# Ants (Hymenoptera: Formicidae) as host and intruder: recent advances and future directions in the study of exploitative strategies

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## Abstract

Despite their reputation for building fortress-like colonies, ants and other social insects have many natural enemies that can infiltrate and exploit them. This profitable strategy, which allows individuals to reap collective benefits while paying few costs of cooperation, has evolved repeatedly in ants. Here, we review recent advances in the study of social parasitism, with three goals: (1) consider how social parasitism arises within the ants, (2) examine the exploitative and defensive tactics employed by parasites and hosts at each stage of their interactions, and (3) integrate recent social parasite species discoveries into an overview of the biogeographic distribution of social parasites. We focus on three common types of interspecific social parasitism: temporary, queen-killing parasites, permanent inquilines (which are usually, but not always, queen-tolerant), and dulotic species that steal heterospecific brood to build their own workforce. We consider only superficially intraspecific interactions and interspecific associations that appear to walk the line between commensal and parasitic. Through our classification of the components of social parasite evolution and our updated assessment of social parasite biogeography, we identify several knowledge gaps in the field and close with some proposed strategies and priorities for future research.

**Key words:** Dulosis, inquiline, temporary social parasite, social parasitism, coevolution, biogeography, latitudinal diversity gradient, review.

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## Introduction

Social insects are known for their coordinated social behavior, elaborate nest structures, and significant ecological impacts (HÖLLDOBLER & WILSON 1990, MICHENER 2000). They are an ongoing focus of research on the evolution and elaboration of social organization (e.g., WILSON 1971, KELLER 1993, BOURKE & FRANKS 1995, REHAN & TOTH 2015, NEGRONI & al. 2016, WEITEKAMP & al. 2017). The "common goods" produced by insect societies are frequent targets of use and exploitation by other organisms. Social parasitism has evolved repeatedly in the eusocial insects and can be used as a tool to understand the costs and benefits of cooperation and cheating (CINI & al. 2019). Ant nests, in particular, frequently harbor a diverse array of social parasites, including ants that socially parasitize other ant species and other myrmecophilous insects (PÉREZ-LACHAUD & LACHAUD 2014). Although the terms "inquiline" and "social parasite" are also used in the myrmecophile literature, non-ant social parasites

will not be covered in this review. This manifestation of social parasitism is a source of fascination from the perspectives of speciation mechanisms, host / parasite coevolutionary arms races, and biogeographic distribution of social parasite pressure, among other topics. This review will examine the current state of knowledge of these facets of ant social parasitism and identify knowledge gaps that could be pursued through future research.

Of the 16,230 valid ant species and subspecies (ANT-WEB 2019), only an estimated 2% are confirmed facultative or obligate social parasites (BUSCHINGER 2009, RABELING & al. 2019). These are unevenly distributed among the ant subfamilies, with the highest proportions found in the subfamilies Myrmicinae (~1.5% of 6772 species) and Formicinae (~3.2% of 3178 species), and fewer in Dolichoderinae (0.3% of 711 species), Pseudomyrmecinae (0.4% of 231 species), and Ectatomminae (0.4% of 264 species) (WARD 1996, LOWE & al. 2002, FEITOSA & al. 2008, HUANG
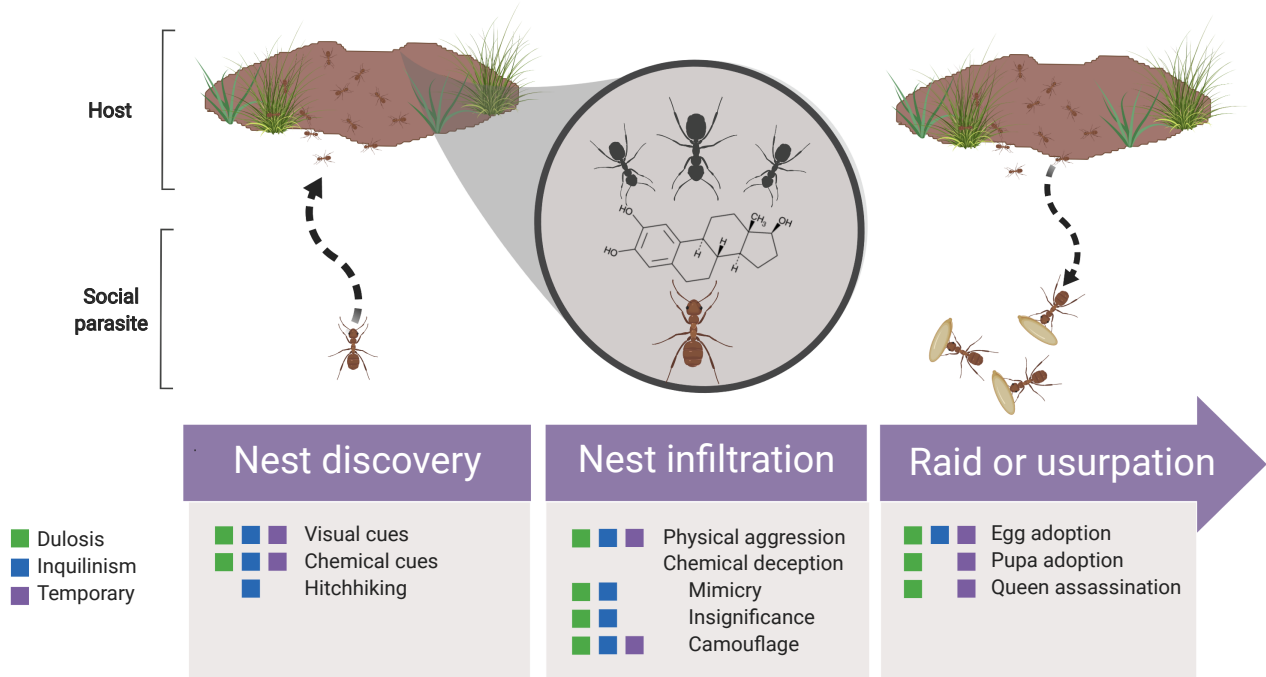
Fig. 1: Summary of the mechanisms of exploitation used by social parasites across the stages of host exploitation: nest discovery, nest infiltration, and raid or usurpation. Colored squares indicate which parasite form utilizes each mechanism of exploitation (green = dulosis; blue = inquilinism; purple = temporary). Created with BioRender.

& Dornhaus 2008, Buschinger 2009). Among socially parasitic ants, we see the repeated, parallel origin of three distinct strategies: temporary social parasitism, permanent inquilinism, and dulosis (Hölldobler & Wilson 1990). Temporary social parasites use host colonies to initiate new nests; newly mated queens enter the host colony and assassinate the queen or queens if present. Remaining host workers assist with parasite brood rearing and other tasks while they persist. The eventual result is a free-living parasite colony. Inquilines likewise enter the host colony as newly mated queens, but rather than killing, they persist side-by-side with the host queen(s). These inquiline social parasites then exploit the labor of host workers to rear offspring. In some cases, inquiline species have lost the worker caste and focus solely on producing sexual offspring (e.g., Talbot 1976, Bourke & Franks 1991, Ward 1996, Sanetra & Buschinger 2000, Cini & al. 2019). Dulotic species steal worker brood (usually pupae) from host nests, and the resulting stolen workers carry out the majority of the tasks in the colonies of the social parasite. Most dulotic species also initiate their colonies through nest usurpation like the temporary social parasites (e.g., d'Ettorre & Heinze 2001); facultative dulotic species such as *Formica sanguinea* may employ either host usurpation (e.g., Mori & Le Moli 1998) or alternative nest founding strategies, such as nest fission (e.g., Pamilo & Varvio-Aho 1979). Although we acknowledge that other relationships can share some characteristics of social parasitism, including intraspecific brood theft (e.g., *Diacamma indicum*), xenobiosis (= nest sharing), and cleptobiosis (= theft of food) (e.g., Lenoir & al. 2001,

Adams & Longino 2007, Powell & al. 2014, Paul & Annagiri 2018), we focus primarily on the aforementioned modes of interspecific parasitism.

Here, we review the current state of research on the emergence of social parasite species and their potential effect on the diversification of free-living ant species. We then investigate the traits of social parasites that facilitate exploitation of hosts, the traits of hosts that mitigate the costs of social parasitism, and the coevolutionary arms race between parasite and host. Finally, we examine our current understanding of the biogeographic distribution of social parasites overall and then zoom in on the distribution and potential for future discovery of each of the three social parasite strategies. While our understanding of social parasite dynamics is expanding rapidly, there are still many questions and research directions that remain virtually unexplored.

**Methods**

There have been excellent reviews of social parasitism over the past 40 years, and many of these helped to inspire our interest in the topic. These reviews vary in their scope, focus, and publication year, but form a solid foundation upon which to build this field. Useful reviews that provide a general overview of social parasitism in ants include Buschinger (1986), Hölldobler & Wilson (1990) chapter 12, d'Ettorre & Heinze (2001; emphasis on dulosis), and Buschinger (2009). Additional reviews focus on chemical ecology of ants (and, in some cases, other social insects), with an emphasis on social parasitism (Lenoir & al. 2001, Akino 2008, Lhomme & Hines

2018), on the coevolutionary dynamics between hosts and parasites (e.g., Brandt & al. 2005a, Cini & al. 2019), on social parasite reproductive strategies (Wolf & Seppä 2016), and on defensive strategies of hosts (Grüter & al. 2018). Meta-analyses investigate whether social parasites conform to Emery's Rule, which states that social parasites are closely related to their hosts (Huang & Dornhaus 2008), and whether host / parasite interactions are shaped by host geographic range size (Suhonen & al. 2019).

In formulating an assessment of the field, this review focused mostly on studies published in the past two decades, many of which were not addressed by previous reviews. A comprehensive survey of relevant literature published between the years 2000 and 2019 was conducted. Older empirical citations include foundational contributions that warrant direct acknowledgment (although some important classical studies were certainly overlooked) and studies that cover topics not represented by the recent literature. An organizational structure for the consideration of coevolutionary dynamics was developed that helps to shed light on understudied aspects of the social parasite lifestyle (Fig. 1). Table S1 (as digital supplementary material to this article, at the journal's web pages) provides a list of recently discovered or studied social parasite / host pairs, with current scientific names based upon their status in the AntWeb database (accessed between January and October 2019). Notably, the nomenclature for some groups is still a topic of debate in the literature and will likely continue to change with future phylogenetic discoveries.

**Emergence of socially parasitic ants**

Social insect colonies produce costly commodities that are beneficial to the group, including workers and nest structures, making them a prime target for exploitation. As a result, social parasitism strategies have evolved convergently in multiple ant lineages (Buschinger 1986, Buschinger 2009; Fig. 2), as well as in wasps (Lopez-Osorio & al. 2015, Cervo 2016, Cini & al. 2019) and bees (Michener 2000, Smith & al. 2013, Lhomme & Hines 2019). Social parasitism within social insect lineages generally involves parasites stealing or co-opting workers for their own benefit and / or occupying the nest structure of their hosts (Hölldobler & Wilson 1990, Buschinger 2009). Although the evolution of social parasitism in eusocial lineages has fascinated researchers for over a century (Emery 1909), we still have much to learn.

Research on speciation mechanisms in ants is still relatively sparse (e.g., Seifert 2010, Purcell & al. 2016), although socially parasitic species have received more attention in proportion to their numbers than other members of Formicidae (Buschinger 1990, Lowe & al. 2002, Sumner & al. 2004b, Rabeling & al. 2014, Leppänen & al. 2016). In this section, we will discuss recent advances in research focused on the origin of social parasites, and, to a lesser extent, on the potential consequences of parasitism on host speciation.

Fig. 2: Dulotic social parasites raid host nests and steal brood. *Polyergus* workers, for example, steal pupae from *Formica* hosts (A, photo by Gary D. Alpert). Inquiline queens live inside the nests of their hosts, often side-by-side with host queens. Small queens of the *Solenopsis phoretica* group actually grasp the petiole and ride on their *Pheidole* host queens (B, photo by Alex Wild).

**Diversification patterns:** Emery (1909) famously commented on the tendency of social parasites and their hosts to be closely related species, a relationship now called "Emery's rule". More recent evidence shows that there is variation in the degree of relationship between parasite and host. Many social parasites are congeners or in sister genera with their hosts, but they are not sister species; this situation is referred to as the "loose" version of Emery's rule (Bourke & Franks 1991, Sumner & al. 2004a, Huang & Dornhaus 2008). A smaller number of social parasites are not closely related to their hosts, as in *Polyrhachis lama*, which parasitizes *Diacamma* sp., a member of a different subfamily (Maschwitz & al. 2000). We also observe variation in patterns of social parasite prevalence along another axis: the degree of diversification of lineages containing social parasites (e.g., Buschinger 1990, Beibl & al. 2005). At one end of the spectrum, some lineages contain only one parasitic species, as seen in *Nylanderia* (Messer & al. 2016), *Ectatomma* (Feitosa & al. 2008), and *Mycocepurus* (Rabeling & Bacci 2010). In contrast, other groups are marked by repeated

emergence and / or continued diversification of social parasite lineages, as in *Lasius* (Janda & al. 2004, Maruyama & al. 2008), *Acromyrmex* (Sumner & al. 2004a, Rabeling & al. 2019), *Myrmica* (Savolainen & Vepsäläinen 2003, Jansen & al. 2010), and *Temnothorax* (Beibl & al. 2005, Feldmeyer & al. 2017, Prebus 2017). Some groups even exhibit transitions in social parasite strategy after the emergence of social parasitism, as in *Formica* (Romiguier & al. 2018) and *Tetramorium* (Sanetra & Buschinger 2000). Many of these insights have been gained through phylogenetic analysis of host and parasite lineages, including in *Lasius* (Janda & al. 2004, Maruyama & al. 2008), *Myrmica* (Jansen & al. 2010), and *Tetramorium* (Sanetra & Buschinger 2000). During the past several years, in particular, phylogenetic inference has been enhanced with the incorporation of transcriptomic or other genomic data in *Formica* (Romiguier & al. 2018) and *Temnothorax* (Feldmeyer & al. 2017, Prebus 2017).

Huang & Dornhaus (2008) explored whether the mechanism of speciation and the consequences of the transition to social parasitism varied with the social parasite strategy. They found that Emery's rule generally applies to inquilinism and temporary parasitism, but not dulosis or xenobiosis. They used the loose Emery's rule definition in their analysis; as a result, their study does not shed light on whether the evolution of some parasitic strategies is more likely to lead to subsequent diversification than others. Given alternative mechanisms shaping the origin of alternative social parasite strategies, this would be an interesting question. Buschinger (1990, 2009) revealed that there were only four host lineages associated with radiations of social parasites employing diverse strategies (e.g., dulosis and inquilinism in the same radiation), and there is now sufficient phylogenetic resolution to revisit this observation with a more formal analysis. Based on their extreme specialization, we predict that the origin of inquilinism may frequently be an evolutionary dead end, with parasites exploiting a single closely related host, but host shifts being unusual and unlikely, as seen in most *Myrmica* social parasites (Jansen & al. 2010, Leppänen & al. 2016). In contrast, dulotic species and temporary social parasites often exploit multiple hosts, and this ability could lead to subsequent speciation through geographic isolation and / or host shifts (Torres & al. 2018).

**Speciation mechanisms:** Building upon arguments put forth by Buschinger (1990), we suggest that biogeographic factors and specialization of social parasites on hosts likely contribute to the diversification outcome of newly evolved social parasites (i.e., whether parasitic lineages give rise to more species or not). Host switching may be a key mechanism mediating diversification of social parasites; for instance, Torres & al. (2018) recently found evidence of host species-associated divergence and, potentially, restricted gene flow in *Polyergus* populations that kidnap brood from different host species in a shared environment. As a result, the diversity and shared distribution of closely related prospective host species could influence the speciation patterns of social parasites. We predict that

parasites associated with relatively speciose host lineages with broadly sympatric distributions will be more speciose themselves. Due to their low densities relative to host species and dependence on adequately high host densities for population persistence, social parasites might also be more susceptible to having isolated geographic lineages. For example, *Leptothorax acervorum* host populations differ in their ability to repel slave making *Harpagoxenus sublaevis* raids, and likewise, populations of the social parasite differ in their ability to manipulate the host (Foitzik & al. 2003). Such geographic variation (sometimes called the geographic mosaic theory; Blatrix & Herbers 2003, Fischer & Foitzik 2004) could lead to eventual speciation following prolonged periods of isolation. Finally, hybridization may facilitate host shifts in some cases and could be investigated as an additional mode of speciation in social parasites. For example, temporary social parasites in the genus *Formica* frequently hybridize (Seifert & al. 2010, Kulmuni & Pamilo 2014, Beresford & al. 2017, Ghenu & al. 2018); it would be interesting to examine whether hybrid queens use a socially parasitic colony founding strategy in these groups and, if so, whether they use the same hosts as parent species. Each of these hypotheses could be tested through phylogenetic methods.

Social parasites and hosts are both undergoing evolutionary change in parallel, as we discuss in the next section. We know very little about whether and how social parasitism contributes to speciation in host species. As in *Leptothorax* species (Foitzik & al. 2003, Fischer & Foitzik 2004), we observe regional variation in the prevalence of social parasites and the defensive tactics employed by the host (Achenbach & Foitzik 2009, Pamminger & al. 2011, Alleman & al. 2018). We propose that regional differences in social traits like colony queen number (e.g., Purcell & al. 2015) and chemical profile diversity (e.g., Martin & al. 2011) could also be shaped in part by social parasite abundance and diversity. If such differences result in genetic incompatibilities or other barriers to mating over evolutionary time, this could mediate parapatric speciation in host lineages.

In addition to observing broad-scale patterns across the phylogeny, we call for more detailed case studies focused on the mechanisms of speciation in social parasites and their hosts. So far, such studies are unevenly distributed, with disproportionate attention paid to potential cases of incipient sympatric speciation, as we see in the ongoing discussion about the status of microgynes of *Myrmica rubra* (e.g., Savolainen & Vepsäläinen 2003, Steiner & al. 2006, Vepsäläinen & al. 2009). We suggest that studies of speciation and genetic differentiation between closely related social parasites, in genera with many social parasite species such as *Polyergus* (Trager 2013), *Formica* (Romiguier & al. 2018), *Temnothorax* (Heinze & al. 2015, Prebus 2017) and *Myrmica* (Savolainen & Vepsäläinen 2003, Jansen & al. 2010), will provide additional insights into the mechanisms underlying diversification in more diverse parasite lineages. Investigating the biogeographic distributions, host species, and habitat,

as well as the patterns of genetic differentiation between related species in these groups, will begin to shed light on the speciation process.

## Mechanisms of exploitation and resistance

In order to infiltrate and exploit their hosts, social parasites employ diverse tactics (d'Ettorre & Heinze 2001, Lenoir & al. 2001, Blatrix & Herbers 2003, Brandt & al. 2005b). This pressure contributes to a variety of host responses that mitigate the costs of parasites or repel them (Foitzik & al. 2001, Foitzik & Herbers 2001, Pamminger & al. 2011, Jongepier & al. 2014, Kaur & al. 2019). Social parasite tactics frequently include chemical and behavioral strategies that either inhibit detection or suppress aggressive responses. Some parasite species, particularly obligate parasites, also have morphological structures that facilitate their exploitative lifestyle. Potential host defenses include aggressive behavioral responses, cryptic positioning of nest entrances, or even shifts in colony social organization (Pamminger & al. 2011, Scharf & al. 2011, Fénéron & al. 2013). In this section, we review known and presumed adaptations of social parasites that improve their ability to parasitize other ants successfully, and the responses of their hosts that aid in avoidance or resistance. We identify instances where coevolution between parasite and host has been investigated directly, and we indicate several knowledge gaps in this area.

To organize our discussion, we consider each stage of the host / parasite interaction separately (Fig. 1). In order to benefit from their host, social parasites need to successfully locate host nests (Stuart 2002, Janda & al. 2004, Huang & Dornhaus 2008, Buschinger 2009), enter the colony (Alloway 1979), and then either exit the colony with stolen brood (dulosis, Buschinger & al. 1980), assassinate the queen(s) (temporary parasites and most dulotic queens, Cover & Sanwald 1988), or persist in the colony (inquilines, Bourke & Franks 1991). Each of these stages may require a unique suite of tactics, both for the social parasites and their hosts. We first describe our current understanding of the relevant traits of social parasites at each of these steps, then we consider the host responses. We close with a discussion of studies that explicitly examine coevolutionary dynamics between host and parasite.

**Traits of social parasites:** N e s t  d i s c o v e r y . Newly mated social parasite queens must first locate a host colony to infiltrate. In addition, workers (known as scouts) seek host colonies in dulotic species (Buschinger & al. 1980). Host discovery behavior is poorly understood in most temporary and inquiline social parasites but has been relatively well explored in several dulotic species. We examine what we know about the behavioral, chemical, and morphological adaptations that might facilitate this phase.

For most ants, one major fitness challenge is locating a suitable nest founding site or an existing colony to enter (for dependent founders or social parasites; Cronin & al. 2013). Entering an existing colony likely provides some

advantages since young queens are buffered from external environmental conditions; however, the low effective population size of ants (Romiguier & al. 2014, Miller 2017) likely makes finding these hosts more challenging than host discovery for parasites of solitary insects. Nest discovery can be challenging to study, because part of the search may take place on the wing and many ant species have a short window of mating flight and nest founding each season (Fowler 1992, Cronin & al. 2013). Many ant species tend to produce large numbers of gynes each year, but relatively few survive to establish successful new colonies (e.g., Ingram & al. 2013). Queens are solitary during this phase of their life cycle and may be exposed to dangers ranging from high predation risk (e.g., Fowler 1992) to desiccation (e.g., Johnson 1998). Thus, in socially parasitic gynes, we expect selection pressure to increase the efficiency of host nest discovery or to mitigate consequences of a slow search. This phase requires further study, but we predict that gynes will be highly sensitive and responsive to host nest odors and / or visual cues. Mechanisms underlying this sensitivity could include morphological, physiological, and behavioral components, such as increased antennal span and a specialized flight behavior depending upon host density and nest type. For example, polygynous *Solenopsis invicta* gynes fly low and slow during their search for a colony to join (Goodisman & al. 2000). For queens seeking nests in this way, we might expect a higher frequency of aposematic coloration, thicker cuticle, or other means of defense to reduce the risks associated with nest searching. Comparing morphological, physiological, and behavioral trait variation between facultative and obligate social parasite queens is one potential way to test these predictions (e.g., Savolainen & Deslippe 1996); we expect obligate social parasites to exhibit traits that are specialized and distinct from free-living relatives.

Alternatively, some social parasite queens may be able to eliminate this risky phase by hitchhiking with host queens (Fig. 2b). Vertical transmission of inquiline social parasites has been observed in *Plagiolepis xene* (see Passera & al. 2001), inferred in *Solenopsis phoretica* (see Davis & Deyrup 2006), and found in other insects that socially parasitize ants, as in socially parasitic beetles (Parmentier 2019). In agreement with the predictions of Brandt & al. (2005b), we speculate that hitchhiking on dispersing queens or dispersing with propagules containing host workers and queen(s) may be a relatively common dispersal mechanism in highly specialized inquilines. To facilitate this transfer, we predict that most inquilines will be small and some may have specialized grasping appendages, allowing them to attach to the bodies of host queens or workers. Indeed, miniaturization has been noted in many different social parasite lineages, including *Acromyrmex* (Soares & al. 2010, Rabeling & al. 2019), *Ectatomma* (Lenoir & al. 2011), *Formica* (Talbot 1976), *Mycocepurus* (Rabeling & al. 2014), *Myrmica* (Schär & Nash 2014) and *Pseudomyrmex* (Ward 1996), among others. Importantly, there are alternative (non-mutually exclusive) explanations for the advantages of small body

size, including a short offspring development time and the ability of parasite larvae to become queens with less food than required to produce host workers (Nonacs & Tobin 1992). In support of a possible role of physical hitchhiking in some inquilines, the mandibular morphology of *S. phoretica* and the collection of a queen from the petiole of a *Pheidole dentata* queen suggest a strong grasping ability (Davis & Deyrup 2006). Likewise, *Tetramorium inquilinum* (=*Teleutomyrmex schneideri*) queens are small compared with their hosts, have unusually large tarsal claws, and spend much of their time riding around on the backs of their host queen (Stuart 2002). Note that the nomenclature of *T. inquilinum* was recently revised (Ward & al. 2015), but that this classification is still a topic of discussion.

Researchers understand some of the dynamics of nest discovery in dulotic species (e.g., Brandt & Foitzik 2004, Pohl & Foitzik 2011, Miller 2017). Many dulotic species send out scouts to seek potential host nests (e.g., Alloway 1979, Topoff & al. 1988, Pohl & Foitzik 2011, Sapp 2017). Detailed monitoring of scout paths and removal experiments demonstrate that *Polyergus topoffi* (formerly *P. breviceps*) scouts systematically reach and search different sectors and that they are essential for raid initiation (Topoff & al. 1988). Other studies have focused more on the characteristics of target colonies favored by dulotic species. In choice trials, the species *Temnothorax* (formerly *Protomognathus*) *americanus*, which forms small colonies consisting of just four or five dulotic workers and about thirty host workers, seems to use host colony size as a cue to determine whether to raid. *Temnothorax* host colonies with more workers are more likely to be raided under some laboratory conditions (Pohl & Foitzik 2011). Miller (2017) found a trade-off in host colony selection, whereby dulotic *T. americanus* colonies were most successful in terms of brood theft and survival rates when they attacked nests with intermediate numbers of workers. She further noted that choice tests might not reflect realistic conditions, since some dulotic species are unlikely to find multiple host nests in the field within the timescale of a choice test (Miller 2017). Finally, Visicchio & al. (2003) showed that *Polyergus rufescens* scouts target *Formica* nests with more brood.

Dulotic species differ in the ways that scouts recruit nestmates to initiate a raid. Buschinger & al. (1980) summarized raid initiation in 12 species that had been well-studied at that point, stating that scouts recruited nestmates via tandem running (in *Harpagoxenus* and *Chalepoxenus* [current valid name *Temnothorax*]), carrying (in *Rossomyrmex*), group recruitment involving scout leading or possible pheromone trail deposition (in *Harpagoxenus*, *Leptothorax*, *Epimyrma* [now *Temnothorax*], and *Formica*), or mass recruitment via pheromone trail (in *Polyergus*). Topoff & al. (1984) demonstrated that *Polyergus topoffi* (formerly *P. breviceps*) scouts orient using visual cues as they return from a host nest. Scouts lead raiders back to the host nest, and both scouts and raiders deposit a chemical trail. Experiments manipulating visual or chemical cues reveal that both were essential for the correct orientation of returning raiders (Topoff & al. 1984). Many questions about the recruitment process remain. For instance, we are only starting to understand the collective decision-making behind raid initiation (Foitzik & al. 2001). In most species, we lack detailed information about the number of scouts relative to non-scouts, and whether scouts also participate in raids (but see Topoff 1990). More remains to be discovered about the factors shaping collective decision-making of host colonies during slave raids, as well. This subject is challenging to study, since collective decisions may rely on ecological and climatic conditions that can only be captured through field studies, but field observations of behavior (particularly inside the nest) are not often feasible.

We also note that social parasites are likely to differ in their nest discovery behaviors, and even closely related species may employ different tactics. For example, queens of both *Lasius interjectus* and *Lasius latipes* enter the host colony immediately after the nuptial flight, while *Lasius claviger* queens hibernate and enter in spring (Raczkowski & Luque 2011). Thus, we should exercise caution in extrapolating tactics and traits across related social parasites. Overall, there are many open questions about nest discovery, and well-designed field and laboratory observations and experiments in a broader range of host / parasite species pairs are needed to advance our understanding of this crucial step in social parasitism.

Nest infiltration. Once the host colony is discovered, parasitic queens or workers need to successfully enter. Some parasites have elaborate strategies that enable them to enter undetected (or be perceived as a nestmate), while others enter forcefully (Kleeberg & Foitzik 2016, Cini & al. 2019, Ruano & al. 2019). Chemical mimicry and camouflage are the most commonly used strategies to facilitate non-aggressive nest infiltration (d'Ettorre & al. 2000, d'Ettorre & Heinze 2001, Lenoir & al. 2001) and chemical tactics are among the best-studied traits of social parasites (reviewed by Dettner & Liepert 1994, d'Ettorre & al. 2000, Lenoir & al. 2001, Akino 2008, Guillem & al. 2014). These chemical tactics frequently involve cuticular hydrocarbons, which are blends of surface chemicals involved in multiple levels of recognition, including nestmate recognition, in social insects. Social parasites often acquire or produce chemical cues to evade host defenses and reduce the degree of aggression (d'Ettorre & Heinze 2001, Brandt & al. 2005b, Martin & al. 2007). The former strategy is called "chemical camouflage" and the latter "chemical mimicry" since their underlying behavioral and physiological mechanisms are quite different. A third strategy is "chemical insignificance", whereby a parasite produces little or no chemical profile (Akino 2008). Although we will utilize these terms as described above, they are used inconsistently in this field and more generally. Some authors define "chemical mimicry" as the imitation of a specifically targeted individual or object, and "chemical camouflage" as the resemblance of background cues, while others focus primarily on the origin of the

cues – they define "chemical mimicry" as a cue that is biosynthesized by the mimic, and "chemical camouflage" as a cue that is acquired from the host (von Beeren & al. 2012). Below, we describe some of the chemical, behavioral, and morphological traits exhibited by temporary social parasites, inquilines, and dulotic species as they enter the host species nest.

Temporary social parasites are often facultative, meaning that queens only sometimes initiate a colony by entering a host nest and assassinating the queen (Hölldobler & Wilson 1990). Some species can also initiate a new nest through independent colony founding, or they can join a conspecific nest (these alternatives are observed in the socially polymorphic species *Formica exsecta*, for instance [Seppä & al. 2004]). This facultative relationship, and the fact that temporary parasites spend the majority of their lifespan in single-species colonies, suggests that there may be less selective pressure for a precisely matching chemical mimicry or camouflage. Indeed, although aggression within parasitized colonies is not usually observed, chemical analysis of mixed colonies sometimes reveals no convergence of CHC profiles, as seen in the host *Lasius fuliginosus* and its undescribed *Lasius* parasite (Liu & al. 2000). Nevertheless, Raczkowski & Luque (2011) showed that *Lasius* host colonies tend to accept gynes of the socially parasitic *L. claviger*, *L. interjectus*, and *L. latipes*, suggesting that these queens either successfully blend in or go undetected by their hosts. Discrimination of social parasite queens by host workers is present in some host / temporary parasite associations, providing indirect evidence of host detection of social parasites. For example, *Formica lugubris* and *Formica aquilonia* experience 40 - 100% queen mortality through aggressive interactions with host workers, following experimental introductions into host colony fragments in the lab (Chernenko & al. 2013). However, there are also cases where temporary parasites exhibit successful chemical mimicry or camouflage. For instance, Ruano & al. (2019) showed that populations containing the temporary social parasite *Formica frontalis* and host *Iberoformica subrufa* converge in CHC composition compared to allopatric populations.

Inquilines remain in the nests of their hosts throughout their life and thus are predicted to benefit most from prolonged and accurate mimicry. Since inquilines are also frequently close relatives of their hosts (Bourke & Franks 1991, Ward 1996), their shared ancestry may facilitate the production of similar CHC profiles. For example, the inquiline *Camponotus universitatis* and congeneric host *Camponotus aethiops* have indistinguishable CHC profiles (Guillem & al. 2014). Chemical camouflage also occurs; for instance, *Temnothorax minutissimus*, an inquiline of *Temnothorax curvispinosus*, grooms the dorsal side of the host queen's head, causing it to gain a similar chemical signature as the host queen, whereas mated young queens have a distinct CHC profile (Johnson 2008). Incipient inquiline species, in contrast, may exhibit chemical insignificance, with reduced production of CHCs. This chemical insignificance is observed in the leaf cutter ant inquiline, *Acromyrmex insinuator*, which parasitizes the host *A. echinatior* (see Lambardi & al. 2007). Interestingly, some inquilines utilize an alternative chemical strategy that serves to suppress nestmate recognition in hosts. For example, the workerless inquiline *Leptothorax kutteri* produces a propaganda substance in the Dufour's gland that causes host workers to attack each other, thereby foregoing their usual vigilant attacks of non-nestmates (Allies & al. 1986).

In our consideration of dulotic species, we first discuss queen nest usurpation and then brood raids conducted by workers. Chemical camouflage is used by usurping *Polyergus samurai* queens in the nests of the host *Formica japonica*; when assassinating the queen in queenright colonies, *P. samurai* queens obtain the CHC profile of the host queen presumably through physical contact. In contrast, queens entering queenless host colonies take on a host worker-like CHC profile (Tsuneoka & Akino 2012). This suggests that *P. samurai* queens may seek out agonistic interactions in part to obtain the queen CHC profile. Greenberg & al. (2007) found that *Polyergus* queens mate during raids (using a potent sex pheromone that rapidly attracts males) and suggested the possibility that queens could take advantage of post-raid confusion to infiltrate a host nest. *Polyergus rufescens* queens also produce decyl butanoate in their Dufour's gland (Visicchio & al. 2000), which may function as an appeasement allomone (Mori & al. 2000) or a repellent of host workers (d'Etorre & al. 2000) when secreted by queens entering the nests of their hosts. Savolainen & Deslippe (1996) examined the size of the Dufour's gland in dulotic species that differed in their dependence on host workers; they found that *Formica* species that are more dependent on stolen host workers tend to have larger Dufour's glands than species that are facultatively dulotic and have relatively few host workers in their nests.

Workers must also successfully enter the host nest to steal brood, and chemical strategies appear to play a vital role in this process as well. Brandt & al. (2006) showed that two species, *Temnothorax americanus* and *Harpagoxenus sublaevis*, generate a propaganda allomone that elicits a "frantic" response from host workers. This substance is produced in the Dufour's gland, but chemical differences between the two parasite species suggest convergent evolution. Dulotic *Temnothorax* species also exhibit chemical profiles with shorter-chained hydrocarbons and a relatively high proportion of *n*-alkanes (compared to other parasitic lifestyles), presumably to elicit less non-nestmate recognition from hosts (Kleeberg & al. 2017). Moreover, these *Temnothorax* parasites exhibit different chemical profiles and/or chemical insignificance depending upon the locally available host species (Brandt & al. 2005b, Kaur & al. 2019). Stealth can also be an essential mechanism of brood theft in ants; in the primitively eusocial ponerine *Diacamma indicum*, thieves that act quickly, stay secretive, and steal unguarded brood (notably, intraspecific brood in this species), tend to be successful (Paul & Annagiri 2018).

**Temporary parasites – queen assassination and host adoption of parasite queens and eggs:** Temporary social parasites take over existing host nests by assassinating the resident queen and taking on the role of egg layer within the colony. Since queen assassination takes place inside the nest, we know little about this process for most species. Instead, both the death of the original queen and the adoption of the usurper and her eggs are often inferred from observations of colonies containing two worker species in one year and then solely the workers of the social parasite the following year (e.g., Talbot 1979).

Researchers understand some of the dynamics of queen assassination behavior and subsequent acceptance (or not) by hosts in a subset of species so far. The queens of *Lasius reginae* eliminate rival queens by rolling them over and strangling them (Hölldobler & Wilson 1990). *Bothriomyrmex decapitans* and *Bothriomyrmex regicidus* queens hold on to the back of a *Tapinoma* queen and slowly cut off her head (Santschi 1906, 1920). When this is accomplished, the *Bothriomyrmex* parasite takes over as the sole reproductive. In laboratory introductions, the temporary social parasite *Lasius* (previously *Acanthomyops*) *murphyi* initially antennates with the host *Lasius neoniger* queen and then remains still in the queen chamber for at least several minutes before beginning to bite the head, thorax, or abdomen of the host queen to pierce the integument (Cover & Sanwald 1988). After the host queen is dead, *L. neoniger* workers accept the parasite queen (sometimes immediately, sometimes within a few days), and foster her eggs. In another *Lasius* parasite / host pair, *L. interjectus* and *L. claviger*, Raczkowski & Luque (2011) noted that an invading *L. interjectus* gyne may only kill one queen in multiple queen colonies in order to gain acceptance. She can then coexist with and exploit the workers produced by the remaining queens in a polygyne *L. claviger* colony. Overall, this queen assassination and acceptance step is critical to the success of the social parasite queens, and a better understanding of the similarities and differences between behavioral and chemical mechanisms across independently derived species, along with estimates of success rates, will shed new light on this process.

**Inquilines – queen and egg adoption:** Inquilines have a different goal once they have successfully entered the nest. They need to survive, produce eggs, and have those eggs adopted and reared by the host workers while their own queen is present. They may do this by partially or totally suppressing host reproduction and/or ensuring that their own offspring receive equal or greater attention than host offspring (e.g., Cini & al. 2019). In *Mycocepurus goeldii*, for example, Rabeling & al. (2014) noted that host reproductive offspring were absent from colonies parasitized by *M. castrator*, even when they were present in neighboring colonies.

Some inquilines, including *Acromyrmex insinuator*, produce workers as well as sexual offspring, and the presence of inquiline workers significantly increases the reproductive output of the social parasite (Sumner & al. 2003).

Both host *A. echinatior* and parasite *A. insinuator* workers can discriminate host and parasite brood, and Sumner & al. (2003) suggested that the parasites may therefore selectively rear conspecifics and suppress production of host reproductive offspring. Soares & al. (2010) similarly identified suppression of reproduction in *Acromyrmex subterraneus* by the inquiline *A. ameliae*.

An alternative strategy to achieve egg adoption is to lay eggs that are as cryptic as possible, as has been observed in some avian brood parasites (e.g., Spottiswoode & Stevens 2011, Feeney & al. 2014). However, the egg odors of some host species are complex and may vary depending upon genetic background, as observed in seven *Formica* species (Helanterä & d'Ettorre 2015); as a result, host workers of some species can distinguish the eggs of social parasites (Chernenko & al. 2011). Still, we know little about how widespread this egg discrimination ability is, and we predict that producing cryptic eggs is likely a convergent trait in ant inquilines, in particular. Egg discrimination assays carried out in numerous host / inquiline pairs could provide a simple preliminary test of this prediction.

**Dulotic species – queen establishment and raids:** Many dulotic species establish colonies by usurping and killing a host queen. Topoff & Zimmerli (1993) used clear observation nests to observe the specific behaviors surrounding usurpation by newly mated *P. topoffi* (previously *P. breviceps*) queens entering a *Formica gnava* host colony. In this case, usurping queens push through defensive workers to rapidly find the queen chamber, where they aggressively bite the resident queen on the head, thorax, and abdomen until she is dead. This process can take half an hour. During this time, the usurping queen licks the wounds of the dying host queen, which appears to be the mechanism by which she gains the colony odor (a similar sequence of events was found in *P. samurai*, as described in the Nest Infiltration section). When the host queen is dead, Topoff & Zimmerli (1993) noted a rapid shift in the worker behavior from frenzied and aggressive to calm. Workers quickly begin to groom the new queen and readily adopt and care for her eggs. This worker adoption of parasite brood is critical for the success of the queen. d'Ettorre & al. (2002) observed that egg adoption may be an ongoing process in *Polyergus* colonies; they found that parasite workers emerging in a usurped *Formica* nest are frequent donors in trophallactic interactions with hosts, which was viewed as a possible appeasement mechanism.

Once the colonies of dulotic species are established, they maintain their workforce by stealing brood (or occasionally workers) from heterospecific colonies. Successful raids consist of scouting, recruitment, fighting (all covered above), and brood removal and transportation (Buschinger & al. 1980). Adoption and integration of stolen brood is the final step dictating the success of dulotic species' raids. By stealing pupae, dulotic species build up their workforce. Pupae eclose in the parasite nest and carry out needed tasks; hosts and parasites share a gestalt odor, but this is shaped primarily by the cuticular

hydrocarbon profile of the stolen host workers (D'ETTORRE & HEINZE 2001). This gestalt odor, in turn, helps to mask the dulotic workers during raids. D'ETTORRE & al. (2002) showed the chemical flexibility of *P. rufescens* workers by introducing worker pupae of this social parasite into the nests of four *Formica* species, one of which is not a natural host. As they predicted, the parasite workers are able to modify their chemical profile to match the "host" workers around them; their chemical profile in isolation closely matches the most frequent host species. BRANDT & al. (2005b) similarly found that *Temnothorax americanus* parasites and enslaved host workers have chemical profiles resembling unparasitized host colonies of *T. longispinosus* and *T. curvispinosus*. They noted regional variation in the CHC profile depending upon the composition of the host community. Intriguingly, they also showed that host species direct more aggression toward enslaved workers than toward free-living non-nestmates in autumn, but not in spring (BRANDT & al. 2005b). Still, workers of both host species are slower to retrieve social parasite eggs than conspecific eggs (SWAN & HARE 2012) showing that there must still be detectable differences between host and parasite brood. Overall, ants usually employ a combination of chemical and physical tactics to successfully adopt pupae through dulosis.

**Host resistance mechanisms:** Mortality and loss of reproductive success due to social parasites exert strong selection pressure on host species (GRÜTER & al. 2018). Mechanisms of avoidance and resistance in host species have received recent research attention (KILNER & LANGMORE 2011, PAMMINGER & al. 2011, GRÜTER & al. 2018). From the host perspective, several stages in the process of social parasitism can be targets for host resistance. Hosts can make their nests more difficult for parasites to find, they can shift their social behavior to make parasite takeover more challenging, they can become more sensitive to social parasite cues and respond to intruders more aggressively, and they can revolt after parasites have taken over their colony or enslaved them (DELATTRE & al. 2012, FÉNÉRON & al. 2013, CREMER & MASRI 2014, METZLER & al. 2016). This subject was recently reviewed (GRÜTER & al. 2018), so we briefly consider our current understanding of resistance mechanisms and propose topics for future study.

Hidden-nest strategy. If social parasites cannot locate nest entrances, they cannot parasitize a given host. Thus, hosts could adjust nest placement to make their nest more difficult to find. However, given the need of a colony to forage and reproduce, and the importance of chemical communication for colony integration, we expect this strategy to be rare. Polydomy may function as a bet-hedging strategy in the presence of social parasites. For temporary parasites or inquilines, not all nests would necessarily contain a queen (ALLOWAY & al. 1982), potentially buffering the colony against some of the consequences of parasitism. For hosts of dulotic species, brood may be distributed among multiple nest structures (DEBOUT & al. 2007), so only a subset would be lost in any given raid.

Variation in social organization. The social structure of the host colony can shape the characteristics of their interactions with social parasites. For example, many ant species exhibit a polymorphism in queen number; recent advances indicate that this is under genetic control, at least in *Solenopsis invicta* (see WANG & al. 2013) and *Formica selysi* (see PURCELL & al. 2014). However, there is no consensus on the ultimate causes of social polymorphism. Single queen (= monogynous) and multiple queen (= polygynous) colonies differ in a suite of traits that may influence their response to social parasites, including worker and queen body size, colony size (e.g., ROSSET & CHAPUISAT 2007), and nestmate recognition precision (MARTIN & al. 2009). The evolution of polygyny is often considered to be a potential preadaptation for social parasitism (e.g., BUSCHINGER 1986, SAVOLAINEN & VEPSÄLÄINEN 2003), but we know less about the effect of colony queen number on contemporary host / parasite interactions. Colonies with a single queen may be more likely to recognize invaders and mount a stronger defense, as seen in *Ectatomma tuberculatum* responding to *E. parasiticum* (see FÉNÉRON & al. 2013) and in *Leptothorax acervorum* responding to *Harpagoxenus sublaevis* (see FOITZIK & al. 2003). On the other hand, temporary social parasite queens would only need to successfully assassinate a single queen, which may increase their chances of successfully taking over the host colony (but see TOPOFF (1999), which states that *Polyergus* queens can systematically kill multiple host queens).

Response to intruders. The defensive response of hosts varies depending upon the strategy employed by the social parasite (SCHARF & al. 2011). Parasite queens that enter the colony rapidly and aggressively elicit an aggressive response from workers, which can result in a high mortality rate for invading queens. This response has been studied in nest fragments in the lab since the sources of social parasite mortality at each stage of nest infiltration are difficult (or impossible) to quantify in field colonies. For example, CHERNENKO & al. (2013) found that host workers of three different *Formica* species attack and successfully kill 40 - 100% of invading temporary social parasite queens of both *F. lugubris* and *F. aquilonia*. Host workers respond aggressively even in the absence of a host queen and further selectively avoid rearing parasite eggs in the laboratory. Some species use previous experience to mount a more effective defense. *Temnothorax longispinosus* colonies are more aggressive and more likely to successfully defend themselves after previous exposure to the dulotic *T. americanus* (KLEEBERG & al. 2014).

The presence of social parasites can also drive hosts to detect a more diverse set of chemical cues. For example, JONGEPIER & FOITZIK (2016) showed that *T. longispinosus* colonies recognize a greater diversity of chemical cues in the presence of their dulotic social parasite, *T. americanus*, than in its absence. Hosts themselves may exhibit greater cuticular hydrocarbon variation in the presence of higher social parasite pressure. *Formica fusca*, which is host to

numerous social parasites, exhibits greater intercolony chemical profile diversity in regions with high parasite pressure compared to regions with lower parasite pressure (Martin & al. 2011).

Worker rebellion. Recent research reveals that host workers have mechanisms to fight back and reduce the fitness of their social parasites even after their nest has been parasitized (e.g., Czechowski & Godzińska 2014). For example, Pamminger & al. (2014) observed that enslaved *Temnothorax longispinosus* workers kill a large proportion of their parasite's offspring. The authors suggested that these rebelling workers gain indirect fitness by reducing parasite pressure on their relatives' colonies, since those tend to be clustered around the parasite colony (see also, Achenbach & Foitzik 2009). In hosts of temporary social parasites, workers of some species can distinguish parasite-laid eggs. For example, *Formica fusca* and *F. lemani* workers favor con-colonial eggs over those produced by the temporary parasite *F. truncorum*, and begin to lay unfertilized male-destined eggs within six days of receiving parasite eggs (Chernenko & al. 2011). Helanterä & Sundström (2007) found that egg discrimination is widespread in ants, and suggested that intracolony conflicts, including social parasitism, likely shape this ability.

**Coevolution between host and parasite:** Directly studying coevolutionary dynamics between host and parasite is more challenging than investigating offensive tactics of parasites or defensive tactics of hosts in turn. We see evidence of coevolutionary dynamics most clearly when we observe host / parasite interactions across different populations and communities (e.g., Brandt & Foitzik 2004, Jongepier & al. 2014, 2015). Brandt & al. (2005b) investigated population-level differences in *T. americanus* and its hosts (*Temnothorax* species) with regard to CHC profiles and host community composition. In populations with a single host, the social parasite closely mimics the host's CHC profile; in contrast, populations with multiple hosts reveal that the parasite's CHC profile is intermediate between distinct hosts (Brandt & al. 2005b). With a similar multi-population comparison, Foitzik & al. (2003) revealed that *Leptothorax acervorum* from unparasitized populations are more successful at repelling *Harpagoxenus sublaevis* raiders than *L. acervorum* from parasitized populations. They further showed that the propaganda substance employed by *H. sublaevis* is highly effective in these parasitized populations. In two cross-population studies on *Temnothorax* ant species and their social parasite *T. americanus*, Jongepier & al. (2014, 2015) found that the ecological success of the social parasite increases with manipulation of collective host behavior, and in response, collective defense portfolios of hosts shift with social parasite pressure.

Another means of investigating coevolutionary dynamics is to examine the strategies of social parasites using different hosts or, potentially, of host species that are parasitized by multiple parasite species. For example, Bauer & al. (2010) demonstrated that the dulotic *Harpa-goxenus sublaevis* attacks two host species. Its intrinsic chemical profile is more similar to the host *Leptothorax muscorum*, which is therefore overexploited. However, because this host is less common than *L. acervorum*, *H. sublaevis* workers will frequently also raid the colonies of the larger-bodied *L. acervorum*, despite facing higher risks. Interestingly, these two host species have strikingly divergent CHC profiles, despite being closely related (Bauer & al. 2010). This comparison allows the researcher to observe both the social parasite strategy and the host strategy, albeit indirectly, across the complex of the parasite with its several hosts. Overall, these studies are more challenging to carry out, but they shed light directly on the interplay between host and parasite, and provide an opportunity to quantify the costs and benefits of these tactics on each side. So far, research of this nature has been limited to a few well-studied systems, most of which happen to involve dulotic social parasites. We call for new studies of geographic variation in host / parasite coevolutionary dynamics across more taxonomically and behaviorally diverse pairs of species.

**Biogeographic distribution of social parasites**
Currently, the majority of the known social parasite species occur in the temperate areas of North America, Europe, and South America (Buschinger 2009; Rabeling & al. 2019). Kutter first pointed out this trend in 1968, followed by Hölldobler & Wilson (1990) and Buschinger (2009) decades later. The temperate distribution pattern contrasts with the biogeographic distribution of free-living ant species, which are distributed along a latitudinal diversity gradient with an increase in biodiversity towards the equator (Economo & al. 2018). Previous reviews of the ant social parasite distribution proposed that this pattern likely reflects a pervasive sampling bias. For example, about one-third of the Swiss ant species are parasitic (Kutter 1968), whereas global social parasite diversity comprises only 2.2% of the world's known ant species. This discrepancy may be attributed to the fact that both Auguste Forel and Heinrich Kutter lived in Switzerland and spent their careers identifying ants around the country. Similar cases have occurred in the United States and Argentina, but not every country has had myrmecologists with a specific interest in discovering and identifying social parasites (Hölldobler & Wilson 1990).

Since ant social parasitism was last reviewed by Buschinger (2009), the overall biogeographic pattern (which Rabeling & al. (2019) refer to as the "Kutter-Wilson Paradox") has not changed substantially (Fig. 3). After describing a new *Acromyrmex* social parasite in Brazil, Rabeling & al. (2019) proposed that the paradox is a genuine biogeographical phenomenon instead of being due solely to sampling bias. They compared historical and current biogeographic patterns and examined the biology and taxonomy of tropical social parasite species and their hosts to arrive at their conclusion. Currently, the proportion of global ant species that are social parasites remains high in the Nearctic (12%) and Palearctic (6%), compared to the Neotropical (1.1%) and Afrotropical (0.6%) ant faunas
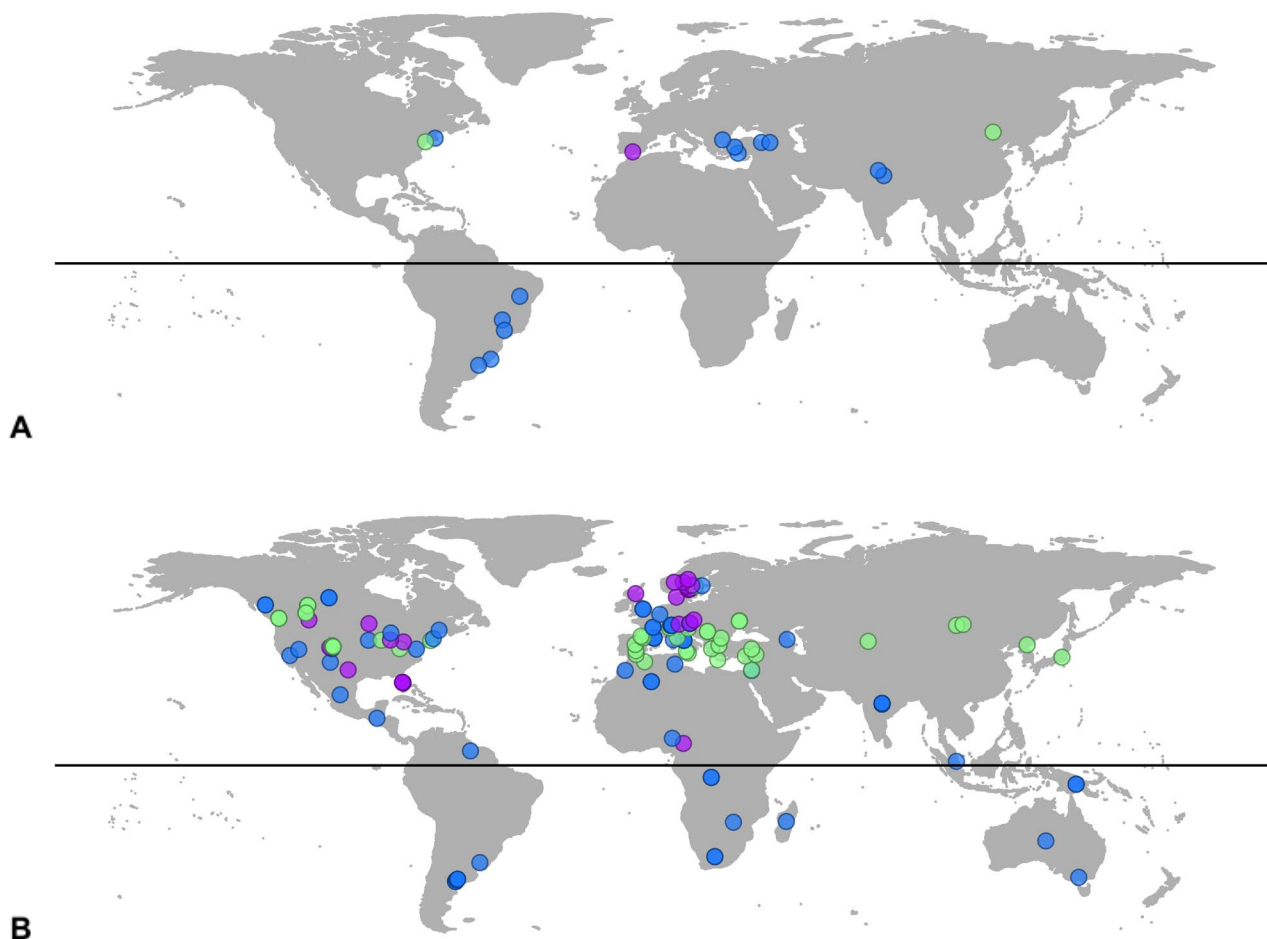
Fig. 3: Distribution of 16 new socially parasitic ant species or relationships described within the last decade (A). Colored circles represent ant species (green = dulosis, blue = inquilinism, purple = temporary). The black horizontal line shows the equator. This is compared with the distribution of the known parasitic ants reported by HÖLLDOBLER & WILSON (1990, B).

(RABELING & al. 2019). Our literature search revealed that 16 new ant social parasite species or relationships were described within the past decade, and these are distributed in both tropical and temperate zones (Fig. 3, Tab. 1). The east coast of South America has seen much activity in this field; contrastingly, none of the newly described parasites occur in Africa or Oceania (Fig. 3). Thus, while RABELING & al. (2019) present a compelling argument in support of the "Kutter-Wilson Paradox", and the newly described ant social parasites are not numerous enough to sway the biogeographic distribution of ant social parasites as a whole, there remains a marked pattern of sampling bias. Specifically, there is a need for a more considerable sampling effort throughout Africa and Oceania.

**Mechanisms underlying the biogeographic gradient:** There are several prevailing hypotheses about mechanisms that could shape a global distribution of socially parasitic ants with greater diversity in temperate regions. WCISLO (1987) suggested that developmental synchrony between host and parasite is crucial for the evolution of brood parasitic behavior, and that populations in temperate regions are more tightly synchronized than in tropical regions. Following this, HÖLLDOBLER &

WILSON (1990) proposed that living in more temperate climates and environments predisposes ant species toward parasitism because cooler temperatures may facilitate the introduction of parasitic queens during the initial development of the symbiosis by dampening the reactions of the host colonies. RABELING & al. (2019) emphasized the importance of species diversity and nest density: while ant faunas in temperate zones are characterized by low species diversity and high nest density, the opposite is true for those in the tropics (LEVINGS & FRANKS 1982, LEVINGS 1983). High nest density and low species diversity might facilitate host discovery by parasites, which is a critical step for successful social parasites (Fig. 1). Another possibility is that polygyny is more common in temperate species than in tropical ones and, as discussed earlier, the emergence of social parasitism may be associated with a polygyne lifestyle (HÖLLDOBLER & WILSON 1990).

To better understand the mechanisms shaping the distribution of social parasites, we can consider biogeographic patterns in each social parasite strategy separately. Overall, dulotic and temporary social parasites are more abundant in colder, northern regions of Europe and North America, than they are in warmer temperate or subtropical

Tab. 1: Socially parasitic ants described since 2010, their hosts, their locations, and their forms of parasitism. * denotes a species that shows many traits of xenobiosis, but most closely fits within the major social parasitism strategy of inquilinism; ** note that the nomenclature of *Teleutomyrmex* was recently revised (Ward & al. 2015), but that this classification is still a topic of discussion.

| Parasite | Host | Form of parasitism | Location found | Author(s) |
|---|---|---|---|---|
| *Acromyrmex charruanus* | *Acromyrmex heyeri* | Inquilinism | Uruguay | Rabeling & al. (2015) |
| *Acromyrmex fowleri* | *Acromyrmex rugosus* | Inquilinism | Brazil | Rabeling & al. (2019) |
| *Camponotus ruseni* | *Camponotus aethiops* | Inquilinism | Turkey | Karaman (2012) |
| *Cephalotes specularis* | *Crematogaster ampla* | Inquilinism* | Brazil | Brandão & al. (2014) |
| *Formica frontalis* | *Iberoformica subrufa* | Temporary | Spain | Ruano & al. (2019) |
| *Mycocepurus castrator* | *Mycocepurus goeldii* | Inquilinism | Brazil | Rabeling & Bacci (2010) |
| *Myrmica latra* | *Myrmica aimonissabaudiae* | Inquilinism | India | Bharti & al. (2016) |
| *Myrmica nefaria* | *Myrmica rupestris* | Inquilinism | India | Bharti (2012) |
| *Nylanderia deceptrix* | *Nylanderia parvula* | Inquilinism | Massachusetts, USA | Messer & al. (2016) |
| *Pheidole acutidens* | *Pheidole nitidula* | Inquilinism | Brazil | Ferreira & al. (2016) |
| *Strongylognathus dao* | *Tetramorium tsushimae* | Dulosis | China | Radchenko & al. (2017) |
| *Temnothorax curtisetosus* | *Temnothorax antigoni* | Inquilinism | Turkey | Salata & Borowiec (2015) |
| *Temnothorax pilagens* | *Temnothorax longispinosus* and *Temnothorax ambiguus* | Dulosis | Michigan, New York, & Vermont, USA | Seifert & al. (2014) |
| *Tetramorium aspina* | *Tetramorium immigrans* | Inquilinism | Turkey | Wagner & al. (2018) |
| *Tetramorium buschingeri (=Teleutomyrmex buschingeri)*** | *Tetramorium chefketi* | Inquilinism | Bulgaria | Kiran & al. (2017) |
| *Tetramorium seiferti (=Teleutomyrmex seiferti)*** | *Tetramorium chefketi* | Inquilinism | Turkey | Kiran & al. (2017) |

regions, even though the free-living ant faunas of these regions otherwise are broadly overlapping. Dulotic species are largely (but not entirely) absent from the tropics (Trager 2013). In contrast, inquiline social parasites are more widely distributed through the temperate and Neotropical regions (Wheeler 1919 & 1925, Kutter 1968, Wilson 1971, Hölldobler & Wilson 1990, Buschinger 2009). Notably, but beyond the scope of this article, cleptobiosis and xenobiosis are rather common in the tropics (Adams & Longino 2007, Breed & al. 2012, Powell & al. 2014). While it is challenging to test hypotheses about the drivers of latitudinal diversity gradients due to many confounding variables and low replication, comparing the properties of each of these strategies may provide novel insights into these patterns. We agree with Rabeling & al. (2019) that the decreasing species diversity and increasing (intraspecific) nest density at higher latitudes might be a large driver of these strategy-specific distributions. All social parasites face host discovery challenges, and these would be more severe in regions with low host nest density. Highly specialized inquilines may minimize this problem by developing modes of vertical transmission (Passera & al. 2001). In contrast, temporary social parasites generally kill the host queen, preventing extended associations with multiple generations of their host. Likewise, dulotic species require continued access to host colonies in order to replenish their population of stolen workers. Thus, discovery of new host nests is expected to be a more significant challenge for these latter species; as a result, we predict that their abundance and prevalence will reflect higher nest densities of host species. For facultative parasites, this constraint may be reduced, since these species can survive without their hosts.

**Future social parasite discovery and status:** We predict that researchers will continue to discover new social parasite species, particularly in tropical environments. To us, it is not clear whether this future discovery will affect the overall diversity gradient of social parasites in general, or any group of social parasites in particular. From our search of social parasite discoveries in the past ten years, we can see that discovery is biased toward inquilines, and that many of these were found in the Neotropics (mainly in Brazil; Fig. 3). We suggest that there are several reasons for the continued discovery of new inquilines. First, specialized inquilines are generally found only within the nests of their hosts, so many standard

diversity survey methods, particularly ones deployed in the tropics (Feitosa & al. 2008, Rabeling & al. 2015, Messer & al. 2016), may fail to detect these species. Second, social parasite population densities are expected to be low, so sampling of multiple complete host colonies would be required for detection. These factors lead us to predict that inquiline social parasites, in particular, will be discovered at a slow but steady pace. We cannot predict the ultimate diversity of this group, because efforts to find them have not been systematic or evenly distributed across the globe.

Discovery of new social parasites and research on rare species will be confounded with ongoing global change. In the *2000 IUCN Red List of Threatened Species*, 94% of all social insects listed as Vulnerable are socially parasitic ants, and these 142 species represent all the socially parasitic ants known at the time (Hilton-Taylor 2000, Chapman & Bourke 2001). Almost certainly, all the currently-known and undiscovered parasitic ant species are highly vulnerable to climate change due to their typically small range sizes, low effective population sizes, and specialized dependent niches.

### Conclusions

Research on social parasites of ants has a long history of important insights, but it is also full of potential for future research. We highlight recent advances in this field, and in doing so, we also point to the many areas that warrant further exploration. Cini & al. (2019) state that social parasites can help to unlock the secrets of insect sociality. We agree that this group of organisms provides insights into the strengths and vulnerabilities of social groups, and into the ecological opportunities that social insects open for other organisms. Through this review, we provide updated information on the current state of knowledge about the diversity, origin, evolutionary dynamics, and biogeographic distribution of socially parasitic ants, which we intend to serve as a resource for future investigators. We end with an overview of the areas that we think are the most promising and wide open for ongoing investigation.

### Avenues for future research

**Speciation mechanisms in social parasites and hosts:** The mode of speciation and the precise pre- and post-zygotic isolating mechanisms that contribute to reproductive isolation are largely unknown in ants. Torres & al. (2018) provide intriguing evidence suggesting that host fidelity may serve to introduce preliminary pre-zygotic barriers into *Polyergus* populations in the Sierra Nevada of California. The possibility that host / parasite interactions and coevolutionary dynamics could promote reproductive barriers is a compelling one, and investigating the diversification patterns in genera with closely related parasites and / or hosts would be a good starting point for understanding the role of interspecific interactions *versus* geographic separation in this process.

**Quantify costs of social parasitism:** Many ant species are long-lived and quantifying the fitness of a queen or colony is challenging even in unparasitized free-living ant colonies. Thus, quantifying the actual fitness cost of social parasitism is a daunting challenge that will require a multi-year commitment with intensive monitoring (depending upon the type of parasitism investigated). However, the rewards would be great, since many of the contemporary research areas focused on coevolution and adaptive strategies assume that social parasitism imposes a substantial cost on the host (and indeed, it must in cases with successful queen assassination). More studies have investigated the risks to parasites during nest infiltration, but there are still significant gaps in our knowledge of the frequency of success of social parasites in most parasite/host associations.

**Comparative demography, both for coevolution and assessment of costs:** One potential approach that could be employed more broadly in this field is to compare population growth, structure, colony turnover, inter-colony parentage, and annual reproductive output between host populations with different levels of social parasite pressure. This more indirect approach would provide some insights into the relative fitness of queens in parasitized and unparasitized populations. Likewise, this comparative approach has been used successfully to identify behaviors and chemical profiles that appear to be coevolving in host/parasite associations in a few systems, but this could be readily expanded.

**Studies of convergent evolution among parasites employing similar strategies/hosts defending against similar parasites:** Another tool to investigate the evolutionary trajectories of different social parasite strategies and to explore the role of coevolution in these relationships will be comparative analyses across taxonomically distinct groups that exhibit similar social parasite strategies. It would be especially beneficial for these investigations to focus on deciphering the similarities and differences between strategies of obligate and facultative social parasites because this might illuminate the evolutionary advantages of each (e.g., Mori & al. 2001).

**Systematic analysis of the biogeographic distribution of each social parasite strategy:** Given the discovery of more social parasites in the past 10 - 20 years (e.g., Fig. 3), we suggest that formal, quantitative biogeographic analyses would be timely, and would provide clarity about whether the observed distribution patterns represent actual distributions or are still artifacts of sampling bias. In particular, we suggest separate assessment of temporary social parasites, inquilines, and dulotic species, since each strategy has different host requirements.

**Genetics / genomics / metagenomics of convergence, adaptive mechanisms, gene reduction:** Contemporary researchers have unprecedented opportunities to pursue genomic lines of research in non-model organisms, yet these studies are lagging in social parasites (but see Cini & al. 2015, Smith & al. 2015, Kaur & al. 2019). Many genetic, genomic, and metagenomic avenues are open for discovery, and we mention just a few. First, across parallel origins of obligate social parasitism, do we

see repeated patterns of genomic structural change, such as gene family expansions or contractions? Second, are the microbiomes of hosts and parasites distinct, or are they shared within a nest? Do microbiome symbionts play a role in any aspect of the social parasite lifestyle (e.g., LIBERTI & al. 2015)? Third, in sister host / parasite species pairs, what regions of the genome distinguish the host and parasite – what genes are present in these regions, and how large and dispersed are they? These genetic data would be especially interesting if compared across species pairs with different divergence histories.

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