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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.

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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

- 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, *Pogonomyrma 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: *Mystridium* '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)

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 nest-mate 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.
- epigaic 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 m² to 100 m² for local analyses of ant diversity up to 100 km² to 100,000 km² 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.

hypogaecic 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.

intracolony 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.

myrmecophile: 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.

sympiosis: 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.

unicolonality: 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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