



Ant Ecology

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

Foreword by E.O. Wilson



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Lori Lach, Catherine L. Parr, and Kirsti L. Abbott

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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 asso-

ciations, 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.

Acknowledgements

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.

We are extremely grateful to Ian Sherman, Helen Eaton, and Elmandi Du Toit from Oxford University Press for providing guidance, advice, and feedback at crucial times and for always being so encouraging of this project. Thank you for putting this book on your portfolio for 2009.

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

- Plate 1** *Adetomyrma* sp. mad01 has been found from only one location in Madagascar. These small, blind, hypogaecic ants have been termed ‘dracula ants’ for their habit of feeding on the haemolymph of their own larvae. (Photo: Alex Wild)
- Plate 2** Ants often defend territories and food resources aggressively (a) *Azteca alfari* (*Cecropia* ant) workers renowned for their aggression immobilize an unfortunate *Odontomachus* sp., and (b) *Oecophylla longinoda* workers pin down a *Polyrhachis* ant that has strayed too far into their territory. (Photos: Alex Wild)
- Plate 3** Ants are involved in an array of mutualistic interactions: (a) *Formica integroides* takes a droplet of honeydew excreted by an aphid, (b) a *Podomyrma* ant tends a lycaenid caterpillar, (c) *Pseudomyrmex* ants feed on special protein-rich food bodies provided by *Acacia* trees, (d) An *Ectatomma* ant feeds from an extrafloral nectary on an *Inga* plant. (Photos: Alex Wild)
- Plate 4** (a) A healthy *Cephalotes atratus* worker and (b) one infected with the nematode *Myrmeconema neotropicum*. Obvious effects of the parasite on the ant include the red gaster, erect posture, and nearly constant gaster flagging. (Photos: Stephen Yanoviak)
- Plate 5** Some ants are specialised seed predators. This worker ant, *Pogonomyrmex desertorum*, is actively harvesting a seed still attached to the plant. (Photo: Alex Wild)
- Plate 6** Members of an ant colony can vary morphologically and functionally. The image here shows the morphological distinctions among a queen (large winged), male (small winged) and worker of a *Camponotus discolor* colony. (Photo: Alex Wild)
- Plate 7** Comparison of queens and workers in relation to mode of colony founding. Species where queens perform non-claustral ICF exhibit low queen/worker size dimorphism (*Myrmecia gulosa*). In contrast, in species with claustral ICF, dimorphism is much larger and wing muscles are enlarged to function as reserves, resulting in a large mesosoma (*Lasius niger*). In species that perform DCF, the mesosoma of ergatoid (= permanently wingless) queens is simplified and closer to that of workers. The size of sole-purpose ergatoid queens varies a lot across species (from top to bottom: *Odontomachus coquereli*, *Cerapachys* sp. 1 from Madagascar, and *Dorylus molestus*). Multi-purpose ergatoid queens are more similar to workers (top: *Myrmiarium* ‘red’ from Madagascar, bottom: *Eutetramorium mocquerysi*). (Photos: www.AntWeb.org and April Nobile)
- Plate 8** Ants undergo complete metamorphosis in their life cycle. Life cycle stages of a twig ant, *Pseudomyrmex gracilis*, are shown: (left to right) an egg, three larval instars, pupa, and adult. (Photo: Alex Wild)
- Plate 9** Replete workers of the honey pot ant, *Myrmecocystus mexicanus*, hang from the ceiling of a nest chamber. They are attended to regularly by workers and sometimes cover

the ceiling of a nest chamber. The repletes' enormously extended crops have been filled with the liquid food for storage. (Photo: Alex Wild)

- Plate 10** Some species exhibit polymorphism. (a) These African driver ants, *Dorylus helvolus*, vary in body size. (b) Workers can also differ in body proportions as well as size; the head of the largest worker of these *Camponotus sansabeanus* is much larger in proportion to its body than that of the smallest worker. (Photos: Alex Wild)
- Plate 11** Two *Wasmannia auropunctata* foragers meet and assess each other. Ants communicate information by touching antennae (antennation). (Photo: Alex Wild)
- Plate 12** Workers ants can lead nestmates to food using tandem running where antennal tapping signals between the two ants control the speed and course of the run. Here, two *Pachycondyla* are tightly connected during a tandem run. (Photo: Alex Wild)
- Plate 13** Ants possess a range of morphological defences: (a) some *Meranoplus* species have a well-developed shield structure on their alitrunk while others possess dense hairs, (b) *Polyrhachis* species often have large petiolar and propodeal spines, (c) *Cataulacus brevisetosus* has heavily sculptured armouring, and (d) *Acromyrmex versicolor* has prickle-like spines covering its head and alitrunk. (Photos: Alex Wild)
- Plate 14** Some of the most notorious invasive ant species (a) the Argentine ant (*Linepithema humile*), (b) the little fire ant (*Wasmannia auropunctata*), (c) the red imported fire ant (*Solenopsis invicta*), (d) the big-headed ant (*Pheidole megacephala*) (Photos: Alex Wild) and (e) the yellow crazy ant (*Anoplolepis gracilipes*) (Photo: Paul Zborowski)
- Plate 15** Argentine ants (*Linepithema humile*) cooperatively attack a much larger Californian harvester ant worker (*Pogonomyrmex subdentatus*). Despite little overlap in resource use, harvester ants disappear from areas invaded by Argentine ants, most likely as a result of aggressive colony raids. (Photo: Alex Wild)

List of Abbreviations

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

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GLOBAL ANT DIVERSITY AND CONSERVATION

Explaining the origin and distribution of biodiversity has been a long-standing goal of ecology. As with other taxa, ant diversity varies among continents and biogeographic regions. Part I provides the evolutionary, biogeographic, and macroecological perspectives necessary to better understand global and regional patterns in ant diversity. This section addresses questions such as how many species and major lineages of ants are there? What is their evolutionary history? How are different taxonomic groups distributed globally? What processes are important in determining diversity in space and time? And, how can we apply this understanding to the conservation of ants?

Chapter 1 unravels the evolutionary history of ants using recent morphological evidence, molecular phylogenetic studies, and new fossil discoveries. Ward reports on the substantial progress that has been made in recent years in identifying major clades of ants and clarifying phylogenetic relationships. Currently there are more than 12,500 described species of ants in 290 genera belonging to 21 extant subfamilies. At the species level, although cataloguing and understanding diversity presents many challenges, advancements have been made with a relatively stable generic classification, several global species revisions, and new technological developments including imaging, Web-based databases, and DNA bar-coding.

Chapter 2 builds on themes presented in the first chapter to focus on biogeographic patterns of global ant diversity. The present-day distribution of ants reflects the combined influence of geography, geology, and climate on the origin, diversification, and spread of lineages. Gondwanaland fragments of South America, Africa, and Australia have the

highest percentage of endemic genera, while species-level hotspot areas include lowland tropical regions. Using phylogenetic-based biogeography, Fisher presents three case studies that demonstrate how information on geography and climatic events can be inferred. Available information on ant extinctions and the palaeogeographic distribution of ant fossils are reviewed.

Taking both global and regional perspectives, Chapter 3 describes diversity patterns and examines the underlying causes of these gradients. Whether for species richness, range size, or body size, ant diversity patterns generally reflect diversity patterns of other terrestrial fauna and flora. Dunn and colleagues summarize patterns of ant diversity along latitudinal and elevational diversity gradients for multiple spatial and taxonomic scales. For each gradient, potential mechanisms are explored. Knowledge about the causes and consequences of ant diversity gradients is likely to provide crucial information for improving our understanding of the effects of climate change on ant diversity.

Given the threats posed by extensive habitat modification and loss globally, especially in tropical areas that harbour exceptional levels of ant diversity and endemism, it is essential that ants are included in conservation efforts. In Chapter 4, Alonso reviews the principal threats, approaches, and challenges to ant conservation and the current status of ant conservation, concluding that attention should be focused on hotspots of richness, endemism, and islands. This chapter provides a clear call to action for all myrmecologists and lists key actions for improved ant conservation in the future.