied on intensive acaricide treatments to control *V. destructor* infestations (Büchler et al. 2010), but the mites have already shown to develop resistance to synthetic acaricides (Sammataro et al. 2005). Chemical treatments have also resulted in the propagation of susceptible honeybee colonies (Büchler et al. 2010), making bees more dependent on the chemicals instead of relying on their natural defences against this pest (de Mattos et al. 2017).

Since the intensification of the beekeeping industry in the Northern Hemisphere, honeybees have always been subjected to selective breeding and domestication to enhance certain traits such as honey production and gentleness (Büchler et al. 2010; Neumann and Blacquière 2016; Uzunov et al. 2017; Guichard et al. 2020). Many European beekeepers also have preferred the Carniolan honeybee (*Apis mellifera carnica*) over local subspecies due to its gentleness and higher honey yields (La R´ua et al. 2009). Although breeding and domestication efforts, as well as the use of certain subspecies like *A. m. carnica*, have improved gentleness and productivity, the overall resilience and health of bee populations have not improved as expected (Guichard et al. 2020). Instead, these efforts have led to a reduction in genetic diversity (Büchler et al. 2010), which is a crucial factor for colony survival under various environmental stressors (Tarpy and Pettis 2013; Leclercq et al. 2018), and the propagation of bees vulnerable to pests and pathogens (Büchler et al. 2010; de Mattos et al. 2017).

The occurrence of *V. destructor* and its associated viruses such as DWV have also been reported in many African countries (Pirk et al. 2016). Unlike European-derived honeybees, African-derived honeybees, by which we refer to the eleven native African *A. mellifera* subspecies that are genetically diverse and adapted to a wide range of climatic conditions (Franck et al. 2001; Aglagane et al. 2023), suffer less from mites infestations and survive without beekeepers' interventions (Akinwande et al. 2012; Begna et al. 2016; Chemurot 2017). Moreover, local beekeepers do not consider this ectoparasite as a threat to their colonies (Gratzer et al. 2021), and no significant colony losses have been attributed to it. This is also true even in countries with highly virulent Korean haplotypes of *V. destructor* (Anderson and Trueman 2000), such as Ethiopia (Begna et al. 2016), Uganda (Chemurot 2017), Kenya (Nganso et al. 2017), and Nigeria (Akinwande et al. 2012), demonstrating the African-derived honeybee's innate resilience against *V. destructor* infestations. African honey bees have also developed tolerance to viral infections such as DWV (Gebremedhn et al. 2020), which contributes to colony losses in the Northern Hemisphere (Martin et al. 2012), as a result of natural selection.

V. destructor-resistant honeybee populations have also been reported in various parts of Europe, such as Norway (Oddie et al. 2017), France (Le Conte et al. 2007), Sweden (Fries et al. 2006), and the Netherlands (Blacquière et al. 2019), as well as in the USA (Seeley 2007). Virus-tolerant bees were also observed in the Gotland honeybee population (Thaduri et al. 2019). However, these populations are limited in number, confined to specific regions, and are still the result of intensive beekeeping practices or management. Therefore, understanding why *V. destructor*-resilient honeybee populations are flourishing in many African countries is crucial for developing effective management strategies to improve honeybee health worldwide. Hence, this review synthesizes existing knowledge about the factors and traits that allow *V. destructor*-resilient honeybee populations in Africa to flourish and aims to translate these insights gained from Africa into more effective approaches for managing the impact of the ectoparasite worldwide.

2. AFRICAN-DERIVED HONEYBEES LIVE IN HARMONY WITH NATURE

2.1. High floral resource diversity and carrying capacity in Africa

Africa is endowed with diverse agro-climatic conditions that support diversified floral

resources (Adi et al. 2014), which in turn sustain over 17.5 million managed honeybee colonies across the entire continent as of 2022 (Fig. 1). Forest beekeeping is the most dominant form of beekeeping in many African countries, followed by backyard beekeeping (Lowore et al. 2018; Lowore 2020; Tarekegn 2022). Backyard beekeeping is widely practiced near home gardens and is highly integrated with crop production, where a variety of plant species and crops are grown intensively (Ababor and Tekle 2018). The integration of beekeeping with crop production and natural forests provides diversified floral resources, which serve as a continuous source of pollen and nectar for honeybee throughout the year (Adi et al. 2014). Although vascular plant alpha diversity is similar between Africa and Europe on a smaller scale (Brummitt et al. 2021; Sabatini et al. 2022; Qian and Qian 2023), honeybee colonies in Africa may benefit more nutritionally from the combination of local alpha diversity, higher beta diversity, and greater floral resource density in their foraging areas. In addition, the population density of managed honeybees in Africa is lower (1 colony/km^2) compared to the population density in Europe (1.2 colonies/km^2) (Visick and Ratnieks 2023), which may reduce the nutritional stress for African-derived honeybees due to less competition for floral resources. Although the presence of high wild bee population density in Africa (Moritz et al. 2007; Visick and Ratnieks 2023) may lead to resource competition with managed bees, the smaller colony size or nest cavity of wild bees compared to managed honeybees (Loftus et al. 2016) may reduce resource competition.

Nutritional status is closely linked to colony health (Branchiccela et al. 2019) and bees fed high-quality diets have stronger immune responses (Corona et al. 2023). Diversified floral resources, providing a variety of nutritional niches, enhance honeybees' immune function and overall resilience to pathogens (Branchiccela et al. 2019; Corona et al. 2023). Hence, the observed strong immune response of African-derived honeybees to viral infections and *V. destructor* infestations, compared to European-derived bees (Gebremedhn et al. 2023), may be partly attributed to the highly diverse floral nutrients available in their environment (Adi et al. 2014). This is primarily because African apiaries are located in areas with a more diverse nutritional offer and larger carrying capacity per colony than European apiaries.

Honeybees adjust their adaptive behaviour, such as swarming, according to the availability of local floral resources (Nuru et al. 2002). Honeybee colonies in Africa reproduce naturally by swarming, and local beekeepers mostly use swarm catching as their colony source rather than using artificial methods (Gebretsadik and Negash 2016). Therefore, the success of swarm catching largely determines the population density of managed honeybee colonies in local African apiaries. This strategy helps to maintain bee populations within the carrying capacity of the environment and prevents overpopulation.

Unlike in Africa, managed honeybee populations in the Northern Hemisphere are concentrated more in urban areas (Frazier et al. 2024), leading to higher colony density (Visick and Ratnieks 2023), and increased shortage of/competition for floral resources. In these regions, nutritional stress, which suppresses the bees' immune responses (Corona et al. 2023), has also been linked with honeybee colony losses, particularly when combined with pesticides and pathogens (VanEngelsdorp et al. 2012; Naug 2009). As a result, most beekeepers in these regions provide supplementary diets to their colonies to reduce nutritional stress (Sultana et al. 2024).

2.2. High genetic diversity in African-derived honeybees

Genetic variation provides traits that enable bees to withstand and adapt to various environmental stressors, including pests and pathogens (Lively 2010; Tarpy and Pettis 2013; Leclercq et al. 2018). In Africa, there are eleven distinct honeybee (*Apis mellifera*) subspecies (Franck et al. 2001; Ilyasov et al. 2020), adapted to the continent's major biogeographic zones, including the Mediterranean north, the Sahel, tropical West and Central Africa, Eastern Africa, and Southern

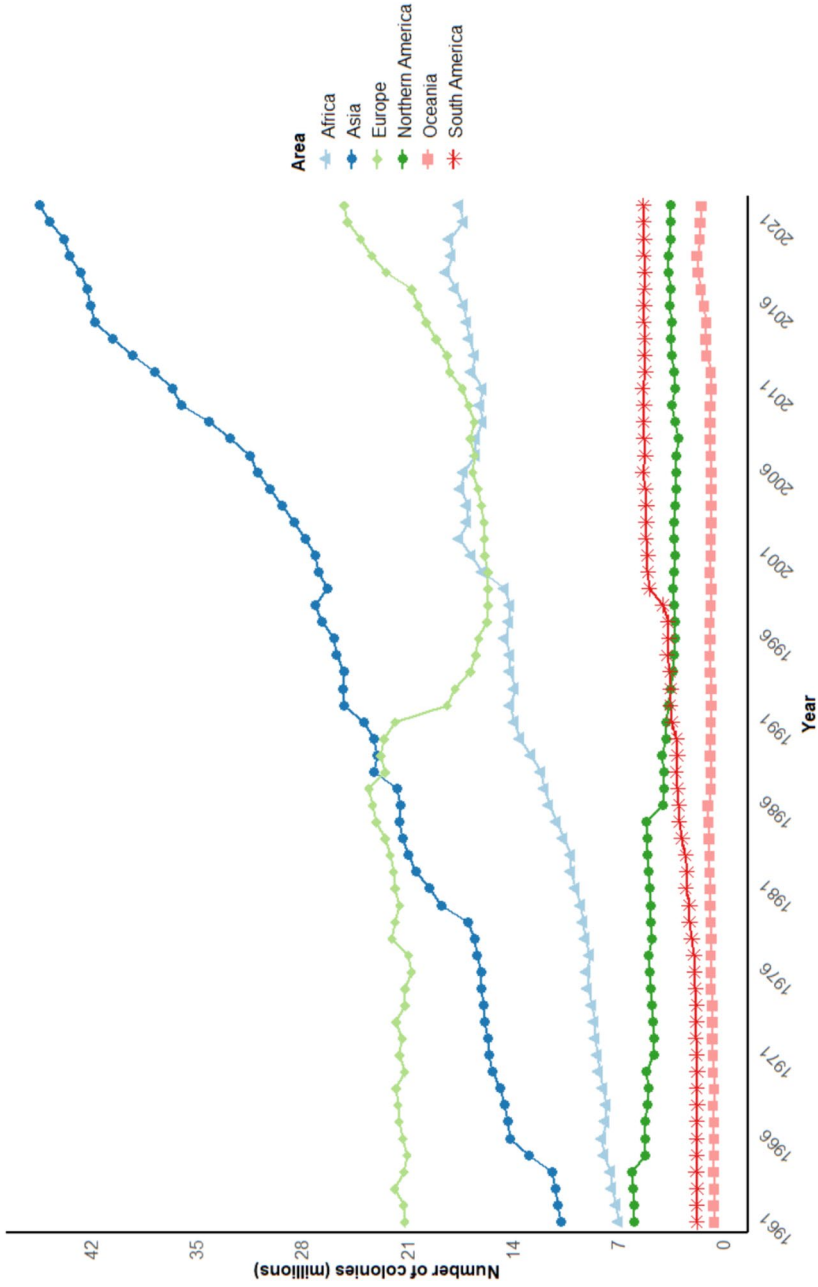

Fig. 1 Trend of managed honeybee colony populations by regions. Source: FAO. 2024. FAOSTAT: Crops and livestock products (Accessed November 2024). https://www.fao.org/faostat/en/#data/QCL

Africa (Ilyasov et al. 2020). These subspecies include *A. m. intermissa*, *A. m. sahariensis*, *A. m. lamarckii*, *A. m. simensis*, *A. m. yemenitica*, *A. m. adansonii*, *A. m. scutellata*, *A. m. capensis*, *A. m. monticola*, and *A. m. litorea*. Genetically, African honeybees are primarily grouped into three evolutionary lineages (Franck et al. 2001): the A lineage, which predominates across sub-Saharan Africa, and the O and Y lineages, mainly found in northeastern Africa. The African lineage is recognized as an important reservoir of genetic diversity (Techer et al. 2017). There is a higher genetic variability in African populations than in European populations (Franck et al. 2001; Techer et al. 2017; Aglagane et al. 2023), despite the decline in European genetic diversity over the past century (Themudo et al. 2020).

Africa's diverse agro-climatic conditions sustain a significantly higher wild bee population density (6.8 colonies/km^2) when compared to Europe (0.26 colonies/km^2) (Moritz et al. 2007; Visick and Ratnieks 2023). Many beekeepers in Africa place their managed honeybees in or near forests where wild bees do nest as well (Ababor and Tekle 2018). Consequently, the high swarming and absconding tendencies of African-derived bees (Hepbum and Radloff 1998; Nuru et al. 2002; Ardestani 2015) may facilitate the genetic mix between wild and managed populations. Following swarming, natural nuptial flights (i.e. natural mating) with about 12 to 15 drones coming from different colonies is the norm in Africa, ensuring genetic mixing between different colonies (Leclercq et al. 2018; Nganso et al. 2024). Local beekeepers use indigenous honeybee subspecies for honey production, helping to maintain the genetic diversity of local honeybee subspecies too. These factors may contribute to the higher genetic variability observed in African-derived bees compared to European-derived bees (Franck et al. 2001; Techer et al. 2017; Aglagane et al. 2023). As a result, this increased genetic diversity may enhance their resilience to environmental stressors, such as the *V. destructor* (Akinwande et al. 2012; Begna et al. 2016; Chemurot 2017; Nganso et al. 2017).

On the other hand, the extensive domestication of honeybees in the Western world's urban areas (Frazier et al. 2024) has led to increased isolation between managed and wild honeybee populations, likely limiting the genetic mix between the two. Moreover, unlike African-derived bees, European-derived honeybees have been subjected to intensive selective breeding that focusses on only a limited set of desirable traits (Büchler et al. 2010; Guichard et al. 2020). For such breeding purposes, a small number of well-performing mother queens are used as breeding stock (Delaney et al. 2009). For instance, in the USA, it is estimated that fewer than 500 queen mothers produce around 1,000,000 daughter queens (Delaney et al. 2009). This large-scale production of many queens from few mother colonies can lead to the (genetic) homogenization of bee populations across large geographic areas. Similarly, Western beekeepers often import honeybee stocks or inseminated queens from commercial breeders (Holmes et al. 2023) or travel to isolated mating stations or islands for more or less controlled fertilization of their virgin queens by drones with specific traits. These practices, however, may contribute to the observed low genetic diversity in indigenous Western honeybee populations (Franck et al. 2001; Techer et al. 2017; Aglagane et al. 2023). This decline in bee genetic diversity has also been suggested as a contributing factor to the high colony losses or the propagation of susceptible colonies in the Northern Hemisphere (Themudo et al. 2020).

2.3. African-derived bees experience low exposure to pesticides

Globally, the total use and intensity of pesticide application have increased at an alarming rate (Figs. 2 and 3). From 1990 to 2022, pesticide use per unit of cropland increased by 94%, with the highest increases seen in the Americas, followed by Asia and Europe (Figs. 2 and 3), highlighting the growing dependence on these chemicals (Sharma et al. 2019). However, the increased use of pesticides has also led to the loss of natural habitats and reduced plant diversity (Sharma et al. 2019), thereby negatively impacting bee

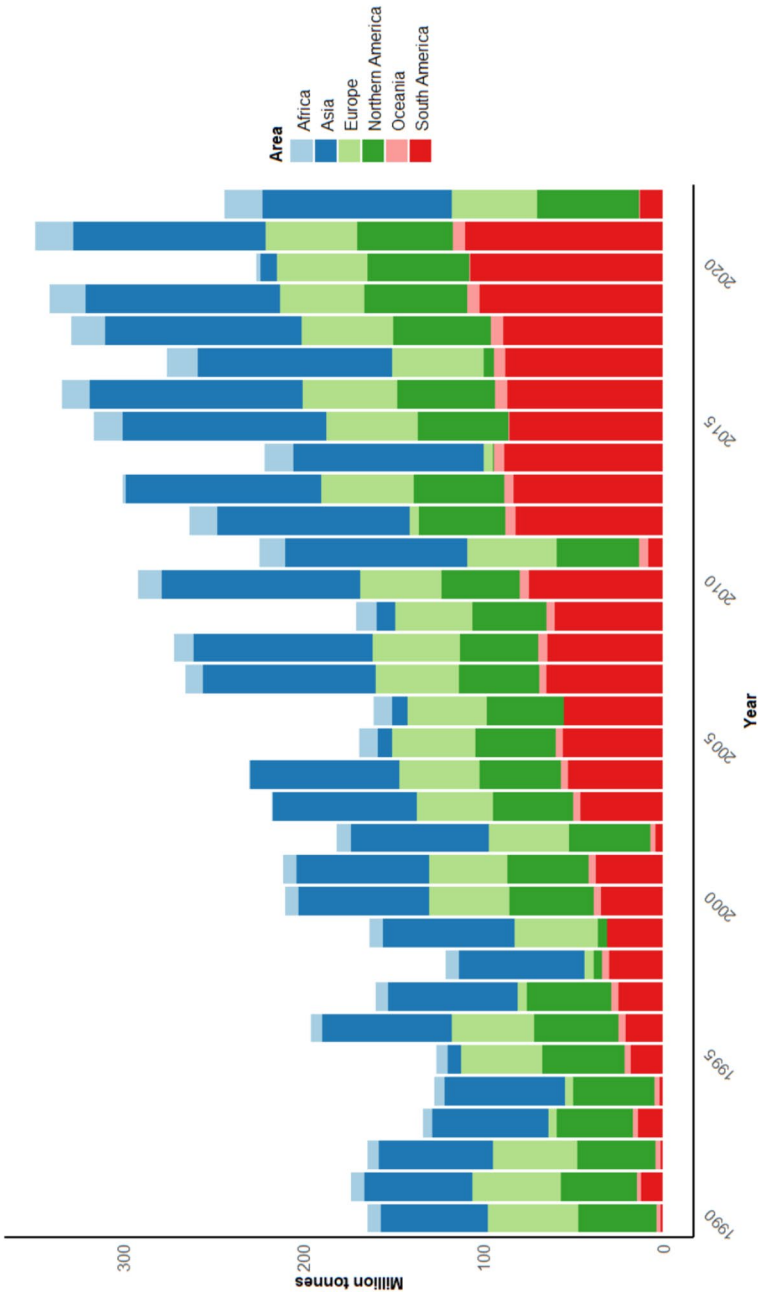

Fig. 2 Total pesticides use by region. Source: FAO. 2024. FAOSTAT: Pesticides Use (Accessed November 2024). http://www.fao.org/faostat/en/#data/RP

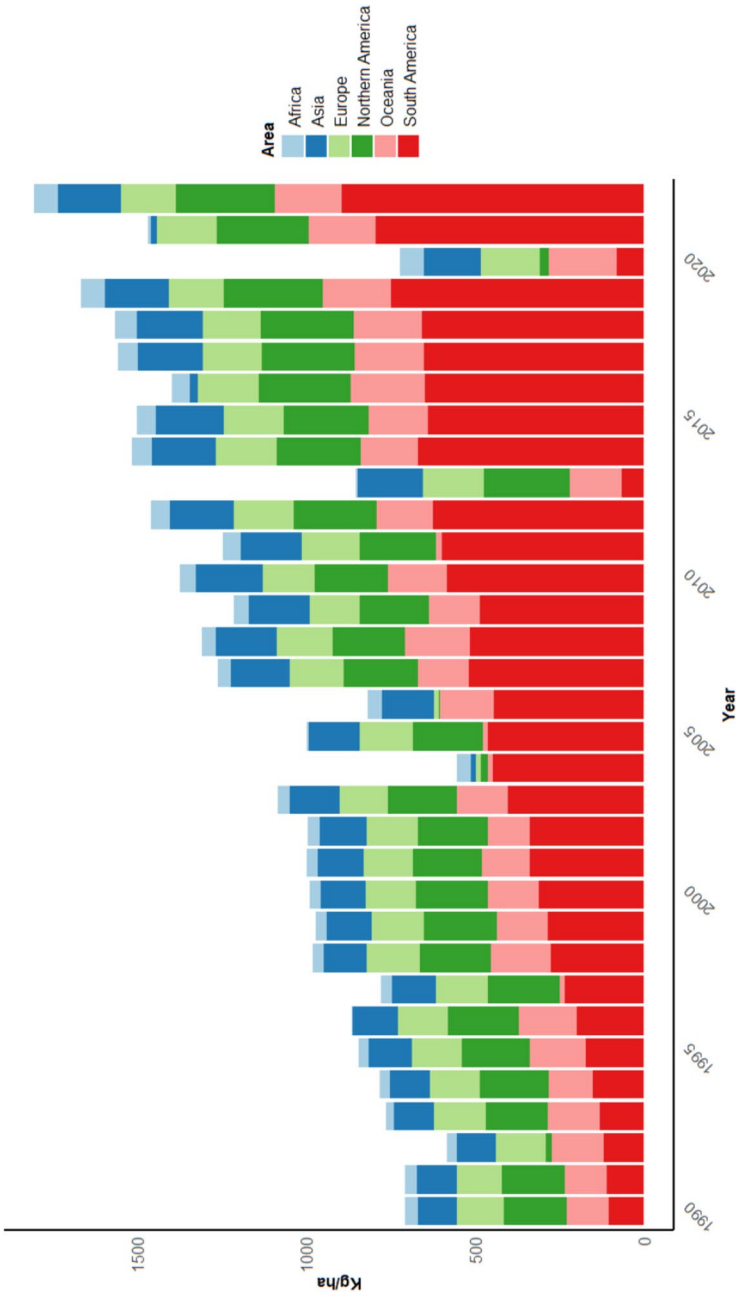

Fig. 3 Pesticides use per area of cropland (Kg/ha) by region. Source: FAO. 2024. FAOSTAT: Pesticides Use per area of cropland (Kg/ha) (Accessed November 2024). http://www.fao.org/faostat/en/#data/RP

nutrition. Pesticides also weaken bees' immune system, making them more vulnerable to pests and pathogens (Pettis et al. 2012; López et al. 2017), and have been associated with honeybee colony losses (Pettis et al. 2012). Moreover, sublethal pesticide doses can also disrupt honeybee navigation and homing abilities, leading to disorientation and loss of foragers (Barascou et al. 2021). This disruption can potentially reduce colony survival, foraging efficiency, and overall colony productivity. In addition, Western beekeepers mostly prefer to set up their apiaries near to urban areas for ease of access or orchards for pollination services, where pesticide use is commonly higher. As a result, the increased use of pesticides (Figs. 2 and 3) due to large-scale commercial farming and urbanization (Sharma et al. 2019) has raised serious concerns among the beekeepers in the West (Perichon et al. 2024).

In Africa, the overall pesticide use has also increased (Gratzer et al. 2021), but the total use and intensity of application remain relatively low compared to other regions in the West (Sharma et al. 2019) (Figs. 2 and 3). This may be because most farmers engage in small-scale farming and rely on traditional methods, such as hand weeding, due to low labour costs. Economic constraints and limited access to agricultural inputs may also prevent local farmers from purchasing and using pesticides. Besides, in many African regions, especially in areas practicing forest beekeeping, there is less agricultural activity and use of agricultural chemicals (Lowore et al. 2018; Lowore 2020; Tarekegn 2022). Together, these factors reduce bees' exposure to pesticides in Africa, thereby reducing their vulnerability to diseases and pests.

However, the growing dependency on pesticide use (Figs. 2 and 3), coupled with the low awareness among farmers about the risks of pesticide use (Sharma et al. 2019) and the ecological and economic benefits of honeybee pollination in Africa (Jacobs et al. 2006), may negatively impact the health of local honeybees in the near future. Therefore, to sustain the health of honeybees, it is crucial to educate farmers about the benefits of honeybee pollination and alternative practices that minimize pesticide use. Strengthening the communication between pesticide applicators and beekeepers before pesticide application is thereby a vital step (Zhang et al. 2023).

2.4. African beekeeping maintains harmony with nature

2.4.1. Low beekeeper intervention

Beekeeping in Africa has a long tradition, dating back about 3500 years, and remains a widespread agricultural activity in the region (Dunne et al. 2021). Beekeeping in most African countries is nature-based, which is rooted in indigenous knowledge, skills, and experience, with minimal interventions by beekeepers (Lowore et al. 2018; Lowore 2020; Tarekegn 2022). This approach, which maintains the harmonious balance with nature, has enabled the production of large quantities of honey and beeswax (FAO 2025) while maintaining the health and genetic diversity of local honeybee populations (Franck et al. 2001; Techer et al. 2017; Aglagane et al. 2023) and allows bees to survive in their natural habitats.

African forest beekeeping, which is the dominant beekeeping practice, utilizes wild honeybee populations without manipulating them (Lowore et al. 2018; Lowore 2020; Tarekegn 2022). This beekeeping practice involves hanging traditional hives on trees for a swarm to colonize them (Fig. 5), which allows bees to select their preferred location and conditions for nesting. It also employs minimal management practices, as beekeepers usually inspect the hives only during the honey harvesting season (Lowore 2020). Traditional hives rely less on artificial foundation, allowing bees to build their combs with a naturally smaller cell size, which is smaller than the standard-cell combs commonly adopted from Europe (Adgaba et al. 2012). When local honeybees are allowed to build comb naturally in foundationless frames, they also develop smaller cell sizes (Gebremedhn et al. 2019). This allows bees to develop natural adaptation mechanisms against pests by shortening their developmental

times (Erickson et al. 1990; Saucy 2014). African worker bees have shorter developmental times (19–20 days) compared to European worker bees (21 days) (Ellis and Ellis 2009), leading to a reduced capped period and less time for *V. destructor* reproduction (Ardestani 2015; van Alphen and Fernhout 2020). Moreover, it has been reported that combs with smaller cell sizes have lower mite infestation rates than those with larger cell sizes (Piccirillo and De Jong 2003). Additionally, when bees naturally build their combs, they develop different cells of different sizes for various purposes, such as worker bee brood, drone bee brood, and honey storage, each with its specific cell size (Yang et al. 2021). This natural cell-building behaviour allows bees to maintain a gender balance between male bees (drones) and female bees (worker bees) within the colony. This balance helps the colony to adjust its population composition according to seasonal needs.

Local beekeepers in Africa harvest honey from traditional hives by removing the entire combs, including brood combs (Fig. 4). Consequently, this way of honey harvesting creates brood-free periods within the colony, which interrupt the mites' reproduction or prolong their phoretic phase, potentially reducing their population growth within the colony. Removing entire combs during honey harvest also encourages bees to build new brood combs (Fig. 4), which are less susceptible to pests than older combs (Piccirillo and De Jong 2004). Altogether, these factors may contribute to the observed lower mites infestations in colonies nested in traditional hives compared to those in framed hives (Gebremedhn et al. 2019; Gela et al. 2023a).

Unlike the conditions in Europe and North America, where honeybees are subjected to intensive selective breeding (Büchler et al. 2010), African-derived honeybees have experienced less intensive breeding and genetic intervention and reproduce naturally through swarming. Following natural swarming, natural mating is the norm in Africa (Leclercq et al. 2018), allowing bees to exhibit their natural behaviours

Fig. 4 Honey harvesting from a traditional hive and development of natural combs. **a** A traditional hive made from local materials such as mud, cow dung, grass, and bamboo. **b** A beekeeper inspecting the hive from the back side during honey harvesting once the bees have moved to the entrance side. **c** The combs removed from the traditional hive during honey harvest. **d** The internal side of the hive after the combs have been removed. **e** The redevelopment of new natural combs by worker bees following the honey harvest

and survive in their natural habitats. Beekeepers' intervention is minimal, as most beekeepers in Africa use swarm catching as a primary source of colonies instead of preventing it (Gebretsadik and Negash 2016). The higher swarming tendency of local honeybee subspecies, compared to European-derived bees, could be attributed to this (Hepbum and Radloff 1998; Ardestani 2015).

When a colony swarms, the old queen often leaves with the swarm and the remaining bees wait for a new queen to emerge, mature, mate, and begin laying eggs. This may create a brood-free period, which interrupts *V. destructor* reproduction in a colony and extends its phoretic phase (Fries et al. 2003a; Akinwande et al. 2012; Begna et al. 2016; Chemurot 2017), thereby delaying the reproductive period of the mites (McMenamin et al. 2017). These factors may contribute to the observed lower mites infestation rate in colonies established through swarming, compared to those established through splitting in Ethiopia (Gebremedhn et al. 2019). Similarly, a reduction in mite populations due to swarming has been observed in Swedish honeybees (Fries et al. 2003b).

According to Akyol et al. (2007), the age of a honeybee queen has an influence on the level of mite infestation in a colony. Colonies headed by younger queens tend to have lower levels of *V. destructor* infestation compared to those headed by older queens. This highlights that the high turnover of honeybee queens due to swarming may also contribute to the reduced levels of mite infestations in African-derived bee colonies. However, the specific mechanisms by which a queen's age influences mite growth are not well understood.

African-derived bees have high absconding tendencies, ranging from 38 to 45% (Nuru et al. 2002; Gebremedhn et al. 2019), and beekeeper interventions to control the high bees' absconding tendencies are minimal. It allows colonies to escape threats like disease, parasites, predators, or resource scarcity by relocating to safer or more resource-rich environments, ensuring that the most adaptable bees survive and reproduce (Shitaneh et al. 2022). It is important to note that hives hanging on trees (Fig. 5) may then act as swarm traps or bait hives for absconding colonies, leading to the formation of wild and resilient colonies.

2.4.2. Allowing natural selection to operate

Natural selection is the primary adaptation mechanism by which traits become common in populations over time due to environmental pressures like pests and pathogens, promoting the survival of colonies better suited to local conditions (Neumann and Blacquière 2016). The minimal intervention by beekeepers in Africa may allow natural selection to operate by reducing artificial influences on bee genetics and behaviour, enabling African-derived honeybees to develop natural defensive traits, such as grooming behaviour, hygienic behaviour, and SMR, to manage *V. destructor* infestations (Allsopp 2006; Strauss et al. 2016; Nganso et al. 2018; Gebremedhn et al. 2019; van Alphen and Fernhout 2020; Gela et al. 2023b).

Honeybee genetic diversity provides a strong foundation for natural selection to operate effectively (Reed 2007; Wallberg et al. 2014). When new environmental challenges arise, the presence of genetic variation among colonies increases the likelihood that some colonies will survive and reproduce more successfully, as they possess traits that are better suited to the changing conditions (Reed 2007; Wallberg et al. 2014). Hence, using indigenous honeybee subspecies which have high genetic diversity in Africa (Franck et al. 2001; Techer et al. 2017; Aglagane et al. 2023) may also allow natural selection to operate and develop resilient bee populations in Africa.

Despite the presence of *V. destructor* in Africa, local honeybees are able to survive without intervention from beekeepers. For example in South Africa, beekeepers initially faced significant colony losses due to the introduction of *V. destructor* (Allsopp 2006), rather than using chemical treatments that interfere with natural selection (van Alphen and Fernhout 2020). In this way, they allowed natural selection to shape the bee populations. Over time, the bees adapted

Fig. 5 Hanging traditional hive for swarming catching in southern Tigray, Ethiopia. Local beekeepers hang traditional hives on trees to be colonized by wild bees

and survived without the use of mite control treatments.

In Cuba, *V. destructor* initially caused high colony losses too, but the country allowed natural selection to operate (Luis et al. 2022). This approach has led to the development of over 220,000 honeybee colonies that are both mite-resistant and highly productive, producing 40–70 kg of honey annually (Luis et al. 2022). Cuba is now an excellent example of what can happen when honeybees are allowed to naturally adapt to *V. destructor* with minimal human interference, resulting in resilient and productive bee populations. In contrast, intensive selective breeding programs in Western countries have been ongoing for decades and have not yet succeeded in producing *V. destructor* resilient honeybee populations (Neumann and Blacquière 2016). This has raised hopes that natural selection may address the *V. destructor* problem (Guichard et al. 2023). Therefore, taking advantage of natural selection, rather than attempting to limit it, and incorporating these principles into modern practices could contribute to the development of more resilient honeybee populations worldwide (Neumann and Blacquière 2016).

2.5. African-derived honeybees have defensive traits

2.5.1. Hygienic behaviour

Hygienic behaviour, that enables worker bees to detect, uncap, and remove diseased or parasitized brood from the colony (Spivak 1996), is one the defence mechanisms of honeybees against various pathogens such as

chalkbrood (Palacio et al. 2010), American foulbrood (Spivak and Reuter 2001), viruses (Schöning et al. 2012), and pests like the *V. destructor* (Spivak 1996). Hygienic behaviour, shaped by natural selection, is also one of the resistance mechanisms that African-derived bees use to manage *V. destructor* infestations (Muli et al. 2014; Gebremedhn et al. 2019; Gela et al. 2023b). However, the contribution of this trait in limiting Varroa mite population growth varies among local honeybee populations. For example, studies in Kenya (*A. mellifera*) (Muli et al. 2014) and Ethiopia (*A. m. simensis*) (Gebremedhn et al. 2019; Gela et al. 2023b) found a negative correlation between hygienic behaviour and *V. destructor* infestation rates, highlighting its contribution on suppressing the mite's population growth. In contrast, no such association was observed for *A. m. scutellata* in Kenya (Nganso et al. 2017). This variation is likely due to differences in environmental conditions and genetic backgrounds (Spivak and Gilliam 1998).

Hygienic bees have the ability to discriminate odours, enabling them to detect and remove diseased brood from the hive at low odour intensities (Masterman et al. 2001), thereby reducing disease spread within the colony (Gramacho and Spivak 2003). This olfactory behaviour is mediated by a number of olfactory proteins, which are primarily found in the antennae of honeybees (Mondet et al. 2015). A recent study examined the expression profiles of key olfactory genes in African-derived bees (Gebremedhn et al. 2023) and found that Ethiopian honeybees exhibit greater expression of the odorant-binding protein *OBP14* than Belgian honeybees. Higher gene expression levels of the odorant binding protein in the antennae of Ethiopian honeybees suggest that reproducing mites might be detected better and cleaned more efficiently (Gebremedhn et al. 2023). High expression of *OBP14* was also observed in *V. destructor*-resistant honeybee populations in New Zealand (Mondet et al. 2015) and Canada (Jiang et al. 2016). These results suggest that the resistance of African-derived bees to *V. destructor* infestations has a molecular basis too.

2.5.2. Suppressed mite reproduction (SMR)

Suppressed mite reproduction (SMR) is another defence mechanism of honeybees that reduces the reproductive success of the ectoparasitic *V. destructor* (Harbo and Harris 2005; Locke and Fries 2011). There are several *V. destructor*-resistant honeybee populations that have been surviving without mite treatments in different European countries, such as the Netherlands (Blacquière et al. 2019), Norway (Oddie et al. 2017), France (Le Conte et al. 2007), and Sweden (Fries et al. 2006), which is mainly attributed to suppressed mite reproduction (SMR). This physiological trait, exclusively expressed during the late larval or pupal stage (Kurze et al. 2016; Scaramella et al. 2023), causes cell-included foundress mites to fail in producing viable offspring or mated female progeny (Corrêa-Marques et al. 2003; Locke and Fries 2011).

The resistance of many African-derived bees to *V. destructor* infestations in countries such as Ethiopia (Gebremedhn et al. 2019), South Africa (Strauss et al. 2016), and Kenya (Nganso et al. 2018) is also largely attributed to SMR. The reproductive success of mites and the number of daughter mites capable of reaching the adult stage and having an available mate are low in these African-derived honeybee populations (Strauss et al. 2016; Gebremedhn et al. 2019). For example, in *A. m. simensis* in Ethiopia (Gebremedhn et al. 2019) and *A. m. scutellate* in South Africa (Strauss et al. 2016), the number of viable female offspring mites produced per foundress mite is 0.27 and 0.3, respectively. These values are much lower than the fecundity value reported for European-derived honeybee subspecies, which is between one and two (Schulz 1984; Fuchs and Langenbach 1989; Corrêa-Marques et al. 2003).

High mite infertility and low proportions of mated female progeny have been identified as key factors explaining the reduced reproductive success of *V. destructor* in African-derived bees (Nganso et al. 2018; Gebremedhn et al. 2019). The low proportions of viable female offspring or mated female progeny are mainly attributed to the failure of the mother mites to produce adult male mites

(Gebremedhn et al. 2019). Therefore, investigating the mechanisms that prevent foundress mites from producing adult male progeny in these African-derived bees may open an interesting research area, as the failure of mother mites to produce adult male offspring is rarely observed outside of African African-derived (Gebremedhn et al. 2019) and Africanized bees (Corrêa-Marques et al. 2003).

2.5.3. Grooming behaviour

Adult mites are capable of attaching to the bees' bodies during phoretic stages (Kurze et al. 2016). In response, worker bees have developed an adaptive behaviour known as grooming behaviour, which allows them to remove, injure, or kill the mites from themselves or their nestmates (Le Conte et al. 2015; Kurze et al. 2016; Guzman-novoa et al. 2018). *V. destructor*-resistant honeybee populations have been identified worldwide, with increased levels of grooming behaviour being a key factor in their resistance (Guzman-novoa et al. 2012). Similarly, African-derived bees also show high grooming behaviour, resulting in up to 80% of investigated fallen mites being damaged (Gela et al. 2023a, b). Moreover, this trait has also been identified as a contributing factor to *V. destructor* resilience of *A. m. intermissa* in Tunisia (Boecking and Ritter 1993), *A. m. intermissa* in Algeria (Dadoun et al. 2020), and *A. m. bandasii* in Ethiopia (Gela et al. 2023b). Nevertheless, the contribution of this trait in limiting the mite population growth varies among different African-derived bee populations, which may be due to genetic or environmental factors. For example, studies conducted in Ethiopian *A. m. simensis* (Gebremedhn et al. 2019) and Kenyan *A. m. scutellata* (Nganso et al. 2017) did not provide evidence supporting grooming behaviour does limit *V. destructor* population growth.

3. CHALLENGES FOR THE AFRICAN BEEKEEPING SECTOR

The resilience of African-derived bees to *V. destructor* is partly attributed to the indigenous beekeepers' management practices characterized by minimal disturbances to the harmony between nature and bees, such as using traditional hives for honey production and swarm catching as sources for new colonies (Gebremedhn et al. 2019). However, the low productivity of local honeybee subspecies is primarily also attributed to these traditional beekeeping management practices (Jacobs et al. 2006; Gratzer et al. 2021). For instance in Ethiopia, traditional hives produce only 5–6 kg of honey annually, while modern hives may yield 35–45 kg (Jacobs et al. 2006). Since local beekeepers harvest honey from the traditional hives by removing entire combs, African honey also often faces quality issues due to the presence of wax, pollen, and other impurities (Jacobs et al. 2006). This may in turn negatively impact its market value (Jacobs et al. 2006).

Hence, to increase productivity and maximize returns for beekeepers, several efforts have been made in different African countries to shift from traditional to modern beekeeping systems (Hailu et al. 2022). However, this transformation has taken place through the adoption of modern beekeeping management practices and technologies from Western beekeeping systems (Hailu et al. 2022). This shift included transferring honeybee colonies from traditional hives to framed hives, using founded sheets or artificial combs with larger cell sizes, and multiplying colonies through advanced methods such as splitting and larval grafting (Gemeda et al. 2020; Hailu et al. 2022). In addition, some efforts even tried to introduce and promote selective breeding to enhance the productivity of local honeybee populations (Negera et al. 2020; Shitaneh et al. 2022).

On the other hand, while the Western modern beekeeping practices such as using framed hives and selective breeding have succeeded in improving economic traits such as honey yield, these efforts have not achieved the desired outcome of producing healthy bee populations (Büchler et al. 2010; Neumann and Blacquière 2016; Uzunov et al. 2017; Guichard et al. 2020; Kovačić et al. 2020). Instead, selective breeding has reduced the genetic diversity of European-derived honeybees (Büchler et al. 2010; Themudo et al. 2020), making it more difficult for populations

to adapt to new threats (Tarpy and Pettis 2013; Leclercq et al. 2018). Western beekeepers also use chemical treatments to control *V. destructor* infestations, making it harder for resistance traits to emerge and spread naturally within bee populations (Kovačić et al. 2020; van Alphen and Fernhout 2020). As a result, these Western modern beekeeping practices have contributed to the propagation of vulnerable bee populations (Büchler et al. 2010). Thus, completely shifting from traditional to modern beekeeping systems in Africa solely relying on Western practices may result in unintended challenges, particularly regarding the health and genetic diversity of local honeybee subspecies (FAO et al. 2021). African beekeeping systems should instead adopt an integrated approach that combines the strengths of traditional practices with modern techniques. This approach may promote commercialization while maintaining the genetic diversity and resilience of African bees to various environmental stressors, such as the *V. destructor*.

4. FUTURE PERSPECTIVES

The natural resilience of African-derived honeybees to *V. destructor* is attributed to a combination of several factors, including defensive traits that develop through natural selection, such as hygienic behaviour (Muli et al. 2014; Gebremedhn et al. 2019; Gela et al. 2023b), grooming behaviour (Boecking and Ritter 1993; Dadoun et al. 2020; Gela et al. 2023b), and SMR (Strauss et al. 2016; Nganso et al. 2018; Gebremedhn et al. 2019). In the past decades, several studies were performed to identify the molecular basis of *V. destructor*-resistance in survivor populations. It was demonstrated that the mechanisms behind these traits are complex and involve multiple genes. However, the search for the molecular basis of *V. destructor*-resistance of African-derived bees has only just started and focused on the occurrence of genetic markers already discovered in survival colonies from the West and the expression of olfactory genes in the antennae. Broadening the study to genome-wide association studies of different African-derived honeybee populations will certainly provide new and valuable information of the mechanisms behind their defensive traits. It could provide several genetic markers for selective breeding purposes in the West, potentially having broader applications across diverse environmental and genetic conditions.

The reproductive success of *V. destructor* in African-derived bees is low (Strauss et al. 2016; Gebremedhn et al. 2019), primarily due to the failure of mother mites to produce adult male offspring. This phenomenon, wherein foundress mites fail to produce male progeny, is rarely observed outside of African (Gebremedhn et al. 2019) and Africanized bees (Corrêa-Marques et al. 2003). Therefore, investigating the factors that prevent foundress mites from producing male offspring in African bees is a promising area of research. This knowledge could be crucial for developing new strategies to combat *V. destructor* infestations in other honeybee populations.

Transitional hives produce higher yields and better honey quality compared to traditional hives (Beyene et al. 2015). Like traditional hives, these hive types allow bees to develop natural combs with smaller cell sizes, and honey harvesting is done by removing honeycombs, facilitating comb recycling. Therefore, promoting transitional hives may improve productivity and maximize returns for beekeepers while sustaining the health of local honeybees, which requires further attention and investigation.

Several potential factors, such as the use of small comb cell size, brood interruption, comb recycling or using new combs, and the use of young queens in a colony, may contribute to the low mite's infestation rates observed in traditional hives. However, these factors may require further investigation to validate their effectiveness and integrate them with modern beekeeping practices.

5. CONCLUSIONS

The results suggest that African-derived honeybees are resilient to a broad set of threats including the ectoparasite *V. destructor* because they live in harmony with nature. Resilience is attributed to a

more bee-friendly environment, to better balanced colony densities, to beekeepers' management practices, and to the bee's behavioural adaptation and physiological and genetic traits. Nature-based beekeeping practices that allow natural selection to operate and maintain the genetic diversity of local honeybee subspecies are the key to their resilience against *V. destructor* infestations.

ACKNOWLEDGEMENTS

The authors acknowledge Dr. Ellen Danneels and Dr. Lina De Smet from Ghent University, Belgium, and Mr. Tesfay Atsbeha from Mekelle Bee Research and Training Centre, for their invaluable inputs during the design and outlining of this review article. The authors also express their appreciation to Ghent University Special Research Fund, Global Minds, and the Tigray Agricultural Research Institute for their financial support.

AUTHOR CONTRIBUTION

Haftom Gebremedhn and Dirk C. de Graaf contributed to the study conception and design. Material preparation, data collection, and analysis were performed by Haftom Gebremedhn. The first draft of the manuscript was written by Haftom Gebremedhn and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

FUNDING

The concept outlined in this review paper forms the common thread of the Better-B project which has received funding from the European Union, the Swiss State Secretariat for Education, Research and Innovation (SERI), and UK Research and Innovation (UKRI) under the UK government's Horizon Europe funding guarantee (grant number 10068544).

DATA AVAILABILITY

In the paper and its supporting materials, the authors declare that the data supporting their findings are available. Any raw data files needed in another format can be obtained from the corresponding author upon reasonable request.

DECLARATIONS

Competing interests The authors declare no competing interests.

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