Supercolonies of ants (Hymenoptera: Formicidae): ecological patterns, behavioural processes and their implications for social evolution

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Abstract

Supercolonies of ants are perhaps the largest non-human animal societies, at their largest spanning several millions of individuals and thousands of nests and in invasive species even crossing oceans. Supercolonies have convergently evolved in several ant groups, and they all share a syndrome of key features. First, their colonies spread by budding, which leads to extensive polydomy and inter-nest movement of individuals. Second, local mating and recruitment of queens lead to extensive polygyny. Their ecological dominance is clear, but their evolutionary maintenance is enigmatic due to low relatedness among cooperating individuals and the lack of clear functional organization above local polydomous units. This review takes a multi-level look at the social evolution of supercolonies in an inclusive fitness perspective, outlining key behavioural, ecological, and genetic processes as well as open questions. Such consideration of cooperation and competition from the gene level to the level of populations of supercolonies is necessary for understanding the history and future of supercolonies.

Key words: Ants, Formicidae, supercolony, unicolonial, polygyny, polydomy, kin selection, inclusive fitness, invasive species, review.

Introduction: Why care about super-colonial ants

Supercolonies of ants, vast networks of nests without territorial borders, are arguably the most massive animal societies, the global human network notwithstanding. As with so many things in myrmecology, they were brought into focus in the seminal works of Edward O. Wilson and Bert Hölldobler, that noted how some secondarily polygynous colonies, that is, colonies that adopt supernumerary queens from their own female offspring, live in populations in "which no colony boundaries exist and local populations are comprised of networks of intercommunicating aggregations of workers, brood, and fertile queens" (Hölldobler & Wilson 1977). This identifies a unicolonial (Wilson 1971) or a supercolonial (Gris & Cherix 1977) lifestyle and its key features: extensive multi-nest colonies with workers, brood, and queens moving freely among neighbouring nests, sometimes ranging several kilometers, so that individuals from the opposite ends of a huge and possibly geographically discontinuous colony identify each other as colony members. Mating and recruitment of queens happen locally, leading to extensive

secondary polygyny, and new nests are formed by budding, leading to polydomy.

Additional momentum for studying supercolonies came with the observation that such colony structures predominate in invasive ant species (Hölldobler & Wilson 1977, McGlynn 1999, Holway & al. 2002), a trend corroborated by recent analyses (Fournier & al. 2019). Supercolonial features predispose species to spread, colonize, and dominate. Intranidal mating allows small propagules, even just a group of workers with diploid and haploid brood (Aron 2001) to establish a colony. Large polydomous networks with no territory boundaries facilitate local dominance and resource monopolization, with potentially disastrous consequences for native ecosystems (Holway & al. 2002). While not all supercolonial species are invasive and not all invasive ants are dominant (Heinze & al. 2006) or supercolonial (Eyer & al. 2020), a lot of what we know about supercolonies is based on studies of invasive populations (Fig. 1). However, there is no need to invoke evolutionary change during invasions as an explanation for
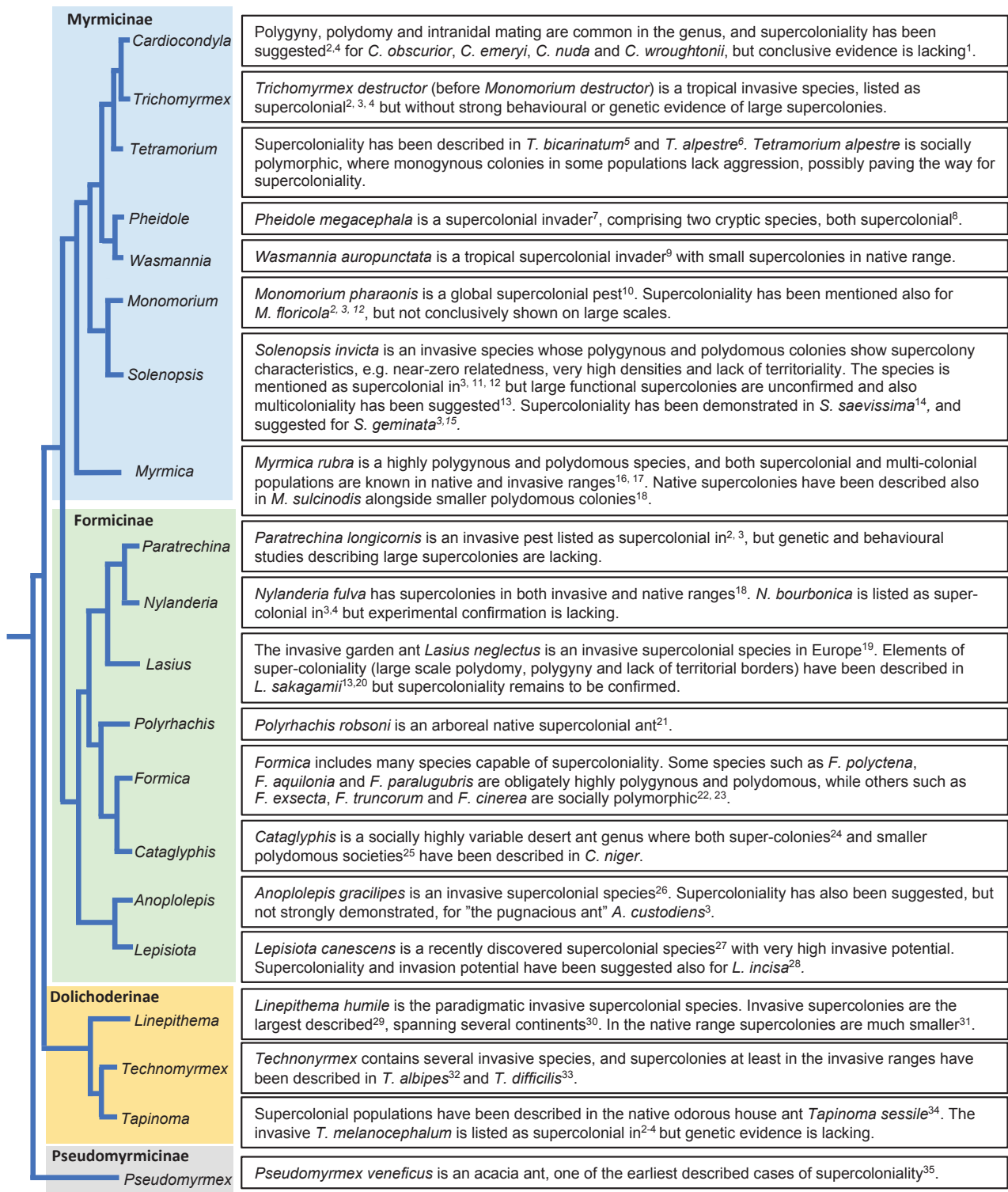
Fig. 1: Examples of invasive and native supercolonial ants. Clockwise from top left: the tawny crazy ant *Nylanderia fulva*, a recently described invasive species in the US (photo Alex Wild / Insects Unlocked / public domain); the yellow crazy ant *Anoplolepis gracilipes*, a highly harmful invasive pest, famous for its destructive effects on native ecosystems on, for example, Christmas Island (photo John Tann / eol.org / cc-by); the little fire ant *Wasmannia auropunctata*, another invasive pest originating from South America (photo Plegadis / Wikimedia commons / public domain); *Formica aquilonia*, a Eurasian boreal mound building wood ant that forms supercolonies in its native woodland habitats (photo Heikki Helanterä).

supercolonies (Pedersen & al. 2006, Helanterä & al. 2009, Moffett 2012). "Small supercolonies" in native range have been observed in, for example, *Linepithema humile* (Mayr, 1868) (Pedersen & al. 2006), *Wasmannia auropunctata* (Roger, 1863) (Foucaud & al. 2009), and *Nylanderia fulva* (Mayr, 1862) (Eyer & al. 2018). The much larger size of invasive supercolonies reflects polydomy and rapid growth in the absence of competition rather than large colonies that arise through loss of aggression.

Another exciting aspect of supercolonies is their enigmatic nature in the light of inclusive fitness logic (Bourke & Franks 1995, Queller & Strassmann 1998, Helanterä & al. 2009, Bourke 2011). While in a typical ant colony (if such a thing exists, see Heinze 2008) workers help their close kin to reproduce, in supercolonies extensive polygyny and movement of individuals between nests brings relatedness among nestmates down, even to zero. This may impede the process of kin selection, which is necessary for maintenance of altruistic worker phenotypes. Nepotism, selfish genotypes, and mutation accumulation are predicted to eventually undermine the success of supercolonies, leading to extinction. This predicted ultimate evolutionary demise is in stark contrast

with the observed ecological success of supercolonies (Helanterä & al. 2009).

Obligate eusociality, where morphologically separated castes are mutually dependent on each other for colony reproduction, evolved in tight nuclear families of singly mated females and their helping daughters (Hughes & al. 2008), but family structures have diverged considerably. A supercolonial lifestyle is an extreme case of such divergence. This lifestyle is limited to ants, dictated by the flightless habits of their workers (Boomsma & al. 2014). The key features of extreme polygyny and polydomy are intertwined. Local recruitment of queens leads to an increase in local density of reproductives and brings about local competition. Local competition is in turn alleviated by local and "dependent" nest founding and local territory expansion of the polydomous colony (Cronin & al. 2013, Boomsma & al. 2014, Hakala & al. 2019). Supercolonial ants can have very different ecologies, either thriving in disturbed habitats with opportunistic nesting preferences or stable habitats with investment heavy nests (Hölldobler & Wilson 1977, Helanterä & al. 2009). In both cases, it is conceivable that local competition is a major selective pressure.

Myrmicinae

Cardiocondyla — Polygyny, polydomy and intranidal mating are common in the genus, and supercoloniality has been suggested[2,4] for *C. obscurior*, *C. emeryi*, *C. nuda* and *C. wroughtonii*, but conclusive evidence is lacking[1].

Trichomyrmex — *Trichomyrmex destructor* (before *Monomorium destructor*) is a tropical invasive species, listed as supercolonial[2,3,4] but without strong behavioural or genetic evidence of large supercolonies.

Tetramorium — Supercoloniality has been described in *T. bicarinatum*[5] and *T. alpestre*[6]. *Tetramorium alpestre* is socially polymorphic, where monogynous colonies in some populations lack aggression, possibly paving the way for supercoloniality.

Pheidole — *Pheidole megacephala* is a supercolonial invader[7], comprising two cryptic species, both supercolonial[8].

Wasmannia — *Wasmannia auropunctata* is a tropical supercolonial invader[9] with small supercolonies in native range.

Monomorium — *Monomorium pharaonis* is a global supercolonial pest[10]. Supercoloniality has been mentioned also for *M. floricola*[2,3,12], but not conclusively shown on large scales.

Solenopsis — *Solenopsis invicta* is an invasive species whose polygynous and polydomous colonies show supercolony characteristics, e.g. near-zero relatedness, very high densities and lack of territoriality. The species is mentioned as supercolonial in[3,11,12] but large functional supercolonies are unconfirmed and also multicoloniality has been suggested[13]. Supercoloniality has been demonstrated in *S. saevissima*[14], and suggested for *S. geminata*[3,15].

Myrmica — *Myrmica rubra* is a highly polygynous and polydomous species, and both supercolonial and multi-colonial populations are known in native and invasive ranges[16,17]. Native supercolonies have been described also in *M. sulcinodis* alongside smaller polydomous colonies[18].

Formicinae

Paratrechina — *Paratrechina longicornis* is an invasive pest listed as supercolonial in[2,3], but genetic and behavioural studies describing large supercolonies are lacking.

Nylanderia — *Nylanderia fulva* has supercolonies in both invasive and native ranges[18]. *N. bourbonica* is listed as super-colonial in[3,4] but experimental confirmation is lacking.

Lasius — The invasive garden ant *Lasius neglectus* is an invasive supercolonial species in Europe[19]. Elements of super-coloniality (large scale polydomy, polygyny and lack of territorial borders) have been described in *L. sakagamii*[13,20] but supercoloniality remains to be confirmed.

Polyrhachis — *Polyrhachis robsoni* is an arboreal native supercolonial ant[21].

Formica — *Formica* includes many species capable of supercoloniality. Some species such as *F. polyctena*, *F. aquilonia* and *F. paralugubris* are obligately highly polygynous and polydomous, while others such as *F. exsecta*, *F. truncorum* and *F. cinerea* are socially polymorphic[22,23].

Cataglyphis — *Cataglyphis* is a socially highly variable desert ant genus where both super-colonies[24] and smaller polydomous societies[25] have been described in *C. niger*.

Anoplolepis — *Anoplolepis gracilipes* is an invasive supercolonial species[26]. Supercoloniality has also been suggested, but not strongly demonstrated, for "the pugnacious ant" *A. custodiens*[3].

Lepisiota — *Lepisiota canescens* is a recently discovered supercolonial species[27] with very high invasive potential. Supercoloniality and invasion potential have been suggested also for *L. incisa*[28].

Dolichoderinae

Linepithema — *Linepithema humile* is the paradigmatic invasive supercolonial species. Invasive supercolonies are the largest described[29], spanning several continents[30]. In the native range supercolonies are much smaller[31].

Technomyrmex — *Technomyrmex* contains several invasive species, and supercolonies at least in the invasive ranges have been described in *T. albipes*[32] and *T. difficilis*[33].

Tapinoma — Supercolonial populations have been described in the native odorous house ant *Tapinoma sessile*[34]. The invasive *T. melanocephalum* is listed as supercolonial in[2-4] but genetic evidence is lacking.

Pseudomyrmicinae

Pseudomyrmex — *Pseudomyrmex veneficus* is an acacia ant, one of the earliest described cases of supercoloniality[35].

Fig. 2: Species where supercoloniality has been demonstrated, or claimed but not strongly demonstrated, and their schematic phylogenetic distribution (phylogeny based on Economo & al. 2018). Literature cited: 1: Heinze & al. 2006, 2: Debout & al. 2007, 3: AntProfiler Database http://134.158.74.46/AntProfiler/, 4: Eyer & Vargo 2021, 5: Astruc & al. 2001, 6: Steiner & al. 2003, 7: Fournier & al. 2009, 8: Fournier & al. 2012, 9: Le Breton & al. 2004, 10: Schmidt & al. 2010, 11: Morel & al. 1990, 12: Helanterä & al. 2009, 13: Kjeldgaard & al. 2020, 14: Lenoir & al. 2016, 15: Ross & al. 2003, 16: Huszár & al. 2014, 17: Chen & al. 2018, 18: Eyer & al. 2018, 19: Ugelvig & al. 2008, 20: Yamauchi & al. 1983, 21: Van Zweden & al. 2007, 22: Borowiec & al. 2021, 23: Rosengren & al. 1993, 24: Leniaud & al. 2011, 25: Saar & al. 2014, 26: Drescher & al. 2010, 27: Sorger & al. 2017, 28: Sithole & al. 2009, 29: Giraud & al. 2002, 30: Van Wilgenburg & al. 2010, 31: Pedersen & al. 2006, 32: Dejean & al. 2010, 33: Sollins 2010, 34: Buczkowski & Bennett 2008, 35: Janzen 1973.
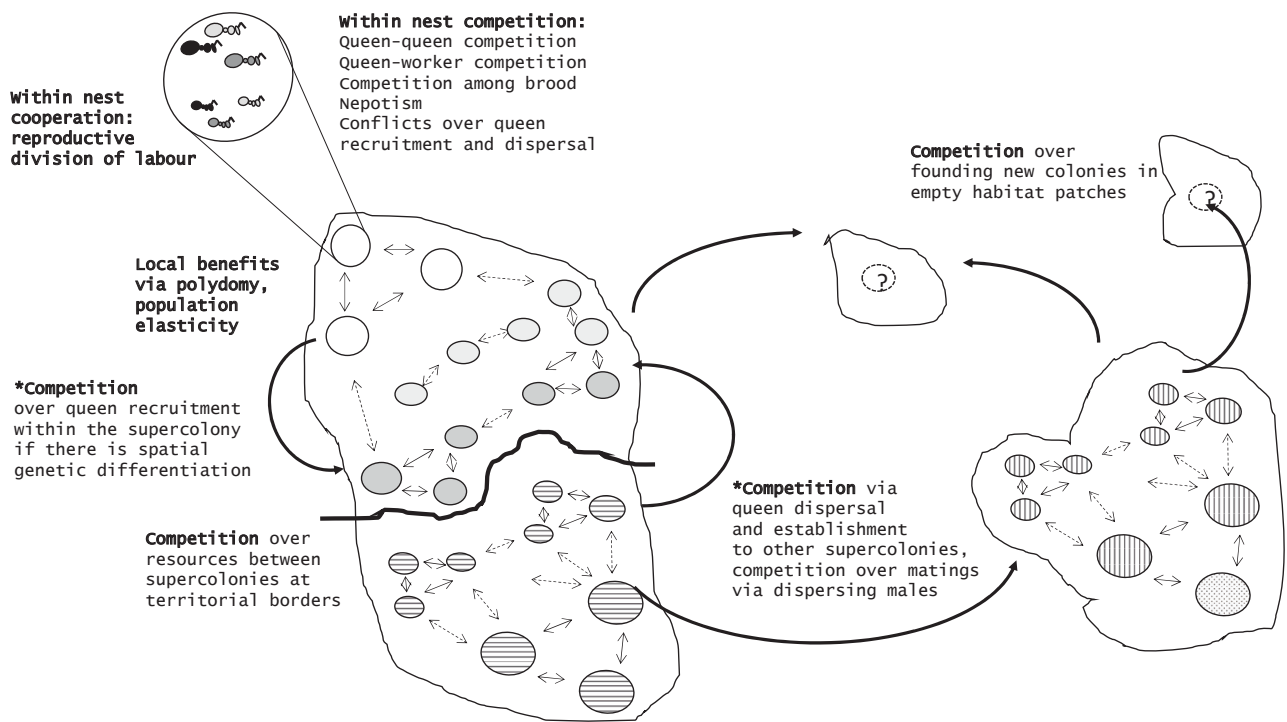
Fig. 3: *Key cooperative and competitive processes of supercolonies. Circles depict nests within supercolonies, thin solid arrows direct interactions such as movement of resources and individuals. Hatched arrows denote recognition and acceptance as a colony member. Thick lines denote territory borders, shapes outline areas of suitable habitat, and thick arrows denote movement of sexuals outside their native nests, within and between supercolonies. The processes marked with an asterisk are ones that apply perhaps exclusively in supercolonies, others are likely to apply to many polygynous and polydomous ants.*

Secondary polygyny and polydomy are both common in ants also outside supercolonies (see Boomsma & al. 2014 and Debout & al. 2007 for reviews, respectively), but supercolonies stand out from just any large polydomous colony. First, "normal" polydomy occurs on scales where cooperation and functional integration between nests is still possible (Debout & al. 2007, Robinson 2014), whereas the vastness of supercolonies precludes direct interaction and functional integration between all nests and individuals. This begs the question of why ants separated by several hundreds of meters, or oceans in the case of the global Argentine ant supercolony (Van Wilgenburg & al. 2010), still recognize each other as colony members and potential cooperators. Second, it has even been suggested that supercolonies represent a new kind of evolutionary entity (Pedersen & al. 2006, Pedersen 2012), perhaps even a novel kind of organismality or individuality (Bourke 2011), but formal explorations of this hypothesis have so far been tentative (Kennedy & al. 2014).

This review sets supercolonies in a kin selection perspective. I highlight selection processes and genetic kin structures at several spatial and temporal scales that are necessary for understanding the origin and maintenance of supercolonies. Furthermore, I review selective processes both at the level of the colonies as (super)organisms, that is, individuals that live, die, and compete with other such "colony-individuals" (Helanterä 2016,

Boomsma & Gawne 2017) and at the level of individuals or genetic lineages within colonies. I also describe our current understanding and outstanding questions in genetics of supercolonies. Finally, I summarize recent and future directions in theoretical understanding of supercolonies.

Diversity in supercoloniality

Defining supercoloniality is far from clear-cut. I discuss the definitions of supercoloniality in Box 1. Main taxa demonstrated or suggested to be supercolonial as well as some key taxa for understanding evolution of supercolonies are summarized in Figure 2. I am not aiming to present an exhaustive list of all species that could be supercolonial, especially as it is clear that new cases continue to be discovered (Sorger & al. 2017, Seifert 2020). Rather than a species by species or population by population discussion of supercolonial qualifications, the key for the remainder of this review is that these are species where potential for forming supercolonies exists, often alongside non-supercolonial populations. This diversity is part of understanding supercolonies.

The size of supercolonies is highly variable. Apart from the gigantic supercolonies observed in invasive species (Giraud & al. 2002, Le Breton & al. 2004, Fournier & al. 2009, Van Wilgenburg & al. 2010), which are outcomes of jump dispersal with human traffic rather than natural dispersal, the largest supercolony described is the "Ishikari

Box 1: How to define a supercolony?

Originally, the lifestyle discussed in this paper was described as "unicolonial" (WILSON 1971), but here, I have chosen to use "supercolony" instead, for two main reasons. First, the term can easily be used for both a supercolony and a supercolonial lifestyle of a species or a population, whereas unicoloniality is suitable for a population or species only, not a colony. Second, it is clear that supercolonies may border each other and live in populations that are not unicolonial. I agree with previous work in that the term "unicolonial" may still appropriately be used for species capable of supercolony formation or when referring to a clearly unicolonial population.

Even the term supercolony is not clear-cut, unfortunately. There are competing and overlapping definitions for what supercolonies or supercolonial species are, recently extensively discussed with a special focus on the Argentine ant (GORDON & HELLER 2012, MOFFETT 2012, PEDERSEN 2012). Here, I synthesize the merits and benefits of the main lines of definitions.

First, supercolonies have been identified as polydomous colonies so large that direct interactions become impossible (PEDERSEN 2012). This identifies a key feature about the ecology of supercolonies that makes them distinct from merely large polydomous colonies, as the borders of behavioural, genetic, and chemical unity extend beyond the functional organization of local nest networks. This, as outlined in the main text, leads to particular evolutionary questions on their stability and maintenance. As a criticism, it has been commented that large ant societies are "anonymous" and most individuals never directly interact anyway. I argue this criticism somewhat loses its momentum, if we focus on resource flows and functional organization rather than one-on-one encounters of workers as the criteria (GORDON & HELLER 2012) for "interactions" that are ecologically relevant. This definition has been narrowed and supplemented by further qualifiers: that a supercolony extends across multiple sites with common origin and interconnected nests within each site and identity by descent across sites as well as closed reproduction, so that mating happens exclusively within supercolonies. The last of these is important for arguing that supercolonies present a distinct type of evolutionary units and seems to apply well to Argentine ants and Pharaoh ants. However, it disqualifies many species commonly agreed to be supercolonial, given the widespread gene flow between supercolonies. Along similar lines, GORDON & HELLER (2012) define a supercolony as a lineage of polydomous colonies with identity by descent that are not functionally coherent.

Alternatively, it has been argued that the key to the definition of a supercolonial species is the ability for indefinite growth, through budding and internal queen recruitment, without losing chemical identity and acceptance as group members (MOFFETT 2012). This definition emphasizes group membership and aggression towards outsiders rather than functional integration, and correctly and importantly identifies the shared key process underlying supercoloniality (rather than an outcome, as the previous definitions), and focuses on abilities held by all members of a species, rather than a definition that would be applied on a colony-by-colony basis. This definition has been further complemented with a qualification of a minimum colony size of a million, which makes the definition more applicable at a colony rather than a species level but faces the unavoidable problems of the arbitrariness of any numerical cut-off. The focus on aggression against outsiders has also been criticized, given the very low levels of aggression by many supercolonial species and sensitivity of such findings to the choice of bioassay (GORDON & HELLER 2012).

It seems that none of the criteria would be sufficient on their own for unambiguously delineating supercoloniality or supercolonies. We need to understand both the patterns of colony size, continuity, and interactions, as well as the underlying process of indefinite growth. Too strong a focus on necessary or sufficient criteria seems unnecessary, and it seems useful to understand supercoloniality as a continuum, with paradigmatic examples such as *Linepithema humile* and *Monomorium pharaonis* at one end, and more variable and flexible species, with less extensive polydomy, such as *Myrmica rubra* and *Solenopsis invicta* lower on the scale. Such a gradation also allows comparing different colonies within a species: not all colonies have reached sizes so large that functional integration or direct interactions become impossible, even if they fulfill the definition of indeterminate growth potential.

supercolony" of *Formica yessensis* WHEELER, 1913 on Hokkaido, Japan. It was estimated to comprise > 45,000 nests, > 300,000,000 workers, and > 1,000,000 queens (HIGASHI 1976). In its native range, the Argentine ant *Linepithema humile* forms colonies spanning from tens to several hundreds of meters (PEDERSEN & al. 2006, HELLER & al. 2008, VOGEL & al. 2009). *Myrmica rubra* (LINNAEUS, 1758), native to Europe and invasive in North America,

may form supercolonies of up to a few hectares (HUSZÁR & al. 2014, CHEN & al. 2018) but also much smaller polydomous colonies (SEPPÄ & PAMILO 1995, WALIN & al. 2001) when suitable habitat patches are small. Many others live in populations that are mosaics of larger and smaller polydomous societies, with no clear dichotomy between supercolonies and non-supercolonial polydomous colonies (PEDERSEN & BOOMSMA 1999, HOLZER & al. 2006, HUSZÁR

& al. 2014). Even clearly dichotomous polymorphism is found: In the fire ant *Solenopsis invicta* Buren, 1972 and a number of *Formica* species, full-sib colonies headed by single queens may locally coexist with polygynous and polydomous, even supercolonial societies (Ross & Shoemaker 1997, Sundström & al. 2005).

Regardless of what species or populations exactly qualify as supercolonial, it is clear that beneath the shared, convergently evolved features their diversity is great. Diversity in morphology, climate, and habitat preferences as well as nesting habits are reviewed in Helanterä & al. (2009). Supercoloniality is not common at the species level as there are some tens of supercolonial species out of > 13,000 described ant species. These species are scattered widely across the major subfamilies of ants, but the hypothesis that supercolonial species are evolutionary dead-ends with a twiggy distribution (Helanterä & al. 2009) remains to be formally tested. However, groups such as *Formica* (Borowiec & al. 2021), *Pheidole* (Fournier & al. 2012), and the *saevissima*-species group of *Solenopsis* (Lenoir & al. 2016, Shreve & al. 2020), where supercolonial or highly polydomous closely related species co-exist, cast a doubt on the generality of the hypothesis as it is possible that supercolonial species have diverged rather than gone extinct.

Kin selection in supercolonies: cooperation and competition at multiple scales

In order to understand the birth and persistence of supercolonies and the associated evolutionary enigma of cooperation despite low relatedness, we need to understand cooperation and conflict at different spatial and temporal scales. In the light of inclusive fitness or kin selection theory, evolutionary altruism (sensu Hamilton 1964a) evolves and prevails among relatives. More technically, the benefits of cooperation must be shared among a more closely related group of individuals than those who compete over genetic representation in the future population. Thus, relatedness among cooperating nestmates and colony-mates needs to be scaled against the relatedness towards competitors. The more a supercolony competes with other supercolonies in the population, the less overwhelming the issue of low local relatedness is. The same applies to within supercolonies: If individuals were able to cooperate with close kin and compete against distantly related individuals, low average local relatedness would not be an issue (Helanterä & al. 2009). This section describes how the key biological features of supercolonies define the scales of cooperation and competition within and between nests and colonies. Figure 3 gives a visual summary of the relevant processes.

Cooperation within nests: are workers helping their relatives?

Understanding the genetic similarity between the reproductive queens and the workers who help is the key to understanding how natural selection operates on social insects (Hamilton 1964b, Queller & Strassmann 1998).

Herein, as said, lies the main issue of kin selection within supercolonies: Given high numbers of queens and mixing of individuals between nests, it is highly unlikely that a worker is helping her mother or another close relative.

Three main points emerge from relatedness among nestmates in supercolonies. First, relatedness is often low, occasionally even statistically indistinguishable from zero. Examples include *Linepithema humile*, *Lasius neglectus* Van Loon & al., 1990, and many species of *Formica*, as reviewed in Helanterä & al. (2009). Second, relatedness varies within species. In some cases, such as *Myrmica rubra* (see Seppä & Walin 1996), there is a continuum starting from near-zero, in others, relatedness varies discontinuously from very low to full-sib with a marked dimorphism in queen numbers – most clearly in *Solenopsis invicta* (see Ross & Fletcher 1985, Ross & al. 1996), and many *Formica* species (Sundström 1993, Goropashnaya & al. 2001, Seppä & al. 2004). Third, relatedness depends on the scale of investigation so that relatedness among nestmates increases when the reference population, with which the allele frequency similarity is compared, is expanded (Chapuisat & al. 1997, Tsutsui & Case 2001, Kümmerli & Keller 2007a, Schultner & al. 2016, Eyer & al. 2018).

Lack of territorial boundaries and apparent mixing of individuals within a behaviourally defined supercolony does not necessarily mean complete lack of kin structure. Isolation by distance arising from population viscosity may mean that individuals in close-by nests are genetically more similar to each other than individuals at opposite ends of the supercolony. Such patterns have been described within supercolonies of, for example, *Linepithema humile* (see Tsutsui & Case 2001, Ingram & Gordon 2003), *Formica pressilabris* Nylander, 1846 (Hakala & al. 2020), *Formica lugubris* Zetterstedt, 1838 (Gyllenstrand & Seppä 2003), *Formica paralugubris* Seifert, 1996 (Chapuisat & al. 1997), *Polyrhachis robsoni* Kohout, 2006 (van Zweden & al. 2007), and *Myrmica rubra* (see Huszár & al. 2014). Supercolonies may also consist of genetically separable clusters even if no behavioural boundaries are seen (Holzer & al. 2009). Thus, even in the absence of borders, dispersal dynamics and movement restriction may lead to local genetic correlations. Whether population structures arising from viscosity are conducive to evolutionary maintenance of cooperation will be discussed below.

Finally, inferring inclusive fitness benefits from snapshot samples of worker relatedness needs to be done with caution. The focus has been on adult workers, but as these are the individuals that move the most across nests, they reflect the minimum levels of relatedness within the society (Helanterä 2009), while the relatedness between workers and queens and brood is more directly relevant for inclusive fitness and could be higher. Higher relatedness between queens or between workers and brood than among workers within nests has been inferred in *Formica exsecta* Nylander, 1846 (Kümmerli & Keller 2007a) and *Formica paralugubris* (see Chapuisat & Keller

1999). Also in *Linepithema humile*, a stronger population structure in queen than worker samples has been observed (Reuter & al. 2001). Furthermore, relatedness patterns may vary seasonally (Schultner & al. 2016), so that workers may be related to the nestmate queens and brood early in their life, even if movement dilutes the relatedness later on.

Direct competition over reproduction within nests

The flipside of cooperation is the potential for conflict and competition. Ant nests are no exception, and queens that avoid dispersal face local competition over reproduction and worker attention. That is, the cohabiting queens are cooperative breeders, sharing the nest and its worker force as a common resource (Rosengren & al. 1993, Boomsma & al. 2014), or even "parasitic" inhabitants of the ecosystem provided by the worker population (Elmes 1973, Hölldobler & Wilson 1977). Such resource sharing inevitably entails an element of competition, even leading to a potential of over-exploitation and a "tragedy of the commons" (Boomsma & al. 2014). However, as genetic studies mainly focus on workers, queen-queen competition is poorly understood, even though it is fundamental to kin selection within nests.

In line with observed low levels of relatedness in workers and brood, genetically effective queen numbers have been estimated to be very high in supercolonies of, for example, *Formica exsecta* (see Kümmerli & Keller 2007b), *Myrmica rubra* (see Huszár & al. 2014), *Myrmica sulcinodis* Nylander, 1846 (Pedersen & Boomsma 1999), and *Linepithema humile* (see Pedersen & al. 2006). An accurate picture of apportionment of reproduction is difficult to come by in field colonies, given the high numbers of queens who share many alleles, and variation in contributions to different sexes and castes (Ross 1988, Fournier & Keller 2001, Kümmerli & Keller 2007b, Libbrecht & al. 2011). Clearly, studies that jointly look at production of workers, males, and gynes are needed for a comprehensive view. Added complexity comes from queen turnover and temporal variation in reproductive shares (see, e.g., Boomsma & al. 2014 for possible scenarios).

To understand patterns of reproductive sharing bottom-up, we must observe the underlying chemical, physiological, and behavioural mechanisms. Little is known about chemical signals or suppression among queens in secondarily polygynous societies. Queens mutually suppress their reproduction in *Solenopsis invicta* (that is by far the best understood highly polygynous species, even if debatable in its supercoloniality, see Tschinkel 2006) and *Linepithema humile* (see Abril & Gómez 2020). Is this a general pattern, and is it similar to the systems of honest fertility signaling in queen-worker interactions (Holman & al. 2010), or is this more competitive in nature, as has been suggested for *S. invicta* (see Tschinkel 2006)? Reproductive competition among queens is likely to be mediated by interactions with workers and involve multiple complex interactions between castes and life-stages

(Warner & al. 2016, Warner & al. 2018), and mere egg laying rates are unlikely to determine reproductive shares (Tschinkel 2006), so careful experimentation is needed.

Workers may compete for reproduction with queens and with each other as well. In polygynous colonies with low relatedness among queens, workers are predicted to prevent each other from reproducing ("worker policing"; Ratnieks 1988, Wenseleers & Ratnieks 2006). However, both the extent of workers laying eggs and the proportions of these eggs reared to males are largely unmapped. Many supercolonial species have sterile workers (Helanterä & al. 2009), but, for example, in *Myrmica*, workers contribute significantly to male production (Smeeton 1981, Evans 1993, Wardlaw & Elmes 1998). Similarly, workers of all *Formica* species have retained the capability to lay eggs, and in at least some supercolonial species they lay eggs in lab colonies even in the presence of a queen (Helanterä & Sundström 2007), suggesting ongoing conflict.

Other kin conflicts within nests

In addition to direct competition for reproduction, low and variable relatedness leads to evolutionary conflicts (Queller & Strassmann 2018) among kin, for example over the reproductive shares or sex allocation of a colony. These conflicts are diverse and complex and vary in how harmful they are to the colony, that is, how well they are resolved (sensu Ratnieks & al. 2006).

First, in colonies where multiple matrilines and patrilines coexist, workers would benefit from directing help to closer than average relatives. Despite the potential conflict, such nepotistic patterns have not been shown in species with highly polygynous societies (e.g., DeHeer & Ross 1997, Keller 1997, Reuter & al. 2001). Nepotism is very rare even in simpler ant societies (but see Hannonen & Sundström 2003 for a case in polygynous but not supercolonial *Formica fusca* Linnaeus, 1758), and lack of kin informative cues is likely a major constraint (Boomsma & d'Ettorre 2013). Cues in adults seem uniform within supercolonies (Brandt & al. 2009, Martin & al. 2009), likely facilitated by trophallaxis (Meurville & LeBouef, 2021), and the inability to recognize close kin is likely to be one key to the maintenance of supercolonies (Helanterä & al. 2009). Theory predicts rarity of nepotism (Keller 1997) as costs to colony productivity and selection against diversity at genetic recognition loci function against nepotism (Ratnieks 1991). Furthermore, variation in brood viability among queens can create nepotism-like patterns with no active discrimination as a cause (Holzer & al. 2006), so correlative results from field studies should be interpreted with caution with respect to the underlying kin selection mechanisms.

However, nepotism concerning brood is an under-investigated possibility. Eggs might carry kin-informative cues as their cues seem to be poorly transferrable and less prone to mixing than surface chemicals of adults (D'Ettorre & al. 2006). Matriline-informative and in some cases even kin-informative cues have been shown to exist

Fig. 4: Conflict among brood in supercolonies: a *Formica* larva eating an egg. Such cannibalism is prevalent in highly polygynous *Formica* supercolonies (photo Unni Pulliainen).

on eggs of supercolonial *Formica* species (Helanterä & d'Ettorre 2015). As kin-recognition abilities of workers through self-matching have been shown in the genus (El-Showk & al. 2010), workers could potentially be able to detect their kin. Theoretically, nepotistic interactions involving brood, especially eggs, could be more likely than nepotistic interactions among adults. Colony-level costs selecting against cues and behaviours are thought to be the main reason for rarity of nepotism (Keller 1997). However, in a highly polygynous colony, there might be a large excess of eggs, and such costs could potentially be low.

Furthermore, we must consider the behaviours of the brood themselves (Schultner & al. 2017). First, it is possible that brood compete with each other via cannibalism (Fig. 4): Consuming nestmate brood is a direct way of getting more resources and removing competitors and thus potentially increasing own chances of developing into a queen. Inclusive fitness models predict that proneness of cannibalizing brood should be higher in polygynous

societies with low relatedness (Schultner & al. 2014). Such an increase in cannibalism with polygyny has been demonstrated in *Formica* ants (Schultner & al. 2013, 2014). More comparative and experimental studies are needed to understand how common such behaviours are and what ultimate factors explain them. However, it is unlikely that such cannibalism would be highly costly for the colonies. Supercolonial *Formica* nests are cohabited by hundreds of queens (Rosengren & al. 1993), likely laying a considerable surplus of eggs so that consumption of eggs does not need to turn into deficit in brood reared, especially if resource recycling is efficient (Chapuisat & al. 1997).

Brood may also compete via begging for food from workers (Creemers & al. 2003, Kaptein & al. 2005, Peignier & al. 2019). General models predict dishonest signaling of hunger when brood does not comprise close relatives (Godfray 1995, Johnstone 2004). While these models wait to be extended into complex haplodiploid societies and more work is needed before we can robustly interpret behaviours of larvae, tentative support for increasing dishonesty in begging in low relatedness societies has been found in *Formica* ants (Peignier & al. 2019). However, as with cannibalism above, colony-level costs of such behaviours are likely negligible.

Finally, a conflict at the very core of a supercolonial lifestyle has perhaps surprisingly been somewhat neglected, that is, the conflicts over the rearing, recruitment, mating, and dispersal of the young reproductive queens (Fig. 5). Theory predicts that old queens have a narrower range of conditions (local kin structures and the expected local competition vs. the chances of breeding elsewhere), in which they should allow supernumerary queens to stay in nests, compared with workers (Crozier & Pamilo 1996). Furthermore, general kin-conflict theory predicts that offspring should be less willing to disperse under risks

Fig. 5: Polygyny in *Formica aquilonia*. While queens are winged and capable of flight, many queens stay in their natal nests, which results in queen numbers rising to hundreds or even thousands per nest (photo left Sanja Hakala, right Heikki Helanterä).

compared with what their mothers would prefer (Motro 1983, Starrfelt & Kokko 2012). Thus, young gynes, the rearing workers, and the old queens could all have different evolutionary optima concerning when to allow gynes to stay at home (Hakala & al. 2019). Importantly, this could be a conflict where costs are actually considerable and the conflict poorly resolved (sensu Ratnieks & al. 2006). It seems unlikely that queen numbers rising to hundreds or even thousands per nest would be optimal for the colony, compared with a situation where most queens would disperse and try to found new colonies elsewhere.

While regulation of queen rearing through worker-larva interactions has been observed in *Monomorium pharaonis* (Linnaeus, 1758), *Myrmica rubra*, and *Solenopsis invicta* (see Bourke & Ratnieks 1999) and workers are known to cull large numbers of queens in *Linepithema humile* (see Keller & al. 1989), the drivers of queen-number regulation are in general poorly understood. In *S. invicta*, the presence of several queens suppresses both the production of new queens as well as the dealation of queens, but recruitment of new queens does not seem to be connected to resident queen numbers (Tschinkel 2006). In polygynous colonies of *Formica exsecta*, rearing of new queens seems well regulated and only occurs when resident queen numbers are low and resource levels suitable (Brown & al. 2003, Kümmerli & Keller 2008). In *Myrmica*, queen production seems to be similarly closely regulated, suggesting that the conflict over queen recruitment is suppressed (Radchenko & Elmes 2010). In *Formica aquilonia*, Yarrow, 1955 between one third and half of the nests seem to produce new queens yearly (Pamilo & Rosengren 1983, Kennedy & al. 2014), and queen numbers are extremely high – even if workers may reject even nestmate queens that are introduced experimentally in the closely related *Formica paralugubris* (see Fortelius & al. 1993, Holzer & al. 2008). Fully understanding the dynamics of this conflict requires simultaneous consideration of variation in queen-dispersal physiology and behavior as well as control over queen rearing, dispersal and recruitment decisions (Hakala & al. 2019). Such conflicts over queen recruitment are even more complex in species with polymorphism in queen size, morphology, and dispersal, observed in, for example, *Polyrhachis robsoni* (see van Zweden & al. 2007), *Myrmica rubra* (see Steiner & al. 2006), and *Solenopsis geminata* (Fabricius, 1804) (McInnes & Tschinkel 1995). The kin conflicts concerning queen behaviour, physiology, and morphology could ultimately even be the drivers of evolution of parasitic inquiline strategies and speciation (Bourke & Franks 1991).

Cooperation between nests: What are the benefits of polydomy and how far do they extend?

Dependent nest founding, likely driven by local competition, leads to polydomous colonies if the nests maintain a functional contact after founding of the satellite (Debout & al. 2007b, Boomsma & al. 2014, Robinson 2014). Such

Fig. 6: Part of a highly polydomous *Formica exsecta* colony in Finnish Lapland (photo: Heikki Helanterä).

polydomy (Fig. 6) provides many potential benefits via, for example, risk spreading, foraging benefits, and ergonomic efficiency (Robinson 2014). For example, having queens spread over several nests decreases vulnerability to predation or disaster, inhabiting multiple nests helps to escape size limitations of nest sites, spatial spread may facilitate food discovery and monopolization and reduce variance in colony success in heterogeneous environments. The balance of these factors likely varies across species or colonies, depending on the typical intensity of competition encountered and reliance of species on stable food resources, such as *Formica* on their persistent aphid trees (Domisch & al. 2016), or opportunistic recruitment to monopolise ephemeral sources by invasive supercolonial species (Holway & al. 2002).

The current benefits of polydomy do not necessarily tell us about the drivers of its origin (Hölldobler & Wilson 1977), and evolutionary cause and effect may be difficult to infer. Thus, mere ecological dominance is a poor explanation for the evolutionary origin and maintenance of polydomy and supercolonies. Rather, we need to understand the scale and structure of cooperation between nests. At what kind of scales are the colonies functionally integrated, compared with genetic structures or aggression patterns (Gordon & Heller 2014)? While benefits of polydomy have been demonstrated in the lab (Stroeymeyt & al. 2017) and in silico (Cook & al. 2013, Burns & al. 2019), our understanding of supercolonial polydomy in the wild is limited to a few important model systems that suggest organization at scales much smaller than whole supercolonies.

The longest studied supercolony in terms of functional organization is the *Linepithema humile* population at Jasper's Ridge Biological Preserve, which has been monitored since 1993 (Gordon & Heller 2014). Rather than a single continuous supercolony, the population consists of polydomous subcolonies that each contract to a small number of very large nests for the winter and expand to larger areas over the summer (Heller & Gordon 2006).

Studies of resource flows using labelled food show that workers come to feed on baits from within a few tens of meters from several nests within each polydomous colony but not between colonies (HELLER & al. 2008). Genetic substructure within the supercolony also suggests that these subcolonies are genetically slightly differentiated from each other, that is, worker and queen movements are likely restricted between them, even if gene flow via males partly dilutes this genetic structure (INGRAM & GORDON 2003). It is clear that the supercolony that has a shared origin does not function as a single complete colony. It remains to be seen whether the small supercolonies of the species in its native range are similarly functionally subdivided.

The other important study system for functional understanding of polydomy is *Formica lugubris* in Northern England (ELLIS & ROBINSON 2014, 2016, BURNS & al. 2020). While there is no genetic, chemical, or aggression assay evidence that the spatially separate polydomous colonies at these sites would form a supercolony, this species is supercolonial in its Central European range (SEIFERT 2018), and insight into nest interactions under polydomy is likely generalizable to supercolonies as well. Trail connections and traffic and resource flows between nests and aphid trees demonstrate that resource sharing among neighbouring nests is based on local features of the network rather than any global feature of the polydomous colony (ELLIS & al. 2014, 2017). Workers mainly transport resources between two nests rather than across the broader network (ELLIS & ROBINSON 2016). Similarly, the success of a nest is strongly dependent on its position in the network. Flows of resources do not seem in any strong way optimised at the polydomous colony-level, given that workers treat also other nests, not just aphid trees, as food resources. Workers seem to have fidelity to a certain nest, and workers with different nest fidelity patterns may simultaneously transport resources to opposite directions (ELLIS & ROBINSON 2016). Clearly, any function at a higher level than a small number of interacting nests is either absent or very poorly coordinated.

Organisation beyond relatively small polydomous units similarly lacks in, for example, *Tapinoma sessile* (SAY, 1836), where the shape of the trail network rather than mere physical proximity dictates patterns of food sharing, and supercolony-wide food sharing is lacking on scales of a few thousand square metres (BUCZKOWSKI & BENNETT 2008). Also noteworthy are the strong seasonal dynamics of nest founding and colony expansion and contraction observed in *Linepithema humile* (see HELLER & GORDON 2006), *Nylanderia fulva* (see OI 2020), *T. sessile* (see BUCZKOWSKI & BENNETT 2008), and *Formica truncorum* FABRICIUS, 1804 (ELIAS & al. 2005). Thus, observations from very limited periods should be generalised with caution. It seems clear that the benefits of supercoloniality are not due to organization beyond that provided by smaller polydomous units. Therefore, the reasons for why individuals across vast distances are treated as colonymates need to be looked for elsewhere.

Competition among nests and colonies: What do aggression bioassays tell us?

Moving beyond the immediate limits of worker movement and resource flows, supercolonies are most often delineated based on aggressive interactions by workers or lack thereof. Lack of aggression is instrumental in understanding the history and future of supercolonies as it reflects the shared descent and genetic and chemical similarity of nests (DRESCHER & al. 2007, UGELVIG & al. 2008, BRANDT & al. 2009, VOGEL & al. 2009, SCHMIDT & al. 2010). However, it does not measure direct and current cooperation but rather the limits of potential cooperation and potential territorial borders.

Aggression studies suggest there are no truly "unicolonial" species, where workers would universally accept all conspecifics as colony members. Aggression occurs between individuals from separate supercolony localities when brought together in bioassays and when they do not share descent. However, from a kin selection point of view, disparate supercolonies that never meet do not compete for resources. Only when genetically distinct supercolonies compete locally, competition alleviates the problems associated with low relatedness within supercolonies locally. While it is common for supercolonies to dominate locally to such an extent that direct interactions with other supercolonies do not occur, there are also numerous cases where direct competition is possible. In the Argentine ant, both native (THOMAS & al. 2007) and invasive (JAQUIÉRY & al. 2005, SUNAMURA & al. 2007) supercolonies, and in some cases even smaller polydomous units (HELLER 2004), may border each other and maintain distinct identities and potential for aggressive territorial encounters (but see BERVILLE & al. 2013 for an apparent exception). Several colonies existing close-by, possibly opening the door to direct competition, have been described also in *Formica polyctena* FOERSTER, 1850 (MABELIS 1979, DRIESSEN & al. 1984), where aggression can lead to the demise of whole colonies, *Myrmica rubra* (native range see HUSZÁR & al. 2014, invasive range see CHEN & al. 2018), *Nylanderia fulva* (see LEBRUN & al. 2019), and *Lepisiota canescens* (EMERY, 1897) (SORGER & al. 2017). Aggression between nests may also occur in complex mosaics in colonies that superficially look like continuous supercolonies (CHEN & al. 2018, HAKALA & al. 2020). However, detailed studies of how often such proximity leads to conflicts over resources, changes in resource ownership, and gain or loss of territory are in most cases largely lacking.

Given the prevalence of aggression bioassays as the preferred method of delineating supercolonies, several points of caution should be made. First, interpretation of bioassay results should consider the importance of choosing the right assay (ROULSTON & al. 2003) and ideally comprise multiple approaches (KRAPF & al. 2019). Conspecific aggression levels demonstrated by many supercolonial species are very low (JANZEN 1973, CHAPUISAT & al. 2005, SCHMIDT & al. 2010, GORDON & HELLER 2014), and the methods used to detect colony borders may lack sensitivity (BJÖRKMAN-CHISWELL & al. 2008, GORDON &

HELLER 2014). Furthermore, under complete habitat monopolization, the encounter rates that determine optimal aggression thresholds may be such that universal acceptance is optimal even if recognition is possible (CHAPUISAT & al. 2005, HOLZER & al. 2006). In such cases, attention should be paid to subtle behaviours such as antennation times and trophallaxis frequencies.

Second, attention should be paid to seasonal and context sensitive variation in colony size and recognition. Seasonal expansions and contractions of colonies have been shown in, for example, *Nylanderia fulva* (see OI 2020), *Tapinoma sessile* (see BUCZKOWSKI & BENNETT 2008), and *Formica truncorum* (see ELIAS & al. 2005), as well as *Linepithema humile* (see HELLER & GORDON 2006). Aggression patterns vary with the season (MABELIS 1979, KATZERKE & al. 2006) and nutritional situations (SORVARI & al. 2008) in *Formica*. Furthermore, encounter rates of workers from different colonies may affect discrimination and responses between specific pairs of colonies, for example, in a "nasty neighbour" effect, where frequently encountered heterocolonial individuals are disproportionately often aggressed, as observed in *Cataglyphis nigra* (ANDRÉ, 1881) (SAAR & al. 2014).

Third, experiments that quantified behaviours beyond short term bioassay aggression have shown that despite initial aggression behaviours may take amicable turns. Experiments in *Linepithema humile* (VÁSQUEZ & SILVERMAN 2008a) and *Monomorium pharaonis* (PONTIERI 2014) have shown colony fusions, especially when genetically and chemically relatively similar nests interact. Furthermore, data on long-term queen survival and reproductive shares are necessary for understanding whether such mergers are mutually beneficial or hostile takeovers. While supercolonies do not in general originally arise through merging of many nests, some genetic data suggest that merging between colonies plays a role, for example, in cases where two strong colonies are unable to outcompete one another, which is certainly a process in need of further attention (PEDERSEN & BOOMSMA 1999, SEPPÄ & al. 2012, HUSZÁR & al. 2014). Merging of supercolonies could also explain the observations of several mtDNA haplotypes in nests of *Lepisiota canescens* (see SORGER & al. 2017) and *Formica paralugubris* (see HOLZER & al. 2009). Based on species where aggression seems to be completely lacking (STEINER & al. 2007, KRAPF & al. 2017), it has also been suggested that in the right kind of ecological settings, supercolonies could arise through absence of discrimination. This interesting hypothesis still awaits empirical support.

The discrepancy between patterns of aggression and scales of functional integration leads to a large open question. Why do differences in local environment and genetic drift not lead to divergence of supercolony parts that are functionally disconnected? If populations are genetically structured, why does discrimination not emerge? Is purifying selection against novel cues generally important for maintaining supercolony unity? A part of the answer certainly comes from assessing the extent of movement of queens and males, that is, gene flow.

Competition via queen recruitment

The bottom line for natural selection is who gets to reproduce. Thus, in addition to understanding supercolony borders and internal structures, we need to understand recruitment of new breeders. If queens or males cross colony borders when mating or establishing as reproductives, the supercolony is competing with non-kin over long time scales even if direct resource competition at territory borders does not occur. In such a case, the problems with low local relatedness are at least partly alleviated. However, recruitment of queens across nests within the supercolony can as well be construed as competition among nests or queens. Thus, we need to understand competition over reproductive positions via mating and queen recruitment at several scales.

In some important cases, establishing as a breeder outside the native colony seems almost impossible. Mating flights are absent or heavily curtailed in, for example, *Linepithema humile* and *Monomorium pharaonis*, and accordingly genetic data in both species suggest very strong colony isolation, both at nuclear and mitochondrial markers, even when supercolonies live next to each other (JAQUIÉRY & al. 2005, VOGEL & al. 2009, SCHMIDT & al. 2010). Behavioural observations also show that even when males of the Argentine ant fly and are allowed to enter nests for mating within a supercolony (PASSERA & KELLER 1994), workers discriminate against males from outside the supercolony, seemingly preventing gene flow altogether (SUNAMURA & al. 2011) and preserving the evolutionary independence of each supercolony (PEDERSEN 2012).

However, the majority of supercolonial species have winged queens (indeed also *Linepithema humile* and *Monomorium pharaonis*) and at least occasional mating flights of supercolonial queens have been observed in several *Formica* species (compiled in SEIFERT 2018: *Formica polyctena, Formica aquilonia, Formica paralugubris, Formica exsecta, Formica pressilabris*), *Myrmica rubra*, and *Myrmica sulcinodis*. Observations of gynes on the flight have been made in at least *Anoplolepis gracilipes* (SMITH, 1857) (HOFFMANN 2014), *Solenopsis geminata, Wasmannia auropunctata* (ROGER, 1863), *Paratrechina longicornis* (LATREILLE, 1802), *Tapinoma melanocephalum* (FABRICIUS, 1793), *Technomyrmex albipes* (SMITH, 1861) (TORRES & al. 2001), and *Technomyrmex difficilis* FOREL, 1892 (WETTERER 2008). In *Pseudomyrmex veneficus* (WHEELER, 1942) (JANZEN 1973) and *Polyrhachis robsoni* (see VAN ZWEDEN & al. 2007), large females are known to be dispersive and capable of independent founding. *Lasius neglectus* queens have been observed flying and suggested to be physiologically capable of independent founding (SEIFERT 2000). The ability of *Pheidole megacephala* (FABRICIUS, 1793) queens to found independently has also been anecdotally observed (WETTERER 2007). Surprisingly little is known about dispersal and colony founding physiology in supercolonial species, but at least in *Formica* it seems that differences between supercolonial and non-supercolonial species are small (HAKALA 2020, but see SUNDSTRÖM 1995), whereas in

Solenopsis invicta, the difference between social types is extensive even if polygyne queens may be capable of rare colony founding (Tschinkel 2006). Thus, despite prevalent local and intranidal mating and natal recruitment of queens, dispersal will play an important role (as also basic theory states, Hamilton & May 1977) when the focus is on population dynamics on long time scales.

In addition to observed mating flights, genetic or experimental data on acceptance and establishment are needed to understand competition through queen recruitment. Genetic data show gene flow between supercolonies and surrounding populations in, for example, *Formica pressilabris* (see Hakala & al. 2020), *Myrmica rubra* (see Huszár & al. 2014), and *Lepisiota canescens* (see Sorger & al. 2017). However, studies utilising sex-specific markers suggest that at least in *Formica lugubris* (see Gyllenstrand & Seppä 2003), *Formica truncorum* (see Gyllenstrand & al. 2005), *Formica exsecta* (see Seppä & al. 2004a), and *Formica paralugubris* (see Holzer & al. 2009) gene flow out from supercolonies is very heavily male biased, and that to some extent, supercolonies may act as sink populations for female dispersal.

Within supercolonies, queens may also disperse (on flight or foot) between nests to compete over reproductive spots. At least in *Formica paralugubris* (see Chapuisat & al. 1997) and *Formica exsecta* (see Kümmerli & Keller 2007a, Kümmerli & Keller 2008), genetic data suggest that this mainly happens between nests close to each other, leading to viscous or structured populations with fairly local competition among the queens. Such assessments of the relative frequencies of different dispersal strategies, considered hand in hand with local kin structures, are necessary for understanding the relevance of different scales of competition, both for the queens and the resident workers.

Experiments similarly show that acceptance of outside queens into nests is possible, especially when nests are queenless. In *Myrmica rubra*, queenless nests are more accepting of queens both within and between colonies, but even queenright nests accepted 1 / 3 of introduced queens in an experiment (Radchenko & Elmes 2010, Sorvari 2017). Similarly, in *Linepithema humile*, the chances of survival of introduced queens were much higher in queenless conditions, but here old queens were introduced rather than young gynes (Vásquez & Silverman 2008b). In *Formica paralugubris* and *Formica exsecta*, both nestmate and non-nestmate queens are accepted into queenright nests (Fortelius & al. 1993, Holzer & al. 2008a, b) although in the former, survival of both nestmates and aliens is low. Thus, workers could be controlling queen numbers even if no discrimination occurs. Acceptance is also higher for unmated than mated queens (Holzer & al. 2008b) and in the presence of nestmate alates (Fortelius & al. 1993). Reproductive success of accepted outsiders might be lower than that of residents (Holzer & al. 2008), which is an important reminder that surviving the introduction does not necessarily tell the whole story.

In contrast to queens, almost nothing is known about competition through the male function. This is slightly surprising given the highly male-biased sex ratios observed in many species. Gene flow has been shown to be male biased in several species of *Formica* (see references above), but this behaviour has not really been cast as competition among supercolonies. This is certainly an area in need of more attention.

Competition over founding new colonies: births of supercolonies

A broad view from social evolution theory justifies seeing insect societies as individuals in their own right, "superorganisms" (Helanterä 2016). In this light, viewing supercolonies as individuals, very little is known at the level of how whole supercolonies compete over representation in the distant future populations (but see Vogel & al. 2009 for an exception). Given the spatial and temporal scales involved, there are obvious practical limitations on such data. Nevertheless, this is an important scale of competition to consider in order to understand supercolony evolution.

First, a large part of what we know of supercolony births comes from invasive species. Spreading patterns show that jump dispersal of small propagules is enough for initiating a supercolony, so the question is how and how often this happens in natural ranges. Spread on waterways through drafting or floating debris is a distinct possibility for species such as *Linepithema humile*, originating from habitats prone to flooding (Vogel & al. 2009), but it is unknown how often this happens. Furthermore, long-term observations suggest that new supercolonies could arise from splitting of existing supercolonies when they grow and contract seasonally (Heller & Gordon 2006). Such dynamics should leave a clear signature in population genetic structures, so that close-by supercolonies are genetically similar, but such a structure was not observed in native *L. humile* populations (Vogel & al. 2009).

Second, the literature cited above on mating flights suggests that establishment of new supercolonies by flying queens is a distinct possibility even if perhaps uncommon. Studies of island species communities of boreal ants (Vepsäläinen & Pisarski 1982, Sorvari 2018) clearly demonstrate that long-distance colony founding occurs in obligately polydomous and polygynous *Formica aquilonia* and *Formica polyctena* and socially polymorphic *Formica exsecta* and *Formica truncorum,* often enough to be ecologically highly relevant. In general, island biogeography should provide a lot of useful information when interpreted in this light.

Very importantly, observing only the extensive "climax" supercolonies is insufficient for understanding how they came to be. To understand how supercolonies compete with each other, we need to look at the population mosaic of colonies of all sizes and ages. These include the incipient supercolonies, supercolonies whose growth is impeded by habitat limits or competition, and cases where supercolonies fail to establish dominance (Castro-Cobo &

al. 2021). For example, *Formica paralugubris, Myrmica rubra,* and *Myrmica sulcinodis* have been described in such mosaics (Pedersen & Boomsma 1999, Holzer & al. 2006, Huszár & al. 2014). The distribution of colony sizes is key to supercolony life cycles, and thus the societies that are smaller than supercolonies are an important piece of the puzzle. The implications of living in very low relatedness societies depend on how much of their lifespan colonies spend in this mature stage (Helanterä 2009) and how many colonies they have competed with or even wiped out on their way to dominance and habitat monopolization.

Deaths of supercolonies

Similar to births, we also need to understand supercolony lifespan and causes of death. As a supercolony that is able to recruit new queens internally is arguably potentially immortal, there are logistic challenges in systematically studying the causes of their demise, and there are few long-term studies of populations of supercolonies. Despite the challenges, there is ample evidence, especially from invasive populations, that supercolonies are mortal indeed (Lester & Gruber 2016). Colony turnover in the native populations of *Linepithema humile* suggests considerable colony mortality (Vogel & al. 2009), and anecdotal evidence suggests that also native *Formica* supercolonies may disappear rapidly (Rosengren & al. 1993). While direct evidence for the cause of death is lacking, in the former case, intra- and interspecific competition and disasters such as flooding were suggested (Vogel & al. 2009). Supercolony mortality caused by competition with conspecific supercolonies is an important part of understanding their dynamics.

Mortality of supercolonies has been observed for several species (Wetterer & al. 2014, Lester & Gruber 2016, Tartally & al. 2016). Likely causes include lethal effects of viruses and microbial pathogens (Lester & Gruber 2016), recently reviewed in Espadaler & Santamaria (2012), Cremer (2019), and Baty & al. (2020), and complex ecological dynamics ("sublethal pathways", Lester & Gruber 2016) due to, for example, collapses of interactions with mutualist partners mediated by overexploitation of their respective hosts, competition over nestsites, and inbreeding effects.

How are supercolony deaths then relevant to scales of competition and kin selection? While competition, pathogens, and the indirect effects they may have on colony success are important for the ecology of supercolonies, the outstanding questions in terms of competition and kin selection are twofold. First, understanding lifespans and causes of death of colonies of all sizes is relevant for understanding competition among supercolonies over extensive temporal and spatial scales. Second, whether supercolony mortality is exclusively due to rare catastrophic events unrelated to internal features of the colonies or whether traits such as competition or pathogens, for which potentially heritable supercolony features play a role, determines which supercolony traits could be shaped by natural selection.

Genetics of supercolonies in the genomic era

Studies of supercolonies using neutral genetic markers have assessed the spatial extent of supercolonies and helped interpret aggression data, shown isolation by distance within colonies, sex biases in gene flow, and helped track invasion histories. While such studies have been instrumental for the current understanding of supercolonies, many open questions remain. Rapid advances in -omics methodologies (see, e.g., Favreau & al. 2018 for a perspective) give tools for deeper understanding of supercolony genomes.

First, at a single supercolony scale, the key question is understanding how genetic homogeneity is maintained or eventually broken in the extremely large supercolonies. Ecological studies underscore that while supercolonies may consist of spatially isolated and functionally separated subcolonies (Gordon & Heller 2014), they comprise genetically and chemically relatively homogenous entities (Brandt & al. 2009, Fournier & al. 2009). Are the societies slowly drifting apart to form subdivided, kin structured populations (Drescher & al. 2010)? Does selection in such a case work in favour of kin recognition (Helanterä & al. 2009) or does it remove rare cues (Crozier 1986, Tsutsui & al. 2000)? Or are movements of either workers or reproductives enough to maintain unity? Genome-wide data (e.g., Warner & al. 2017, Privman & al. 2018) add resolution to describing genetic structures and help distinguish neutral and selective processes underlying homogeneity of supercolonies, especially those at gene loci underlying cuticular chemistry and nestmate recognition.

Zooming out to populations comprised of several supercolonies, each supercolony is an isolated subpopulation with a small effective size due to genetic bottlenecks at colony founding (Sundström & al. 2005, Seppä 2008), and as such under strong demographic effects of drift on genetic variation, compared with efficacy of natural selection. Supercolonies within a species can in extreme cases even be thought of as evolving as "independent lineages" (Schmidt & al. 2010, Pedersen 2012), although in many cases, differentiation is not so extreme as populations exchange sexuals, as discussed above. Thus, supercolonial species seem an excellent general model case for understanding local adaptation and intraspecific divergence under strong demographic effects.

At the intersection of kin selection and genomics, a crucial prediction on the potential evolutionary fate of supercolonies can be tested (Queller & Strassmann 1998, Helanterä & al. 2009). Theory predicts that in low relatedness societies selection on the worker phenotypes should be diminished as selection affects genes in sterile individuals only indirectly (Linksvayer & Wade 2009). For example, a harmful mutation in a hypothetical gene that would only affect sterile worker traits would not be selected against if the indirect negative effects on queen reproduction befall distant relatives not carrying that mutation. If relatedness is zero, natural selection on such a gene would be nonexistent, which is predicted to lead to

downfall of supercolonies through mutation accumulation. Similarly, any gene with positive effects on the worker traits would not spread through selection. However, there are reasons why demonstrating such an effect could be difficult. First, gene flow from non-supercolonial, high relatedness populations may in many species provide a rescue (Queller & Strassmann 1998). Second, caste biases in gene expression tend to be highly life-stage, tissue, and context sensitive, so that genes only affecting worker traits may be very few (Mikheyev & Linksvayer 2015, Morandin & al. 2015, Warner & al. 2019). However, when experimental context and tissue specific gene expression are carefully controlled for, there is some evidence that worker expressed genes evolve under relaxed selection in *Monomorium pharaonis* – further data across species is clearly needed (Warner & al. 2017).

At the same time, supercolonies have many fascinating features whose adaptive genetic basis is yet to be discovered, such as changes in queen dispersal and mating behaviours, genetics of nestmate recognition and communication. Genomics of social traits are of evolutionary interest as such traits are predicted to evolve rapidly. First, rapid evolution could stem from arms-race dynamics related to conflicts inherent in many social traits (Brockhurst & al. 2014). Second, genes with caste biased or in general plastic expression are predicted to evolve rapidly due to both adaptive and neutral reasons (Helanterä & Uller 2014). Genomic studies in *Solenopsis invicta* suggest that caste biased genes in general evolve rapidly (Hunt & al. 2011, 2013), and signatures of both ancient and recent positive selection in genes with putative social functions, such as caste regulation, chemical communication, and neurological functions, have been observed in *S. invicta* (see Privman & al. 2018, Dang & al. 2019). Understanding how repeatable such findings are across supercolonial species and across supercolonies within species is a highly interesting question, as is the question of whether supercolonial ants are different from other social insects in these respects, given their specific population features.

A separate question highly pertinent to genetic understanding of supercolonial traits is the role of "supergenes" in queen-number polymorphisms and their evolutionary maintenance. In both *Solenopsis* fire ants (Wang & al. 2013, Cohen & Privman 2020, Yan & al. 2020) and *Formica* (Purcell & al. 2014, Brelsford & al. 2020), queen number variation is associated with so called supergenes or "social chromosomes" (but note that this applies also to non-supercolonial, monodomous species with queen number variation). These large groups of linked genes provide several interesting prospects for further research. First, their gene contents, such as genes associated with processing chemical information and environmental perception, provide information on loci causal in regulation of queen numbers and morph specific evolution (Pracana & al. 2017, Cohanim & al. 2018, Martinez-Ruiz & al. 2020), which may guide genomic investigations in other species without social chromosomes. Second, they seem to harbour interesting selfish genetic elements (Keller & Ross 1998, Avril & al. 2020) and are thus interesting model cases for the role of intragenomic conflicts in shaping polymorphic traits at a higher level of organisation. Third, they add another model system to supergene studies, a topic that combines diverse adaptations ranging from mating types in plants (Branco & al. 2018), lekking strategies in birds (Küpper & al. 2015) to colour mimicry in butterflies (Joron & al. 2011).

Supercolonial ant species are also potentially very interesting for speciation genetic studies. This is because propensity for intranidal mating, dependent colony founding, and polygyny (Seifert & al. 2010) could shelter queens from negative consequences of inter-specific matings that could prove fatal in a solitary insect or a lone founding queen. Together with large population differentiation, limited gene flow, and haplodiploidy (Nouhaud & al. 2020), extreme polygyny creates a combination conducive to speciation and maintenance of hybrids in the population that facilitates studying the incompatibilities underlying speciation. *Formica* (Beresford & al. 2017), *Solenopsis* (Cohen & Privman 2019), and *Pheidole* (Fournier & al. 2012) are interesting cases at least, given the presence of closely related species with potential for supercoloniality. Furthermore, sympatric speciation via inquilines (Bourke & Franks 1991) could provide opportunities to study genomics of incipient speciation.

Finally, individual and colony traits in supercolonies are interesting from a quantitative genetics perspective. Beyond supergenes (Wang & al. 2013, Purcell & al. 2014), heritability and genetic architecture of colony level traits is little known in any ant species in the wild (but see Gordon 2013), and the complexity of supercolonies further widens the knowledge gap. In insect societies, genes of other individuals influence the developmental and selective environment of individual and group traits. Thus, the sib-social or indirect genetic effects are a major determinant of phenotypic variation and responses to social selection (Linksvayer 2006, 2015). The few existing quantitative genetic studies show that the architecture of both individual and nest level traits is complex (Linksvayer 2006, Libbrecht & Keller 2013), but also that sociobiologically highly relevant colony level traits are heritable and respond to selection – including foraging activity, aggression levels, and cuticular odour profiles (Walsh & al. 2020a, 2020b). As studying trait heritability and change in natural populations of supercolonies is likely to be challenging, such laboratory studies are crucial for a complete picture on evolutionary change as they provide a complementary perspective to ecological, experimental, and gene sequence data.

An expanded theoretical framework

While ecological and genetic data are the key to understanding each case study, a theoretical framework helps to structure the understanding, guides empirical research by providing novel testable predictions, and facilitates broad comparisons between superficially disparate biological

systems. This section will briefly discuss supercolonies in the light of existing theory as well as prospects for novel theory.

First, supercolonies deliver an important lesson on how to apply inclusive fitness predictions to case studies. For example, simple verbal theory predicts that selfish and nepotistic genotypes should eventually take over when relatedness is very low (Helanterä & al. 2009). However, as discussed above, understanding what the relevant relatednesses are requires ecological understanding. Furthermore, apparent persistence of a supercolonial lifestyle despite extreme predicted conflicts forces us to think about limits of adaptation in social settings more generally. Do individuals have access to information about the kin structures they live in or their relatedness towards particular individuals they encounter, and which individuals have the power to drive their evolutionary optima in societies (Beekman & Ratnieks 2003, Ratnieks & al. 2006)? Understanding when (and when not) predicted conflicts break out requires knowledge of mechanistic details. The little explored conflicts over queen recruitment and dispersal are likely to benefit from similar thorough considerations of constraints of social adaptations.

Second, repeated and convergent evolution of a supercolonial syndrome is a great model case for social niche construction (Ryan & al. 2016). Some of the conceptual connotations of niche-construction theory are perhaps controversial (Scott-Phillips & al. 2014), but the core idea should not be: Social traits co-evolve and modify each other's selective regime. Kin structures that provide the selective regime for social traits depend on other social traits, such as dispersal and mating decisions. General models show such feedbacks between, for example, cooperation and population clustering (Powers & al. 2011), mating behaviours, sex ratios and evolution of altruism (Rautiala & al. 2017), and budding dispersal and sex ratios (Gardner & al. 2009) as well as discrimination behaviours and availability of recognition cues (Crozier 1986, Ratnieks 1991). Many specific traits of supercolonial species would likely benefit from similar treatments, such as the interactions between kin structures, sex and caste allocation, and dispersal and mating strategies, especially taking into account haplodiploidy and the associated sex asymmetries in relatedness, the inbreeding risks associated with local mating, and the evolutionary conflicts among colony members.

Third, a broader view may help to shed further light on the balance of cooperation and competition among kin in viscous populations where dispersal within supercolonies is limited. In simple models, population viscosity impedes cooperation, as the benefits of cooperation among closeby kin are cancelled out by increased kin competition (reviewed in Helanterä & al. 2009). However, this assumes that cooperative behaviours themselves do not affect local carrying capacity or other demographic features such as group survival. If patches are "elastic" so that increased cooperation increases local carrying capacity, the negative effects of increasing density of related individuals may be alleviated (Van Dyken 2010). It is easy to see how supercolonial (and many other) ant societies could work this way, through, for example, enhancing habitat quality by tending mutualists (Rosengren & al. 1993) or eliminating competitors disproportionately effectively with increasing density.

More broadly, different types of cooperative or altruistic behaviours depend in different ways on dispersal and kin competition (Van Dyken & Wade 2012a, 2012b). Survival and fecundity altruism (such as nest defence and reproductive division of labour, respectively) are selected for under plentiful resources but create local competition. Local competition, in contrast, selects for resource efficiency and resource enhancement altruism (e.g., effective foraging through pheromone trails and tending of mutualists, respectively) that in turn improve the resource situation (Van Dyken & Wade 2012a). Thus, while each type of altruism is eventually self-limiting, diverse altruistic traits may coevolve in a "runaway" manner (Van Dyken & Wade 2012b). There seems to be a lot of scope for more detailed theories applying to supercolony life histories to shed light on how the genetic structures and their determinants together with the ecology and functioning of the polydomous colonies feedback on each other.

Concluding perspectives

In an earlier review on supercolonial ants (Helanterä & al. 2009), we concluded that kin selection theory helps to explain the rarity of supercoloniality. This review, I hope, also shows that kin selection theory also helps us understand the key processes that potentially explain the maintenance of supercolonies and calls for a multi-level approach to supercolonies, from genes to populations of whole supercolonies competing.

A very general message is that understanding early drivers of evolution of any extreme trait from its present benefits and costs is challenging. Understanding supercolonies benefits from zooming out from the most extreme cases in two ways.

First, supercolonies need to be understood as colonies in a population consisting of a continuum of sizes. Each supercolony starts small at some point in time, selection on colony traits happens throughout its lifetime, and conspecific colonies of all sizes are relevant competitors. Looking at the huge supercolony that has outcompeted everything in its path may be a poor guide to understanding which features made it win the competition and how many (unrelated) competitors it wiped out on its way to dominance. Low relatedness at the end of the game is not the whole story.

Second, zooming out from the supercolonial species to their phylogenetic background is needed. As supercoloniality is built on a syndrome of traits, reconstructing the order in which those traits arose is illuminating (Borowiec & al. 2021). Similar reconstructions have shed light on, for example, evolution of sociality in termites (Inward & al. 2007) and vespid wasps (Hunt 1999), but analysis of supercolonies has the added benefit that there

is a large number of separate origins to compare. Such analyses should be supported by theoretical analyses of trait coevolution. Similarly, phylogenetic analyses are needed for rigorously testing the unresolved question of supercoloniality as an evolutionary dead-end.

Zooming out is complemented by zooming in. There are many outstanding questions and features described in only a few species that need careful experimental, genetic, physiological, and ecological dissection in more species to gain an understanding of convergent patterns and idiosyncratic solutions. How many queens try to disperse and how many establish locally, and who controls that? What about the males? How is this reflected in gene flow patterns and variation in individual dispersal traits? What is the balance of selection and neutral processes underlying social evolution in small, isolated populations, possibly complicated by supergenes? How do queens compete and communicate in highly polygynous nests? At what scales are the benefits of a polydomous organization shared?

It is unlikely that any ant researcher ever was worried about running out of questions, but supercolonies certainly have a lot to offer. Each species is an interesting case on its own, but there is also immense potential for comparative and theoretical work that combines the species level findings into a big picture, illuminative of key principles of social evolution.

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