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Climate change: impact on honey bee populations and diseases

Y. Le Conte [1] & M. Navajas [2]

(1) French National Institute for Agronomic Research (*Institut National de la Recherche Agronomique - INRA*), UMR 406 Abeilles et Environment (INRA/UAPV), Laboratoire Biologie et Protection de l'Abeille, Site Agroparc, Domaine Saint-Paul, 84914 Avignon Cedex 9, France
(2) French National Institute for Agronomic Research (INRA), UMR CBGP (INRA/IRD/CIRAD/Montpellier SupAgro), Campus International de Baillarguet, CS 30016, 34988 Montferrier-sur-Lez Cedex, France

Summary

The European honey bee, *Apis mellifera*, is the most economically valuable pollinator of agricultural crops worldwide. Bees are also crucial in maintaining biodiversity by pollinating numerous plant species whose fertilisation requires an obligatory pollinator. *Apis mellifera* is a species that has shown great adaptive potential, as it is found almost everywhere in the world and in highly diverse climates. In a context of climate change, the variability of the honey bee's life-history traits as regards temperature and the environment shows that the species possesses such plasticity and genetic variability that this could give rise to the selection of development cycles suited to new environmental conditions.

Although we do not know the precise impact of potential environmental changes on honey bees as a result of climate change, there is a large body of data at our disposal indicating that environmental changes have a direct influence on honey bee development. In this article, the authors examine the potential impact of climate change on honey bee behaviour, physiology and distribution, as well as on the evolution of the honey bee's interaction with diseases.

Conservation measures will be needed to prevent the loss of this rich genetic diversity of honey bees and to preserve ecotypes that are so valuable for world biodiversity.

Key words

Adaptation – Apis – Biodiversity – Conservation – Disease – Ecotype – Honey bee – Genetic diversity.

Introduction

Bees of the *Apis* genus are distributed throughout the world in highly diverse climates. The *Apis mellifera* species, whose distribution range extends to sub-Saharan Africa, northern Europe and Central Asia, is found in a wide variety of environments, including the oases of the African desert, the Alps, the fringes of the tundra and the mists of the United Kingdom. Its ecotypes have adapted remarkably well to their biotopes. The other honey bee species of the *Apis* genus are distributed around Asia, particularly tropical south-east Asia (33).

Climate change estimations predict upheavals in certain regions of the world a few decades from now, with encroaching deserts, a retreating icecap, snowmelt, changing rainfall patterns and a greater frequency of extreme climate events generally.

A change in climatic conditions is bound to have an impact on the survival of these ecotypes or of honey bee species that are closely associated with their environment. Migration and changes in their lifecycle and behaviour could help them to survive in new biotopes. As the honey bee's genetic variability will be crucial to its adaptation, we would do well to ensure that we preserve this genetic variability. Honey bees will also need to adapt to a whole array of predators, parasites and pathogens surrounding them. Not only will the relationships between hosts and parasites change, honey bees will have to cope with new stresses arising from trade-facilitated transfers of pathogens among honey bee species. In such a context, climate change could create new opportunities for establishing honey bees in undreamt-of regions or habitats.

The honey bee: an economically valuable species

The long-term survival of farming worldwide relies in part on insect pollinators. In monetary terms, they contribute an estimated US$ 117 billion per year (7); around 35% of agricultural crops depend directly on pollinators (18) and 84% of cultivated plant species are involved with the activity of these insects (41). The European honey bee, *Apis mellifera*, is the most economically valuable pollinator of agricultural crops worldwide (17). Honey bees are also crucial for maintaining biodiversity because they pollinate numerous plant species that require an obligatory pollinator for fertilisation (1, 24). In a context of climate change, plant phenology will be modified, especially the flowering period. A new bioclimatic and economic balance will shape the types and distribution of agricultural crops, as well as those of spontaneous vegetation (38). Climate change could destabilise relationships between flowers and pollinators, and pollinators will need to be protected to ensure that they continue their pollination function, which is so important for the economy and for the ecological balance.

The European honey bee, *Apis mellifera*, and its south-east Asian cousins

Ten honey bee species of the *Apis* genus have so far been identified (3). The distribution of these species is highly uneven (Fig. 1). *Apis mellifera*, which originates from Africa, has followed two waves of colonisation in Eurasia (40) and has been exported to other continents. The nine other species have remained in the areas where they

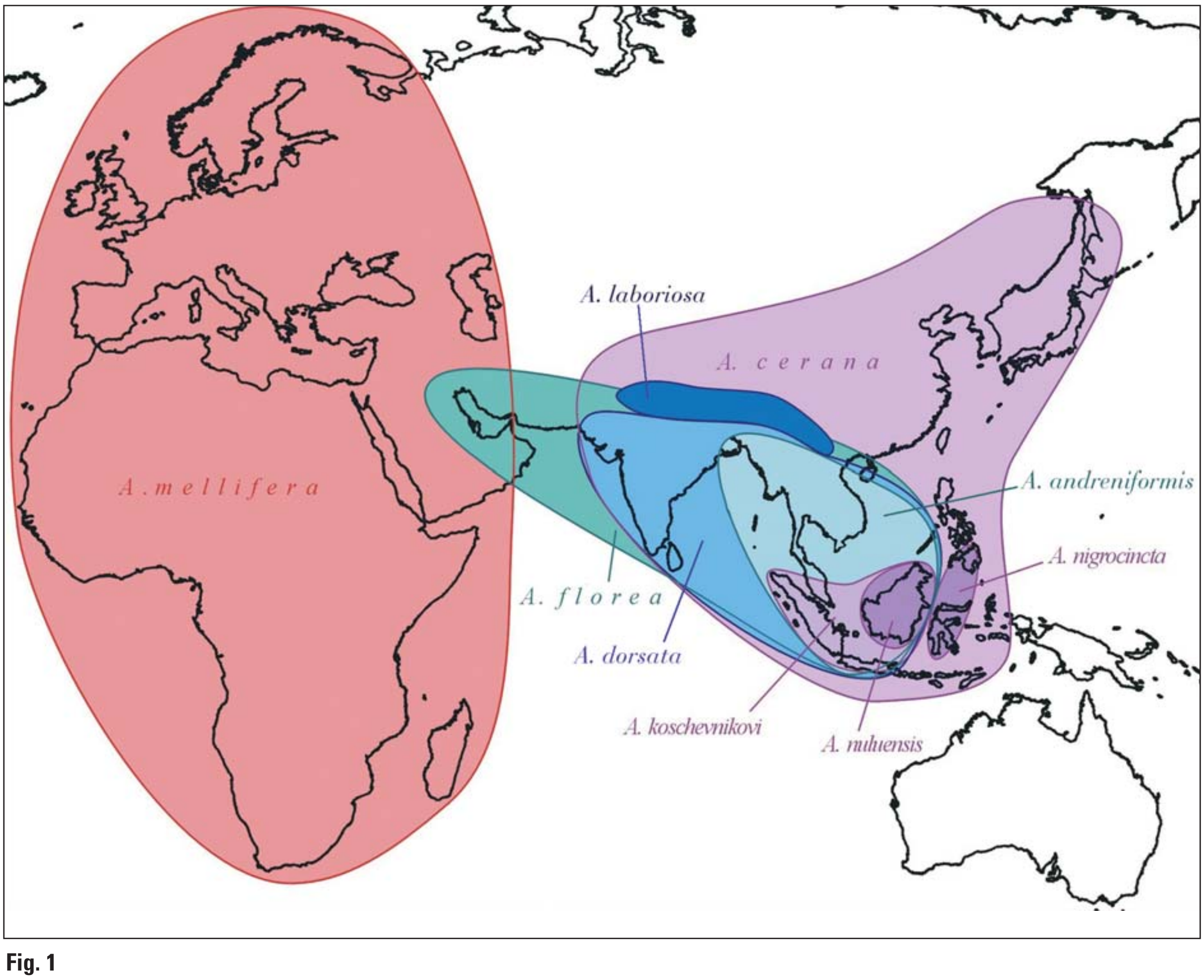

Fig. 1
Distribution of species of the *Apis* genus
(amended in accordance with Franck *et al.*, [10])

originated, in Asia, which is the most likely birthplace of the *Apis* genus.

The Asian species of *Apis mellifera* are much less productive than the European races. As they live in a mild tropical climate, they have no need to amass large food stores because they can find flowers to meet their needs throughout the year (33). In contrast, the European races of *Apis mellifera* have evolved towards a honey harvesting and storage strategy that enables them to last the winter. The need to survive often harsh winters exerts a strong selection pressure; in part this explains the better honey-producing capacities of *Apis mellifera* (21). *Apis mellifera*'s excellent yield capacity has led it to be used by beekeepers in all regions of the world. It is now found in Asia, where it cohabits with other species of the *Apis* genus, as well as in the Americas and Australia, where it was imported by the colonists.

The domestic honey bee, *Apis mellifera*, has 25 sub-species or races

Apis mellifera is the most widely-distributed honey bee in the world because of its great honey-harvesting potential. From a morphological, behavioural and genetic standpoint, *Apis mellifera* closely resembles *Apis cerana,* whose distribution range extends from Japan to the easternmost fringes of the Near East. The two species are thought to have diverged around 8 million years ago (33).

The original distribution range of *Apis mellifera* is Europe, Africa and the Middle East as far as Afghanistan, Kazakhstan and eastern Russia. The species includes 25 sub-species or geographic races described by morphometry and molecular analysis and grouped into evolutionary branches on the basis of their morphological similarities (Fig. 2). Each race is defined according to the morphological, behavioural, physiological and ecological characteristics which it has evolved to suit its individual climatic and environmental conditions. The races of the 'A' branch are typically African, although the races can differ markedly one from another. The races of the 'C' branch, such as *Apis mellifera carnica, ligustica* and *cecropia*, live along the north-eastern coasts of the Mediterranean Sea and are morphologically similar to the races of the 'O' branch in the Near and Middle East. The races of the 'M' branch, such as *Apis mellifera* and iberiensis, are typical of Western Europe, but also share some similarities with the North African races (10, 33).

A recent molecular study using SNP markers confirmed the significance of the evolutionary branches of *Apis mellifera* (40). It revealed that the species had originated in Africa. Two branches have colonised Europe, one by travelling from the Middle East to Italy, and the other from Spain to Denmark. The two most genetically dissimilar races are *Apis mellifera mellifera* and *Apis mellifera ligustica.*

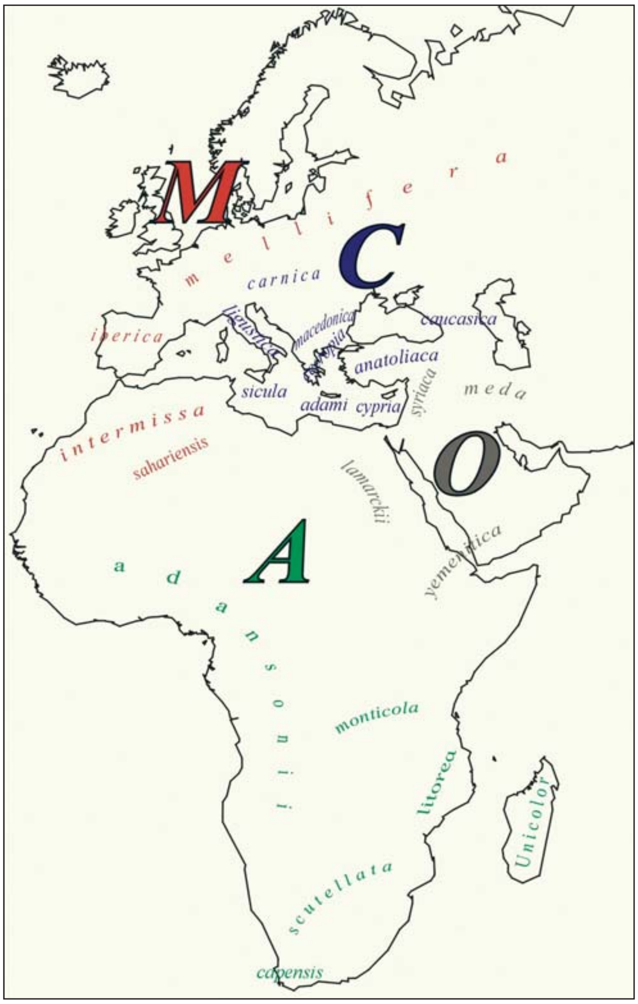

Fig. 2
Main geographic races of *Apis mellifera*
(according to Franck *et al.* [10])
Apis mellifera races are classed into four evolutionary branches (A, M, C and O) according to their morphological differences (established by Ruttner in 1988)

The genetic pool of these races is evolving continually in response to natural selection, with bees adapting not only to changes in their environment but also in response to human apicultural practices (21). Any contact between these races and imported races, or with pathogens, can alter their characteristics markedly. *Apis mellifera ligustica*, *Apis mellifera mellifera* and *Apis mellifera caucacica* have been exported worldwide, as far as Asia, where they have come into contact with other honey bee species as well as with new parasites and pathogens (16).

Bee diseases and parasites

Numerous predators, parasites (mites) and pathogens (protozoa, bacteria and viruses) prey upon the honey bee.

Mites

The honey bee tracheal mite, *Acarapis woodi*, is a parasite of *Apis mellifera* and *Apis cerana*. It lodges itself in the trachea of worker bees, where it breeds, and eventually suffocates them (34). Although it was a pest in the 20th Century, the tracheal mite is now no longer a major problem for world apiculture.

Tropilaelaps spp. is a parasitic mite of *Apis dorsata* honey bees in tropical Asia. The introduction of *Apis mellifera* into the distribution range of *Apis dorsata* has provided the *Tropilaelaps* mite with a new host. A recent study based on molecular markers has identified at least four *Tropilaelaps* species in Asia, although *T. clareae* is the only one that is parasitic to *Apis mellifera* (2). In this region of the world, *Apis mellifera* is also prey to another parasitic mite, *Varroa destructor*, with the two species engaged in fierce competition for parasitism. *Tropilaelaps* are brood parasites, feeding on the haemolymph of the bee brood and breeding there. A proliferation of these parasites can kill honey bee colonies and encourage the emergence of other pathogens. The mite is so reliant on brood that it dies after more than seven days without it.

The *Varroa* mite, *Varroa destructor* (Fig. 3), is a pest that destroys colonies of *Apis mellifera* worldwide, with the exception of Australia where it is not yet present. Scientists tend to attribute honey bee mortality largely to the *Varroa* mite. Originally a parasite of the Asian honey bee, *Apis cerana*, it was transferred to the European honey bee, *Apis mellifera*, in the mid-twentieth century by exchanges of genetic material among many countries (28). Left untreated, colonies infested with the *Varroa* parasite die after two to three years. It is impossible to eradicate this parasitic infection. *Varroa* mites help to diminish the honey bee's immune response and encourage the development of viral infections (13). They are also active vectors in the transmission of viruses and bacteria (43, 44).

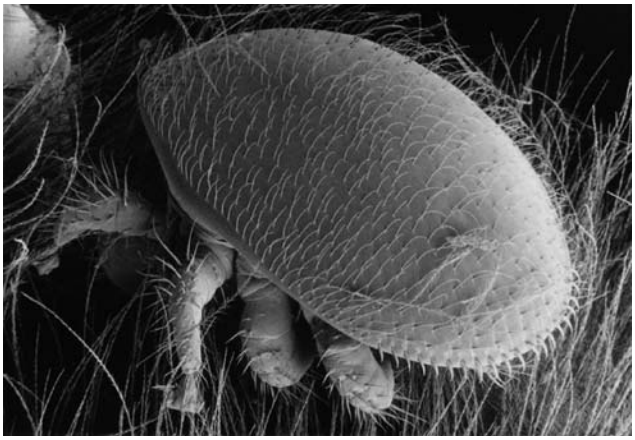

Fig. 3
Microphotograph of a female *Varroa destructor* mite obtained by scanning electronic microscopy (dorsal view)
Photo by E. Erbe and R. Ochoa, USDA-SEL-EMU

The problems with *Varroa* parasite control are typical of those encountered in curbing any insect pest population. *Varroa* are becoming resistant to the acaricides used by beekeepers to control them (25). The recent discovery in several parts of the world (notably the United States of America [USA] [14] and Europe [19]) of honey bee colonies able to tolerate heavy infestations of *Varroa destructor* opens the door to lasting solutions for controlling the parasite. The biological basis of this tolerance has begun to be unravelled using innovative genomic methods that suggest that honey bee tolerance of *Varroa* is determined more by behaviour than by immunological factors (26).

Protozoa

Nosema apis is a microsporidian that attacks the midgut wall of adult honey bees. The disease can develop with no visible symptoms or manifest itself as a weakening of the colony, possibly ending in death. Colony infestation is latent. The disease tends to emerge mainly in early spring following long, wet winters: during winter, honey bees are prevented from going outside and drop their excrement inside the hive, forming a source of contagion for other bees. After this, the disease spreads rapidly. Even though *Nosema apis* exhibits signs common with other diseases, the disease can be identified by certain signs observable when inspecting the colony and in the laboratory (16).

Nosema cerana is another microsporidian species that resembles *Nosema apis* (12). It is a parasite of *Apis cerana* and has been transferred to *Apis mellifera* by exchanges of genetic material. It was recently identified in Europe (12, 15). Since then, it has been found the world over. *Nosema cerana* does not cause the same signs in honey bees as *Nosema apis*. Only molecular techniques can differentiate between the two microsporidians (15). This parasite is considered to be responsible for sharply dwindling honey bee populations in Spain (15).

Bacteria

The bacteria pathogenic to honey bees attack the brood.

American foulbrood, a disease that has been known since ancient times, is caused by *Bacillus larvae*. This serious, highly contagious disease occurs across the globe (16).

European foulbrood is caused by *Melissicoccus pluton*, in association with other bacteria. It tends to gain a foothold in weakened colonies in spring and at first is benign. A supply of pollen from outside the nest is usually all colonies need to overcome the disease, although heavy losses have been reported in the past (16).

At present, only antibiotics are effective in treating these protozoa and foulbroods, but they are no longer authorised because of the hazard of residues in honey.

Viruses

Eighteen different viruses have been identified in honey bees of the *Apis* genus. Some of these viruses are highly anecdotal, while others are latent and can be extremely prolific among the bees in our hives without causing any noticeable signs (37). For reasons as yet unknown, these viruses can become highly pathogenic to honey bees, causing trembling and paralysis that are observable at the colony entrance. This is the case with chronic paralysis virus (CPV) and acute paralysis virus (APV). It is not yet known how these viruses act to kill bees. No treatment exists to control such viruses, which can weaken or kill the colony. These pathologies can be stemmed by a supply of quality pollen from foraging bees. *Varroa* weakens the bee's immune system and encourages viral growth (4).

Impact of climate change on honey bees

Climate change can impact on honey bees at different levels. It can have a direct influence on honey bee behaviour and physiology. It can alter the quality of the floral environment and increase or reduce colony harvesting capacity and development. It can define new honey bee distribution ranges and give rise to new competitive relationships among species and races, as well as among their parasites and pathogens. Beekeepers will also be obliged to change their apiculture methods. They will favour moving their hives to new foraging areas and importing foreign races to test their value in the new environments.

Impact of climate change on honey bee behaviour, physiology and distribution

The European honey bee, *Apis mellifera*, has the potential to adapt to hot climates. For instance, *Apis mellifera sahariensis* is found in the oases of the Sahara, where it has adapted to local bloom (such as palm flowers) and extreme heat (33). In the USA, honey bees can develop in the Arizona Desert. The survival requirement for these bees is a supply of water, which they use in large quantities to raise their larvae and to regulate the brood temperature to between 34°C and 35°C. In an arid environment, desert flowers are unable to provide the bees with enough water and they die. According to climate change predictions, desert regions will become even drier, leading to the disappearance of oases and their honey bees. *Apis mellifera sahariensis* is highly unlikely to migrate naturally to more favourable desert areas because oases are very isolated and not conducive to long-distance migration or swarming. It is therefore vital to envisage conservation measures to transfer this bee to zones favourable to its development, lest we lose this ecotype that is so valuable for world biodiversity.

Climate change can influence the honey bee development cycle. It is generally agreed that each race of honey bees develops at its own rate (21). Any sort of climate change or movement of a race of honey bees from one geographical region to an alien one is therefore bound to have measurable consequences. In cool regions, honey bees spend the winter clustered in a tight ball and use their honey stores to provide them with the energy they need to survive until spring. The honey bee's capacity to accumulate energy reserves and to manage the colony's development exerts significant adaptive pressure. In the spring, when the weather becomes more clement, the queen starts to lay eggs and the colony develops and increases the size of the worker population. A cold snap lasting several weeks may occur during which the honey bees are unable to harvest. The large size of the honey bee population causes such a rapid depletion of stores that the colony can die of starvation. It is something that can easily happen to hybrid bees (crosses of several races by bee breeders), which develop very fast in spring. In contrast, local ecotypes that are better adapted to the environmental conditions are more cautious and develop more slowly in spring until after this cold snap, when they breed very rapidly. In this way they avoid jeopardising the colony's survival. A distinction therefore needs to be made between local ecotypes, which need to adjust their development and stores to the climate, and hybrid bees selected by bee breeders. Hybrids have not been bred to build up food stores, the queen does not adjust her egg-laying and the workers do not adjust their larvae-rearing, with the result that the bees are unable to survive without the assistance of a beekeeper to provide them with unlimited supplies of sugar solution (21). The variability of the honey bee's life-history traits as regards temperature and the environment shows such plasticity and genetic variability that this could give rise to the selection of development cycles suited to new climatic conditions.

Bees adjust their behaviour to weather conditions. They do not go out when it rains and, in extremely hot weather, they gather water to keep the colony cool.

Would climate-induced changes in flora provide honey bees with the conditions for viability?

Climate influences flower development and nectar and pollen production, which are directly linked with colonies' foraging activity and development (42). Bees must build up sufficient honey stores to enable them to survive the winter. The nurse worker bees must consume enough pollen to feed the larvae through their pharyngeal glands. A major effect of climate change on honey bees stems from changes in the distribution of the flower species (38) on which the bees depend for food. Will plants be able to survive the rapid advent of drought conditions or, on the contrary, wetter seasons? If they can, will conditions be optimal for flowers to produce the nectar and pollen needed for honey bees to develop? Although we do not know the precise impact that these factors could have on honey bees in a context of climate change, there is a large body of data at our disposal indicating that environmental changes have a direct influence on honey bee development. We are aware of the impact that rain can have on honey harvesting by bees. For instance, when acacia flowers are washed by rain, they are no longer attractive to honey bees (Fig. 4) as it dilutes their nectar too much. Likewise, an overly dry climate will reduce the production of flower nectar for honey bees to harvest: lavender flowers produce no nectar when the weather is too dry, which makes harvesting by bees a largely hypothetical matter. In extreme situations, honey bees can die of starvation unless the beekeeper is vigilant (Fig. 5).

The honeydew produced by stinging insects from certain plant species is also climate-dependent. In Alsace, very special conditions are required for the development and growth of balsam fir aphid populations, whose honeydew is highly attractive to honey bees (16). On the other hand, certain types of honeydew cause dysentery in honey bees. What effects will climate change have on honeydew production?

The food shortages stemming from an excessively dry climate, which reduces pollen production and impoverishes its nutritional quality, are currently the subject of much debate (36). Honey bees that are born in autumn spend the entire winter in the hive and form the backbone of the colony in spring. A pollen diet is very important for rearing the future workers (23). A pollen shortage induced by autumn drought will have the effect of depriving bees in winter, weakening their immune system and making them more susceptible to pathogens, and shortening their lifespan.

Tropical climates may evolve towards more distinct seasons with dry periods. In this case, Asian honey bees would need to rapidly step up their honey-harvesting strategy to amass sufficient stores to survive periods without flowers. Or else they could develop a migration strategy, as has *Apis dorsata*, a giant honey bee of the *Apis* genus. *Apis dorsata* colonies build their nests in the open air, consisting of a very big, single comb of up to two metres in length. *Apis dorsata* tend to be gregarious, which gives them a distinct advantage in the joint defence of their nests against predators. *Apis dorsata* honey bees readily migrate in response to seasons, flowering patterns or disruption. They abandon their nests and can fly distances of up to 200 kilometres to escape starvation or predators. After leaving their nests unoccupied for several months (or in some cases one or two years) the same honey bee colony returns

Fig. 4
Bee foraging on acacia
Acacia-flower foraging is highly climate-dependent. Rain can diminish a potentially large nectar harvest
Photo by Yves Le Conte

Fig. 5
Bee foraging on lavender
Lavender-honey harvesting is unpredictable. Drought often curbs the production of nectar by lavender flowers
Photo by Yves Le Conte

to colonise the same nest in the same tree every year (27, 30). A plausible scenario is that, to guarantee their survival, these honey bees will migrate in step with the evolution and disruptions of local flower species, and that they will switch their migration sites, abandoning regions that have become too arid. What will happen to honey bee species that do not migrate? If there is large-scale natural swarming, these species will be able to swarm to more favourable regions and abandon their regions of origin. Failing that, they will need to evolve rapidly towards a harvesting strategy to enable them to survive during periods with no flowers.

A commonly-cited textbook example is that of the Landes ecotype in south-western France. In the Landes region, the colonies develop in step with heather bloom, which is the main natural resource for these honey bees. The Landes ecotype has therefore modelled its development on that of the plant (20) (Fig. 6). A change in climate is bound to alter the flora. What will this do to the heather and to this honey bee ecotype?

Consequences for the geographical distribution of *Apis mellifera mellifera* and other races

Natural movements

As with other arthropods (5), climate change will lead to a reduction or an increase in the areas available to honey bees. Bees will abandon areas that evolve towards drought and migrate towards the fringes of such areas. In contrast, honey bees will colonise cold areas that were initially hostile to them.

Fig. 6
Bee foraging on heather
Colonies of the Landes ecotype of the European dark bee *Apis mellifera mellifera* in south-western France have modelled their development on heather bloom
Photo by Joël Blaize

A well-studied example is that of the Africanised honey bee. The Africanised honey bee's geographical distribution has now extended as far as Argentina and the USA, where it has come to a halt (9, 32). According to researchers, this is because the climatic conditions beyond that are too cold for the Africanised honey bee. Global warming is therefore conducive to the bee's expansion outside its current distribution range. Moreover, the Africanised honey bee is less susceptible to the *Varroa* mite than European honey bees (22). It is therefore expected to form feral colonies and to adapt more easily than other races, which is what is happening in the USA at present.

Movements instigated by beekeepers

Beekeepers are expected to change their transhumance habits and abandon areas that have become too dry in favour of wetter areas. They will most probably be tempted to continue importing queens of other races to test their potential to adapt to new climates. Although such imports will increase the genetic diversity of honey bee populations, they will also act as vectors for the introduction of new pathogens or of new bee haplotypes of varying usefulness, as in the past (see the Africanised honey bee).

Bringing imported honey bees into contact with local races and ecotypes facilitates a genetic admixture that may aid the survival of the species but will also tend to eradicate local ecotypes and pure races through genetic pollution.

Potential for adaptation: genetic variability

Apis mellifera is a species that has shown great adaptive capacity, as it is found almost everywhere in the world and in highly diverse climates. Imported to the Americas by the colonists, it has co-evolved with humans and has spread throughout the continent, from north to south. It may be assumed that, as the species has great biodiversity, it will be able to use its genetic variability (6) to adapt to climate change. In contrast, the Asian species have remained in Asia, which might indicate lesser adaptability to different environments and fragility in the face of climate change. *Apis mellifera* seems to have more adaptive potential than its Asian cousins, which have low yields and have been subject to little transhumance. Humans, with whom *Apis mellifera* has co-evolved for several centuries, will certainly be decisive in helping honey bees to survive in hostile environments and in preserving the biodiversity of these species. Beekeeping is an essential pollination and production support tool in this respect. However, if bee ecotypes are no longer suited to their biotopes, feral colonies will need to evolve rapidly to survive without human assistance.

Trade in honey bees: a factor of diversity and environmental adaptability?

French beekeepers have imported honey bees from virtually the world over. Interracial hybrids, bred by artificially inseminating queens, can produce yields up to double those of the black honey bee (*Apis mellifera mellifera*) (11). Royal jelly producers are working with foreign races because the French dark bee is highly productive (16). A network for importing foreign queens has therefore been established in France for a very long time. However, these hybrids and other races are often less well-adapted and more susceptible to disease than local races. In France, there are therefore those who defend the local dark race, as these ecotypes are well adapted to their biotope, whilst others choose to import and use hybrid bees to ensure better harvests. The result of these opposing trends is wide genetic diversity in France, owing to continuing hybrid imports and to the genetic pollution of local honey bees.

In North America, it is prohibited to import queen bees for health reasons. In spite of the huge sums spent on preventing such imports, American honey bees have more diseases than European ones. In the USA, a few large-scale queen bee breeders are responsible for renewing the stock, with each breeder selling hundreds of thousands of queens. They raise their queens from just a few of their best strains, which reduces the genetic diversity of the honey bee population and so weakens the bees' defences against various pathogens.

In a global warming perspective, France's situation is assuredly a more comfortable one, as French honey bees are endowed with greater genetic diversity and therefore have greater adaptive potential. The same is not necessarily true of other European countries that ban imports and select their stock rigorously.

This is an idea to be considered in the context of the spontaneous emergence of lines of *Varroa*-resistant honey bees, as has occurred in France with the emergence of honey bee colonies that have survived for more than ten years without any treatment against the *Varroa* mite (19). However, countries that select their honey bees and import very few, such as Germany and the USA, have not yet detected any *Varroa* mite resistance in their honey bees.

Molecular biology is a useful tool for measuring the genetic diversity of honey bee populations and linking it with their adaptability to climate change and to different pathogens (40). Genomics is another useful tool that has become available following the recent sequencing of the bee genome (39), which will enable us to gain a better understanding of the co-evolution mechanisms between honey bees and their pathogens (26). A deeper understanding of these mechanisms will lead to better management of honey bee populations and to the detection of the genes involved in new bee phenotypes.

Diseases and parasites: changes in disease profiles and incidence

Different diseases in different parts of the world

Current disease profiles and potential changes in distribution arising from climate change

Some known pathogens are distributed worldwide. They include: *Varroa destructor* in the case of *Apis mellifera* and *Apis cerana*; bacteria that cause American and European foulbrood; *Nosema apis* and *N. cerana*; and numerous viruses affecting *Apis mellifera*. These pathogens tend to have different haplotypes of varying virulence. Climate change can encourage the transfer of these haplotypes to honey bee populations.

Other pathogens or haplotypes have more limited distribution ranges, such as *Tropilaelaps*, which to date has been found only in Asia (34). Climate change will lead to movements of honey bees of different species and races, bringing them into contact with pathogens with which they have never co-evolved, as has occurred with *Varroa destructor* and *Apis mellifera*. In the space of a few decades last century, two extremely homogeneous haplotypes of this honey bee parasite were sufficient to invade virtually the entire *Apis mellifera* distribution range (35). History therefore shows that such encounters can be catastrophic and that honey bees will need human assistance to survive. Honey bee movements may be spontaneous and linked to changes in geographical distribution, or the result of exchanges of bees among beekeepers.

There could be changes in the geographical distribution of diseases whose expression depends on climatic factors. This has happened with chalkbrood disease, which is caused by the fungus *Ascosphera apis*, which develops mainly in a humid environment.

How will the pathogen/bee interaction evolve?

Recent results from a metagenomic study by American researchers on honey bee populations suffering from colony collapse disorder are highly instructive in this respect (8). They have shown that honey bee colonies are infested by numerous pathogens, including imported ones. There is therefore a high likelihood that as yet unidentified pathogens exist on certain honey bee species or races. Pathogen species infesting different honey bee races or species can be brought into contact with new hosts. The recent discovery of *Nosema cerana* (15) and the Israeli acute paralysis virus (8) among *Apis mellifera* is a potent example of the role humans can play in movements of honey bee populations. Climate change could modify the interactions among these different pathogens. *Tropilaelaps* is an interesting case in point. The *Tropilaelaps* mite does not yet infest *Apis mellifera* because this honey bee's development cycle includes a period without brood, on which the mite is utterly reliant for its survival (34). However, if climate change induces warmer winters, *Apis mellifera* would have to adapt towards a continual brood cycle, which would render it a potential host for *Tropilaelaps*.

Consequences for bee health and socioeconomic impact

Honey bees will require human protection, if only because of their importance for agricultural production and markets. It seems clear that bees will come into contact with new pathogens. The high mortality rate and colony collapses that we are currently seeing demonstrate the fragility of honey bee populations worldwide. As has been the case with the *Varroa* threat to *Apis mellifera*, our honey bees will need to be aided with medicines and appropriate control methods to prevent them from becoming extinct.

Climate change can facilitate the emergence of new invasive species

Numerous examples have revealed the fragility of the host–parasite balance and shown that even slight climate changes impact on the establishment of invasive species that are currently at the fringes of the honey bees' distribution range.

The situation of honey bees can also evolve when predators colonise new areas. A stark example is that of the bee-eater, a magnificent bird that feeds on *Hymenoptera* and bees. The bee-eater originated in the Mediterranean region but has extended its distribution range, causing only minimal harm to beekeepers so far. In France it is now found north of the Loire. A second example is an apiary pest, the small hive beetle (*Aethina tumida*), which originated in South Africa and develops on the weakest honey bee colonies. The parasite was imported into the USA, probably on citrus fruit on which the beetle can also develop. It has compounded the problems of American beekeepers, especially in hot and humid regions. The cold climate has halted the beetle's northward progression. Climate change will promote the extension of its distribution range. Measures have been taken to prevent this insect pest from being imported into Europe, where it is considered a potential hazard.

Socioeconomic aspects

Not only bees, but beekeepers too, will need to adapt to changes in climate and flora. This means that some regions that are now hostile to beekeeping will become of interest to beekeepers, whilst other foraging areas will have to be abandoned. A decisive factor in beekeepers' choices will be the adaptiveness of honey plants to climate change.

Beekeepers will also need to adapt their bees to climate change, abandoning local ecotypes or races in favour of better-adapted honey bees. This means that measures must be envisaged to conserve honey bee races and ecotypes to limit the loss of bee biodiversity. An appealing technique is sperm cryopreservation.

Recent cases of mortality

Since 1995, we have been seeing heavy mortality among *Apis mellifera* worldwide. The consensus among researchers is that a combination of factors is responsible for this honey bee mortality. Pesticides kill many colonies every year. New pathogens have been added to the already long list of honey bee diseases. However, researchers agree that the bees' environment and stress, both of which are influenced by climate change, have been decisive factors in this heavy mortality (29, 31). There appear to be strong interactions between diseases, pesticides, environment and climate. Climate change has an action on each of these factors. To understand the effect of climate change on the evolution of honey bee populations, each of these factors will need to be taken into account.

Conclusion

Widespread mortality in the *Apis mellifera* honey bee worldwide aptly demonstrates the fragility of this species, whose survival relies on an increasingly hostile environment. The reasons given to explain this phenomenon include pesticide use, new diseases, stress and a combination of these factors. As a result, climate change will shift the balance between the honey bee, its plant environment and its diseases. The honey bee has shown a great capacity to colonise widely diverse environments and its genetic variability should enable it to adapt to such climate change. However, the fear is that climate-induced stress will in future compound the various factors already endangering the species in certain regions of the world.

If humans modify the honey bee's environment, they also have a duty to take conservation measures to prevent the loss of this rich genetic diversity of bees. To understand the factors favouring the extinction of honey bees, it will be necessary to conduct fundamental research aimed at ascertaining the causes of mortality, as well as the effect of human-induced environmental change. Environmental impact studies in the field, as well as the use of modern genomics methods made possible by the recent sequencing of the bee genome, are expected to play a prominent role in discovering the vital stress factors for these species.

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