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Ant Ecology

Edited by Lori Lach | Catherine L. Parr | Kirsti L. Abbott

Foreword by E.O. Wilson

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Contents

Foreword

Edward O. Wilson

This book devoted to the many dimensions of ant ecology has been delivered at the right time. The number of biologists who include ants in their research, especially in ecology and sociobiology, and thus the overall capability of research, is rising swiftly. So is the number of myrmecologists, those who study ants as their primary objective. So numerous have these researchers become, and such is the high overall quality of their work, that myrmecology is poised to take its place among such more immediately recognizable taxon-defined disciplines as ornithology, herpetology, and nematology. Myrmecology can be properly regarded as a part of entomology, but is no longer subordinate to it.

When I began my own studies on ants as a teenager, in 1946, there were fewer than a dozen myrmecologists in the United States actively publishing, not including narrowly focused economic entomologists. There were two in South America, and several more each in Europe, Australia, and Asia. Today the number worldwide is in the hundreds, and rising steeply. As the surviving myrmecologist with the longest continuous track record of research (65 years), I have recently, at last stopped trying to keep up with all of the literature. If I and a few other old timers can be said to have been carrying the torch of myrmecology, I am happy to have it wrested from our grasp and hurried forward.

There are compelling additional reasons why the discipline should continue to grow and take its place among the prominent biological sciences. Ants make up most of the insect biomass, and they weigh more than all the land vertebrates combined save human beings. In part they have accomplished this feat by elaborate symbioses, including, variously among species sapsucker herds, ant-plant associations, arboreal ant gardens, elaiosome-mediated seed dispersal, and fungus gardens. In some species, most notably the *Oecophylla* weaver ants and leafcutter garden ants, we find the most elaborate nonhuman systems of communication and division of labor. Their systems are rivaled only by those of the apine bees and macrotermitine mound-building termites.

The communication systems have shown us to what degree it is possible for pheromone communication to evolve, and what its ultimate limitations may be, on this or perhaps any other planet. By studying self-organization as simple colonies evolve into superorganisms, myrmecologists have made important advances in defining the process of group selection. They have disclosed some of the true nature of emergent traits during the emergence of new levels of biological organizations.

Yet while the scientific natural history of ants has grown to maturity during the past two centuries of research, telling us much about basic habits and the life cycles of hundreds of species, and while the past half century has added a great deal of information about how ant colonies are put together, myrmecologists have only begun to explore the ecology of ants. We understand little of the environmental factors that shaped the social adaptations of these insects, how assemblages of species have evolved as an evolutionary product. We have only begun to explore the full impact of ants on the natural ecosystems of the planet and those they share with humanity.

The authors of the present volume have made an important contribution by summarizing much of what we have learned about the ecology of ants and by suggesting the shape of what is to come.

Preface

From scorching, barren deserts to humid tropical forests, from deep in the soil to high in the tree canopies, ants are everywhere! Their near-ubiquitous occurrence on every continent except Antarctica, combined with their enormous abundance and high diversity make ants deserved of special attention.

Ants are one of the few insect groups that can be reliably identified to family by just about anyone, regardless of age or background. They are the wise and hard-working creatures of biblical and fable lore, the endearing underdogs of Hollywood animation to some (and exaggerated villains of B-grade films to others), the unwitting victims of children with magnifying glasses, and the unwanted guests of picnics. Politicians, economists, and traffic planners are among the non-biologists who have mined ant society structure for potential application to human behaviour. Understanding of ant behaviour and collective intelligence has contributed to advances in robot development, computer science, telecommunication networks, and the stock market.

To myrmecologists – those who study ants – ants are the 'premier soil turners, channelers of energy, and dominatrices of the insect fauna' (Hölldobler and Wilson 1990). Indeed, it would be difficult to overstate the importance of ants in the functioning of terrestrial ecosystems. Estimated to number between 25,000 and 30,000 species, currently just more than 12,500 ant species are described, accounting for less than 1% of all described insect species (Bolton *et al*. 2006; May 1988). Despite their relatively small contribution to overall global biodiversity, they are omnipresent in virtually every terrestrial habitat. The estimated 10,000 trillion individual ants alive at any one time weigh about as much as all human beings combined (Hölldobler and Wilson 1994). Sustaining and sheltering their sheer numbers dictates that ants engage in a variety of ecological roles: competitors, predators, prey, scavengers, mutualists, gardeners, and soil engineers.

In their need for food and shelter, they are like any other organism on the planet. But as eusocial organisms, ants have evolved to partition reproduction and resource acquisition among different individuals. This division of labour has dramatic consequences for the ecology of ants. With the exception of colony-founding events, queens stay in protected nest enclaves with the sole purpose of producing eggs. The workers are responsible for foraging, maintaining and defending the colony, and only very rarely reproduce. Since a single worker is only one of many that undertakes these tasks and does not represent a reproductive unit, its survival is not integral to the longevity of the colony. These observations were once thought 'fatal to' the theory of natural selection (Darwin 1859); how could worker ants evolve if they are incapable of reproducing? Recasting ants as 'superorganisms', and framing their social organization within the context of kin selection, where natural selection acts on the colony, and workers maximize colony efficiency in the absence of 'interindividual conflict for reproductive privilege', resolves this natural selection conundrum and goes a long way towards explaining why eusocial insects have been so successful: organized groups outcompete individuals, and larger groups outcompete smaller ones of the same species (Hölldobler and Wilson 2008).

Thus, in ecology the importance of ants is reflected by their ubiquity and the great number of interactions in which they are capable of participating within an ecological community. As such, the study of ants has led to significant advances in our understanding of insect evolution, global diversity patterns, competitive interactions, mutualisms, ecosystem responses to change, and biological invasions. But ants are also important to study and understand because they are different; their status as superorganisms places them at a level of organization between individuals and ecosystems (Hölldobler and Wilson 2008). Their social structure provides a rich ground for exploring how division of labour affects the acquisition of resources, foraging and defensive behaviours, and coevolution with the flora and fauna with which they interact. In turn, how elements of their social structure, such as colony founding, caste differentiation, and nestmate recognition, are influenced by their environment deserves investigation.

Why *Ant Ecology?*

Several excellent texts have described the social organization and evolution of social insect societies (e.g., Bourke and Franks 1995; Crozier and Pamilo 1996; Gordon 1999; Hölldobler and Wilson 1990). Our purpose in compiling this book was fourfold: to complement and build on these fundamental works, to highlight the contributions of myrmecology to ecology more broadly, to synthesize the current state of knowledge, and to add to the growing body of work that seeks to promote interest in insects both among ecologists and in the world of conservation. We also seek to inspire current and future myrmecologists to seize the opportunities presented by the gaps in research that are identified throughout the book. We hope that this volume will appeal to community and behavioural ecologists, population biologists, macroecologists, evolutionary biologists, as well as those involved with conservation and natural resource management.

Ecology is not a linearly structured science; it is as complex and interconnected as the world that it seeks to understand. Ant ecology is no different. Thus, although we have organized the book into four parts: Global Ant Diversity and Conservation, Community Dynamics, Population Ecology, and Invasive Ants, the boundaries between them blur and blend. Each section begins with a brief introduction that identifies common themes and defines terms applicable to the subsequent four chapters. The first three sections provide a firm foundation in ant ecology, while the fourth applies this foundation to the problem of ant invasions. Interspersed throughout the book are short boxes that further explain important techniques, terms, or methods, or highlight an interesting discovery, debate, or application relevant to the chapter. A notable strength of the book is that it draws on the knowledge and experience of so many myrmecologists and ecologists; 53 authors and 55 reviewers from around the world have contributed their ideas, time, and energy to the pages that follow.

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Ant Ecology was conceived in boundless enthusiasm at the seaside café Chocolate Fish in Wellington, New Zealand, on 30 August 2006. Since then many individuals have helped and supported us through the process of turning our ambitious proposal into this tangible volume.

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We are most indebted to our authors, who joined us in this journey and remained committed and patient with us throughout. Edited volumes such as this benefit from the variety of perspectives brought to the project by each author, and the creativity of each contributor in describing his or her own part of this amazing scientific discipline. Many authors contributed to the terms and definitions in the glossary, and we thank them for their diligence.

The dazzling array of weird and wonderful ants and their fascinating biologies are brought to life through images supplied by Alex Wild. We sincerely thank you for such superb photographs. We thank Andrew Mercer for providing the domain (www.funkyant.com) that hosted all the *Ant Ecology* emails, and Pat Lach for her incredible patience and hard work in compiling the reference list. We are very grateful to Adam Beaumont, Dan Borg, Stephanie Chapple, Natalie Funtera, Jeremy Gibson, Courtney Johnson, Emily McGuire, Mike Parr, and Amber Tritt who put in some long hours proofreading, commenting on chapters and text boxes, and providing us with non-myrmecologists' perspectives on it all.

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List of Plates

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List of Abbreviations

AFLP	Amplified Fragment Length Polymorphism
ANeT	Asian Ant Network
BAP	Biodiversity Action Plan
BDFFP	Biological Dynamics Forest Fragment Project
CHC	Cuticular Hydrocarbon
COI	Cytochrome c Oxidase I, also Cytochrome Oxidase I
CR	Critically Endangered
DCF	Dependent Colony Foundation
DIVA	Dispersal-Vicariance Analysis
DD	Data Deficient
EFN	Extrafloral Nectary
EPBC Act	Environment Protection and Biodiversity Conservation Act
EN	Endangered
EX	Extinct
EXW	Extinct in the Wild
FB	Food Bodies
GALS	Giant African Land Snail
GBIF	Global Biodiversity Information Facility
CBA	Cost–Benefit Analysis
GIS	Geographic Information System
IBA	Important Bird Areas
ICF	Independent Colony Foundation
ICZN	International Code of Zoological Nomenclature
IGR	Insect Growth Regulator
ISPM	International Standards for Phytosanitary Measure
IPM	Integrated Pest Management
JH	Juvenile Hormone
KBA	Key Biodiversity Areas
LC	Least Concern
LLAMA	Leaf Litter Arthropods of Mesoamerica
GCM	Geometric Constraints Model
mtDNA	mitochondrial DNA
MTE	Metabolic Theory of Ecology
Mya	Million years ago
NT	Near Threatened
NPP	Net Primary Productivity
SISG	Social Insects Specialist Group
SSC	Species Survival Commission
SRLI	Sampled Red List Index
USDA	United States Department of Agriculture
VU	Vulnerable
YCA	Yellow Crazy Ant

Chapter 11

Nestmate Recognition

Patrizia d'Ettorre and Alain Lenoir

11.1 Introduction

> '. . . it begins to seem that some ability to recognize kin and to react accordingly will be found in any social animal if looked for carefully enough'.
>
> —Hamilton (1987, p. 426)

Recognition of kin or group members is essential to the evolution of social behaviour, whether living in a small family group or in a society of millions of individuals, such as a mature *Atta* colony. Research on kin recognition has been prolific, and a good synthesis was achieved about 20 years ago, with the publication of two edited volumes, one by Fletcher and Michener (1987) – the source of the Hamilton quote above – and the other by Hepper (1991). Moreover, the contribution by Holmes and Sherman (1983), who investigated the *how* and *why* of kin recognition in one of the first models – the ground squirrel – deserves mentioning. The early history of Hamiltonian-based research on kin recognition, especially in vertebrates, has been nicely summarized more recently by Holmes (2004).

In this chapter, we review the recent literature on ant-recognition systems. We are aware that our approach is far from being comprehensive, but our aim here is to concisely highlight what we believe is the essential knowledge gained so far, with the hope of generating further studies aimed at filling some of the research gaps and answering what we think are important, but still unresolved questions.

Since terminology is often an issue that could easily shift the focus from a biological problem to a semantic one, we begin with defining a few key terms, and classifying some of the fundamental features of recognition systems. A minimum of two participants is required to play the recognition game: a *cue-bearer*, which shows the cues correlating with some significant factor, and an *evaluator*, which identifies and then assesses these cues by comparing them with some kind of template (see Liebert and Starks 2004 for a review of the alternative terminology used in recognition research). When this process takes place, we can usually observe an act of discrimination, for example, aggression. However, the absence of detectable discrimination does not necessarily mean that recognition did not occur, since recognition is defined as the internal neural or cognitive process that can also happen without producing any observable discrimination. Unfortunately, our knowledge of the strictly internal neural processes underlying recognition is still in its infancy, and thus the two terms are often used as functional synonyms.

An efficient way of studying recognition systems is to disentangle them by analysing three distinct components: the *expression* (also called production), the *perception*, and the *action* component (Gamboa *et al*. 1991; Sherman *et al*. 1997; Starks 2004). The expression component refers to all the processes involved to produce or acquire recognition cues (labels) by the cue-bearer; the perception concerns the evaluator and it is the process by which the evaluator detects, identifies the labels, and compare these with some kind of template; the action component is the response of the evaluator, usually a discriminating behaviour that we can somehow observe and quantify.

Later in this chapter, we specifically address the expression of recognition cues in ants, whereas here we give an essential, but a more general overview of the possible mechanisms underlying recognition, all of which might be relevant for ants. Several different classifications have been proposed by different authors (reviewed by Liebert and Starks 2004; Mateo 2004) and there has been a long debate on what should be defined as 'true' kin recognition (e.g. Grafen 1990; Sherman *et al*. 1997). We believe that the distinction originally made by Waldman (1987) has indeed some general heuristic value. Recognition is defined as *indirect* when the evaluator relies on some contextual cues, such as spatial location. In some particular circumstances, any individual encountered in a closed nest is reliably a group member, and the evaluator does not need to assess cues that are actually on the putative cue-bearer. In contrast, recognition is *direct* when it is based on phenotypic cues that are actually borne by other individuals (cue-bearers).

11.2 Mechanisms of recognition

The following recognition mechanisms (see also Figure 11.1) have all found theoretical and, most significantly, empirical support in different groups of organisms, from amoebae to insects and vertebrates. This is not to be viewed as a hierarchical classification; there is no 'best' mechanism of recognition, and the proposed ones are not necessarily mutually exclusive. The underlying forces that have favoured the selection of one mechanism in a particular social species can be successfully investigated only by taking into account ecological constraints and life history trade-offs.

(a) Prior association: During its development or early stage in life, the focal individual (evaluator) learns cues from the other individuals that are most frequently encountered. These become 'familiar' individuals, who are thus treated as kin (or fellows; see Section 11.3), while individuals who are not familiar are always

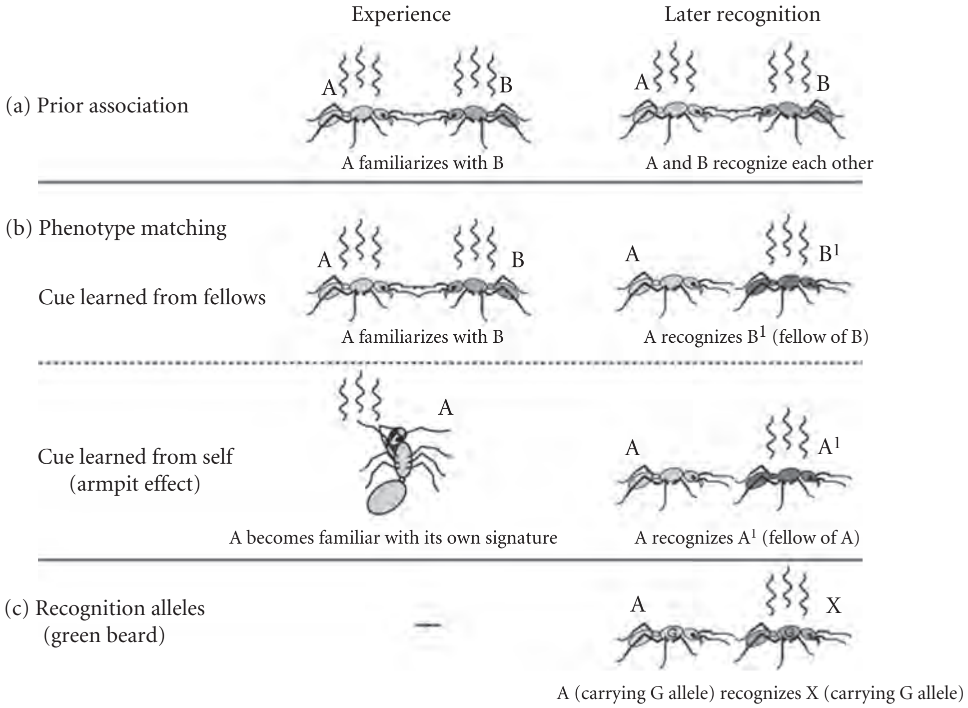

Figure 11.1 There are a range of possible mechanisms of direct recognition (see text Section 11.2). Inspired by Wyatt (2003).

treated as non-kin, independently of their relatedness with the evaluator.

(b) Phenotype matching: The focal individual learns cues to construct an internal, neural template. Once the template is in place, every encountered cue-bearer is compared with the evaluator's template, and recognition is based on the degree of similarity between label and template. The source of cues to be learned in order to form the template could come from other individuals (e.g. nestmates) or from the focal individual itself. The latter case is called self-referent phenotype matching (or armpit effect; cf. Dawkins 1982).

The difference between 'prior association' and 'phenotype matching' is that with the first mechanism only individuals that have been already encountered (familiar) can be recognized as kin (or fellow), whereas the second mechanism allows recognition of never-encountered individuals as kin, if they match the evaluator's *Gestalt* template (see Section 11.3.3).

(c) Recognition alleles (green beard): This is a concept proposed by Hamilton (1964) and then named by Dawkins (1976), the 'green-beard effect'. An allele at a single locus – or closely linked genes – could cause the expression of (*a*) a detectable phenotypic cue (a green beard), (*b*) the ability to recognize this same cue in other individuals independently of relatedness and (*c*) the preferential treatment of individuals expressing the cue. The same gene should encode all three functions (cue, recognition, and altruism), and thus this mechanism is not expected to occur frequently (see Grafen 1998). However, the green-beard effect has been shown in the red imported fire ant, *Solenopsis invicta* (Keller and Ross 1998) and has recently found additional theoretical support (Jansen and van Baalen 2006).

This recognition mechanism does not require any form of learning, contrary to the previous other mechanisms, which are based on cue-learning. However, it is very difficult to experimentally distinguish between self-referent phenotype matching and recognition alleles (cf. Crozier 1987; Mateo 2004).

11.3 Kin and nestmate recognition

When studying ants and social insects in general, a clear distinction should be made between kin and nestmate recognition. These two phenomena are essentially different. Efficient discrimination between colony members and aliens (nestmate recognition) is crucial for the organization of insect societies, since it prevents robbery and parasitism from outside (cf. Hölldobler and Wilson 1990). Nestmate recognition is typically manifested by rejecting alien intruders, thus it occurs between colonies and among unrelated individuals. Kin recognition, in contrast, could take place at a different level, within the colony. Whilst insect societies are usually composed of related individuals, the degrees of relatedness among nestmates within the same colony can vary. If the queen mates with more than one male (polyandry), the colony will contain workers from different patrilines, a mixture of full-sisters and half-sisters; the obvious example being the honeybee (cf. Tarpy *et al*. 2004). Obligate multiple mating is also the rule in some ant species, such as army ants (Kronauer *et al*. 2007a), leaf-cutting ants (Villesen *et al*. 2002), harvester ants *Pogonomyrmex badius* (Rheindt *et al*. 2004) and *Cataglyphis cursor* (Pearcy *et al*. 2004). Another possible complex scenario is the presence of multiple queens in the same colony (polygyny), which gives rise to the coexistence of several matrilines. Multiple queens with multiple matings (e.g. Kellner *et al*. 2007) can yield several patrilines and matrilines in the same colony.

11.3.1 Is kin recognition expected in social insects?

Kin and nestmate recognition coincide in ants only when colonies are headed by a singly mated single queen, and there is no queen turnover. In this case, workers are all full-sisters and there is no need to discriminate among different kinds of kin. By contrast, when different patrilines or matrilines coexist in the same colony, discriminating full-sisters versus half sisters could be advantageous for the single worker, which would benefit from favouring its full-sisters. However, kin recognition leading to nepotistic behaviour is expected to be selected

Box 11.1 Recognition between different species: natural and artificial mixed colonies of ants

Christine Errard

Social parasitism is the coexistence in the same nest of two species of social insects, one of which profits (the parasite), and the other of which generally suffers (the host). Many ant species are known to be engaged in some form of parasitic association with other ants (xenobiosis, temporary parasitism, dulosis or slavery, permanent parasitism, or inquilinism). Social parasitism in ants is a relatively rare form of parasitism, with about 220 cases described (~2% of all described ant species), though new parasitic species continue to be discovered. Social parasitism is not equally spread among the subfamilies; it is absent in the primitive subfamilies Ponerinae (with one exception) and Nothomyrmeciinae, and it is concentrated in certain genera in the Myrmicinae and Formicinae (Hölldobler and Wilson, 1990).

Social parasites have evolved to overcome the host nestmate recognition code, penetrate the host colony, and achieve social integration with their new colony. Newly eclosed social parasites, like all callow ants, are characterized by cuticular 'chemical insignificance' (odourlessness), which allows them to bypass the colony odour barrier (Schmid-Hempel 1998) at the time of usurpation of the host's nest. This is followed by a 'chemical integration' period when they acquire the specific chemical cues ('labels') of the host colony and incorporate them into their 'template' (internal representation of the environment chemical cues) by a learning process. Chemical integration is achieved by camouflage, in which the parasite gets cues from the host via contact with nest material and via allogrooming, and trophallaxis with the host (for reviews, see Dettner and Liepert 1994; Lenoir *et al*. 2001). For example, the xenobiotic ant *Formicoxenus provancheri* acquires the odour of its host, *Myrmica incompleta*, in the first days of its adult life and maintains the camouflage by intense host grooming (Lenoir *et al*. 1997). The slave-making ant *Polyergus rufescens* has not only evolved a species odour (chemical profile) that matches closely that of its most important and usual host species, *Formica cunicularia*, but it has also evolved the ability to modify its chemical profile should it penetrate any other *Formica* host species (e.g. *F. gagates*, rare host; *F. selysi*, non-natural host) to obtain social integration into host colonies. This chemical flexibility, possible only with the young parasite (newly emerged callows), could facilitate the change to different host species, if the main host species becomes rare (d'Ettorre *et al*. 2002a).

Artificially mixed-species groups composed of two non-chemically related ant species (Figure 11.1.1) provide a good tool for testing the chemical insignificance and chemical integration phases of alien-ant adoption and isolating the different parameters affecting recognition (e.g. label and template formation and plasticity). To achieve mixing, callow workers of each species are selected and removed from their mother colonies within 5 h of emergence and before they can interact with other colony members. Ten to fifteen workers of each species are combined and kept queenless and without brood, for at least three months before conducting the bioassays (dyadic encounters).

Figure 11.1.1 Food exchange between workers of *Manica rubida* (Myrmicinae) (left) and *Formica selysi* (Formicinae) (right) reared in an artificial mixed-species group created five hours after their emergence. (Photo: Y. Leclerc)

In mixed groups of *F. selysi* and *Manica rubida* callow ants, individuals acquire chemical cues characteristic of their allospecific nestmates via social interactions, thus progressively

continues

Box 11.1 continued

achieving a unified chemical profile (*Gestalt* i.e. mixture of the odours of the two associated species), that permits the two species to inhabit the same nest without displaying aggression (Errard 1994a). The reference cues are learned by the young imago shortly after emergence, the first interactions with their nurses (homospecific as well as heterospecific) being decisive. So, during their sensitive or critical period, the young ants are able to learn the odour of their nearest social environment, which strongly influences the recognition of colonial memberships during all their adult life (Errard 1994b). However, experimental mixed-species groups of *Manica rubida* with either *Myrmica rubra, Tetramorium bicarinatum*, or *F. selysi* show that the process of cue learning (see Chapter 11) during the sensitive period varies according to the specific chemical cues of the associated species. The post-imaginal learning, template reforming, and decision-making seem to be more precisely tuned (higher potential to discriminate between profiles) when the two species' chemical complexes are similar (Errard *et al*. 2006). The use of mixed-species groups of *F. selysi* and *Ma. rubida* also enables the exploration of the possible role of the volatile chemical cues within the nest that may affect the template formation during the early social experience of the ants. For example, *Ma. rubida* workers that were imprinted on *F. selysi* Dufour's gland constituents were always amicable towards the non-familiar *F. selysi* workers, indicating that undecane, the major product of *F. selysi* Dufour's gland, affects template formation in *Ma. rubida* workers. These results support the hypothesis that the perception of learned volatile cues permits a general recognition process that precedes the identification of cuticular chemical cues by contacts (Errard *et al*. 2008).

against at the colony level (Keller 1997; Boomsma *et al*. 2003).

Indeed, there is very limited – and controversial – evidence for nepotism in social insects (cf. Wenseleers 2007). In honeybees, several studies investigated the possible occurrence of nepotistic queen-rearing, but results have been equivocal or negative (review in Breed *et al*. 1994; see also Tilley and Oldroyd 1997; Moritz *et al*. 2005). In ants, only one study, conducted on the polygynous species *Formica fusca*, clearly suggested that workers indeed favour their own close kin when rearing eggs and larvae (Hannonen and Sundström 2003). However, a different study on another polygynous species, *Formica exsecta*, showed that workers do not discriminate between highly related and unrelated brood, but that brood viability differs between queens and this difference in viability could be sufficient to explain a relatedness pattern that could be interpreted as evidence for nepotism (Holzer *et al*. 2006b). This is in accordance with other studies that also failed to demonstrate nepotism in multiple queen colonies (e.g. De Heer and Ross 1997; Clémencet *et al*. 2007). Thus, the occurrence of nepotism remains controversial in ants, and we agree with previous authors who have suggested that recognition studies in ants usually deal with nestmate rather than kin recognition (e.g. Vander Meer and Morel 1998).

This does not mean that kin selection has to be discharged as one of the crucial forces for developing recognition systems in social insects. Kin selection has likely been very important for the evolution of eusociality in insects, but ecological pressures have contributed in shaping more complex societies where nestmate recognition conveyed higher advantages, and therefore kinship has been largely replaced by 'nestmateship' (cf. Lenoir *et al*. 1999). Thus, in social insect colonies, especially in the complex ant societies, individuals cooperate on the basis of familiarity and not necessarily on the basis of genetic relatedness. This familiarity has been termed 'fellowship' by Jaisson (1991, and references therein), and its strength has been elegantly shown by forming experimentally mixed colonies of phylogenetically distant ant species (e.g. Errard *et al*. 2006; Box 11.1). This is not a mere laboratory artefact, since natural mixed colonies do occur in the case of social parasitism (Lenoir *et al*. 2001).

11.3.2 How can recognition systems be stable?

For recognition to be possible, individuals must be somehow different: a polymorphism of labels is required. This cue diversity is supposed to be the expression of an underlying genetic variation: a polymorphism of genetic markers. When there is a high cost for being rejected, as in the case of a conspecific alien intruder that is attacked when attempting to enter an ant colony, individuals bearing rare labels will suffer costs at high probability. In contrast, individuals bearing common labels will very often match the template of evaluators and will suffer the cost of rejection only in few cases. The expected evolutionary scenario would result in rare labels being selected against with the consequent loss of the original genetic polymorphism. Eventually, all individuals in a population will be carrying the same genetic markers and recognition of friends and enemies would be impossible. Yet, polymorphic cue systems can be continuously observed. This paradox has been addressed for the first time in mathematical terms by Ross Crozier (review in Crozier 1987) and is known as the Crozier paradox (Tsutsui 2004). The subsequent debate has generated an array of verbal and mathematical models (discussed by Gardner and West 2007), and it now appears that the original suggestion by Crozier, that genetic marker diversity allowing recognition must be maintained by selection for something else, such as balancing selection imposed by host–parasite interactions, is indeed very likely (Rousset and Roze 2007).

In ants, nestmate recognition may be important, not only in competition between species and colonies, but also in mate choice. However, the phenomenon has not been extensively studied and, to our knowledge, only the following example is known. In *Leptothorax gredleri*, cuticular hydrocarbons of males and reproductive females are colony-specific and might thus act as a chemical cue (or signal) to avoid mating with sibs (Oppelt *et al*. 2008).

11.3.3 In search of the nestmate recognition cues

We have seen how in the context of nestmate recognition, which is vital for colony defence and is typically expressed by the action of rejecting alien intruders, recognition cues need not be directly correlated with genetic relatedness, since this would allow disruptive nepotism within the colony. One way of achieving nestmate recognition without allowing kin recognition is simply to mix things up by forming a cocktail of recognition cues. Cues produced by individuals may be combined to create a common colony odour (the *Gestalt* model; Crozier and Dix 1979). We have also seen that polymorphic cues are needed to discriminate between nestmates and non-nestmates. Insects live in a world of odours, thus we expect to find chemical cues that vary among colonies and are relatively uniform within a colony. Cuticular hydrocarbons appear to fit all the requirements needed to act as labels in the process of nestmate recognition in social insects. Insect cuticles are covered by waxy substances (mostly long-chain hydrocarbons from 20 to 35 carbon atoms) that probably evolved originally to avoid desiccation and were later used as recognition cues (Blomquist *et al*. 1998). Ants and other social insects show a complex pattern of cuticular hydrocarbons, which varies in quality among species and quantity (relative amount) within species, thus representing an ideal multi-component signal with the level of polymorphism required for recognition to be effective (Figure 11.2). These substances can be both genetically and environmentally determined and are permanently mixed to form a uniform blend. Trophallaxis and allogrooming are the main ways to obtain this uniform colony odour (Boulay *et al*. 2000; Chapuisat *et al*. 2005). It has been confirmed that the post-pharyngeal gland (a head gland specific to the Formicidae) serves as a reservoir to concentrate and mix the hydrocarbons (review in Lenoir *et al*. 1999) that are transported by a lipophorin protein (Lucas *et al*. 2004).

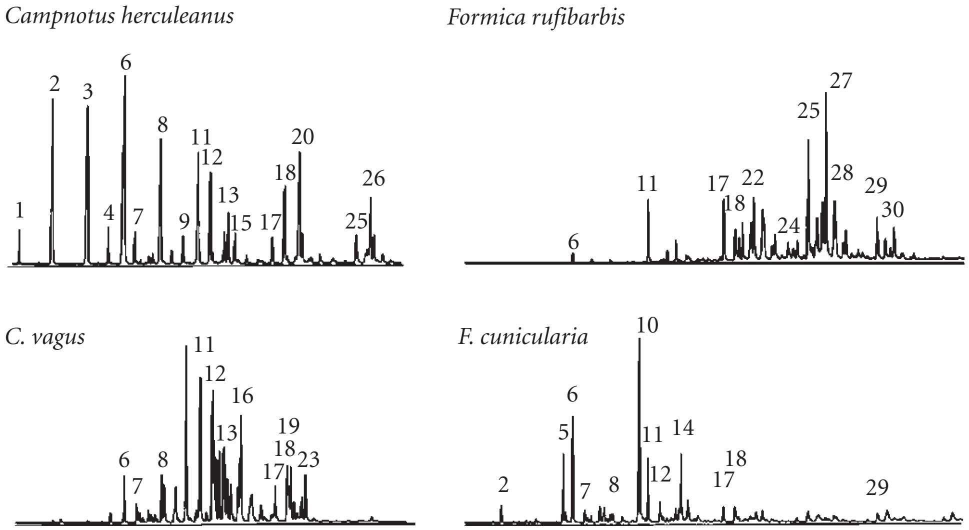

Figure 11.2 Gas-chromatograms showing the cuticular profiles of four different ant species. Some of the identified peaks are indicated as a reference: (1) n-C_{22}; (2) n-C_{23}; (3) n-C_{24}; (4) 2-meC_{24}; (5)$C_{25:1}$; (6) n-C_{25}; (7) 9- + 11-meC_{25}; (8) n-C_{26}; (9) 2-meC_{26}; (10) $C_{27:1}$; (11) n-C_{27}; (12) 11- + 13-meC_{27}; (13) 5-meC_{27}; (14) $C_{28:1}$; (15) n-C_{28}; (16) 10-meC_{28}; (17) n-C_{29}; (18) 11- + 13-meC_{29}; (19) 7-meC_{29}; (20) 7,13-dimeC_{29}; (21) 5,11-dimeC_{29}; (22) 12-meC_{30}; (23) n-C_{31}; (24) 13- + 15-meC_{31}; (25) 7-meC_{31}; (26) 5,13-dimeC_{31}; (27) 3,11-dimeC_{31}; (28) 15- + 17-meC_{33}; (29) 5-meC_{33}.

11.4 What do we know about recognition cues in ants?

Apart from the edited volumes on kin recognition cited earlier (see Section 11.1), which contain important chapters on social insects, there have been a number of comprehensive reviews more focused on the role of cuticular hydrocarbons, especially in ants (Lenoir *et al*. 1999; Singer 1998; Vander Meer and Morel 1998). These have stimulated an impressive body of research aimed at understanding the recognition code of ants. Our review here focuses on recent literature, and we encourage the reader to go back to these reviews for the basic knowledge.

11.4.1 'Bar-coding' and single compound recognition

Cuticular hydrocarbon (CHC) profiles are used by social insects to discriminate nestmates from non-nestmates according various levels: species, colonial, intra-colonial (castes, subcastes, reproductive status), and sometimes inter-individual. Recognition could occur through a process similar to reading a bar-code. Humans use bar-coding as a new promising tool for species identification via the mitochondrial gene cytochrome oxidase (COI). In modern taxonomy, it is especially helpful to discriminate cryptic species (Hebert *et al*. 2003; Hebert and Gregory 2005). In ants, bar-coding using cuticular hydrocarbons for species identification is theoretically possible and cheaper, but only few data are currently available, for instance on the genus *Cataglyphis* (cf. Dahbi *et al*. 1996; Oldham *et al*. 1999), the *Pachycondyla villosa* complex (Lucas *et al*. 2002) and the *Tetramorium caespitum/impurum* complex with six chemotypes (Steiner *et al*. 2002). In a recent study, the two sympatric colour morphs (red and black) of *Camponotus rufifemur* appeared to be chemically different with almost no hydrocarbons in common (Menzel *et al*. 2008). They may be two different species. Another study investigated 13 species of the genus *Formica* (Martin *et al*. 2008b) and a large program of species identification using CHCs is certainly an interesting challenge to be pursued. In termites, chemosystematics seems to be more advanced as phylogenetic analyses with cytochrome oxidase or microsatellites corroborate results obtained with chemical characterization (Copren *et al*. 2005; Dronnet *et al*. 2006).

New techniques have been used to discriminate between different species, colonies, and castes by measuring cuticular hydrocarbons levels with infrared photoacoustic spectroscopy, for example, for *Ectatomma* (Antonialli *et al*. 2007; Antonialli *et al*. 2008) and for *Oecophylla smaragdina* (Newey *et al*. 2008). Using spectroscopy may be a faster and less-expensive alternative to the analysis of cuticular hydrocarbons with gas chromatography or mass-spectrometry.

How many compounds are necessary for bar-code recognition among ants? Generally, bar-code discrimination cannot be based on one or a few compounds, but requires a complex blend of non-volatile compounds (Boomsma and Franks 2006). However, single compounds might play a role in within-colony discrimination, for example by characterizing the queen or reproductive individuals. In *Pachycondyla inversa*, the hydrocarbon 3,11-dimethylheptacosane is very abundant only on the cuticle of the queen and dominant egg-laying workers in queen-less colonies (Heinze *et al*. 2002b). Electro-antennography showed that workers react preferentially to this compound, which is correlated with ovarian activity and is likely to assume the role of a fertility signal (d'Ettorre *et al*. 2004). In *Dinoponera quadriceps*, this function is attributed to 9-hentriacontene (Monnin *et al*. 1998, 2002). However, evidence, although strong, remains correlative, and the role of these substances has not yet been demonstrated experimentally.

Other questions involve the respective role of the different hydrocarbon classes. The saturated *n*-alkanes have been considered to be important mainly for protection against desiccation, while branched alkanes appear to play a major role in nestmate recognition. In *Pachycondyla* species, internally branched methyl- and dimethyl-alkanes are indeed involved in recognition (Lucas *et al*. 2005). In *Camponotus cruentatus*, the colonial specificity is very important (see later) and trimethyl-alkanes, which are unusually abundant in this species, could play a central role (Boulay *et al*. 2007a). The picture is certainly more complex than previously thought, since recent data reveal different – and sometimes contrasting – results. In *Linepithema humile* and *Aphaenogaster cockerelli*, by using inert support such as glass beads or pieces of cotton coated with different hydrocarbon mixtures, it has been shown that a combination of at least two CHC classes is necessary to elicit an aggressive response. However, interestingly, no single class is more important than the others in eliciting the response (Greene and Gordon 2007b). In *Formica*, experiments involving glass beads and synthetic hydrocarbons showed that alkenes may have a more important role. In *F. japonica*, both *n*-alkanes and 9-alkenes are necessary to discriminate nestmates from aliens (Akino *et al*. 2004). But in *F. exsecta*, despite the cuticular profile being composed of alkanes and Z9-alkenes, aggression is elicited only by the alkenes (Martin *et al*. 2008b). Thus, more experiments are necessary to elucidate the roles of the various hydrocarbons classes, which appear to differ among species.

11.4.2 Cuticular hydrocarbons and task specificity

A correlation between the task an ant worker is performing and its CHCs is well known. For instance, ants modify their CHC profile when they become older and begin to forage. The role of juvenile hormone (JH) in temporal polyethism was first discovered in bees and wasps (Giray *et al*. 2005; Robinson 1985) and it has been recently confirmed in ants. The topical application of JH accelerates CHC modifications in the transition from brood-tender to forager in *Myrmicaria eumenoides* (Lengyel *et al*. 2007). Juvenile hormone has also been shown to be involved in the expression of possible fertility signals. Topical applications of a JH analogue (Cuvillier-Hot *et al*. 2004) could induce a decrease in fertility and a change of the cuticular profile in the monogynous queenless ant *Streblognathus peetersi*. Thus, cuticular hydrocarbons could inform nestmates about the hormonal state connected to dominance and fertility in a particular individual. Indeed, in *S. peetersi*, alpha workers are characterized by low levels of JH (Brent *et al*. 2006).

Despite much correlative evidence, experiments directly testing synthetic hydrocarbons and the role of different hydrocarbon classes are only few. The harvester ant *Pogonomyrmex barbatus* provides an interesting example. The CHCs are used for nestmate recognition in this species (Wagner *et al*. 2000), but the relative abundance of *n*-alkanes is 20% higher in foragers than in workers performing colony maintenance activities (Wagner *et al*. 1998). This might help prevent desiccation since these workers are foraging in a desert environment. Moreover, a particular group of workers, called patrollers, can stimulate foraging activity when a new seed source is discovered. These patrollers have a distinct CHC profile, and a series of elegant experiments showed that dropping glass beads coated with patroller CHC extracts inside the nest could mimic returning patrollers and induce foraging activity (Greene and Gordon 2003).

11.4.3 The genetic basis of cuticular hydrocarbon profile

Direct genetic control over CHCs is well known in *Drosophila* (Ferveur 2005). In social insects, there is also evidence that hydrocarbon composition, and therefore nestmate recognition cues, can be in part genetically determined. Nestmate recognition appears to be genetically based in *Formica polyctena*. Field experiments conducted on nests in pine forests of Germany showed the existence of a strong relationship between genetic distance and aggressive behaviour. This can be pictured as a sort of 'genetic gestalt': genetically related nests tend to show little aggressive behaviour (genetically determined recognition cues, namely CHCs), but there is no correlation between physical nest distance and aggression (Beye *et al*. 1997). Likewise, aggression increases with genetic distance between nests in *Formica pratensis*. But here dispersion often occurs by fission (a form of 'dependent colony foundation', see Chapter 9) and thus neighbouring nests tend to be more closely related than distant nests and are less aggressive to them (Beye *et al*. 1998). Moreover, the relative importance of environmentally and genetically determined cues in this species can vary according to the social structure (monodomy or polydomy (cf. Pirk *et al*. 2001). Similarly, the variation observed in the cuticular compounds of 12 populations of *Petalomyrmex phylax* from Cameroon could be explained by a combination of both genetic and social factors (number of queens), and by the spatial distribution of populations (Dalecky *et al*. 2007).

By contrast, there is no correlation between genetic distance and nestmate discrimination in *Plagiolepis pygmaea* (Thurin and Aron 2008) and in *Formica selysi* (Rosset *et al*. 2007). It is worth noting that in *F. selysi* these authors observed that there is no difference in nestmate recognition ability between workers of single- and multiple-queen colonies. Rosset *et al*. (2007) also suggested that workers might be able to detect a signal that is characteristic of the social structure (monogyny versus polygyny). However, this signal is not known, and it would be necessary to compare the odour profiles of the two types of colonies. In the super-colonies of *Formica paralugubris*, whereby individuals mix freely among separated nests, the ability to discriminate between nestmates and non-nestmates is maintained between populations, as indicated by longer antennation bouts, and aggression increases with geographic and genetic distance (Holzer *et al*. 2006a; see Plate 11 for more on antennation).

In conclusion, general patterns are difficult to find since the relative importance of genetic and environmental factors in shaping nestmate recognition cues seems to be linked to the particular life history of the different species. We discuss possible environmental factors in Section 11.5.

11.4.4 The discovery of very long chain hydrocarbons and other compounds

The recent use of high temperature gas-chromatography columns allowed the identification of new hydrocarbons with longer chains on the ant cuticle, which have remained undetected with the commonly used columns. The discovery of these long-chain hydrocarbons opens new avenues for research in some fields such as host–parasite interactions. Usually, social parasites mimic their host CHCs (chemical mimicry, cf.Lenoir *et al*. 2001), but *Acromyrmex insinuator* do not mimic their host. Instead, this social parasite is chemically insignificant in the 'normal' C29–C35 range, where it has a very low total amount of CHCs, but it possesses large quantities of unsaturated C43–C45 hydrocarbons. The role of these CHCs is not known; it has been suggested that they are difficult to perceive, and hence may support, the chemical insignificance hypothesis. They may also function as a 'sponge' and absorb traces of lighter hydrocarbons that are used as nestmate recognition cues so to blur them

(Lambardi *et al*. 2007). However, it is too early to draw any conclusion, and this discovery calls for reinvestigating the chemical profile of all the ant species with high temperature GC-columns. For example, *Formica truncorum* was supposed to have a very simple CHC composition, with few compounds and not heavier than C31 (Boomsma *et al*. 2003). In fact, they have long-chain hydrocarbons, from 34 to 45 carbon atoms, accounting for 55% of the total CHC profile (Akino 2006). Apparently, this does not change the colonial identity, and the chemical signature of the colony is maintained with or without these long-chain hydrocarbons. Some ants will be shown not to have long-chain CHCs anyway, like *Formica japonica* (Akino 2006), whereas all the *Formica s. str*. species have C25–C37 chains (Martin et al. 2008a). *Pachycondyla villosa* has also very long chains CHCs, up to C45 (Lucas *et al*. 2004). The hydrocarbon profile of the tropical *Camponotus rufifemur* consists almost exclusively of methyl-branched alkenes from C35 up to C49 (Menzel *et al*. 2008). Interestingly, *Petalomyrmex phylax* from Cameroon has a long set of C32–C42 alkenes, and there is a geographical south bias towards substances that have a higher molecular weight (Dalecky *et al*. 2007), suggesting a role of environmental factors.

Other classes of compounds may be involved in ant nestmate discrimination. It is long known that free fatty acids and esters also exist on the insect cuticle, and steroids have been recently discovered (see parabiosis, Section 11.5.2). Cholesterol has been found in large quantities in males of *Leptothorax gredleri* (Oppelt *et al*. 2008). If these compounds have a role in recognition, it needs to be further investigated.

11.4.5 The possible role of volatiles

Cuticular hydrocarbons, which are not very volatile, have long been considered responsible for nestmate recognition as this occurs generally at very short distance between individuals: a few millimetres or maximum 1 cm (Brandstaetter *et al*. 2008; Cuvillier-Hot *et al*. 2005). Nevertheless, more volatile substances might also play a role, and nestmate recognition perhaps does not always rely only on CHCs. In two *Atta* species both inter- and intraspecific recognition seem to be mediated by alarm pheromone constituents as well as by substances from abdominal exocrine secretions (Hernandez *et al*. 2006). Akino and Yamaoka (2000) suggested that in *Lasius fuliginosus*, volatiles could act as a transient cue at short distances, while non-volatiles would serve as definitive signals for recognition of nestmates. Volatiles from the Dufour's gland are implicated in *Camponotus fellah* nestmate recognition (Katzav-Gozansky *et al*. 2004, 2008). However, here the chemical nature of the volatile cues still remains uncertain. Some simple alkanes may play a role, for example callow *Manica rubida* workers in mixed-species groups with *Formica selysi* can imprint on volatile alkanes (in particular undecane) from the *F. selysi* Dufour's gland and incorporate them into their own template. Since undecane is not present in the glandular secretion of *M. rubida*, it is learned from the *Formica* group-mates (Errard *et al*. 2008). We suggest that the role of volatiles has probably been largely underestimated, and thus requires more attention in future studies.

11.5 The ecological context

One of the principal reasons of the ecological success of social insects is their ability to exploit and monopolize food sources at the colony level. For this, they need to discriminate and exclude competitors. However, nestmate recognition plays different roles in different ecological contexts.

11.5.1 Inside the nest: role of nest material and food

Inside the nest, ants do not need to discriminate nestmates from non-nestmates as they are all supposed to be fellows (Jaisson 1991). The nest entrance is usually patrolled by very efficient guards, and aliens are not admitted into the nest. Thus, it is frequently observed that when an intruder manages to enter the nest, it is accepted. This is illustrated by the case of alate females of *Cardiocondyla elegans*, which are transported by workers into unrelated nests: outside the nest they are subject to aggression, but aggression ceases once they are inside (Lenoir *et al*. 2006). It is generally considered that nurses inside the nest are less aggressive than foragers. The walls of the nest chambers are probably saturated with hydrocarbons and other substances secreted by the ants, but their chemical identity is not known. Various myrmecophile beetles and crickets rub against the inner walls of the nest to obtain the colony odour and be tolerated by passive chemical mimicry (Lenoir *et al*. 2001).

The nest odour is important when the colony needs to emigrate. Explorers use it to mark the new nest, and when ants are given a choice, they will prefer a nest marked with colony odour over an unmarked one (e.g. *Lasius niger*; Depickère *et al*. 2004; *Temnothorax albipennis*; Franks *et al*. 2007a). On the contrary, workers of *Aphaenogaster araneoides*, which frequently migrate to a new nest, strongly avoid nests marked with colony extracts. This absence of nest marking might prevent detection by predaceous army ants (McGlynn 2007). The colony marks laid by minor workers of *Pheidole pallidula* are also used in ant clustering (Sempo *et al*. 2006). The aggregative role of cuticular hydrocarbons has also been documented in other insects, such as gregarious cockroaches. Recently, an elegant study showed that cockroaches indeed aggregate with robots impregnated with the CHCs of congeners (Halloy *et al*. 2007).

In wasps and honeybees, the nest is made with paper and/or wax that captures and retains odours and produces some key components used in recognition. Leaf-cutting ants can be compared to wasps and honeybees because the garden fungus is composed of degrading leaves and emits numerous substances influencing the nest odour. In *Acromyrmex*, the fungus absorbs the cuticular hydrocarbons of the ants and its odour is thus colony-specific (Bot *et al*. 2001b; Viana *et al*. 2001). Logically, the nest odour is influenced by the nature of the leaf used as substrate for the fungus, as was demonstrated in *Acromyrmex* long ago (Jutsum *et al*. 1979). That the diet (privet, roses, or bramble) can influence nestmate recognition has been confirmed more recently (Richard *et al*. 2004). The variation in chemical profiles of *Acromyrmex echiniator* and *A. octospinosus* ants is at least partly explained by the genetic differences in amides, aldehydes, and methyl esters, originating probably from the fungus. The fungus garden is therefore an important independent source of chemicals contributing more to the *Gestalt* than the innate chemicals of ants (Richard *et al*. 2007). In ant–plant interactions (see later) we do not know how the colony odour is influenced by the host plant, thus this is a promising field of research. *Allomerus* ants, for instance, build in their *Hirtella* host plants galleries pierced with numerous holes serving as traps to capture insect prey. A fungus that has not yet been identified is associated with the nest and probably produces compounds that are included in the ant colony odour (Dejean *et al*. 2005b).

The colony odour appears to be particularly influenced by environmental factors, such as food, in tramp species. For example, in *Linepithema humile*, the diet can significantly modify both CHCs and nestmate recognition (Liang and Silverman 2000). Similar behavioural results have been obtained in the crazy ant *Paratrechina longicornis*, although the chemical profiles were not analyzed and the study is based on laboratory observations only (Say-Piau and Chow-Yang 2003).

11.5.2 Outside the nest: territory-marking and foraging trails

Markings outside the nest may take different forms depending on the ecological context and the role of the species in the community. Workers mark the nest entrance with colony-specific chemicals to prevent intrusions. Thus, nest marking can play an important role in nestmate recognition. In *Myrmica rubra* and *Pheidole pallidula*, workers probably use their legs to transfer secretions onto the ground (Cammaerts and Cammaerts 1998; 2000b). In *Messor capitatus*, territorial marking near the nest entrance is made colony-specific by faecal spots containing hydrocarbons identical to those of the cuticle (Grasso *et al*. 2005). Wenseleers *et al*. (2002) showed that the readiness to fight in the desert ant *Cataglyphis fortis* was high for ants near the nest entrance and declined at 5–20 m. This clearly indicates that aggression is displayed in the context of the nest, and thus has more to do with nestmate recognition than with territory defence.

In some species, nestmate recognition is less strict, as shown by low inter-colonial aggression. Non-nestmate intruders are able to enter the nest in 60% of trials in *Myrmecia nigriceps* and up to 50% in *Cataglyphis cursor* (Lenoir *et al*. 1988; van

Wilgenburg *et al*. 2007). Here foragers can share food sources, and tolerance is probably favoured by high relatedness between neighbouring colonies since *C. cursor* reproduces by fission (Lenoir *et al*. 1990; Lenoir *et al*. 1988; Mayade *et al*. 1993). Another example is *Ectatomma tuberculatum*, which forms open colonies and forages in trees that are not defended as territories (Zinck *et al*. 2008). In confrontation tests between ants of different aggressive colonies, the 'winner' is generally the ant that is on its own territory (Fresneau and Errard 1994). This 'bourgeois strategy' has been investigated in *Cataglyphis niger* where the chemical cue advertising the ownership comes from the cloacal gland (Wenseleers *et al*. 2002). Some ant species might mark their entire home range with colony-specific chemicals. However, various species apparently mark their home range in a way that is not colony-specific, as has been observed in two *Tetramorium* species (Cammaerts and Cammaerts 2000a) and in *Lasius niger* (Devigne and Detrain 2002). In general, the identity of the marking substances is not known. The differences in all these data on 'territorial pheromones' may be explained by the different contexts used in the studies: for example, in *Myrmica* it refers to walking speed, while in others it refers to fighting advantages.

The famous wood-ant *Formica* wars with hundreds of corpses at the frontiers of colonies in spring and the ants' cannibalistic behaviour have impressed the human imagination (Mabelis 1979). Some ant species do have a real territory, which is actively defended and marked chemically according to the strict definition of Hölldobler and Wilson (1990). Territorial ants, such as *Pogonomyrmex* (Hölldobler 1974), usually form large over-dispersed colonies where the nest distribution allows foraging on non-overlapping areas or trunk trails thus reducing the number of aggressive interactions. Generally, these ants learn the colonial identity of their neighbours and consequently are less aggressive towards these known neighbours than towards complete strangers, a phenomenon called 'dear enemy' (see review in Knaden and Wehner 2003). On the contrary, in *Camponotus cruentatus*, where colonies have very different CHC profiles, the territories can overlap by 40%, but workers fiercely defend food sources against neighbouring colonies without any 'dear enemy' effect (Boulay *et al*. 2007a).

In the tropical rainforests, many ant species have evolved an arboreal life, some species are dominant and form very large colonies with absolute territories defended against neighbouring colonies of their own or other species. They are distributed in a mosaic pattern (Blüthgen and Stork 2007; Dejean *et al*. 2007a; see also Chapter 5). Weaver ants *Oecophylla* are a typical example of territorial arboreal ants, which mark the leaves with rectal pheromones that can persist for more than nine months under the tropical rains (Dejean and Beugnon 1991). These marks are used by other ant species to avoid the *Oecophylla* territories (Offenberg 2007). Herbivorous beetles are also able to detect these pheromones and avoid feeding on *Oecophylla* ant trees (Offenberg *et al*. 2004). Here again, we do not know the identity of the chemical signals.

Plant-ants are obligate associates of specialized plants called myrmecophytes (i.e. plants offering to their guest ants special structures called domatia; see Chapter 6). In these ant species, one colony generally occupies one tree for nesting and foraging, the tree being a real territory (Dejean *et al*. 2007a). When the distribution of trees is over-dispersed, the colonies tend to be isolated. In two *Allomerus* species in Guyana, it has been observed that intra-specific aggressiveness is very low, while interspecific conflicts between different species are very violent. This does not mean that the ants have lost nestmate recognition, but the strictly arboreal life of these ants and the distance between trees, which make the encounters almost impossible, may explain the loss of intra-specific aggression (Grangier *et al*. 2008).

Territorial ants are dominant in the ant community, and defend their territory not only against conspecific, but also against allospecific intruders (see Chapter 5). *Camponotus cruentatus* is a good example of ecologically dominant ant in the Mediterranean region, whereas *Aphaenogaster senilis*, which is not territorial, is subordinate (Figure 11.3). Subordinate ants use several strategies to avoid conflicts with the dominant ones, for example foraging in a different time-window leading to temporal partitioning (Cerdá *et al*. 1997). Are ants able to recognize the other species? Evidence suggests

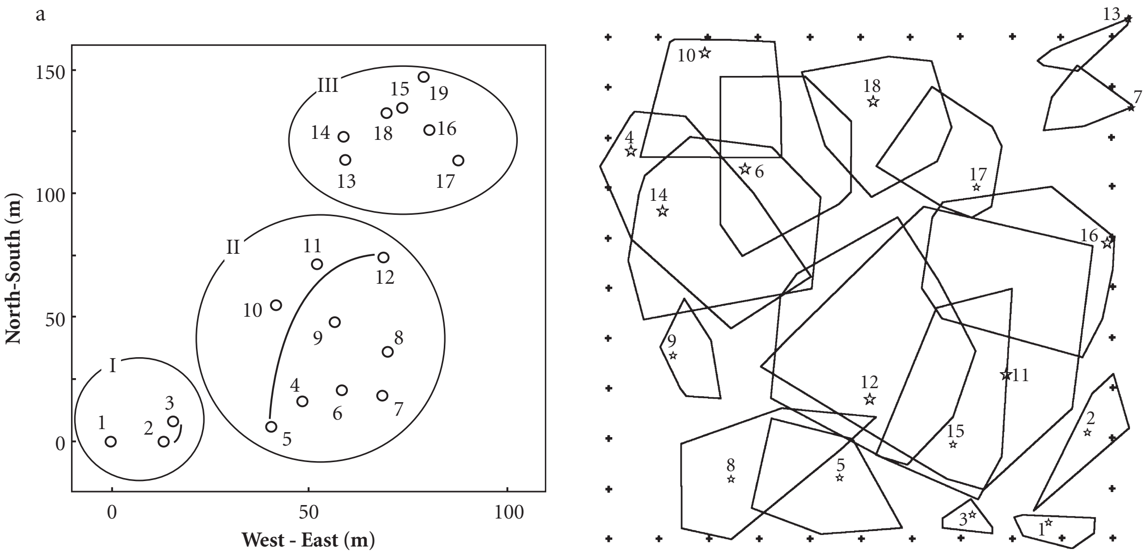

Figure 11.3 (a) Distribution map of *Aphaenogaster senilis* nests in Doñana National Park (Andalousia, South Spain, sea level). This ant species reproduces by dependent colony foundation and inter-nest aggression is low. Nests are presented in three groups according to their behavioural indices of aggression and chemical distances. Intra-group aggression is low, indicating a possible common ancestor fissioning group. Nests 2–3 and 5–12 have probably recently been founded. (Modified from Ichinose *et al*. 2005) (b) Map of 18 major nests of *Camponotus cruentatus* localised on or near the 50 x 50 studied plot in Sierra de Cazorla (South Spain, 1400 m asl). The polygons delimit the area within which 95% of the workers of a given nest forage. The overlap between the different areas is 44%. Nevertheless, food sources are fiercely defended against any other neighbour. Hydrocarbon profiles of the colonies are strictly different. (Modified from Boulay *et al.* 2007a)

that they do, for instance, *Camponotus foreli* workers always attack *Cataglyphis iberica*, whose colonies are then eliminated, while they tolerate *A. senilis* (Cerdá and Retana 1998).

Trails can contain colony-specific components also outside the territory, on the non-defended home range. In *Lasius nipponensis* (cf. *L. fuliginosus*) and *L. japonicus* (cf *L. niger*) trails are used by one colony only. The trail pheromone is not colony-specific, but the specificity is given by footprint hydrocarbons that are almost identical to CHCs (Akino and Yamaoka 2005a,b). This prevents the exploitation of trails by neighbouring colonies. A more elaborate association is parabiosis, where two (or more) species share the same nest and use the same trails. This phenomenon is frequent in Neotropical ant gardens (reviewed by Menzel *et al.* 2008). Since parabiotic species need to tolerate heterospecific ants as nestmates, they must have modified their recognition system. Habituation to the others' odour seems to be the mechanism. In the association between *Odontomachus mayi* and *Crematogaster limata*, the ants have completely different chemical profiles, and the learning is limited to the partner colony only (Orivel *et al*. 1997). In the rainforest of Borneo, there is the interesting case of parabiotic association between *Crematogaster modigliani* and *Camponotus rufifemur*. The latter is tolerant towards any colony of *Cr. modiglianii*, but not towards other *Crematogaster* species (Menzel *et al.* 2008). This might be explained by the unusual cuticular profiles of these species, which are covered by a set of steroids that have not yet been identified. The composition of these steroids differs between colonies, but is more similar for the two species of the same parabiotic nest. Whether steroids play a role in nestmate recognition is under investigation. The reduced discrimination of heterospecific nestmates might be caused by transfer of *Ca. rufifemur* hydrocarbons to the *Cr. modiglianii* profile.

Extremely long-chain hydrocarbons may be difficult to detect by antennal receptors, and hence result in chemical insignificance (Menzel *et al*. 2008). This species-specific, but not colony-specific tolerance contrasts with the above results, indicating that recognition in parabiosis may be due to a different learning process and different templates.

11.6 Concluding remarks

The amazing ecological success of ants is due in part to their ability to discriminate nestmates from non-nestmates, not only individuals belonging to colonies of the same species, but also to other species. Inside the colony, ants, for example, *Pogonomyrmex barbatus*, recognize individuals performing different tasks and can also discriminate social status (Sections 11.4.1 and 11.4.2). Outside the colony, ants know their surroundings, their nest entrance, and home range. The current body of evidence suggests that nestmate recognition in ants is mostly based on a mechanism of phenotype matching, even if other mechanisms cannot be excluded. Early in its development, an individual worker would learn the relevant cues from its fellows and build a template representing the colony odour profile. This is similar to the process of imprinting, and has been shown in several ant species (Jaisson 1991). In many cases, we have clear proof that cuticular hydrocarbons are among the relevant recognition cues, and that the colony odour is formed by mixing together the cues of basically all the colony members via social interactions (allogrooming and trophallaxis with the involvement of the post-pharyngeal gland (cf. Lenoir *et al*. 2001; Lenoir *et al*. 1999). Thus, the colony odour is not the simple sum of cues of the different individuals, but it is a new configuration, a pattern of elements resulting into a unified whole (*Gestalt*).

Depending on the life histories and the ecological and evolutionary constraints of the different ant species, the proportion of cues that are genetically and environmentally determined will vary (Sections 11.4.3 and 11.5.1). When the environmental component of the cue-expression is significant, the internal template of each individual needs to be flexible to adapt constantly to the changes in the local environment. Since nestmates and non-nestmates may have overlapping cues, the discriminating response of ants – similarly to other social organisms – cannot be perfect, and is likely regulated according to an acceptance–rejection threshold. Indeed, the acceptance threshold model (Reeve 1989) predicts that recognition systems are not fixed, but context-dependent, and the threshold should vary according to the cost and benefits of accepting non-nestmates and rejecting nestmates (recognition errors). The model has been tested in a host–social parasite system and has been supported by the observation of a significant adaptive behavioural flexibility (level of aggression) of the host species linked to the seasonal dynamics of the social parasite (d'Ettorre *et al*. 2004). According to the threshold model, aggression as a result of non-nestmate discrimination is an 'all-or-none' response: either there is aggression or not, but the threshold as well as the template can vary (Liebert and Starks 2004). Alternatively, the graded model proposes that ants progressively vary their level of aggression according to the difference between the template and the pattern of cues borne by the encountered individual (Lenoir *et al*. 1999). Evidence for a graded model in nestmate discrimination is given by the observation that longer antennation time is required when the chemical signature (cues) differs slightly from the template (Dahbi and Lenoir 1998; Holzer *et al*. 2006a). However, these two models are by no means mutually exclusive.

In some particular circumstances, ants have been shown to have unexpectedly sophisticated recognition abilities. This is the case of co-founding queens of *Pachycondyla villosa* and *P. inversa*, which are capable of individual recognition (d'Ettorre and Heinze 2005; Dreier *et al*. 2007). Unrelated queens found new colonies together, but when they first meet they aggressively establish a dominance hierarchy that later controls the partitioning of work and reproduction. Individual recognition in these small societies is advantageous because it facilitates the maintenance of stable dominance hierarchies and avoids the cost of repeated aggressive encounters. We know that individual recognition in *Pachycondyla* ant queens is based on the long-term memory of chemical cues, but there is no direct proof that these cues are indeed cuticular hydrocarbons, although the cuticular chemical profiles of queens are neither associated with dominance nor with fertility, and nestmate queens do not share a common odour.

Recent results suggest that ant workers of *Cataglyphis niger* can also discriminate different individuals. By using a habituation–discrimination paradigm (Nowbahari 2007) showed that adult workers learn the cues of individual ants that they have encountered and recognize them in subsequent encounters. Workers are less aggressive towards familiar non-nestmates than towards unfamiliar ones.

Finally, ants are apparently capable of a sort of 'latent learning'; for example they can learn what to do or not to do when they are confronted with the choice of a new nest using both pheromones and landmark cues. Thus, ants are possibly able to make plans for the future (Franks *et al*. 2007b).

11.7 Future directions

Despite the recent advances in analytical technology and the flourishing of studies in the last decades, the recognition code of ants and other social insects is far from being ultimately deciphered. As a usual occurrence in science – and this is one of the reasons why it is so fascinating – while investigating old questions, researchers find new questions instead of clear answers. We would like to draw attention to some issues that need to be considered and therefore constitute the ground for promising future studies.

- Is there something other than cuticular hydrocarbons acting as recognition labels?

Cuticular hydrocarbons have long been considered as the best candidates for recognition cues (cf. Howse 1975); however, although their importance has been confirmed in many cases, recent findings beg for exploring the potential role of other compounds by following new research directions. We have already discussed the possible implication of volatile chemicals from exocrine glands in Section 11.4.5. Here we point out a recent study that looked at a different category of substances. Paper wasps hibernate in particular safe locations that can be used by subsequent generations of foundresses. Turillazzi *et al*. (2006) experimentally showed that these hibernation sites are marked with venom secretions and cuticular peptides. A proteinaceous pheromone has also been recently identified as having a role in termite egg recognition (Matsuura *et al*. 2007). Thus, the unexplored world of proteins and peptides opens its doors to social insect recognition. With their complex tridimensional structure, cuticular peptides could contain essential information themselves, but could also somehow embed cuticular hydrocarbons and thus change their physical and chemical properties. This might explain why isolated hydrocarbons do not always elicit a behavioural response when used alone in experimental designs.

- Does recognition always need long-term memory and integrated information processing?

The label-template matching model discussed earlier (Section 11.6) requires learning the recognition cues and forming an internal neural template that is stored somewhere in the memory and can possibly be updated. This process implies information processing at high brain centres (e.g. mushroom bodies). Is there any other parsimonious alternative? The idea of habituation, which is the simplest form of learning not necessarily requiring high brain centres, is usually dismissed (Vander Meer and Morel 1998). However, a recent study suggests that even a simpler process, receptor adaptation, which does not involve any learning, could account for recognition of non-nestmates. Ozaki *et al*. (2005) described a sensory sensillum on the antennae of *Camponotus japonicus* with a surprising function. This sensillum responds specifically to non-nestmate CHC blends and does not react to nestmates' CHC extracts. A peripheral recognition mechanism in detecting colony-specific chemical signals is thus possible (but see Leonhardt *et al*. 2007). Such a mechanism cannot account for within-colony discrimination, and we know that ants are able to detect different classes of nestmates, but these results cannot be ignored, and more studies are needed to disentangle the different mechanisms that might intervene at different levels of recognition.

- Is there an ant queen pheromone?

The ant queen pheromone is like the Metastasian Arabian phoenix: everyone says it exists, but no one knows where it is. Three recent reviews have addressed this enigma from different angles (Hefetz 2007; Le Conte and Hefetz 2008; Peeters and Liebig 2009), thus we hope that it will be solved soon, at least in some ant species. There is evidence that cuticular hydrocarbons are involved in signalling queen fertility, but there is no direct proof so far. In *Aphaenogaster senilis*, the queen signal may involve the Dufour's gland secretion more than CHCs, and this ant is probably a good experimental model system because a simple biological test can be exploited: when the queen is removed, the workers immediately reorient the developing of worker larvae to produce gynes (Boulay *et al*. 2007b).

- Can recognition be studied in the laboratory?

Most of our current knowledge on recognition systems in ants is derived from laboratory assays. How much do these reflect the natural situation? This question has rarely been addressed and we believe it is an important one. Roulston *et al*. (2003) used the Argentine ant *Linepithema humile* as a model to compare four different laboratory aggression bioassays largely used to study nestmate discrimination in ants. The assays included interactions between one live and one dead ant, two live ants, five against five live ants, and one ant introduced to a foreign colony. All assays using live ants gave comparable results, independently of the scoring method used, but pairing a live and a dead produced inconsistent results and lowered aggression levels. Nevertheless, isolated aggressive acts did not necessarily predict whole colony interactions, as some colonies that fought in bioassays merged when the entire colonies were allowed to interact. Thus, aggression tests may give only limited information about interactions between colonies. This does not mean that we should stop working in the laboratory. Some particular questions can only be addressed under controlled conditions, as when trying to disentangle behavioral and chemical cues underlying recognition (cf. Guerrieri and d'Ettorre 2008; Lucas *et al*. 2005). Nevertheless, we would like to stress that laboratory results should be interpreted with caution, and we encourage researchers to trust their doubts and to go back to the field as much as possible.

11.8 Summary

The ability to recognize group members is a key characteristic of social life. Ants are typically very efficient in recognizing non-group members, and they aggressively reject them in order to protect their colonies from robbery and parasitism. There is a range of different recognition mechanisms including prior association, phenotype matching, and recognition alleles. The concept of kin recognition should be considered different from that of nestmate recognition in ants and other social insects. Most of the available studies address the nestmate recognition level, namely the discrimination of nestmates (colony members) from non-nestmates (strangers), independently of actual relatedness. Indirect and direct evidence identify long-chain cuticular hydrocarbons as the best candidates to act as recognition cues in ants, even if other chemical substances could also play a role, at least in some ant species. The relative importance of genetic and environmental factors on the expression and variation of the cuticular hydrocarbon profile is then analyzed in connection with ecological factors and life history characterizing the diversity of ant species. There are many ongoing debates and unanswered questions about recognition cues and mechanisms. The recognition systems of ants are extremely complex.

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Glossary

active constituent: A chemical in a bait matrix that mediates ant control; includes direct toxins and juvenile hormone analogues.

aculeate wasps: A group of wasps in which the egg-laying ovipositor has been modified to form a sting; most closely related group to ants.

adaptive management: A natural resource management approach that incorporates systematic experimentation and monitoring to compare alternative management actions and update these actions accordingly.

agricultural intensification: generally associated with crop specialization, increasing mechanization, and generalized use of agrochemicals and other external inputs in the crop field.

agroforestry: Agricultural systems incorporating trees.

alate: Winged reproductive; can refer to either queens or males.

allometry: A non-linear scaling relationship between the size of an organism and the size of any of its body parts. For example, head width increases more than leg length as body size increases. The opposite is isometry, where proportions between body parts stay constant across a range of body sizes.

altruism: Lifetime improvement of a beneficiary's reproductive success at the expense of the lifetime reproductive success of the altruist.

ant garden: Ant nest consisting of epiphytic plants that profit from the association with the ants.

ant mosaics: Spatial patchworks of two or more dominant ant species that have non-overlapping territories.

antennation: Investigation of an encountered ant with the antennae; the interaction allows nestmate recognition at contact or at very short distance.

arboreal ants: Ants that live and forage above the ground in trees and other vegetation.

assemblage: A taxonomic subset of a community.

bait matrix: Substance in which active constituents are delivered to ants. Matrices can be liquid (predominantly water, but sometimes other attractive substances such as sugar or honey) or solid (typically corn grit or fishmeal).

Bergmann's rule: The hypothesis that size of individuals (or for social organisms, colonies) increases with elevation and latitude.

biodiversity: Variation in life on Earth at all levels of biological organization (genetic, species, ecosystem).

biodiversity hotspot: An area of significant biodiversity containing at least 0.5% or 1,500 species of global vascular plants as endemics, and having lost at least 70% of its primary vegetation (see: www.conservation.org). Recently Conservation International has included areas of high irreplaceability but low vulnerability as hotspots.

biogeography: Study of the distribution of biodiversity in space and time, and includes physiological, morphological, and genetic perspectives.

bioregion: See **ecoregion.**

bivouac: Temporary nest structure formed by army and driver ants. The structure consists of a mass of tightly locked individuals that protects the queen and the larvae within it.

brachypterous queen: Queen with short wings that are ineffective for flying.

brood: Immature ant individuals, including eggs, all larval stages and pupae.

budding: A synonym for **dependent colony foundation**, originally meant for polygynous species whose nests remain interconnected; often used interchangeably with the term fission.

carton nest: Nest structures built actively by ants from different substrates such as detritus, earth, plant-fibres or trichomes, or silk collected from spiders.

caste: A group of female individuals distinguished from another group within the colony, by function or morphology. See also **functional caste definition** and **morphological caste definition**.

caste determination: The process by which embryological development of a female ant is determined as either worker or queen; also see **genetic caste determination, environmental caste determination**, and **hybridization-mediated caste determination**.

central place foraging: A means of collecting food in which the forager returns to a central place to deliver food (e.g. in nesting birds or in most social insects).

cheater: A species that takes advantage of one or more benefits exchanged between two mutualists at a cost to one or both of the mutualists.

chemical insignificance: Absence or low quantities of cuticular hydrocarbons that allows acceptance in a social insect colony; characteristic of newly emerged individuals and of some social parasites.

clade: A monophyletic group; a group of biological taxa that includes a single common ancestor and all its descendants.

claustral: A mode of independent colony foundation in which the queen has sufficient metabolic reserves to raise her first brood of workers without a need to forage outside the nest.

cognitive map: A map-like representation of spatial locations stored in the brain.

colony: Eusocial society of cooperating individuals of the same ant species.

colony closure: Inaccessibility of a colony to organisms other than members of the colony.

colony fusion: Merging of two mature colonies into one.

colony odour: The colony specific blend of non-volatile substances (mostly hydrocarbons) found on the cuticle of individuals and shared among all colony members.

colony size: Number of individuals in a colony, mainly depending on the number of workers in the colony.

colony structure: The caste, demographic, genealogical, and spatial make-up of a colony.

community: Interacting, coexisting assemblages of organisms.

co-occurrence analysis: A method for testing for non-random patterns of species occurrences.

correlated random walk: A random walk (an individual turns by a random angle after each step of a given distance), with the added aspect that turning angles are normally distributed around the previous direction of the movement.

crown group ants: Clade composed of the most recent common ancestor of all living ants and their descendants.

cue: A trait that can be used in communication to extract relevant information although it has not evolved for that purpose (see also **signal**).

cuticular hydrocarbons: Lipids found on the cuticle. In social insects, a blend of long-chain hydrocarbons forms the specific colony odour and play role in protecting against insects from desiccation and in communication.

deforestation: Removal of trees (sometimes complete extraction) from forested areas; usually by logging and/or burning.

dependent colony foundation (DCF): Initiation of a new colony by a group of nestmate queen(s) and workers that leave the maternal nest together; accordingly queens never go through a solitary stage; dispersal is on the ground and thus short ranged.

diaspore: A plant dispersal unit consisting of a seed plus any additional tissues.

diploid male vortex: Reduced allelic diversity in a population at the sex-determining locus (e.g. resulting from inbreeding and population size reduction); reduced heterozygosity at the locus increases production of nonviable, diploid males which reduces population growth rate and thus further reduces allelic diversity at the sex determining locus in the population.

discovery–dominance trade-off: The inverse relationship between the ability of a species to discover food and its ability to dominate resources (either behaviorally or numerically).

domain: The geometric area of interest, may be spatial (a mountain range, the globe, a continent) or temporal.

domatia: Plant structures including hollow thorns, stems, and leaf pouches in which colonies of ants reside.

dominance–impoverishment rule: A relationship between ant species richness and dominant species in a community. The fewer ant species in a local community, the more likely it is to be behaviourally dominated by one or two species with large, aggressive colonies. In many studies, however, the direction of this causality has been reversed, and emphasis has been placed on the effect dominants have on species richness, not vice versa.

ecological gradient: A pattern, usually in richness, abundance, or body size, along an ecological axis. Common ecological axes are temperature, elevation, latitude, and net primary productivity.

ecoregion: A large unit of land or water containing geographically distinct communities associated with particular combinations of environmental conditions.

ecosystem engineers: Organisms that directly or indirectly modify ecosystem properties (e.g. the availability of resources for other species) by causing physical changes in biotic or abiotic material.

ecosystem services: Benefits humans derive from ecosystems, including provisioning services such as food and water, regulating services such as regulation of floods, drought, land degradation, and disease, supporting services such as soil formation and nutrient cycling and cultural services such as recreational, spiritual, religious, and other non-material benefits.

elaiosome: Lipid and protein-rich fleshy structures attached to seeds of many plants reliant upon ants for seed dispersal, consumed by many ant species.

endemic species: Species ecologically unique to a specifically defined place and not found elsewhere.

environmental caste determination: Exclusively non-genetic caste determination.

epigaeic ants: ground-active ants; forage primarily on the ground.

epigenetic: Changes in gene expression not involving changes in the underlying nucleotide sequence.

eradication: The intentional extirpation of geographically discrete populations of a species, irrespective of whether other discrete populations still remain within the landscape.

ergatoid queen: Under the functional caste definition, a queen with worker-like external morphology (permanently lacking wings and with a simplified mesosoma and fused sclerites); distinct from dealate queen, which is a winged queen that has shed her wings. A ‘multi-purpose’ ergatoid queen can either function as reproductive or perform worker-like sterile tasks, and is similar to workers in size. ‘Sole-purpose’ ergatoid queens function only as reproductives and may be similar to workers in size or extremely dimorphic. Identical with gamergate under the morphological caste definition.

ergatomorphic queen: see **ergatoid queen.**

eusociality: True sociality defined by reproductive division of labour between female castes, cooperative brood care, and the presence of workers of a later generation to the queen(s).

exotic species: species not native to an area of interest.

extent: The domain or scope of an analysis. For example an analysis of New World terrestrial latitudes (North and South America) has a scope of 148° of latitude (ranging from 55°S to ~83°N) or ~16,500 km (see also **grain**).

extinction: The death of every member of a population, an entire species or higher taxon from some area of interest.

extrafloral nectary: A structure on a plant that produces nectar in a location other than within a flower.

facultative polygyny: Polygyny that is not essential for a colony to remain viable. Colonies that display facultative polygyny can switch between monogyny and polygyny.

female calling: The emission, typically of pheromones, by a reproductive female in order to attract males to her.

fission: A synonym for dependent colony foundation, originally meant for monogynous species where colonies reproduce by dividing into two equal parts; often used interchangeably with the term budding.

fitness: The reproductive rate of a genotype.

food bodies: Lipid and protein-rich structures found on some species of plants; believed to have evolved in symbiotic interactions with ants.

formicoid: A well-supported clade that includes three widespread and species-rich ant subfamilies – Dolichoderinae, Formicinae, and Myrmicinae – as well as army ants and relatives (dorylomorphs), bulldog ants (Myrmeciinae), big-eyed arboreal ants (Pseudomyrmecinae), and a few other smaller groups.

functional caste definition: Definition of caste by role in the colony. Under the functional caste definition a queen is a mated individual laying both male- and female-destined eggs, independent of her external morphology, and a worker is an unmated individual that may lay male-destined eggs; compare with **morphological caste definition**.

functional monogyny: Presence of more than one mated female capable of reproduction in a colony, only one of which lays eggs.

fungus garden: The cultivation of basidiomycete fungi as a food source by ants of the Attini tribe.

gamergate: A mated and egg-laying individual with worker-like external morphology; identical with ergatomorphic queen under the functional caste definition.

genetic caste determination: Caste determination encoded in nucleotide sequences; possibly modulated by environmental influences.

Gestalt model: Establishment of a common colony odour by sharing the recognition cues (by trophallaxis and/or allogrooming).

Gondwana: Also called Gondwanaland; southern hemisphere supercontinent in the Palaeozoic Era (248 to 545 Mya), formed with the break up of Pangaea; subsequent splitting resulted in the origins of the modern continents (Antarctica, South America, Africa, Australia-New Guinea) as well as Madagascar, New Zealand, the Arabian peninsula, and the Indian subcontinent.

grain: The resolution of an analysis, can range from 1 m^2 to 100 m^2 for local analyses of ant diversity up to 100 km^2 to 100,000 km^2 for regional or hemispheric scale analyses. Also see '**extent**'.

granary: A nest chamber in seed-harvesting ants in which the ants store plant seeds they have collected.

granivore: An organism that consumes seeds as a main food source.

group selection: Natural selection that works to the advantage of a group of not necessarily related individuals.

gyne: Broad term for a female reproductive; queens are functioning gynes.

habitat disturbance: Any event that removes biomass from a habitat.

habitat specialist: Species that can live and reproduce only in a particular type of habitat.

habitat transformation: Any event that reduces available resources or changes the microclimate or structure of a habitat.

haplodiploid: See **male haploidy**.

haplometrosis: Foundation of a new colony by a single queen.

honeydew: The carbohydrate-rich excreta of hemipterans that feed on plant sap, often collected and fed upon by ants.

hybridization-mediated caste-determination: Genetic caste determination in hybrids fixed in populations, workers bear the genomes of both parental species, but queens that of only one.

hypogaeic ants: Ants that forage and live underground.

inbreeding: Mating between related individuals.

inbreeding depression: Decreased population vitality in terms of growth, survival, or fecundity following inbreeding.

inclusive fitness: The fitness of an individual, taking into account not only that individual's own success in passing on genes to the next generation, but also the success of all its kin, that is, those bearing some portion of the same genotype; see also **kin selection** and **fitness**.

independent colony foundation (ICF): Initiation of a new colony by a solitary queen who raises her first brood of workers without the help of workers from the maternal nest, generally after dispersal flight and mating. See also claustral and non-claustral.

inquilinism: Extreme parasitic state where the parasitic species lacks a worker caste and is thus fully dependent on its host's workers to complete its life cycle.

insect growth regulator: Chemical used in ant baits that halts normal development of insects. They typically affect all stages of development including eggs, larvae, pupae, and adults. In reproductive individuals ovaries are compromised and production of eggs becomes limited or stops altogether. Includes juvenile hormone analogues.

integrated pest management (IPM): Pest control strategy that uses a range of complementary techniques to manage pest populations. It aims to also reduce reliance on chemicals. Techniques used include mechanical and physical devices, genetic, biological, and cultural control, as well as chemical control.

interspecific competition: Competition between and among individuals of different species.

intracolonial relatedness: Degree of average relatedness across all individuals of the colony; extreme values are 0.75 under monogyny–monandry and 0.0 in a spatially extensive supercolony.

intranidal: Within the nest.

intraspecific competition: Competition between individuals of the same species.

invasive: Those ant species that demonstrate ecological, environmental, or economic impacts.

invasive alien species: A species that has been introduced to an area and is invasive; distinct from alien, exotic, introduced, tramp, and other terms that only denote origin.

IUCN Red List of Threatened Species: A list of taxa deemed threatened by IUCN criteria, it provides taxonomic, conservation status, and distribution information (http://www.iucnredlist.org).

juvenile hormone analogue: Synthetic version of a biological juvenile hormone. These hormones regulate many aspects of insect physiology. The juvenile hormone analogues used in ant baits most commonly halt development of workers before becoming adults (at various stages).

keystone species: A species whose impact on its community or ecosystem is disproportionately large relative to its abundance; also a species that regulates local species diversity in lower trophic levels.

kin selection: Natural selection mediated by interactions between relatives. Under Hamilton's formulation, an individual's fitness is divided into personal reproductive success and the effects of the individual on the reproductive success of others weighted by relatedness, a formulation under which reproductive self-sacrifice is selected for if the transmission of genes identical to genes in the altruist by relatives is increased sufficiently.

leaf litter: The layer of decaying leaves, rotting wood, and other organic material that accumulates on the ground, typically under woody vegetation.

macrogyne: The larger queen morph under queen dimorphism.

male aggregation: The mating arrangement whereby males from different nests assemble in a group for queens to join them for the purpose of insemination.

male haploidy: Genetic system in which males are haploid; in Hymenoptera this results from normal males arising from unfertilized eggs and females from fertilized ones. Males are thus a genetic subsample of their mother which results in a relatedness asymmetry in the colony. Generally seen as a synonym for haplodiploidy.

mesosoma: in the Apocrita, the fused thorax and first abdominal segment

metapleural gland: Gland on the alitrunk that is peculiar to ants, although not all ant species possess it. Produces and secretes antibiotics that can prevent the growth of bacteria and fungi on the ants and inside their nest.

microgyne: The smaller queen morph under queen dimorphism.

monandry: Mating of a queen with just one male.

monodomy: The use of a single nest by a colony. Serially monodomous colonies construct more than one nest but live in only one of them at a time.

monogyny: Possessing a single queen. Primary monogyny is monogyny resulting from haplometrosis. Secondary monogyny results from pleometrosis in which only one of the founding queens persists.

monophyletic: See **clade**.

morphological caste definition: Definition of caste under which a queen is morphologically distinguishable from a worker; not applicable to all ant species; to be distinguished from the **Functional caste definition**.

morphospecies: Species that are distinguished solely on the basis of appearance.

multicoloniality: Colony structure characterized by distinct colony and nest boundaries within a population.

multi-level selection: Selection operating at several levels including individual, patriline, matriline, nest, colony, and population.

mutualism: An interaction between two species that is mutually beneficial to the fitness of each. Obligate mutualisms are required for the persistence of a species, facultative mutualisms are not required for the persistence of a species.

myrmechophile: An organism that lives in association with ants.

myrmecochore: A plant that depends in whole or in part upon ants for seed dispersal.

myrmecochory: Ant dispersal of seeds.

myrmecophyte: A plant that permanently hosts a colony of ants in specialized domatia and usually provides food in the form of food bodies or extrafloral nectar.

natural enemy: A predator, parasite, parasitoid, pathogen, or herbivore adversely affecting the species or group of species being described.

nest: Dwelling of a colony.

nest chamber: Cavity within a nest, distinct from tunnels.

nest odour: Mixture of all substances found inside or at vicinity of the nest, including the colony odour, which allows orientation to and recognition of the nest.

nestmate recognition: Recognition of individuals of the same nest sharing a common colony odour allowing altruistic behaviours towards nestmates and discrimination and rejection of non-nestmates.

net diversification: The difference between the rate of extinction and the rate of speciation.

net primary productivity (NPP): A measure of the grams of carbon per unit area per unit time sequestered.

non-claustral: Mode of independent colony foundation where the queen has limited metabolic reserves and needs to forage outside the nest regularly to feed her first brood of workers.

null models: Models that exclude some process of interest in order to consider the pattern expected in its absence. A null model of diversity along gradients is used to examine the pattern of diversity that would be expected in the absence of climatic drivers of diversity.

nutrient balance: Ratio of nutrients (e.g. carbohydrate–protein balance) contained in food. Food that is ingested that diverges from the optimum for an organism requires the excess nutrients to be excreted so that the balance is achieved.

nutritional upgrading: Enhancement of nutritional value of food sources by endosymbiotic bacteria either via recycling of excretions or production of higher quality nutrients from lower quality ones, e.g. production of essential amino acids from non-essential ones.

obligate polygyny: Polygyny that is necessary or essential for the species to ensure full viability and reproduction success of a colony.

oligogyny: A special case of polygyny in which colonies possess a low and limited number of queens that are intolerant of each other and frequently occupy different parts of the nest.

omnivore: A consumer feeding on both plant- and animal-based diets; a mixture of primary and secondary consumption.

parabiosis: Association of two or more ant species in the same nest, involves cooperation of the two colonies but separation of brood.

paraphyletic: A group of biological taxa that contains a common ancestor, but does not contain all descendents of that ancestor.

parataxonomist: A biodiversity collection and inventory specialist, usually recruited from local areas and trained by professional biologists, who typically collects specimens, prepares them and sorts them into morphospecies.

pest risk analysis (PRA): Combination of risk assessment and risk management for a particular pest threat. Pest Risk Analysis aims to directly link the severity of the risk to management objectives and priorities.

pheromone: A chemical substance (or a specific blend of substances) that mediates communication between members of the same species. By contrast, allelomones mediate communication between members of different species (and are further distinguished in allomones, kairomones, and synomones). Pheromones are called releasers if they trigger an immediate behavioural response in the receiver; and primers if they cause physiological changes in the receiver that can eventually result in a behavioural response.

phragmosis: Blocking of the entrance of the nest by a body part, usually the head; usually performed by a morphologically specialized worker subcaste.

phylogenetic diversity: A measure of biodiversity based on the length of evolutionary pathways that connect a given set of taxa (sum of the length of branches of a phylogeny).

phylogeny: The evolutionary development and history of a particular taxonomic group, usually a species or higher taxonomic grouping; constructed using molecular sequencing data and morphological data matrices.

physogastry: Enlargement of the gaster by stretching of the intersegmental membranes, allowing for increased ovarian activity.

pleometrosis: Foundation of a new colony by two or more cooperating queens.

polyandry: Mating of a queen with more than one male.

polydomy: The use of two or more spatially separated nests by one colony.

polyethism: Functional specialization of different workers of the colony leading to a division of labour among workers; may be as a function of age (age polyethism) or permanent, involving specializations of individuals over their entire adult life, sometimes but not always accompanied by morphological adaptation, see also **caste**.

polygyny: Possessing more than one queen, distinct from oligogyny in that several to very many queens mix freely within the nest. Primary polygyny results from pleiometrosis. Secondary polygyny develops from a colony founded by a single queen that later adopts other queens. Serial polygyny is a derived strategy under monogyny whereby after the queen's death she is replaced by a daughter-queen to avoid colony dissolution, resulting in temporary coexistence of worker offspring of different queens.

polymorphism: Substantial differences in the size and/or shape of non-gyne females in the same colony; see also **worker subcastes**.

population viscosity: A measure of the genetic isolation-by-distance effect across colonies of a population.

post-pharyngeal gland: A gland positioned in the head, mainly found in Formicinae, that produces salivary secretions and functions as a reservoir of hydrocarbons that are shared between individuals by trophallaxis.

propaganda pheromone: A volatile substance used by social parasites to influence workers of a host ant colony.

proventriculus: Valve-like muscular and sclerotized structure separating the crop from the midgut. The proventriculus is important in ants feeding largely on liquids since it dams the efflux of liquid from the crop into the midgut and therefore allows storage of large volumes of liquid in the crop.

queen: A mated female reproductively active and able to produce offspring of both sexes; frequently queens differ in their external morphology from workers, mainly by wings, and by larger mesosoma size.

queen dimorphism: Existence of two distinct queen phenotypes in a species.

Rapoport's rule (also Rapoport pattern): The hypothesis that there is a positive relationship between range size and latitude.

rare species: Species with low abundance that are infrequently encountered; may have a widespread or localized distribution.

relatedness asymmetry: The state of one individual being more related to another than the other is to it, e.g., under male haploidy, a father is twice as related to a daughter as she is to him, and sisters are more related to each other than their brothers are to them.

replete: A worker with her crop full of sweet liquids for provision; an example of permanent polyethism, not present in all species.

selective logging: A type of logging where only certain, usually economically important, tree species are removed from forests.

sex allocation: Proportion of investment in either male or female reproductive function, generally measured as the proportion of investment into producing males to queens.

sex determining locus: The genetic locus that governs sex determination whereby heterozygosity results in females but homozygosity in non-viable, diploid males; viable males are haploid. Not yet identified in ants.

sex ratio: Proportion of reproductive individuals of both sexes produced.

signal: A trait that evolves in a signaller to provide information to a receiver in a way that induces a change in the behaviour of the receiver for the benefit of the signaller (see also **cue**).

silvopastoral system: Pasture or grazing systems that include trees.

social parasite: Ant species that live in the nest of another genetically distinct ant species almost exclusively producing sexual offspring while remaining reproductively isolated from their hosts.

soil bioturbation: Movement of soils; caused by ants through the formation of mounds, subterranean galleries and chambers, and the movement of soil particles along the soil profile.

soldier: A distinct worker phenotype that is functionally specialized for the role of colony defence.

speciation: The evolutionary process by which one species forms a new species.

species diversity: Species richness weighted by some measure of abundance such as number of individuals or biomass. Many people use the term species diversity when they are actually referring to species richness.

species richness: Number of different species in a sample, location, region, habitat, ecosystem, or other biological unit.

stable isotope: Any of the different types of atoms of the same chemical element that differ in atomic mass and do not decay.

stable isotope analysis: The measurement of the ratio of two stable isotopes of an element typically to estimate the relative contributions of multiple resources to a consumer or the consumer's trophic position.

stem group ants: All the taxa in a clade preceding a major cladogenesis event. For ants a group containing all organisms more closely related to ants than to any other extant taxa; can refer to extinct taxa that are outside the crown group but that are inferred to be more closely related to ants than to any other living aculeate wasps.

supercolony: An ant colony with multiple queens integrated harmoniously over a large area. Individuals freely mix among nests across spatially separate parts of the colony.

symbiosis: The close and often long-term relationship between different species that is frequently, but not always beneficial to one or both species.

systematics: Study of relationships among taxa through time involving the systematic classification of organisms and the evolutionary relationships among them.

taxon cycle: Sequential stages of expansion and contraction of the ranges of species; often linked with shifts in ecological distribution.

taxonomy (Linnaean): A method of classifying living things; originally devised by Carolus Linnaeus. It uses a combination of a genus name and a single specific characterizing word (species name) to uniquely identify each species.

template: Internal (neural) representation of the colony odour believed to be learned just after emergence (sometimes during the preimaginal period) and constantly updated.

tending: The collective actions of ants collecting honeydew and closely associating with honeydew-producing herbivorous hemipterans.

threatened species: Species that are at risk of extinction due to human activities that directly or indirectly affect their life or their habitat.

trophallaxis: The exchange of either regurgitated or excreted liquid food that occurs among members of an ant colony.

trophic egg: Egg laid for later consumption by another individual in the colony; frequently understood as a term for eggs that also are inviable.

trophic level: A quantitative description of the position a species or group of species occupies in a food chain, with primary producers being the first trophic level, herbivores the second, primary predators the third, and secondary predators the fourth.

trophobiont: see **trophobiosis**.

trophobiosis: A symbiotic association between organisms where food is obtained or provided. The provider of food in the association is referred to as a trophobiont.

umbrella taxon: A taxon for which protection also confers protection on coexisting organisms.

unicoloniality: Colony structure characterized dependent colony foundation, inbreeding, and the lack of distinct colony boundaries within a population.

worker: Female ant, typically incapable of producing offspring, and differing morphologically from the queen by absence of wings and frequently smaller mesosoma size.

worker policing: Destruction of an egg laid by one worker by another worker, to avoid a reduction of relative fitness by the egg-destroyer.

worker subcastes: Extreme case of worker polymorphism in that worker phenotypes differ in a strong deviation from isometry; a morphological adaptation to permanent polyethism.

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