

# Hybridization and invasiveness in social insects – The good, the bad and the hybrid

Denis Fournier and Serge Aron



Hybridization may help drive biological invasions by reducing Allee effects, increasing genetic variation, and generating novel adaptive genotypes/phenotypes. Social insects (ants, bees, wasps, and termites) are among the world's worst invasive species. In this review, we study the relationship between hybridization and invasiveness in social insects. We examine three types of hybridization based on the reproductive characteristics of first-generation hybrids. We discuss several examples of the association between hybridization and invasiveness, which are predominantly found in bees and termites. However, hybridization also occurs in several non-invasive species, and highly invasive species are not consistently associated with hybridization events, indicating that hybridization is not a main driver of invasiveness in social insects. We discuss why hybridization is not more commonly seen in invasive social insects.

## Address

Evolutionary Biology and Ecology, Université libre de Bruxelles, Brussels, Belgium

Corresponding author: Aron, Serge ([saron@ulb.ac.be](mailto:saron@ulb.ac.be))

**Current Opinion in Insect Science** 2021, 46:1–9

This review comes from a themed issue on **Social insects**

Edited by **Michael Goodisman** and **Brendan Hunt**

<https://doi.org/10.1016/j.cois.2020.12.004>

2214-5745/© 2021 Elsevier Inc. All rights reserved.

## Introduction

When species or populations end up beyond their native ranges, they often pose a threat to local biodiversity [1]. The removal of geographic barriers increases contacts between native and non-native populations, which have each been genetically shaped over the course of allopatric divergence; this new geographical proximity may lead to hybridization [2,3]. Admixture and introgression may also result, and all three phenomena can significantly affect the genetic make-up, long-term survival, and evolution of populations and species; furthermore, they may eliminate the barriers that prevent the establishment, spread, and range expansion of invasive species [4,5,6<sup>\*\*</sup>,7,8<sup>\*\*</sup>] (Figure 1). Hybridization can reduce Allee

effects by allowing invaders to access mates [9<sup>\*\*</sup>]. Admixture increases standing genetic variation and may generate novel adaptive genetic combinations [6<sup>\*\*</sup>,8<sup>\*\*</sup>]. Introgression allows allele flow from the native to the introduced population, boosting genetic variation and giving rise to new genotypes/phenotypes that are or can become adaptive in the new environment [6<sup>\*\*</sup>,8<sup>\*\*</sup>].

Three main types of hybridization have been defined based on the reproductive properties of first-generation hybrids ( $F_1$ ) and the phylogenetic distances between hybridizing species [10,11<sup>\*\*</sup>]. Type 1 hybridization results in sterile or non-viable  $F_1$  offspring because of genetic incompatibilities, the loss of local adaptations, and/or the breakdown of co-adapted genes. These fitness costs may lead to demographic decline in one or both species. Type 2 hybridization results in fertile  $F_1$  offspring. However, in these hybrids, no chromosomal recombination occurs during meiosis; their offspring are thus clonal or hemiclinal, displaying a single parental genome. Type 2 hybridization gives rise to unusual modes of reproduction such as polyploidy, gynogenesis, parthenogenesis, androgenesis, or hybridogenesis. Type 3 hybridization is characterized by interbreeding between related taxa that results in viable, fertile hybrids whose presence mediates gene flow and introgression between the parental species. It increases genetic diversity within populations by introducing alleles that can help organisms adapt to environmental stochasticity [12].

## Invasive social insects

The ecological success of social insects (bees, ants, wasps, and termites) is largely attributed to their division of labor—colonies are composed of a reproductive caste (queens and males) and a non-reproductive caste (workers) [13]. As a result of anthropogenic activities, several social insect species have become invasive around the world [14–17].

Hybridization occurs in both invasive and non-invasive social insects. Natural hybridization appears to be most common in ants and has causes and consequences at both the individual and social levels [18]. However, it remains unclear whether hybridization favors the invasiveness of social insects or whether it is simply the outcome of range expansion.

In this short review, we examine the relationship between hybridization and invasiveness in social insects. We use the hybridization types described above [10,11<sup>\*\*</sup>], which

**Glossary**

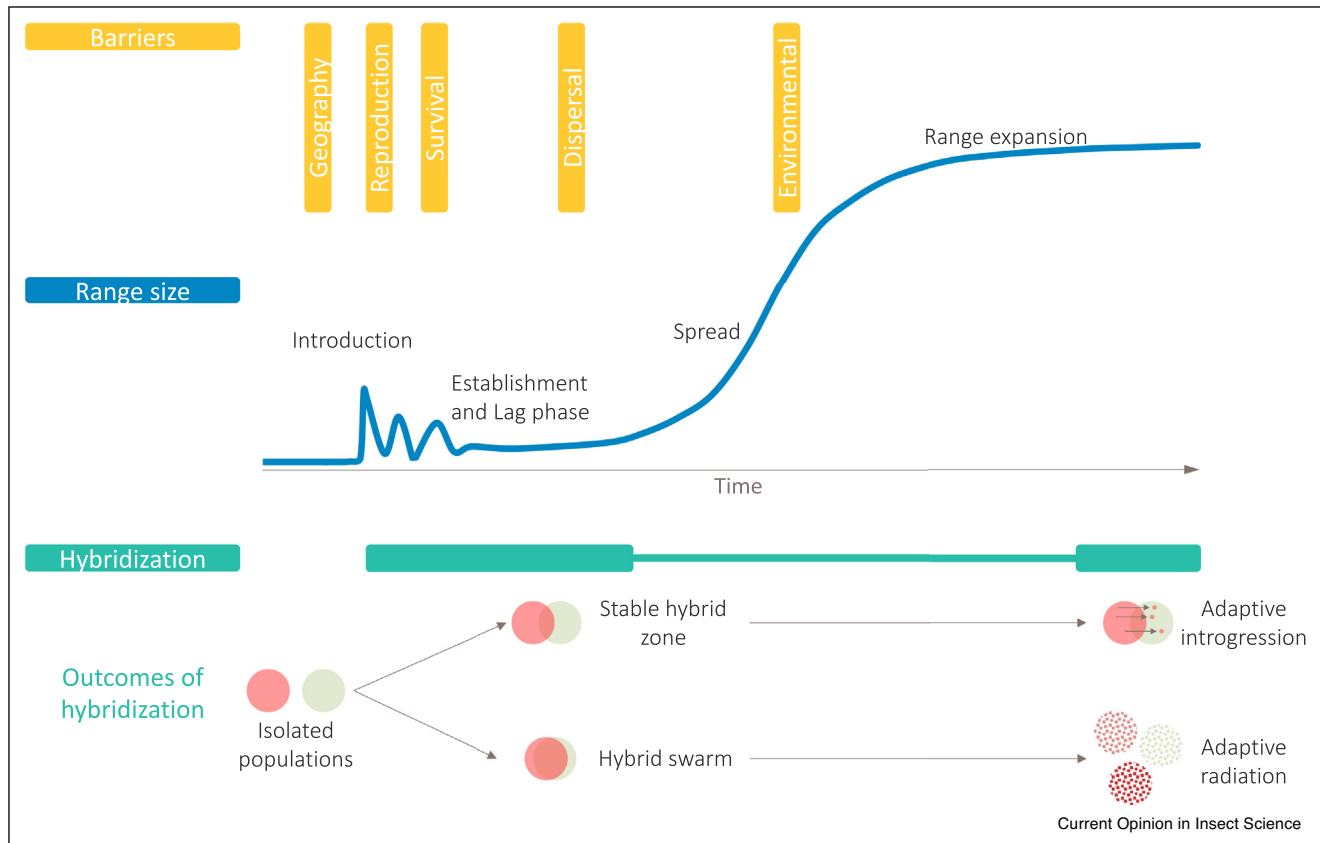
**Admixture:** Genomic mixing resulting from interbreeding between genetically distinct groups  
**Allee effect:** Positive association between population size and population growth  
**Androgenesis:** A mode of reproduction involving the development of an embryo bearing only paternal chromosomes  
**Gene flow:** Transfer of genes between different groups of organisms  
**Gynogenesis:** A mode of parthenogenesis where oocyte development requires stimulation by a sperm cell, but to which the male gamete contributes no genetic material; gynogenesis and androgenesis are forms of uniparental inheritance  
**Hybridization:** Interbreeding between genetically distinct groups (e. g. different genetic lineages, populations, species, or genera)  
**Hybridogenesis:** A form of reproduction where both the maternal and paternal genomes are expressed in somatic tissues, but the germline is purely maternal  
**Introgression:** Gene flow from one genetically distinct group to another, due to hybridization  
**Parthenogenesis:** A mode of reproduction in which an oocyte can develop into an embryo without being fertilized by a sperm cell

seem to be the most appropriate given the diverse reproductive strategies of social insects.

**Hybridization in invasive social insects**

Hybridization has been documented in social insects identified as invasive by the IUCN and in species not (yet) classified as invasive but that pose an equivalent threat to biodiversity (Table 1). Marked differences exist in the taxonomic distribution of invasive species, hybridization frequency, and hybridization type. Ants are the most common invasive social insects. Hybridization occurs in about 50% of the invasive ant species studied so far, which means the phenomenon is not more frequent in invasive versus non-invasive ants (Table 1). Type 2 hybridization (introgression absent) and Type 3 hybridization (introgression present) are equally common. In contrast, far fewer bee, wasp, and termite species appear

Figure 1



A framework for describing biological invasions.

The invasion process can be represented as a number of stages and barriers that invasive species or populations must overcome to be successful. Range size depends on the time since arrival and the nature of the barriers encountered. Hybridization may favor invasiveness by diminishing Allee effects, generating novel gene combinations, and/or promoting the introgression of adaptive, 'ready-to-use' alleles. Adapted from Refs. [4,5,7,8\*\*].

Table 1

## Hybridization in invasive social insects

Species	IUCN - GISD	Evidence for hybridization and/or introgression	Type of hybridization	Direction of introgression	References
<b>Ants</b>					
<i>Anoplolepis gracilipes</i>	Yes	Microsatellite markers	2		[27]
<i>Dorylus molestus</i> × <i>D. wilverthi</i>	No	Microsatellite and mitochondrial (COII) markers; morphometric analyses	3		[72]
<i>Lasius alienus</i> × <i>L. niger</i>	No	Allozymes	3	Unidirectional ( <i>L. alienus</i> queens mate with <i>L. niger</i> males)	[73]
<i>Myrmica rubra</i>	Yes	Microsatellite and mitochondrial (COI, cyt b) markers	3	Unidirectional (usually, microgynous males mate with macrogynous females)	[74]
<i>Myrmica scabrinodis</i>	No	Mitochondrial (COI, cyt b) markers	3 <sup>a</sup>		[75]
<i>Myrmica scabrinodis</i> × <i>M. vandeli</i>	No	Geometric morphometrics	3	Bidirectional <sup>a</sup>	[76]
<i>Nylanderia fulva</i>	No	Microsatellite markers	2		[33]
<i>Paratrechina longicornis</i>	Yes	Microsatellite markers	2		[26,77]
<i>Solenopsis geminata</i> × <i>S. saevissima</i>	Yes	Microsatellite markers; distribution, bioclimatic, and coloration data	3	Introgression of genes from <i>S. geminata</i>	[78]
<i>Solenopsis geminata</i> × <i>S. xyloni</i>	Yes	Laboratory experiments	3 <sup>a</sup>	Unidirectional ( <i>S. geminata</i> males mate with <i>S. xyloni</i> queens)	[35]
<i>Solenopsis invicta</i> × <i>S. richteri</i>	Yes	SNP and mitochondrial (COI) markers, allozymes; microarrays; venom alkaloids, cuticular hydrocarbons; behavioural assays; body mass, water content and thermotolerance	3	Bidirectional	[36–41,42*,79]
<i>Solenopsis quinquecupis</i> × <i>S. invicta</i>	Yes	Allozymes and mitochondrial (COI) markers	3	Unidirectional (introgression from <i>S. invicta</i> and <i>S. richteri</i> to <i>S. quinquecupis</i> )	[43]
<i>Tapinoma darioi</i> sp.n. × <i>T. magnum</i>	No	Mitochondrial (COI) markers	3	Unidirectional	[80]
<i>Tetramorium caespitum</i> × <i>T. immigrans</i>	No	Microsatellites, mitochondrial (COI) and AFLP markers; morphometrics	3	Bidirectional	[81,82]
<i>Vollenhovia emeryi</i>	No	Microsatellite markers	2		[25]
<i>Wasmannia auropunctata</i>	Yes	Microsatellite markers	2		[24,83]
<i>Acromyrmex octospinosus</i>	Yes	No evidence			
<i>Lasius neglectus</i>	Yes	No evidence			
<i>Linepithema humile</i>	Yes	No evidence			
<i>Monomorium destructor</i>	Yes	No evidence			
<i>Monomorium floricola</i>	Yes	No evidence			
<i>Monomorium pharaonis</i>	Yes	No evidence			
<i>Nylanderia pubens</i>	Yes	No evidence			
<i>Ooceraea biroi</i>	No	No evidence			
<i>Pachycondyla chinensis</i>	Yes	No evidence			
<i>Pheidole megacephala</i>	Yes	No evidence			
<i>Solenopsis papuana</i>	Yes	No evidence			
<i>Tapinoma melanocephalum</i>	Yes	No evidence			
<i>Technomyrmex albipes</i>	Yes	No evidence			
<b>Bees</b>					
<i>Apis mellifera scutellata</i>	Yes	Mitochondrial (COI, COII) and SNP markers; whole-genome sequences; morphometric analyses	3	Bidirectional	[45,46,47*,69*]
<i>Apis m. scutellata</i> × <i>A. m. capensis</i>	Yes	Mitochondrial (COI, COII), nuclear ( <i>Z-locus</i> ) markers	3	Bidirectional	[57,71*]
<i>Apis mellifera scutellata</i> × <i>Apis m. ligustica</i>	Yes	Microsatellite markers	3		[48,49]
<i>Apis mellifera</i> × <i>A. cerana</i>	No	Artificial insemination; nuclear (EF1 $\alpha$ ) marker	1		[19]

**Table 1 (Continued)**

Species	IUCN - GISD	Evidence for hybridization and/or introgression	Type of hybridization	Direction of introgression	References
<i>Bombus terrestris</i>	No	Laboratory experiments; microsatellite markers			[84,85]
<i>Bombus t. terrestris</i> × <i>B. t. hypocrita sapporoensis</i>	No	Laboratory experiments	1		[20,21,23]
<i>Bombus t. terrestris</i> × <i>B. h. hypocrita</i>	No	Laboratory experiments	1		[20]
<i>Bombus t. terrestris</i> × <i>B. ignitus</i>	No	Laboratory experiments	1		[23]
<i>Bombus t. terrestris</i> × <i>B. t. lusitanicus</i>	No	RAD-seq and mitochondrial (COI) markers; mitogenome	3	Unidirectional <sup>a</sup> (introgression from commercial into native bumblebees)	[50,51]
Termites					
<i>Coptotermes formosanus</i> × <i>C. gestroi</i>	Yes	Laboratory tests crossing; mitochondrial (COII) markers	3	Unidirectional <sup>a</sup> (introgression of <i>C. gestroi</i> genes)	[52,53,54*,55*,56]
<i>Nasutitermes corniger</i> × <i>N. ephratae</i>	No	Laboratory tests crossing	3 <sup>a</sup>	Bidirectional	[86]
<i>Pseudacanthotermes spiniger</i> × <i>P. militaris</i>	No	Laboratory experiments	1		[87]
<i>Reticulitermes flaviceps</i> × <i>R. chinensis</i>	No	Microsatellite markers; laboratory experiments			[88]
<i>Reticulitermes grassei</i> × <i>R. banyulensis</i>	No	Mitochondrial (COI, COII) and nuclear (ITS2) markers; cuticular hydrocarbons	3		[89]
<i>Reticulitermes lucifugus corsicus</i>	No	Microsatellite, mitochondrial (COII) and nuclear (ITS2) markers	3	Bidirectional	[90]
<i>Zootermopsis nevadensis nuttingi</i> × <i>Z. n. nevadensis</i>	No	Microsatellite and mitochondrial (COI) markers	3	Bidirectional (greater gene flow from <i>Z. n. nuttingi</i> to <i>Z. n. nevadensis</i> populations)	[91]
Wasps					
<i>Polistes chinensis antennalis</i>	Yes	No evidence			
<i>Polistes dominula</i>	No	No evidence			
<i>Vespa mandarina</i>	No	No evidence			
<i>Vespa velutina nigrithorax</i>	Yes	No evidence			
<i>Vespula germanica</i>	Yes	No evidence			
<i>Vespula pennsylvanica</i>	Yes	No evidence			
<i>Vespula vulgaris</i>	Yes	No evidence			

Twenty-six social insects are currently classified as invasive by the Global Invasive Species Database (GISD), which is managed by the Invasive Species Specialist Group (ISSG) of the IUCN Species Survival Commission. To this list, we have added 24 species that cause equivalent threats to biodiversity and that might be classified as invasive in the future. Provided are genetic, chemical, morphometric, and experimental data related to the presence of hybridization and/or introgression, hybridization type (as per [10,11\*]); see text for details, and the direction of introgression.

<sup>a</sup> Type of hybridization and/or direction of introgression requires additional studies to be confirmed.

to have become invasive. Hybridization (mainly Type 3) appears to occur in almost all the invasive bees and termites studied to date; it has yet to be observed in invasive wasps. That said, major differences exist in what is known about each species. Hereafter, we will thus focus on the best characterized examples.

### Type 1 hybridization

F<sub>1</sub> hybrid queens are rarely observed under natural conditions, suggesting they have low fitness and/or low viability. For instance, artificial cross-insemination between *Apis mellifera* and *A. cerana* resulted in completely sterile queens [19]. In some cases, F<sub>1</sub> hybrid queens can produce viable workers capable of caring for

brood [18]. In theory, the ability to produce workers may play a key role in invasion success because workers could help maintain and expand recently arrived propagules. Additionally, in some species, workers can produce males, who could then mate with native or invasive queens. This is the case for the bumble bee *Bombus terrestris*, a species used to provide commercial pollination services worldwide. *B. terrestris* naturally occurs in the western Palaearctic but has spread well beyond its native range after its queens escaped from greenhouses. In Japan, *B. terrestris* males and native bumble bee queens frequently interbreed in the wild (20.2% and 30.2% of *B. hypocrita hypocrita* and *B. h. sapporoensis* queens, respectively) [20]. An initial study showed that such mating events

can yield F<sub>1</sub> hybrid queens and workers and that hybrid workers can lay unfertilized eggs that developed into adult males [21]. However, subsequent laboratory studies found that hybridization disrupted reproduction because the native species produced non-viable eggs [21–23]. It thus appears that hybridization reduces the fitness of native species, facilitating its replacement by invasive species.

### Type 2 hybridization

Four ant species (*Wasmannia auropunctata* [24], *Vollenhovia emeryi* [25], *Paratrechina longicornis* [26], and *Anoplolepis gracilipes* [27]) independently evolved a genetic caste determination system that reduces the cost of inbreeding and circumvents the fitness costs of hybridization for female reproductives [24,28]. Sterile workers develop from F<sub>1</sub> hybrid crosses, whereas reproductives develop from pure lineages. Queens arise from thelytokous parthenogenesis and solely transmit maternal genes across generations. Males arise from androgenesis and solely transmit paternal genes. Consequently, the queen and male genomes (i.e. the *germline* of the colony) follow separate evolutionary branches, while the worker genome (the *soma*) combines two genetically distant lineages [24,29]. The broad range of alleles in hybrid workers may boost colony fitness via direct and social heterosis, resulting in the more efficient division of labor among workers, greater pathogen resistance, and/or higher tolerance of environmental variability [30–32]. This caste determination system also reduces Allee effects, notably the demographic challenges in small founding populations due to mate scarcity [9<sup>•</sup>,28].

In the same vein, in invasive populations of *Nylanderia fulva* [33], postzygotic selection maintains a distorted pattern of genetic inheritance: females generally carry maternally inherited alleles, and males generally carry paternally inherited alleles. Such reproductive phenomena may ultimately lead male and female reproductives to form distinct genetic lineages.

### Type 3 hybridization

The relationship between hybridization and invasiveness is illustrated by some examples. In *Solenopsis* fire ants, hybridization events between *Solenopsis geminata* and *Solenopsis xyloni* have been documented in several populations in areas where these species are sympatric. Colonies of *S. xyloni* contain multiple queens that have each mated with a single male. Queens mated with a male of their own species produce only reproductive offspring; in contrast, queens mated with a *S. geminata* male produce only workers [34]. In such areas, all *S. xyloni* colonies are composed exclusively of F<sub>1</sub> hybrid workers, which indicates there is a selective advantage to hybridization. Laboratory experiments have shown that hybrid workers display greater foraging efficiency than do pure *S. geminata* workers and greater

competitive hardiness than pure *S. xyloni* workers [35]. Thus, hybrid workers may be sufficiently competitive to co-exist alongside *S. geminata* and to, eventually, extend their distribution range.

While no hybridization has been documented between *Solenopsis invicta* and *S. richteri* in the species' native range (temperate areas of Argentina), they have admixed following their introduction into North America. Hybridization seems to have had several positive effects. First, hybrids can inherit the highly toxic alkaloids of *S. invicta*, which can be deployed in competition for resources [36]. Second, hybrids are more tolerant of low temperatures than are pure workers of either species [37,38], which has allowed them to expand northward within their invasive range [39]. Third, in the lab, hybrid workers discover new baits and recruit nestmates more quickly than do pure workers from native populations [40], which may favor colony growth and, subsequently, population density. However, the reproductive potential of hybrids remains unstudied [41,42<sup>•</sup>]. While *Solenopsis quinquecupis* appears to be reproductively isolated in its native range, it engages in recurrent hybridization with both *S. invicta* and *S. richteri* in its introduced range in the US [43].

The European fire ant *Myrmica rubra* was introduced from its native Eurasia into eastern North America, where the species can reach high densities. Colonies can contain two types of queens: large queens (i.e. macrogynes) and small, socially parasitic queens (i.e. microgynes). Macrogyne generate most of the workforce. Analyses of nuclear and mtDNA have shown that the host and its parasite are closely related, suggesting that there is incomplete lineage sorting and that hybrid introgression is still occurring [44]. If and how this reproductive system affects invasiveness is unknown.

Hybridization between the South African subspecies *Apis mellifera scutellata* and the European honey bee (EHB) results in a very aggressive hybrid—the 'Africanized' honey bee (AHB), or 'killer bee'. In this case, there is bidirectional flow of maternal and paternal genes between EHBs and AHBs. In feral AHB populations in Texas, the mean frequency of European nuclear genes ranged from 25 to 37% [45]. Representation of the AHB genome has rapidly expanded from South America to the southwestern US, a process in which worker aggressiveness has likely played a pivotal role [45,46,47<sup>•</sup>]. Interestingly, the Texas AHB population was the source of the 'gentle' AHB in Puerto Rico, in which a selective sweep favored specific alleles at certain loci [48,49]. What has emerged is a trait mosaic in which the EHB's lower level of aggressiveness is combined with an enhanced resistance to AHB ectoparasites [48,49].

While contact between *Bombus terrestris* and local species in Japan resulted in Type 1 hybrids (see above), interbreeding

and introgression has affected wild native *B. terrestris lusitanicus* populations in Spain [50,51]. Introgressed alleles from *B. terrestris* might be less suited to the warmer conditions of Spain, possibly diminishing fitness in native populations.

In termites, *Coptotermes formosanus* and *Coptotermes gestroi* are among the most invasive and destructive species. They occur sympatrically in their invasive range in Florida, where they overlap in their swarming seasons. Inter-specific (pre)mating behavior has been observed, suggesting hybridization occurs under natural conditions. In laboratory experiments, conspecific and heterospecific incipient colonies display equal establishment rates, but after one year of foundation heterospecific colonies grow twice as fast as conspecific colonies, perhaps due to the benefits of heterosis. Furthermore, hybrid workers display a thermal tolerance range that encompasses the ranges of both parental species, potentially expanding the windows of activity in hybrid populations and favoring their further spread [52,53,54\*,55\*]. However, after two years from foundation, reduction in the molting rates of individuals in hybrid colonies cancels out growth rate differences [56].

### Why is there not more hybridization in invasive species?

The examples above suggest that hybridization might facilitate invasiveness in social insects by increasing genetic diversity within populations and promoting allele introgression, thus facilitating adaptation to environmental conditions. Moreover, in Hymenoptera, hybridization only affects the production of females since males develop from unfertilized eggs. Although cross-mated queens may have reduced fitness because their reproductive female offspring will be sterile, they can still produce fertile sons. As long as hybrid workers are viable and can rear the brood, these males will live to potentially mate with native females [18,57]. This dynamic may help invasive populations become established.

Some invasive ants appear to largely avoid hybridization's negative effects on the fitness of female reproductives via a genetic caste determination system—male and female reproductives are asexually produced, while non-reproductive, hybrid workers are sexually produced (see Type 2 hybridization). While the two components of this system may, respectively, (i) help diminish Allee effects during the introduction and establishment phases and (ii) increase genetic diversity in the workforce, this reproductive set-up cannot fully explain the success of invasive ants. First, hybridization occurs in several non-invasive species (e.g. *Cataglyphis*, *Pogonomyrmex*, *Lasius*; [58–64]), and the introduction and spread of several highly invasive species are not associated with hybridization events (Table 1). Second, in the well-studied little fire ant, *Wasmannia auropunctata*, there is not a clear relationship between hybridization and invasiveness as clonal/hybrid

populations are not necessarily ecologically dominant [65]. In contrast, the presence of invasive populations is always correlated with anthropogenic disturbance, suggesting that human activities lead to ecological changes that select for alternative reproductive tactics [24,65].

In contrast to what is seen in ants, hybridization and invasiveness are strongly associated in termites. This relationship may have arisen because diploid organisms such as termites are less affected by hybridization's deleterious effects than are haplodiploid organisms like ants [66,67]. When males are haploid, hybrid incompatibilities apply to the whole genome and are not restricted to the autosomes and/or sexual chromosomes, as typically seen in diploids. Surprisingly, hybridization has never yet been observed in wasps.

The question thus arises: If hybridization significantly promotes range expansion and novel, adaptive genetic combinations, why is it not more common in invasive social insects? There may be at least three explanations. First, hybridization may have yet to be detected in some species due to a lack of research and/or sampling limitations. Second, prezygotic reproductive barriers might prevent breeding among more distantly related species. Postzygotic barriers might reinforce selection against hybrid offspring by reducing their viability or reproductive capacity, and/or by preventing introgression back towards the parental species. Third, hybridization may have fitness costs ([6\*\*] and references therein), as illustrated in the following three examples. (i) Hybrid offspring may be less fit than their parents. Deleterious hybridization will then be selected against in peripheral populations, which are usually more vulnerable to extinction, and in hybrid zones, which will become evolutionary dead ends rather than sources of dispersal. (ii) If hybrids preferentially mate with hybrids and outperform their parents, hybrids may become reproductively isolated in an area bounded by the ranges of their parental species. (iii) Introgression may lead rare species to go extinct via genome swamping by more common species. Thus, for hybridization to drive range expansion, introgression must confer genetic benefits without destroying species integrity.

### Conclusion

Future studies should clarify the adaptive pathways underlying the invasive success of social insects and the role of hybridization and introgression in this process. Among these, integrating models of hybrid zone dynamics in 'classical' ecological niche modelling could prove useful in predicting (and preventing) future expansion of invasive species, especially of cryptic species complex or populations that share similar ecological niche and life history traits with native populations. Genomics offer new opportunities to identify signatures of hybridization, to estimate historical and current admixture events, and to

analyze levels of selection that prevent hybridizing species from merging [68\*\*,69\*]. Comparative transcriptomics will allow researchers to identify (*i*) genes and gene combinations involved in reproductive barriers that maintain hybridizing species isolated, as well as (*ii*) introgression and its potential consequences on adaptation and phenotypic plasticity [68\*\*]. Gene drive technologies may help to control or eradicate invasive populations through the super Mendelian inheritance of a genetic trait, for example, by the promulgation of severe deleterious traits in invasive populations or by jeopardizing the reproduction of invasive individuals [70]. Clearly, combining ecological modelling, -omics approaches and experimental evolutionary biology will help to build a framework for biodiversity conservation.

## Funding

This work was supported by grants from the Belgian FRS-FNRS (Fonds National pour la Recherche Scientifique; # J.0151.16 and T.0140.18 to S.A.; # 2.4594.12 and J.0110.17 to D.F.) and the Université libre de Bruxelles (Fonds Defay to D.F.).

## Conflict of interest statement

Nothing declared.

## Acknowledgements

We thank J. Pearce-Duvt for her language editing services and two anonymous referees for their valuable comments and editorial suggestions.

## References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest

1. Simberloff D, Rejmanek M (Eds): *Encyclopedia of Biological Invasions*. University of California Press; 2011.
  2. McFarlane SE, Pemberton JM: **Detecting the true extent of introgression during anthropogenic hybridization**. *Trends Ecol Evol* 2019, **34**:315-326.
  3. Viard F, Riginos C, Bierne N: **Anthropogenic hybridization at sea: three evolutionary questions relevant to invasive species management**. *Philos Trans R Soc Lond B: Biol Sci* 2020, **375**:20190547.
  4. Prentis PJ, Wilson JRU, Dormontt EE, Richardson DM, Lowe AJ: **Adaptive evolution in invasive species**. *Trends Plant Sci* 2008, **13**:288-294.
  5. Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM: **A proposed unified framework for biological invasions**. *Trends Ecol Evol* 2011, **26**:333-339.
  6. Pfennig KS, Kelly AL, Pierce AA: **Hybridization as a facilitator of species range expansion**. *Proc R Soc B: Biol Sci* 2016, **283**:20161329
- A clear description and evaluation of how hybridization contributes to species range expansion through the relative role of the introgression of adaptive alleles, the increased genetic variation and the maintenance of population size.
7. Zenni RD, Dickie IA, Wingfield MJ, Hirsch H, Crous CJ, Meyerson LA, Burgess TI, Zimmermann TG, Klock MM, Siemann E *et al.*: **Evolutionary dynamics of tree invasions: complementing the unified framework for biological invasions**. *AoB Plants* 2016, **9**:plw085.
  8. Grabenstein KC, Taylor SA: **Breaking barriers: causes, consequences, and experimental utility of human-mediated hybridization**. *Trends Ecol Evol* 2018, **33**:198-212
- A recent synthesis of the mechanisms by which disturbance promotes hybridization and that highlights the utility of human-induced hybridization for understanding evolution. The authors draw up a non-exhaustive list of cases of disturbance-mediated hybridization, and design a workflow documenting human-induced hybridization and identifying the mechanisms causing species barrier breakdown.
9. Mesgaran MB, Lewis MA, Ades PK, Donohue K, Ohadi S, Li C, Cousens RD: **Hybridization can facilitate species invasions, even without enhancing local adaptation**. *Proc Natl Acad Sci U S A* 2016, **113**:10210-10214
- By combining both theoretical and experimental approaches, this paper shows how hybridization can help introduced populations to overcome Allee effects by allowing a mate-limited colonizing species to mate with local species. The results are of interest to invasion management strategies as they point out the necessity to better understand the relationship between sister groups, cryptic species complex and neighbouring populations that already share similar ecological niche and life history traits.
10. Quilodrán CS, Montoya-Burgos JI, Currat M: **Modelling interspecific hybridization with genome exclusion to identify conservation actions: the case of native and invasive *Pelophylax* waterfrogs**. *Evol Appl* 2015, **8**:199-210.
  11. Quilodrán CS, Montoya-Burgos JI, Currat M: **Harmonizing hybridization dissonance in conservation**. *Commun Biol* 2020, **3**:391
- This paper defines a framework for the understanding of the ecological and evolutionary consequences of hybridization, and proposes that human-induced hybridization be a tool to enhance the adaptation to changing environmental conditions or to increase the genetic diversity of groups affected by inbreeding depression.
12. Mallet J: **Hybridization as an invasion of the genome**. *Trends Ecol Evol* 2005, **20**:229-237.
  13. Wilson EO: *The Insect Societies*. Harvard University Press; 1971.
  14. Suarez AV, McGlynn TP, Tsutsui ND: **Biogeographic and taxonomic patterns of introduced ants**. In *Ant Ecology*. Edited by Lach L, Parr C, Abbott K. Oxford University Press; 2010:233-244.
  15. Goulson D: **Effects of introduced bees on native ecosystems**. *Ann Rev Ecol Syst* 2003, **34**:1-26.
  16. Beggs JR, Brockerhoff EG, Corley JC, Kenis M, Masciocchi M, Muller F, Rome Q, Villemant C: **Ecological effects and management of invasive alien *Vespidae***. *BioControl* 2011, **56**:505-526.
  17. Evans TA, Forschler BT, Grace JK: **Biology of invasive termites: a worldwide review**. *Ann Rev Entomol* 2013, **58**:455-474.
  18. Feldhaar H, Foitzik S, Heinze J: **Lifelong commitment to the wrong partner: hybridization in ants**. *Philos Trans R Soc Lond Ser B* 2008, **363**:2891-2899.
  19. Gloag R, Tan K, Wang Y, Song W, Luo W, Buchman G, Beekman M, Oldroyd BP: **No evidence of queen thelytoky following interspecific crosses of the honey bees *Apis cerana* and *Apis mellifera***. *Insectes Soc* 2017, **64**:241-246.
  20. Kondo NI, Yamanaka D, Kanbe Y, Kunitake YK, Yoneda M, Tsuchida K, Goka K: **Reproductive disturbance of Japanese bumblebees by the introduced European bumblebee *Bombus terrestris***. *Naturwissenschaften* 2009, **96**:467-475.
  21. Yoon H-J, Park I-G, Lee K-Y, Kim M-A, Jin B-R: **Interspecific hybridization of the Korean native bumblebee *Bombus hypocrita sapporoensis* and the European bumblebee *B. terrestris***. *Int J Ind Entomol* 2011, **23**:167-174.
  22. Kanbe Y, Okada I, Yoneda M, Goka K, Tsuchida K: **Interspecific mating of the introduced bumblebee *Bombus terrestris* and the native Japanese bumblebee *Bombus hypocrita sapporoensis* results in inviable hybrids**. *Naturwissenschaften* 2008, **95**:1003-1008.
  23. Tsuchida K, Yamaguchi A, Kanbe Y, Goka K: **Reproductive interference in an introduced bumblebee: polyandry may mitigate negative reproductive impact**. *Insects* 2019, **10**:59.

24. Fournier D, Estoup A, Orivel J, Foucaud J, Jourdan H, Le Breton J, Keller L: **Clonal reproduction by males and females in the little fire ant.** *Nature* 2005, **435**:1230-1234.
25. Ohkawara K, Nakayama M, Satoh A, Trindl A, Heinze J: **Clonal reproduction and genetic caste differences in a queen-polymorphic ant, *Vollenhovia emeryi*.** *Biol Lett* 2006, **2**:359-363.
26. Pearcy M, Goodisman MAD, Keller L: **Sib mating without inbreeding in the longhorn crazy ant.** *Proc R Soc B: Biol Sci* 2011, **278**:2677-2681.
27. Gruber MAM, Hoffmann BD, Ritchie PA, Lester PJ: **The conundrum of the yellow crazy ant (*Anoplolepis gracilipes*) reproductive mode: no evidence for dependent lineage genetic caste determination.** *Insectes Soc* 2013, **60**:135-145.
28. Foucaud J, Orivel J, Loiseau A, Delabie JHC, Jourdan H, Konghouleux D, Vonshak M, Tindo M, Mercier J-L, Fresneau D *et al.*: **Worldwide invasion by the little fire ant: routes of introduction and eco-evolutionary pathways.** *Evolut Appl* 2010, **3**:363-374.
29. Queller D: **Evolutionary biology: males from Mars.** *Nature* 2005, **435**:1167-1168.
30. Burke JM, Arnold ML: **Genetics and the fitness of hybrids.** *Ann Rev Genet* 2001, **35**:31-52.
31. Nonacs P, Kapheim KM: **Social heterosis and the maintenance of genetic diversity.** *J Evol Biol* 2007, **20**:2253-2265.
32. Chapman NC, Harpur BA, Lim J, Rinderer TE, Allsopp MH, Zayed A, Oldroyd BP: **Hybrid origins of Australian honeybees (*Apis mellifera*).** *Apidologie* 2016, **47**:26-34.
33. Eyer P-A, Blumenfeld AJ, Vargo EL: **Sexually antagonistic selection promotes genetic divergence between males and females in an ant.** *Proc Natl Acad Sci USA* 2019, **116**:24157-24163.
34. Tschinkel WR: *The Fire Ants*. Harvard University Press; 2006.
35. Axen HJ, Wildermuth A, Helms Cahan S: **Environmental filtering of foraging strategies mediates patterns of coexistence in the fire ants *Solenopsis geminata* and *Solenopsis xyloni*, and their interspecific hybrids.** *Ecol Entomol* 2014, **39**:290-299.
36. Chen L, Hu Q-B, Fadamiro HY: **Reduction of venom alkaloids in *Solenopsis richteri* × *Solenopsis invicta* hybrid: an attempt to identify new alkaloidal components.** *J Agric Food Chem* 2010, **58**:11534-11542.
37. Xu M, Lu Z, Lu Y-Y, Balusu RR, Ajayi OS, Fadamiro HY, Appel AG, Chen L: **Cuticular hydrocarbon chemistry, an important factor shaping the current distribution pattern of the imported fire ants in the USA.** *J Insect Physiol* 2018, **110**:34-43.
38. Ajayi OS, Appel AG, Chen L, Fadamiro HY: **Comparative cutaneous water loss and desiccation tolerance of four *Solenopsis* spp. (Hymenoptera: Formicidae) in the southeastern United States.** *Insects* 2020, **11**:418.
39. Gardner WA, Diffie S, Vander Meer RK, Brinkman MA: **Distribution of the fire ant (Hymenoptera: Formicidae) hybrid in Georgia.** *J Entomol Sci* 2008, **43**:133-137.
40. Gibbons L, Simberloff D: **Interaction of hybrid imported fire ants (*Solenopsis invicta* × *S. richteri*) with native ants at baits in Southeastern Tennessee.** *Southeast Nat* 2005, **4**:303-320.
41. Pandey M, Adesso KM, Archer RS, Valles SM, Baysal-Gurel F, Ganter PF, Youssef NN, Oliver JB: **Worker size, geographical distribution, and introgressive hybridization of invasive *Solenopsis invicta* and *Solenopsis richteri* (Hymenoptera: Formicidae) in Tennessee.** *Environ Entomol* 2019, **48**:727-732.
42. Cohen P, Privman E: **Speciation and hybridization in invasive fire ants.** *BMC Evol Biol* 2019, **19**:111  
A population genomic survey of native and introduced populations of *Solenopsis invicta* and *S. richteri* shows that the reproductive barrier between the two species is maintained for approximately 200 000 generations in their native range and breached in the introduced range where the two species freely hybridize. These results lay the foundations for further studies on the molecular bases of reproductive isolation of invasive populations.
43. Ross KG, Shoemaker DD: **Species delimitation in native South American fire ants.** *Mol Ecol* 2005, **14**:3419-3438.
44. Leppänen J, Vepsäläinen K, Savolainen R: **Phylogeography of the ant *Myrmica rubra* and its inquiline social parasite.** *Ecol Evol* 2011, **1**:46-62.
45. Pinto MA, Rubink WL, Patton JC, Coulson RN, Johnston JS: **Africanization in the United States: replacement of feral European honeybees (*Apis mellifera* L.) by an African hybrid swarm.** *Genetics* 2005, **170**:1653-1665.
46. Kono Y, Kohn JR, Wicker-Thomas C: **Range and frequency of Africanized honey bees in California (USA).** *PLoS One* 2015, **10**:e0137407.
47. Nelson RM, Wallberg A, Simões ZLP, Lawson DJ, Webster MT: **Genomewide analysis of admixture and adaptation in the Africanized honeybee.** *Mol Ecol* 2017, **26**:3603-3617  
Whole-genome sequencing of Africanized honeybees revealed that some alleles at functional sites with European ancestry are at a selective advantage in the Africanized population. This region is associated with reproductive and behavioral (foraging) traits in worker bees and could help adaptation to new environments.
48. Galindo-Cardona A, Acevedo-Gonzalez JP, Rivera-Marchand B, Giray T: **Genetic structure of the gentle Africanized honey bee population (gAHB) in Puerto Rico.** *BMC Genetics* 2013, **14**:65.
49. Acevedo-Gonzalez JP, Galindo-Cardona A, Avalos A, Whitfield CW, Rodriguez DM, Uribe-Rubio JL, Giray T: **Colonization history and population differentiation of the Honey Bees (*Apis mellifera* L.) in Puerto Rico.** *Ecol Evol* 2019, **9**:10895-10902.
50. Seabra SG, Silva SE, Nunes VL, Sousa VC, Martins J, Marabuto E, Rodrigues ASB, Pina-Martins F, Laurentino TG, Rebelo MT *et al.*: **Genomic signatures of introgression between commercial and native bumblebees, *Bombus terrestris*, in western Iberian Peninsula—implications for conservation and trade regulation.** *Evol Appl* 2019, **12**:679-691.
51. Cejas D, López-López A, Muñoz I, Ormosa C, De la Rúa P: **Unveiling introgression in bumblebee (*Bombus terrestris*) populations through mitogenome-based markers.** *Anim Genet* 2020, **51**:70-77.
52. Chouvenec T, Helmick EE, Su N-Y: **Hybridization of two major termite invaders as a consequence of human activity.** *PLoS One* 2015, **10**:e0120745.
53. Su N-Y, Chouvenec T, Li H-F: **Potential hybridization between two invasive termite species, *Coptotermes formosanus* and *C. gestroi* (Isoptera: Rhinotermitidae), and its biological and economic implications.** *Insects* 2017, **8**:14.
54. Patel JS, Tong RL, Chouvenec T, Su N-Y: **Comparison of temperature-dependent survivorship and wood-consumption rate among two invasive subterranean termite species (Blattodea: Rhinotermitidae: *Coptotermes*) and their hybrids.** *J Econ Entomol* 2019, **112**:300-304  
Laboratory experiments on two invasive subterranean termites show that hybrids exhibit greater thermo-tolerance than parental species. In contrast, wood-consumption rates do not differ. Hybrids may thus have the ability to spread over the full geographic range of both parental species.
55. Patel JS, Chouvenec T, Su N-Y: **Temperature preference of two invasive subterranean termite species and their hybrids (Blattodea: Rhinotermitidae: *Coptotermes*).** *J Econ Entomol* 2019, **112**:2888-2893  
Laboratory experiments on two invasive subterranean termites show that hybrids exhibit greater thermo-tolerance than parental species. In contrast, wood-consumption rates do not differ. Hybrids may thus have the ability to spread over the full geographic range of both parental species.
56. Lee S-B, Chouvenec T, Patel JS, Su N-Y: **Altered mobility and accumulation of inefficient workers in juvenile hybrid termite colonies.** *Front Ecol Evol* 2020, **8**:589762.
57. Moritz RFA, Beye M, Hepburn HR: **Estimating the contribution of laying workers to population fitness in African honeybees (*Apis mellifera*) with molecular markers.** *Insectes Soc* 1998, **45**:277-287.
58. Seifert B: **Interspecific hybridisations in natural populations of ants by example of a regional fauna (Hymenoptera, Formicidae).** *Insectes Soc* 1999, **46**:45-52.



59. Helms Cahan S, Keller L: **Complex hybrid origin of genetic caste determination in harvester ants.** *Nature* 2003, **424**:306-309.
60. Umphrey GJ: **Sperm parasitism in ants: selection for interspecific mating and hybridization.** *Ecology* 2006, **87**:2148-2159.
61. Kulmuni J, Seifert B, Pamilo P: **Segregation distortion causes large-scale differences between male and female genomes in hybrid ants.** *Proc Natl Acad Sci U S A* 2010, **107**:7371-7376.
62. Wenseleers T, Van Oystaeyen A: **Unusual modes of reproduction in social insects: shedding light on the evolutionary paradox of sex.** *BioEssays* 2011, **33**:927-937.
63. Seifert B: **Hybridization in the European carpenter ants *Camponotus herculeanus* and *C. ligniperda* (Hymenoptera: Formicidae).** *Insectes Soc* 2019, **66**:365-374.
64. Kuhn A, Darras H, Paknia O, Aron S: **Repeated evolution of queen parthenogenesis and social hybridogenesis in *Cataglyphis* desert ants.** *Mol Ecol* 2020, **29**:549-564.
65. Foucaud J, Orivel J, Fournier D, Delabie JHC, Loiseau A, Le Breton J, Cerdan P, Estoup A: **Reproductive system, social organization, human disturbance and ecological dominance in native populations of the little fire ant, *Wasmannia auropunctata*.** *Mol Ecol* 2009, **18**:5059-5073.
66. Haldane JBS: **Sex ratio and unisexual sterility in hybrid animals.** *J Genet* 1922, **12**:101-109.
67. Beukeboom LW, Koevoets T, Morales HE, Ferber S, van de Zande L: **Hybrid incompatibilities are affected by dominance and dosage in the haplodiploid wasp *Nasonia*.** *Front Genet* 2015, **6**:140.
68. Abbott RJ, Barton NH, Good JM: **Genomics of hybridization and its evolutionary consequences.** *Mol Ecol* 2016, **25**:2325-2332  
 This paper introduces a special issue on the genomics of hybridization. It provides an update on genomic methods used to detect and characterize hybridization, on the adaptive significance of introgression and isolating barriers, and puts hybridization and hybrid genomes in the context of biological conservation.
69. Calfee E, Agra MN, Palacio MA, Ramirez SR, Coop G: **Selection and hybridization shaped the rapid spread of African honey bee ancestry in the Americas.** *PLoS One* 2020, **16**:e1009038  
 By comparing populations of *scutellata* European hybrid honeybees in North and South America, the authors identified several loci with an excess of *scutellata* or European ancestry due to selection. Whole genome sequencing shows that *scutellata* European hybrid bees maintain high genetic diversity and competitive fitness despite their rapid expansion.
70. Teem JL, Alphey L, Descamps S, Edgington MP, Edwards O, Gemmill N, Harvey-Samuel T, Melnick RL, Oh KP, Piaggio AJ et al.: **Genetic biocontrol for invasive species.** *Front Bioeng Biotechnol* 2020, **8**:542.
71. Eimanifar A, Pieplow JT, Asem A, Ellis JD: **Genetic diversity and population structure of two subspecies of western honey bees (*Apis mellifera* L.) in the Republic of South Africa as revealed by microsatellite genotyping.** *PeerJ* 2020, **2020**:8280  
 This work shows the expansion and the genetic introgression of *A.m. capensis* into *A.m. scutellata*, and highlights the invasive potential of *A.m. capensis*.
72. Kronauer DJC, Peters MK, Schöning C, Boomsma JJ: **Hybridization in East African swarm-raiding army ants.** *Front Zool* 2011, **8**:20.
73. Pearson B: **Hybridisation between the ant species *Lasius niger* and *Lasius alienus*: the genetic evidence.** *Insectes Soc* 1983, **30**:402-411.
74. Leppänen J, Seppä P, Vepsäläinen K, Savolainen R: **Genetic divergence between the sympatric queen morphs of the ant *Myrmica rubra*.** *Mol Ecol* 2015, **24**:2463-2476.
75. Ebsen JR, Boomsma JJ, Nash DR: **Phylogeography and cryptic speciation in the *Myrmica scabrinodis* Nylander, 1846 species complex (Hymenoptera: Formicidae), and their conservation implications.** *Insect Conserv Diver* 2019, **12**:467-1846480.
76. Bagherian Yazdi A, Münch W, Seifert B: **A first demonstration of interspecific hybridization in *Myrmica* ants by geometric morphometrics (Hymenoptera: Formicidae).** *Myrmecol News* 2012, **17**:121-131.
77. Tseng S-P, Darras H, Lee C-Y, Yoshimura T, Keller L, Yang C-CS: **Isolation and characterization of novel microsatellite markers for a globally distributed invasive ant *Paratrechina longicornis* (Hymenoptera: Formicidae).** *Eur J Entomol* 2019, **116**:253-257.
78. Ross KG, Gotzek D, Ascunce MS, Shoemaker DD: **Species delimitation: a case study in a problematic ant taxon.** *Syst Biol* 2010, **59**:162-184.
79. Ometto L, Shoemaker D, Ross KG, Keller L: **Evolution of gene expression in fire ants: the effects of developmental stage, caste, and species.** *Mol Biol Evol* 2011, **28**:1381-1392.
80. Seifert B, D'Eustacchio D, Kaufmann B, Centorame M, Lorite P, Modica MV: **Four species within the supercolonial ants of the *Tapinoma nigerrimum* complex revealed by integrative taxonomy (Hymenoptera: Formicidae).** *Myrmecol News* 2017, **24**:123-144.
81. Wagner HC, Arthofer W, Seifert B, Muster C, Steiner FM, Schlick-Steiner BC: **Light at the end of the tunnel: integrative taxonomy delimits cryptic species in the *Tetramorium caespitum* complex (Hymenoptera: Formicidae).** *Myrmecol News* 2017, **25**:95-129.
82. Cordonnier M, Gayet T, Escarguel G, Kaufmann B: **From hybridization to introgression between two closely related sympatric ant species.** *J Zool Syst Evol Res* 2019, **57**:778-788.
83. Rey O, Facon B, Foucaud J, Loiseau A, Estoup A: **Androgenesis is a maternal trait in the invasive ant *Wasmannia auropunctata*.** *Proc R Soc B: Biol Sci* 2013, **280**:20131181.
84. Kraus FB, Szentgyörgyi H, Rožej E, Rhode M, Moroń D, Woyciechowski M, Moritz RFA: **Greenhouse bumblebees (*Bombus terrestris*) spread their genes into the wild.** *Conserv Genet* 2010, **12**:187-192.
85. Gosterit A, Baskar VC: **Impacts of commercialization on the developmental characteristics of native *Bombus terrestris* (L.) colonies.** *Insectes Soc* 2016, **63**:609-614.
86. Hartke TR, Rosengaus RB: **Heterospecific pairing and hybridization between *Nasutitermes corniger* and *N. ephratae*.** *Naturwissenschaften* 2011, **98**:745-753.
87. Connétable S, Robert A, Bordereau C: **Dispersal flight and colony development in the fungus-growing termites *Pseudacanthotermes spiniger* and *P. militaris*.** *Insectes Soc* 2012, **59**:269-277.
88. Wu J, Xu H, Hassan A, Huang Q: **Interspecific hybridization between the two sympatric termite *Reticulitermes* species under laboratory conditions.** *Insects* 2020, **11**:14.
89. Lefebvre T, Vargo EL, Zimmermann M, Dupont S, Kutnik M, Bagnères A-G: **Subterranean termite phylogeography reveals multiple postglacial colonization events in southwestern Europe.** *Ecol Evol* 2016, **6**:5987-6004.
90. Lefebvre T, Châline N, Limousin D, Dupont S, Bagnères A-G: **From speciation to introgressive hybridization: the phylogeographic structure of an island subspecies of termite, *Reticulitermes lucifugus corsicus*.** *BMC Evol Biol* 2008, **8**:38.
91. Aldrich BT, Kambhampati S: **Preliminary analysis of a hybrid zone between two subspecies of *Zootermopsis nevadensis*.** *Insectes Soc* 2009, **56**:439-450.