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# Breeding structure and invasiveness in social insects

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Plasticity in life history traits is commonly used to explain the invasion success of social insects. While intraspecific plasticity is often recognized, interspecific variability is easily overlooked, whereby different species exhibit different strategies. The presence of many queens per colony and the collapse of colony boundaries have favored invasiveness for many ant species. However, these strategies are absent from other successful social invaders. Here, we report that various life-history traits may differentially enhance the invasion success in social insects. We suggest that other aspects of their breeding system, like asexual reproduction, intranidal mating and pre-adaptation to inbreeding may enhance their invasion success. Thorough comparative studies between native and introduced populations or studies of closely related species will help identify additional traits favoring the invasion success of social insects, and ultimately provide a more comprehensive picture of the evolutionary factors enhancing invasiveness across this phylogenetically and ecologically diverse group.

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## Introduction

The rise of worldwide trade has facilitated the movement of many species of plants and animals outside of their native ranges. These species are usually introduced in the urban environment, a rapidly growing ecosystem that is becoming a major part of modern landscapes. Species introductions are often associated with radical changes in the abiotic and biotic pressures these species have evolved to face in their native and natural ranges [1,2]. These sudden ecological changes are frequently accompanied by a reduction in genetic diversity through bottlenecks, which may generate co-adapted gene complexes conferring novel and advantageous traits in the invaded environment. The myriad of novel pressures that

introduced, bottlenecked populations may encounter within a short timeframe therefore represents an unprecedented potent evolutionary force.

Social insects are particularly successful invaders, representing around 40% of the top 100 invasive invertebrates [3<sup>••</sup>,4,5]. These invaders frequently triumph in the competition for ecological resources allowing them to spread in their new introduced range, outcompeting native species, despite these latter species being shaped by natural selection to fit their local conditions. In addition to their behavioral, physiological and morphological variation [6], social insects display extreme plasticity in their breeding systems that may influence their invasion success. Many invasive populations exhibit variation from the classical mating system and colony structure, consisting of a colony headed by a single queen (and a king in the case of termites) inhabiting one nest. Species invasions have occurred many times independently within and across each lineage of social insects: ants, bees, wasps and termites. This provides an outstanding opportunity to identify key life history traits enhancing invasion success in this phylogenetically and ecologically diverse group. In this review, we examine whether different invasive social insects share common mating systems and colony breeding structures, or whether they evolve unorthodox mating systems allowing them to circumvent the loss of genetic diversity to successfully establish, dominate and spread in their novel environment. We discuss how reiterated transitions from native natural environments into introduced urban landscapes by different social insect species can provide insights into the direction and the repeatability of evolution of these life history traits in this group.

## Number of reproductives per colony

Many invasive social insect colonies are headed by numerous reproductive queens (polygyny) [3<sup>••</sup>,7–9]. This type of breeding system increases colony survival, freeing the colony of the fate of a single queen, and greater colony growth due to an increased production of workers [10]. It enhances invasion success through the production and allocation of a large number of workers to dominate resources [11]. Polygyny also increases the chance that a queen is included in a propagule that gets transported and successfully establishes after its introduction (i.e. propagule pressure) [8,12]. It increases the chance of introduction, establishment and further spread within the introduced range through additional human-mediated jump dispersal. Notably, the reproduction of multiple unrelated queens within a colony decreases relatedness among nestmates. As extreme polygyny eliminates indirect fitness, it challenges kin selection and calls into

question the long-term evolutionary stability of this breeding structure [13].

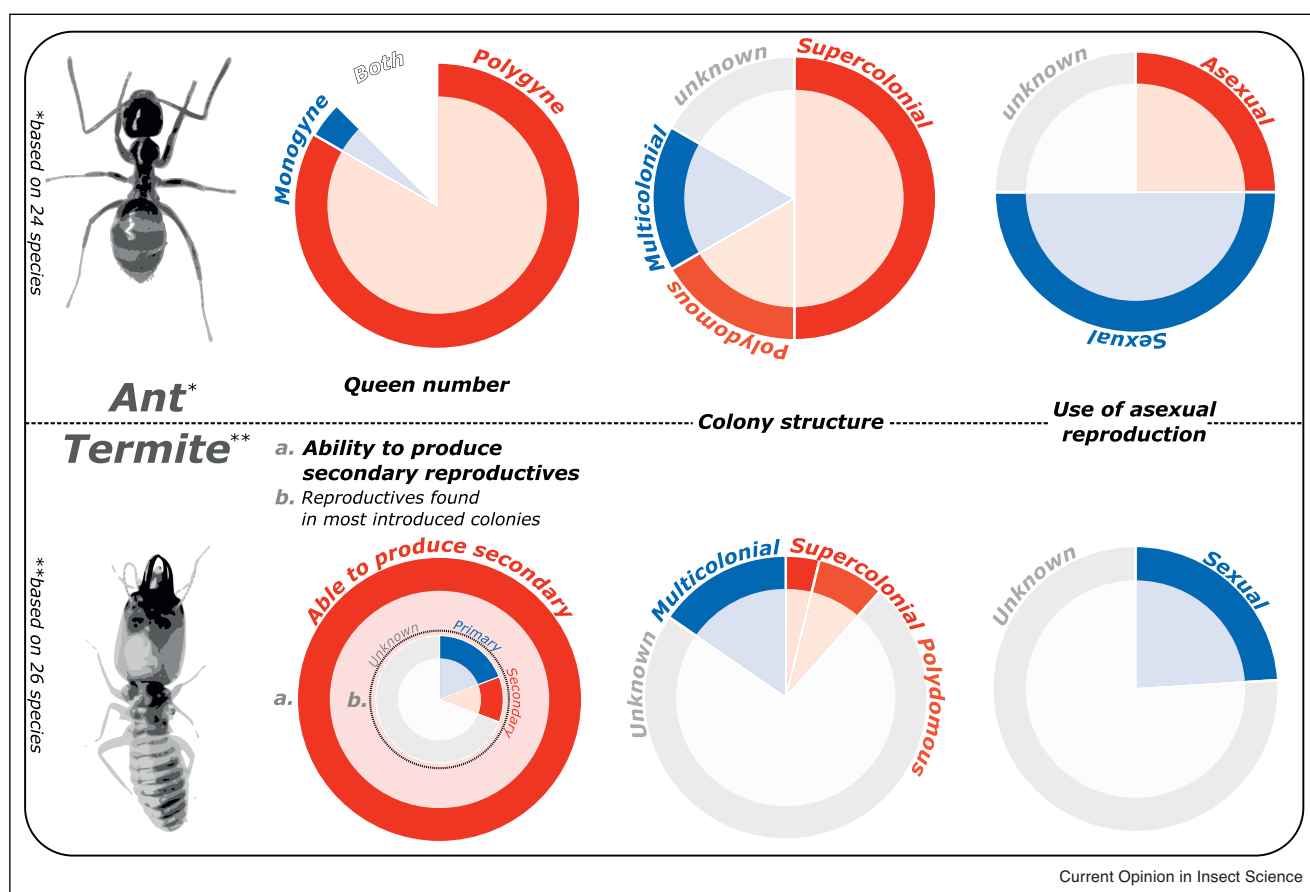
#### Ants

The occurrence of multiple queens in introduced colonies has been observed in many invasive ant species (Figure 1). This feature has been extensively reviewed in invasive ants and is undeniably associated with invasion success in this group [14]. Notably, some exceptions still occur suggesting that polygyny is not strictly required for successful invasion in ants, as a few species establish and spread despite some of their colonies being monogyne, such as *Tetramorium immigrans* [15<sup>\*</sup>], *Brachymyrmex patagonicus* [16<sup>\*</sup>], or the monogyne forms of *Solenopsis invicta* [17] and *S. geminata* [18]. Notably, most of these species are not completely monogyne, but exhibit a flexible breeding structure, including both monogyne and polygyne colonies.

#### Wasps

Increased polygyny has been described in introduced wasps, especially in the *Vespula* genus including three well-known invasive species, *Vespula germanica*, *Vespula vulgaris* and *Vespula pensylvanica*. In some parts of their ranges, colonies may survive winter and shift from an annual to a perennial colony cycle, with colonies living for multiple years [19]. This change allows the recruitment of queens, enabling the development of large polygyne colonies over several years. However, this shift to a polygyne breeding structure is more likely the result of milder winters in their invaded ranges [20], than an actual post-introduction change of their colony breeding structure. Indeed, similar variation in queen number and overwintering of colonies has been reported in the native range of *V. pensylvanica* in California [21]. The weak nestmate discrimination already present in its native range may pre-adapt this species to transition to polygyny, favoring the adoption of foreign queens in late season

Figure 1



Number of reproductives per nests, colony structure and use of asexual reproduction in invasive ants and termites. In termites, the number of reproductives per nest is divided into (a) their ability to produce additional secondary reproductives and (b) the actual type of reproductives found in most introduced colonies. The data used to generate this figure, and the associated references, are provided in Supplementary material Table S1.

[22\*]. Plasticity of this trait in the native range may therefore represent a pre-existing condition that facilitated their invasion, rather than a novel evolution in invasive populations of these wasp species.

### Bees

Interestingly, polygyny has not been reported in invasive social bees. Although *Bombus terrestris* or the Africanized and European honey bees *Apis mellifera* are among the most widespread invaders [23], none of them exhibit a polygyne breeding structure. Their worldwide distributions most likely stem from their extensive transport for pollinator services than their ecological dominance. *A. mellifera* colonies have indeed suffered high mortality in many regions in both its native and introduced ranges, with beekeepers struggling to keep them alive [24].

### Termites

The hypothesis of enhanced invasion success with high numbers of reproductives has received less support in invasive termites (Figure 1). Instead, their invasion success has been suggested to stem from the easy generation of new reproductives, rather than their actual number. In most lower termite species and some higher termites, workers and/or larvae can differentiate into secondary (neotenic) reproductives. This feature allows any group of foraging workers trapped in a transported piece of wood to readily produce secondary reproductives, and thereby become a viable propagule [4,25]. Yet, introduced populations of invasive termites that have been studied exhibit a small proportion of colonies headed by secondary reproductives (i.e. extended families), and even then, these may have only a few secondary reproductives present, as in *Coptotermes formosanus* [26]. Invasive populations of the higher termite *Nasutitermes corniger* have multiple primary reproductives that can arise from either multiple kings and queens engaging in cooperative founding and/or the production of supplemental kings and queens within the nest [27]. This suggests that the production of multiple reproductives within colonies, either neotenic or primary reproductives, may favor the establishment and rapid spread of an invasive species. However, it is less clear whether this strategy is used to achieve local dominance of already established colonies in a given environment in the way many ants dominate their invasive ranges with highly polygyne colonies. Interestingly, the production of neotenic and supplemental primary reproductives by termites and highly polygyne ant colonies are both characterized by intranidal mating, which may reduce biotic and abiotic pressures of the novel environment during the vulnerable dispersal and colony foundation stages. *Reticulitermes flavipes* and *Reticulitermes urbis* may represent the exception, as all colonies in their introduced ranges are headed by hundreds of secondary reproductives [28]. In these species, the high number of reproductives allows colonies to be unusually populous and spatially expansive.

### Supercoloniality — reduced aggression toward non-nestmates

In addition to polygyny, social structure may also drastically change between native and invasive ranges. Social structure ranges from monodomy, whereby each colony occupies a single nest, to polydomy, where colonies comprise several nests exchanging workers, brood and reproductive queens [29–32]. In some invasive species, the lack of aggression between workers from different nests enables the formation of supercolonies — an extensive polydomous colony [8]. This social structure reduces intraspecific competition, leading to a dense network of interconnected nests, genetically undistinguishable from each other. It therefore allows invasive populations to reach tremendous densities and outcompete native species by allocating a large number of workers to monopolize resources [8]. Similar to polygyny, the collapse of colony boundaries eliminates relatedness among nestmates, and therefore workers' indirect fitness. Consequently, unicoloniality is often described as an evolutionary dead-end, with no unicolonial species but only unicolonial populations [29].

Although unicoloniality is undeniably associated with many ant invasions (Figure 1), the number and size of the supercolonies encountered within introduced ranges can differ greatly among and within species. The entire invasive range of some invasive species may comprise a single huge supercolony spanning several thousand km, such as *Wasmannia auropunctata*, *Nylanderia fulva* and *Pheidole megacephala* [33–35]. While in other species, the invasive range may consist of several supercolonies, such as *Anoplolepis gracilipes* [36,37]. Sometimes, the number and size of the supercolonies may even be highly variable between populations of the same species, such as the Argentine ant *L. humile*. In this species, the invasive range in California comprises five supercolonies from 1 to 1000 km in length [38]; while the invasive range in southern Europe is made of only two supercolonies, one is 6000 km long, whereas the other is only a few km long [39]. In invasive populations of *Myrmica rubra*, *Brachyponera chinensis* and *Technomyrmex albipes*, colonies occupy several interconnected nests, forming small supercolonies (<1 km) [40\*\*,41,42]. This variation in supercolony size raises the question of where a 'large polydomous colony' ends and a 'supercolony' begins [29,43]. It is noteworthy to point out that some invasive populations are not unicolonial, rather each colony inhabits only a single nest. Such a pattern is observed in *B. patagonicus* [16\*], *T. immigrans* [15\*] or even both social forms of the highly invasive *S. invicta* [44].

The formation of supercolonies is less prevalent in termite species, and has been described in only a single species (Figure 1). In *R. urbis*, the introduced population in Italy and France consists of a single supercolony without aggression among different nests that gradually

expands through budding [45]. To a lesser extent, introduced colonies of *R. flavipes* are spatially expansive, with no genetic differentiation among workers separated by up to 1.5 km [46]. Although most colonies are still genetically distinct from each other, the absence of intraspecific antagonism between non-nestmates allows frequent fusions between colonies [47]. Overall, these findings also call attention to the threshold between supercolonies and large expansive polydomous colonies. Importantly, these traits also occur to a lesser degree in the native range [48], a pre-existing trait that may have enhanced the invasion success of this species.

### Unorthodox reproductive strategies

Several additional mating strategies have been suggested to favor invasive social insects, allowing them to overcome or reduce the loss of genetic diversity within introduced populations. In the invasive bee *Apis cerana*, multiple matings per queen (polyandry) may artificially increase the number of migrants (i.e. through stored sperm), thus extending genetic diversity brought from the native population [49\*\*,50]. This diversity is later transmitted directly through the production of new queens by the founding queen, and indirectly through the production of males by workers, daughters of the founding queen [51\*]. In the Asian needle ant *B. chinensis*, introduced colonies have similarly low levels of genetic diversity as those in the native range, although the introduced population experienced a severe bottleneck [40\*\*]. Inbreeding pre-exists in the native range, where generations of sibmating may have reduced inbreeding depression through the purifying selection of deleterious alleles, and thus lower the cost of a genetic bottleneck during introduction [40\*\*]. In the invasive wasp *V. germanica*, drones avoid aggregating with their nestmates during nuptial flights, therefore reducing the chance of inbreeding [52].

In addition, thelytokous parthenogenesis seems particularly prevalent in invasive species (Figure 1), which suggests this unorthodox mating strategy may provide evolutionary advantages to invade. In the tropical fire ant *S. geminata*, polygyne colonies produce queens asexually but workers are produced sexually via mating with males from the sexually reproducing monogyne colonies [53\*\*]. However, this strategy does not prevent the production of diploid males by polygyne colonies, sometimes representing 100% of the sampled adult males [18]. In response, polygyne colonies minimize this cost by the founding of nests by the cooperation of multiple queens and cannibalism of diploid male larvae [54\*]. Parthenogenesis is also present in some invasive populations of the ant species *W. auropunctata*, *Vollenhovia emeryi*, *A. gracilipes* and *Paratrechina longicornis*, where new queens are clones of their mothers while sons are clones of their fathers. This twofold asexuality segregates female and male gene pools into two distinct lineages [37,55–57]. Workers arise

from the hybridization of these lineages (i.e. through sexual reproduction), and are therefore 100% heterozygous. A single queen may therefore invade a new population, and its daughter queens and sons can interbreed without suffering inbreeding depression [56]. Notably, a similar outcome is achieved in the invasive population of the sexually reproducing ant *N. fulva*. In this species, sexually antagonistic selection selects for different alleles in males and females for specific loci, which results in completely heterozygous females (i.e. sexually produced) at a substantial part of the genome [58\*\*].

In some clonal populations of the ant *Mycocepurus smithii*, unmated queens can produce both new queens and workers asexually, while sexual reproduction is still prevalent in other populations [59,60]. In this species, a single clonal queen can invade a new population without the need for mating. Strategies with similar outcomes are reported in the queenless ants *Pristomyrmex punctatus* and *Ooceraea biroi*, in which all workers (and ergatoid queens for *P. punctatus*) are capable of thelytokous reproduction [61,62]. In these species, any small colony fragment has the potential to become a viable propagule without the necessity of mating [63].

Interestingly, although the use of unorthodox reproductive mating strategies to overcome genetic depletion [64–68] or to remove the need of mating [69] has been reported in some non-invasive termite species. Yet, these mating strategies seem unrelated to invasiveness in this group. In some species, secondary queens arise through thelytokous parthenogenesis after the primary queen dies [66]. The mating of these secondary queens with the primary king to which they are unrelated (a breeding system known as asexual queen succession; AQS) maintains the heterozygosity among the offspring while purging the primary queen-derived genomes of deleterious mutations [66]. Interestingly, neither of the two invasive species of the genus *Reticulitermes* reproduce by AQS, despite this genus comprising at least three AQS species [65–67].

### Conclusion

In today's world, where global trade lowers geographical barriers and human activity constantly reshapes ecological borders, biological invasion of many species, including social insects, represents one of the major economic and ecological threats. Determining whether native and invasive populations display different breeding structures and mating systems represents the first step in this investigation. The second step is to determine when the shift arises, distinguishing between existing phenotypic plasticity of this trait in the native range or its adaptive evolution in the introduced range, potentially enhanced by genetic drift following introduction events. Species introductions are characterized by gradients of potential adaptive drivers (e.g. competition, predation, pathogens,



food, and pollution). Assessing variation of a trait along these gradients in both native and introduced ranges may provide insights into its evolutionary trajectories. Species invasions therefore provide fortuitous experimental settings to investigate the range of social insect mating strategies and their evolution in response to a number of adaptive drivers. Identifying the drivers of trait differences in both the native and introduced ranges will broaden our understanding of the mechanisms linking species invasions and mating systems in this group.

### Conflict of interest statement

Nothing declared.

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### Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.cois.2021.01.004>.

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