

**IMPACT OF HUMAN MANAGEMENT ON THE
HOST-PARASITE INTERACTIONS BETWEEN
APIS AND *VARROA***

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von Herrn Alexis Louis Beurepaire

geb. Am 04.07.1988 in Roubaix, France

Gutachter / in:

1. Prof. Dr. Robin F.A. Moritz (Molecular Ecology group Martin-Luther-Universität, Halle, Deutschland)
2. Prof. Dr. Robert J. Paxton (General Zoology group, Martin-Luther-Universität, Halle, Deutschland)
3. Prof. Dr. Christian W. W. Pirk (Zoology and Entomology group, University of Pretoria, South Africa)

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GENERAL INTRODUCTION

Interactions between humans and honeybees (genus *Apis*) date back to prehistoric time (Crane, 1999). The relationships between our ancestors and these insects began when man still lived in caves, and bee colonies were hunted for their honey and brood which formed a highly nutritive resource (Crane, 1986; Crittenden, 2011). Today, these interactions have intensified and honeybees have become very popular due to their ecological (Hepburn and Radloff, 2011) and economical value (Klein et al., 2007). Also the scientific world has been fascinated by honeybees for millennia, and many features of the biology of these species have sparked the interest of researchers worldwide (Winston, 1987).

Apis is a moderately diverse genus, including at least nine species (Hepburn and Radloff, 2011). Eight of these species are native to East and South-East Asia, whereas the last one, *A. mellifera*, is endemic to Western Asia, Africa and Europe (Ruttner, 1988). These species have particular characteristics separating them from the rest of the Apidae family, such as extreme multiple mating by queens (Palmer and Oldroyd, 2000), reproduction via swarms that make a clear break from the nest (Oldroyd and Wongsiri, 2006) and reuse of brood cells for brood rearing or honey storage (Oldroyd and Wongsiri, 2006). Honeybees are commonly grouped in three subgenera: *Microapis* (the dwarf honeybees), *Apis* (the cavity-nesting honeybees) and *Megapis* (the giant honeybees). These subgenera are primarily reflecting the morphological differences among the species, but other traits vary among these groups such as the architecture of their nests and the time and location of their reproductive swarms (Otis et al., 2000).

In addition to these biological differences, human influence is different among the subgenera. This is especially pronounced in the cavity-nesting species, where management has become more and more intense over time (Oldroyd and Wongsiri, 2006). Contrary to the dwarf and giant honeybees, these species build multiple combs in cavities which can easily be

identified. Hence, their colonies can be frequently harvested without destroying the totality of the brood and represented a very valuable and sustainable food source for prehistoric men. Later on, the development of hives further enhanced the intensity of the interactions, and led to the domestication of some species like the Western honeybee (*A. mellifera*) and the Eastern hive bee (*A. cerana*). Finally, the development of transportation tools and selective breeding in *A. mellifera* has profoundly changed the population dynamics of this species. Today, wild colonies of *A. mellifera* and *A. cerana* are still common in some parts of the world, but are often in close contact with managed apiaries (Pirk et al., 2016).

Honeybees are eusocial insects nesting in colonies headed by a single polyandrous queen which lives for several years. Two major natural events shape the dynamics of these colonies: reproductive swarming and migration. In all honeybee species, reproductive swarming is initiated when colonies are strong enough and start producing sexual individuals (queens and drones). In natural conditions, this event is initiated by the current queen leaving the colony to start a new colony with approximately half the worker force. A few days later, a next generation of queens emerge. After mating in a swarm, one of these daughter queens will take over the colony. In parallel, migration is frequent in Asian honeybees and common in some subspecies of *A. mellifera* (Hepburn and Radloff, 2011). This event is characterized by absconding of the queens together with the entire colonies' working force because of resource depletion. Hence, this behaviour is highly influenced by the availability of pollen and nectar in the surrounding of the nests. Remarkably, the distance the colonies travel varies greatly between species and subspecies (Oldroyd and Wongsiri, 2006).

Altogether, natural reproductive swarming and migration result in a loss of part or whole colonies and significantly reduce the honey and bee product yield of a given colony. Obviously, this is not in the interest of beekeepers that tend to prevent these natural events as much as possible by manipulating food resources (i.e. feeding colonies) or managing reproduction (i.e. by placing

more brood frame and/or destroying queen cells). Thus, the influence of humans on the dynamics of managed honeybee colonies is colossal. Yet, the most extreme human impact on honeybees results from the transportation of colonies (Moritz et al., 2005; Mutinelli, 2011). As a result of a long period of domestication and because of its high productivity, *A. mellifera* was introduced in almost all the regions of the globe. Several risks are associated with these introductions (Goulson, 2003) including for instance competition for floral or nesting resources with other pollinators (Gilpin et al., 2016; Paini, 2004), interspecific hybridization (Li, 1998) and pathogen transmission between native and introduced species (Morse and Flottum, 1997; Pirk et al., 2016).

In fact, the most harmful parasite of *A. mellifera*, *Varroa destructor* (Anderson and Trueman, 2000) has been transferred to the western honeybee because of transportation of colonies outside of their native range (Crane, 1978). This ectoparasite was originally confined to South-East Asia where its native host is the eastern hive bee, *A. cerana* (Anderson and Trueman, 2000). But after the introduction of *A. mellifera* in the natural range of *V. destructor*, the mite successfully established in colonies of the western honeybee and consequently spread worldwide due to the transfer of infected colonies from Asia (Rosenkranz et al., 2010; Wilfert et al., 2016). Today, *V. destructor* represents a major global threat for *A. mellifera* (Boecking and Genersch, 2008; Dainat et al., 2012; De la Rúa et al., 2009; Le Conte et al., 2010).

The *Varroa* genus includes at least four species, all initially infecting Asian cavity-nesting honeybees. In addition, there is strong evidence that at least two distinct species from the Philippines could be added to this list (Anderson and Trueman, 2000). The life cycle of the mite is composed of a series of reproductive and phoretic phases (Sammataro et al., 2000). Reproduction takes place in the honeybee brood cells where one or several mature foundress(es) enter at the prepupal stage one or two days prior to capping and hide in the bottom of the cell on the remaining brood food. Approximately 70 hours after the cell is sealed by the honeybee workers, the mite(s) lay a first haploid male egg (Ifantidis, 1983). Subsequent female eggs are produced

every 30 hours after that point, and once the offsprings are mature they mate with each other. Thus, when only one foundress infests a cell, brother and sister mate together. This may change if more than one mite originally invades the cell and offsprings from different mothers admix (Fuchs and Langenbach, 1989). Not all the offsprings will have time to reach maturity before the pupa emerges. In each of her reproductive cycle, a female will produce in average 1.3-1.45 mature daughters when infesting a worker cell and close to double this amount in a drone cell, due to the longer time of development of honeybee males (Martin, 1995, 1994). However, the reproductive success of the mites is negatively correlated to the number of foundresses invading the brood cell (Fuchs and Langenbach, 1989). Once the honeybee emerges, all mature females leave the cell and the male(s) die(s). In general, the females perform several distinct mating cycles during their lifespan, ranging from two or three under field conditions (Fries and Rosenkranz, 1996; Martin and Kemp, 1997) to as many as seven in the laboratory (de Ruijter, 1987). Between each cycle, a mite stays a few days in a phoretic phase while feeding directly on adult bees.

To date, only two species of the genus *Varroa* (*V. destructor* and *V. jacobsoni*) have been detected in *A. mellifera* colonies (Anderson and Trueman, 2000; Roberts et al., 2015) and only one (*V. destructor*) is found outside its natural range. These mites impact honeybee colonies on two different levels. On the one hand, the parasite feeds on the haemolymph of the brood and adults, weakening these individuals. On the other hand it plays an important role as a vector and/or symbiont of multiple honeybee viruses (Boecking and Genersch, 2008; Di Prisco et al., 2016; Genersch and Aubert, 2010; Martin et al., 2012; McMenemy and Genersch, 2015), which seems to cause even more devastation than the feeding itself.

While the mite is very harmful for *A. mellifera*, *V. destructor* has very moderate effects on *A. cerana* (Peng et al., 1987). These differences of sensibility to *V. destructor* between the two hosts are reflecting the period these two honeybee species have been in contact and co-evolved with the mite. Host-parasite coevolution is generally perceived as reciprocal selection on host

resistance and parasite infectivity (Thompson, 1994). On the one hand, there is a strong selection on host defences to limit the fitness impacts of parasites. On the other hand, parasites must constantly adapt to overcome these defences and enhance their transmission. As generations pass and this evolutionary arms race goes on, adaptations evolve in both parts and a fluctuating equilibrium may be reached. This evolutionary theory was defined by Van Valen (1973) as the “Red Queen Hypothesis”. In the long term, this powerful evolutionary force can drive entire population apart (Fumagalli et al., 2011; Paterson et al., 2010). As results of this coevolution, several behavioural traits of *A. cerana* have evolved to hinder the growth of *Varroa* populations such as an effective hygienic behaviour (Peng et al., 1987; Rath and Drescher, 1990; Rath, 1999), “entombment” of the drones if they are too heavily infected (Rath, 1992) and social apoptosis (Page et al., 2016). In addition, the mite mainly reproduces in drone brood in the colonies of the Asian host, not impeding directly the worker development and colony productivity (Koeniger et al., 1983; but see De Jong, 1988).

In contrast, *V. destructor* remains a major global threat to colonies of *A. mellifera* despite many generations of interactions between these species. In most parts of the world, the parasite can cause rapid colony death if no treatments are performed by beekeepers (Martin, 1998). This is mainly due to the fact that the mite can also reproduce in the highly available worker cells in the western honeybee, causing an annual increase of the parasite population up to 2000-fold (Martin and Medina, 2004; Vandame et al., 2000). However, adaptations of the western honeybee towards *V. destructor* have arisen independently in different parts of the world (Locke, 2015) and defence mechanisms such as hygienic and grooming behaviour are also present in some *A. mellifera* populations (Fries et al., 1996; Kurze et al., 2016). Although these adaptations are less effective in controlling the mite than in *A. cerana*, they can significantly improve the survival of *A. mellifera* colonies (Büchler et al. 2010; Rinderer et al. 2010; Locke et al. 2012).

In addition to these behavioural adaptations, the population dynamics of the host might play a significant role in reducing the impact of *V. destructor* infestation. For instance, the frequent migration of colonies represents consecutive bottlenecks hindering the growth of parasite populations, as only a limited number of phoretic mites reaches the new nests, where less brood is available for them to reproduce. This migrating behaviour is found in some African subspecies of *A. mellifera* and may explain why these populations were originally able to survive *V. destructor* infection, and could develop adaptations to further tolerate mite infestation (Pirk et al. 2014; Strauss et al. 2016).

Despite the numerous projects on the coevolution between the genera *Apis* and *Varroa*, most studies have focused on the host or the parasite independently. Yet, the mite is highly dependent on the honeybee colony development to reproduce and in return strongly influences the health status of its host (Seeley et al. 2015). Hence, the population dynamics of the parasite can also influence the outcome of the infestation. For instance, infestation of brood cells with too many foundresses may result in negative reproductive success in *V. destructor* (Fuchs and Langenbach 1989; Donzé and Guerin 1997). Up to now, all colonies of *A. mellifera* which developed tolerance to the parasite have in common the fact that they were not actively managed (Locke 2015). This characteristic highlights the important role of beekeeping on the development of the parasite infection. By interfering with the population dynamics of both, the honeybee and the mite, humans can greatly modify the interactions between these organisms.

To fully understand the relationships between the genera *Apis* and *Varroa* and the importance of human interference in this system, both the parasite and the host have to be considered simultaneously. If one wants to investigate the interaction dynamics between any host and parasite at the population level, it is important to first understand the population structure of the host, then that of the parasite to finally address potential interactions. The aim of this thesis is to study the genetic structure of honeybees and their parasite in order to assess the main biological

parameters influencing the population dynamics in *Apis* and *Varroa*. In all three of the following chapters, microsatellite markers were used to estimate several parameters reflecting the levels of genetic diversity and gene flow of different populations and species of honeybees and the mite. Among other things, the level of human impact varies greatly between these populations and species. The conclusions we can draw from the research conducted in this thesis will therefore help understanding how the population dynamics honeybees and *Varroa* may be altered by human management. More particularly, this work will bring new insights on the way beekeeping can hinder adaptations in the host populations and influence the virulence, the transmission and/or the dispersal of the parasite.

Chapter I

Extensive population admixture on drone congregation areas of the giant honeybee, *Apis dorsata* (Fabricius, 1793)

A. Beaurepaire, F. B. Kraus, G. Koeniger, N. Koeniger, H. Lim and R. F. A. Moritz

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Preface

To visualize how the genetic diversity of honeybee populations is maintained in the wild, I first dissected mating strategies of the giant honeybee *Apis dorsata*. This species is characterized by long distance seasonal migration (Koeniger and Koeniger 1980), nest aggregation in the same trees (Paar *et al.* 2004; Rattanawanee *et al.* 2013), nest site fidelity (Neumann *et al.* 2000; Paar *et al.* 2000) and tremendous intracolony levels of genetic diversity as a single queen can mate with over a hundred males (Moritz *et al.* 1995). In addition, as *A. dorsata* cannot be kept in apiaries, it is almost free of any impact of bee management. Thus, this work brings new insights into the colony dynamics of wild honeybees that can then be compared with the available knowledge on managed honeybee populations in order to understand the epidemiological consequences of beekeeping with regard on the spread of parasites and potential selection for resistant host types.

Apis dorsata often forms dense colony aggregations which can include up to 200 often closely related nests in the same location, setting the stage for inbred mating. Yet, like in all other *Apis* species, *A. dorsata* queens mate in mid-air on lek like drone congregation areas (DCAs) where large numbers of males gather in flight (Figure I.1). This study aims at providing insights on the reproductive behaviour of the drones of *Apis* in the wild and help understanding how these individuals may contribute to the gene flow of honeybees in space and time. Because drones are preferentially targeted by *Varroa* in honeybee colonies (Boot et al., 1995), the selection pressure on these individuals is tremendous. Thus, understanding the dispersal abilities of honeybee males will help inferring how adaptations towards parasites such as *Varroa* can spread among colonies and populations.

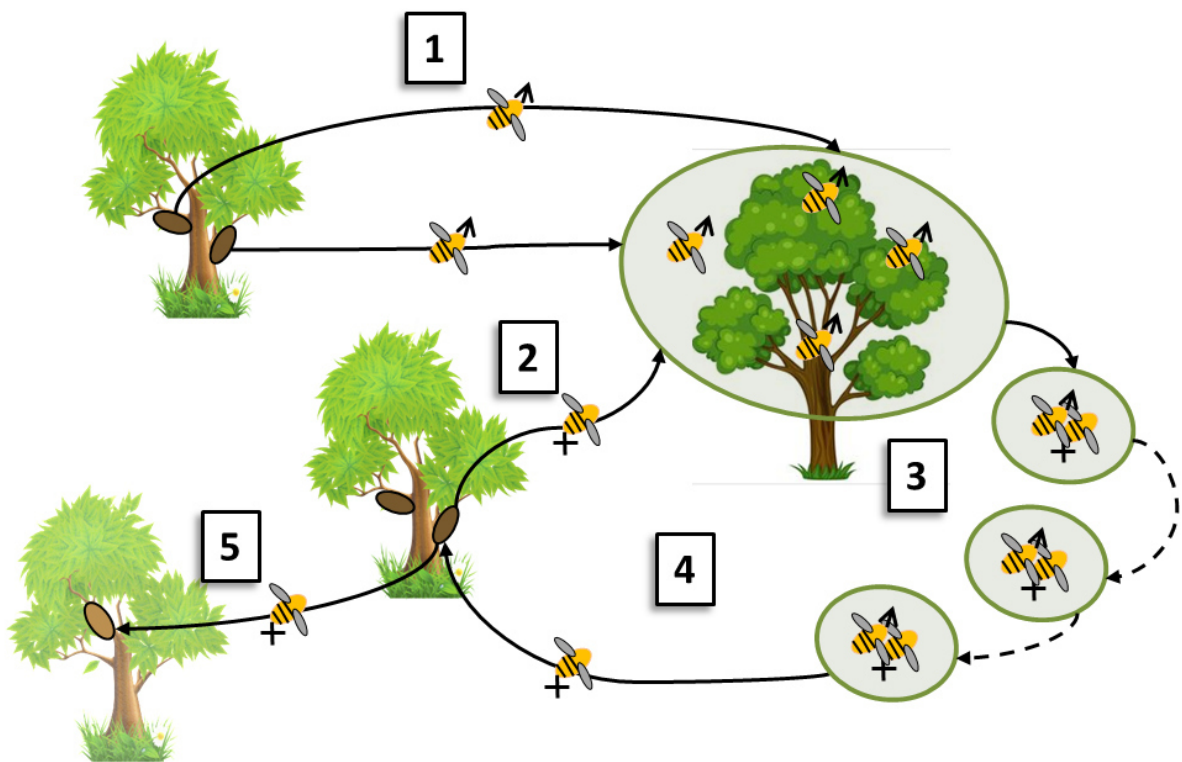


Figure I.1 – Reproduction in *Apis dorsata*

Figure illustrating the reproduction of *A. dorsata*. **1.** Drones fly to the canopy of a tall emergent tree; **2.** Virgin queens join them once the DCAs are formed; **3.** Within the DCAs, queens mate in average with 44.2 ± 27.15 drones over up to six consecutive days; **4.** Once mating is finished, the queens return to their natal nest; **5.** The freshly mated queens will then leave with a part of the workers to found a new colony or take over their natal nest.

Chapter II

Seasonal cycle of inbreeding and recombination of the parasitic mite *Varroa destructor* in honeybee colonies and its implications for the selection of acaricide resistance

Alexis L. Beaurepaire, Klemens J. Krieger and Robin F.A. Moritz

Keywords: Population Genetics, Host-Parasite Coevolution, Population Dynamics, Microsatellites, *Varroa destructor*, *Apis mellifera*

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Preface

After investigating the reproduction of wild honeybees, the aim of this second chapter is to bring new insights into the genetic structure of *V. destructor*. In the first global survey of the genetic diversity of this parasite, Solignac et al. (2005) claimed that the invasive types of the mite were two partly isolated clones. Although this can be explained by the bottlenecks following *V. destructor* spill-over and invasion of the mite and due to its incestuous reproduction system involving brother-sister mating in the cell (Figure II.1), these claims are not compatible with other observations on the biology of this parasite. In fact, when *V. destructor* faces strong selection pressure, the emergence and the spread of adaptations can be very swift, such as in the case of acaricide resistance (Milani, 1999). Yet, for adaptations to arise and spread so rapidly significant levels of genetic variation must be maintained in the populations of the mite and gene flow must be significant; which is not coherent under a strict inbreeding hypothesis.

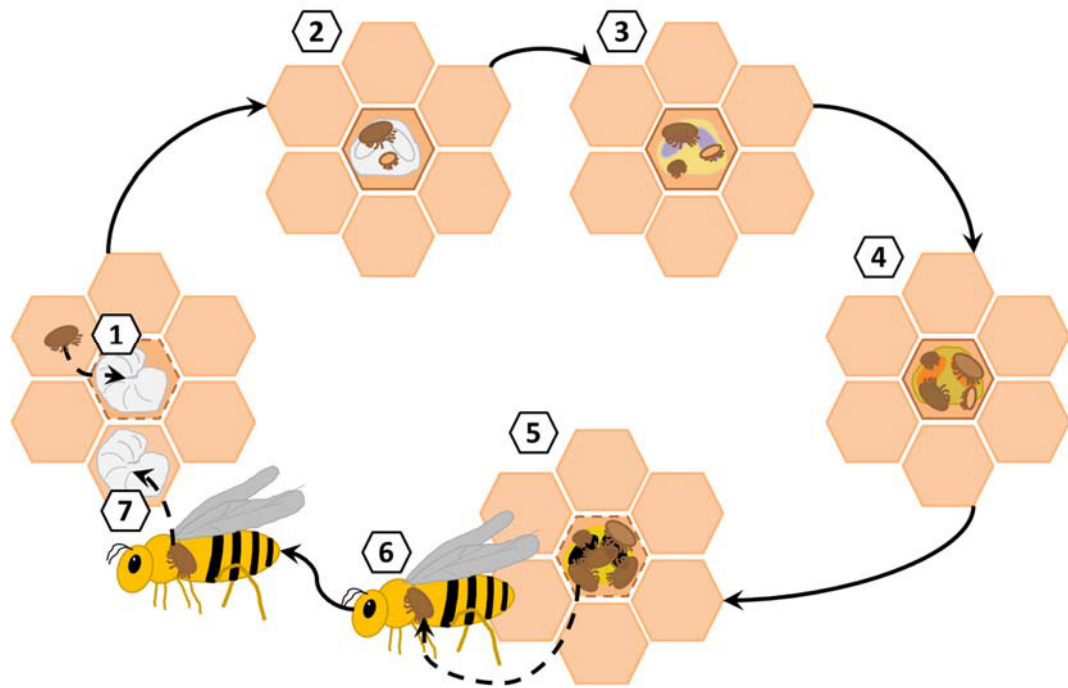


Figure II.1 – Single mite reproduction in *Varroa*

Figure illustrating the life cycle of a *V. destructor* female in case of a single mite infestation. **1:** The mite enters a honeybee brood cell with a fifth instar larva; **2:** At approximately 70H post-capping, the foundress produces a first unfertilized, haploid egg which will develop into a male; **3:** The foundress lays females eggs every 30H; **4:** Once they are mature (approximately 160H for males, 140H for females), mating takes place between brothers and sisters; **5:** Once the infected bee hatches, the mature females exit; **6:** These females spend some time on a phoretic phase, attached to adult bees and dispersing within and/or between colonies; **7:** After this phoretic stage, the mated females can infect new brood cells and a new cycle can start again.

To clarify these aspects of the biology of *V. destructor*, this study aims at tracking the temporal evolution of the mite inbred lineages in colonies of *A. mellifera*. Given the particular reproductive system of the mite (Figure II.1), a model reflecting temporal evolution of inbreeding in *V. destructor* is compared to empirical data. This part will provide crucial information to determine the main mechanisms involved in the selection and the spread of adaptations in this supposedly almost clonal system.

Chapter III

Host specificity in the honeybee parasitic mite, *Varroa* spp. in *Apis mellifera* and *Apis cerana*

Alexis L. Beaufrepaire, Tuan A. Truong, Alejandro C. Fajardo, Tam Q. Dinh, Cleofas Cervancia
and Robin F. A. Moritz

Keywords: Host-Parasite Coevolution, Reproductive Isolation, Hybridisation, Parasite Spill-over, *Varroa*, *Apis*

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Preface

After investigating the genetic structure of the honeybees and *V. destructor* separately, the third and last part of this thesis aims at comparing populations of the mite between its two hosts (*A. cerana* and *A. mellifera*) and over several regions of the Philippines and Vietnam. In Asia, beekeeping of *A. cerana* is less and less popular and the native bee is often replaced with *A. mellifera*, which is gentler, more productive and less prone to abscond. However, keeping the western honeybee requires intense management practices, contrary to the native bee that can be transferred to boxes from wild nests. For these reasons, beekeepers often possess a large number of *A. mellifera* hives and sometimes a few colonies of *A. cerana* located on the same apiary (Figure III.1). These mixed-species apiaries represent a great opportunity to study the patterns of intra- and inter-specific transmission of the parasite as well as the effect of colony dynamics of *A. cerana* and *A. mellifera* on the genetic structure of mites sharing the same environmental conditions.

To date, only two haplogroups of *V. destructor* from Korea and Japan have been reported in *A. mellifera* colonies (Anderson and Trueman, 2000). This observation is surprising given that the western honeybee has been introduced to most parts of Asia and is currently in contact with many more haplotypes of the parasite (Figure III.1). Yet, analyses of the mitochondrial genome of other Asian *Varroa* haplotypes revealed a high host specificity in Vietnam (Fuchs et al., 2000) and Thailand (Rueppell et al., 2011; Warrit et al., 2006).

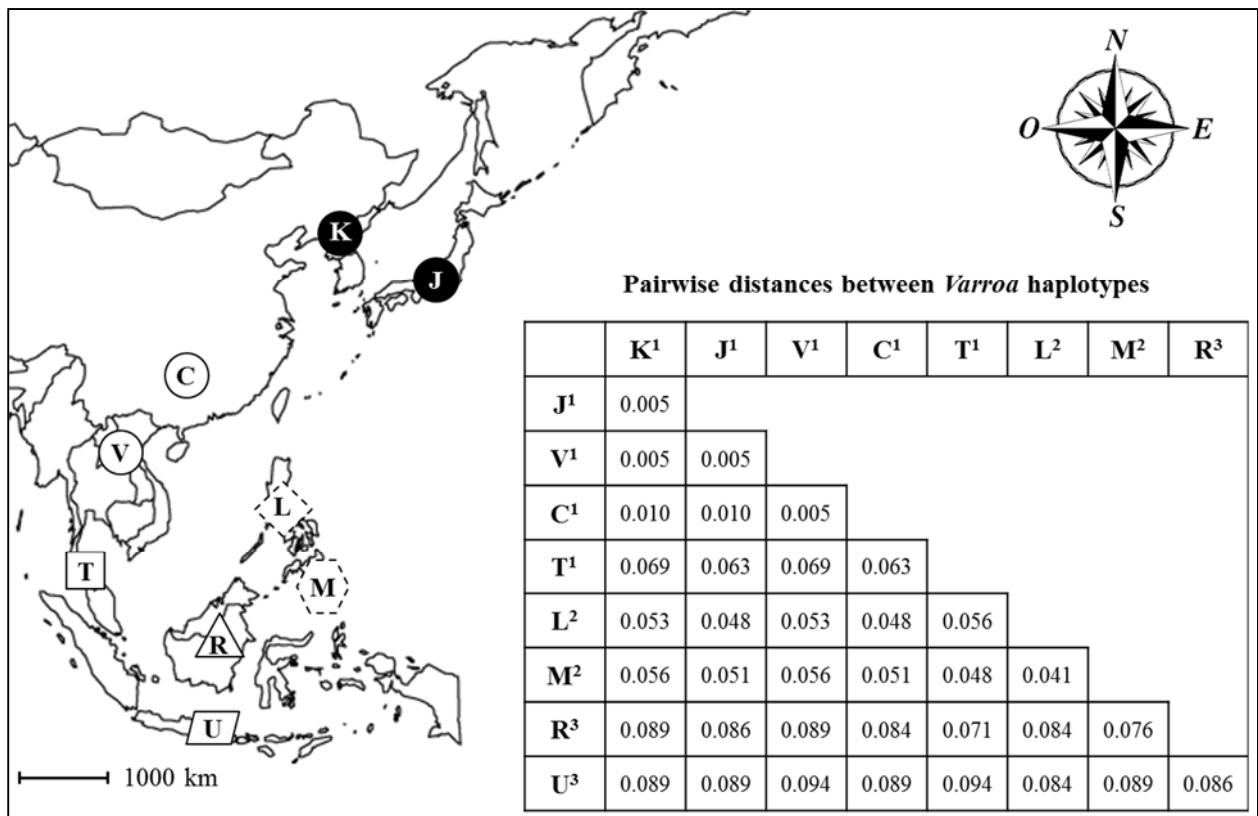


Figure III.1 – Comparison of the major *Varroa* haplogroups in Asia

Map indicating the distribution of the main *Varroa* haplogroups in Asia. The different solid line forms stand for different species (circle: *V. destructor*, square: *V. jacobsoni* from Thailand, triangle: *V. rindereri*, parallelogram: *V. underwoodi*) and the two dashed line forms are hypothetical species (diamond: *Varroa Luzon* sp., hexagon: *Varroa Mindanao* sp.). The two circles filled with black (K and J) represent the two *V. destructor* haplogroups which managed to switch to *A. mellifera* and are nowadays found in other regions of Asia. The matrix illustrates the pairwise distance (*p*-distance, calculated as proportion of nucleotide sites at which the two compared sequences are different) between these Cytochrome Oxidase I (COI) haplogroups (one sequence per group). The locations of the forms on the map indicate the region where the mites providing the sequences used in the matrix were sampled. References for the sequences: ¹: 1088bp COI sequences from Navajas et al. (2010), ²: 458bp COI sequences from Anderson and Trueman (2000), ³: Anderson and Fuchs (1998).

Interestingly, hybridization between these different haplotypes may occur but cannot be detected with mitochondrial markers. To date, only Solignac et al. (2005) have addressed the hybridization potential among distinct *V. destructor* haplotypes. They reported in their study that over 8% of the mites they analysed from Japan (where the Korean and Japanese haplotypes are found in sympatry) were direct F1 hybrids, indicating that these events can be common where hosts switches can occur. The following study aims at identifying the probability of recombination between the multiple haplotypes found in Vietnam and in the Philippines. As these hybrids may represent potential new threats for honeybee health, these results will help assessing the risks generated by the transportation of *A. mellifera* to Asia. In addition, this work will provide details on the influence of *A. mellifera* and *A. cerana* colonies dynamics and the effects of the differential beekeeping management of these hosts on the population structure of the mite.

GENERAL DISCUSSION

This thesis aims at bringing new insights into the coevolution between *Apis* and *Varroa* as well as the impact of beekeeping on this system. This is achieved by analyzing the spatio-temporal genetic structure of these organisms in order to assess the main parameters shaping their interactions. The first paragraphs of this discussion will summarize the knowledge on the population dynamics of honeybees and their parasitic mites based on the three chapters of this thesis and available literature. This will provide a strong foundation to further investigate how new adaptations can emerge and disperse in the populations of hosts and parasites. The second part will address how these adaptations can interact in a natural setting. Finally, the third and last part of this discussion will focus on how beekeeping and human management can destabilize the arms race between the genera *Apis* and *Varroa*.

1. Selection and Spread of Adaptations in *Apis* and *Varroa*

Genetic variation is paramount for adaptations to take place in a host-parasite system. This variation originates through mutations in the genome of organisms and is shaped by multiple parameters relative to their biological traits and surrounding environment (Hughes et al., 2008). The aim of this first part is to highlight which of these parameters influence the selection and the spread of adaptations in *Apis* and *Varroa* separately before looking at their interactions.

1.1. Selection and Spread of Adaptations in *Apis*

Several parameters are influencing the selection of adaptations in *Apis*. For a more comprehensive understanding, these parameters will be displayed here chronologically according to the life cycle of a honeybee colony.

A first parameter that will influence the selection of adaptations to *Varroa* in honeybees is the ploidy of the brood (Figure IV.1). In honeybees, sex of individuals is determined by their ploidy; with males being haploid and females diploid. In addition, selection operates only on drones and queens, unless the workers reproduce (Barron et al., 2001). As the infestation of *V. destructor* in queen cells is very low (Calderone et al., 2002), drones will be particularly targeted by the selective pressure induced by the parasite. Interestingly, the parasite is exclusively reproducing in male brood in *A. cerana* in natural conditions (Tewarson et al., 1992). Therefore, the selection of adaptations in that host species is likely to be particularly swift because in case of high parasite infestation any male cell will be highly infested and under strong selective pressure. In *A. mellifera*, despite the fact that *V. destructor* prefers drone cells (Boot et al., 1995), the overall selective pressure on males may be lower because the mite can also reproduce in worker cells. In addition, haplo-diploidy can also directly influence the selection of adaptations (Kidner and Moritz, 2015; O'Donnell and Beshers, 2004), for example by direct selection of recessive alleles in the haploid males.

After an initial selection has occurred in the brood, mating will further affect the selection and the spread of adaptations in honeybees (Figure IV.1). Reproduction in *Apis* is very demanding and any resource loss before the mating flight may significantly decrease the reproductive success of the drones and queens. As the result of the first chapter of this thesis highlights, this is particularly pronounced for honeybee males that have to disperse, fly over long distances, and finally race after a queen to mate with. Hence, only the drones which are less affected and/or more adapted to *Varroa* will successfully reproduce in DCAs. This panmictic reproduction system will tend to rapidly distribute any resistance allele within and between populations. Altogether, due to their high level of polyandry, honeybees retain a substantial amount of genetic diversity at the colony level (Sherman et al., 1998; Tarpy et al., 2004). If selection operates on drones -as may be

the case for adaptations to *Varroa*- any adaptive trait will be quickly disseminated within and between populations.

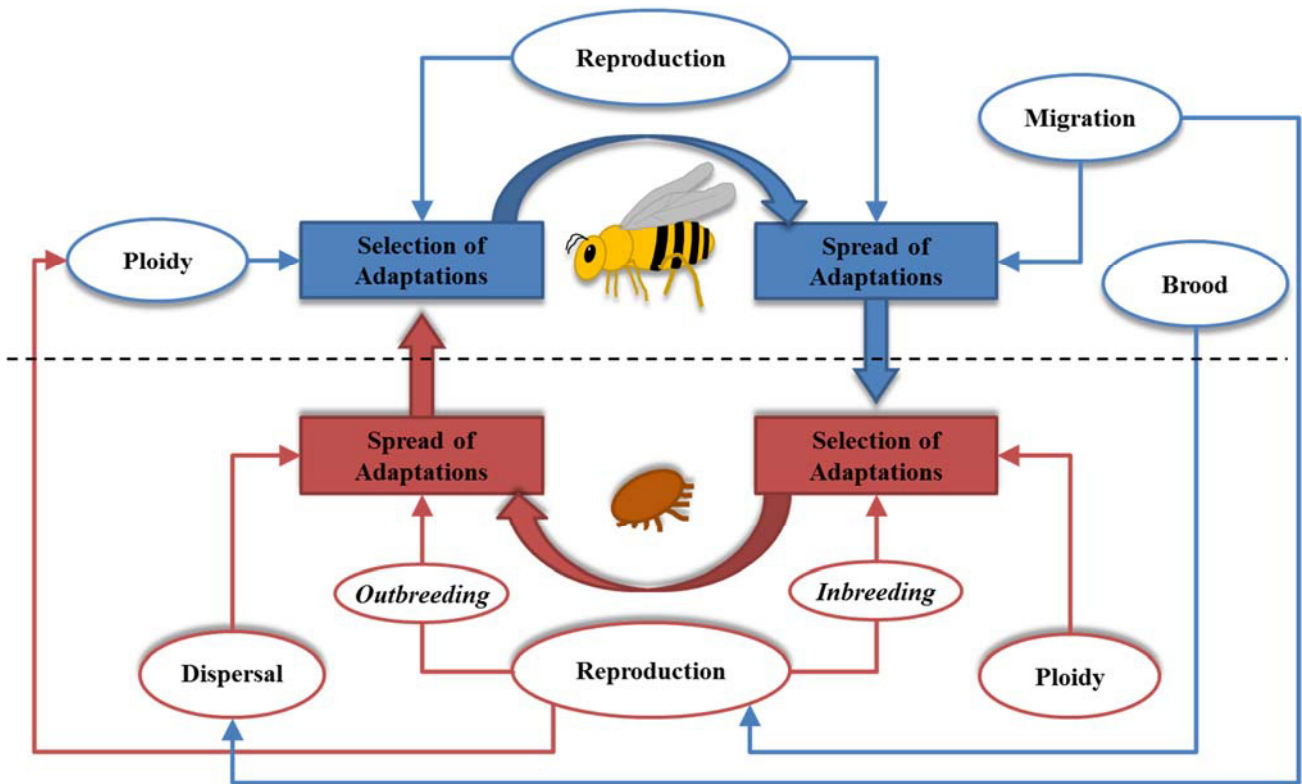


Figure IV.1– Main parameters involved in the arms race between *Apis* and *Varroa*

Figure summarizing how the different parameters of the populations of *Apis* (in blue) and *Varroa* (in red) discussed in this thesis can influence the interactions between these two organisms. The arrows indicate where each parameter acts more predominantly.

To date, no details are available on the genetic diversity and structure of *A. cerana* DCAs. However, the eastern hive bee also forms swarms including large number of drones in which the queens mate multiple times (Koeniger and Koeniger, 2000; Oldroyd and Wongsiri, 2006). Hence, as for *A. mellifera* and *A. dorsata*, DCAs are likely to play a similarly important role in the gene flow of *A. cerana*. Although there is still a lot to learn on this topic, the consequences of the honeybee lek-like reproductive system are clear: enhancing the gene flow between colonies and subpopulations and promoting high levels of intracolony genetic diversity.

In addition to that, migration will increase the gene flow and enhance the spread of adaptations within and among honeybee populations over even larger scales (Hepburn and Radloff, 2011). Noticeably, the influence of this parameter is variable, as the tendency for migratory swarming is different between *Apis* species and populations, and highly dependent on the environment (Oldroyd and Wongsiri, 2006).

1.2. Selection and Spread of adaptations in *Varroa*

The study of the temporal dynamics of *V. destructor* populations in temperate regions suggests a seasonal increase of multiple cell infestation correlated to the brood availability of the host. Thus, both inbreeding and outbreeding may vary over time in very tight dependency on the host colony dynamics. These two phases can have a bilateral influence on the selection and spread of alleles in the populations of *Varroa* (Figure IV.1).

Initially, when a large amount of brood is available early in the season, *V. destructor* reproduces mainly through inbred mating and a phase of swift selection may take place. Inbreeding is often considered to be deleterious although it may also be beneficial if the costs associated with incestuous mating do not exceed certain thresholds (Keller and Waller, 2002; Kokko and Ots, 2006). The first and most important benefit of inbreeding is the reduction of the cost of sex (Maynard-Smith, 1978). In *V. destructor*, the indirect reduction of the cost of sex (e.g. the genome of the mother passes entirely to the next generation when she performs inbred mating) is coupled to a direct reduction in exposure to the host defences, as actively looking for multiple infestations may reinforce the time being vulnerable to the host grooming behaviour. The second benefit is that inbreeding can enhance the expression of advantageous recessive phenotypes in diploid organisms. This way, inbreeding may boost the fixation of adaptations such as acaricide resistance alleles in *V. destructor*. Finally, inbreeding is the most effective way of purging deleterious

mutations from diploid individuals (Muller, 1964, 1950). However, this is not as important in haplo-diploid organisms such as *V. destructor*, in which their elimination is also achieved by selection on haploid males (Crozier, 1970; Kidner and Moritz, 2016; O'Donnell and Beshers, 2004).

Later in the season, as the mite infestation builds up in the honeybee colony and/or the brood availability decreases, the proportion of multiple cell infestations increases. Multiple infestations may not always result in outbreeding if the different foundresses are from the same lineage or if the multiple lineages found in a cell do not admix. Yet, the overall heterozygosity increases in *V. destructor* populations at that stage, suggesting that at least a few lineages recombine. In addition to this lineage recombination, the dispersal of mites between colonies due to honeybee worker drift is also frequent in late summer and fall (Forfert et al., 2015; Greatti et al., 1992) and may further spread the mite and their alleles among colonies.

2. Natural interactions between *Varroa* and *Apis*

As explained in the previous paragraphs, cycles of in- and out-breeding in *V. destructor* are very tightly linked to the colony dynamics of its host. Accordingly, the demography of different *Apis* species, subspecies and populations can shape the genetic structure of mite populations. The next paragraphs will aim at dissecting the main parameters involved in the arms race opposing the different species and populations of *Apis* and *Varroa* in order to further understand the potential influence of their population dynamics on the coevolution between these organisms.

2.1. Interactions between *Varroa* and *A. cerana*

Due to a longer period of coevolution with *V. destructor*, *A. cerana* is not as much affected by the mite as *A. mellifera* (Peng et al., 1987a). In addition to the differences in behaviour of the

host (i.e. grooming) and the parasite (i.e. preference for reproduction in drone brood), the colony dynamics of the honeybees can play an important role in the reduction of the impact of the mite.

Reproductive and migrating swarms are very frequent in *A. cerana*, especially in the tropical and subtropical distribution of this species (Oldroyd and Wongsiri, 2006). Because there is a pause in egg-laying during these events and mite reproduction is not possible, the parasite prevalence in colonies that swarm is significantly lower (Fries et al., 2003; Loftus et al., 2016). In addition, the length of the swarming period will also greatly influence the reproduction of the mite, because longer periods of phoretic stage significantly decrease its reproductive success (Rosenkranz and Bartalszky, 1996). In tropical regions, colonies of *A. cerana* can swarm for weeks (Oldroyd and Wongsiri, 2006). After the colonies have started a new nest, only a few drone cells will be available at the beginning for the surviving mites to reproduce. Thus, swarming events will significantly affect the population size but also the growth rate of their parasites in the new colonies.

New colony founding events in *A. cerana* may also lead to high levels of multiple infestation and recombination of mite lineages due to the small amount of drone brood, potentially breaking any local adaptation of the mite. Accordingly, significantly higher levels of heterozygosity were observed in *V. destructor* and *V. jacobsoni* populations infecting *A. cerana* compared to *A. mellifera* mites (third chapter of this thesis; Roberts et al., 2015). Although this may in part be due to the host switch, it could also reflect the impact of the swarming behaviour on the mite's genetic structure. Comparing mites from sympatric managed and wild colonies of *A. cerana* would help exploring this hypothesis.

2.2. Interactions between *Varroa* and *A. mellifera*

The first contacts between *A. mellifera* and *V. destructor* occurred about two centuries ago in Eastern Russia (Danka et al., 1995). However, most populations of the Western honeybee

affected by the mite nowadays were only exposed to the parasite in the last decades. Hence, the relationship between *A. mellifera* and *V. destructor* is very recent in terms of evolutionary time scales (Oldroyd, 1999). This short period of coevolution may partially explain why the mite is more virulent in its new host (Fries et al., 2001). In addition, as mite reproductive cycles are much more frequent than the generations of its host, adaptations of the parasite may take place more rapidly (Hafner et al., 1994). Yet, many populations of *A. mellifera* have developed adaptations to *Varroa* infestation (Locke, 2015). Interestingly, all of the populations have in common the fact that they are wild or feral. However, not all wild and feral Western honeybee populations show these adaptations to the mite. Some specific traits of these populations probably predisposed them to adapt so rapidly to the parasite (Loftus et al., 2016).

As breeding of resistant honeybee populations is believed to be the most promising and sustainable solution against *Varroa* (Büchler et al., 2010; Rinderer et al., 2010), many studies have focused on analyzing the resistance and tolerance traits in these surviving populations. The results of these studies highlighted the importance of the colony dynamics to decrease the impact of the parasite. Like in *A. cerana*, frequent swarming and absconding may have initially limited the population size and population growth of the mite and therefore its deleterious impact (Loftus et al., 2016). Additionally, the density of colonies being smaller in nature compared to managed apiaries, horizontal transmission may be much reduced in feral and wild *A. mellifera*. This is well illustrated in the African *A. mellifera* subspecies, which generally tend to survive *Varroa* infestation more than the European subspecies (Allsopp, 2006; Ritter, 1993; Rosenkranz, 1999; Strauss et al., 2014). One of these subspecies, *A. mellifera scutellata*, presents an interesting set of characteristics which further enhance its tolerance to parasites, such as high rates of absconding, smaller colony size and faster colony development (Moritz and Jordan, 1992; Schneider et al., 2004). In some *A. mellifera* populations, high mite death and infertility rates are common (Le Conte et al., 2007; Locke and Fries, 2011; Moretto, 2002; Strauss et al., 2016). Interestingly, this

feature may be influenced by the host, as the brood of some subspecies appears to be less attractive to the mite (Frey et al., 2013; Guzmán-novoa et al., 1999) due to different components of the brood cuticle volatiles (Behrens et al., 2011; Lattorff et al., 2015).

Therefore, many mechanisms to hinder the mite's population growth may have been present, or have evolved in the resistant and tolerant honeybee populations. Yet, a common point among these studies is that the variability of the parasite has been neglected. Importantly, the genetic variation found in *V. destructor* (second and third chapters of this thesis; Dynes et al., 2016) is coupled with a significant diversity in the phenotypes of the mite, such as their level of acaricide resistance (González-Cabrera et al., 2016; Milani, 1999) and their ability to mimic cuticular hydrocarbons of their host (Le Conte et al., 2015). The study of *A. mellifera* in the Arnot forest (USA) reflects well the importance of considering the parasite variation as well when looking at honeybee resistance and tolerance (Seeley, 2007). That study revealed that the low impact of *V. destructor* in the honeybee population in Arnot forest may have nothing to do with the host, but could be explained by the lower virulence of the mite infecting these populations (de Guzman and Rinderer, 1999).

3. Interference of beekeeping on *Varroa* and *Apis* interactions

The introduction of *A. mellifera* in Asia is certainly the most extreme and extensive way humans have influenced the relationships between honeybees and their pathogens (Moritz et al., 2005; Mutinelli, 2011). It resulted in numerous parasites and pathogens spill-over besides *Varroa* (Anderson and Trueman, 2000), such as *Tropilaelaps* (Anderson and Morgan, 2007), *Nosema ceranae* (Fries, 2010), multiple viruses (Forsgren et al., 2015; Yañez et al., 2015) and most likely other yet unknown organisms. Today, the impact of *A. mellifera* on the health of Asian honeybees is poorly understood (Chantawannakul et al., 2015; Oldroyd et al., 2009). But as the transportation

of *A. mellifera* into other regions of the globe changed the pathosphere of other pollinators (Fürst et al., 2014; Graystock et al., 2015), its congeneric species may be also greatly affected.

In addition to these effects at the global scale, transhumance is also affecting honeybee health at smaller ranges. This is the case in the USA, where millions of colonies are transported every year all over the country to pollinate different crops. This non-natural migration is not only causing high stress for the honeybees, but may also greatly facilitate the horizontal transmission of *Varroa* and the spread of the mite and other pathogens over the country (Cavigli et al., 2016; Cox-Foster et al., 2007; Dynes et al., 2016). Hence, it is not surprising to see that beekeepers think that this parasite is at least partially implicated (31.7%) in the high colony losses experienced in the USA over the last decades (van Engelsdorp et al., 2008). In addition to that, the movement of managed honeybee colonies in the vicinity of feral or wild resistant populations may result in the rapid loss of natural adaptations (Pirk et al., 2016). Due to the high admixture in the DCAs, adaptations of the feral or wild colonies would rapidly decrease in frequency in the regions such as in Europe where managed honeybees are dominant (Jaffé et al., 2009).

Horizontal transmission of honeybee parasites may also be enhanced by beekeeping practices at the apiary level (Fries et al., 2001). In nature, honeybee colonies are found in low densities because nesting sites such as tree hollows are scattered around the landscape. By keeping many colonies in a reduced area, beekeepers drastically enhance the population densities of honeybees and the interactions between individuals of different colonies, with inevitable consequences on the transmission and the virulence of their parasites (Bull, 1994). A direct effect of these high densities is the common use of feeding sites between the colonies. Honeybees from different colonies may exchange parasites readily as they intensively use common floral resources (Durrer and Schmid-Hempel, 1994; Kevan et al., 1990). In addition, the drifting and robbing of honeybees are greatly enhanced when colonies are placed in high densities (Greatti et al., 1992; Pfeiffer and Crailsheim, 1998). Finally, the movement of combs from one colony to another by

beekeepers (i.e. to strengthen a weak colony) or the use of contaminated material will also greatly facilitate horizontal transmission of parasites and pathogens.

Once transmission has occurred between colonies, it does not take long for a parasite to spread in a nest. The density of individuals being very high in honeybees nests, once a few workers get in contact with a new parasite, the time needed for this organism to spread between individuals and throughout the entire nest is much reduced (Schmid-Hempel, 1998). At this level again, humans may facilitate the transmission of *Varroa*. Beekeepers commonly prevent their colonies from absconding by feeding them extra pollen. This is common in *A. mellifera*, but also in managed *A. cerana* colonies in Asia, where this practice is very popular to restrain the tendency of this species to abscond (personal observations). However, by doing so, beekeepers let the brood accumulate in the colonies, offering great opportunities for *Varroa* populations to build up.

Inversely, beekeeping may also reduce the rate of vertical transmission in *Varroa*. As beekeepers want to optimize honey production they often prevent natural reproductive swarming and purchase queens from professional breeders as they want to keep other traits of their bees (i.e. low aggressiveness). This will tend to homogenize the genetic diversity in their apiaries and may increase the overall susceptibility of their colonies (Schmid-Hempel, 2011; Sherman et al., 1998).

Interestingly, the rate of vertical and horizontal transmission of parasites can also influence their virulence (Bull, 1994; Fries et al., 2001). On the one hand, vertical transmission may select for decreased virulence of parasites, as in that case the successful reproduction of the pest depends on its hosts fitness. On the other hand, if the rate of horizontal transmission is too high, this trade-off may disappear as the costs associated with parasite virulence are lower. In fact, reproduction does not occur naturally in most managed *A. mellifera* colonies in contrast to unmanaged populations of the western honeybee and *A. cerana*. Therefore, transmission is mostly horizontal in managed colonies, which may explain why *V. destructor* is more virulent in *A. mellifera*.

Finally, control strategies also greatly influence the populations of parasites and their effect on hosts. For instance, the use of treatments against *V. destructor* may result in swift selection as documented on the second chapter of this thesis. Even with elaborated strategies involving multiple compound turnovers, the impact of the acaricide residues (e.g. Martel et al., 2007) on the selection of resistance are hard to predict. Furthermore, acaricides can indirectly impact other mite traits. Fitness trade-offs associated with pesticide resistance have been documented in many organisms (Georghiou and Taylor, 1977) but have not yet been thoroughly explored in *Varroa*.

Thus, many more parameters have to be included in order to design efficient control strategies of *V. destructor*. Management of this pest by involving the arms race with its host seems to be the most adapted control strategy in the case of *V. destructor* as it can result in the evolution of a complex set of effective counter-adaptations towards this particularly dynamic parasite.

CONCLUDING REMARKS

As genetic variation greatly influences the outcome of the arms race between hosts and parasites, one may be tempted to think that more diversity gives a better advantage in this type of coevolution. If so, *A. mellifera* would possess a clear lead over its ectoparasite *V. destructor*. As a matter of fact, the results exposed in this thesis confirmed that the populations of *Varroa* possess much lower levels of genetic diversity compared to honeybees which are characterized by extreme intracolony diversity. This is due to polyandry and high gene flow between colonies because of a very effective population admixture in DCAs. However, the successful invasion and spread of the inbred mite around the globe shows that the interactions between *Varroa* and *Apis* are complex and that other features of their biology are involved in the coevolution among these organisms. Among other things, the ability of the mite to mimic the cuticular hydrocarbons of its host to avoid detection (Le Conte et al., 2015; Martin et al., 2001) and of the honeybee to manipulate these signals to detect infected cells (Salvy et al., 2001) illustrate very well the dynamism of the ongoing arms race between *V. destructor* and *A. mellifera*.

So far, most knowledge on the biology of honeybees concerns *A. mellifera* and much less effort has been put in studying the other *Apis* species. Yet, many more studies are needed to fully appreciate the diversity of honeybees in Asia (Hepburn and Radloff, 2011; Oldroyd and Wongsiri, 2006). Among other things, these studies should aim at comparing the genetic structure of other honeybees' DCAs and try to identify the biotic and/or abiotic factors influencing the dispersal behaviour of honeybee drones and queens. In addition, the fact that *A. cerana* and other species of cavity-nesting bees (*A. koschevnikovi*, *A. nuluensis* and *A. nigrocincta*) are found in sympatry in some parts of Southeast Asia and that these species can be either managed or wild provides great opportunities to test for the impact of beekeeping on honeybee health.

Curiously, the genetic structure of *Varroa* populations has started to be explored only recently despite the importance of this parasite for honeybee health and the fact that microsatellite markers were developed over a decade ago (Evans, 2000; Solignac et al., 2003b). Contrary to previous suggestions based on very few individuals per colonies and populations (Solignac et al., 2005), the analyses of the colony level structure presented here show that the levels of genetic diversity in *V. destructor* are considerable and that the population structure of this parasite is very dynamic both in space and time. However, if these findings may be reflected in mites infecting *A. mellifera* in temperate climate, it is important to keep in mind that these observations may not apply to all *Varroa* species and populations. Notably, the dynamics of *V. destructor* populations are also greatly influenced by the climate, natural flowering resources and density of colonies (Giacobino et al., 2016; Leza et al., 2016). Comparing the spatio-temporal evolution of the genetic structure of mites from diverse locations reflecting these biotic and abiotic factors would greatly help optimising control strategies of the mite by adapting these strategies to their environment.

In addition, the interactions between *Apis* and *Varroa* will inevitably influence the dynamics of their populations. To date, not much is known on the interactions between these genera in Asia. For the conservation of honeybees, it is reassuring to see that *Varroa* is not able to spill-back to *A. cerana* in Vietnam and the Philippines, although this may not be the case in other locations. Interestingly, a study showed that in Thailand -where different haplotypes of the host and species of parasite live in sympatry- the Mainland host lineage is infected by several mite species but not the Sundaland type (Warritt et al., 2006). These different host lineages may exhibit different resistance traits against the mite. Therefore, further work on the co-phylogeny of these species is also needed to determine patterns of association between the different hosts and parasites in Asia.

Finally, many other organisms parasitize Asian honeybees, some of which have not been thoroughly studied yet (Chantawannakul et al., 2015). As *A. mellifera* beekeeping is rapidly expanding in Asia (Moritz et al., 2005; Moritz and Erler, 2016; Pirk et al., 2016), new spill-overs

could lead to very rapid global spread of these pests as in the case of *V. destructor* (Muñoz, 2008; Wilfert et al., 2016). Inversely, the spread of non-native mites via the transportation of *A. mellifera* between different regions of Asia could additionally threaten the Asian honeybees. In addition, the impact of other organisms such as viruses (McMahon et al., 2016; Wilfert et al., 2016) and the effect of the environment (Costa et al., 2012; De Jong et al., 1984; Giacobino et al., 2016; Leza et al., 2016) are likely to play important roles in the interactions between *Apis* and *Varroa*. Despite the fact that wild honeybee populations may quickly adapt to invasive *Varroa* haplotypes, the transfer of non-native viruses facilitated by this vector could change the outcome of the arms race (Di Prisco et al., 2016; Manley et al., 2015; Wilfert et al., 2016). Understanding how these different organisms interact represents a new challenging question in the fascinating disciplines of host-parasite coevolution and honeybee research.

SUMMARY

Honeybees (genus *Apis*) and humans have been interacting for millennia. These interactions have intensified over time and the development of beekeeping. Nowadays, the most extensive impact of beekeeping on honeybee populations is certainly the transportation of colonies of the western honeybee, *Apis mellifera*. Because of honey and bee product business, this species has been introduced to most regions of the world, among which South-East Asia. After being transported there, *A. mellifera* came in contact with other *Apis* species, together with many new parasites and pathogens. Among these, the ectoparasitic mite *Varroa destructor* managed to switch from *Apis cerana*, its original host, to the introduced western honeybee. Today, the parasite has spread to most parts of the globe and most colonies of *A. mellifera* cannot survive without beekeeping management practice such as acaricide treatments. Thus, beekeeping influence on this host-parasite system is not limited to dispersal of the honeybees. Consequently, understanding how human management practices impact the interactions between *Apis* and *Varroa* is crucial to develop efficient management strategies of the mite.

The aim of my PhD was to investigate the population structure and genetic diversity of different populations and species of honeybees and *Varroa* in order to understand their dynamics and infer how beekeeping can disrupt the interactions between these organisms. To do so, I used molecular tools to analyse how these populations and species disperse and reproduce. I first studied a wild honeybee species, *Apis dorsata*, in order to understand how diverse and dynamic *Apis* species are without human interference. I then looked at the dynamic of *V. destructor*, and more specifically how the mite population structure evolves in space and time. In the third and last part of this thesis, I investigated the factors shaping the population

structure of different mite populations by comparing the dispersal and hybridisation potential of *Varroa* between hosts and populations in Asia.

Altogether, my results show that wild *Apis* population are very dynamic and that reproduction contributes greatly to the admixture of their populations. The second part of this thesis revealed that *V. destructor* is more diverse than previously claimed and its populations very dynamic. In this parasite species, inbreeding and recombination fluctuate over time according to the availability of its host brood. The third chapter of this work highlighted great differences in the host specificity between haplogroups and species of *Varroa*. Although mites from *A. cerana* and *A. mellifera* did never switch hosts in northern Vietnam, we found that a potential new species found in Luzon, the Philippines, is able to infect both hosts.

With these findings and the available literature, I discussed how beekeeping may change the dynamic of *Apis* and *Varroa* population and disrupt their natural host-parasite interactions. Evidences of *A. mellifera* populations surviving infestation with *Varroa* have gotten more and more numerous in the last years. A common point between these populations is that beekeeping influence was very limited, or even non-existent, permitting natural adaptations against the parasite to evolve and spread. As an alternative to chemical treatment, these natural adaptations may be used for selective breeding and could help limiting the impact of the pest on colonies of *A. mellifera*. However, if the biology of *Varroa* and *Apis* are not taken into account in future control strategies, mites counter-adaptations may develop and spread very quickly. In addition, new mite populations will likely switch host in Asia as *A. mellifera* beekeeping keeps developing in that part of the globe. Thus, all breeding efforts will be futile if the biology of the host and the parasite are not taken into account. Therefore, the work summarized in this thesis can provide knowledge to help designing new control strategies that are more sustainable and help preventing new host switches of the parasite in South-East Asia.

ZUSAMMENFASSUNG

Die Honigbiene (*Apis*) und der Mensch interagieren miteinander seit Jahrtausenden. Diese Wechselbeziehung nahm im Laufe der Zeit immer mehr zu und das Imkern entstand. Der größte Einfluss des Menschen heute, ist die Verbreitung der westlichen Honigbiene *Apis mellifera* in alle Welt. Da Honig und Bienenprodukte überall beliebt sind, wurde diese domestizierte Art in fast allen Teilen der Welt eingeführt, so auch in Süd-Ost Asien. Nach ihrer Ankunft kam sie dort mit den einheimischen Bienenarten, sowie deren Parasiten und Pathogenen, in Kontakt. *Varroa destructor*, einem Ektoparasit, gelang es schlussendlich von *Apis cerana*, seinem ursprünglichen Wirt zur eingeführten westlichen Honigbiene zu wechseln. Inzwischen hat sich der Parasit auf der ganzen Welt ausgebreitet und die meisten *A. mellifera* Kolonien können nicht mehr ohne imkerische Maßnahmen, wie den Einsatz von Akariziden, überleben.

Deshalb ist der Einfluss des Menschen auf das Wirts-Parasiten System heute nicht mehr nur auf die Verbreitung der Honigbiene beschränkt. So ist es ausschlaggebend zu verstehen in welchem Maße sich das Imkern auf die Interaktionen zwischen *Apis* und *Varroa* auswirkt, um effektive Strategien zur Bekämpfung der Milbe zu entwickeln.

Das Ziel meiner Doktorarbeit war es die Populationsstruktur und genetische Diversität verschiedener Populationen und Arten von Honigbienen und *Varroa* zu untersuchen, um die Wechselwirkungen zwischen diesen Organismen besser zu verstehen und herauszufinden wie der Mensch am effektivsten in dieses System eingreifen kann. Um das zu erreichen verwendete ich molekulare Werkzeuge um zu analysieren wie sich Populationen und Arten beider Organismen verbreiten und vermehren. Zuerst untersuchte ich die wilde Honigbienen Art *Apis dorsata*, um zu verstehen wie divers und dynamisch *Apis* Arten ohne menschlichen Einfluss sind.

Dann sah ich mir die Dynamik von *V. destructor* an und wie die Populationsstruktur der Milbe sich über Zeit und Raum verändert. Im dritten und letzten Teil meiner Arbeit untersuchte ich welche Faktoren die Populationsstruktur von verschiedenen Milbenpopulationen

beeinflussten, indem ich das Verbreitungs- und Hybridisierungspotential von *Varroa* zwischen verschiedenen Wirten und Wirtspopulationen in Asien verglich.

Meine Ergebnisse zeigen, dass wilde *Apis* Populationen sehr dynamisch sind und die Reproduktion einen wichtigen Teil zur Diversität in den Populationen beiträgt. Der zweite Teil dieser Arbeit zeigte, dass *V. destructor* diverser ist als bisher angenommen und die Populationen sehr dynamisch sind. Inzucht und Rekombinationen fluktuieren in diesem Parasit über die Zeit, abhängig von der Verfügbarkeit der Wirtsbrut. Das dritte Kapitel zeigte große Unterschiede in der Wirtsspezifität von Haplogruppen und Arten von *Varroa* auf. Obwohl Milben von *A. cerana* und *A. mellifera* in Nordvietnam nie den Wirt wechselten, fanden wir eine potentielle neuer Art in Luzon, auf den Philippinen, die in der Lage ist beide Wirte zu infizieren.

Ich diskutierte meine Ergebnisse auf Basis der momentan vorhandenen Literatur, um aufzuzeigen wie imkern die Dynamik zwischen *Apis* und *Varroa* Populationen beeinflussen könnte. Es gibt zunehmend Hinweise auf *A. mellifera* Populationen, die den Befall durch *Varroa* überleben. Eine Gemeinsamkeit zwischen diesen Populationen ist, dass der menschliche Einfluss so gering wie möglich oder sogar gar nicht vorhanden war und so natürliche Anpassungen gegen den Parasiten entstehen und verbreitet werden konnten.

Diese natürlichen Anpassungen könnten eine Alternative zur chemischen Behandlung darstellen, für selektive Züchtung genutzt werden und so den Einfluss des Schädlings auf die Kolonien von *A. mellifera* minimieren. Wenn jedoch in zukünftigen Strategien die Biologie von *Varroa* und *Apis* nicht berücksichtigt wird könnte die Milbe sich den Resistenzen in den neuen Kolonien anpassen und weiterhin *A. mellifera* Kolonien weltweit bedrohen. Es ist außerdem wahrscheinlich, dass neue Milbenarten den Wirtswechsel zu *A. mellifera* in Asien vollziehen, wenn deren Haltung dort weiterhin zunimmt. Alle Züchtungsbemühungen könnten zunichte gemacht werden, wenn diese Punkte nicht berücksichtigt werden. Die Ergebnisse dieser Arbeit

sollen deshalb helfen neue nachhaltige Kontrollstrategien zu entwickeln um zu verhindern, dass es zu weitere Wirtswechsel des Parasiten in Süd-Ost Asien kommt.

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APPENDIX A - Eidesstattliche Erklärung

Halle, den 29-09-2016

Hiermit erkläre ich an Eides statt, dass diese Arbeit von mir bisher weder bei der Naturwissenschaftlichen Fakultät I – Biowissenschaften – der Martin-Luther-Universität Halle-Wittenberg, noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion eingereicht wurde.

Ich erkläre, dass ich mich bisher noch nicht um den Doktorgrad beworben habe. Ferner erkläre ich, dass ich diese Arbeit selbstständig und nur unter Zuhilfenahme der angegebenen Quellen und Hilfsmittel angefertigt habe. Die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen sind als solche kenntlich gemacht worden.

Alexis Beaurepaire

APPENDIX B - CURRICULUM VITAE

M.Sc. Alexis BEAUREPAIRE

Molecular Ecology Research group
Martin-Luther University Halle-Wittenberg
Room 125b, Hoher Weg 4
06108 Halle (Saale)
Tel: +49-(0)1573-6900685
alexis.beaurepaire@zoologie.uni-halle.de

PERSONAL INFORMATION

Birthdate 4 July 1988
Birth location Roubaix, Nord-Pas-de-Calais, France
Nationality French

EDUCATION

12. 11 –Currently **PhD candidate** - Martin-Luther Universität Halle-Wittenberg, Molecular Ecology Research Group. Supervised by Prof. Robin F.A. Moritz
Research Project: “Coevolution between *Varroa destructor* and its honeybee hosts”

2010-2011 **MSc (2nd year) Biology of Organisms and Populations**
Université de Bourgogne, Dijon, France

2009-2010 **MSc (1st year) Biodiversity of Aquatic and Continental Ecosystems**
Université des Sciences et Technologies de Lille, Lille, France

2008-2009 **BSc Biology of organisms and populations – ERASMUS**
University of Oulu, Oulu, Finland

2006-2008 **BSc Biology of organisms and populations**
Université des sciences et technologies de Lille, Lille, France

INTERNSHIPS AND WORKSHOPS

February 2012 Workshop in “Honey bee genetics” in the University of Murcia (Spain), organised by Dr. Pilar De la Rúa

01. 11 – 06. 11 Training - Université de Bourgogne supervised by Pr. Thierry Rigaud
Research Project: “Diversity and genetic structure of an acanthocephalan parasite, *Pomphorynchus laevis*”

03. 10 – 06. 10 Training - Université de Lille 1 supervised by Dr. Fabrice Roux
Research Project: “Genetic basis of an adaptative trait: study of the life history traits of *Arabidopsis thaliana*”

SCIENTIFIC AWARDS

- December 2014** Anne Keymer Student Talk Prize (highly commended) at the BES-SFE meeting in Lille, France
- September 2014** DAAD conference grant for the Sixth Eurbee Congress in Murcia, Spain

CONFERENCE PRESENTATIONS (PARTIAL LIST)

September 2016

- December 2014** “Extensive Population Admixture at Drone Congregation Areas of the giant honey bee, *Apis dorsata*”, Oral participation at the BES and SFE meeting in Lille, France
- October 2014** “Impact of the introduction of the Western honey bee, *Apis mellifera* on the native Asian honey bees”, lecture at the Higrade course, *Helmholtz Zentrum Für Umweltforschung, Halle, Germany*
- September 2014** “Genetic diversity of the *Varroa* mite in Northern Vietnam”, Oral participations at the Sixth EurBee Congress, Murcia, Spain
- March 2012** “Impacts of intensive land-use systems on the populations of Asian honey bees”, Poster at the Bienentagung, Bonn, Germany

ADDITIONAL SKILLS

- Spoken Languages**
- | | |
|---------|----------------|
| French | Mother tongue |
| English | Advanced level |
| Spanish | Medium level |
| German | Beginner level |
- Computer programs** MS Office, R, InkScape, MEGA, Network, DnaSP, BioEdit, Fstat, Genepop, Arlequin, Structure, Distruct, MSA, MS-Toolkit, ADEGENET, Geneious, CLC Genomic workbench...
- Reviewing activities** Apidologie, Entomologica, Journal of Apicultural Research, Scientific Report

TEACHING, MENTORING

- Summer courses** Computer courses – Population Genetics software
- Student trainings** Supervision of Bachelor students and Master students