Evolutionary biologists find delight in tracing their study topics back to Charles Darwin, and ant researchers are no exception. The dulotic habit of many ant species was highlighted by Darwin as one of the most sophisticated adaptive outcomes of natural selection (1). Dulotic ants raid nests of other ant species for pupae, so that when workers eclose from the raided pupae they start working for their dulotic host nest. Thus, dulotic ants gain work force with little investment, whereas the captured workers are deprived of evolutionary fitness. The wonderful ways in which ant species exploit each other’s behaviors to get their brood reared do not stop here, however. Some species are temporary social parasites whose queens infiltrate nests of other species and kill the resident queen, so that the host workers start rearing the parasite’s young, and the colony gradually turns into a colony of the parasitic species. So-called inquilines, workerless social parasites, live permanently in colonies of their host species alongside the host queens, relying on the host workers for rearing their offspring (2). Social parasitism is found outside ants as well, in wasps, bees, and even in birds such as cuckoos and cowbirds, but the diversity of such strategies is the highest in ants. In PNAS, Borowiec et al. (3) use phylogenomics to reconstruct the evolutionary routes to parasitic strategies taken by Formica ants and their connections to dispersal and nest-founding strategies more generally.

Formica is a Holarctic ant genus that comprises the mound-building wood ants and their relatives, dominant in temperate and boreal ecosystems from coniferous forests to peat bogs to prairie. All the main types of social parasitism are found within the genus. In addition to diversity in social parasitism, Formica are remarkably diverse in their social ecologies: Some species live inconspicuous and submissive lives in underground nests with some hundreds of workers and one or a few queens; more dominant species build impressive mounds or thatches and may form extensive nest networks, “supercolonies,” so that a single multinest colony easily spans several hectares, with tens or hundreds of thousands of workers and hundreds of queens in each nest (4). The phylogeny constructed by Borowiec et al. (3) traces the origin of the genus to the Old World ca. 30 Ma ago, with repeated colonization of the Nearctic. They use ultraconserved elements in the genome to construct the family tree of the genus and map findings of an extensive natural history literature as well as their personal observations on variation in social parasitism, queen dispersal behaviors, and nest-founding behaviors into the family tree, which allows reconstructing ancestral states of behavior and timing of transitions in strategies. Formica is not the only ant genus with all the three major types of social parasites, but the phylogenetic reconstruction suggests that the evolutionary routes Formica ants have taken to different parasitic strategies stand out from earlier described cases. In Formica both dulosis and inquiline social parasitism have evolved from ancestors with temporary parasite lifestyles. Elsewhere, as in Acromyrmex leafcutter ants (5) and Myrmica red ants (6), inquilineism has evolved independent of temporary parasitism, with inquilines occasionally parasitizing closely related species, possibly even via sympatric speciation (6). Thus, these remarkably sophisticated strategies may convergevolently evolve from different evolutionary backgrounds.

Mapping trait covariation into a phylogeny is a powerful method for understanding the coevolution of traits; Borowiec et al. show that parasitic strategies are strongly interconnected with variation in colony-founding and dispersal strategies of young queens (3). Evolution of these strategies is driven by competition (7). Competition against other ants, including conspecifics, is a key feature of ant ecology, and colony founding and early growth are the key stages when the risk of succumbing to competitors is at its highest. The ancestral Formica already had diverse solutions to this problem, each with its own pros and cons (Fig. 1). Some queens disperse on the wing and attempt to establish their own nest,
Dispersal and reproductive strategies of an ant queen

**Ancestral *Formica* strategies**

**Budding:**
- **Start a new nest on foot with help of nestmate workers**
- **Pros:** Aleviates local competition resulting from philopatry
- **Cons:** Vulnerable strategy in the long run, as dependent on the local habitat and poor at spreading long distances

**Philopatry:**
- **Stay at home and reproduce alongside kin**
- **Pros:** Dispersal and colony founding risks avoided
- **Cons:** Increases local competition

**Independent colony founding:**
- **Disperse from natal nest by flight, start colony and rear first workers alone**
- **Pros:** Allows colonizing new empty areas
- **Cons:** Very risky

**Temporal social parasitism:**
- **Start a new nest on foot with help of nestmate workers**
- **Pros:** Allows colonizing new areas with decreased colony founding risks
- **Cons:** Infiltrating host colonies is risky and requires novel adaptations

**Intraspecific social parasitism:**
- **Leave natal nest and seek adoption in a conspecific nest**
- **Pros:** Avoids local competition and investment into colony founding
- **Cons:** Infiltrating host colonies is risky and requires novel adaptations

**Temporary social parasitism:**
- **Start colony via temporary social parasitism and complement own worker force by raiding also later in colony life**
- **Pros:** Allows colonizing new areas with decreased colony founding risks
- **Cons:** Requires novel adaptations and leads to irreversible dependence on host populations.

**Modern *Formica* strategies**

**Dulosis:**
- **Start colony via temporary social parasitism and complement own worker force by raiding also later in colony life**
- **Pros:** Allows colonizing new areas with decreased colony founding risks
- **Cons:** Requires novel adaptations and may lead to irreversible dependence on host populations.

**Inquilinism:**
- **Start colony via temporary social parasitism and complement own worker force by raiding also later in colony life**
- **Pros:** Allows colonizing new areas with decreased colony founding risks
- **Cons:** Requires novel adaptations and leads to irreversible dependence on host populations.

Fig. 1. The range of dispersal and reproductive strategies available for a young ant queen. Strategies on the left (darker orange shading) represent the options used by the ancestors of modern *Formica* 30 Ma. In modern *Formica* the strategies have diverged to include the parasitic strategies on the right (lighter orange shading), with intraspecific social parasitism as a likely evolutionary intermediate.

sometimes joining forces with another queen (pleometrosis), a risky strategy with potentially high payoffs if a pristine habitat devoid of competitors is found. Some stay in their natal nest with their mothers and siblings and some join nestmate workers to initiate a new satellite nest on foot nearby, leading to “polydomous” colonies that inhabit many interconnected nests, although this latter strategy was probably rare ancestrally (3).

All these strategies still exist in *Formica*, but a major evolutionary turn was taken ca. 18 Ma ago, when the ancestor of the modern *difficilis, integra, rula, dakotensis, sanguinea*, and *exsecta* groups replaced the risky independent founding option with a temporary parasitic strategy to be used when dispersing from the natal site. Thus, the burdens of nest founding and rearing early brood were outsourced to the host species. It seems likely that parasitizing conspecific nests was an evolutionary intermediate on the way. The option of staying at home and expanding the colony via budding was retained and in some cases developed further to supercoloniality. This combination of strategies seems very successful, as in these species groups we can find the most dominant *Formica* species.

Thus, *Formica* ants have two strategies available, with very different strengths and weaknesses. One is good for local dominance but very poor in reaching new areas, and the other is good for reaching new ground but demands abilities to infiltrate host nests. Interestingly, most species are polymorphic in their strategies and thus seem to get the best of both worlds. The importance of different strategies differs between species. Species like *Formica aquilonia* seem to rely almost exclusively on budding, whereas temporary parasitism is prevalent in, e.g., *integra* and *difficilis* groups (3). In some species the variation is extensive. For example, *Formica truncorum* and *Formica exsecta* may live either in populations comprising many separate single queen nests founded via temporary social parasitism or form supercolonies comprising hundreds of interconnected nests founded via budding (4).

The origins and maintenance of the variation in strategies needs to be understood bottom-up, from the social evolution of dispersal decisions taken by young queens. While dispersal abilities are highly relevant for a species’ ability to colonize new ground, and thus essential for long-term success, the selective pressures still need to be looked for at an individual level. Dispersal is selected for only if the immediate fitness prospects are higher outside than at home. Success outside depends on independent founding chances or on availability of potential hosts, the success in invading them, and the competition faced after successful establishment. The payoffs of staying at home depend on the local family situation. Alongside gains through personal reproduction, effects on relatives need to be considered. Staying at home to reproduce is costly if it increases competition for resources and leads to irreversible dependence on host populations. The payoffs of staying at home depend on the local family situation. Alongside gains through personal reproduction, effects on relatives need to be considered. Staying at home to reproduce is costly if it increases competition for resources and leads to irreversible dependence on host populations.

The origins and maintenance of the variation in strategies needs to be understood bottom-up, from the social evolution of dispersal decisions taken by young queens. While dispersal abilities are highly relevant for a species’ ability to colonize new ground, and thus essential for long-term success, the selective pressures still need to be looked for at an individual level. Dispersal is selected for only if the immediate fitness prospects are higher outside than at home. Success outside depends on independent founding chances or on availability of potential hosts, the success in invading them, and the competition faced after successful establishment. The payoffs of staying at home depend on the local family situation. Alongside gains through personal reproduction, effects on relatives need to be considered. Staying at home to reproduce is costly if it increases competition for resources and leads to irreversible dependence on host populations.

Downloaded by guest on October 9, 2021
While studies of kin conflicts in Formica have been very successful, the ecologically very fundamental conflict over queen dispersal and recruitment still needs careful attention.

Maintenance of dispersal polymorphism seems puzzling when the different strategies require such different adaptations. Parasites need to fly, find a mate, and locate and infiltrate host colonies, which sometimes requires remarkable precision in chemical mimicry (10). Those who stay at home can focus just on egg laying and competing for worker attention and have no use for wings, flight muscles, or chemical mimicry. In addition to understanding the heterogeneity of selection pressures through behavior and ecology, we can look into comparative and functional genomics of plasticity of life histories to solve this puzzle. Interestingly, maintenance of polymorphism in Formica might be facilitated by genetic linkage, as a supergene has been shown to underlie differences in queen number regulation intimately linked to dispersal behaviors, perhaps facilitating co-inheritance of coadapted alleles in key genes (11). While this far this supergene has only been studied in detail in in a nonparasitic species, Formica selysi, the same polymorphism extends throughout the genus, making Formica a very promising system for comparative genomics.

While flexibility and plasticity prevail in temporary parasitism, dulosis and inquilineism seem to be irreversible strategies as both evolved once in Formica and no reversals back to a free-living life are seen. In leafcutter ants, inquiline strategies are accompanied by gene losses and genome erosion, similar to other tight interspecies interactions in which sometimes requires remarkable precision in chemical mimicry. In addition to understanding the heterogeneity of selection pressures through behavior and ecology, we can look into comparative and functional genomics of plasticity of life histories to solve this puzzle. Interestingly, maintenance of polymorphism in Formica might be facilitated by genetic linkage, as a supergene has been shown to underlie differences in queen number regulation intimately linked to dispersal behaviors, perhaps facilitating co-inheritance of coadapted alleles in key genes (11). While this far this supergene has only been studied in detail in in a nonparasitic species, Formica selysi, the same polymorphism extends throughout the genus, making Formica a very promising system for comparative genomics.

While flexibility and plasticity prevail in temporary parasitism, dulosis and inquilineism seem to be irreversible strategies as both evolved once in Formica and no reversals back to a free-living life are seen. In leafcutter ants, inquiline strategies are accompanied by gene losses and genome erosion, similar to other tight interspecies interactions such as obligate nonsocial parasitism and intracellular symbioses (5). Formica provides an interesting group for studying possible genome erosion and host–parasite coevolution in dulotic species, both for comparisons to other ants such as Temnothorax acorn ants (12) but also for observing parallel genomic evolution in an unusually large group of dulotic species that share a common ancestor.

Colony-founding strategies arise from selective processes at individual and colony levels but have far-reaching consequences at the population level. They are a nexus where within-colony conflicts, morphological evolution of the queen caste, genome evolution, community dynamics, and intricate mechanisms of host–parasite coevolution combine in complex coevolutionary feedback loops (9). The work of Borowiec et al. (3) is a beautiful example of how such complex interactions can be tackled by combining genomic methods with a wealth of meticulous natural history observations into a big picture that in turn inspires and guides more detailed hypotheses and their tests.

Phylogenetic comparative work has produced some of the most compelling examples of our understanding of evolution of social traits, and Formica have the potential to offer similar insight into a complex of traits with huge ecological significance. As this text started with Darwin, it is fitting to close with him as well, hitting the nail on the head when writing about the coordinated traits underlying social parasitism, although this time in cuckoo strategies in birds (1): “It has been objected that I have not noticed other related instincts and adaptations of structure in the cuckoo, which are spoken of as necessarily co-ordinated. But in all cases, speculation on an instinct known to us only in a single species, is useless.”

1. C. R. Darwin, On the Origin of Species by Means of Natural Selection, or Preservation of Favoured Races in the Struggle for Life (John Murray, London, 1859).
2. A. Buschinger, Social parasitism among ants: A review (Hymenoptera: Formicidae). Myrmecol. News 12, 219–235 (2009).
3. M. L. Borowiec, S. P. Cover, C. Rabeling, The evolution of social parasitism in Formica ants revealed by a global phylogeny. Proc. Natl. Acad. Sci. U.S.A. 118, e2026029118 (2021).
4. L. Sundström, P. Peppà, P. Pamilo, Genetic population structure and dispersal patterns in Formica ants — A review. Ann. Zool. Fennici 42, 163–177 (2005).
5. L. Schrader et al., Relaxed selection underlies genome erosion in socially parasitic ant species. Nat. Commun. 12, 1–13 (2021).
6. G. Jensen, R. Savolainen, K. Vepsäläinen, Phylogeny, divergence-time estimation, biogeography and social parasite-host relationships of the Holarctic ant genus Myrmica (Hymenoptera: Formicidae). Mol. Phylogenet. Evol. 56, 294–304 (2010).
7. J. J. Boomsma, D. B. Hüsztár, J. S. Pedersen, The evolution of multiqueen breeding in eusocial lineages with permanent physically differentiated castes. Anim. Behav. 92, 241–252 (2014).
8. W. D. Hamilton, R. M. May, Dispersal in stable habitats. Nature 269, 578–581 (1977).
9. S. Hakala, P. Seppä, H. Helanterä, Evolution of dispersal in ants (Hymenoptera: Formicidae): A review on the dispersal strategies of sessile superorganisms. Myrmecol. News 29, 35–55 (2019).
10. C. A. Johnson, H. Topoff, R. K. Vander Meer, B. Lavine, Do these eggs smell funny to you?: An experimental study of egg discrimination by hosts of the social parasite Polyergus breviceps (Hymenoptera: Formicidae). Behav. Ecol. Sociobiol. 57, 245–255 (2005).
11. A. Brelsford et al., An ancient and eroded social supergene is widespread across Formica ants. Curr. Biol. 30, 304–311.e4 (2020).
12. B. Feldmeyer, D. Elsner, A. Alleman, S. Foitzik, Species-specific genes under selection characterize the co-evolution of slavemaker and host lifestyles. BMC Evol. Biol. 17, 237 (2017).