Review Article

Title

Speciation in ants: Unlocking ant diversity to study speciation (Hymenoptera: Formicidae)

Name(s) of author(s)

Patrick Heidbreder, Patrick Krapf, Marit Kuijt, Beatriz Portinha, Michel Chapuisat & Jonna Kulmuni

Key words: Formicidae, ants, speciation, reproductive isolation, hybridization, diversification, review

Address(es) of author(s)

Patrick Heidbreder (contact author), Organismal and Evolutionary Biology Research Programme, University of Helsinki, Rm 5202, Viikinkaari 1, 00790 Helsinki, Finland. E-Mail: patrick.heidbreder@helsinki.fi

Patrick Krapf, Organismal and Evolutionary Biology Research Programme, University of Helsinki, Rm 5202, Viikinkaari 1, 00790 Helsinki, Finland. Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Postbus 94240, 1090 GE Amsterdam, Netherlands. E-mail: patrick.krapf@helsinki.fi

Marit Kuijt, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Postbus 94240, 1090 GE Amsterdam, Netherlands. E-mail: m.kuijt@uva.nl

Beatriz Portinha, Organismal and Evolutionary Biology Research Programme, University of Helsinki, Rm 5202, Viikinkaari 1, 00790 Helsinki, Finland. cE3c, Centre for Ecology, Evolution and Environmental changes & CHANGE, Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal. E-Mail: beatriz.portinha@helsinki.fi

Michel Chapuisat, Department of Ecology and Evolution, Université de Lausanne, BIO-3123, Biophore - CH-1015 Lausanne, Switzerland. E-mail: michel.chapuisat@unil.ch

Jonna Kulmuni (contact author), Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Postbus 94240, 1090 GE Amsterdam, Netherlands. Organismal and Evolutionary Biology Research Programme, University of Helsinki, Viikinkaari 1, 00790 Helsinki, Finland. E-mail: j.k.kulmuni@uva.nl

Number of pages: 19
Number of figures: 2
Number of tables: 0

Abstract

Ants are among the most abundant terrestrial animals and play key roles in ecosystems across the globe. Their taxonomic and ecological diversity makes them a prime taxon for contributing to our understanding of the patterns and processes of speciation.However, studies often do not explicitly link their results to the broader framework of speciation and reproductive isolation. Here we combine macroevolutionary work on ant diversification with microevolutionary studies on reproductive isolation and hybridization to review what is known about ant speciation. We also discuss how two key features, sociality and haplodiploidy, could impact speciation and hybridization in ants. We find that, although key innovations as drivers of ant diversification have been studied, several gaps exist in our understanding of reproductive isolating mechanisms in ants. However, general population features or traits such as co-evolution within mutualistic or parasitic relationships suggest that reproductive isolating mechanisms are generalizable across the tree of life. We suggest that ants provide a sound system to study general aspects of speciation, especially hybridization, the genomic basis of intrinsic postzygotic isolation, and species interactions as drivers of reproductive isolation between species.

1. Introduction

1.1 Ants and speciation

With a conservative estimate of 20 quadrillion individuals and a total biomass of 12 megatons of dry carbon, exceeding that of wild birds and mammals (SCHULTHEISS & al. 2022), ants (Hymenoptera: Formicidae) are among the most abundant terrestrial animal species (SCHULTHEISS & al. 2022). They play a central role in land ecosystems and are important ecosystem service providers, conducting various tasks such as bioturbation (i.e., reworking of soils and sediments), nutrient cycling (e.g. decomposition of organic matter), and seed dispersal (HANDEL & BEATTIE 1990, PARR & al. 2016). Moreover, ants have predation and symbiotic relationships that shape the surrounding invertebrate and plant communities. With this abundance and ecological importance of ants comes their taxonomic diversity.

Ants started diversifying in the late Cretaceous, roughly ~100 Mya, coupled with the proliferation of angiosperm forests and accompanying herbivores (MOREAU & al. 2006). Genetic innovations—sociality, large colony sizes, caste polymorphism, and increased longevity and fecundity—evolved rapidly, within ~20 My (ROMIGUIER & al. 2022). Today, over 14,000 ant species are described worldwide (BOLTON 2025), with many more still undetected or undescribed. Here we review what is known about the processes of speciation in ants, and how this group can provide answers to open questions in the field of speciation.

In the 100 million years of their existence, ants have acquired an essentially global distribution, excluding Antarctica and some islands (WILSON & TAYLOR 1967, HÖLLDOBLER & WILSON 1990). For example, Iceland does not have native ants, but with travel and trade, some species now occur there. High species and geographic diversity establish ants as a prime target for taxonomic studies, naturally tying into questions of speciation. Interestingly, although ants are the focus of numerous taxonomic studies, there has been less emphasis on understanding general speciation questions using ants (Fig. 1). We seek to tie together the strong taxonomic work on ants with the methods and discourse of speciation research.

Speciation as a field broadly studies the processes that generate biological discontinuity, that is, what leads to the emergence and persistence of new species. Current work aims to understand species and speciation through the buildup of reproductive isolation (STANKOWSKI & RAVINET 2021). To understand speciation, one needs to understand how reproductive isolation evolves. The term reproductive isolation can be defined in quantitative or qualitative terms (WESTRAM & al. 2022). Qualitatively, reproductive isolating mechanisms are characteristics of species that reduce or prevent successful reproduction with members of other species (KULMUNI, BUTLIN, & al. 2020). Quantifying the contribution of different reproductive isolating mechanisms across taxa provides a way to integrate and relate the common isolating mechanisms and their impact on the speciation process across the tree of life. Open questions in the field include the impact of gene flow during speciation, the dynamics of the buildup of reproductive isolation, and the frequency and evolutionary importance of hybridization (hybridization being reproduction between diverging lineages BARTON & HEWITT 1985) .

In reviewing the literature on ant speciation research we find that, while there has been much research on the taxonomic distinctions of ants (i.e., species revisions, evolutionary histories, and the classification of new species), the results of these studies are often not put back into the broader context of speciation (Fig. 1). That is, while ant speciation research makes much use of the latest methods, including genomic, morphological, paleontological, behavioral, and terminology of speciation (e.g. geographic modes of speciation including allopatry, parapatry and sympatry), they are used to define the histories and differences of particular species, rather than to contribute to the broad understanding of the patterns and processes of speciation and the build of up reproductive isolation (but see e.g. SAVOLAINEN & VEPSÄLÄINEN 2003, BLACHER & al. 2022). We see this as both a gap and an opportunity. The extensive and diverse research on ants can provide a general understanding of how speciation patterns apply to ants, and in turn, identify areas in which ants may be particularly well suited to furthering our understanding of the speciation process.

In this review we focus on four main areas of ant speciation bridging from macroevolutionary patterns to microevolutionary processes. We cover 1) patterns of macroevolutionary diversification in ants, 2) reproductive isolating mechanisms, 3) hybridization and 4) interactions with other organisms as drivers of speciation. We conclude with open questions and avenues to explore in future research.

1.2 Key factors affecting speciation in ants

Ants have two key features that may impact the process of speciation and outcomes of hybridization. These are sociality and haplodiploidy, both of which could speed up the evolution of reproductive isolation and lead to faster speciation under some conditions (Socias-Martínez & Peckre 2023). The complete and lifetime morphological assignment to distinct castes from early development↓one of which is a permanently non-reproductive worker caste↓that occurs in most ant species, is the hallmark of obligatory eusociality (or superorganismality), one of the major evolutionary transitions (Wheeler 1986, Helanterä 2016, Boomsma & Gawne 2018, Boomsma 2022). Social organization in ants can vary from monogyny (single queen per nest) to polygyny (multiple, up to hundreds of queens per nest) and supercoloniality (nests within a population are connected, each nest containing hundreds of queens). Polygyny and supercoloniality are frequently associated with reduced dispersal and mating within or near the natal colony, leading to differentiation between populations and low effective size within populations (Sundström & al. 2005). Together these factors could lead to the build-up of genetic differentiation and reproductive isolation. Supercoloniality however, seems to be an evolutionary dead-end; as relatedness approaches zero, the process of kin selection and maintenance of altruistic worker phenotypes is impeded, leading to nepotism, mutation accumulation, and ultimately to the extinction of supercolonies (Helanterä 2022).

Sociality is not conflict free. The division of labor between queens and workers is associated with multiple potential conflicts caused by asymmetries in relatedness (Queller & Strassmann 2002, Meunier & al. 2008). Such kin conflicts have been suggested to result in sympatric speciation via social parasitism in *Myrmica* (Savolainen & Vepsäläinen 2003) and in fungus growing ants (Rabeling & al. 2014) (See section 4.1 Interactions with plants, fungi, and other organisms as drivers of speciation). More generally, many species of ants are workerless social parasites, raising interesting questions on how and when they diverged from their hosts (Wilson 1971, Buschinger 2009, Rabeling 2021, Trible & al. 2023). Additionally, sociality changes the selective pressures operating on hybrids (See section 3 Hybridization and its implications in ants). Sterility of hybrids is no issue if hybrids develop into workers, as in *Pogonomyrmex* harvester ants (Cahan & al. 2002, Helms Cahan & Keller 2003). Cooperative breeding and polygyny also allow hybrid queens with high egg mortality to persist and reproduce (Beresford & al. 2017). This interaction between sociality and hybridization may shape ant evolution differently from other classic hybridizing taxa such as cichlids or *Heliconius* butterflies, and may play a role in the high rates of hybridization observed in ants.

Finally, ants are haplodiploid, potentially affecting the tempo of speciation. Haplodiploidy in ants is a result of arrhenotokous reproduction, where unfertilized eggs from queens develop into males and fertilized eggs into diploid females. The existence of haploid males can lead to more efficient purging of deleterious mutations (Avery 1984, Werren 1993) and to faster fixation of recessive beneficial mutations (Nouhaud & al. 2020). This faster molecular evolution in haplodiploid organisms compared to diploids could also promote the rapid evolution of reproductive isolation, in a much similar way as the faster-X effect (Meisel & Connallon 2013).

2. Patterns of macroevolutionary diversification in ants

2.1 Early ants and modern ant development

The ant fossil record begins around 99 million years ago, during the mid-Cretaceous period. This fossil record, which mainly consists of specimens preserved in amber, includes representatives of extinct ant subfamilies, like the Sphecomyrminae, and extant ones, like the Formicinae, Aneuretinae, Dolichoderinae, and Ponerinae (LaPolla & al. 2013, Perfilieva 2023). These fossils are mainly found in the Neotropics, but specimens occur more globally, pointing to an earlier initial divergence of the Formicidae family (Brendon E. Boudinot & al. 2022, Perfilieva 2023). This is supported by molecular data: studies estimating divergence times using molecular clocks suggest that ants began diversifying between 139 and 158 million years ago, stemming from a wasp-like ancestor (Moreau & al. 2006, Perrichot & al. 2008, Moreau & Bell 2013). These early ants likely lived in soil environments as predators, hunting small invertebrates (Lucky & al. 2013). Furthermore, they had already evolved sociality, based on differences in body sizes found in fossils (Grimaldi & Agosti 2000, Brendon E Boudinot & al. 2022).

A distinct pattern of species richness in modern ants shows a concentration in tropical regions, particularly in the Neotropics and Asia (Kaspari & al. 2004). Different hypotheses have been tested for this phenomenon, including the tropical conservation hypothesis (Wiens & Donoghue 2004), the distribution-rate hypothesis (Pianka 1966), and the ecological regulation hypothesis (Pianka 1966). A study by Economo and colleagues (Economo & al. 2018) found that the tropical conservation hypothesis, which proposes that tropic-adapted species have existed for longer, since temperate environments only developed later, is the most likely. The same study did not find support for the distribution-rate hypothesis, which proposes that the tropical environment causes a higher diversification rate. The Neotropics, where ant lineages likely originated, have the highest diversity, whereas other ecological regions with similar climates have lower diversity, supporting the tropical conservation hypothesis rather than the distribution-rate hypothesis (Pie 2016). However, the tropical conservation hypothesis does not explain the observed diversification patterns by itself, since some very old lineages do not have as much diversity as would be expected under this hypothesis (Economo & al. 2019). Therefore, other causes for shifts in ant diversification rates are undeniable.

In general, positive shifts in diversification rate are often associated with either increased ecological opportunity, e.g., dispersal to, and colonization of, a new environment, or with the evolution of a key innovation, such as a novel trait that offers a competitive advantage to an organism or allows it to expand into a previously inaccessible environmental niche space (Simpson 1949). Below we discuss both mechanisms as drivers of ant diversification.

2.2 Increased ecological opportunity as a driver of ant diversification

Increased ecological opportunity allows species to diversify by adapting to new environments and inhabiting different parts of a new niche, driving adaptive radiation and diversification. In ants, ecological opportunities in part promoted the diversity we see now. Around 50 million years ago, fossils indicate an increase in ant diversity. The most accepted hypothesis of this spike in divergence is that ants evolved and speciated alongside the divergence of angiosperms (Moreau & al. 2006). Angiosperm forest floors are much more diverse than gymnosperm forests, which allowed ants to diverge across terrestrial habitats and live in canopies (Moreau & al. 2006). Predatory ants also benefited from the increased insect abundance that accompanied angiosperm expansion. This shift in food availability may have driven the evolution of specialized foraging behaviors, such as honeydew-feeding in Formicinae and Dolichoderinae. The ability to exploit liquid food sources likely led to the evolution of repletes and semi-replete major workers in some species, enhancing their survival in resource-scarce environments.

A non-mutually exclusive hypothesis that might explain the Formicidae diversification is the dynastic succession hypothesis (Wilson & Hölldobler 2005). It suggests that the early establishment of ants in ecosystems provided them with opportunities to diversify and fill ecological niches with limited competition. Fossil evidence from Eocene amber deposits demonstrates that Formicinae ants were among the first to exploit tree canopies, taking advantage of the expanding angiosperm-dominated forests of the time (Perkovsky 2009, Ward & al. 2015). Additionally, mutualistic interactions, such as protecting plants from herbivores in exchange for shelter or nectar, further cement their ecological roles. This mutualism is supported by fossil and modern evidence, showing that Formicinae ants have long been integral to arboreal ecosystems (Ward & Brady 2003).

2.3 Key innovations in the diversification of ants

Hodges and Arnold (Hodges & Arnold 1995) defined key innovations as “biological traits that promote lineage diversification via mechanisms that increase the rate of speciation and/or decrease the rate of extinction”. In Hymenoptera, several key innovations (like wasp-waists, stingers, and parasitoidism) have been studied. However, secondary phytophagy, i.e. the secondary transitions to plant feeding, was found to be the most important key innovation in the diversification of the order (Blaimer & al. 2023). This is in line with the evolution of angiosperms alongside the Formicidae, as mentioned before. Despite suggestions on the role of sociality in ant diversification, it is not considered a key innovation, as both termites and ants were social for tens of millions of years before independent evolutionary events led to radiations within specific subgroups (Barden & Engel 2020).

One key innovation that has specifically influenced ant diversification is claustral colony founding. In species that show this trait, queens rely on stored energy reserves to establish new colonies without needing to leave the nest to forage. This adaptation reduces early mortality risks from predation and competition, providing a significant survival advantage. Claustrality has independently evolved in three lineages: Formicinae, Myrmicinae, and Dolichoderinae, and is thought to contribute to their high diversification rates by allowing them to establish colonies that are protected from predators and enemy ant species present in the in surrounding environment (WILSON & NOWAK 2014).

A predation adaptation found in some genera of the subfamilies Ponerinae, Myrmicinae, and Formicinae, is the spring-loaded trap-jaw mechanism (MOREAU & BELL 2013, LARABEE & SUAREZ 2014). This adaptation enhances the hunting efficiency of their bearers, allowing them to secure niches that require precision and fast predation (LARABEE & al. 2016). This innovation has thus caused an ecological niche expansion and allowed these genera to diversify. Indeed, the diversification rate in ant lineages with trap-jaw mechanism is 0.064, which is twice the overall rate of diversification in their Ponerinae subfamily (LARABEE & al. 2016). A higher diversification in genera with the trap-jaw mechanism has also been observed within the subfamily Myrmicinae (A*nochetus* + *Odontomachus* and *Pyramica* + *Strumigenys*; MOREAU & BELL 2013). The convergent pattern in two separate subfamilies strongly suggests that the trap-jaw mechanism is an innovation promoting species diversification. Booher & al. (2021) further support this with finding that diversification in *Strumigenys* came after the evolution of the trap jaw mechanism. However, as noted by Larabee & Suarez (2014), while the phylogenetic evidence of the trap jaw a key innovation is mounting, it remains to be demonstrated that the trap jaw has allowed ants to enter new adaptive zones and improved the ecological performance versus non-trap jaw species.

Key innovations can also be defensive. The Formicinae subfamily famously produces formic acid, which is a unique chemical defense (WILSON & HÖLLDOBLER 2005). Especially in the tropics, formic acid is suggested to be an advantage because there are many interspecies interactions. The evolution of formic acid is associated with an increase in speciation rate, likely because these ants were able to thrive in environments where they normally would not, due to many natural enemies. Similarly, in the Dolichoderinae subfamily, the evolutionary success of this group can be attributed to their sophisticated chemical communication strategies (WARD & al. 2010). This increases the efficiency of both foraging and colony expansion, saving energy for reproduction.

3. Reproductive isolating mechanisms in ants

3.1 Reproductive isolating mechanisms as a common framework to understand speciation across taxa

As highlighted in the introduction, traditional speciation research investigating reproductive isolating mechanisms and quantifying reproductive isolation between pairs of ant species is rare (Blacher & al. 2022). This is in stark contrast to the number of studies interested in ant hybridization (Fig. 1). Seifert (2023) aims to bridge this gap by suggesting prezygotic isolation in *Cardiocondyla* and *Myrmoxenus* based on a lack of hybridization in the field, although there is no systematic study of what mechanism could be responsible for this isolation (but see Gusten & Buschinger 1997). Research on ant speciation often focuses on hybridizing species (Schwander & al. 2008, Kulmuni, Nouhaud, & al. 2020, Blacher & al. 2022, Portinha & al. 2022), potential sympatric speciation between socially parasitic species and their non-parasitic host species (Savolainen & Vepsäläinen 2003, Rabeling & al. 2014), and the divergence of entire genus and species groups using a macroevolutionary perspective (Moreau & al. 2006, Goropashnaya & al. 2012). Studies of reproductive isolation are mostly restricted to species belonging to the genera *Formica*, *Myrmica* and *Solenopsis*. In this section we review what is known about prezygotic and postzygotic isolating mechanisms in ants.

3.2 Mechanisms of prezygotic isolation in ants

Prezygotic reproductive isolation refers to mechanisms that operate before zygote formation and impede the transfer of gametes to individuals of the other species (Coyne & Orr 2004). These could be temporal, where gametes are released at different times of the year or individuals of the two species mate at different times of the day. Prezygotic isolation can also be spatial, where individuals of the two species live in different habitats, on different host plants or in different geographical regions, or result from behavioral differences, for example mismatches in courtship behavior, like between *Drosophila* species (Markow 1981, Schug & al. 2008) Some isolating mechanisms are further classified as prezygotic-postmating, where mating has occurred but sperm is not viable in the reproductive tract of the other species or has problems fertilizing the egg.

Temporal variation in mating flight time is a prime candidate for prezygotic isolating mechanism in ants. Species within a genus vary in the timing of their mating flight (McCluskey 1992), ranging from a few days to over two months. For example, despite prevalent hybridization between the wood ants *Formica aquilonia* and *F. polyctena*, they experience a temporal barrier and have diverged in mating flight times (Douwes 2012). In Finland, at its range margin *F. polyctena* hybridizes extensively with *F. aquilonia* and forms stable hybrid populations (Beresford & al. 2017, Satokangas & al. 2023). These hybrids are more numerous than *F. polyctena*, but harbor many characteristics of *F. polyctena*, like preference for warmer microhabitat and high polygyny (Satokangas & al. 2023). Further temporal isolation is observed between hybrids and *F. aquilonia*, as their flight times differ significantly, indicating a temporal prezygotic barrier that could eventually lead to speciation between the hybrids and one of their parental species (Krapf & al. 2025 unpublished data). Similar findings have been made for *Pogonomyrmex rugosus* and two independent lineages arising via hybridization. The two hybrid lineages not only fly at different times compared to *P. rugosus,* but they also have strong preference to mate within and between hybrid lineages, rather than with *P. rugosus* (SCHWANDER & al. 2008). While nuptial flight timings in ants have been described as generally consistent within species (MCCLUSKEY 1992), differences in flight times have been observed within the geographic range of a single species, *P. rugosus*, based on differing environmental cues across the range (HELMS & CAHAN 2010). Additionally, a reduction of nuptial and dispersal flights in some European species (SEIFERT 2010) may also support intraspecific divergence in flight timings as a route for initial prezygotic divergence.

Spatial isolation is a classic barrier to reproduction. While allopatry across islands (SARNAT & MOREAU 2011) or continents (SCHÄR & al. 2018) has certainly acted as an isolation barrier, habitat differentiation can also drive divergence in a sympatric or parapatric context. Therefore, ecological speciation or niche divergence is increasingly appreciated as a driver of species differentiation. The idea is that divergent selection for adaptation to niches in a heterogeneous environment drives genetic differentiation, along with reduced opportunities for mating due to the occupation of different habitats. Habitat often varies between ant species. For example, Véle & al. (2009) describe differentiation in average habitat preference between *Formica fusca*, *F. pratensis, F. sanguinea* and *F. truncorum* across soil and air temperatures, light intensity, and forest and ground cover. Such divergence can be explained by historical separation across refugia, as occurred in other *Formica* species (GOROPASHNAYA & al. 2004), and in two *Temnothorax* species (Pusch & al. 2006). Evidence for environment or habitat as an explicit driver of divergence is limited and best explored within species. In the leaf cutter ant *Atta cephalotes*, Muñoz-Valencia and colleagues (2022) found significant isolation by environment between populations separated by the Andes mountains, even after accounting for isolation by distance and isolation by barrier, though these factors likely interact. Studies of species diversification on broader taxonomic and geographic scales in *Stenamma* (BRANSTETTER 2012) and *Temnothorax* (PREBUS 2017) suggest habitat transitions coinciding with global cooling, but we lack data on how habitat would have led to isolation. We note that premating isolation due to habitat can be insufficient on its own to prevent gene flow, as seen in *Formica rufa* group, where habitat preference, even at the species level, is an incomplete barrier to gene flow for many species pairs (SATOKANGAS & al. 2023). Premating batteries may also shift or disappear with range changes, as seen in the fire ants *Solenopsis invicta* and *S. richteri*, which experience no gene flow in their native ranges in southern South America yet readily hybridize at the contact zone of their introduced ranges in North America (COHEN & PRIVMAN 2019).

As ants rely heavily on chemical communication and chemical cues for mate choice and nestmate recognition, these cues and recognition mechanisms are potential prezygotic barriers. Nestmate and species recognition have been under intense investigation in the context of kin recognition and social parasitism. Nestmate recognition in ants is largely based on antennal recognition of cuticular hydrocarbon (CHC) profiles (Fielde 1901, Fielde 1903), a complex blend of non-volatile chemicals present on the ant cuticle (Martin & Drijfhout 2009). Thus, CHCs could create much of the basis for mate recognition and mate choice in ants, providing mechanisms which could act as a starting point for prezygotic isolation. CHC profiles are species-specific and stable across geography in *Formica* (Martin & al. 2008) but may also be acquired or modified by the environment (Beibl & al. 2007), potentially allowing for divergence of recognition signals and eventually speciation driven by the environment. There is consistent evidence for mating preferences accompanying differences in CHC profiles (Morrison Iii & Witte 2011). Blacher & al. (2022) found a strong preference for conspecifics in mate choice experiments between *Formica selysi* and *F. cinerea*, coinciding with distinct CHC profiles. Beibl & al. (2007) found that sexuals of the dulotic ant *Chalepoxenus muellerianus* reared in their natural host's nests versus an alternative species host discriminated against each other. This suggests that mate choice cues in dulotic ants could diverge following host switching. The process of mate choice and CHC recognition are complex and associated with errors. This is highlighted by hybridization, which may asymmetrically impact mate preference of hybrid for either of the parent species (Beresford 2021).

Ant nests are full of resources, and social parasites have evolved to exploit these. Social parasitism in ants can be considered a form of brood parasitism (Rabeling 2021), whereby sexuals from one species rely on the social behavior and resources of a host species. In some cases, speciation via the evolution of social parasitism has been suggested to occur sympatrically, the parasite evolving from the host (See 4.2 Social parasitism as a driver of speciation). This initial divergence is very likely based on prezygotic isolating mechanism, like temporal isolation or differences in swarming behavior between the sexuals of the incipient parasitic species mating within the nest and the ones of the host species dispersing by flight (Rabeling 2021). Speciation can also occur when a socially parasitic lineage exploiting multiple host species becomes reproductively isolated based on host specificity as has occurred in wasps (Hambäck & al. 2024).

3.3 Mechanisms of postzygotic isolation in ants

Postzygotic isolating mechanisms operate after zygote formation and can be either intrinsic or extrinsic. Probably the best known intrinsic postzygotic isolating mechanisms are Bateson-Dobzhansky-Muller incompatibilities (Bateson 1909, Dobzhansky 1936, Muller 1942), that is, allele combinations from the two parental species are incompatible in hybrids, which reduces their viability or causes sterility. Extrinsic postzygotic isolating mechanisms reduce the fitness of hybrid individuals in specific environments. For example, in mimetic *Heliconius* butterflies, hybrids between *Heliconius melpomene* and *H. cydno* are fully viable, but they have novel wing patterns, so that the predators do not recognize them as butterflies they have learned to avoid and predate them (Merrill & al. 2012, Brower 2013).

The contrast between haploid males and diploid females in ants provides an ideal opportunity to map recessive intrinsic incompatibilities (Nouhaud & al. 2020). Heterospecific allele combinations that are lacking from haploid males but found in diploid female hybrids can be used to scan for candidate incompatibility loci. Intrinsic incompatibilities and their genomic extent have been studied in *Formica* wood ants (Kulmuni & al. 2010, Kulmuni & al. 2020). Recessive intrinsic incompatibilities are selected against in haploid hybrid males during development but masked in diploid females, leading to inviability of hybrid males, a hallmark of Haldane's rule. These patterns have been observed in *Formica polyctena* × *F. aquilonia* hybrids, where selection during development removed males with specific introgressed alleles, but these alleles were present in females as heterozygotes (Kulmuni & al. 2010, Kulmuni & Pamilo 2014a). Later studies have shown that intrinsic incompatibilities between these species are genome-wide (Kulmuni & Pamilo 2014, Kulmuni, Nouhaud, & al. 2020), yet reproductive isolation is incomplete (Satokangas & al. 2023) and gene flow between the species has occurred asymmetrically throughout their divergence (Portinha & al. 2022). Some of the genome-wide incompatibilities between *Formica polyctena* × *F. aquilonia* may be extrinsic, since frequency of introgressed alleles has been shown to correlate with spring temperature (Martin-Roy & al. 2021).

Although ants are an ideal study system to map the genomic location and extent of recessive incompatibilities, genomic studies of barrier loci in ants are surprisingly rare. Instead, some studies relied on behavioral experiments and viability analysis to study postzygotic isolation in ants. Strong postzygotic isolation in the form of hybrid inviability is observed in hybrids between *Pogonomyrmex rugosus* and one hybrid lineage (H). Genetic caste determination system of the hybrid *Pogonomyrmex* lineages is one of the unique consequences of hybridization in ants, where mating with one's own lineage produces new queens and males whereas mating with another lineage produces workers. The system is suggested to circumvent hybrid sterility, and to reap the benefits of increased genetic diversity in the female workers. There is strong prezygotic isolation between *Pogonomyrmex rugosus* and another hybrid lineage (H1), and the few heterospecific matings that do occur produce mainly inviable offspring, aborted at egg stage (Schwander & al. 2008). Indirect evidence of intrinsic incompatibility leading to inviability of males is also found in *Tetramorium*, where *Tetramorium immigrans*, *T. caespitum* and hybrid colonies are found in the field, but based on microsatellite analysis, no hybrid males were inferred from the worker genotypes (Cordonnier & al. 2020).

Incompatibilities could also be cytonuclear, induced by endosymbionts or by the co-evolution between the mitochondria and nucleus (Barnard-Kubow & al. 2016). *Wolbachia* are a genus of bacteria found in the ovaries and testes of various invertebrate species, including many species of ants (Wenseleers & al. 1998). Infection by *Wolbachia* can result in cytoplasmic incompatibility (CI), parthenogenesis, and feminization in insects (reviewed in Werren 1997). Due to these effects, *Wolbachia* has been put forth as a possible factor causing reproductive isolation between infected and non-infected populations (Degnan & al. 2004). While good evidence of isolation due to *Wolbachia* has been found for example in mosquitos, *Culex pipiens* (Laven 1967), and multiple *Drosophila* species (Bourtzis & O'Neill 1998, Veneti & al. 2012), the effects of *Wolbachia* in *Formicidea* are still relatively unknown (Russell 2012, Ramalho & al. 2021), but do include cytoplasmic incompatibility and potential for male killing. For example, *Wolbachia*-induced unidirectional cytoplasmic incompatibility was recently discovered between Old and New World populations of *Cardiocondyla obscurior* (Ün & al. 2021), preventing hybridization between populations of these species that carry different strains of *Wolbachia* (Degnan & al. 2004). This mechanism could eventually lead to speciation. In addition to speciation through direct reproductive isolation, coevolution between *Wolbachia* and the host can lead to interdependencies which, if disrupted by hybridization, could lead to incompatibilities. For example, Wolbachia provides nutrients by supplementing vitamin B in *Tapinoma melanocephalum* (Cheng & al. 2019).

Goodisman and colleagues (1998) developed a theoretical framework for cytonuclear interactions between haplodiploid species and applied it to a North American hybrid zone between the imported red fire ant *Solenopsis invicta* and the black imported fire ant *S. richteri*. These species do not hybridize in their native South American range, but they do in their introduced range (Ross & Robertson 1990) in North America. Shoemaker & al. (2006) show, through mtDNA based phylogenies, that the introduced populations lost their *Wolbachia* endosymbionts during their invasion of North America, which Feldhaar & al. (2008) interpret as the possible loss of a postzygotic barrier to hybridization driven by cytoplasmic incompatibility. Interesting cytonuclear patterns are also found in *Formica* hybrids. Beresford & al. (2017) identified a pattern of cytonuclear mismatch in *F. aquilonia* × *F. polyctena* hybrids, where nuclear *F. polyctena*-like individuals tend to carry *F. aquilonia*-like mitochondrial haplotypes, and vice-versa. This cytonuclear mismatch does not seem to negatively affect the fitness of these hybrids and therefore does not constitute a reproductive isolation mechanism in this specific system.

4. Hybridization and its implications in ants

When considering the mechanisms of reproductive isolation and speciation in ants, we are inevitably led to studies of hybridization. Hybridization occurs when different species, subspecies or genetically distinct lineages mate and produce offspring that carry genetic material from both parents. Hybridization in ants has been a topic of interest throughout the late 20th century, with studies of hybridization between fire ant species introduced to North America (Meer & al. 1985) and between *Formica* species in Central Europe (Seifert 1999). Furthermore, a recent comparative study developed an approach to detect F1 hybrids from single genome data and found that hybridization is especially prevalent in ants (Weyna & al. 2022). High rates of hybridization could further lead to hybrid speciation, as several studies have documented mechanisms that isolate hybrids from one of both of their parental species (Schwander & al. 2008, Blacher & al. 2022, Satokangas & al. 2023). More generally, hybridization provides novel combinations of ancient genetic variants, which can lead to rapid specialization and speciation, as demonstrated in the adaptive radiation of lake Victoria cichlid fishes, for example (Marques & al. 2019, Meier & al. 2023) While not necessarily focused on speciation itself, the growing research on hybridizing ant species has expanded our understanding of reproductive isolation mechanisms between ant species and revealed interesting evolutionary consequences of hybridization in ants.

As described above, ants are haplodiploid and social organisms, so that males are produced asexually. These factors modulate the way ants are affected by hybridization. When a gyne mates with a male from another species, this leads to asymmetry between sexes; all the females (queens and workers) are F1 hybrids, but as males are produced asexually by the mother (i.e., pure parental queen), they are not hybrids. Hybrid males occur only in the F2, and these hybrid males are the sons of F1 queens (Koevoets & Beukeboom 2009), which means that hybrid males trail behind hybrid females by one generation. The delayed appearance of hybrid males after an interspecific crossing means that there are reduced opportunities for introgression between the nuclear genome of the hybridizing species in haplodiploids compared to diploids, while the mitochondrial genome is always available for introgression in hybrid diploid females. Therefore, there is potential for biased mitochondrial introgression, relative to nuclear introgression, in haplodiploid hybrid organisms compared to diploid organisms, as found by Patten & al. (2015) through mathematical modelling.

To produce F2 and further generation hybrids, the sexual hybrid individuals must be fertile. If hybrids are sterile, it is difficult to establish a stable hybrid lineage, unless hybrids are produced by repeated interspecific matings. This is a severe limitation in ants, as queens usually mate only once after their emergence and store the sperm in their spermatheca for later use, meaning that they are “stuck” with the same genetic material for the entirety of their reproductive lives. Multiple matings can lessen this problem and there is evidence for frequent, but usually low level, polyandry (i.e., mating with multiple males by queens) in ants (Schmid-Hempel & Crozier 1999). For example, (Pamilo 1993) found that about 60% of *F. aquilonia* queens mate with multiple males, but that the number of matings is low (1-6). Overall, the number of male mates per queen is very variable across ant species, ranging from one up to 25 in some army ants (Boomsma & Van Der Have 2002, Kronauer & al. 2011, Barth & al. 2014). If a pure species queen mated with a heterospecific male can produce viable hybrid workers, but no hybrid sexuals, she can rescue her fitness by producing pure males asexually, and/or by mating multiply to secure intra-specific partners (Feldhaar & al. 2008). Various forms of social hybridogenesis have been described in ants, with hybrid workers resulting from inter-lineage matings, while males are produced asexually, and queens either asexually or from intra-lineage crosses (Leniaud & al. 2012, Lavanchy & Schwander 2019). The case of *Pogonomyrmex* harvester ants presents an interesting implementation of this solution. The distribution of the species *P. rugosus* and *P. barbatus* overlap in southwest New Mexico (North America), where hybrid populations show strong genetic caste determination (Julian & al. 2002). Helms Cahan & Keller (2003) identified four genetic lineages (H1, H2, J1, J2) and showed that inter-lineage matings produce workers, while intra-lineage matings produce queens; these lineages are essential to the caste-functionality of the colonies in these populations. Anderson & al. (2006) found evidence that this genetic caste determination was obtained by introgression from *P. barbatus* in *P. rugosus*, following inter-specific hybridization. Later, Schwander & al. (2008) found that the H1 and H2 lineages are almost completely reproductively isolated from one of their parental species, *P. rugosus*, due to the combined effects of asynchronous mating flights and assortative mating (pre-zygotic reproductive isolation mechanisms), and hybrid inviability, as the majority of eggs produced in backcrosses with *P. rugosus* die before reaching the larval stage (post-zygotic mechanism). This hybrid *Pogonomyrmex* system highlights how sociality provides original ways by which hybrid lineages can circumvent post-zygotic reproductive barriers.

In later generation hybrids, the dynamics and purging of hybrid incompatibilities differ between haplodiploid and diploid organisms. A codominant incompatibility in diploids is expressed equally in males and females and carries the same fitness costs to all individuals, implying a long and somewhat “softer” selective process working on the resolution of hybrid incompatibilities. However, with haplodiploidy, all hybrid incompatibilities behave like dominant incompatibilities in the haploid males and are exposed to selection (e.g. Beukeboom & al. 2015). This translates into higher fitness costs for males than for females in the short term, which is predicted to speed up the population-wide sorting/purging progress in the long term (Kulmuni & al. 2024). As such, these genetic incompatibilities may be resolved faster in haplodiploid hybrid populations than they are in diploid populations. If hybrid incompatibilities are not lethal, hybrid ants could escape the costs of hybridization imposed by these incompatibilities more quickly than diploid hybrid organisms.

If the hurdles of incompatibilities are buffered by social conditions, a population of hybrids could persist through time. In the case of highly polygynous supercolonial mound-building wood ants (Stockan & Robinson 2016), the presence of multiple reproductive queens coupled with nest budding could facilitate the maintenance of hybrid queens despite strong hybrid incompatibilities and low hybrid hatching rate (Martin-Roy & al. 2021). Even if the hatching rate of hybrid queens is low, hundreds of reproductive queens could allow survival of the colony. Furthermore, such low fitness females are buffered from environmental conditions within the stable nest environment. Hybrid queens with low egg hatching rates or high larval mortality would be quickly eliminated in solitary species, or in social monogynous species with independent colony founding.

The interplay between sociality and haplodiploidy fundamentally shapes how hybridization and interspecific gene flow unfold in ants, with complex outcomes and unusual hybridogenetic systems that often differ from expectations derived from diploids. These factors may influence the course of speciation, highlighting the need to consider social structure and reproductive mechanisms when studying the origin and persistence of species in ants.

5. Interactions with other organisms as drivers of speciation

Ants display a diverse set of lifestyles and behaviors (Hölldobler & Wilson 1990). In addition to the various social behaviors mentioned above, they can cultivate plants, tend fungi or other animals as food sources, and parasitize other species (Hölldobler & Wilson 1990). These interactions with other organisms, be them plants (Nelsen & al. 2018), fungi (Dejean & al. 2023), or other animals (Stadler & Dixon 2005, Parmentier & al. 2020), likely promoted ant diversification and speciation, and led to the evolution of highly specialized, if not unique characteristics and lifestyles. Much research exists on the evolution, taxonomy and distribution of these interactions and resulting lifestyles, but fewer studies specifically investigate reproductive isolating mechanisms that could have led to speciation in these cases. Below, we will discuss ant-plant interactions, trophobionts (e.g., sap-sucking insects), fungus-growers, and social parasitism as case studies. We highlight which reproductive isolating mechanisms might act in each case and how they could be investigated in future research.

5.1 Interactions with plants, fungi, and other organisms as drivers of speciation

Ants can interact with plants, fungi, and other organisms on various intensity levels ranging from facultative and generalised to obligatory and highly specialised (Delabie 2001, Nelsen & al. 2018, Parmentier & al. 2020, Dejean & al. 2023). Under the right conditions, such interactions can promote the development of prezygotic barriers and lead to speciation (Ward 1993).

Ant-plant co-evolution has led to the evolution of specialized resources provided by plants for ants, such as nest sites or food, and reciprocally of nutrients and protection against herbivores provided by the ants to the plants (Hölldobler & Wilson 1990, Bronstein & al. 2006, Nelsen & al. 2018). For example, ant-plant interactions are known between plants of the genus *Vachellia* and acacia ants in the *Pseudomyrmex ferrugineus* group (Ward & Branstetter 2017) or the dolichoderine ant *Philidris nagasau* attending six *Squamellaria* epiphyte plant species (Chomicki & Renner 2016). After such interactions have formed, they may allow dispersal and persistence in slightly different habitats than the ancestral lineage, promoting reproductive isolation in allopatry or parapatry. For example, in the *P. ferrugineus* group reproductive isolation due to geographical isolation is assumed to be the driving speciation force (Ward 1993): With the shift of ants to open habitats ~6 Mya (Ward & Branstetter 2017), fewer ant colonies may have been in the nearby surroundings and thus fewer possibilities to mate, promoting reproductive isolation. Similarly, the dolichderine ant *P. nagasau* seems to be endemic to the Fiji Islands, which likely has promoted reproductive isolation in allopatry after arriving there (CHOMICKI & al. 2016). Notably, *Philidris* species have received little attention so far, so that other obligate interactions may be found to further elucidate the speciation event in this genus.

Ants have also evolved symbiotic associations with fungi (MUELLER & al. 2005). Attini ants are the most famous examples of obligatory mutualism in which ants nourish various fungus cultivars with leaves and use the fungi bodies as food (SCHULTZ & BRADY 2008). Notably, leaf-cutter ants of the genus *Atta* have obligate mutualistic interactions with a single fungus species, *Leucoagaricus gongylophorus* (MIKHEYEV & al. 2006, SCHULTZ & al. 2024). This co-evolution occurred via several changes in both partners and promoted reproductive isolation and speciation in the *Atta* genus: Ants and fungus lose the ability to produce arginine (BRANSTETTER & al. 2017) and to break down lignin (NYGAARD & al. 2016), respectively, thus being dependent on the partner, or the obligate vertical transmission of the fungus by dispersing queens (MUELLER & al. 2001).

As in ant-plant interactions, geographic isolation but also ecological and behavioral differences have likely driven speciation in *Atta* species, which have spread from Central America to the southern parts of South America (BARRERA & al. 2021). For example, *A. colombica* is mainly found in lower-elevation regions in Central America to north-western South America, while sympatric *A. cephalotes* is present in higher-elevation regions across South America (BARRERA & al. 2021), which suggests that geographic and ecological barriers may have promoted reproductive isolation and speciation. Additionally, some species are separated geographically but also use different plants. For example, *A. vollenweideri* and *A. goiana* forage mainly for monocotyledonous plants, while *A. saltensis* and *A. opaciceps* only use dicotyledonous plants (BARRERA & al. 2021), suggesting that they could have speciated geographically and behaviorally. Indeed, behavioral differences may further drive speciation. For example, *A. cubana* occurs sympatrically with *A. insularis* on the island of Cuba and uses coastal regions and sandy soils as nesting sites, while *A. insularis* prefers forest and grassland habitats (FONTENLA 1995, BARRERA & al. 2021). These differences in habitat preferences may have led to a change in the CHC bouquet and thus to reproductive isolation. However, there is a clear interplay between behavior (selecting nest substrate) and ecology (habitat) in this case. The potential barriers and reproductive isolating mechanisms discussed above await for further testing.

Ants also interact with other organisms that can promote speciation, such as trophobionts (e.g., caterpillars and sap-sucking insects; STADLER & DIXON 2005, PARMENTIER & al. 2020) or endosymbionts such as *Wolbachia* or *Blochmannia* (ROUSSET & al. 1992, DEGNAN & al. 2004). Ants tend trophobionts, protect them against predators, and trophobionts provide food by excreting a sugary solution called honeydew (DELABIE 2001, STADLER & DIXON 2005). Such interactions can range from facultative to obligate (Stadler and Dixon, 2005) and 25% of more than 4,000 aphid species are tended by ants; PARKER & KRONAUER 2021). Ant species of the genus *Acropyga* have an obligate trophobiotic interaction with mealybugs of the genera *Eumyrmococcus, Neochavesia,* and *Xenococcus* (all subfamily Rhizoecinae). This interaction formed 15-20 Mya (LaPolla 2005) and seems to have driven speciation. For example, mealybugs have only been found inside *Acropyga* nests, ants only feed on honeydew provided by the mealybugs, and *Acropyga* gynes carry mealybugs in their mandibles during mating flights to start a new "herd" in the new colony (a behavior termed "trophophoresy"; LaPolla & al. 2002). Additionally, ants and mealybugs only live belowground and are found in Arizona (USA) and Mexico (LaPolla & al. 2002). These close interactions between the partners suggest that behavioral and geographical barriers could have led to reproductive isolation and speciation. However, to elucidate whether these interactions are species-specific, several ant species in the genus as well as their mealybugs should be collected, and mealybugs should be switched among ant species. If the interactions between ants and mealybugs are species-specific, this would provide support for ecological speciation.

Endosymbionts such as *Wolbachia* or *Blochmannia* can induce changes in sexual reproduction and lead to reproductive isolation and speciation (Rousset & al. 1992, Degnan & al. 2004). A well-known example of co-speciation includes *Camponotus* ants and their endosymbionts *Blochmannia* (Degnan & al. 2004), with each *Camponotus* species having its own vertically transmitted endosymbiont (Manthey & al. 2022). Notably, *Blochmannia* genes are evolving about 30 times faster than *Camponotus* genes, and both rates of molecular evolution are positively correlated (Manthey & al. 2022). This rapid gene evolution may have led to *Blochmannia* diversification and thus to *Camponotus* co-speciation and can, in the future, promote reproductive isolation and speciation.

5.2 Social parasitism as a driver of speciation

Social parasitism is the 'parasitic dependence of a social insect species on one or several free-living social species' (Buschinger 2009). It has evolved at least 60 times independently in six different, distantly related ant subfamilies and can be found in over 400 species (Rabeling 2021). Four types of social parasitism are distinguished, namely ant guests (xenobiosis), temporary social parasitism, permanent social parasitism with dulosis ('slave-making'), and permanent social parasitism without dulosis (inquilinism; Bourke & Franks 1991, Buschinger 2009, Rabeling 2021). All temporary and permanent parasites are closely related to their respective host species ((Emery 1909; later termed 'Emery's rule'; Wilson 1971). Today, a *strict form* of Emery's rule (i.e., parasites are the closest relatives to their host (Ward 1989) is distinguished from a *loose form* (i.e., parasites and their hosts are closely related). Two hypotheses following Emery's rule have been postulated to explain how social parasitism evolved (Bourke & Franks 1991): The *intraspecific* hypothesis suggests that a social parasite evolves directly from its host in sympatry (strict Emery's rule), while the *interspecific* hypothesis suggests that a non-parasitic species evolves a parasitic behavior allopatrically and starts parasitising another non-parasitic species (loose Emery's rule). For both hypotheses, polygyny and polydomy seem to be a prerequisite

(Bourke & Franks 1991, Buschinger 2009, Rabeling 2021): Polygyny allows the adoption of non-nestmate queens, and polydomy to easily find other host colonies. Both traits are common in genera containing socially parasitic species, such as *Acromyrmex* (Rabeling & al. 2014), *Formica* (Borowiec & al. 2021), *Lasius* (Brendon E. Boudinot & al. 2022), *Myrmecia* (Douglas & Brown 1959, Mera-Rodríguez & al. 2023), and *Myrmica* (Savolainen & Vepsäläinen 2003).

Whether social parasite evolved in sympatry or allopatry has implications on how reproductive isolation builds and thus on the process of speciation. For example, inquilines seem to speciate more frequently in sympatry (intraspecific hypothesis), while temporary and dulotic social parasites seem to speciate in allopatry (interspecific hypothesis; Rabeling 2021, Mera-Rodríguez & al. 2023), but see also Talbot 1976, Fischer & al. 2020 for allopatric speciation of inquilines). In one case, a socially parasitic lineage evolved quickly and intraspecifically, within lab-bred colonies of asexual workers of clonal raider ants (Trible & al. 2023). Winged, queen-like individuals appeared suddenly, and these clonal "social parasites" had lost heterozygosity at a large genomic region, suggesting that a pre-existing genetic module, or supergene, equipped them with the necessary behavioral, morphological and physiological specialization (Chapuisat 2023, Trible & al. 2023).

In non-clonal ants, reproductive isolation can also occur intraspecifically and in sympatry, via several ways frequently observed in inquilines (Buschinger 2009, Rabeling 2021): (i) Socially parasitic offspring are smaller (i.e. microgynes) and have a shorter developmental time than regular-size sexual offspring of the host, which can lead to assortative mating and temporal reproductive isolation. A smaller body size of social parasites has been observed in *Acromyrmex* (Schultz & al. 1998, Mera-Rodríguez & al. 2023), *Ectatomma* (Nettel-Hernanz & al. 2015), *Myrmica* (Savolainen & Vepsäläinen 2003, Leppänen & al. 2015 but see also Steiner & al. 2006), *Nylanderia* (Messer & al. 2016), *Plagiolepis* (Aron & al. 2004), and *Pseudomyrmex* (Ward & Branstetter 2022). (ii) Sexuals of social parasites mate inside or close to the nest, which also allows assortative mating and promotes spatial reproductive isolation. This shift in mating system has been observed in *Mycocepurus* (Rabeling & al. 2014) and *Myrmica* (Savolainen & Vepsäläinen 2003), and is suspected for *Nylanderia* (Messer & al. 2016). (iii) At later stages in the speciation continuum, gene flow and hybridisation between host and social parasite cease (Mera-Rodríguez & al. 2023) and their male genitalia differ largely, leading to complete reproductive isolation, as observed in *Mycocepurus* (Rabeling & al. 2014). (iv) Parasitic queens may also suppress the production of host sexual offspring, as observed in *Mycocepurus* (Rabeling & al. 2014).

For allopatric speciation of social parasites, evidence for reproductive isolation is indirect (Buschinger, 2009) and has been found in the genera *Formica* (Borowiec & al. 2021), *Pheidole* (Fischer & al. 2020), and *Temnothorax* (Prebus 2017), based on phylogenomic reconstructions. Comparisons mainly comprise temporary and dulotic social parasites, but also examples of inquiline species (Rabeling 2021). A non-parasitic species can evolve some parasitic behavior in allopatry and start parasitizing other, free-living species (Rabeling 2021). For example, *Formica* temporary social parasites seem to have evolved after the loss of independent colony foundation (Borowiec & al. 2021). In theory, if a species splits into two allopatric daughter species A and B, queens of species A may start to "cheat" and rely on nearby colonies of other species for colony foundation. After secondary contact, species A may start parasitizing species B, while remaining reproductively isolated (Bourke & Franks 1991). Dulosis seems to have evolved in *Formica* ants from temporary social parasitism (Borowiec & al. 2021). Three scenarios for its development have been proposed (Buschinger 2009, Borowiec & al. 2021, and references in both): (1) A species is highly territorial and competitive, allowing it to invade weaker or smaller colonies and kill them, (2) A species may predate on brood and food of other species, or (3) A species transports brood over longer distances. Socially parasitic ants and their hosts thus provide excellent systems to test models of sympatric and allopatric speciation, and examine how behavioral, social, ecological and genetic changes jointly lead to reproductive isolation.

Conclusions and outlook

Thanks to their ubiquity, geographic spread, and ecological diversity, ants provide an ideal system to study speciation. Numerous species pairs with known ecology and life histories can allow for testing ecological divergence, while frequent hybridization provides opportunities for studying the impact of gene flow on genomic divergence, both key areas of current speciation research. Furthermore, the wealth of research addressing ant taxonomy, ecology, and distributions, means that reproductive isolation mechanisms could be tested and compared across many groups of closely related species. These comparative analyses would allow, for example, insights into the relative importance and timing of the evolution of pre- and post-zygotic barriers, or the role of intrinsic and extrinsic factors in the speciation process. Additionally, the genomic data on ants is accumulating. Together with the possibility of accessing population samples of haploid male genomes without the need for phasing will allow for mapping species barriers across the genome, as well as addressing the importance of chromosomal inversions and supergenes in speciation and reproductive isolation.

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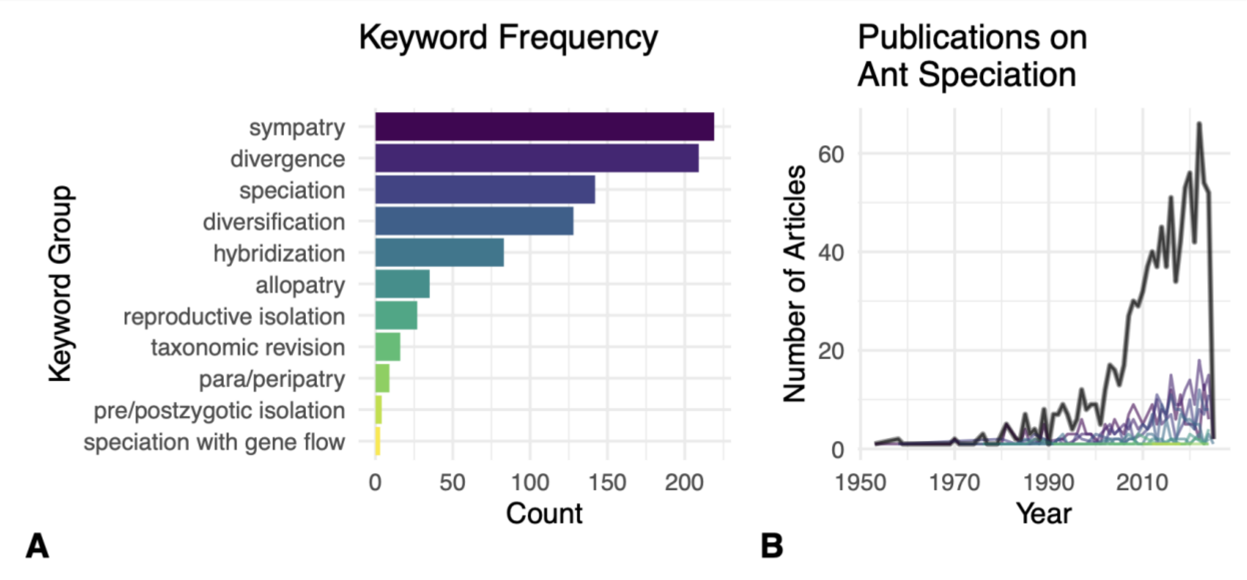
Table and figure captions

Fig. 1: Speciation research on ants is not usually performed under the framework of reproductive isolation. A) Counts of each keyword together with “ant”, “ants”, or “Formicidae” in the literature search including 2,665 published articles found from Web of Science, Google Scholar, and Scopus. B) Time series by year for the number of articles containing any of the keywords included in the search, line colors match bar colors and labels in the bar chart, while the black line shows total publications.


Keyword Frequency
Keyword Group
sympatry
divergence
speciation
diversification
hybridization
allopatry
reproductive isolation
taxonomic revision
para/peripatry
pre/postzygotic isolation
speciation with gene flow
0
50
100
150
200
Count
A
Publications on Ant Speciation
Number of Articles
0
20
40
60
1950
1970
1990
2010
Year
B