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Insects: The Disregarded Domestication Histories

Thomas Lecocq

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Abstract

Domestication has irrevocably impacted human evolution. The domestication process/pathways have been the focus of abundant research for plants and vertebrates. Advances in genetics and archeology have allowed tremendous progresses in the understanding of domestication for these organisms. In contrast, insects' domestication has comparatively received far less attention to date. Yet, insects are the most common animal group on Earth and provide many valuable ecosystem services to humans. Therefore, the aims of this chapter are (i) to provide an overview of main ancient and recent insect domestication histories and (ii) to reread them by the light of the domestication process, pathways, triggers, and consequences observed in other animal species. Some of the considered species (i.e., silkworm and honey bee) have been chosen because they are among the few insects commonly acknowledged as domesticated, while others allow illustrating alternative domestication patterns. The overview of current literature shows similar human-directed pathway and domestication syndrome (e.g., increased tameness, decreased aggressiveness, modified reproduction) between several insect species.

Keywords: domestication level, domestication pathways, domestication syndrome, insect species

1. Introduction

Domestication is one of the most important developments in human history [1]. Beginning during the Late Pleistocene with dog domestication [2, 3], it has irrevocably impacted human history, demography, and evolution leading to our current civilizations [1, 4–6]. Domesticated species play important roles for humans in many aspects of our daily life by providing food, biological control agents, pets, sporting animals, basic materials, and laboratory models [1, 7, 8]. This considerable importance in our culture, survival, and way of life has always aroused the

curiosity of scientists and nonscientists. An extraction from the database Scopus of articles and reviews published since 1960 in Life Science Area (i.e., agricultural and biological sciences; biochemistry, genetics and molecular biology; environmental science; multidisciplinary) for which the term “domestication” is cited in the title, the abstract, or the keywords inventories 6199 documents (database accessed on August 31, 2018). However, despite this profusion of literature, significant questions regarding the domestication process, the domesticated species notion, or the domestication histories still remain [9–11].

The notions of domesticated species and domestication process are among the most confusing and controversial concepts in biology [12–14]. Vivid debates are continually fuelled by clashes of conflicting, although complementary, visions of botanists, mammalogists, ornithologists, ichthyologists, archeologists, geneticists, and sociologists. The achievement of a consensual view is impeded by the complexity of the domestication phenomenon, which involves many phylogenetically distant species and occurs in several different social and cultural contexts [1]. Nevertheless, there were some attempts to unify the alternative points of view to some extent [1, 12, 13, 15–17]. For the purpose of this chapter, domestication can, thereby, be considered as the process in which populations are bred in man-controlled environment and modified across succeeding generations from their wild ancestors in ways making them more useful to humans who control, increasingly during the process, their reproduction and food supply [1, 12, 15–17]. This process does not involve all populations of a particular species: some populations can undergo domestication, while other populations do not. The domestication process is a continuum that can be divided into five key steps (the so-called “domestication levels”) based on the degree of human control over the population life cycle and the degree of gene flow from wild counterparts [12]. This classification had been primarily developed for fish species [12, 18] but can be extended to other species (**Figure 1**). At the early stage (level 1) of the domestication process, the first attempts of acclimatization of a wild population to man-controlled environments are made [12]. These environments can be captive or “ranch” conditions quite isolated from wild populations where living conditions, diet, and food are controlled by humans [19]. The next stages correspond to an increasing control of the life cycle by humans: level 2—a part of life cycle is controlled by humans in man-controlled environments, but “seed” materials are collected in the wild to maintain rearing of the species (i.e., capture-based production; e.g., [20]); level 3—the life cycle is fully controlled by humans in man-controlled environments, but significant gene flow from the wild still occurs due to spontaneous introgressions or intentional wild specimen introductions by breeders [21]; level 4—the life cycle is fully controlled by humans in man-controlled environments without wild inputs [12]. The last stage (level 5) corresponds to the development of selective breeding programs or organism engineering to intentionally modify some traits of the human-controlled populations (e.g., [22–24]). Seen from this perspective, a species can be considered as domesticated when it reaches, along this continuum, a threshold arbitrarily defined according to a particular scientific or legislative context. The resulting subjective definition of domesticated species is thus eluded from this chapter.

The domestication process is set during a temporal succession of interactions between a species and humans: the so-called “domestication pathways” [10, 25]. An overview of published domestication histories allows identifying three main pathways [10, 15, 25, 26]. In the commensal pathway, there is no intentional action on the part of humans but, as people manipulated their



Figure 1. Domestication process and insect domestication level. Numbers 0–5 refer to the domestication levels [12, 18]. Characteristics of each domestication level are provided on the left. Lines and points near the insect species names show the range of domestication degrees observed among populations of the species.

immediate surroundings, some populations of wild species have been attracted to elements of the human niche. The tamer, less aggressive individuals with shorter fight or flight distances of a wild species establish a profitable commensal relationship with humans. Later, succeeding generations of such individuals shift from cynanthropy to domestication through captivity setting up and human-controlled breeding. The dog and the cat are the archetypal commensal pathway species [10]. Contrary to the former, the prey pathway begins with human actions, but the primary human motive is not to domesticate but to increase food resources. Actually, it is initiated when humans modify their hunting strategies into game-management strategies to increase prey availability, perhaps as a response to localized pressure on the supply of prey. Over time and with the more responsive populations (e.g., the more docile individuals), these game-management/keeping strategies turn into herd-management strategies based on

a sustained multigenerational control over movements, feeding, and reproduction of populations corresponding to a domestication process. Species that have followed this prey pathway are, for instance, large terrestrial herbivorous mammals [26]. At last, the directed pathway is the only one that begins with a deliberate and directed process initiated by humans in order to domesticate populations of a wild species [26]. Most modern domestic species such as pets [27], transport animals [10], and aquatic species [12, 28] have arisen because of this pathway [10]. The three pathways are theoretical conceptualizations of domestication process, but many species have a more complex history involving several pathways (e.g., pigs [10, 25, 29]).

When the domestication process begins, it results in long-term genetic differentiation and, finally, in the evolution of distinct changes in phenotypic traits [16, 30]. The differentiation of populations undergoing a domestication process can be initiated early in their domestication history and despite persistent gene flow from wild populations [21, 31–34]. The resulting specific morphology, physiology, and behavior constitute the “domestication syndrome” that tends to be more or less similar among different species of a particular organism group [35–40]. Overall, these specificities include domestication traits (i.e., facilitating the early stage of domestication) and improvement traits (i.e., appearing at latter stages of domestication) [35]. The first are shared by all domesticates and generally fixed during the first stages of domestication, while the latter are observed in some domesticated populations when higher human impacts on breeding happens [10]. These changes are driven by (i) selection pressures created by both unintentional and deliberate human actions as well as by human-modified environments and/or by (ii) a relaxation of the selection occurring in the wild [10, 41, 42].

The domestication process, pathways, and consequences on plants (e.g., [1, 37, 43]), mammals (e.g., [1, 10, 26]), birds (e.g., [44, 45]), and fishes (e.g., [12, 28]) have been the focus of an abundant research from Darwin’s works [46]. However, insects’ domestication has comparatively received far less attention to date [47]. Yet, insects are the most common animal group on Earth: they make up about 75% of all animal species [48, 49]. They play an important role in pollination, waste bioconversion, biocontrol, raw material supplying, food production, medical application, and human cultures. Strangely, major reviews on domestication give the impression that so few have been domesticated [10, 11, 15, 25, 26]. An overview of current literature shows how insect domestication has been overlooked: the database Scopus inventories only 68 papers that focus on it and most of them on only two species (i.e., the silkworm and the honey bee). Actually, most insect rearing/breeding/farming histories have not been considered as domestication processes although they can be interpreted as such. Therefore, the aims of this chapter are (i) to provide an overview of main ancient and recent insect domestication histories and (ii) to reread them by the light of the domestication process, pathways, triggers, and consequences observed in other animal species. Some of the considered species (silkworm and honey bee) have been chosen because they are among the few insects commonly acknowledged as domesticated species, while others have been considered since they allow illustrating alternative domestication patterns.

2. The silkworm and the sericulture

Silkworm is the caterpillar of the moth *Bombyx mori* (Lepidoptera, Bombycidae). It is one of the most important insects in human economy because the species is the primary producer of silk

[50, 51]. Although silk has a tiny percentage of the global textile fiber market (i.e., less than 0.2%; the yearly worldwide production is about 200,000 metric tons of silk [51]), the annual turnover of the China National Silk Import and Export Corporation alone is more than 2 billion US\$ [19, 51]. Moreover, silk production provides employments to several million persons in rural and semirural areas across the world [19] (e.g., 8 millions in India [51]). Beside its economic importance, *B. mori* is an edible insect [19], a health food [19], a pet [19], and model species for basic research because of its short life cycle and adaptation to laboratory culture [52–55].

2.1. *Bombyx mori* life cycle and production

The silkworm life cycle is strongly controlled by humans in indoor facilities with controlled environmental conditions [51]. New eggs are incubated in rearing facilities where their hatching can be scheduled and synchronized by humans through chemical treatments and photothermal controls (e.g., black boxing practices) [51]. The newly hatched caterpillars are transferred to rearing tray (i.e., brushing process) and fed by humans with man-produced plants (e.g., mulberry leaves) [51]. After several molts, caterpillars climb on man-provided supports and spin their silken cocoons. Then, cocoons are collected and *B. mori* specimens are killed before metamorphosis since proteolytic enzymes released to make a hole in the cocoon by the adults are destructive to the silk [51]. Some cocoons are allowed to survive in order to produce adults for breeding [51]. In contrast to closely related wild moth species (e.g., *B. mandarina*) that fly for reproduction or evasion from predators, *B. mori* adults are not capable of functional flight due to their too big/heavy body and their small wings [51]. Therefore, *B. mori* completely relies on human assistance in finding a mate and a laying support [51]. The *B. mori* oviposition site selection is also controlled by humans (i.e., egg laying occurs on man-offered mulberry plant or on filter paper) [51, 56].

2.2. Domestication history and pathway of *Bombyx mori*

Bombyx mori is one of the few insects commonly acknowledged as truly domesticated and as a stunning case in point of insect domestication [47, 52, 57, 58]. Several archeological and molecular studies have tried to trace the history of its domestication (e.g., [57, 59–62]). The silkworm was domesticated roughly 7500 years ago from Chinese populations of *B. mandarina*, an extant wild silk moth of East Asia [57, 59, 60, 63]. The domestication of the silkworm is thought to be a directed pathway [10] starting at a single event [61]. Long-term bidirectional significant gene flow occurred between wild and domesticated silkworm populations during the first 3500 years of the domestication [59] most likely because of accidental escapes and intentional hybridizations by breeders to produce desirable strains [52, 59, 64]. Nowadays, low gene flow presumably still exists with *B. mandarina* [65].

Even though silk spread rapidly across Eurasia, its production remained exclusively Chinese for several millennia [62, 66]. Indeed, the sericulture (i.e., the raising silkworms for silk production) spread only to Korea and Japan around 2000 years ago [57, 60] and was even later introduced to Central Asia and Europe (i.e., the Byzantines acquired the sericulture methods by 522 CE) through the Silk Road [57, 66]. This silkworm production expansion is one of the most tremendous examples of the direct and indirect consequences of the animal domestication on the human history [57]. Indeed, the opening of Silk Road has dramatically impacted

human history by triggering cultural/technical/good exchanges as well as population movements and disease spread out (e.g., bubonic plague) between Eurasian civilizations while its closing forced the merchants to take to the sea to ply their trade triggering the Age of Discovery [51, 66]. The industrial revolution and the increasing demand in Europe led to a peak of the sericulture by the eighteenth and nineteenth centuries before declining due to silkworm disease breakouts and the raising of cotton industry [51].

2.3. Consequences and progress of the domestication process in *Bombyx mori*

Bombyx mori displays significant specificities compared to its phylogenetically nearest wild counterpart [67–71]. Some of these traits can be considered as (i) domestication traits reinforced by or (ii) improvement traits fostered by selective pressures shaped by unintentional/deliberate human actions and human-modified environments: an increased cocoon size, larger body size, higher silk production, higher growth rate, larger tolerance to human presence/handling, higher ability to live in crowded conditions, and a better feed efficiency [51, 52, 57]. Conversely, other specificities could be explained by a relaxation of the selection occurring in the wild (e.g., predation pressure): leucism (meaning the loss of camouflage) and disability to fly [51, 68]. These last changes have made *B. mori* entirely dependent upon humans for survival, feeding, and reproduction [51, 52]. Moreover, independent selective breeding programs and different breeding environments (i.e., from temperate to tropical climate) have led to the development of more than 1000 inbred lines or strains of domesticated silkworms across the world [51, 57, 60, 72]. Since *B. mori* (i) has its life cycle fully controlled by humans in captivity, (ii) is entirely dependent on humans for reproduction, (ii) and undergoes selective breeding and genetic improvement to harvest maximum output, they are one of the few insect species at a very advanced domestication stage (Level 5; **Figure 1**). While they are not as extreme as the *B. mori* case, other moth species used for silk production have their life cycle under human control and dependence such as *Samia cynthia* (i.e., ericulture; see [73, 74]).

3. The honey bees: beekeeping or apiculture?

Honey bees are eusocial insect species distinguished by their production and storage of honey and their construction of colonial nests from wax [75]. They belong to the same genus (Hymenoptera, Apidae, *Apis* spp.) that includes 11 species and many subspecies native from the Old World [75, 76]. The dwarf honey bees (*A. florea* and *A. andreniformis*) are small species from southern and southeastern Asia that make small open nests in trees and shrubs [75, 77, 78]. These species produce honey that is harvested and eaten by local human populations [77, 79]. The giant honey bees (*A. binghami*, *A. breviligula*, *A. dorsata*, and *A. laboriosa*) are aggressive species inhabiting forest areas of South and Southeast Asia [80–82]. They produce honey and wax in their open nest on trees, cliffs, or buildings that are harvested by indigenous people [83–85]. *Apis koschevnikovi* and *A. nuluensis* are cavity-nesting species that occur in the tropical evergreen forests of Borneo [86, 87]. *Apis nigrocincta* is a cavity-nesting species reported in Sulawesi [75]. The western honey bee (*A. mellifera*) and the eastern honey bee (*A. cerana*) are cavity-nesting species native throughout (i) Africa, the Middle East, and Europe and (ii) South and Southeast Asia, respectively [75]. All *Apis* species are important pollinators for many ecosystems [88].

Although other species like *A. dorsata* or *A. cerana* can be important for human economy and feeding in certain countries, none achieves the crucial economic, agricultural, scientific, and environmental importance of *A. mellifera* [89–91]. Its importance relies on its pollination activity as well as on its production of honey, wax, venom, pollen pellets, propolis, and royal jelly [92].

3.1. *Apis mellifera* life cycle and production

Unlike most of other bee species, honey bees produce perennial colonies with large number of individuals that (i) belong to different castes (i.e., workers that are sterile females, drones that are males, and queen that is the reproductive female) and (ii) are not able to survive by themselves for extended periods [75]. In the nest, there is a labor division between castes: (i) the workers harvest pollen and nectar on flowers to feed larvae, queen, and other workers as well as to store food as honey [89, 93] and protect the nest from predators and (ii) queen ensures the production of new queens, drones, and workers [75]. The colony is considered as a superorganism since it is a collection of agents, which can act in concert to produce phenomena (e.g., colony exhibit homeostasis and emergent behavior) governed by the collective [94]. When environmental conditions are favorable (i.e., abundance of food), new queens are produced while old queen with up to two-thirds of the workers leaves the nest in a swarm to find a new location to establish a new nest [89]. In the old nest, new queens compete until only one remains and the survivor takes the nest control [89]. Then, the new queen goes on one or more nuptial flights and mates with several drones [95]. Once mating is done, the queen remains in the hive and lays eggs [89]. The swarming behavior and the takeover of the old nest by the new queen can be interpreted as the reproduction of the superorganism.

Humans can control the life cycle of the superorganism by providing man-made hives for the colony to live and store food [89]. This allows humans to easily collect honey and other products that hive produces rather than to scavenge these products in the wild. More advanced practices allow apiarists to control colony reproduction by restricting swarming behavior and controlling mating by artificial insemination [96, 97].

3.2. Domestication history, traits, and pathway of *Apis mellifera*

Molecular dating suggests that *A. mellifera* expanded its distribution around 1 million years ago [98, 99] from a still debated ancestral range [76, 90, 98–102]. During its range expansion, the western honey bee experienced local adaptations [103] and geographic differentiations leading to the current substantial phenotypic variation across its extensive geographic range [101]. This intraspecific variability has been used to develop an extensive classification of 29 subspecies (or “races”) [76]. These taxa are now lumped into four major groups based on morphological, genetical, ecological, physiological, and behavioral traits: the African, Western/Northern European, Eastern European, and Middle East populations (review in [100]). The European groups exhibit phenotypic adaptations to survive colder winters, whereas the African group is more aggressive and shows a greater tendency to swarm [101].

Humans began harvesting wax and honey from honey bee colonies at least 9000 years ago [104, 105]. They originally scavenged these products from wild nests [89, 104, 105]. However, the demand for honey outgrew its natural availability as human populations became larger and

sedentary [106]. This context presumably triggered the beekeeping development by providing hives to honey bees that make it easier to harvest their honey and wax by humans [105]. At the beginnings of beekeeping, honey bees were not “bred” so much as “kept”: humans provided rudimentary containers (often destroyed during honey harvesting) and hoped that wild bee colonies would take up residence without later swarming [105]. Over time, humans increased their control on bees by developing swarming control device (i.e., queen excluder [96]), reproduction control (e.g., artificial insemination [97]), mass breeding (e.g., [107]), selective breeding programs (e.g., [108–110]), and new strains (e.g., Buckfast strain [111] or Africanized honey bees [112]).

The honey bees’ domestication concerns only *A. mellifera* and *A. cerana* (see details about the later species in [89]) most likely because they display intrinsic features that facilitated the domestication process: (i) cavity-nesting habit making hives suitable for these species, (ii) hygienic behavior (i.e., detection and removal of diseased brood and wastes) limiting diseases, and (iii) adaptations to tropical and temperate climate facilitating the apiculture development across the world [89, 110], for example, *A. mellifera*. Moreover, differentiations in traits facilitating beekeeping are observed at the subspecies level. Subsequently, some particular subspecies were preferably domesticated by humans. For instance, non-African subspecies have been more widely used by most beekeepers since they can survive in temperate regions, have a low tendency to swarm, and low aggressiveness [101].

Domestication history of honey bees has been investigated through molecular datasets that highlight several domestication events followed by introgression between subspecies [90, 113, 114]. Although the honey bee domestication history has been regarded as a directed pathway [10], the evolution from early beekeeping practices to modern apiculture practices can be seen as similar to the prey pathway in which game-keeping strategies turns into control over movements, feeding, and reproduction. However, it is likely than directed and prey pathways occurred during honey bee domestication history since several domestication events happened [90, 113, 114].

3.3. Is *Apis mellifera* domesticated?

Many authors acknowledge (often without justification) the domesticated status of *A. mellifera* (e.g., [10, 16, 47, 58, 89, 102, 115–117]). In contrast, *A. mellifera* has been considered as never properly domesticated but only as managed species by other authors (e.g., [110, 114]; however, some of these scientists acknowledge an ongoing domestication process) because (i) their biology, physiology, and behavior are seen as largely unchanged from their wild counterparts [114], (ii) honey bees are able to survive without human’s help [118], (iii) there is extensive gene flow between wild/feral and managed bees in native range due to the difficulties to achieve controlled mating [119]. However, these points should be reconsidered. First, the comparison of phenotypes between “wild” and “nonwild” populations is difficult in a large part of the species range. Indeed, colonies that are found in the wild may have escaped from a managed colony, and therefore, they may not be wild [120]. In Europe, it is unlikely that there are any truly wild subpopulations left due to this gene flow [120]. This means that the differentiation fostered by the domestication process can be blurred by the large amount of feral populations in the wild. Nevertheless, there are significant behavioral changes observed in man-controlled honey bees stocks such as multiple queen colonies (i.e., colonies conserved several queens without

deadly competition between them [121]), decreased aggressiveness, higher honey production, increased foraging zeal, and disinclination to swarm of some strains [111]. These specificities can be interpreted as improvement traits within a domestication syndrome. Second, many other species acknowledged as “domesticated” can survive in the wild (e.g., feral populations of rabbits, cats, and dogs [122]; although fast initial decline in fitness of domesticated escapees in the wild is expected [123]). Moreover, the ability of honey bees to survive in the wild could be overestimated since most *A. mellifera* are not considered to be self-sustaining as veterinary treatments against the mite *Varroa destructor* among other parasites is often provided [120]. Third, gene flow between “nonwild” and wild populations is commonly observed during the domestication process (see [21, 124, 125]). Actually, the debate about the status of domesticated animal for *A. mellifera* exemplifies the subjectivity of the domestic species threshold. Beside this controversial definition, *A. mellifera* shows that different conspecific populations can be at different stages of the domestication process. Indeed, there is no control by humans over the life cycle of wild populations that are commonly observed for the African group [126–128]. In contrast, many populations belonging to the European groups have a life cycle completed in man-made environment (i.e., hives) and controlled by humans (i.e., control of superorganism reproduction), feed on domesticated crops (i.e., humans can actively control the honey bee food supply for honey production or crop pollination) and/or on artificial food provided by humans (i.e., sugar syrup) [129], and some of them undergo selective breeding programs [108–111]. Therefore, the domestication levels of *A. mellifera* range from 0 to 5 according to the population considered.

4. The bumble bees and the stingless bees: the other bee domestications

About 90% of world’s plant species are pollinated by animals [130–132], and the main animal pollinators in most ecosystems are bees [88]. Although other taxa like butterflies, flies, beetles, wasps, or vertebrates can be important pollinators in certain habitats or for particular plants [133, 134], none achieves the numerical dominance as flower visitors worldwide as bees [130, 131]. The pollination efficiency of bees has been used by humans to improve their crop yields. The western honey bees is the most commonly used species in managed pollination service [76, 135]. This species pollinates nearly half of the top 115 global food commodities and is capable of increasing the yields of 96% of animal-pollinated crops [117, 136]. However, the lack of sufficient stocks of honey bees to ensure pollination service [115, 137], the aggressiveness of Africanized honey bees (i.e., obtained by man-made hybridization between African and European subspecies of *A. mellifera* to breed a strain of bees that would produce more honey and be better adapted to tropical conditions) in Neotropics [138], and the poor pollination efficiency of *A. mellifera* for some plants, as well as the requirement of maintaining the honey bee colonies outside the flowering period of valuable crops [139] have triggered or restarted the domestication of other bee species: the bumble bees and the stingless bees.

4.1. The bumble bees

Bumble bees (Hymenoptera, Apidae, *Bombus* spp.) are social insects with a nearly worldwide distribution with their largest species diversity in temperate and cold areas [75, 140]. Except in

tropical regions, bumble bees produce annual colonies (i.e., colony dies after the production of new queens and males). They have several adaptations such as their ability to “buzz pollinate” (i.e., sonication) and their insulated bodies that make them ideal pollinators for many valuable crops (e.g., raspberry and tomatoes) for which honey bees are quite inefficient pollinators [139–141]. Moreover, bumble bee colonies can be easily shipped and can be maintained without specialists’ help in crops fields [139]. However, they do not produce honey or hive material suitable for mass market sales [117]. Therefore, their commercial importance is only based on their pollination efficiency on particular crops, mainly in greenhouses [117]. First trials of bombiculture were attempted by researchers at the beginning of the twentieth century [142, 143], but bumble bee mass production started during the 1980s [139, 144]. At least five species have undergone domestication process for pollinator production (*B. ignites*, *B. impatiens*, *B. lucorum*, *B. occidentalis*, and *B. terrestris*) and many more for research purpose [139, 142–145]. Their domestication history follows a directed pathway with several domestication events since several bumble bee breeders started independently the production of the same taxon [139, 144]. *Bombus terrestris* is the most traded species: more than 2 million colonies are yearly produced and shipped throughout the world (review in [146]). The species is mass produced in indoor facilities in which the whole life cycle is controlled by humans [139]. The choice of the most effective bumble bee species for mass production has been made through the test of several species [139]. Most of them have been proved to be poorer choices (e.g., more aggressive, hard to feed, low production success), and their domestication programs have been abandoned [139, 144]. This means that the domestication process of such species (e.g., *B. lapidarius* [139]) has regressed after a period of human interest.

Although domestication of bumble bees has been acknowledged by various authors (e.g., [139, 147]), comparison between breeders’ stocks and wild populations is still lacking to highlight potential domestication syndrome in *Bombus* species. Nevertheless, the domestication programs of the five most produced species are already quite advanced (Level 4, **Figure 1**) since current bumble bee breeders’ stocks experience low gene flow with their wild counterparts. However, no selective breeding program has been reported to date.

4.2. The stingless bees

Stingless bees (Hymenoptera, Apidae, Meliponini) are social bees with perennial colonies (i.e., nest can remain active for more than 50 years) occurring in most tropical or subtropical areas [75, 148]. They are known for their pollen/honey production and their pollination efficiency for several valuable crops (e.g., coffee, Avocado, Strawberry, Rambutan) [138, 148]. Meliponiculture dates back to the Maya civilization and is nowadays practiced in Australia and Central/South America [148–150]. Nevertheless, their domestication process has not progressed so far (Level 2, **Figure 1**) since most of the meliponiculture is mainly a capture production that consists in attracting stingless bee swarms and maintaining the colonies in artificial wooden hives [148, 150].

5. Cochineal insects

Scale insects (Hemiptera, Coccoidea) are the third large insect groups including species that are, sometimes, considered as domesticated [47, 58, 151]: cochineals, lac scales, *Ceroplastes*

species, and *Ericerus* species. These species are economically valuable for the substances that they produce under proper farming [152]. *Dactylopius coccus* and *Kerria lacca* are among the most produced scale insects.

5.1. *Dactylopius coccus*

Cochineal is an important source of red for dyes, lake pigments, cosmetics, and food/pharmaceutical colorants [151, 153]. Indeed, the red dye is mainly composed of carmine, which is a pigment obtained from the scale insects belonging to *Dactylopius* genus (Hemiptera, Dactyloidea) or some *Porphyrophora* species (Hemiptera, Margarodidae) [151, 153–155]. Nowadays, most of the carmine production is based on the farming of *D. coccus* inhabiting (sub)tropical South and Central America [151, 153].

The species is used as a source of carmine in Mesoamerica and South America since the pre-Columbian times [156]. The earliest known cochineal-dyed textiles dates back to the twelfth century, but first evidence of cochineal farming is estimated to the tenth century [155–157]. The center of domestication is thought to be in Mexico [157]. Carmine became an important export good during the Spanish colonial period [156]. Later, the species was introduced in other areas such as Australia, Canary Islands, South Africa, and South Asia [156]. In the middle of the nineteenth century, the production of cochineal fell sharply due to the development of artificial red dyes. Consequently, the cochineal trade almost totally disappeared in the twentieth century. Since the 1970s, cochineal production was restarted due to the discovery of carcinogenic and hazardous properties of synthesized dyes [155].

Dactylopius coccus females are wingless sessile parasites of cacti in the genus *Opuntia* [151, 153, 155]. After mating with winged males, females give birth to nymph that are airborne transported by the wind to new host plants. Since the *D. coccus* females depend on *Opuntia* plants, their production takes place in cactus farms producing domesticated plant species [156, 158]. Cochineals are produced by infesting cacti plants and harvesting the insects by hand 90 days later. During this period, humans actively control potential predators [159]. At the end of the process, some cochineals are left to reproduce, while others are collected for carmine extraction.

Dactylopius coccus has been considered as a domesticated species [47, 58, 151], since it is reliant on human propagation and protection for survival at least in some regions [159]. Moreover, most of *D. coccus* is produced in man-controlled environments (i.e., cactus farms). Nevertheless, humans poorly control the species reproduction and gene flow with wild populations is frequent; yet more recent developments are improving this control (e.g., environment-control microtunnels in Mexico [58]). Overall, the domestication process of *D. coccus* (level 3, **Figure 1**) is far behind the ones of silkworms and honey bees. Since comparison between farmed and wild cochineals is lacking, potential domestication syndrome is unknown.

5.2. *Kerria lacca*

Lac is an important commercial resin of several utilities (e.g., material construction, cosmetics, medicine). It is a resinous secretion of lac insect species from Asia and Central America

[160, 161]. *Kerria lacca* (Hemiptera, Kerriidae) is one of the main species used for lac production [160, 161]. Its life cycle is similar to *D. coccus* with winged males and wingless sessile females that parasite several hundred host plants [161, 162]. For several centuries, lac yields were collected from the wild on infested host plants by local human populations [161]. During the nineteenth century, the increase of exportation from Asia triggered the development of artificial inoculation and mass production [161] through a domestication history that can be interpreted as a prey pathway (i.e., human control on the species was triggered by the need of increasing lac supply). Similarly to *D. coccus*, the domestication process of *K. lacca* is at an early stage (level 3, **Figure 1**) since the current production involved only host plant, lac crop, and lac pest management.

6. Farmed edible and medicinal insects

Humans have been eating insects for millennia [58, 163]. However, human entomophagy is a long-standing taboo in westernized societies [19, 58, 164]. This can explain why insect farming for human food supply has been largely absent from the main agricultural innovations and domestications with few exceptions such as honey bees, silkworms (i.e., pupae is a by-product of silk production), and scale insects [19, 73]. Yet, more than 2 billion of people eat insect regularly since there are a source of protein, fat, vitamins, and minerals frequently stored and sold in developing countries (review in [73, 164]). Across the world, more than 2000 insect species are considered as edible for human food or animal feed [19, 58, 164, 165]. Beside food, insects provide many natural products for drugs to treat human diseases [166, 167].

Overall, the most commonly consumed insects by humans or livestock/pets are beetles (Coleoptera) (31%), caterpillars (Lepidoptera) (18%), bees/wasps/ants (Hymenoptera) (14%) as well as crickets (Orthoptera) (13%) [19, 58, 73, 163–165]. Most of these insects, as well as those used as entomocuticals, are harvested in the wild [163] but some of these species are farmed for sale and profit [19, 73]. Currently, commercially farmed insects include (i) the house cricket (*Acheta domesticus*), the palm weevil (*Rhynchophorus ferrugineus*), the giant water bug (*Lethocerus indicus*), and water beetles (various species of Coleoptera) for human consumption [58, 168, 169] and (ii) bees, wasps, flies, butterflies, moths, and cockroaches for drug production [167]. Even in small-scale production in developing countries [19], their production implies that their life cycle is controlled by human in captive conditions isolated from their wild counterparts in order to meet regulations about human food production (i.e., hygienic standards, sterile conditions) as well as limiting pathogen spillover from/to the wild [19, 164, 169–171]. Such conditions are conducive for an advanced domestication process (Level 4, **Figure 1**) through a directed pathway. Conversely, other species are produced through an increasing human manipulation of their environment to increase insect yields and to ensure their long-term availability as food [172]. For instance, edible social wasps (Hymenoptera, Vespidae, *Vespula flaviceps*, and *V. shidai* in Japan) are traditionally managed by keeping wasp nests collected in the wild in hive boxes during one season to improve yields [173]. However, current attempts to improve the practice involves efforts to maintain new queens in captive condition over several generations [173], paving the ways to a prey domestication pathway.

7. Biological control agents and sterile insect technique

Addressing the needs of the increasing human population will require a 60% increase in global food production by 2050 [174]. Insects could aid in achieving this objective by providing food production [19, 164] as well as pollination service (see Section 4) and biological control of pests [175].

Biological control is a method of controlling pests such as arthropods, weeds, and plant diseases using predator (e.g., ladybugs to control aphids [176], herbivorous, or parasite species [175]). Parasitoids are among the most widely used biological control agents (e.g., [177, 178]). In these species, female deposits its egg inside or outside a host where emerged parasitoid larva continues to feed resulting in the host death [178–180]. This parasitic way of life is used by humans to target hosts that are pests. Whiteflies parasitoids (Hymenoptera, Aphelinidae, Encyrtidae, Eulophidae, Platygasteridae, Pteromalidae, and Signiphoridae) are an example of insects used in greenhouses to control major crop pests (i.e., the whiteflies; Hemiptera: Aleyrodidae) [177, 180]. As many other parasitoids (e.g., fly *Eucelatoria*, the beetle *Chrysolina*, and the wasp *Aphytis*), they are massively produced in captive conditions by humans before being shipped across the world [180]. The full control of their life cycle by humans is needed in order to ensure that the production (i) matches with the appropriate release dates when susceptible host species is at a suitable phase of development [181] and (ii) is available on a yearlong basis to respond to demand across the world [178, 182].

The sterile insect technique (SIT) is an alternative approach to control main pests (e.g., [183–185]) or disease vectors (e.g., [186–188]). This method implies to massively release sterile males (sterilized through the effects of irradiation on the reproductive cells) of an insect species into a target environment to compete with wild males for reproduction [183–185]. Ultimately, mass releases allow limiting offspring production of a particular pest and promoting its eradication (e.g., [184]). Mass-rearing production with a life cycle fully controlled by humans is needed to produce the large quantity of insect required by SIT [183].

The required full control of life cycle of pest insects for SIT or biological control agents means that an advanced domestication process is reached (up to 5 since some patented strains are available [189]). In the context of SIT, several studies have investigated the differences between wild and mass-produced males in order to ensure that released sterile males are able to compete with wild males (e.g., [183, 190]). These studies show that the domestication process has triggered several ecological and behavioral divergences between produced and wild populations as well as a decreased fitness of produced populations in the wild (e.g., [183, 190]).

8. Insects as pets

Archeological pieces of evidence show that insects have been used as pets for centuries [191]. Nowadays, crickets, grasshoppers, beetles, cockroaches, silkworms, ants, honey bees, bumble bees, mantises, and stick/leaf insects are bred by humans as a pleasing activity or for teaching purpose [192–194]. Conversely to vertebrates [8, 195–197], there is no, to my knowledge, scientific

literature addressing the domestication of pet insects. However, some of these pet insects are produced for other purpose such as honey bees, silkworms, and house crickets for which a domestication process is acknowledged (see previous sections). For other species, such as hissing cockroach (*Gromphadorhina portentosa*), mass/small-scale, and/or amateur production are practiced [198–202]. As for other “exotic” pets (e.g., [18]), these productions involve (i) a full control by humans on the life cycle in captive conditions since a large part of the production is completed out of the species native range and (ii), thus, an advanced domestication process (level 4, **Figure 1**).

9. Insects for laboratory research

Animals are widely used as model species in biology and biomedical sciences. Some insect species have been used for laboratory experiments for several decades (e.g., silkworms, honey bees, and other species [54, 203, 204]), especially the fruit flies (*Drosophila* spp.) [205–207].

Drosophila species first entered laboratories about 1900 and are now standard laboratory animals [208, 209]. As they become an instrument for scientific production, *Drosophila* have been massively produced in laboratory conditions in which life cycle, feeding, and mating are highly controlled by humans [208, 210–212]. This human control along with the strain development and artificial selection for particular purposes [208, 213–216] reflect an advanced domestication process of some populations (level 5, **Figure 1**), while there are many wild populations (e.g., [206, 217, 218]).

Conversely to most other insect species, domestication of *Drosophila* populations has been the focus of several studies since it has been considered as a model system to understand the consequences of the domestication process on genomes and phenotypes [219]. Indeed, fruit flies are easy and cheaply to bred and have a rapid generation time (i.e., at least a dozen generations per year) [206, 220]. This allows comparing several populations that have or not been subject to different domestication histories (e.g., [221–223]) or even monitoring evolutionary trajectories of population undergoing a domestication process since their foundation from the wild [219, 224–226]. This has allowed studying domestication process in well-defined laboratory experiments with replication and specific environmental controls for several *Drosophila* species. An overview of these experiments allows highlighting the domestication consequences for *Drosophila* taxa. Different studies highlight that “domesticated” populations display genetic specificity and accumulation of deleterious mutations, inbreeding depression as well as increasing of fertility, tameness, and manageability due to selection for human-accommodating phenotypes and/or the relaxation of selection on traits adapted in nature [219, 220, 222, 227–230]. Moreover, the evolutionary convergence is observed between long-established laboratory populations [219, 220, 222, 227–230].

10. Conclusions

10.1. Are insect species undergoing domestication processes?

Although few stunning cases (e.g., *B. mori*) have been the focus of abundant research, scientific literature has poorly investigated insect domestication to date. The main reason of this

is that insect domestication for human food supply has been largely absent from the agricultural development with few exceptions [19, 73]. Moreover, it is likely that insect domestication study has been hindered by the complexity and the subjectivity of the definition of domesticated species (e.g., for *A. mellifera* [10, 16, 47, 117–119, 58, 89, 102, 110, 114–116]). The difficulty of defining a threshold along a continuous process is a common problem in biology (see similar debate about the status and the process for the species status *versus* speciation in [231–233]). Consequently, the study of the process is often set aside or eluded due to debates on a particular threshold. In insects, many scientific articles or books (e.g., [234]) have analyzed or reviewed the breeding/productions of various insect species without explicitly describing these processes as domestication. Yet, the human control on the life cycle (i.e., on individuals' life cycle in noneusocial species or on superorganism's life cycle in honey bees) of most produced insect species is congruent with a domestication process (**Figure 1**; *sensu* [12]). Since a large number of insect populations are produced in captive conditions isolated from their wild counterparts (**Figure 1**), many species can be considered as undergoing a domestication process. Moreover, new domestication processes can be expected in the near future due to current challenges to increase human food/sanitary security (e.g., [19, 164, 175, 186–188]) or to address new demands for pets (i.e., similar development to the ornamental fish trade (e.g., [18, 235–237])).

10.2. Domestication patterns in insects

Domestication events in insects are no less complex than in crops and vertebrates. Domestication histories can involve (i) one (e.g., silkworms [61]) or several (e.g., in honey bees and bumble bees [113, 139]) domestication events and (ii) one (e.g., bumble bees [139]) or potentially several domestication pathways (e.g., honey bees). In most insect species (i.e., except for few extreme cases such as silkworms), different populations of a particular taxon can reach different degrees of progress in the domestication process (e.g., from wild status to an advanced domestication level in *B. terrestris*). Gene flow between populations at different domestication degrees is commonly observed in insects [59, 65, 119] but they do not hinder development of domestication syndrome (see next section).

Some insect species undergo domestication processes for several centuries (e.g., *B. mori* and *A. mellifera*; [57, 59, 60, 63, 89, 104, 105]), while domestications of most insects produced as biological control agents, pets, and laboratory organisms, or for SIT strategies and entomocentrals' production have been recently initiated. These recent domestications have been made possible thanks to the advances in technology of captive environment control and animal food production since the nineteenth century [1]. Indeed, most insect domestications are thought to follow a directed pathway, which requires rapidly a full control of life cycle by humans in man-controlled environments. This implies the use of efficient environment and food control technologies. Technological advances have made possible or easier the domestication of species, which could not be domesticated in the past, paving the way to a new wave of domestication (similarly to aquatic species [28]).

As for vertebrate species (see review in [1, 12]), some intrinsic features can hinder the development of domestication processes: (i) a diet that cannot be easily supplied by humans (e.g., oligolectic bee species feeding only on few plant species), (ii) long life-cycle (e.g., periodical cicadas that spend most of their 13- and 17-year lives underground at larval stage), (iii) bad

disposition (e.g., some wasp species), or (iv) reluctance to breed in captivity. Nevertheless, modern technology could potentially allow domesticating any insect species. Indeed, current insect production involves species with very different ecologies (i.e., terrestrial taxa, e.g., silkworm [51]; aquatic species, e.g., water beetles [168]), behavior (i.e., solitary insects, e.g., silkworm [51]; eusocial species, e.g., honey bees [89]), and development (i.e., Endopterygota, e.g., honey bees [89]; Exopterygota, e.g., house crickets [19]); representative of the insect biodiversity. However, new domestication processes, which presumably occur only through directed or prey pathways for insects, are only initiated by humans to provide response to needs or demands of humanity. This means that the domestication of a species that could meet human needs/demands already addressed by another produced species is unlikely [1, 238]. Instead, all species that have recently undergone a domestication process and then have been massively produced are those which provide response to new needs or demands of humanity such as bumble bees (i.e., pollination in greenhouses), hissing cockroach (i.e., pet), or *Drosophila* flies (i.e., laboratory organism) [139, 199, 208, 209].

An overview of current insect productions in man-controlled captive conditions shows that insect taxa are used to address very different human needs (e.g., food [19], raw materials [234], pets [194]). Moreover, many insect taxa that are primary produced to address a specific demand tend to be later used to serve several human needs as observed in the domestication histories of several mammal species. For instance, *A. mellifera* that produces honey (i.e., the primary use) and edible pupae can be considered as the insect equivalent of dairy cows, which are valued not only for their milk but also as meat [19]. Moreover, honey bees provide several raw materials (wax), health food (royal jelly), entomoceticals (venom), ecosystem service (pollination), model specimens for research [204], and pleasure (recreational beekeeping) to humans [92].

10.3. Domestication consequences and their shaping factors

Overall, differentiations between wild populations and their counterparts undergoing a domestication process have been poorly studied in insect species. Yet, such divergences and convergences of various phenotypic traits that differentiate domesticates from their wild progenitors can be expected under the domestication syndrome hypothesis [36]. In mammals, the domestication syndrome tends to comprise changes in tameness, aggressiveness, coat color/pigmentation, body morphology, reproductive alterations, hormone, neurotransmitter concentrations, and brain composition [36]. Some of these changes can be observed when comparing *B. mori* and its phylogenetically nearest wild counterpart [67–71] in tameness (i.e., larger tolerance to human presence/handling), aggressiveness (i.e., toward conspecifics since *B. mori* has higher ability to live in crowded conditions), morphology (i.e., leucism, larger body size), and reproduction/development (i.e., bigger cocoon and higher silk production, higher growth rate, altered pre-mating behavior) [51, 52, 57, 68]. Comparison of silkworm specificities with phenotypes of man-produced *Drosophila* flies and honey bees shows some convergences: higher tameness (i.e., fruit flies), lower aggressiveness toward humans and conspecifics (i.e., in *A. mellifera*), modified reproduction (e.g., higher fertility in fruit flies; changes in reproduction, e.g., limited swarming in *A. mellifera*), and morphology (i.e., specific color patterns of man-controlled strains/races) [111, 121, 219, 220, 222, 227–230]. These specificities concern domestication traits facilitating the domestication by humans (e.g., aggressiveness in honey bees) as well as improvement traits (e.g., higher honey production in *A. mellifera*; higher silk production in *B. mori*) that increase the manageability and the animal production efficiency/profitability for humans.

Specificities of populations undergoing a domestication process have been most likely shaped by unintentional/deliberate human actions, human-controlled environments, relaxation of the selection occurring in the wild or both as in other animal species [10, 41, 42]. For instance, the inability of *B. mori* to fly could result from a relaxation of selection in the wild (i.e., silkworm are protected and fed in captive conditions by humans) and/or a human pressure for “nonflying” insects (i.e., this facilitates the handling by humans). Similarly, the lower aggressiveness of honey bees can result from a lower predation pressure (i.e., human protection of hives) as well as from human selection for less aggressive populations. Inadvertent human habituation and unintentional conditioning could also be a primary selective agent in insect domestication as suggested to explain developmental and reproductive differences between *Drosophila* strains [220].

From a genetic point of view, animals in captive environment are expected to rapidly display genetic changes corresponding to adaptations to captive breeding [239]. Indeed, the specific selective pressure occurring in domestication environments promotes selection for domestication syndrome gene variants [11]. This selection on man-controlled populations can shape specific genotypes even when gene flow from the wild still occurs [21, 59]. Changes in traits linked to valuable resources for humans or morphology have been showed to have a genetic basis (e.g., specificity of silk gland transcriptomes [67] and melanin synthesis [68] of *B. mori*). Similarly, behavior modifications commonly observed in insect domestication syndrome (e.g., tameness, aggressiveness, manageability by humans) can be explained by mutations on neurogenetic genes affecting overall locomotion and activity as suggested in man-produced populations of *Drosophila* species and mammals [36, 220]. Therefore, large mutational target of neurogenetic genes can explain the evolution of specific behavior in animal populations undergoing domestication processes [220]. These neurogenomic loci collectively provide a large genomic substrate for variation to accumulate, and then selection and drift to act, to transform behavior [220].

10.4. Future prospects

The study of domestication of insect is still at a nascent stage. Some “model species” such as *A. mellifera*, *B. mori*, and *Drosophila* spp. have been the focus of several studies to understand domestication process. However, genetic bases of domestication-fostered modifications as well as the characterization of these modifications are poorly known. Therefore, further studies are needed to generalize domestication patterns as well as to understand genomic basis of domestication process.

Conflict of interest

The author declares no conflict of interest.

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