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Review Article

# Evolution of dispersal in ants (Hymenoptera: Formicidae): a review on the dispersal strategies of sessile superorganisms

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**Abstract**

The extreme diversity of dispersal strategies in ants is unique among terrestrial animals. The nature of ant colonies as social, perennial, and sessile superorganisms is the basis for understanding this diversity, together with the inclusive-fitness framework for social evolution. We review ant dispersal strategies, with the aim of identifying future research directions on ant dispersal and its evolution. We list ultimate and proximate determinants of dispersal traits and the ecological and evolutionary consequences of dispersal for population structures and dynamics, as well as species communities. We outline the eco-evolutionary feedbacks between the multitude of traits affecting dispersal evolution and the likely evolutionary routes and ecological drivers in transitions among the diverse ant dispersal strategies. We conclude by presenting a research framework to fill the gaps in current knowledge, including comparative studies of colony life histories and population structures and theoretical models of the eco-evolutionary dynamics affecting dispersal, in an inclusive-fitness framework.

**Key words:** Colony founding, dispersal conflict, inbreeding, inclusive fitness, kin competition, kin selection, local resource competition, mating flight, mating system, philopatry, resource allocation, sex bias.

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## Introduction

Dispersal is any movement of organisms that can potentially lead to gene flow (Ronce 2007). Movement at all spatial scales, both within and between habitat patches, can qualify as dispersal. Dispersal allows organisms to colonize new areas and thus survive environmental changes should their current habitats become unsuitable. Indeed, the ability to find new habitats and resources in variable environments is considered one of the ultimate causes for dispersal (Van Valen 1971). As natural populations are threatened by habitat fragmentation and climate change, as well as the spread of invasive species, dispersal is also a key consideration in conservation planning (Pressey & al. 2007).

Local resource competition is another ultimate cause for dispersal. From an inclusive-fitness perspective, competition with relatives is harmful, and dispersing away from them is favored by kin selection (Hamilton & May 1977). Staying close to one's relatives and mating with them may also cause inbreeding depression, and lower both direct and indirect fitness (Bengtsson 1978, Motro 1991, Perrin & Goudet 2001). This highlights that dispersal is a social trait and includes both elements of cooperation and conflict among individuals. Thus, selection for dispersal needs to be considered in an inclusive-fitness or multi-level selection framework (Poethke & al. 2007).

Dispersal is a complex process with three distinct phases: emigration (dispersal decision), movement, and immigration that includes establishment as a reproducer in the destination (Bowler & Benton 2004, Ronce 2007). Thus, dispersal comprises multiple traits, potentially responding to multiple selection pressures (Starrfelt & Kokko 2012). As these traits may be genetically corre-

Tab. 1: Overview of the ant nest founding strategies and the typical mating locations and dispersal strategies connected to them. Note that a species can use a combination of several strategies and this is very common in some cases (such as polygynous colonies having alternative strategies). The dispersal strategy mentioned here refers to the individuals, not the species. When mating happens within the gyne's natal colony, the male can be either a disperser from a foreign colony, or a philopatric individual from the same colony. * Nest refers to a single nest mound / cavity / structure, colony refers to the whole society. A colony can consist of one or several nests (monodomy or polydomy, respectively) or be a nestless one (in army ants).

lated and plastic, the genetic architecture of dispersal is potentially very complex (Saastamoinen & al. 2017). This makes predicting responses to selection difficult, especially since the evolutionary role of phenotypic plasticity may be more substantial than conventionally appreciated (Pfennig & al. 2010).

To truly appreciate dispersal and its consequences requires understanding both its ultimate and proximate causes, and their interactions (Bowler & Benton 2004). In this review, we bring together the theoretical context of dispersal evolution with empirical studies on behavior, genetics, physiology and ecology of ants. Our aim is twofold: to show that studying dispersal can further our understanding of social evolution in ants, and to show that ants offer an excellent study system for future work inferring dispersal evolution and the selection pressures affecting it.

**Dispersal of the superorganism:** Natal dispersal of winged young queens and males has been suggested to be the ancestral dispersal strategy in ants (Hölldobler & Wilson 1990). As colonies of most ant species are sessile and queens do not leave the established colonies (Wilson 1971), this is the only stage where dispersal happens in most ants. Thus, ant colonies are superorganisms that disperse through their mobile offspring like plants do through their pollen and seeds, and sessile marine invertebrates, such as corals, through their sperm, eggs and larvae (Hölldobler & Wilson 2008, Helanterä 2016). The young adult queens (gynes) are the propagules founding new colonies and can disperse both before and after fertilization. They mate within a short time period before colony founding, with one or several males, and store the sperm in their bodies for the rest of their lives (Boomsma 2013). The males are haploid and their sperm is clonal, so gene flow through their movement resembles pollen dispersal. In many species males are sperm limited and only mate once (Passera & Keller 1992), although in some taxa they can mate more than once and possibly in different locations (Shik & al. 2013).

Most ants have sessile colonies and are thus central place foragers. This makes escaping local competition over resources, especially nest sites and food, an important selection pressure for dispersal. Because ant workers are wingless, ants are especially effective in utilizing resources in the immediate proximity of their colonies (Peeters & Ito 2015) and central place foraging affects ants more than social insects with winged workers. Even if not all ants defend their territories (Savolainen & Vepsalainen 1988), the central place foraging lifestyle is likely to result in selection for dispersal beyond the foraging area of the natal colony. The necessity of dispersal in ants is further enhanced by competition between generations, and the low likelihood of nest site and resource inheritance. In many species, the queens are long lived and their colonies can exist in the same location up to a few decades (Wilson 1971). Colony life spans of even a few decades have been recorded in, for example, *Myrmecocystus* and *Formica* (see Chew 1987, Pamilo 1991c). Thus, ants, along with some perennial bees such as the honey bee, differ from most other social hymenopterans by controlling local resources over long timescales (Wilson 1971).

However, female offspring may skip dispersal and stay in their long-lived natal colonies as extra queens. Polygyny (see Tab. 1) is a form of cooperative breeding where multiple queens share the same colony and resources, including the worker force. It is common throughout the ant phylogeny and indeed often arises through philopatry of daughters of the colony (Keller 1995, Heinze 2007, Boomsma & al. 2014). Thus, the theoretical prediction (Kokko & Lundberg 2001) that natal philopatry and cooperation are favored in nest-site limited systems, where dispersal is risky and survival of territory owners high, seems to fit well with the evolution of secondary polygyny (Tab. 1) in ants. However, in addition to cooperation, polygyny also introduces potential for conflict among co-breeders (see sections "Social selection pressures" and "Consequences of dispersal").

In this review, we consider leaving the natal colony always as dispersal, even when the spatial scale is small. Dispersing at all spatial scales is costly and risky (Bonte & al. 2012). The abovementioned idiosyncrasies of ants further add to the risks. Especially the last phases of dispersal, including mating, colony founding and establishment as a reproducer in a competitive community, are critical phases in ant life cycles, and a stage for eco-evolutionary feedbacks where many aspects of ant lives intertwine. Research on ant dispersal has touched on many of these aspects, as demonstrated with detailed examples below. However, an overarching framework for understanding these complex interactions is still needed, and we conclude the review by proposing the building blocks of a research program aiming to better understand the evolution of ant dispersal.

## Diversity of ant dispersal strategies

Here, we explain the diversity of ant dispersal strategies and show how mating and colony founding are integrally tied to dispersal. We point out some of the main constrains on ant dispersal, both on wing and by foot, and discuss how dispersal differs between the sexes. Ant flight ecology and the selection pressures affecting the movement phase

| Nest / colony* founding strategy | Definition | Typical mating location | Queen dispersal | Male Dispersal | Example taxa |
|---|---|---|---|---|---|
| **Independent, non-claustral** (Hölldobler & Wilson 1990, Brown & Bonhoeffer 2003) | Queens forage for food during nest-founding | Away from the colony | By flight | By flight | Ponerinae, Myrmeciinae (Peeters 1997) |
| **Independent, claustral** (Peeters & Ito 2001) | Queens do not forage but stay enclosed in the nest chamber during nest-founding | Away from the colony | By flight | By flight | Prevalent in Formicinae, Myrmicinae (Hölldobler & Wilson 1990) |
| **Pleometrosis (= primary polygyny)** (Hölldobler & Wilson 1977) | Several queens found the nest together; the nest usually reverts later to a single-queen state (= monogyny) | Away from the colony | By flight | By flight | *Lasius niger* (see Sommer & Hölldobler 1995), *Pachycondyla* (see Trunzer & al. 1998), *Pogonomyrmex californicus* (see Johnson 2004) |
| **Dependent, fissioning** (Bourke & Franks 1995, Cronin & al. 2013) | Existing colony splits into two, workers carry gynes to new locations | At the gyne's colony | On foot with workers | By flight, or no dispersal | *Cataglyphis cursor* (see Lenoir & al. 1988), all army ants (Schneirla 1971) |
| **Dependent, budding** (Bourke & Franks 1995, Cronin & al. 2013) | Workers found new nests close to the original ones and carry the queens with them either as juveniles or as adults; often leads to polydomy | At the gyne's colony | On foot with workers | By flight, or no dispersal | Many *Formica* ants (Rosengren & Pamilo 1983) |
| **Polydomy** (Debout & al. 2007) | Existing nest splits by budding but the parts retain connection; does not necessarily fit the definition of dispersal, unless the colony grows very big and queens are moved from nest to nest; makes dispersal avoidance more profitable by enhancing the colony's ability to gather resources | None, or see budding | No dispersal, or see budding | No dispersal, or see budding | Many species of *Crematogaster, Leptothorax, Camponotus, Formica* (see Debout & al. 2007) |
| **Secondary polygyny** (Rosengren & al. 1993, Crozier & Pamilo 1996, Boomsma & al. 2014) | Queens seek adoption to existing colony as extra queens; the recruiting colony can be a foreign one (dispersal) or the natal colony (philopatry); often connected to budding and polydomy | Away from the colony, or at the gyne's colony | By flight, or no dispersal | By flight, or no dispersal | Many *Formica* ants (Rosengren & al. 1993), many *Myrmica* ants (Keller 1993, Seppä 1996) |
| **Supercoloniality** (Pedersen 2006, Boomsma & al. 2014) | Extreme polydomous polygyny, where colonies cover large areas; can function as a distingt dispersal strategy due to the invasive potential on continuous habitat | At the gyne's colony | No dispersal except within the colony | By flight, or no dispersal except within the colony | *Linepithema humile* (see Giraud & al. 2002), many *Formica* ants (Rosengren & al. 1993) |
| **Temporary social parasitism** (Buschinger 1986, 2009) | Queens exploit colonies of other species as stepping stones for founding their own colonies | Away from the colony | By flight | By flight | Several *Formica* and *Lasius* species (Buschinger 2009) |
| **Inquiline parasitism** (Buschinger 1986, 2009) | Queens exploit colonies of other ant species, usually without ever producing own workers | Away from the colony, or at the gyne's colony | Dispersal limited in various ways | Dispersal limited in various ways | Several species of *Leptothorax* and *Plagiolepis* (Buschinger 2009) |
| **Xenobiosis** (Buschinger 1986, 2009) | Queens found their nests inside the nests of other ant species, and exploit some of the host's resources, but produce their own workers | Away from the colony, or at the gyne's colony | Dispersal limited in various ways | Dispersal limited in various ways | *Formicoxenus* and *Polyrhachis* (Buschinger 2009) |

of dispersal were recently reviewed by Helms (2018), and are outside the scope of the current review.

**Colony founding as an integral part of dispersal:** Colony founding by queens is the final immigration phase of dispersal, directly for the gynes and indirectly for the males. This is the phase of dispersal that has received most attention in ant research and through which ant dispersal is most commonly described. Due to these reasons, we continue using the colony founding terminology for describing ant dispersal strategies (see Tab. 1 for summary of the main colony founding strategies and their effects on dispersal, and explanation of the terms that will be used hereafter). However, dispersal is successful only after the dispersing individual reproduces in the new location, resulting in gene flow (Ronce 2007). In population genetic terms, only colonies producing sexual offspring can be considered successful, but from the ecological perspective, colonies often have an effect on local communities already during their growth phase when they concentrate on worker production (Oster & Wilson 1978). The growth phase can be considerably long, for example in *Pogonomyrmex barbatus* (Smith, 1858) it takes about five years (Gordon 1995, Gordon & Wagner 1999).

Phylogenetic reconstruction shows that ancestral ant queens used non-claustral colony founding (Keller & al. 2014). Modifications to this ancestral strategy have evolved several times in different ant taxa, most likely to reduce the high costs of dispersal (Heinze & Tsuji 1995), but the proposed evolutionary pathways between the strategies have mostly not been formally tested. In line with the general notion that dispersal has high potential for evolution (Saastamoinen & al. 2017), closely related species can use different strategies, and reversals to ancestral strategies have occurred (e.g., Keller 1991, Brown & Bonhoeffer 2003, Johnson 2010). We will discuss the possible evolutionary pathways in detail in "Evolutionary transitions in dispersal", and specify the knowledge gaps and research needs in "Conclusions and future directions."

**Dispersal ability and resources:** The queens and males of many ants are strong flyers (Helms 2018) and based on studies on colonization and community ecology (Vepsäläinen & Pisarski 1982, Vasconcelos 1999), it is obvious that many species are pioneers that commonly colonize new habitats and at least some individuals of these species disperse long distances. For example in *Lasius niger* (Linnaeus, 1758), populations in Northwestern Europe seem to be genetically uniform, suggesting regular long range dispersal (Boomsma & Van Der Have 1998), consistent with the pioneer lifestyle of the species.

However, measurements of flight distances have been reported for only a few species, sometimes with small sample sizes (Helms 2018). There are also plenty of taxa whose colony structures and life cycles have not been studied at all, especially among ponerine ants (Peeters 1997). Furthermore, knowing average dispersal distances is not enough. Dispersal distribution in natural populations of most organisms is fat-tailed, meaning that most individuals do not disperse much at all and the rest have large variation in their dispersal distances (Lowe & McPeek 2014). As the whole distribution of dispersal distances is likely to affect the population level consequences of dispersal, assessing also the intraspecific variation in ants is an important aspect of future research.

In the absence of direct data on flight, the flight ability can be roughly inferred from morphological traits such as the wing muscle mass to body mass ratio (Marden 1987, 2000). Flying ants carry large amounts of resources, especially the claustrally founding gynes that need fat and storage proteins for energy during colony founding (Wheeler & Buck 1995, Wheeler & Martínez 1995, Wheeler & Buck 1996). Such queens have larger abdomens and smaller muscles compared with the gynes using other nest founding methods and might therefore be less skilled in flying and less able to fly long distances (Helms & Kaspari 2014, 2015). In contrast, non-claustral gynes have worker-like large heads and strong neck muscles for foraging during colony founding and thus face restrictions in their thorax architecture and flight muscle size (Keller & al. 2014). This makes the relationship of colony founding strategy and flight ability complex in ants. Also pleometrosis and parasitic strategies can change the queen's need for resources and therefore affect wing muscle to body mass ratios.

In addition to flying, several ant species also disperse on foot, especially the queens but in some cases also the males (Heinze & Tsuji 1995). This results in shortened dispersal distance and patterns of isolation by distance across small geographical scales (Peeters & Aron 2017). Especially dependent colony founding through budding or fissioning compromises the colonization ability of a species (Peeters & Molet 2009). Transition to dependent founding changes colony resource allocation: The resources for dispersal are not only allocated to the queens, but also indirectly to the workers that assist them in colony founding (Peeters & Ito 2001, Peeters 2012). In some species budding leads to polydomy, which enhances the colony's ability to gather resources, expands the colony area, and affects local competition (Debout & al. 2007, see "Social selection pressures").

**Dispersal polymorphism in queens:** Variation in resource allocation leads to variation in dispersal ability among individuals. For example in fire ants, the heavier summer gynes with better resources disperse smaller distances and found nests alone, while the leaner overwintered gynes fly further, and sneak into established colonies as intraspecific parasites (Helms & Godfrey 2016). Regardless of whether this is an adaptive parasitic strategy or just starved individuals making the best of a bad job, such variation has ecological and evolutionary consequences through effects on the selective regime of dispersal traits.

Clear-cut dispersal polymorphism is widespread among insects (Zera & Denno 1997). Such polymorphism is suggested to evolve when different selection pressures select for and against dispersal at the same time (Mathias & al. 2001). Dispersal polymorphism exists in ant queens,

too. Especially in dependently founding ants there are queen polymorphic species, with flying and completely flightless morphs, convergently evolved in several taxa (Peeters 2012). The genetic and developmental basis of such polymorphism is largely unknown, but for example in *Harpagoxenus* and *Leptothorax*, polymorphism seems to be caused by a single-locus mutation (Bourke 1987, Heinze & Buschinger 1989, Heinze & Tsuji 1995). In *Myrmica* ants, several species have queen size morphs, microgynes that are more commonly philopatric or even parasitic without producing their own workers, and macrogynes that usually participate in long range dispersal. In *Myrmica rubra* (Linnaeus, 1758) the two morphs are clearly distinct in size and behavior, and also genetically partially differentiated (Vepsäläinen & al. 2009, Leppänen & al. 2015), whereas in *Myrmica ruginodis* Nylander, 1846 the correlation between dispersal strategy and size is not as strong (Wolf & al. 2018). Similar queen size dimorphism exists also in several *Leptothorax* species (Hamaguchi & Kinomura 1996, Rüppell & Heinze 1999, Rüppell & al. 2001).

Variation in dispersal strategies may also exist with no obvious external morphological differences. For example, many *Formica* species have both monogynous and polygynous, even supercolonial, populations as a result of different dispersal strategies (Rosengren & al. 1993). In the polygynous populations, some individuals are philopatric and stay in their natal colonies, while some disperse and found their nests independently or via temporary parasitism (Collingwood 1979). Recently such intraspecific variation in dispersal has been linked to genetic architecture (Libbrecht & al. 2013). So-called social chromosomes, first found in *Solenopsis invicta* Buren, 1972 (Ross & Keller 1998, Krieger & Ross 2002, Wang & al. 2013) and later in *Formica selysi* Bondroit, 1918 (Purcell & al. 2014) seem to be connected to dispersal behavior of colonies: One type of the linkage group is associated with monogynous colonies where extra queens are not accepted, and the other type with highly polygynous colonies where workers readily accept extra queens.

In general, the genetic architecture of dispersal evolution is still largely unknown, both empirically and theoretically (Saastamoinen & al. 2017), but the different types of ant dispersal polymorphisms hold promise for being good model systems for such questions in the future.

**Dispersal strategies of ant males:** Ant males are traditionally seen only as the vehicles of sperm, and not much more. Their role inside the colonies during their development has not evoked much interest (Schultner & al. 2017), and their life outside the colonies is usually described by a single word: short. Ant males can potentially allocate all their resources to mating and dispersal, and do not need to invest in longevity, for example through costly immune defenses (Boomsma & al. 2005, Stürup & al. 2014). Detailed studies on male ants have focused on only a few species, such as *Atta* leaf-cutter ants (e.g., Baer & Boomsma 2006, Stürup & al. 2011). As male behavior and mating strategies vary a lot in other social Hymenopterans (Alcock & al. 1978, Boomsma & al. 2005), also ant males should be investigated more.

Fig. 1: *Formica pratensis* male has left the natal nest and climbed to a tree branch above it, ready to fly. Photograph by S. Hakala.

Dispersal coevolves with mate localization in ants (Peeters & Aron 2017) and studies on mating behavior are the main source of information about male dispersal. Traditionally, two main ways of mate localization are distinguished: In the male-aggregation system, both sexes join synchronous mating swarms away from their natal colonies, whereas in the female-calling system, males find gynes that advertise themselves with pheromones near their natal nests, with no clear synchrony in the flights among sexes (Hölldobler & Bartz 1985, Kaspari & al. 2001, Peeters & Aron 2017). Female calling is associated with male biased dispersal so that gynes fly only after mating, or not at all (Peeters & Aron 2017, Helms 2018). Female calling systems sometimes mean long search times for males, which has occasionally resulted in increased male life spans, and special morphological adaptations such as functional mandibles for feeding (Shik & Kaspari 2009, Shik & al. 2012). The division between the two mating systems is not necessarily strict in all taxa. For example in some *Formica* species (Fig. 1), individual gynes have been reported to either fly away from their natal nest or wait close by and males answer this with specific patrolling behavior for locating them (Kannowski & Johnson 1969).

Even less is known about within species variation in male behavior. In supercolonial *Linepithema humile* (Mayr, 1868), males are shown to either mate at their natal colony or to disperse and mate with gynes in other colonies (Passera & Keller 1993) and similar variation in behavior exists in *Formica* (Rosengren & Pamilo 1983). Also socially polymorphic species such as *Leptothorax acervorum* (Fabricius, 1793) (Hammond & al. 2001) or several *Myrmica* species (Seppä 1996) are likely candidates for such behavioral variation. In *Formica exsecta* Nylander, 1846, males are dimorphic, with monogynous colonies predominantly producing larger males that are suggested to be better at competing over mating opportunities locally, and polygynous colonies producing smaller, possibly more dispersive males (Fortelius & al. 1987).

The most dramatic within-species variation occurs in *Cardiocondyla* ants (Stuart 1987, Heinze & al. 1998): A winged male morph disperses, and a wingless, philopatric fighter morph mates in the natal colony and fights with other wingless males for mating opportunities.

Outside *Cardiocondyla*, flightless males are rare and found mainly in highly specialized species where also queen dispersal is restricted, such as social parasites *Formicoxenus* (see Härkönen & Sorvari 2017), or supercolonial *Monomorium pharaonis* (Linnaeus, 1758), whose males do have wings but still do not fly (Bolton 1986, Fowler & al. 1993). This can be contrasted with at least 16 different subfamilies with completely flightless queens (Peeters 2012) and even more taxa with otherwise limited female dispersal (Heinze & Tsuji 1995). Such apparent difference in the dispersal ability and propensity between the sexes begs for a systematic investigation of sex-biased dispersal in ants, both in terms of population genetics and the dispersal morphology and physiology.

**Sex-biased dispersal:** Sex-biased dispersal strategies are expected when there are differences in the trade-offs between dispersal and reproduction between the sexes (Zera & Denno 1997, Marden 2000, Perrin & Goudet 2001). These can arise when the sexes are competing for different resources during their adult lives (Li & Kokko in press). Classical theoretical considerations (Greenwood 1980) and empirical patterns from mainly vertebrates (Trochet & al. 2016) show that dispersal is biased towards the sex that has more to gain (or less to lose) from increased dispersal, mainly driven by the number of mating partners and local resource competition connected to parental care. In insects, dispersal strategies commonly differ between the sexes (Zera & Denno 1997), but the drivers of sex bias in invertebrates have not been systematically tested.

Accordingly, male bias in dispersal can be predicted to be more common in ants, as ant queens experience resource allocation trade-offs between flight and colony founding (See section "Dispersal ability and resources"). Since ant males do not live beyond dispersal and mating, and only compete over access to matings, selection can optimize them for these functions with fewer trade-offs, making males more likely to be the more dispersing sex. Many of the derived dispersal and nest founding strategies in ants can be roughly explained by selection that reduces the relative allocation to flight in queens (Heinze & Tsuji 1995), and are associated with female-calling mating system where males fly more in search for mating partners (Peeters & Aron 2017, Helms 2018), symptomatic of coevolution between sexes.

Male-biased dispersal is indeed often reported in ants (Sundström & al. 2005, Foitzik & al. 2009), even in species like *Formica exsecta* (see Sundström & al. 2003), whose monogynous life histories are thought to correlate with male-aggregation mating systems and dispersal of both sexes. However, a clear majority of studies on sex-biased dispersal focus on species where male bias is predicted (Johansson & al. 2018), such as species with completely flightless queens [e.g., *Nothomyrmecia macrops* Clark, 1934 (Sanetra & Crozier 2003); *Proformica longiseta* Collingwood, 1978 (Seppä & al. 2006, Sanllorente & al. 2015), army ants (Berghoff & al. 2008, Barth & al. 2013, Soare & al. 2014)]. Not surprisingly, dispersal and gene flow are heavily male-biased in these species. When sex-biased gene flow was assessed in a well-dispersing pioneer species *Formica fusca* Linnaeus, 1758, a slight female bias was observed (Johansson & al. 2018). Thus, species that do not have derived dispersal strategies should be studied more in order to gain a better understanding of sex biases in ant dispersal. Considering the idiosyncrasies of ant life histories, further investigation of the theoretical basis of sex-biased dispersal in ants would produce precise, testable hypotheses for these studies.

For the rest of this review, our discussion mostly focuses on queen dispersal, merely because males are largely overlooked in literature. Nevertheless, the examples and open questions reviewed here make it clear that male dispersal behavior is worth a closer look in the future.

**Is colony relocation dispersal?** In addition to natal dispersal, ants can move short distances by relocating the whole colony, with workers carrying brood and queen(s) to a new location (Smallwood 1982, McGlynn 2012). Colony relocation behavior has been reported throughout the ant phylogeny (McGlynn 2012). This behavior resembles dependent colony founding, and is also comparable with it in movement scale (Bouchet & al. 2013). This kind of small-scale movement is not usually considered dispersal, and the colonization potential of relocation is obviously small. But considering the long colony lifespan in some ants, regular nest relocation can lead to covering significant distances over longer time scales and should thus not be completely dismissed as a potential form of dispersal.

Colony relocation is most commonly a response to changing environmental conditions or disturbances (McGlynn 2012), for example colonies being built in substances that do not last for long times, such as small pieces of damp rotten wood, as in *Mystrium oberthueri* Forel, 1897 (Bouchet & al. 2013). In some other species, colonies are shown to relocate whenever they find a better quality site than the one they currently occupy, e.g., *Temnothorax albipennis* (Curtis, 1854) (Dornhaus & al. 2004). The same environmental challenges that lead to relocations can be also connected to polydomy and many polydomous species readily relocate their nests, sometimes in seasonally changing nest networks (Debout & al. 2007). Some ant species even have highly specialized behavioral strategies for colony relocation, such as self-assembled waterproof rafts in *Solenopsis invicta* to survive flooding (Mlot & al. 2011).

The most conspicuous case of colony relocation are army ants, where mobility defines the entire lifestyle: Army ants are group predators whose colonies regularly move from one location to another, without building permanent nest structures. As their queens are flightless, new colonies are produced through fission (Wilson 1958, Brady 2003). They can shift their colony as an answer to unfavorable environmental conditions, just as other ants,

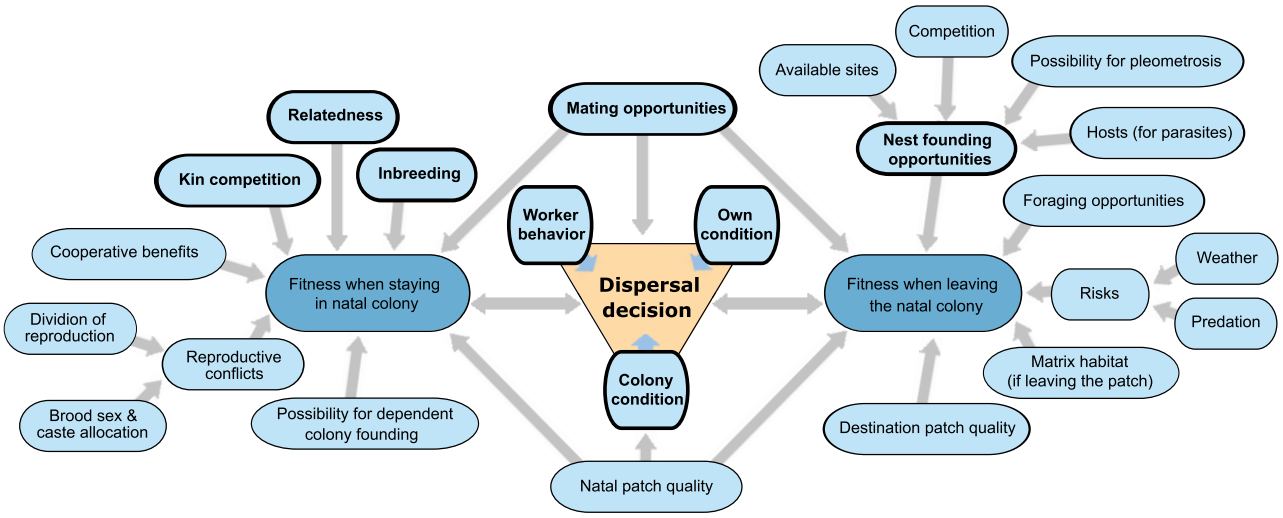


Fig. 2: Individual-level factors affecting the evolution of dispersal behavior. An individuals' decision to stay in the natal nest or to leave it – and later the decision to leave the natal habitat patch or not - depends on several factors that affect its fitness (indicated with arrows). The most influential ultimate and proximate factors are highlighted in bold. Most factors also interact with each other, and especially relatedness is a central factor that affects all social interactions. Inside the natal colony, the dispersing individual has direct information mainly about its own condition, colony condition and worker behavior (all of which closely interact). The other factors affect dispersal evolution mainly through natural selection, as ecological, social, and evolutionary feedbacks. The fitness benefits differ among the possible scenarios, and choosing one scenario has costs of lost opportunities from the other scenarios.

but they also have specialized emigration behavior. They move up to 450 meters at a time, either in a regular cycle or in a more irregular manner, depending on the taxon (Schneirla 1971). "True army ants" has been suggested to be a non-monophyletic group in the subfamily Dorylinae (Brady & al. 2006), and lifestyles with similar characteristics have also evolved in other more distantly related taxa (Kronauer 2009).

Colony relocation behavior, especially on the army ant scale, is an evolutionary transition of the superorganism from a sessile lifestyle towards a mobile one. Similar transitions have occurred in marine taxa (e.g., in feather stars (Nakano & al. 2002)), but the phenomenon has not been theoretically analyzed. The fact that such transitions in ant lifestyle and dispersal strategies are possible underlines their evolutionary flexibility.

## Multiple causes and selection pressures of dispersal

Dispersal is a multicausal process, and several different selection pressures affect it, sometimes in opposite directions (Starrfelt & Kokko 2012). The importance of the three ultimate causes for dispersal (inbreeding avoidance, avoidance of kin competition, colonization of new habitats) varies between taxa and depends on their ecology and evolutionary history (Bowler & Benton 2004). Importantly, the selection pressures predicted to affect the existence, rate or the range of dispersal are partially different (Lowe & McPeek 2014). Direct selection for dispersal plays a role mostly in the onset of dispersal and less so during the movement phase (Burgess & al. 2016). Thus, whether young ant sexuals leave the natal colony or stay and mate within it, is likely under direct selection for dispersal, but the range of their movement is affected by more proximate ecological and local selection pressures.

In this section, we list and discuss the determinants of dispersal decisions of individuals (summarized in Fig. 2). We start by exploring the ultimate causes, i.e., the selection pressures for dispersal in an inclusive-fitness framework, and discuss where the power over dispersal lies in ant societies. These sections deal with theoretical predictions, and the relative importance of these causes in natural populations should be systematically investigated with comparative data, due to the multitude of ecological and proximate causes affecting dispersal (Bowler & Benton 2004). At the end of this section we briefly explain the main proximate causes that shape the realized dispersal and gene flow in natural populations, and reflect on the condition dependency of dispersal decisions.

**Inbreeding avoidance:** Inbreeding avoidance is likely to be an important cause selecting for dispersal in ants. As in other haplo-diploid hymenopterans with complementary sex determination system (CSD), the effect of inbreeding is considered to be particularly harmful, because it results in inviable or sterile diploid males (Cook & Crozier 1995, Zayed & Packer 2005). CSD has recently been shown to exist in *Vollenhovia emeryi* Wheeler, 1906 (Miyakawa & Mikheyev 2015) and diploid males have been reported in many other ant taxa, consistent with the existence of CSD (Cook 1993). Other costs of inbreeding have been demonstrated in *Formica exsecta* (see Haag-Liautard & al. 2009) and *Cardiocondyla obscurior*

(Wheeler, 1929) (Schrempf & al. 2006). In order to avoid inbreeding, at least one of the sexes has to leave the natal colony and mate elsewhere, which can lead to sex-biased dispersal strategies (Pusey 1987, Motro 1991, Gros & al. 2008, section "Sex-biased dispersal").

Local mating between two offspring of the same colony seems to be limited to derived strategies, such as parasitic nest founding strategies, secondary polygyny or the fighter male morphs in *Cardiocondyla*. In *Cardiocondyla elegans* (Emery, 1869), workers actively carry gynes from one colony to another to allow them to mate with unrelated males, which seems to be a behavioral adaptation to avoid inbreeding (Lenoir & al. 2007). It is likely that in some of the locally mating ant taxa either CSD based on many loci or alternative sex determination mechanisms have evolved to counter the harmful effect of CSD and inbreeding (Buschinger 1989, Schrempf & al. 2006). Also clonal reproduction contributes to inbreeding-avoidance in some ant lineages, and it has been suggested to be an important pre-adaptation to the colonization success of some of the invasive, supercolonial species (Pearcy & al. 2011, Wenseleers & Van Oystaeyen 2011). In polygyne and supercolonial ant societies, the high number and low relatedness of egg-laying queens reduces the risk of inbreeding, but the risk still remains as polygyny is often the result of the daughters of the society staying and mating locally.

Many ant species commonly produce only or mainly single sex broods (Pamilo & Rosengren 1983, Nonacs 1986, Cook & Crozier 1995), which is often explained through worker control of sex ratios in response to relatedness asymmetries (Trivers & Hare 1976, Boomsma & Grafen 1990, Boomsma & Grafen 1991, Meunier & al. 2008). However, it also contributes to inbreeding avoidance. Split sex ratios force individuals to find mating partners outside the nest, ensuring dispersal even when it would otherwise be unfavorable for the individuals.

**Social selection pressures:** According to general theory, resource competition with relatives is harmful and dispersing away from them is favored by kin selection (Hamilton & May 1977), and the negative effects of competition among kin can cancel out the benefits of local cooperation in simple scenarios (Taylor 1992, West & al. 2002). However, more complex models show limited dispersal and population viscosity to be beneficial for social organisms (Lehmann & al. 2008, Kümmerli & al. 2009). This complexity, together with the difficulty of specifying the spatial scale over which cooperation and competition occur in nature (West & al. 2002) makes it hard to pinpoint which selection pressures have the highest impact on dispersal.

Indeed, one of the most interesting aspects of queen philopatry is the possibility to make the colony more successful, as polygyny allows producing a larger worker force. Especially when resource competition is strong, cooperative strategies connected to better resource deployment may be favored (Van Dyken & Wade 2012). According to Rosengren & al. (1993), this could explain the prevalence of polygyny in aphid farming *Formica* ants. If their ability to attend aphid livestock increases with increasing number of worker-producing queens, they can possibly even create more resources than the habitat originally had, overcoming some of the resource limitations that would otherwise lead to harmful kin competition. Polygyny is also connected to polydomy and budding dispersal in many ants, including *Formica* (Rosengren & Pamilo 1983, Debout & al. 2007, Ellis & Robinson 2014). This has been suggested to explain why queen philopatry and polygyny are so prevalent in ants compared with all other social insect taxa (Boomsma & al. 2014).

Recruitment of new queens potentially complicates the selection pressures affecting dispersal (see also "Colony allocation decisions and conflicts"). The number of queens and the division of reproduction among them affect expected direct fitness opportunities of a philopatric young queen. For example in functionally monogynous species where only one of the nestmate queens reproduces at a time, such as *Leptothorax* sp. (Heinze & Smith 1990), direct fitness is gained only in the case of possible resource inheritance in older age. In other species, all of the queens can reproduce simultaneously, as in for example *Temnothorax* (Guénard & al. 2016) and *Myrmica* ants (Evans 1996), which could make staying a safe strategy. The division of reproduction can also be more subtle. For example, in *Solenopsis invicta* (see Ross 1988) and *Formica exsecta* (see Kümmerli & Keller 2007) some queens produce mostly workers while others concentrate on sexual production.

Furthermore, the reproductive tenure of philopatric, polygynous queens is often relatively short compared with dispersing monogynous queens (Keller & Passera 1990, Tsuji & Tsuji 1996). For example, in facultatively polygynous *Formica fusca*, queens in polygynous nests have a shorter life than queens in monogynous nests (Bargum & al. 2007). However, this is compensated for by the facts that by staying in the polygynous colony, the queen both avoids the risks of dispersal and can immediately start producing sexual offspring instead of having to produce workers first (Keller & Passera 1990, Tsuji & Tsuji 1996).

Finally, the fitness consequences of staying in the natal colony depend on multiple allocation decisions within the colony, whose evolution in turn may depend on the kin structure of the nest (Crozier & Pamilo 1996). For example, colony sex and caste allocation may be predicted to affect the dispersal decision, all else being equal: The optimal choice for a single gyne could depend on the number of other competing gynes and the choices they make (Rosengren & al. 1993). The future allocation decisions also directly affect the fitness of any queen that decides to stay in the colony. As dispersal decisions alter the social environment within the colony, it is very difficult to fully assess the fitness consequences of philopatry vs. dispersal (Keller 1993), and truly understanding the social selection pressures requires understanding the eco-evolutionary feedbacks on dispersal (see "Consequences of dispersal").

**Conflict over dispersal:** The optimal dispersal behavior is predicted to differ between parent and offspring perspectives. For the parents, the fitness of each offspring is equally valuable, but for the offspring their own fitness is more valuable than that of their siblings. From a parent's point of view, high levels of risk can be tolerable, but the dispersing individual's risk tolerance threshold is lower, which leads to a potential parent-offspring conflict over dispersal (Motro 1983). In addition to dispersal itself, also the distance can be under conflict, as parents favor longer distances while the dispersers themselves would rather choose to stay close (Starrfelt & Kokko 2010). The strength of the conflicts depends on the ecological setting, and the conflict is stronger when dispersal is very risky (Motro 1983).

In ants and other social insects, there is potential for a three-way conflict over dispersal, because the colony structure complicates the situation. In addition to the parent-offspring conflict (Motro 1983) between the mother queen and the dispersing sexual offspring, also the queen and the workers may have conflicting inclusive-fitness interests. As in other conflicts in insect societies, relatedness influences what are the optimal strategies for each player and whether there is potential for conflict (Ratnieks & Reeve 1992, Crozier & Pamilo 1996, Ratnieks & al. 2006). The dispersal conflict is expected to be amplified when relatedness asymmetries within the society increase. That is, the dispersing individuals are expected to value their direct fitness more, when indirect fitness effects are diluted through low relatedness to others. However, the exact shape of the potential three way conflicts and whether they manifest as actual conflicts remain to be studied.

**Power over dispersal:** Actualization and outcome of potential dispersal conflicts depend on which party has most power to control dispersal (Beekman & Ratnieks 2003). In some organisms, dispersal is strictly under maternal control: For example, in plants the offspring have no power over dispersal decisions (Motro 1983). In animals, the division of power is usually more equal: For example, in marine invertebrates, the parent controls the development and release of the planktonic larvae, but the larvae have power over their own behavior after that (Marshall & Morgan 2011).

In ants, workers take care of brood, and sex allocation is in many cases consistent with worker control (Meunier & al. 2008). Thus, workers may affect the dispersal patterns by controlling the sex ratios of the brood and the gyne-worker ratio of the female brood (Ratnieks & al. 2006). Workers can also indirectly affect the dispersal behavior of individual dispersers, since dispersal decisions are often condition dependent (Bowler & Benton 2004), and workers have the possibility to control larval development and thus the condition of dispersing individuals. However, the relative contribution of workers and the individuals themselves has been assessed only in a few cases. Studies on the genetic architecture behind the mass of individuals have revealed complex interactions between individual genotype and the social or indirect genetic effect


Fig. 3: (a) *Lasius flavus* gynes and workers have climbed on a rock above their nest. The workers of this subterranean species are rarely seen above ground expect at the onset of dispersal. (b) *Lasius niger* males emerging from their nest. Photographs by S. Hakala.

of rearing workers (Linksvayer 2015). In a cross-rearing experiment on *Solenopsis invicta*, the origin of rearing workers seemed to affect larval development even more than the genetic background of the larvae, which would suggest great worker power (Keller & Ross 1993), whereas in a cross-rearing experiment on *Temnothorax curvispinosus* (Mayr, 1866), there were direct (the genotype of the individual itself), maternal, and worker effects on the gyne's mass at maturation, and direct and worker effects on the male mass (Linksvayer 2006). It seems that the development of larvae is an outcome of both their own phenotype and their social environment (Fjerdingstad 2005, Linksvayer 2015, Schultner & al. 2017).

Worker control over the development of dispersers does not guarantee that the latter are willing to disperse. However, as workers outnumber the dispersing individuals, it seems likely that they have power over the actual dispersal decision as well (Beekman & Ratnieks 2003, Fig. 3a & b). Worker behavior at the onset of dispersal has not been studied quantitatively, but there are anecdotes of workers controlling the movement of winged individuals and forcing them out of the colony at the appropriate time (e.g., Talbot 1956). In mammals, forced natal dispersal is common, although aggression is not usually targeted towards relatives, but rather towards unrelated juvenile individuals competing for resources (Wolff 1993). Behavioral studies are needed to assess the role of aggression towards gynes at the onset of dispersal and the likelihood of forced dispersal in ants. In supercolonial *Linepithema humile*, execution of older egg-laying queens is common, as workers kill up to 90% of the queens in their colonies each spring, possibly to control the relatedness and queen number (Keller & al. 1989, Inoue & al. 2015), which could be a delayed manifestation of an unresolved conflict over dispersal. But with no theoretical assessment of the direct benefits of such behavior to the workers, this remains speculative and begs further investigation.

In independently founding species, gynes and males control their own movement after leaving the natal colony, and the gynes choose where they settle to found a colony. In contrast, in dependently founding species, workers have almost full control over all stages of dispersal. Workers choose which gynes (or queens, or queen-destined brood) to carry to a new location. Dependent colony founding has evolved when the success rate of independent colony founding is low due to environmental reasons (Molet & al. 2008, Cronin & al. 2013). As higher dispersal risks theoretically also result in stronger conflicts over dispersal (Motro 1983), dependent colony founding could also resolve the dispersal conflict, as it both decreases the risk for the gynes and allows workers to alleviate local competition by moving queens to new nests.

**Environmental selection pressures:** Evolution of dispersal, and especially of dispersal distance, is strongly linked to local environmental factors. The ecological setting affects dispersal, either immediately through facultative and condition dependent decisions based on the information individuals are able to obtain (Kokko 2003, Clobert & al. 2009), or through natural selection.

Theoretically, colonizing new habitats is an important selection pressure for dispersal (Van Valen 1971, Olivieri & al. 1995). However, the time scale for such selection is long, because it plays out only when current habitat becomes unsuitable. Thus, selection for dispersal through the need for colonizing new habitats likely depends on selection for decreasing fitness variance in a lineage, rather than increasing immediate mean fitness (i.e., bet-hedging, Starrfelt & Kokko 2012). Also the spatial scale of colonizing new habitats is large in ants: For central place foragers, even short-range dispersal is often enough to mitigate the harmful effects of kin competition, but finding new habitats requires long-range dispersal. Thus, it is not clear how strong direct selection for colonizing new habitats can be. In general, long range dispersal is probably rarely maintained purely for dispersal alone, but is often a byproduct of traits selected for other reasons, such as avoiding predators and finding mating partners (Van Dyck & Baguette 2005, Nathan & al. 2008, Burgess & al. 2016).

Fig. 4: *Crematogaster* sp. gyne after leaving the natal colony, making further dispersal decisions on the go. Note the big mesosoma with strong flight muscles. Photograph by Alejandro Santillana, published as a part of the "Insects Unlocked" project.

In general, long-range dispersal away from the current patch increases when local resource competition is high due to small size, low quality, or high competitor density of the current patch (Poethke & Hovestadt 2002, Clobert & al. 2009). To our knowledge, studies assessing the relation of habitat quality and individual dispersal decisions have not been done on ants. However, it is clear that habitat quality impacts colony condition and thus affects the overall dispersal patterns through the amount and quality of dispersers the colony produces. As an extreme example, in *Cardiocondyla* the colony condition affects which male morph it produces: Under good conditions, the less costly wingless males are produced, while the more costly, substantially larger winged males appear in unfavorable conditions (Cremer & Heinze 2003). Similar condition dependency might affect the quality of dispersers in other ant species as well. Variation in individual quality, in turn, affects single dispersal events, so that not all individuals disperse the same way (Clobert & al. 2009, Lowe & McPeek 2014). For example in *Formica truncorum* (Fabricius, 1804), the individuals in better physical condition seem to be more likely to initiate dispersal (Sundström 1995). There are no studies measuring how dispersal distances correlate with individual condition in ants.

After the decision for long range dispersal has been made, patch connectivity and quality of surrounding habitat matrix affect the success of dispersal (Hanski 1999, Fahrig 2001), as does the predation pressure (Helms

2018). Individuals are likely to base their decisions on information about their immediate surroundings and their own physical condition (Fig. 4), whereas conditions further away and at a later time point are more likely to work through eco-evolutionary feedbacks.

**Consequences of dispersal**

Dispersal has important consequences on different spatial and temporal scales. In dispersal, individual and population level processes are connected through ecological and evolutionary feedbacks that interact through population dynamics. Ecological feedbacks result from resource availability and social interactions, while evolutionary feedbacks result from different fitness benefits of alternative strategies (Bowler & Benton 2004). Separating causes and consequences of dispersal is partly arbitrary and full understanding of dispersal requires understanding the eco-evolutionary feedbacks at play. In this section we briefly list consequences of dispersal, but mostly discuss the potential feedbacks affecting ant dispersal, even though research on these questions still largely awaits to be done.

**Colony allocation decisions and conflicts:** Taking co-evolving dispersal and mating strategies into account can deepen our understanding of social conflicts within ant societies. Relatedness among different members of the colony has been shown to affect many allocation and behavioral decisions and is also predicted to affect dispersal decisions and thresholds of accepting additional philopatric queens in the colonies (Pamilo 1991a, b, Bourke & Franks 1995, Crozier & Pamilo 1996). If some of the queens avoid dispersal and stay in their natal colony, relatedness is also immediately altered, which could lead to interesting feedback loops.

The potential conflict over queen number is influenced by the dispersal optima of the parents (queen and colony) and the offspring (gynes and males). The optimal dispersal rules of gynes have not been assessed by detailed theory, but a simple prediction is that they should seek adoption more readily than the colonies are willing to allow (Motro 1983). For workers, the difference between inclusive-fitness effects of accepting or rejecting an extra queen into the colony decreases with increasing queen number (Crozier & Pamilo 1996). Thus, if the queen number increases enough (due to any reason), additional queens have only negligible effects on the relatedness between nestmate and the workers. Eventually, the selection to control queen number may be weakened or even overrun by other selection pressures. This kind of feedbacks might in part explain extremely high queen numbers per nest (tens and even hundreds), such as those found in *Formica* ants (Rosengren & al. 1993) and other supercolonial species, even though multiple other causes may explain the original switch to polygyny.

Dispersal decisions can also be predicted to affect other within-colony conflicts. The higher the number of queens per nest is, the more are workers predicted to police reproduction by other workers, which over time resolves the queen-worker conflict over male production (Ratnieks & al. 2006). Similarly, the more queens are recruited back into their natal colonies, the smaller the queen-worker conflict over sex ratio is predicted to be. This is because having multiple queens dilutes the relatedness asymmetries between workers and the male and female brood, and the sex ratio optima of both parties converge towards 1:1 (Trivers & Hare 1976, Bourke & Franks 1995). However, in practice the sex ratios in sexual brood might not reach exactly 1:1 in polygynous societies, because part of the worker force can be considered an investment in the gynes that stay and start laying eggs in the natal colony (Pamilo 1990), in a similar manner as in dependently founding species where the resource allocation for gynes happens partly through the workers that help them found colonies (Peeters 2012). This kind of indirect resource allocation makes it hard to consider the exact fitness consequences of these dispersal strategies.

There is also another potential feedback between dispersal and sex ratios in ant colonies: Local mate competition caused by philopatric males skewing optimal sex ratios towards females could explain at least part of the observed sex ratio bias (Alexander & Sherman 1977). This hypothesis has not gained large support among social insect researchers as local mate competition has been deemed unlikely in species with mating flights and male-aggregation mating system – but the hypothesis may have been dismissed prematurely (Helanterä 2016). Local mate competition theories can be useful especially when explaining female biased allocation connected to derived dispersal strategies, such as completely flightless ants (e.g., *Cardiocondyla* sp. (Schrempf & al. 2005)), social parasites (e.g., *Plagiolepis xene* Stärcke, 1936 (Aron & al. 1999)) or highly polygynous species (e.g., *Myrmica sulcinodis* Nylander, 1846 (Pedersen & Boomsma 1998)).

**Population dynamics:** Dispersal has the potential to alter population dynamics and different dispersal strategies may impact persistence of populations over evolutionary time scales. Population genetics offers excellent tools for inferring large-scale patterns of dispersal (Balloux & Lugon-Moulin 2002).

In most studied ant taxa the spatial scale of dispersal seems to be small and the resulting population structures genetically viscous (Rissing & Pollock 1986, Seppä & Pamilo 1995, Ross & al. 1997, Sundström & al. 2005). As suggested already by Hölldobler & Wilson (1977), this holds true especially in polygynous species and populations, showing that social structure and dispersal are tightly linked in ants (Sundström & al. 2005). Especially species using only dependent founding have very viscous populations due to reduced gyne dispersal (Sanetra & Crozier 2003, Berghoff & al. 2008, Barth & al. 2013, Sanllorente & al. 2015, Peeters & Aron 2017). However, this may be a biased view, as species using strategies with limited gyne dispersal have been studied more (Seppä 2009, Johansson & al. 2018). In contrast, lack of viscosity has been shown in a handful of species, e.g., in *Lasius ni-*

*ger* (see Boomsma & Van Der Have 1998), *Formica fusca* (see Johansson & al. 2018), and *Temnothorax rugatulus* (Emery, 1895) (Rüppell & al. 2001). More balanced sampling of species and careful consideration of the spatial scales used would show if short distance dispersal and population genetic viscosity are general traits in ants, and which are the correlated life history traits.

Climate change will put pressure for range shifts on natural populations (Helms & Bridge 2017), and additionally habitat fragmentation affects them (Sundström & al. 2005, Seppä 2009). The high extinction risk of isolated populations is demonstrated for example in tree-living ant communities where the ant assemblages in isolated trees are sensitive to local extinctions (Gove & al. 2009). Especially the species using strategies of limited gyne dispersal (dependent colony founding, high levels of polygyny, the flightless social parasites) are particularly at risk for facing colonization problems. Although these strategies may be beneficial locally, they can lead to extinction when the local habitat becomes unsuitable. The dispersal abilities and extinction risks of ant taxa using strategies of limited gyne dispersal should be properly assessed.

Even in well dispersing species, search efficiency for suitable habitats may affect population structure. For example, *Lasius neoniger* Emery, 1893 and *Solenopsis molesta* Emery, 1895 gynes were shown to be inefficient in returning to their preferred habitat when displaced, indicating that they cannot search for it effectively (Wilson & Hunt 1966). Ant populations indeed seem to be patchy over large spatial scales, with species often not occurring in locations with suitable habitat (Wilson 1955, Levings 1983). This indicates that ant dispersal is either not strong enough in terms of propagule pressure or not informed enough in terms of their patch-finding ability, to guarantee high occupancy everywhere. Such chance effects might lead to problems in case the suitable habitat becomes rarer.

**Community dynamics:** Interspecific variation in dispersal has an important role in community dynamics. Island biogeography theories (MacArthur & Wilson 1967, Kadmon & Allouche 2007) predict that more isolated or fragmented habitats are expected to have poorer ant communities. The limited dispersal of many ant species may strengthen such patterns. Brühl & al. (2003) indeed show that in Malaysian rainforest, a bigger continuous forest area has twice as diverse ant community than the fragmented areas, which is rather worrying from conservation perspective.

Ant community research has focused on two main factors: how different environmental conditions shape the communities and what is the role of competitiveness (e.g., Davidson 1980, Levings 1983, Savolainen & Vepsalainen 1988, Andersen 1992, Bestelmeyer 2000). Competitive abilities of the species already present at a location affect the success of new dispersers trying to settle (Vepsäläinen & Pisarski 1982). Colonies in ant communities are often evenly spaced both intra- and interspecifically (Levings & Traniello 1981, Levings & Franks 1982, Chew 1987), demonstrating that new colonies are founded within equal distances from the existing ones in order to minimize competition – or colonies compete until only some survive. In *Myrmecocystus mimicus* Wheeler, 1908 workers of nearby colonies are shown to prevent colony founding (Hölldobler 1981).

In this light, possible correlations between competitiveness and dispersal ability should be influential for the formation of ant communities. Overall, Vepsäläinen & Pisarski (1982) stressed how important the species' dispersal and colony founding characteristics are in the structures of ant communities: Better dispersing species generally reach new areas more easily and might get advantage for early settlement regardless of their competitive abilities, whereas, for example, social parasite species cannot settle in an area where their host species does not already exist.

Also within-species variation in dispersal behavior plays a role in community dynamics (Lowe & McPeek 2014), and since it is rather large in many ant species, and correlates with their social structures, its role in ant communities should be assessed. The dispersing individuals may have different traits or trait values than the more philopatric individuals of the same species and these traits can shape the species communities more than generally appreciated.

**Evolutionary transitions in dispersal:** We have argued that dispersal is both a social trait and a determinant of the kin structures that create the selective regime for social traits. Thus, dispersal is prone to eco-evolutionary feedbacks. To understand the evolutionary transitions in ant dispersal strategies (Fig. 5), we need to understand how such feedbacks affect the different aspects of dispersal. At the moment, such questions are largely unanswerable due to lack of data on dispersal traits across the whole ant phylogeny. Below, we briefly list some examples of traits and feedbacks that may prove to be important. Our speculation focuses mostly on the kin-selected adaptive consequences. As both species specific idiosyncrasies and broader ecological selection pressures undoubtedly contribute to the variation observed, we stress that the predictions we outline are best tested with observing trends in broad phylogenetic comparisons.

The first major evolutionary step in ant dispersal is the switch from non-claustral to claustral colony founding. While it is easy to see how high risks during the founding stage select for such a strategy (Hölldobler & Wilson 1990), the switch requires a large suite of changes on the metabolism and size of the queens (Brown & Bonhoeffer 2003), accompanied with miniaturization of the workers to reduce the cost of the first worker brood (Peeters & Ito 2015). In order to understand the consequences of such changes, we need to understand correlates of larger resource allocation per queen accompanied with smaller resource allocation per worker, and how they affect further evolution. Possible correlates include further changes in worker sizes and numbers (which could consequently change the ecological status of the species) and changes in mating systems, driven by changes in operative sex

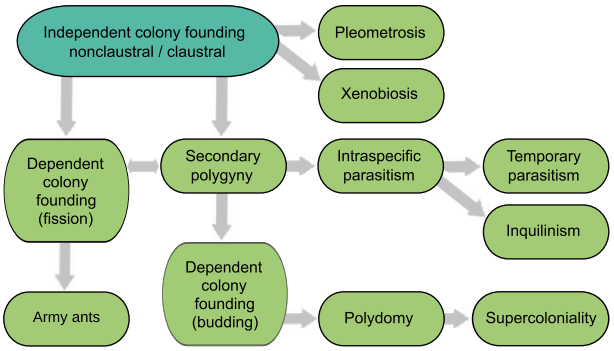


Fig. 5: The proposed evolutionary paths between colony founding strategies (see Tab. 1 for explanations of the terms). The evolutionary pathways from one dispersal and nest founding strategy to another have been widely discussed in the literature (see main text for details and references), but comprehensive phylogenetic analyses have not been made so far. Here, we present a hypothesis for the most likely evolutionary scenario for the switches between strategies. The arrows indicate the evolutionary direction from ancestral to more derived strategy, but also reverting back seems to occur commonly. The ancestral strategy in ants is independent, non-claustral colony founding, from which claustral founding has evolved (Keller & al. 2014). Army ants have arisen from non-claustral ancestors and pleometrotic species are usually claustral, but further analysis is needed to conclusively distinguish which of the two independent nest founding strategies is ancestral to some of the other strategies, and they are therefore grouped here.

ratios. As both reversals to non-claustral founding and intra-specific variation in claustrality occur (Stille 1996, Brown & Bonhoeffer 2003), it seems that claustrality is evolutionarily reversible. An important question in need of empirical and theoretical attention is whether claustral or non-claustral founding is more likely to lead to further transitions to other strategies, such as dependent colony founding.

Pleometrosis is a strategy that usually occurs combined with claustral colony founding (Bernasconi & Strassmann 1999), but is also possible in non-claustral species (e.g., *Pogonomyrmex californicus* (Buckley, 1867) Johnson 2004). This strategy requires synchronized mating flights, and large numbers of individuals to ensure colony founding partners. It remains poorly understood whether pleometrosis is associated with more or less investment per queen at the colony level and how that affects dispersal distances or the population densities. In addition to the ecological correlates for this strategy, we need to understand the selection pressures arising from social interaction among the founding queens and their first workers, such as the effects of honest or dishonest signaling of queen condition and productivity (Rissing & Pollock 1986, Nonacs 1992, Holman & al. 2010).

The next evolutionary steps towards more derived dispersal strategies, dependent colony founding and polygyny, answer similar ecological demands: They are both predicted to evolve when the dispersal risks are high and the colony-founding success is low, for example due to high competition, nest site limitation, habitat patchiness or predation (Bourke & Franks 1995, Cronin & al. 2013, Boomsma & al. 2014). Both of these strategies are very variable, and have evolved several times in vastly different ant taxa, meaning that no single explanation for their evolution is enough. It has been suggested that selection against dispersal may lead to readoption of queens in their natal colonies, which then can lead to the evolution of dependent colony founding (Bourke & Franks 1995, Heinze & Tsuji 1995, Cronin & al. 2013). Polygyny and dependent founding indeed often co-occur (Keller 1991, Cronin & al. 2013). However, this is not a general rule, and a direct causal link between these strategies does not always exist as dependent founding has evolved also independently from polygyny (Cronin & al. 2013). In the case of these strategies, potential feedbacks are less speculative, as local recruitment of queens changes the local kin structures and resource allocation that drive dispersal itself. For the gynes, it may be beneficial to exploit the colony resources instead of taking the risks of dispersal, especially when relatedness is low.

Low success of long-range dispersal leads to selection for limited dispersal and more philopatric behavior in insects and can create evolutionary prospects for morphological and behavioral changes leading to stayer morphs (Harrison 1980, Zera & Denno 1997). In ants, long distance dispersal can in extreme cases disappear completely, as in flightless dependently founding gynes (Peeters 2012) or in some of the supercolonial species (Helanterä & al. 2009). Paradoxically, supercoloniality is a successful dispersal method in continuous habitats – even though the gynes may not be good at dispersing, the colonies spread efficiently by budding. For example, wood ants have colonized Northern Eurasia very fast after the last glaciation (Pamilo & al. 2016). Even more extreme cases can be found in invasive species across their introduced habitats: For example, *Linepithema humile* has spread through the Mediterranean coast as a single supercolony since the 19th century (Giraud & al. 2002, Wetterer & al. 2009). Regardless, both supercoloniality and dependent colony founding lead to colonization problems in fragmented habitats, which may partly contribute to the notion that such lifestyles are evolutionary dead ends. Even though they are beneficial strategies locally and on shorter time scales, and seem to have evolved rather easily in several ant taxa, they do not necessarily survive and radiate on evolutionary time scales (Helanterä & al. 2009, Peeters 2012).

It has been suggested that parasitic nest founding strategies (temporary parasitism and inquilism) are an evolutionary consequence of selection for selfish philopatry within polygynous societies, leading to intraspecific parasitism and after a host shift or speciation, to interspecific parasitism (Buschinger 2009, Boomsma & al. 2014). The third type of social parasitism affecting dispersal evolution, xenobiosis, seems to follow a different evolution-

ary pathway. Xenobiotic species are not closely related to their hosts, and their development is not tied to the host resource allocation, as they take care of their own brood (Buschinger 2009). Dependency on host resources, and possible coevolution with host colony allocation decisions and caste determination, may direct also dispersal evolution of parasitic species. Small size, which is especially common among inquilines (Buschinger 2009), helps deceptive development into queens with the amount of resources the host allocates for the development of its own workers (Nonacs & Tobin 1992). As small queen size likely further selects against independent founding, this should result in the parasites being more strictly dependent on their hosts.

It is clear that all parasite species are somehow restricted in their dispersal because they can only settle on locations where one or more of their host species already live (Vepsäläinen & Pisarski 1982, Buschinger 1986). Especially inquilines and xenobiotic species can be seen as extreme habitat specialists, because the host nests are the only suitable habitat for these species. This is suggested to be a reason why these species have so often lost their flight ability: Dispersal by wing has a high risk of flying to areas without suitable hosts (Brandt & al. 2005). In contrast, temporary parasites have kept their flight ability, and consequently colonization ability, more frequently (Buschinger 2009). Connectivity and continuity of the host populations need to be considered in order to understand the evolution of the parasitic strategies, since all social parasites coevolve with their hosts, but the coevolutionary dynamics may direct the evolution of different strategies to different directions (Brandt & al. 2005).

**Conclusions and future directions**

We identify four key areas where further research would help to understand the causes and consequences of ant dispersal: comparative analyses on dispersal evolution and life history traits, gene flow analyses with non-biased species sampling, understanding the genetic architecture of the traits relevant for dispersal, and formulating testable theories for ant dispersal.

First, comprehensive data on colony life-history traits are needed for a wide variety of ant taxa, including at least sizes of different castes and resident queen numbers, as well as behavioral data on dispersal and mating. Ideally also details on allocation ratios and individual morphology should be documented. Importantly, these data should be collected for males, too, as they are currently seriously understudied. This dire need for comparative colony life-history data has been identified for a long time (Starr 2006) and the coordinated efforts to build databases have recently given hope for progress (Parr & al. 2017). Phylogenetic comparative analyses combined with environmental data (climate, local communities) have proven insightful in other social evolution contexts, such as understanding the relation between cooperative breeding and habitat harshness (Cornwallis & al. 2017, Griesser & al. 2017). Such analyses would allow teasing apart the crucial preadaptations and possible correlates for the evolution of different dispersal strategies, in addition to understanding the ecological drivers. Also the long-standing hypotheses of certain dispersal strategies as evolutionary dead ends (supercoloniality, dependent colony founding, parasitic strategies) should be subjected to rigorous tests.

Second, as dispersal is a multi-phase process, and the observation of movement does not comprise data on successful gene flow, descriptive population genetic structure data are needed. These data should be collected without the current biases with respect to the life histories of the taxa. While these are labor-intensive data, the increasing cost efficiency of genotyping, and the possibilities of using museum samples (Wandeler & al. 2007) means that this is achievable for a large number of species. Data on the dispersal strategies and environmental conditions should be incorporated in the analysis and studies on larger spatial scales are also needed. Modern landscape genetic methods that do not require identifying discrete populations are a useful option for analyzing this kind of data (Manel & al. 2003, Manel & Holderegger 2013).

Third, experimental and genomics approaches allow further understanding of the basis of dispersal related phenotypes and the potential constraints of adaptation (Saastamoinen & al. 2017). Investigating the relative roles of direct and indirect genetic effects (Linksvayer 2015) on developmental outcomes and behavioral decisions may shed light on how the traits potentially respond to selection. Sequencing approaches complement the picture by allowing to understand the role of plastic gene expression underlying dispersal phenotypes, possible pleiotropic constraints and elements of parallel and lineage specific evolution of the genomic underpinnings of dispersal phenotypes.

Fourth, careful theoretical work on co-evolving traits in ant dispersal is needed to make the most of the comparative data. Models of coevolution of social traits and population structures have demonstrated strong feedbacks. For example, Powers & al. (2011) show that population structure drives social evolution, but also that social behavior affects the population structure and therefore enhances the evolutionary process. Van Dyken & Wade (2012) stress how important it is to consider the connection between the evolution and the ecology of social behavior, when studying the evolution of different altruistic strategies. Similar dynamics of social niche construction (Ryan & al. 2016) are likely at work in the dispersal evolution of ants. Also the possible social conflicts over dispersal among multiple actors in the colonies should be incorporated in the future models on ant dispersal. Similarly to models of sexual selection and sexual conflict (Chapman & al. 2003), traits of one class of individuals are the key selective pressures to the other class. Testable models of sex-biased dispersal in ants, in connection to evolution of mate location, have potential to illuminate some of the open questions of the field, especially since empirical tests of kin-selection based theories of sex-biased dispersal remain surprisingly scarce overall (Li & Kokko in press).

Considering the ecological importance of ants, it is surprising how little is still known of their dispersal and colonization behavior. Even though ants are seemingly robust and numerous, their effective population sizes are often very small, which makes them more vulnerable than one might think (Seppä 2009). In this light, understanding ant dispersal has direct conservation relevance in environments undergoing rapid human induced change. In order to understand vulnerability of ant populations, dispersal is a key process at the intersection of behavior and population dynamics. To understand dispersal, we need to understand its ecological context, individual level determinants and evolutionary history.

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