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Cooperation and conflict in ant (Hymenoptera: Formicidae) farming mutualisms – a review

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Abstract

Farming practices, in which one organism (here: "the host") promotes the growth of the organism it relies on for food (here: "the symbiont"), are not restricted to human hosts. Among the non-human farmers, ants are particularly successful. Farming is an example of mutualism: an interaction between different species which is beneficial for all those involved. The evolutionary stability of mutualism in the light of potential conflicts of interests between the partners still remains incompletely understood. Various mechanisms may aid alignment of differing interests and resolve host-symbiont conflicts. Farming mutualisms are well-suited for studying these mechanisms. The three most important arenas of potential conflict in farming mutualisms concern symbiont reproduction, symbiont transmission / dispersal and symbiont (genetic) diversity. Here, these three symbiont characteristics and the control mechanisms governing them are reviewed for the two best-known cases of ant farming: (1) fungus-growing by attine ants and (2) Homoptera-tending by various groups of ants. Cross-system comparison of these ant farming systems highlights several universal patterns potentially governing the evolutionary stability of these successful mutualisms: Many systems are characterised by reduced symbiont dispersal and diversity (often in association with asexual reproduction and vertical transmission), possibly promoted by specific ant behaviours, such as creation of protective environments. Frequently, these systems function as networks, with the focal species interacting with additional species, highlighting a promising new take on classic mutualisms.

Key words: Aphids, attine ants, dispersal, diversity, evolutionary stability, fungus, reproduction, scale insects, transmission.

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Introduction

The evolution of plant and animal domestication has been a key factor in the success of the human species, allowing its populations to grow vastly, invade new habitats and sustain high densities (RINDOS 1984, LARSEN 1995, SMITH 2007a, b, LALAND & BOOGERT 2010). Farming (or "cultivation mutualism"; HATA & al. 2010, PION & al. 2013), in which one organism (here: the "host") promotes the growth of another organism (here: the "symbiont") it relies on for food, however, is not restricted to humans. Non-human farming practices range from primitive ("proto-farming") to highly sophisticated. Primitive forms include the farming of bacteria by amoebae or fungi (BROCK & al. 2011, PION & al. 2013), non-active ("passive") farming of fungi by snails (SILLIMAN & NEWELL 2003) and of algae by sloths (PAULI & al. 2014), and damselfish actively growing gardens of algae (HATA & KATO 2006, HATA & al. 2010). More advanced farming includes specialised Homopteran husbandry for "milk" and "meat" by ants (WAY 1963, STADLER & DIXON 2008) and sophisticated systems of fungus growing by beetles (FARRELL & al. 2001, BIEDERMANN & TABORSKY 2011), ants (WEBER 1972, CURRIE 2001, MUELLER 2002, MUELLER & al. 2005, POULSEN & BOOMSMA 2005), and termites (AANEN & al. 2002, 2009).

The systems that involve ants as "farmers" are some of the most specialised and best studied cases of non-human farming. Having evolved millions of years ago, the farming ants' niche-construction through cultivation and rearing of their own food sources likely played a large role in the ecological success of these species, possibly allowing them to reach remarkably high population densities (HÖLLDOBLER & WILSON 1990, MUELLER & GERARDO 2002, OLIVER & al. 2008, IVENS & al. 2012a).

Farming systems are examples of mutualisms, cases of cooperation between different species (BRONSTEIN 1994). This implies that both partner species involved receive net benefits from engaging in the interaction. In the case of farming, the mutualistic interaction typically takes the form of food exchanged for services (grooming, protection). Evolutionary theory predicts mutualism to be inherently unstable: Even though the established relationship will be beneficial for the two interacting species, there is continued selection pressure on the separate partners to reap the

benefits from the interaction without paying the costs of their investment (HERRE & al. 1999, BRONSTEIN 2001, BERGSTORM & al. 2002, SACHS & SIMMS 2006). This continued selection on the partners to invest little but take much could ultimately lead to one of the partners evolving into a parasite of the other, or to extinction of the system as a whole, due to an overabundance of "free-riders" or conflicts of interests between the partners (SACHS & SIMMS 2006). The most pressing questions on mutualism evolution seek to explain how such mutualism breakdowns are prevented: which mechanisms ensure that mutualists associate with the right partners? And how are mutualists prevented from "defecting" (ARCHETTI & al. 2011a)?

Having persisted during a long co-evolutionary trajectory and yet being typically asymmetric, the intimate relationships between the farmers (the "hosts") and their close-living mutualistic crops or herds (the "symbionts") make interesting study cases for our understanding of mutualism stability. This review aims to evaluate our current knowledge on conflicts and cooperation in ant farming systems and to outline new avenues for study, by focusing on the two best-known cases of ant nutritional farming: fungus-growing attine ants and Homoptera-tending ants.

Conflicts of interests in farming mutualisms: theoretical background

Farming mutualisms are generally asymmetric, with the host often being larger, longer lived and represented by a single reproductive entity (individual, colony). The symbiont interacts often as a group of multiple individuals, has a short generation time and is smaller. In farming systems, these partner species tend to be dependent on each other for survival (the host eats (part of) the symbiont to survive and thus controls its survival). In such intimate, asymmetric interactions, the interests of the partners will never be fully aligned and conflict lurks around the corner. Host and symbiont are theoretically predicted to be in conflict about three topics in particular: (1) symbiont reproductive mode, (2) symbiont transmission and dispersal, and (3) symbiont diversity (FRANK 1996b, HERRE & al. 1999, MUELLER 2002). Historically, these considered "arenas of conflict" are symbiont-biased; this stems from the original assumption that hosts are generally controlling there symbionts. Although host control over mutualistic symbionts is indeed thought to be essential for evolutionary stability of mutualisms (FRANK 1996b, HERRE & al. 1999, SACHS & al. 2004, ARCHETTI & al. 2011b), the question whether the hosts are in complete control remains unanswered. Below, I will introduce these three arenas, their possible resolutions and the preferred options for both partners in more detail (Tab. 1).

Arena 1: Symbiont reproduction

The symbiont's mode of reproduction can be sexual, clonal or a mixed strategy of both. It would be in the interest of the host to prevent the symbiont from sexually reproducing: Energy allocation towards sexual reproduction is avoided and beneficial combinations of genes are preserved, for lack of recombination (FRANK 1994). For the symbiont it would be beneficial to sexually reproduce to avoid inbreeding effects and remain resilient in changing environments, for example through recombination or bet-hedging (Tab. 1). The scope for host control of symbiont reproduction is two-fold. Directly, the host can actively suppress sexual reproduction by preventing its symbiont to mate. Indirectly, hosts can promote asexual reproduction by creating a protective environment for symbionts (LAW & LEWIS 1983, LAW 1985, WULFF 1985). In such a stable niche, the benefits of asexual reproduction (a higher reproductive rate and not having to search for a mate) outweigh the cost of a reduced ability to cope with fluctuating environments. In this case, host control may thus emerge as a by-product of genotypic predictability.

Arena 2: Symbiont transmission and dispersal

Symbionts can be either horizontally or vertically transmitted. Under horizontal transmission, symbionts disperse independently from their host. Typically, at the beginning of a host generation, hosts associate with symbionts that are unrelated to the symbionts of their parents. Under vertical transmission, symbionts are transmitted directly to descendants of their previous hosts during host reproduction. Vertical symbiont transmission can be beneficial to both partners: Not only do mutualists no longer incur costs of seeking a partner, it also promotes co-dependency between the partners (DOUGLAS 1998a, LAW & DIECKMANN 1998, HERRE & al. 1999, SACHS & al. 2004, VAUTRIN & al. 2008). In fact, it is for this latter reason that vertical transmission is considered one of the most important mechanisms in mutualism evolution. Repeated co-reproduction creates a positive feedback loop (termed "partner fidelity feedback") between the fitness of both interacting partners: Cooperation will indirectly, via the partner, benefit the actor, thus increasing the evolutionary incentive to cooperate (EWALD 1987, BULL & RICE 1991, YAMAMURA 1993, FOSTER & WENSELEERS 2006, VAUTRIN & al. 2008, WEYL & al. 2010, ARCHETTI & al. 2011a, SACHS & al. 2011, FREDERICKSON 2013). Horizontal transmission, on the other hand, allows the symbiont to escape less beneficial interactions, explore new habitats and avoid competition with close relatives (HAMILTON & MAY 1977). Also, horizontal transmission allows the host to choose among potential symbionts and select the best partners (termed "partner choice") (BULL & RICE 1991, HOEKSEMA & BRUNA 2000, FOSTER & WENSELEERS 2006, WEYL & al. 2010, ARCHETTI & al. 2011a). Several models have indeed shown that, provided horizontal transmission remains local and mutualists have the ability to choose their partners, stable mutualism can evolve under horizontal transmission as well (GENKAI-KATO & YAMAMURA 1999, WILKINSON & SHERRATT 2001). Another potential benefit of horizontal transmission for the hosts is the possibility to only take on costly symbionts when environmental conditions require the interaction.

Host control over transmission can be direct, by preventing independent dispersal / horizontal transmission and indirect, by providing an environment with decreased incentive to disperse.

Arena 3: Symbiont diversity

Symbionts can be farmed in either polycultures or monocultures. From the symbiont's viewpoint, some diversity might be preferred, because this would prevent competition with close relatives (FRANK 1996b, BOT & al. 2001). However, some argue that only the indirect benefits ensured by the high relatedness found in monoculture farm-

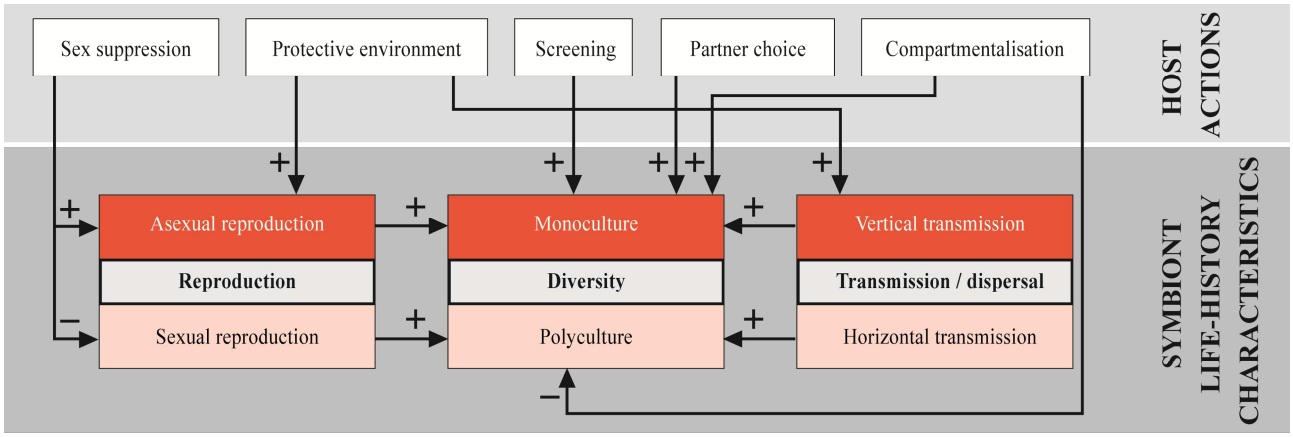

Fig. 1: Flow diagram of host actions and symbiont traits involved in farming mutualism conflict resolution. The top panel lists host actions, the lower panel lists symbiont life-history characteristics and their arenas of potential conflict with their possible outcomes (symbiont reproduction, diversity, transmission / dispersal in bold panels). Two sets of outcomes are often observed in nature: asexual reproduction, monoculture and vertical transmission (in bright red) and sexual reproduction, polyculture and horizontal transmission (in light red). Arrows show relationships and plus and minus signs indicate the nature of the relationship (positive or negative).

Tab. 1: The three arenas of conflict in farming mutualisms. For each arena, its possible outcomes are listed as well as the respective theorised benefits for host and symbiont of these outcomes.

Arena of conflict	**Possible outcomes**	**Host perspective**	**Symbiont perspective**
Symbiont reproduction	Asexual	– Beneficial gene combinations are preserved (beneficial in stable environments). – Less productivity loss due to symbiont energy allocation to sexual reproduction.	– All genes are passed on to the next generation. – No energy and time loss due to searching for mates.
	Sexual	– Symbiont with higher adaptive potential (beneficial in changing environments).	– Adaptations to changing environments are promoted through mechanisms such as bet-hedging and increased genetic diversity.
Symbiont transmission and dispersal	Horizontal	– Partner choice can take effect: good symbionts can be chosen, bad symbionts can be avoided or replaced. – When symbiont is temporarily not needed, the costs of having one can be avoided by not involving in an association.	– Competition with close relatives can be avoided. – Escape from the host is possible.
	Vertical	– Ensures having a (good) symbiont in the next generation (partner fidelity). – Host / symbiont co-evolution can occur, increasing productivity.	– Ensures having a host in the next generation. – Host / symbiont co-evolution can occur, increasing productivity.
Symbiont diversity	Monoculture	– Increased productivity through uniform farming conditions. – Harmful competition between symbionts is avoided.	– Symbionts that are consumed by their host gain indirect fitness benefits via dispersing / reproducing relatives.
	Polyculture	– Increased productivity through increased diversity (diversity-productivity relationship). – Symbiont community is more resilient against specialised parasites.	– Competition with close relatives is avoided. – Opportunity to outcompete other symbionts.

ing can outweigh the costs of individual symbionts being eaten by the hosts (AANEN & al. 2009, BOOMSMA 2011). Mutualistic hosts are predicted to also favour predominant or exclusive monocultures if coexistence of multiple strains or species within the same host causes costly competition (FRANK 1996b, VAUTRIN & al. 2008) or free-riding by cheating symbionts, leading to a direct reduction in overall productivity (e.g., BRONSTEIN 2001, KIERS & DENISON 2008). Moreover, competition among symbionts may select for virulent competitive traits that can indirectly also harm the host (WULFF 1985, FRANK 1996b). Finally, uniform conditions allowed by monoculture may increase mutualism productivity in undisturbed environments (LAW 1985, DOUGLAS 1998a). This latter argument, however, remains debated, because a community of multiple symbionts might also offer a broader spectrum of services or might be less vulnerable to parasites (e.g., VAN BORM & al. 2002, PALMER & al. 2010). In addition, existing variation among

the symbionts available provides the hosts with the opportunity to exert partner choice. The stabilizing effect of partner choice, however, will only have effect if at least some variation to choose from remains in the population (FOSTER & KOKKO 2006, MCNAMARA & LEIMAR 2010, FREDERICKSON 2013, HEATH & STINCHCOMBE 2013).

Host control over symbiont diversity generally happens through specific mechanisms of symbiont screening upon admission (ARCHETTI & al. 2011b) or symbiont rewarding / sanctioning in response to performance (KIERS & DENISON 2008, WEYL & al. 2010, ARCHETTI & al. 2011a). In addition, hosts can employ simple mechanisms such as positive frequency-dependent propagation or separation of symbionts in time or space ("compartmentalization") to reduce symbiont diversity (e.g., AANEN & al. 2009, PALMER & al. 2010).

Interdependence of stabilizing mechanisms

Clearly, these three arenas of conflict and their possible outcomes are not independent and all three are closely intertwined in a complicated web of costs and benefits of possible outcomes, host control mechanisms and symbiont life history characteristics (Fig. 1) (HERRE & al. 1999). The conflicts can thus be resolved in a cascade of cost-benefit balances, which will favour certain combinations of symbiont traits over others. Indeed, two sets of outcomes are often found in nature: (1) asexual reproduction, vertical transmission and monocultures versus (2) sexual reproduction, horizontal transmission and polycultures. The first set would be expected under complete host control. Below, I will review the symbiont characteristics commonly found in two well-known examples of ant farming: fungus-growing and Homoptera-tending (Fig. 2).

Fungus-growing ants

Biology and evolution

Fungus-growing ants, also commonly referred to as "attine ants" (subfamily Myrmicinae, tribe Attini) are a tribe of > 230 species that depend on the fungus they cultivate in their nest for food. The ants inoculate, groom, eat and disperse their symbiont fungus, making the fungus-growing ant – fungus systems classic examples of non-human agriculture (Fig. 2a). Attine ants are exclusively New World species and occur primarily in the Neotropics, with the northern limit of their range likely set by the cold-tolerance of their symbiotic fungus (SCHULTZ & BRADY 2008, MEHDIABADI & SCHULTZ 2010, MUELLER & al. 2011a). With high densities and diverse fungal substrates (ranging from arthropod carcasses to freshly cut leaves and flowers) fungus-growing ants are of major ecological and economic importance throughout their range (WEBER 1966, 1972, MEHDIABADI & SCHULTZ 2010).

Fungus-growing behaviour in attine ants evolved approximately 50 million years ago (SCHULTZ & BRADY 2008, MIKHEYEV & al. 2010). All fungi cultivated by attine ants are basidiomycete fungi belonging to the tribe Leucocoprineae (MUELLER & al. 1998, VO & al. 2009, MEHDIABADI & SCHULTZ 2010, MEHDIABADI & al. 2012). Cophylogenies between the attine ants and their fungi show a history of close co-evolution, with major evolutionary transitions to coral farming, yeast farming and fungal farming on cut leaves being well-represented; these major transitions are generally reflected in the distinction between "lower attines" and the more derived clade "higher attines" (MUELLER & al. 1998, MUELLER & GERARDO 2002, VILLESEN & al. 2004, DE FINE LICHT & al. 2010, MEHDIABADI & SCHULTZ 2010, MIKHEYEV & al. 2010, MEHDIABADI & al. 2012).

Fig. 2: Three examples of ant farming of fungi (a), root aphids (b) and mealybugs (c) for food. (a) *Acromyrmex* leaf-cutter ants tending their fungus garden (photo: D.R. Nash); (b) subterranean *Lasius* ants tending *Prociphilus* aphids (photo: D.J.C. Kronauer); (c) an *Acropyga* queen and male mating while the queen is holding an adult female *Eumyrmococcus* mealybug in her mandibles, an example of trophophoresy (photo: S. Kuribayashi).

The ants are obligately dependent on the fungus for food: While adults are known to consume the fungus, it is the exclusive diet of the larvae (WEBER 1972, MUELLER 2002 (and references therein), SCHIØTT & al. 2010). The fungus is presumably also dependent on the ants for survival,

although free-living strains of lower attine fungi have been found (MUELLER & al. 1998, VO & al. 2009). These fungi might therefore be considered facultative mutualists, whereas the higher attine fungi are considered obligate mutualists (MEHDIABADI & al. 2012). The obligate relationship between the higher attines and their fungi has led to some of the most specialised adaptations in the mutualistic partners: leaf-cutter ants have workers that are morphologically specialised to cut leaves that serve as substrate to the fungus and the fungus grows specialised structures (the "gongylidia") for the ants to feed on and to transfer digestive enzymes to the ants to manure substrate (MEHDIABADI & SCHULTZ 2010, SCHIØTT & al. 2010, DE FINE LICHT & al. 2013).

Symbiont reproduction

All fungus-growing ants inoculate and disperse their fungus vegetatively (see below). This led to the assumption of exclusive clonal reproduction in the domesticated fungi (WEBER 1966). Although clonal reproduction was indeed confirmed molecularly for fungi both inside and outside ant gardens (CHAPELA & al. 1994, MUELLER & al. 1996), a later AFLP study yielded mixed evidence: Next to signs of predominant clonal reproduction, these data also indicated recent genetic exchange between domesticated fungi and their free-living counterparts (MUELLER & al. 1998). This result and the symbiont's capacity for meiosis were later confirmed by MIKHEYEV & al. (2006). The co-evolution between fungus-growing ants and their fungus thus seems more diffuse than previously assumed, and may be best interpreted as one-to-many co-evolution rather than one-to-one (MIKHEYEV & al. 2006).

The exact mechanisms underlying the observed recombination remain unresolved to date. Occasional sporulation or hyphal fusion inside the ant nests are the most plausible explanations. In support of the former, fruiting bodies of cultivated fungus have occasionally been observed both in the field and in the laboratory and some of the spores produced by these fruiting bodies proved to be viable (WEBER 1966, MUELLER & al. 1998, PAGNOCCA & al. 2001, MUELLER 2002, VO & al. 2009). In support of the latter, SEN & al. (2010) found signs of recombination between different fungal strains grown together in chimeric gardens in a laboratory set-up, although these findings remained inconclusive.

In line with theoretical predictions that hosts would prefer asexual symbiont reproduction, ants have been reported to destroy incipient basidiocarps as well as display distressed behaviour when fruiting bodies erupt from their garden (reviewed in MUELLER 2002). Ants may also be able to indirectly prevent fungal sexual reproduction. Factors such as fungal biomass and mixing of strains are known to promote basidiocarp formation in basidiomycete fungi (MUELLER 2002). Reproductive choice may therefore not be under exclusive control of the fungus, but could also be influenced by ant farming behaviour.

Symbiont transmission and dispersal

Presumably, attine ants vertically transmit their fungal crops. Upon leaving the nest to mate and found a colony of their own, gynes (virgin queens) take a small piece of fungal mycelium with them (WEBER 1966, 1972, MUELLER 2002, MEHDIABADI & SCHULTZ 2010). The young queens then use this fungal inoculate to initiate their own garden. This natural history ensures strong partner fidelity between maternal lines of ants and their domesticated fungi and should result in matching co-phylogenies between ant hosts and their fungal symbionts. In fact, vertical transmission and dispersal of fungi by the ants might have been the starting point of this mutualism: this "dispersal first" hypothesis predicts that the interaction originated from ants consuming a fungus that already used them as dispersal vectors (MUELLER & al. 2001).

However, several phylogenetic and population genetic studies showed signatures of frequent lateral transfer of fungi between colonies (horizontal transmission) in both lower attines and higher attines (MUELLER & al. 1998, GREEN & al. 2002, MIKHEYEV & al. 2007). In addition, the fungus of *Atta* species occurring in the northern range limit of the genus was shown to be capable of independent long-distance dispersal (MUELLER & al. 2011b). On the other hand, the matching co-phylogenies between attine ants and their fungal crops, have been mostly attributed to long-term vertical transmission. This is clearly exemplified by the phylogeny of fungi cultivated by *Cyphomyrmex* ants, which shows strong partner fidelity over millions of years with ant speciation events linked to rare cultivar switches (MEHDIABADI & al. 2012).

What are the mechanisms behind occasional cultivar exchanges? Cultivar switches can happen either indirectly, when ants domesticate a fungus that previously escaped another garden to resume its free-living form (MUELLER & al. 1998, VO & al. 2009, MUELLER & al. 2011b) or directly, when ant colonies steal gardens from neighbouring colonies (MUELLER 2002). Indeed, colonies adopt an alien fungus as their new resident fungus when deprived of their own garden, either when allowed to steal the garden of their neighbours (ADAMS & al. 2000) or when force-fed experimentally (e.g., BOT & al. 2001, VIANA & al. 2001, IVENS & al. 2009, POULSEN & al. 2009). The ability and readiness to adopt a new fungal crop differs between incipient and mature colonies, with incipient colonies more readily accepting another fungus (BOT & al. 2001, IVENS & al. 2009, POULSEN & al. 2009). This response is attributed to "garden-reinforcement" (see details below in the section on symbiont diversity), in which the ants imprint on their fungal strain by feeding on it during the first three to four weeks of colony existence (POULSEN & al. 2009). Considerable fitness costs for both fungus and ants are involved with cultivar switching, such as delayed development of incipient colonies and lower garden biomass, smaller colony size and lower reproductive output in mature colonies (MEHDIABADI 2005, POULSEN & al. 2009). These fitness costs are likely caused by ant-fungal mismatching: For example, the ants' physiology may be adapted to another symbiont, leading to inhibited larval growth when fed on "sub-optimal" fungi. Likewise the ants' foraging strategy and system of garden hygiene, including the specialized "pesticides" the ants and their mutualistic bacteria produce, may function sub-optimally when paired with a novel fungus (CURRIE 2001, SEAL & TSCHINKEL 2007, SEAL & MUELLER 2014). These findings indicate co-adaptation between original ant-fungus pairs, constraining the potential of frequent exchange.

Who is in control of fungal transmission and exchange? At first glance, one would assume the ants to be in con-

trol, since they can (and do) decide which fungus enters the garden and decide which fungus is vertically transmitted. However, the fungus may possess manipulative powers that can coerce ants into dispersing it or in rejecting intruding fungi (see below) (MUELLER 2002). And while the ants may actively suppress fungal escape (and horizontal transmission) by destroying emerging fruiting bodies, the fungus is likely in control of the timing of escape and with ant control unlikely to be 100% effective, may occasionally succeed.

Symbiont diversity

The fungi are likely grown in monocultures, following from three natural history specifics of attine fungus growing: First, the fungus garden is started by the foundress with a single inoculum, second, since most species are monogynous, there will be no competing inoculi in the garden and third, the fungus is subsequentially clonally propagated within the garden (MEHDIABADI & SCHULTZ 2010, MUELLER & al. 2010). Genetic monocultures were confirmed in the gardens of *Acromyrmex* and *Atta*, even stably over multiple years (POULSEN & BOOMSMA 2005, MUELLER & al. 2010). However, SEN & al. (2010) reported rare cases of polycultures in gardens of laboratory colonies of *Atta texana* (BUCKLEY, 1860), which had been offered multiple potential cultivars. The ant-fungus pairs used in this experiment were collected in the Northern range limit of ant fungus-growing. Elsewhere, these Northern fungal populations have been shown to exhibit less variation and recombination; I hypothesise here that this lower population variability in the fungi may have also led to the ants' discriminatory ability to be less effective, leading to polycultures instead of exclusive monocultures (SEN & al. 2010, MUELLER & al. 2011b).

Monocultures of fungus gardens are upheld by a mechanism of threefold incompatibility between the resident mutualist pair and intruding fungi: Direct ant-fungus incompatibility, direct fungus-fungus incompatibility (chemical warfare between genetically different Basidiomycete fungi growing in close proximity of each other) and indirect fungus-fungus incompatibility via the ant workers (WORRALL 1997, BOT & al. 2001, POULSEN & BOOMSMA 2005). Ants manure their garden with so-called "fecal droplets" (WEBER 1972, BOT & al. 2001, POULSEN & BOOMSMA 2005, SCHIØTT & al. 2010), which contain fungus-derived compounds, such as enzymes and, presumably, incompatibility compounds (RØNHEDE & al. 2004, POULSEN & BOOMSMA 2005, SCHIØTT & al. 2010, DE FINE LICHT & al. 2013). Higher attines ingest these compounds when harvesting the gongylidia, but do not digest them (SCHIØTT & al. 2010, DE FINE LICHT & al. 2013). Via these presumed incompatibility compounds in the fecal droplets the fungus prevents entering alien fungi from establishing (WORRALL 1997, BOT & al. 2001, POULSEN & BOOMSMA 2005). As expected, incompatibility through "manure imprinting" is transient: After ten days of force-feeding mature *Acromyrmex* colonies will accept a new fungus as their resident fungus (BOT & al. 2001, POULSEN & BOOMSMA 2005) and *Atta* colonies can be made to accept fungi by "purging" them on a non-fungus diet prior to the experiment (SEN & al. 2010).

Does the fungal control on garden diversity leave the ants with no say in the matter? Attine ants have displayed discriminatory ability between fungi repeatedly. Not only do they distinguish between their own and resident fungi (see above), *Cyphomyrmex* and leaf-cutter ant *Atta texana* also showed clear preferences in café style partner choice experiments, although *Atta* chose to combine several fungi into one garden (ADVANI & MUELLER 2006, SEN & al. 2010). Ants most likely exert partner choice based on the fungal hydrocarbon profile, which has been shown to be partly heritable and partly environmental (e.g., via diet dependent or brood) (VIANA & al. 2001, RICHARD & al. 2007).

Other examples

Fungiculture is not restricted to attine ants. Other ants, however, do not culture their fungus directly for food: *Lasius* and *Azteca* ants culture fungus in their nest for structural purposes (SCHLICK-STEINER & al. 2008, MAYER & VOGLMAYR 2009) and *Allomerus* plant-ants use their fungus for prey-capture (DEJEAN & al. 2005, RUIZ-GONZALEZ & al. 2011) as well as nutrient recycling. The latter behaviour was also observed for plant-ant *Petalomyrmex phylax* SNELLING, 1979 (DEFOSSEZ & al. 2011, LEROY & al. 2011). Because direct consumption of the fungus by the ants has not been recorded in these cases, they are not strictly considered examples of "farming" (HATA & al. 2010, PION & al. 2013, but see LAUTH & al. 2011), although, for example, *P. phylax* displays all behaviours commonly associated with "cultivation" such as feeding of the fungus, and its protection and transport (DEFOSSEZ & al. 2009, 2011).

Nevertheless, interesting parallels on the symbiont characteristics reviewed here can be observed between these cases of ant fungiculture and the attine fungus growing. For example, the fungus cultured by *Petalomyrmex phylax* presumably reproduces asexually; fruiting bodies have not been found (DEFOSSEZ & al. 2009). In addition, *Lasius* transmits some of its fungi vertically (SCHLICK-STEINER & al. 2008) and the fungus of *Allomerus* ants grows in monocultures (RUIZ-GONZALEZ & al. 2011). These parallels indicate that, although these fungi are not cultured for food, these systems might be subject to similar evolutionary host-symbiont dynamics.

Homoptera-tending ants
Evolution and biology

Tending of Homoptera (specifically aphids and scale insects, now formally included in the Sternorrhyncha; MCGAVIN 1993) by ants is wide-spread in nature (WAY 1963, STADLER & DIXON 2005, 2008). Ants feed on honeydew excreted by the Homoptera, which feed on host plants or trees. These interactions are increasingly recognised to be of major ecological and economic importance, especially when the ants or Homoptera are invasive species or affect crop plants (DELABIE 2001, BUCKLEY 1987, NESS & BRONSTEIN 2004, STYRSKY & EUBANKS 2007, HELMS 2013, ROSS & SHUKER 2009).

Aphid-tending behaviour occurs throughout the ant phylogeny, but most tending species can be found in the subfamilies Formicinae, Dolichoderinae and Myrmicinae, suggesting multiple gains and losses (HÖLLDOBLER & WILSON 1990, DELABIE 2001, MOREAU & al. 2006, OLIVER & al. 2008). About 1000 of the 4000 known aphid species (Aphididae) are tended by ants (i.e., myrmecophilous) (BRISTOW 1991, STADLER & DIXON 2005). Ant-aphid in-

teractions are generally considered textbook examples of mutualism; both ants and aphids presumably profit from the interactions. However, the relatively restricted occurrence of these interactions suggests that ant-aphid mutualism is not "all roses" and that the benefits may not outweigh the costs in all circumstances, rendering these associations evolutionarily unstable (BUCKLEY 1987, BRISTOW 1991, STADLER & DIXON 1999, SHINGLETON & STERN 2003, STADLER & al. 2003, STADLER & DIXON 2005, YAO 2014).

Of the 32 families of scale insects known, the soft scales (Coccidae) and mealybugs (Pseudococcidae) are best known for being tended by ants. Myrmecophilous species are also found among the hard scale insects (Stictococcidae, which are obligate myrmecophiles) and armoured scales (Diaspididae) (DELABIE 2001, STADLER & DIXON 2008, ROSS & SHUKER 2009). The interactions studied in most detail include the highly specialised, mutually obligate, association of *Acropyga* sp. ants with xenococcine mealybugs (SCHNEIDER & LAPOLLA 2011), Asian *Dolichoderus* "herdsmen" ants tending mealybugs and other scale insects (MASCHWITZ & HÄNEL 1985) as well as weaver ants *Oecophylla longinoda* (LATREILLE, 1802) and *O. smaragdina* (FABRICIUS, 1775) and Argentine ant *Linepithema humile* (MAYR, 1868) tending scale insects (WAY 1963, BACH 1991).

The earliest fossil records of aphid-tending by ants date its evolution back to 23 - 38 mya (HÖLLDOBLER & WILSON 1990). The oldest fossils of *Acropyga* sp. ants carrying their mealybugs stem suggest that ant-scale insect interactions evolved at least 15 - 20 mya (JOHNSON & al. 2001, LAPOLLA 2005). With fungus-farming dated back to 50 mya, ants were thus likely farmers before herders (but see LAPOLLA & al. 2006).

Many research efforts have sought to qualify and quantify costs and benefits of ant-Homoptera interactions. For the ants, Homoptera serve as important resources: The honeydew they excrete provides both carbohydrates and amino acids (WAY 1963, BUCKLEY 1987). In addition to milking them, ants prey on their aphids, thereby obtaining additional protein (PONTIN 1958, 1961, WAY 1963, SMART 1991, SAKATA 1994, OFFENBERG 2001). The interaction between armoured scale insects and *Melissotarsus* ants is the only known exclusively meat-based ant-Homoptera interaction: These scale insects do not feed on plant phloem sap and therefore do not produce honeydew (BEN-DOV & FISCHER 2010, SCHNEIDER & al. 2013). Yet, their tending ants likely depend on them for food: The armoured scales make up the majority of the possible prey inside the ants' galleries, and the ants' stunted legs prevent them from foraging outside of their galleries (BEN-DOV & FISCHER 2010, SCHNEIDER & al. 2013). Having a continuous food source nearby also likely allows Homoptera-tending ants to reach high densities, inhabit otherwise poor habitats and possibly invade new habitats (WAY 1963, BUCKLEY 1987, SEIFERT 2007, STADLER & DIXON 2008, IVENS & al. 2012a, HELMS 2013). Costs of Homoptera tending for ants remain unknown, although the observed shift from milking to preying on their aphid herd when "easier" sugar sources are provided, suggests the ants experience costs of active tending (OFFENBERG 2001).

The cost-benefit ratio of being ant-tended is less clear-cut for the Homoptera. The benefits are well-established: Ants provide their herds with active protection from predators and parasites (EL-ZIADY & KENNEDY 1956, ZWÖLFER 1958, PONTIN 1959, BARTLETT 1961, WAY 1963, PAUL 1977, HILL & BLACKMORE 1980, BUCKLEY 1987, BACH 1991, STADLER & DIXON 1999, BILLICK & al. 2007, NIELSEN & al. 2010) and provide sanitation by removing excess honeydew (EL-ZIADY & KENNEDY 1956, BANKS & NIXON 1958, ZWÖLFER 1958, WAY 1963, PAUL 1977, HILL & BLACKMORE 1980, BACH 1991). Often, the ants also provide their herds with protective sheltering or underground chambers (ZWÖLFER 1958, WAY 1963, MASCHWITZ & HÄNEL 1985, SEIBERT 1992) as well as brood care (WAY 1963, PONTIN 1978, MATSUURA & YASHIRO 2006) and dispersal to host plants (WAY 1963). This active tending behaviour by ants, along with the ants' ability to limit Homopteran dispersal (see below), causes colonies of tended Homoptera to be often larger than untended colonies (EL-ZIADY & KENNEDY 1956, WAY 1963, ADDICOTT 1979, STADLER & DIXON 2005, 2008). In fact, scale insects might only be prone to sooty molds at the densities reached when ant-attended; the ants thus indirectly create the need for scale insects to be cleaned by them (WAY 1963).

Tended aphids, however, can also incur costs of ant-attendance as exemplified by restricted reproduction and dispersal rates (WAY 1963, BUCKLEY 1987, STADLER & DIXON 1998, 1999, YAO & al. 2000, STADLER & DIXON 2005). These costs may stem from a trade-off between investment in life history traits and increased honeydew production. Indeed, when tended, aphids increase their feeding rate as well as the quantity and composition of their honeydew (BANKS & NIXON 1958, YAO & AKIMOTO 2001). Determining the costs and benefits of ant-attendance has thus not been straightforward and can be context-dependent (ADDICOTT 1979, STADLER & DIXON 1999, YOO & HOLWAY 2011) as well as transient over consecutive generations (TEGELAAR & al. 2013).

Possibly resulting from these diffuse selection pressures of costs and benefits associated with ant-attendance, observed specificity in ant-Homoptera associations is moderate at best, with the highest levels of specificity observed in tropical ant-scale insect interactions (WAY 1963). Most myrmecophilous Homoptera can be associated with multiple species of ants and vice versa (WAY 1963, STADLER & DIXON 2005); the same scale insect aggregations can even be tended by several ant species in succession or during different times of the day (HILL & BLACKMORE 1980), although the aggregations have a higher fitness when tended by their "primary" host ant species (EASTWOOD 2004). One-to-one evolution is thus unlikely in these systems (SHINGLETON & STERN 2003). In line with this, aphids can be both obligately or facultatively myrmecophilous and also ant species differ in whether they are solely dependent on aphids for food or not (STADLER & al. 2003, STADLER & DIXON 2005). Obligate interactions, nevertheless, do exist. Both the interactions of the herdsmen ants and *Acropyga* ants and their mealybugs are assumed to be mutually obligate and also *Melissotarsus* are considered obligate coccidophiles; likewise are both ant *Lasius flavus* (FABRICIUS, 1782) and some of its root aphids presumably obligately associated (FLANDERS 1957, PONTIN 1958, 1959, 1961, WAY 1963, PAUL 1977, PONTIN 1978, HEIE 1980, MASCHWITZ & HÄNEL 1985, SMART 1991, LAPOLLA & al. 2002, SEIFERT 2007, SCHNEIDER & LAPOLLA 2011, SCHNEIDER & al. 2013).

Despite this assumed diffuse co-evolution, morphological and behavioural adaptations to a lifestyle together exist in both ants and Homoptera. The most conspicuous morphological adaptation to myrmecophily in aphids is the "trophobiotic organ", an array of long hairs in the anal region that can hold a droplet of honeydew for ants to "harvest" (ZWÖLFER 1958, WAY 1963, HÖLLDOBLER & WILSON 1990). Myrmecophilous scale insects have a similar structure as well as other adaptations, such as modified respiration in Myzolecaniinae (WAY 1963, GULLAN & KOSZTARAB 1997, DELABIE 2001). In addition, myrmecophilous aphids tend to have morphological traits correlated with a protected environment: shorter cornicles (which otherwise produce protective wax), shorter legs and a longer rostrum (which takes longer to retract). Although these latter traits are widely cited as adaptations to myrmecophily, BRISTOW's (1991) comparative analysis showed that these traits may have been pre-existing; pre-disposing now-myrmecophilous species to associations with ants. This hypothesis was later confirmed in a comparative analysis of mouthpart lengths in *Chaitoporus* (see SHINGLETON & al. 2005). Also obligate myrmecophilous Pseudococcidae have shorter legs and are consequently more sessile than facultatively ant-tended species (WAY 1963). Perhaps the most striking adaptation to myrmecophily is observed in mealybug *Hippeococcus*, which lost its bacterial endosymbiont responsible for assimilation of essential nutrients and became dependent on being fed by *Dolichoderus* ants for nutrient acquisition (ROSS & SHUKER 2009).

The ants mostly show behavioural adaptations to Homoptera-tending, apart from presumed morphological adaptations in the subfamilies Formicinae and Dolichoderinae to their proventriculus and gaster, which allow large quantities of honeydew or nectar to be passed around within colonies (STADLER & DIXON 2005, OLIVER & al. 2008). Ants actively protect, tend and clean their herds – behaviours that likely originate from brood care behaviour (EL-ZIADY & KENNEDY 1956, WAY 1963, YAO & al. 2000, STADLER & DIXON 2005, 2008). Ant defensive behaviours towards predators and parasites are quite specialised, with conserved stereotypical components (NAULT & al. 1976, MONDOR & ADDICOTT 2007). For example, the alarm pheromone of native aphid species can elicit protective behaviour from locally invasive Argentine ants (MONDOR & ADDICOTT 2007).

Symbiont reproduction

Aphids can reproduce both sexually and asexually, with many species being "holocyclic" (multiple generations of asexual reproduction followed by a sexual generation), although also "anholocyclic" (exclusive asexual reproduction) species or populations occur (SIMON & al. 2002). Alates (winged aphids) are typically produced to facilitate an obligate host plant shift for sexual reproduction, but also viviparous dispersers can occur in species without shift hosts (MÜLLER & al. 2001). Also scale insects can reproduce both sexually and asexually, with a high incidence of the latter (GULLAN & KOSZTARAB 1997, ROSS & SHUKER 2009). Scale insects never require an obligate host plant shift for sexual reproduction. The occurrence of different reproductive strategies indicates that there is scope for conflict over Homopteran investment into reproduction. This potential conflict could not only concern the Homopteran mode of reproduction, but also the rate at which they reproduce (both in terms of number of reproductive cycles and the number of offspring produced during each cycle).

Concerning the mode of reproduction: Most above-ground myrmecophilous aphids are presumably holocyclic (HEIE 1980). This was confirmed by population genetic studies of the above-ground, facultative myrmecophilous black bean aphid *Aphis fabae* (SCOPOLI, 1763), which is tended by *Lasius niger* (LINNEAUS, 1758) (VANTAUX & al. 2011a) and several species of *Tuberculatus* aphids, which are tended by *Formica* ants (SEIBERT 1992, YAO & AKIMOTO 2009, YAO 2010). In contrast, presumably obligately myrmecophilous root aphids, which occur in nests of subterranean ant *L. flavus*, showed predominant, if not exclusive, asexual reproduction (IVENS & al. 2012b).

Little is known about the potential relationship between the mode of reproduction and myrmecophily in scale insects. Only the mealybug *Paraputo anomala* (NEWSTEAD, 1910), which is presumably vertically transmitted by its host ant *Aphomomyrmex afer* EMERY, 1899 is known to be exclusively parthenogenetic (GAUME & al. 2000). Two more ant-tended scale insects are presumably parthenogenetic: *Malaicoccus* sp. mealybugs reproduce viviparously inside nests of their *Dolichoderus* host ants and males of these scale insects have never been observed (MASCHWITZ & HÄNEL 1985). Likewise, armoured scale insects reproduce inside their host ant's galleries (BEN-DOV & FISCHER 2010). However, *Acropyga* ant gynes have been observed to carry gravid, oviparous scale insect females on their mating flights (LAPOLLA & SPEARMAN 2007, SCHNEIDER & LAPOLLA 2011) and of one of their mealybugs *Xenococcus annandalei* (SILVESTRI, 1924), males have been described (GULLAN & KOSZTARAB 1997), suggesting that these mealybugs maintained sexual reproduction.

Tended aphid populations display altered reproductive rates. Often, these rates are increased as was, for example, shown for *Aphis fabae* when tended by *Lasius niger* and for cotton aphid *A. gossypii* (GLOVER, 1877) when tended by Argentine ants (EL-ZIADY & KENNEDY 1956, MONDOR & al. 2008). Also preference studies of aphid attendance by *L. niger* showed increased reproductive rates in the preferred species *Metopeurum fuscoviride* (STROYAN, 1950), as well as prolonged colony survival until the time sexuals were produced. Interestingly, ant preference studies showed that sexually reproducing aphids were only observed in colonies of the preferred aphid species and never in other, less-preferred, species (FLATT & WEISSER 2000, FISCHER & al. 2001). Several studies indicate that also in scale insects reproductive rates and densities increase under ant-attendance, most likely resulting from the ants' protective services (BARTLETT 1961, WAY 1963, BACH 1991).

Decreased reproductive rates in tended aphids, however, are also frequently observed and are considered a major cost of ant-attendance (YAO & al. 2000, STADLER & DIXON 2005, 2008). Although colonies of *Tuberculatus quercicola* (MATSUMURA, 1917), are longer lived when attended by *Formica yessensis* WHEELER, 1913, they produce fewer embryos (YAO & al. 2000). Likewise, STADLER & DIXON (1998) showed lower reproductive rates in the *L. niger*-tended aphid *Aphis fabae cirsiiacanthoides*

(SCOPOLI, 1763), associated with prolonged developmental time, smaller gonads and fewer well-developed embryos. TEGELAAR & al. (2013), showed that this lowered reproductive output was caused by the aphids producing smaller embryos when ant-attended. Interestingly, this effect was transient and later generations displayed normal reproductive rates.

What mechanisms cause these changes in reproductive mode and rates associated with ant-attendance? Ants could potentially control aphid sexual reproduction in species with an obligate host plant shift by selectively preying on alate aphids or otherwise delaying dispersal (see below). Indeed, it has been hypothesised that tended aphids evolved to become monoecious (i.e., lose their obligate host shift), possibly in response to ants clipping wings of alate aphids (WAY 1963). Indirectly, by keeping aphid colony sizes at bay through preying, ants prevent crowding, which is commonly known to induce sexual reproduction and alate production (HALES & al. 1997). Also *Oecophylla* and *Acropyga* actively regulate the numbers of their tended scale insects; the latter do this by placing their mealybugs alternately on productive roots (FLANDERS 1957, WAY 1963). Likewise, the exclusive asexual reproduction in some root aphids tended by *Lasius flavus* could be induced by the constant, subterranean environments created by the ants, which do not allow sex-inducing cues such as photoperiod or temperature to reach critical threshold levels (MORAN 1992, HALES & al. 1997, RISPE & al. 1998, SIMON & al. 2002). Also physiological trade-offs due to increased feeding rates in response to ant-attendance may lead to reduced reproductive rates (BANKS & NIXON 1958). This effect does not need to be ant-controlled: the results on trans-generational effects of ant-attendance on *Aphis fabae*, show that aphids may be in control over their own reproductive investment, responding to increased partner fidelity by investing into, for example, honeydew production rather than offspring production.

Symbiont transmission and dispersal

Also here, I consider both the mode of transmission and, for horizontal transmission, the frequency of transmission and dispersal.

Vertical transmission of Homoptera has only been observed for scale insects and never for aphids (WAY 1963, HÖLLDOBLER & WILSON 1990, DELABIE 2001, LAPOLLA 2005, STADLER & DIXON 2008). In two independently evolved cases, gynes bring scale insects in their mouth on their mating flight (termed "trophophoresy" (LAPOLLA & al. 2002, LAPOLLA 2005). *Tetraponera binghami* (FOREL, 1902) ants bring crawlers (the dispersing stage of scale insects) on their mating flight. These crawlers may, however, be taken from the ants' natal or a neighbouring nest (KLEIN & al. 1992, WARD 2001); a population genetic study on both the ants and their mealybugs would be needed to show whether this is a true case of vertical transmission from generation to generation. The best-known case of ant-scale insect vertical transmission is that of *Acropyga* ants and their xenococcine mealybugs, with 12 of the ~ 30 *Acropyga* species having been confirmed to carry mealybugs on their mating flights (Fig. 2c) (FLANDERS 1957, HÖLLDOBLER & WILSON 1990, SCHNEIDER & LAPOLLA 2011). This is an ancient example of vertical transmission with fossils showing alate *Acropyga* queens carrying mealybugs (JOHNSON & al. 2001, LAPOLLA 2005) and a molecular cophylogeny of these species could possibly elucidate the coevolutionary history, much like has been done for attine ants and their fungus (e.g., MUELLER & al. 1998). A third, putative, case of vertical transmission is that of ant *Aphomomyrmex* with mealybug *Paraputo anomala*. In the field, many founding queens are already associated with mealybugs (even sometimes attached to a queen) before production of their first brood (GAUME & al. 2000). Since *P. anomala* is parthenogenetic, this would be the only example of ant-Homoptera farming in which the symbiont is both vertically transmitted and clonally reproducing, making the system directly comparable to higher attine fungus-farming (GAUME & al. 2000). Interestingly, *A. afer* also farms another coccid species, which presumably transmits horizontally between ant nests (GAUME & al. 2000). Lastly, also *Melissotarsus* presumably play a role in colony founding of their armoured scale insects, but the exact transmission mechanism remains unknown to date (BEN-DOV & FISCHER 2010, SCHNEIDER & al. 2013).

The case closest to vertical transmission observed in aphid-tending ants is that of new nests of ant *Formica yennensis*, which start by budding from their maternal colony and continue to tend their natal colonies of *Tuberculatus quercicola* aphids (YAO & AKIMOTO 2009). Since these aphids are holocyclic and also produce alates, this cannot be considered a true case of vertical transmission in which new generations of both mutualistic partners co-disperse. Yet, a mechanism like this causes the same host-symbiont combination to be "reproduced" in multiple colonies. Similarly, mealybugs climb on the back of *Dolichoderus* herdsmen ants when they start a new colony by fission (MASCHWITZ & HÄNEL 1985, JOHNSON & al. 2001). These ants also give their mealybugs a ride when there is imminent danger, or when relocating the colonies once resources at the current location are depleted (MASCHWITZ & HÄNEL 1985). Also other ants, such as *Oecophylla*, *Pheidole*, *Tetraponera* and *Linepithema*, have been shown to actively disperse their scale insect herds to feeding locations or newly built nests (KLEIN & al. 1992, DELABIE 2001, SACCHETT & al. 2009).

Even though aphids horizontally transmit to their ant hosts, dispersal frequencies in ant-tended aphids are significantly reduced. Population genetic signatures of restricted dispersal have been shown for tended *Tuberculatus* aphids (YAO & AKIMOTO 2009, YAO 2010, YAO & KANBE 2012) and four species of ant-tended root aphids (IVENS & al. 2012b). Likewise VANTAUX & al. (2011a) found a population of *Aphis fabae* tended by *Lasius niger* to be highly structured, although genetic differentiation between the aphid subcolonies was not statistically affected by ant-attendance. Indeed, ant-attended aphids commonly have low numbers of alates (EL-ZIADY & KENNEDY 1956, JOHNSON 1959, WAY 1963, KLEINJAN & MITTLER 1975, MÜLLER & al. 2001, YAO 2010, TEGELAAR & al. 2011, IVENS & al. 2012b, TEGELAAR & LEIMAR 2014, but see STADLER & DIXON 1999), although at least some of these aphids have similar levels of alates and dispersal as their non-attended counterparts later in the season, albeit significantly delayed (EL-ZIADY & KENNEDY 1956, KINDLMANN & al. 2007). Delayed dispersal poses an additional cost of ant attendance for these aphids when competing with non-attended species for the same host plants (KINDLMANN & al. 2007).

The reduced levels of dispersal in ant-tended aphids are likely ant-mediated. Ants have several ways of suppressing the numbers of alates developing in their Homopteran herds. First, by population regulation through culling ants control aphid densities and thereby prevent crowding, an important inducer of wing development (WAY 1963, HALES & al. 1997, MÜLLER & al. 2001). Second, ants can suppress aphid dispersal directly by biting off wings of alate aphids, which has been reported for *Lasius* sp. and its root aphids (ZWÖLFER 1958). Third, ants can chemically suppress aphid dispersal. Ant secreted semiochemicals tranquilize aphids, thereby inhibiting dispersal through walking (OLIVER & al. 2007) as well as reducing the aphids' capability to perceive tactile contact, and thus, crowding. Aphids also respond less strongly to their alarm pheromones when ants are around (NAULT & al. 1976). Lastly, ants can chemically inhibit aphid wing development as was shown for secretions from the mandibular glands of ant *Formica fusca* LINNAEUS, 1758 (KLEINJAN & MITTLER 1975). Although ants could potentially constrain scale insect dispersal via preferential preying on crawlers, no records of this exist. In fact, BACH (1991) observed higher numbers of crawlers in ant-tended scale insects. No studies have tested any other mechanisms of dispersal inhibition, such as through semiochemicals.

Apart from ant-mediated reduction in aphid dispersal, myrmecophilous aphid species may actually have been predisposed for myrmecophily by their overall lower levels of mobility and lower numbers of alates (STADLER & al. 2003). Likewise can the observed lower levels of dispersal and flight muscle development in ant-tended *Tuberculatus* species be interpreted as both an adaptation to ant attendance or a predisposition (YAO 2010, YAO & KATAGIRI 2011).

Symbiont diversity

Single ant colonies can simultaneously tend multiple species of aphids (PONTIN 1978, GODSKE 1991, FISCHER & al. 2001, IVENS & al. 2012a). However, mixed aphid colonies, with multiple species on a single stem or in a single aphid chamber are rare (MUIR 1959, GODSKE 1991, FISCHER & al. 2001, IVENS & al. 2012a). Are these ant-tended colonies also genetic monocultures, with only a single clone per species? Indeed, IVENS & al. (2012a) found aphid chambers in subterranean *Lasius flavus* nests to be almost exclusively inhabited by single clones. Also VANTAUX & al. (2011a) observed that at least one third of the colonies of facultatively ant-attended, free-living aphid *Aphis fabae* were genetic monocultures and mixed colonies harbored only two to four clones. Colony-level diversity increased over time, following settlement of new clones. This contrasted findings on *Tuberculatus* aphid colonies, in which diversity erodes over time (YAO & AKIMOTO 2009). Ant-attended *Tuberculatus* colonies also harbor less genetic diversity than colonies of non-attended *Tuberculatus* (YAO 2010). However, more of such comparative evidence would be needed to verify that within-species clonal diversity in ant-tended aphid colonies is indeed even lower than the low to intermediate diversity generally observed in aphid colonies (reviewed in ABBOT 2011).

Little is known about the diversity of scale insect herds. Ant *Aphomomyrmex afer* is found associated with two species of scale insects. Most *A. afer* colonies are only associated with one at a time (GAUME & al. 2000). Likewise, herdsmen ants typically tend a single species, and when additional mealybugs or coccids are found in the colonies these receive less attention from the ants, suggesting discriminatory ability in the ants (MASCHWITZ & HÄNEL 1985). In the galleries of *Melissotarsus* many organisms can be found simultaneously, but the mutualistic armoured scales are most abundant (SCHNEIDER & al. 2013). The genetic diversity of single-species scale insect herds has never been assessed; this would be a promising avenue for future research.

Does the observed low level of diversity among aphid "livestock" stem from active partner choice by the ants or does it simply result from aphid clonal reproduction in combination with low levels of dispersal? There is theoretical potential for ants to exert partner choice in ant-Homoptera mutualisms. Quality differences, in terms of honeydew quantity and composition, do indeed exist both among aphid species (VÖLKL & al. 1999, FISCHER & al. 2001) and clones of the same species (VANTAUX & al. 2011b) as well as between scale insects (EWART & METCALF 1956). Aboveground ants indeed display discriminatory ability between aphids with different honeydew composition; most notably do ants prefer aphid species excreting melezitose-rich honeydew (KISS 1981, VÖLKL & al. 1999, WOODRING & al. 2004), although ants do not discriminate between clones with differing melezitose excretion (VANTAUX & al. 2012). Interestingly, Homoptera may not be in full control over honeydew composition: Their bacterial endosymbionts (such as *Buchnera* in aphids) likely influence it (DOUGLAS 1998b, HANSEN & MORAN 2011, YAO 2014). Ants do even show discriminatory ability beyond honeydew: *Lasius niger* ants are able to recognise aphids that were previously tended by nest mates as well as aphids that gave honeydew before; and will choose not to prey on them (SAKATA 1994); Fire ant *Solenopsis invicta* BUREN, 1972 is able to discriminate between healthy and parasitised aphids (VINSON & SCARBOROUGH 1991). In another choice experiment, however, *L. flavus* did not spend more time with its own aphids than with aphids from neighbouring colonies (IVENS & al. 2012c). These discriminatory choices may well be based on cuticular hydrocarbons (CHC) transferred from ants to aphids during tending, similar to the mechanism observed in fungal recognition by fungus-growing ants. Indeed, *L. niger* is able to discriminate between myrmecophilous and non-myrmecophilous aphids based on their CHC (LANG & MENZEL 2011). Also *L. fuji* RADCHENKO, 2005 ants tend to be less aggressive towards aphid dummies with which they share CHC and *Stomaphis yanonis* (TAKAHASHI, 1960) aphids mimic these ants' CHC, presumably to prevent being preyed upon (ENDO & ITINO 2012, 2013).

Discussion

Ant farming systems are good candidate systems for the study of host-symbiont conflicts in mutualisms. Here, I reviewed which outcomes are observed with regard to three potential arenas of conflict (Reproduction: sexual or asexual reproduction; Transmission: vertical or horizontal transmission; Diversity: monoculture or polyculture; Tab. 1, Fig. 1) in three systems of ant farming: fungus-growing attine ants, aphid-tending ants and scale insect-tending ants. Generally, in all three biological systems both outcomes theorised for each arena occur, with two exceptions: poly-

Tab. 2: Observed symbiont traits, their underlying mechanisms and observed control of symbiont traits by the host ants or the symbionts themselves in the three reviewed systems of ant-farming: Fungus-growing ants, aphid-tending ants, and scale insect-tending ants (both "Homoptera"-tending). Underlined traits are most commonly found.

System		Arena of conflict	Observed symbiont trait	Underlying mechanism	Observed control in partners	
					Host	Symbiont
Fungus-growing ants	Attine ants	Symbiont reproduction	Asexual	Vegetative inoculation by ants	– Performs inoculation – Suppresses fruiting bodies (directly and indirectly)	Suppresses chance of hyphal fusion by enforcing monoculture
			Sexual	– Fruiting bodies – hyphal fusion	–	Can develop fruiting bodies
		Symbiont transmission	Vertical	Vegetatively via ants	Chooses which fungus to disperse	Controls its own transmission by enforcing monoculture
			Horizontal	– Free-living fungus, escape – Garden stealing by ants	– Suppression fruiting bodies – Choice to steal / accept new fungus	– Formation of fruiting bodies – Ant imprinting on fungus prevents horizontal transmission
		Symbiont diversity	Monoculture	Threefold resident-alien fungus incompatibility	Imprinting in ants	Direct and indirect incompatibility enforces monoculture
			Polyculture	–	–	–
Homoptera-tending ants	Aphid-tending ants	Symbiont reproduction	Asexual, reduced reproductive rates	Low numbers of alates, reduced reproductive development	– Provision of constant subterranean environment – Direct (chemical, physical) and indirect (aphid colony size control) suppression of alates	Increased investment into feeding and honeydew production
			Sexual, increased reproductive rates	Obligately holocyclic, increased aphid colony sizes	Large colony sizes following protection	Alate and oviparae development
		Symbiont transmission / dispersal	Limited dispersal rates	Ant-mediated reduction in alates and mobility	– Physical and chemical reduction of mobility – Indirect reduction in alate numbers – Protective environment reduces incentive to disperse	Reduced investment into alate production
			Horizontal transmission	Independent dispersal by aphids, acceptance by ants	Limited partner choice in ants	Dispersal by aphids
		Symbiont diversity	Frequent, but not exclusive monocultures	Repeated clonal reproduction, reduced dispersal in combination with occasional settlement	Potential partner choice in ants	Clonal reproduction combined with reduced dispersal
	Scale insect-tending ants	Symbiont reproduction	Asexual reproduction, Sexual reproduction	Influencing mechanisms unknown	NA	NA
			Increased reproductive rates	Increased fecundity through protection	– Protective services – Population regulation (selective preying, selective root access)	–
		Symbiont dispersal	Vertical transmission	Trophophoresy, back-riding by scale insects, budding	Choice who to bring	Choice to disperse with ant
			Horizontal transmission	Colony acceptance for tending by ants	NA	NA
		Symbiont diversity	Species-level polyculture	Mechanisms unknown	NA	NA

culture fungus gardens and vertical transmission of aphids by ants have both never been observed in the field (Tab. 2).

Protective environments

Strikingly, both in systems of fungus-growing and Homoptera-tending, there are examples of ants creating an environmentally constant, protective environment for their herds or crops. Usually, these enclosed galleries occur inside the ant nests and they are often subterranean. Previously, creation of such predictable environments has been predicted to promote the evolution of mutualism (LAW & LEWIS 1983, LAW 1985), because those circumstances no longer call for symbiont sexual reproduction and horizontal transmission, two features that usually allow organisms to deal with fluctuating environments. Consequently, host-symbiont associations would no longer be dissolved as frequently, resulting in improved alignment between the partners. Therefore, I hypothesise here that these frequently observed ant behaviours of building protective chambers may have played an important role in the evolution of the farming systems we observe to date and may be an essential part of the success of these systems.

Reevaluating host control

Historically, host-symbiont conflict resolutions have often been attributed to host control (FRANK 1996a, HERRE & al. 1999, MUELLER 2002). This means that it would be expected that the observed symbiont traits result mainly from mechanisms of ant control over their crops and herds. However, in most of the cases reviewed above, the observed symbiont traits are controlled by both host and symbiont, suggesting that in those arenas, interests are now largely aligned, possibly as a result of long-term co-evolution (Tab. 2). Nevertheless, traditionally, experimental studies on ant farming systems tend to be ant-biased. To be able to assess the full extent of symbiont-control, in particular for the two ant-Homoptera systems, future studies of, for example, partner choice should ideally test the existence of symbiont preferences as well.

Ant farming as study system for mutualism

Here, I reviewed examples of ant farming in the context of mutualism evolution, with mutualism defined as an interaction between different species, with net benefits for both. However, although the interacting species clearly receive benefits, can we be sure these are always net benefits? In that case, the costs of being completely dependent on the symbiont for food would have to outweigh the benefits for the host. And in case of the symbiont, in particular the Homoptera on which the ants prey frequently, the benefits of increased population growth would have to outweigh the costs of being eaten. Although quantification of the exact costs and benefits for the partner species in currently known farming systems is still work in progress, shifting our focus to free-living relatives of mutualistic species can shed light on these questions. When those species involved in the farming interaction have higher overall reproductive success than their free-living relatives, the system can indeed be considered a mutualism (AANEN 2010). Following this latter argument, both the fungus-growing ant system and the ant-aphid systems in which tended aphid colonies displayed increased reproductive rates (e.g., *Metopeurum fuscoviride* tended by *Lasius niger* (see FLATT & WEISSER 2000) can be considered true mutualisms. However, it is important to bear in mind that, once we have assessed the costs and benefits involved for all partners during future research efforts, some of the systems reviewed above might turn out to be cases of parasitism rather than mutualism, with one species being "trapped" in the interaction, doing worse than its free-living relatives.

Although some of the ant-scale insect interactions have been studied in detail, more detailed genetic and experimental studies are still lacking. Such studies would allow for more detailed cross-system comparisons, facilitating tests for universal patterns governing farming mutualisms. The *Aphomomyrmex afer* - *Paraputo anomala* system is especially promising, because it represents a system with vertical transmission of an asexual mealybug, which often occurs in monocultures. In addition, *A. afer* ants are not only known to tend a second (horizontally transmitted) scale insect but also to keep fungus gardens (GAUME & al. 2000, BLATRIX & al. 2013). Within- and between ant nest population genetic analyses of *P. anomala* and the other symbionts would provide information for direct comparison to the fungus-growing ant systems.

Towards a species community view of mutualism

Traditionally, mutualism theory is developed for one-to-one interactions and classic mutualisms are often regarded as such. However, apart from the host ants and their symbionts, each of the reviewed farming systems involves several other organisms as well. For example, the attine-fungus systems do include several mutualistic bacteria as well as a specialised parasitic fungus and in the ant-Homoptera systems the host plants and endosymbionts of the Homoptera can largely influence honeydew composition, the "currency" of those interactions (DOUGLAS 1998b, CURRIE 2001, HANSEN & MORAN 2011, YAO 2014). These additional organisms can be both mutualists and parasites of the system; either way they will have profound effects on the ultimate cost-benefit ratio of the focal interactions and, consequently, selection pressures on all partners involved. Leaving these additional partners "out of the equation" might therefore lead to misinterpretation of the observed dynamics of the system. Extending our view to regarding host-symbiont mutualisms as ecological networks of co-evolving species instead, may provide one of the most promising new avenues towards a more general understanding of factors governing the evolution and maintenance of mutualism (INGS & al. 2009).

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