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Polydomy: the organisation and adaptive function of complex nest systems in ants

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Many ant species spread their colonies between multiple spatially separated but socially connected nests, a phenomenon known as polydomy. Polydomous species are ecologically and phylogenetically diverse, and often economically significant as invasive pests. Benefits of polydomy may include risk spreading, efficient resource exploitation and ergonomic factors. Very little is known about the costs of polydomy; facultatively polydomous species are good candidates for identifying costs. Analysing polydomous colony structure provides insights into which costs and benefits are driving the colony organisation; for example, a cross-species analysis of inter-nest trail networks shows structural features related to long-distance transport efficiency. Deeper understanding of polydomy will shed light on key issues in evolutionary and behavioural ecology, and also benefit both conservation and pest control.

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Introduction: what is polydomy, and why is it important?

The idea of an ant colony as a cooperative group of closely related ants that live together in a single nest may seem appealingly obvious; however, many ants defy this paradigm for at least part of their life-cycle. Over 150 ant species, so far, are known to instead spread their colony across multiple spatially separated but socially connected nests. This phenomenon is known as polydomy (Box 1, Figure 1) and has evolved many times independently among the ants — polydomous species are phylogenetically and ecologically diverse. It is likely that different evolutionary drivers have been responsible for different origins of polydomy, especially as polydomy occurs in both polygynous and monogynous species (Box 1) [1]. The prevalence of polydomy poses a significant challenge to the traditional view of a social insect colony as a 'factory within a fortress' [2].

Studies of the organisation of behaviour in social insect colonies are important in behavioural ecology, explaining collective behaviours such as foraging, division of labour and nest construction [3]. However, the majority of these studies assume that a colony is operating from a single nest. Many processes operate differently under the spatial structure provided by multiple nests, so studying these behaviours in the context of polydomy is important to complete our understanding. Taking polydomy into account is essential also for the definition of colony boundaries [1,4–9] and this in turn is important for several reasons, both fundamental and applied. In social insects, such as ants, the colony can be seen as the reproductive unit, and thus the unit on which natural selection is operating. To understand the evolutionary ecology of these species, we need to be able to define a colony so we know at what scales we would expect to see cooperation, intra-colony reproductive conflict and inter-colony competition. For example, in populations that are highly polydomous or even unicolonial (Box 1, Figure 1), genetic variation between nests may be so low that individuals helping nestmates are no longer differentially helping their kin. Without kin-selection via differential benefits to relatives, the selection for worker traits is predicted to weaken, while selfish reproductive strategies will be selected for [10]. Together, these processes should contribute to making extreme polydomy an unstable strategy over evolutionary time [10]. Over rather shorter timescales, when individuals from polydomous species are sampled, knowing colony identity is important so that, in addition to the nest, the polydomous colony can be included as a grouping factor [11,12]. Relying on nest alone to provide independent replication may give pseudoreplicated or misleading results. For example, genetic differentiation between nests of the same polydomous colony can be low [13] and if nests such as these were sampled and assumed to be independent, then this could lead to artificially low values for within-nest relatedness.

Polydomous species are often highly ecologically successful with far-reaching ecosystem impacts, some even becoming invasive pests [14••,15–18]. All of the ant species on the list of the world's 100 worst invasive species are polydomous [19]. Polydomy poses significant challenges to pest control because of the difficulties of treating a spatially dispersed colony that can repopulate

Box 1 Glossary

Monodomy: An ant colony is housed in a single nest, that is, the nest houses all queens, all brood and at least the majority of workers (Figure 1a).

Polydomy: An ant colony simultaneously occupies at least two spatially separated but socially connected nests (Figure 1b,c).

Nest: A nest houses both workers and brood, but not necessarily a queen [1].

Social connection: Socially connected nests share or exchange resources, for example, food or workers.

Unicoloniality: A population of an ant species functions as a single large polydomous colony (Figure 1c).

Multicoloniality: A population of an ant species consists of colonies (monodomous or polydomous) that function independently and usually interact agonistically (Figure 1a,b).

Polygyny: At least two reproductively active queens are present in a colony. The colony may be monodomous or polydomous: if it is polydomous, the queens may or may not be dispersed between multiple nests.

Monogyny: Only one reproductively active queen is present in a colony; the colony may be monodomous or polydomous.

an area from a single overlooked nest [20]. These problems also apply to conservation, for the opposite reason: an ant population may seem healthy because many nests are present, but these may represent a very small number of actual colonies, leading to risks associated with small effective population size.

In conclusion, understanding polydomy is essential to understanding the evolutionary and behavioural ecology of ants, and for effectively and accurately sampling and studying polydomous colonies. This review focuses on recent developments in the study of the ecological costs and benefits of polydomy, and on how polydomous colony structure relates to function.

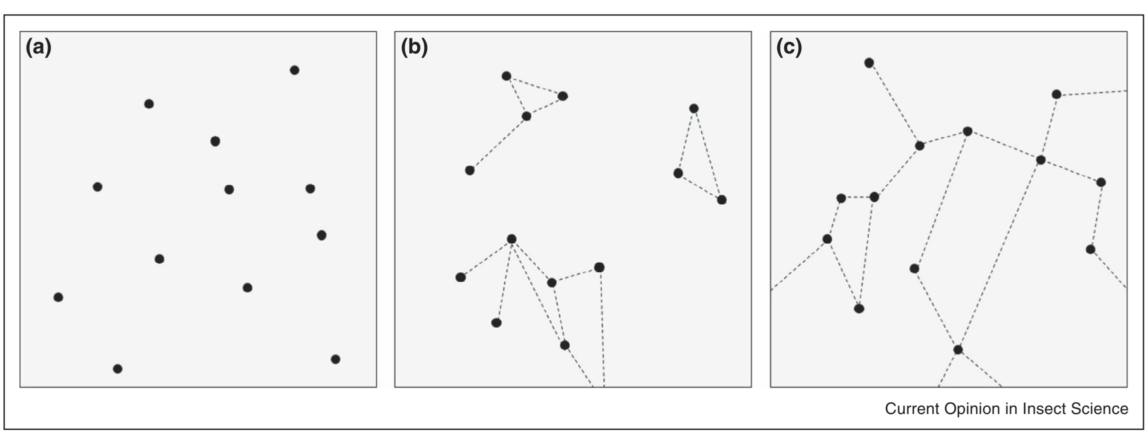
Benefits of polydomy

Polydomy allows colonies to create new nests without going through the high-risk bottleneck of single-queen nest foundation. Local foundation of socially connected nests provides a relatively low-risk way of spreading into a new area. For polygynous species, this also offers a method of colony reproduction, because a budded nest or group of nests can later become socially separated from the 'parent' colony and function independently. Indeed, polydomy is likely to have arisen from processes of incomplete budding or nest migration. Other ecological factors related to polydomy, while not necessarily having been drivers of the evolutionary origin of polydomy, may still confer current adaptive benefits. These include risk spreading, foraging advantages and ergonomic benefits (Figure 2). Below, some examples of recent advances and gaps in our knowledge regarding the adaptive function of polydomy in relation to these three areas are highlighted.

Risk spreading

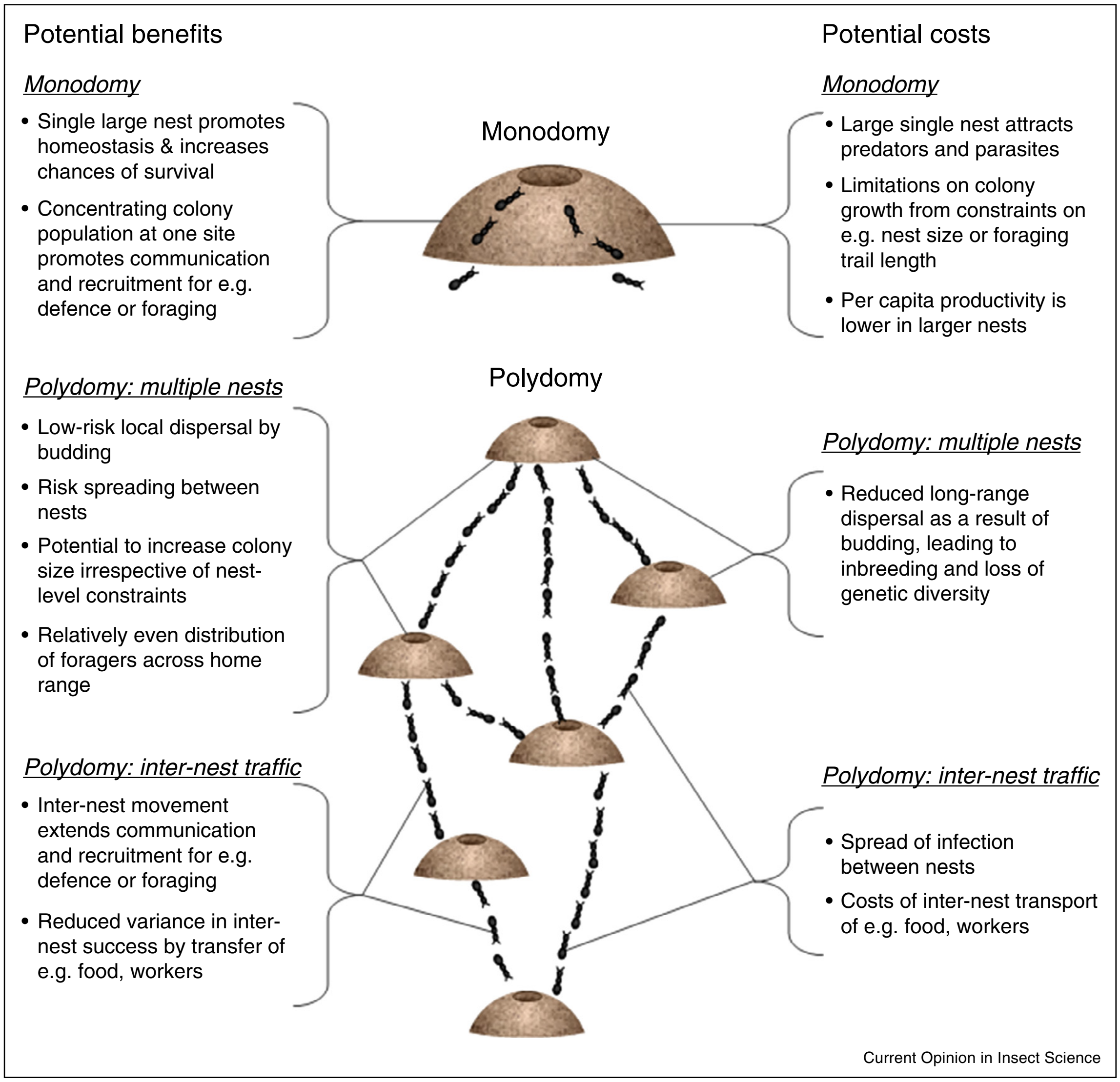
It seems intuitively obvious that spreading a colony over multiple nest sites makes the colony less reliant on the survival of any particular nest. This applies most obviously to polygynous species, but even in monogynous polydomous species, sexual brood is often transported to queenless nests, making the survival of the queenright nest less critical than it would otherwise be. This has obvious potential to be beneficial if a nest suffers predation or attack by conspecifics [21,22], or indeed pest control attempts [23–25]. However, clear evidence of the adaptive benefit of polydomy in these contexts is lacking. Multiple nests may also be useful if local conditions change, because the inhabitants of a nest that becomes unsuitable can relocate [26] to other more successful nests. An additional possible risk-spreading benefit to polydomy could be the potential to isolate pathogens or parasites by cutting off contact with an

Figure 1



Schematic representation of different forms of colony organisation. • = ant nest; – = social connection: these could be inter-nest trails, or more diffuse movement of individuals between nests. **(a)** a multicolonial population of monodomous ant colonies; **(b)** a multicolonial population of polydomous ant colonies; **(c)** a unicolonial polydomous ant population.

Figure 2



Summary of potential costs and benefits of different nesting strategies. The costs and benefits of polydomy are separated into those arising from splitting the colony into multiple nests and those associated with inter-nest traffic, whether via trails or more diffuse movement of individuals. The potential cost and benefits do not apply equally to all ant species.

infected nest — although having well-connected nests could have the opposite effect of allowing an infection to spread rapidly throughout a colony or unicolonial population [27].

Resource discovery and exploitation

Ant colonies are generally thought of as central-place foragers, but polydomous colonies can have several 'centres' to which food is retrieved. Theoretical models predict that this may reduce the time to discover new food sources, because resources are more likely to be close to a nest from which foragers are searching [28,29]. However, if large-scale recruitment is required to exploit a resource, then modelling predicts that polydomous colonies might be expected to lose out, because their population of potential recruits is dispersed [29]. This cost can be reduced by involving multiple nests in the recruitment process [12,30] or by recruiting from persistent foraging trails [31]. Moderate polydomy could be a form of discovery-dominance trade-off, in which having dispersed nests improves a colony's ability to find new resources (because scouts are spread relatively evenly over the foraging area) but nests are still large enough to provide enough workers to dominate a resource. As well as decreasing discovery time, polydomy can also decrease the initial food retrieval time. Modelling predicts that long foraging trails can be a limitation on colony growth in monodomous species [32]; becoming polydomous could be important to reduce this cost. In heterogeneous environments, polydomous colonies can then redistribute food from successfully foraging nests to other nests [33•]. This ability to transfer colony members and food (or specific nutrients) between nests, and the spatial dispersal of the foraging workforce, should reduce variance in foraging success for polydomous colonies.

Nest size and colony size ergonomics

For monodomous colonies, colony size (number of individuals) and nest size (physical volume occupied) are closely related. Polydomy allows colonies to break out of the confines of this relationship, making it possible to increase colony size, even when there are constraints on individual nest size. Constraints may be physical, for example, in cavity-dwelling *Temnothorax rugulatus*, colonies become polydomous when the density of individuals in the nest cavity is high [34], suggesting this species uses polydomy to respond to crowding in nest sites that cannot be enlarged. Another cavity-dwelling species, the 'turtle ant' *Cephalotes rohweri*, also becomes polydomous when it outgrows its first cavity. This species has a morphological caste specialised to 'plug' and defend the entrances to the cavities. The distribution of these specialists among the nests of the colony balances their two roles: continuing defence of occupied cavities and staking claim to new cavities [35••]. In addition to physical constraints, nest size may also be constrained if larger nests are attractive to parasites or predators [22] or by ergonomic factors, such as decreasing productivity per capita as worker number in a nest increases. This counter-intuitive relationship is known as 'Michener's paradox', and may be accounted for by resource limitation and increased number of inactive workers in larger nests [36••]. There is potentially a trade-off between the decrease in productivity with increasing worker number, and the benefit of increased homeostasis (more predictable foraging success, greater chance of survival) as worker number increases [36••]. Polydomy may provide a middle ground, where nests are small enough to keep productivity high, and flexibility in movement of food and workers between nests improves predictability of foraging success and survival. However, among wood ants (*Formica rufa* group) at a single site in Finland, polydomous species (*F. aquilonia* and *F. polyctena*) actually had larger nests than locally monodomous species (*F. lugubris*, *F. rufa*) suggesting that there was no trade-off between nest size and nest number, at least at the species level [37]. More data are needed on how ergonomic pressures influence polydomy, and to what extent polydomy can be a way of allowing colonies to grow beyond nest size constraints.

Costs of polydomy

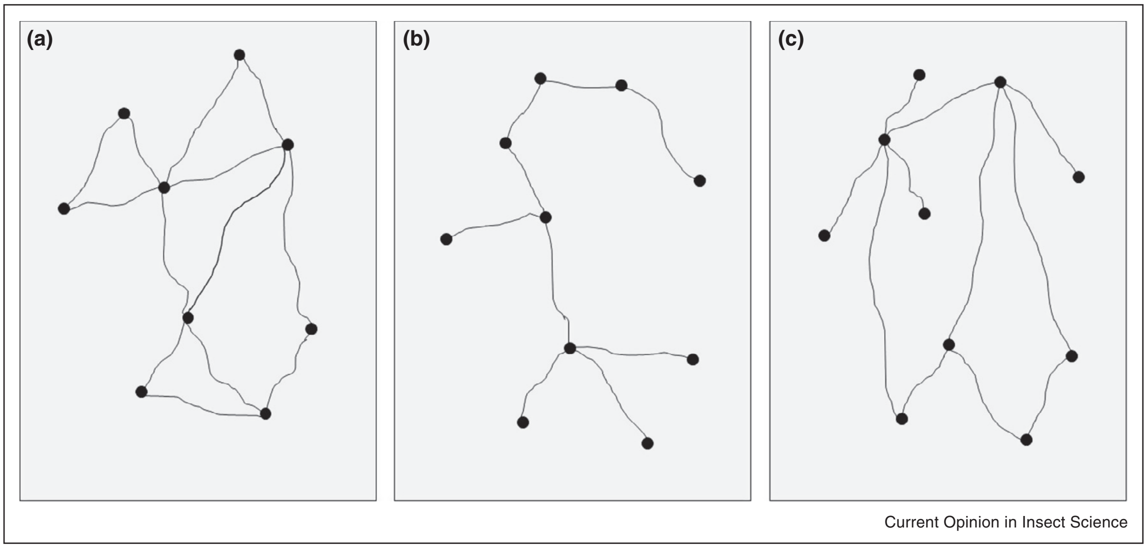
While polydomy is a widespread social structure in ants, monodomy appears to be even more common, so much so that it is often the default expectation of those studying ants. This means that, while some effort has been made to explain the benefits of polydomy, the equally important benefits of monodomy (or the relative costs of polydomy) have received less attention (Figure 2). One potential cost of polydomy is that by dispersing resources across multiple nests, they may become spread too thinly, for example, dispersed foragers reducing exploitation ability [29]. There are also energetic costs of inter-nest transport and the risk of costly resource loss during transportation, particularly loss of brood being transported to queenless nests in monogynous polydomous colonies (Box 1) [38]. Genetic costs may also occur as a result of using local budding as the main means of colony reproduction: specifically, long-distance dispersal ability may be reduced and inbreeding increased, leading to a loss of genetic diversity locally [39]. Many species of ants are facultatively polydomous, becoming polydomous (or increasing the level of polydomy) only at certain times of year or under certain conditions [40••,41–44]. These are good candidate species for identifying the costs and benefits driving the choice of one nesting strategy over another.

Organisational structure of polydomous colonies

Polydomous colonies range from the simplest structure, two connected nests, to complexes of many thousands of nests [45,46]. The social connections between polydomous colonies can be broadly categorised into three types: first, sharing resources (e.g. food, nest material); second, movement of colony members (e.g. brood, queens, workers, particular task groups); third, sharing information (e.g. recruiting ants from other nests to food; passing alarm signals between nests). Some interactions fall into more than one category, for example movement of replete workers would transfer both food resources and colony members. These interactions can result in cooperation between nests, for example, in exploiting a large food resource, and also potentially in competition, for example, over a limited workforce. Another consequence is that nest-level division of labour may occur. For example, particular nests within the colony may specialise on rearing brood of a particular stage as a consequence of local thermal conditions [47] or on foraging due to the location of stable food resources [33•].

Even among closely located nests, food sharing is not uniform, indicating that there is structure to inter-nest connections [48]. Inter-nest connections are often visible as trails: these connecting trails are sometimes mapped, though rarely analysed (but see [33•,49•]). Analysing the trail networks within polydomous colonies is important, because it provides insights into which of the costs and benefits suggested above are driving the colony structure. For example, in the context of risk-spreading, minimising the impact of a predator could suggest dense network

Figure 3



Schematic representation of different forms of connection structure within a hypothetical polydomous colony. • = ant nest, lines indicate inter-nest trails. **(a)** Nests are densely connected; **(b)** nests are connected by the minimum number of trails possible; **(c)** this intermediate form is the most common structure among real polydomous colonies [49•]. Nests connect mostly to nearest neighbours, but some long-distance connections are present also.

connections to neighbours, so that rapid evacuation from a nest under attack (or rapid recruitment of additional defenders) is possible (Figure 3a). Conversely, if the pressure driving polydomous colony structure is to limit the spread of infection, a formation closer to the minimum spanning tree (MST) which uses the fewest possible trails to connect all nests would be expected, as this would allow an infected nest to be easily isolated from the colony (Figure 3b). Analysis of colony maps from six ant species showed that colonies generally occupy an intermediate position: while not highly dense networks, they do have more trails than the MST would predict, indicating that trail costs (e.g. infection spread, trail maintenance) are not the main drivers of colony structure [49•]. The presence of extra trails suggests that robustness in colony cohesion may be important. In addition, in the networks studied, nests did not connect only to neighbours, but also frequently to distant nests (Figure 3c). These long-distance connections greatly increased the efficiency of the network, suggesting that effective information transfer or resource transportation has influenced the structure [49•]. A similar pattern of food sharing between distant nests is seen in *Lasius neoniger* [50].

If resource exploitation benefits are significant for polydomous colonies, then trail structure and nest location should be influenced by food patches, particularly as polydomy is generally associated with the exploitation of clumped resources [51]. There is some evidence for this: in *Formica exsecta*, inter-nest trails are formed primarily as a side-effect of shared food resources [52], and in a polydomous *F. lugubris* population, trails connecting nests that differed more in their amount of foraging were stronger than trails between nests with more equal foraging, suggesting an important food-redistribution role to the interconnection structure [33•]. Differences in foraging provision between nests of the same colony can have direct fitness implications, for example affecting oviposition rate in the Argentine ant *Linepithema humile* [42]. More work is needed to determine how the structure of polydomous colonies develops and changes in response to environmental challenges.

Future directions

Polydomy is an intriguing strategy of colony organisation, with many possible benefits including risk-spreading, improved foraging organisation and reducing the impact of nest-size limitations on colony growth. There are also potential costs to polydomy, which have been relatively under studied. Studying the structure of polydomous colonies helps to demonstrate what benefits drive the organisation of the connections between nests. Areas of interest for future study include:

- To what extent is the level of selection in a polydomous species the individual nest, and to what extent the whole colony?
- How does polydomous organisation in ants compare to analogous systems in other groups, for example, polydomous termites, or bees and wasps with very high levels of inter-nest movement [53,54]?

- Do polydomous colonies gain fitness benefits from risk-spreading, improved foraging or other ecological consequences of polydomy?
- Do the benefits of rapid resource discovery and retrieval offset the costs of later resource redistribution?
- How important is avoiding ergonomic constraints, such as decreasing per capita productivity, in promoting polydomy?
- How does polydomy impact on reproductive conflict, particularly in monogynous polydomous species?
- How does individual-level task specialisation interact with division of labour at the nest level?
- How do polydomous colonies use their nesting structure to respond to local change?
- What drives transitions/regional patterns in facultatively polydomous species?
- How consistent across taxa and environments are organisational features of polydomy?

Although there have been many recent additions to our knowledge of polydomy, there are still large and numerous gaps in what we know about how and why colonies distribute themselves between multiple nests. Deeper understanding of this social organisation strategy will shed light on key issues in evolutionary and behavioural ecology, and also be of benefit to both the conservation and the control of polydomous ant species.

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