A Field Guide to the Ants of New England

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A Field Guide to the Ants of New England

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To everyone who wants to learn more about the ants that share our planet

I spent long hours with them [the nation of ants], *and yet did not get bored. They would come and give us hope that life had not come to a halt.*

—Ahmed Errachidi, from *A Handful of Walnuts*

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Preface

Why ants, why New England, why a field guide? For the past three years, we have repeatedly been asked these questions. The short answers are: ants are important, fascinating, and cool; New England is where we live, work, and play; and field guides bridge the gap between ant farms and technical keys and encourage everyone to look more closely at what Professor E. O. Wilson calls the "little things that run the world." But now that this field guide is in front of you, you deserve some more detailed answers.

Ants are fascinating animals and are familiar to people around the world. Yet most people know little or nothing about their diversity, natural history, ecology, or evolution. What are these ants? How many different kinds are there? What do they eat? Before we wrote this book, most of our parents, nieces, nephews, students, friends, and colleagues had no idea that there are over 130 species of ants in New England alone! Now they know better.

Ants are some of the most important actors in the ecological theater (see Chapter 2). In many places, ants make up the largest proportion of animal biomass. If you put all the ants on one side of a scale and all of the animals (including humans) of any other kind on the other, ants most likely would be heavier. They eat animals (dead or alive), plants, and fungi; disperse seeds; and turn over more soil than earthworms. They are everywhere: inside and outside, in the soil of forests and meadows, in and on trees, under the sink and in the rafters, and in between the cracks in the pavement. Aspects of our own human societies are mirrored in ant societies. Workers cooperate and divide up labor within colonies, but different colonies fight for food and space, battle over territories, and even parasitize or enslave one another. This is not always a mirror into which we want to look, however; their lives and behaviors have been caricatured in many books and movies, from H. G. Wells's *Empire of the Ants* (1905) through Gordon Douglas's *Them* (1954) to Eric Darnell and Tim Johnson's *Antz* (1998). Because ants are important, fascinating, and cool, we set out to write a book for people interested in learning more about them and their world.

Ants occur on every continent except Antarctica and in habitats ranging from the Arctic tundra to dry deserts and tropical rainforests. Ants live where people are and where they have been, including rural villages, suburban towns, and densely populated cities, as well as in abandoned mines and overgrown vacant lots. New England is a manageable microcosm of the larger world. We divide the region politically into six states—Maine, New Hampshire, Vermont, Massachusetts, Connecticut, and Rhode Island—but ants, like Boston Red Sox fans, show little respect for state boundaries. Instead, ants are tied to ecoregions: coastal plains with their beaches, dunes, and pine barrens; upland coniferous, deciduous, and mixed forests; the farm fields and old fields in between; and the wetlands, rivers, lakes, and streams that connect all of these habitats (see Chapter 1). This range of habitats and the variable climate of New England are similar to those of much of the eastern United States and Canada, so the utility of this guide extends well beyond New England. In the descriptions of individual species (Chapter 5), we include over a dozen species that currently reach the edges of their range on New England's borders in Canada and New York. As the climate changes, some of these may make their way into New England itself.

Ants, like birds, butterflies, and dragonflies, are enchanting to observe in the field and are downright spectacular when viewed through a hand lens or a dissecting microscope. The ant fauna of New England displays a stunning variety of sizes, colors, sculpturing, armor, ornamentation, and hairiness. In brief, ants are beautiful. The creations of advertisers, computer graphics artists, cinematographers, and toy makers often are inspired by ants, and it is aesthetically pleasing to study their features at the same time that we identify them. In this guide, we celebrate such beauty. At the same time, we have designed this book for beginners first learning how to identify ants and for the experts who make their living studying them.

With only a little background and practice, and a hand lens, amateur naturalists, teachers, and students of all ages can learn to identify the common groups (genera) of ants. In fact, the illustrated key to the genera printed on the inside front cover of this field guide is designed to be used while observing ants with a 10 hand lens—no microscope required! The modest diversity of New England ants (just over 130 species in 31 genera and 6 subfamilies) makes them practical subjects for studies of biodiversity and conservation in the classroom and the field. It can be hard to determine the precise identity of an ant in the field because they are small. However, accurate species identification of pinned specimens under a dissecting microscope is easier because ants have distinctive features visible on their bodies. It is easy to distinguish among many ants once you know what to look for. With this guide, anyone can learn the manageable group of New England ants.

Ant species are identified by using keys (see Chapters 4 and 5). The first comprehensive key to all of the ants of North America was published in 1950, has never been revised, and is now out of print. A complete key to the genera of North American ants was published only in 2007. Before we wrote this book, the identification of ant species from any particular region would require dozens of specialized keys that were published in obscure journals and that contained only a few line drawings illustrating the most important features or characteristics. Many of these keys could be deciphered and used only after you already knew how to identify the species!

Using identification keys is an exercise in deduction, but it need not be an exercise in frustration. Although scientists have developed specialized vocabularies for each group of organisms and myrmecologists (literally, "students of ants") have developed their own arsenal of distinctive terms, our keys use relatively simple language, and all terms are illustrated (see Chapter 4 and the diagrams printed on the inside back cover). The keys themselves are copiously illustrated: over 500 original drawings (both black-and-white and color) greatly aid their use. Each species is described on its own page, with additional drawings and color photographs taken in the field of the workers, their nests, and their habitats. Simple maps illustrate where in New England each species has been collected through 2011.

The world's climate is changing rapidly, and New England is changing, too. Ants will respond to these changes: southern species may move northward into New England, and northern species may take refuge on high mountain peaks or emigrate to Canada. This book not only provides an introduction to the tools and techniques of observing and collecting ants (Chapter 3) but also summarizes the current (as of 2012) patterns of species distributions (see the maps in Chapter 5 and the discussion in Chapter 6). Your observations will help test hypotheses about how the distributions of ants will change as the climate changes. The data associated with the species' distribution maps and the analysis of their distribution are publicly available at the book's Web site (http://NEants.net). Although ants have been collected in many New England parks and towns, many other locations are entirely unexplored. Go outside, explore the forests and fields, learn about the ants, and add to this growing body of data. Together, we will continue to learn about the world of ants.

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Acknowledgments

It is a cliché to say that it takes a village (or at least an anthill) to write a book, but it is really true for a book that brings together so much knowledge of natural history, taxonomy, ecology, and evolutionary biology in one place. First and foremost, we thank Stefan Cover and André Francoeur, myrmecologists extraordinaire, who spent countless hours teaching us the intricacies of New England ant taxonomy and sharing their lifetimes of expertise with us. James Trager brought us up to speed on *Polyergus* taxonomy, and Bernice DeMarco shared her evolving ideas about the subtle differences among *Aphaenogaster* species. The keys have been tested and the text critiqued by Stefan, André, and James, along with many other of our students and colleagues: Katie Bennett, David Cappaert, Israel Del Toro, Mark Deyrup, Richard Haradon, Clarisse Hart, Michael Kaspari, Dave McDonald, Mike and Shannon Pelini, Alex Wild, and two anonymous reviewers, along with all of the participants in the 2011 Humboldt Field Research Institute Seminar on the Ants of New England: Jennifer Apple, Amy Arnett, Sharon Bewick, Rob Chapman, Rob Clark, Aaron Fairweather, Jonathan Mays, Juan Sanchez, Tony Scalise, Rogério Silva, and Conrad Vispo. They found many mistakes and unclear couplets in our draft keys; we take responsibility for any errors that remain.

The authors shared in the writing and editing of the entire book. All of the illustrations were drawn from New England specimens by coauthor Elizabeth Farnsworth. Yale University Press scanned the drawings for the book; the originals are stored in the Harvard Forest Archives in Petersham, Massachusetts. Most of the photographs were taken by coauthors Gary Alpert and Aaron Ellison; additional photographs were contributed by Adam Clark, Elaine and Julius Ellison, Elizabeth Farnsworth, André Francoeur, Nick Gotelli, Benoit Guénard, Rick Hawkins, Sara Lewandowski, Billie Jean Moran, Tom Murray, Claude Pilon, Mike Quinn, Thomas Shahan, Alex Wild, and the Yale Peabody Museum. Each photograph in the book is imprinted with the initials of the photographer; refer to the Internet Resources at the end of the book for a list of Web sites where you can enjoy more fine photography by Tom, Claude, Mike, Thomas, and Alex. (The aerial photograph of the Thimble Islands on p. 296 is © Peabody Museum of Natural History, Yale University, New Haven, Connecticut.) Ed Kamens showed Aaron Ellison around Yale's Saybrook College to photograph the only New England habitat of *Paratrechina longicornis* known to date, and Shirley Ellison spent a day with Aaron locating *Nylanderia flavipes* to photograph in the field. Brian Hall (Harvard Forest) helped us with some of the mapping. Donat Agosti (American Museum of Natural History), Barry Bolton (British Museum of

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Although all of us have been watching and studying ants for many years, we can trace the genesis of this particular book to a statewide ant-collecting blitz we conducted across Massachusetts in 2007 on properties owned by the Massachusetts Audubon Society (MAS) and The Trustees of Reservations (TTOR). Taber Allison (MAS), Robert Buchsbaum (MAS), Paul Goldstein (Field Museum, Chicago), Russ Hopping (TTOR), Julie Richburg (TTOR), and Ernie Steinauer (MAS) provided encouragement and logistical support for that study. The Universities of Connecticut (UCMS), Maine (UMDE), Massachusetts (UMEC), New Hampshire (UNHC), Rhode Island (URIC), and Vermont (UVCC), along with Cornell University (CUIC), Pennsylvania State University (PSUC), Acadia National Park, the Maine Forest Service (ELMF), the American Museum of Natural History (AMNH), the Academy of Natural Sciences (ANS), Harvard's Museum of Comparative Zoology (MCZ), the Yale Peabody Museum (PMNH), and the Canadian National Collection of Insects (CNC), opened their collections to us, allowing us to accumulate tens of thousands of historical records of ant occurrences. We are grateful to the faculty and curators at these institutions, not only for helping us access the collections but also for doing such a great job curating them: Rebecca Cole-Will (Acadia National Park); Andy Bennett, Gary Gibson, and John Huber (CNC); Rick Hoebeke (CUIC); Charlene Donohue (ELMF); Stefan Cover (MCZ); Ray Pupedis (PMNH); Jane O'Donnell and Dave Wagner (UCMS); Frank Drummond and Ellie Groden (UMDE); Don Chandler (UNHC); Howie Ginsberg (URIC); and the late Kurt Pickett (UVCC). Charlene Donohue, forest entomologist with the state of Maine and president of the Maine Entomological Society, rounded up specimens from the Maine State collections, those of David Bourque and Dana Michaud, and many more from other members of the society; she, along with Amy Arnett (Unity College, Maine), Beth Choate (University of Maine), Richard Haradon (Essex, Massachusetts), Daniel Jennings (University of Maine), Andrew McKenna-Foster (Maria Mitchell Natural History Museum, Nantucket, Massachusetts), Mark Mello (the Lloyd Center for the Environment, Dartmouth, Massachusetts), Joan Milam (University of Massachusetts), Beetle Bob Nelson (Colby College), Joe Simonis (Cornell University), and Scott Smyers (Oxbow Associates, Massachusetts), sent us ants—sometimes tens of thousands of them—to identify; and Chelsea Carr, Israel Del Toro, Terrance Dunn, Clarisse Hart, Samantha Hilerio, Mark Johnston, Kelly McBride, Dave McDonald, Mike Pelini, and Rogério Silva cheerfully sorted and helped to identify them. Eldridge Adams (University of Connecticut) sent us his unpublished distributional records for *Myrmica rubra,* and Gary Ouellette (College Park, Maryland) sent us unpublished collection records for Kennebec County, Maine. We especially thank Israel Del Toro, who created a unified database of all of the aforementioned specimens, along with thousands more he collected himself from Virginia to Maine in 2010. These data are part of his Ph.D. dissertation work at the University of Massachusetts, and we are grateful that he shared the database with us so we could construct accurate distribution maps. Dave Lubertazzi (MCZ), Rogério Silva (University of São Paulo), and Michael Weiser (North Carolina State University) contributed additional georeferenced data from the MCZ to Israel's database.

Finally, nothing in this world happens for free. Our research on ants has been generously supported by the Arthur Green Fund of the MCZ, the Conservation and Research Foundation, MAS, the Massachusetts Natural Heritage and Endangered Species Program, the Nantucket Conservation Foundation, TTOR, the U.S. Department of Energy (award DE-FG02-08ER64510), and the U.S. National Science Foundation (awards DEB 02-35128, DBI 04-52254, DEB 05-41680, DEB 06-20443, and DBI 10-03938). To all, we are grateful.

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1.
Ants and the New England Landscape

New Englanders live in a changeable climate. Locals quip, "If you don't like the weather, wait ten minutes." But we don't always appreciate how diverse our landscape is. We lack the grand mountains of western North America (our tallest, Mount Washington, is just over 2,000 m high), and it may seem to the casual observer that New England is one large suburb from Portland, Maine, to Fairfield, Connecticut. But from an ant's-eye view, even a change in elevation of only 100 m or a shift in latitude of only 1° (about 110 km) can determine whether a nest can survive. Subtle differences in soil texture, bedrock chemistry, moisture, and temperature all make a huge difference to an ant. To better understand our ants, we start by introducing you to the geological and environmental diversity of New England.

Ancient History Shapes Today's Environment

New England gardeners grumble that their soils are a messy jumble of rocks, but they rarely consider where those rocks came from. The bedrock of New England is the product of hundreds of millions of years of geological drama involving continental collisions, mountain building, glacial scouring, and other upheavals. Our oldest rocks date back over 1 billion years, visible in the Grenville gneiss outcrops on Clarksburg Mountain in the southern Green Mountains of western Vermont. Common bedrock types in New England include the familiar hard, acidic granites of New Hampshire and Maine (remnants of the European tectonic plate that pulled away 200 million years ago with the breakup of the supercontinent Pangaea); the volcanic redstones and basalts of west-central Massachusetts and Connecticut (the >200-million-year-old Metacomet Range); marbles and limestones from 500-million-year-old beaches and reefs in valleys of western Massachusetts and Vermont; and the much older, highly metamorphic gneisses and schists of the Berkshire and Taconic Mountains. The composition of the bedrock profoundly influences the chemistry and texture of the soils derived from them as they weather and erode.

The glaciers that have periodically scoured the New England landscape have been the major agents of weathering and erosion. As many as four major glaciation events occurred between 1.6 million and 14,000 years ago—with continent-sized ice sheets spreading south and covering all of New England during periods of extreme cold, then receding north as the climate warmed, leaving behind rocks and fresh soil ready for ants (and other animals and plants) to recolonize (Figure 1.1).

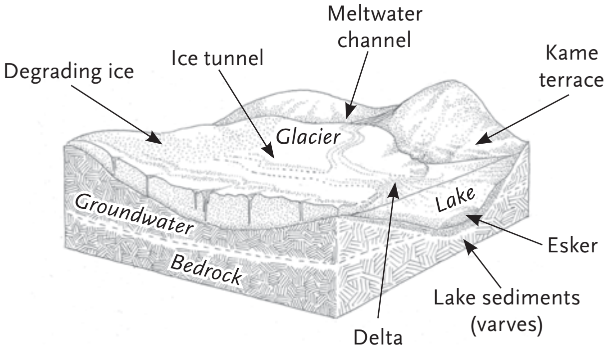

Figure 1.1. A cross section of the land and water formations resulting from glacial development and retreat. Drawing by Elizabeth Farnsworth.

We think of glaciers as pristine, bluish rivers of ice, but in fact they are huge, dirty conveyor belts laden with gravel, sand, and silt. Glaciers move like gigantic bulldozers, reworking and depositing rocks and sediments through a combination of movement and meltwater. Glaciers have left many characteristic signatures, including eskers (sinewy, sandy ridges from the glacier's underbelly visible in central Massachusetts and the Connecticut River valley of New Hampshire and Vermont); drumlins (spoon-shaped hills composed of till overlying knobs of rock, especially common on Cape Ann); kames (terraces of till pushed up against the flanks of hills visible along many valleys in Vermont); kettles (bogs and wet depressions left on the coastal plain by stranded icebergs that melted in place); and sandy outwash plains and deltas (formed as melting glaciers discharged their loads in places such as the Katama Plains of Martha's Vineyard, the Montague Sandplains of Massachusetts, and the dunes and deltas of the Connecticut River valley). Glacial melting and recession (deglaciation) took place in fits and starts. When the leading edge (or toe) of a glacier pushed forward as fast as it was melting, lots of reworking of sediments occurred, even though the glacier appeared to remain stuck in place. Enormous piles of unsorted rock debris, called moraines, were dumped unceremoniously, concentrated, and mounded up at the glacier's toe. Long Island is a terminal moraine formed at the southernmost extent of the glacier; Block Island, Martha's Vineyard, Nantucket, and Buzzards Bay were all formed as the most recent (Wisconsian) glacier paused for a few thousand years as it receded north from the last glacial maximum, 21,000 years ago.

Moraines occasionally created dams, stopping the flow of melting ice and creating temporary glacial lakes, of which Lake Hitchcock in the Connecticut River valley was one of the largest. This lake stretched nearly 650 km from what is now New Britain, Connecticut, to St. Johnsbury, Vermont. When the dam burst about 12,400 years ago, it left behind layers of sediment that had been deposited at the bottom of the lake for thousands of years. Today, the rich mixture of clays and sands from these former lake bottoms underlies the floodplain of the Connecticut River and is the basis for the most fertile agricultural soils in New England; sweet asparagus, leaf tobacco, and the Labor Day Ant, *Lasius neoniger,* are hallmarks of this soil in the Pioneer Valley of Massachusetts.

When the glaciers at last loosened their icy grip on New England about 12,000 years ago, a period of rapid climatic change (both warming and cooling) ensued, allowing plants—and ants—to recolonize from the unglaciated south. A period of especially dry, warm weather (the so-called Hypsithermal) prevailed between 9,000 and 5,000 years ago; this warming may have been enhanced by small changes in Earth's angle of tilt relative to the sun. During the Hypsithermal, New England supported expansive grasslands reminiscent of today's Midwestern prairies. Remnants of these grasslands still persist in coastal areas of Maine, Massachusetts, Rhode Island, and the islands of Massachusetts, including Martha's Vineyard and Nantucket, that lie to the south of Cape Cod. Ants such as *Formica knighti, F. reflexa,* and *F. ulkei,* which are common in Midwestern prairies, can still be found in New England in these isolated grassland fragments.

Never content to remain stable for long, Earth's climate cooled sharply between 1500 and 1850 A.D. This 350-year Little Ice Age gave New England a reprise of cold summers and often deadly winters. Did ants pack up and move south, or did boreal species such as *Myrmica brevispinosa* and *Formica hewitti* expand their range, only to shrink back to their alpine redoubts when the climate warmed again? Although the biogeographic history of species' range shifts is difficult to trace, the signatures of these great climatic changes are reflected in the composition of the ant fauna we see today (see Chapter 6).

It's All About the Soil

What do continental collisions and titanic ice ages mean to an ant? Most New England ant species are creatures of the soil, and much of New England's soil has been ground (so to speak) out of bedrock by ice and water. Many ants are quite choosy about the soils they inhabit. Some, like *Solenopsis* cf. *texana,* will nest only in the purest fine sands of windy beaches. Add even a minute amount of clay into the mix, and they are replaced by their less finicky cousin, *S. molesta*. And no ground-nesting ant prefers soggy soil; even bog ants (*Myrmica lobifrons*) seek out dry microhabitats, nesting and foraging in the relatively high ground atop hummocks of *Sphagnum* moss.

Stable soils, such as till, consist of well-defined layers or horizons topped by a shallow organic surface composed of decaying plant litter. Just below the litter layer is the A horizon, where organic material is constantly being mixed with mineral soil by soil dwellers like ants and earthworms. Farmers also deepen this layer with their plows; even in soils that have been fallow or reverted to forests long ago, this plow layer (usually about 0.5 m deep) is still visible today. Iron, clay, aluminum, and other minerals leach from the A horizon and accumulate in the underlying mineral soil (the B horizon). Beneath these zones, in the C horizon, new soil is created through the erosion of underlying bedrock.

For an ant colony to survive the cold New England winters, most ground-dwelling ants need to dig nests that reach well below the frost line: at least 1 m deep, extending well into the B or C horizon. As we discuss in Chapter 2, ants performing the simple routines of nest housecleaning also have profound effects on the chemistry, aeration, and recycling of mineral soils brought up from the B horizon. Because ground-dwelling ants must excavate soil to build and maintain their nests, many species are very sensitive to soil texture, which is defined by the relative proportions of sand, silt, and clay. It is less clear whether ants also are sensitive to soil chemistry. For example, are some species more commonly associated with high-pH, basic soils derived from limestone, or are they more commonly associated with lower-pH, acidic soils derived from granite? More observations and experimental research are sorely needed in this area.

However, not all ants nest in pure soil. The familiar Eastern Carpenter Ant, *Camponotus pennsylvanicus,* carves its nests in decaying wood (mostly in dead limbs or hollow trunks of living trees, fallen logs, and yes, sometimes in wet or rotting wood in houses). Other species, such as *Temnothorax longispinosus,* nest in dead, hollow twigs. Still others, such as *C. caryae* and *T. schaumi,* nest under bark high in tree canopies. Many species of *Lasius,* especially the citronella ants in the *claviger* group, seek the shelter of rocks, digging out nests beneath them (and scurrying willy-nilly when you happen to pick up that rock). Still others, including *T. ambiguus* and the species that enslave it, such as *Protomognathus americanus,* nest in tiny acorns! Finally, some "tramp" species (tiny, mostly tropical, ants that breed rapidly and disperse over long distances), including the Crazy Ant (*Paratrechina longicornis*) and the Pharaoh Ant (*Monomorium pharaonis*), colonize basements, kitchens, and other nooks of human habitation—the only New England habitats reliably warm enough to shelter them year-round.

But Vegetation Matters, Too

Both soils and climate heavily influence the composition of vegetation in different regions of New England. New England's climate varies considerably from the coast (with its maritime influences) to inland (with its continental influences). Cold coastal waters are slow to warm up in the spring and keep air temperatures cooler on Cape Cod than in the interior well into the early summer. Likewise, the mountains of our region experience much cooler temperatures throughout the year than do lower-elevation sites, shaping the plant communities that occur from north to south and from summit to valley. Because temperature and vegetation go hand in hand, ecologists classify New England broadly into five ecoregions—areas that share similar climates, growing seasons, and plant community types (Figure 1.2). If you travel along a transect from northern Maine to southwestern Connecticut, collecting ants along the way, you will find very different suites of species inhabiting these ecoregions. We discuss general patterns here and look at potential causes of these patterns more closely in Chapter 6.

Northern and western Maine, most of New Hampshire and Vermont, the Berkshire Mountains and Worcester Plateau of Massachusetts, and the Litchfield Hills of Connecticut are in the Northeastern Highlands ecoregion. This ecoregion is cloaked in boreal forests dominated by hardy spruces, firs, white pines, and northern hardwoods including oaks, American Beech, and Sugar Maple. Bogs reminiscent of Alaskan tundra are the predominant wetlands in this ecoregion. Our highest peaks—Mount Katahdin in Maine, Mount Mansfield and Camel's Hump in Vermont, Mount Washington and the other high peaks of the Presidential Range in New Hampshire,

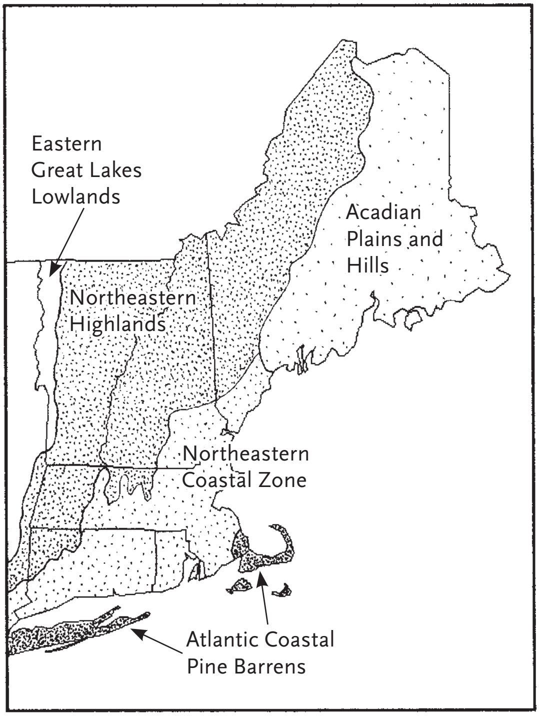

Figure 1.2. The five ecoregions of New England. Drawing by Elizabeth Farnsworth.

and Mount Greylock in Massachusetts—have low-lying alpine vegetation that has clung to these summits since the glaciers receded. Boreal and cold-climate ant species such as *Camponotus herculeanus, Formica hewitti, F. podzolica,* and *Myrmica brevispinosa* extend their ranges into New England only in the Northeastern Highlands.

Down East Maine (the low-elevation regions of central and northeastern Maine), with its rolling plains, low hills, many lakes and ponds, and a rocky coastline, forms the Acadian Plains and Hills ecoregion. This ecoregion is characterized by a mixture of northern deciduous hardwoods (predominantly Red Oak, Sugar Maple, and American Beech) and evergreen conifers (spruces, firs, Eastern Larch, and Northern White Cedar). Productive farms, pastures, and blueberry barrens punctuate the forest and are home to prairie ant species such as *Formica ulkei* and *F. knighti*. Down East Maine's unique coastal raised bogs perch atop granite bedrock and host bog specialists and cold-climate ant species, including *Dolichoderus mariae, Formica neorufibarbis, Myrmica alaskensis,* and *M. lobifrons*.

The Northeastern Coastal Zone ecoregion consists of the southern part of coastal Maine, coastal New Hampshire, all of Rhode Island except Block Island, and the portions of Connecticut and Massachusetts (excluding Cape Cod and its offshore islands) that are lower in elevation than 300 m above sea level. The temperate and diverse mix of vegetation in this ecoregion consists of deciduous forests, grasslands, and sedge meadows that extend south from New England into the Mid-Atlantic coastal plain and piedmont. Southern woodland ant species, such as *Camponotus americanus, C. castaneus, C. chromaiodes,* and *Formica creightoni,* are characteristic of this ecoregion.

Cape Cod, Martha's Vineyard, Nantucket, and Block Island, together with New York's Long Island, are in the Atlantic Coastal Pine Barrens. This unique ecoregion is dominated by Pitch Pine, Black Oak, Chestnut Oak, and blueberries growing on sandy soils. The once extensive pine barrens have been modified heavily by human activities, and only small remnants of true pine barrens—a globally threatened ecosystem—remain in New England. Many southern species of ants, notably *Pheidole pilifera, Monomorium viride, Solenopsis* cf. *texana,* and *Temnothorax texanus* are found in this ecoregion.

Finally, the Lake Champlain valley at the northwestern edge of Vermont is part of the Eastern Great Lakes Lowlands ecoregion. Before European settlement, the forests here were dominated by hardwood trees more characteristic of Mid-Atlantic latitudes, including Beech, White Oak, ashes, and hickories. The rich soils of the Champlain valley encouraged farming, and now most of this ecoregion is devoted to agriculture and residential development. Nevertheless, some southern ant species, such as *Camponotus* *chromaiodes,* find the comparatively warm (for New England) climate around Burlington most hospitable.

Small-scale differences in vegetation within ecoregions profoundly influence microclimate, and ants respond accordingly. Having tiny bodies with large surface-area-to-volume ratios, ants are very sensitive to temperature and thus to the plant communities around them. Warmer south-facing slopes of hills will support different ant species (and vegetation) from cooler, north-facing slopes. Deciduous hardwoods and evergreen conifers reflect the sun's rays differently, thereby influencing the temperature on the ground; in winter or summer you have only to walk from a clearing to the deep shade of a conifer forest to appreciate the difference in temperature. On a balmy spring day when the temperature reaches 15° C—the minimum average yearly temperature at which most ant nests really wake up—you will find an abundance of species in oak glades. Just a few meters away, under a dense canopy of hemlock trees, only one or two cold-tolerant species, such as *Aphaenogaster picea,* will be out and about.

Of course, land cover is not static over time, and therefore neither is the ant fauna. What happens if you clear-cut that dense hemlock stand? Suddenly warm sun floods the forest floor, which is now covered with twigs, branches, and other coarse woody debris. Different species of ants, especially *Formica* species, quickly colonize these newly logged patches in the forest. Three years later, a thick tangle of raspberries and impassable stands of young birches will have taken hold. These may discourage humans from passing through, but other species thrive in these dynamic habitats. Twenty years on, as the free-for-all scramble among the plants has begun to calm down, a more stable mixture of pines and maples will have overtopped the fly-by-night birches; look for *Camponotus novaeboracensis* nesting in fallen birch logs and under bark. Hemlocks and shade-tolerant oaks lurk in the understory, waiting for one of those pines to fall and open up a light gap in which they can grow. In a hundred years or more, a tall forest of mixed conifers and hardwoods will have grown up; look among the acorns for tiny *Temnothorax curvispinosus* nests, in the leaf litter for small nests of the handsome *Stenamma impar,* and in standing dead tree trunks for larger nests of *C. nearcticus.* And a few ant species, such as *Lasius speculiventris,* nest mostly in the moist soils of the oldest forests, especially those that were never logged.

In many ways, this type of ecological succession mirrors the historical pattern of land cover change in New England over the past three centuries. Arriving in the 1600s, early European colonists documented vast stands of old-growth coniferous and mixed-deciduous forests interspersed with clearings and occasional burns made by Native American hunters and farmers. Following settlement, nearly 80% of New England's forests, especially in the Connecticut River valley and the Champlain basin, was cleared in the 1700s to make way for crops, pastures, and cities (Figure 1.3).

In the wake of the Industrial Revolution, subsistence farming largely disappeared from New England, and by the early 1900s abandoned farmlands slowly began to revert to forest. This succession proceeded from field to old field to forest, and today the majority of the New England landscape is forested once again (Figure 1.4).

New England's agricultural history remains visible in the ubiquitous stone walls built by European colonists and their oxen (Figure 1.5). These stone walls are also good places to look for ants; *Stigmatomma pallipes,* for example, often forages between the rocks. Unfortunately, suburban developments and urban sprawl are making inroads into forests, and some elements of mature forests, including many understory orchids and other herbaceous plants, may never fully recover. Although the seeds of many spring woodland flowers are dispersed by ants, especially by *Aphaenogaster picea* and *Myrmica punctiventris,* the seedlings are rapidly eaten by burgeoning populations of deer, which are no longer held in check because their native predators (mountain lions or catamounts, wolves, and lynxes) are now extinct or very rare.

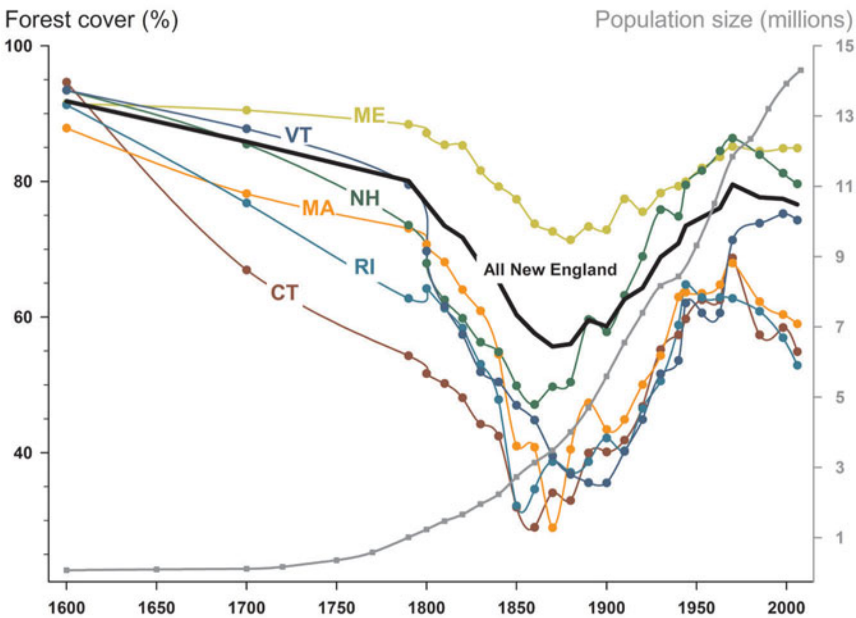

Figure 1.3. The forest cover of each of the six New England states (as a percent of total state area) and of all of New England (as a percent of total area) since European settlement, along with total New England population size since 1600. Data courtesy of Brian Hall and David Foster, Harvard Forest.

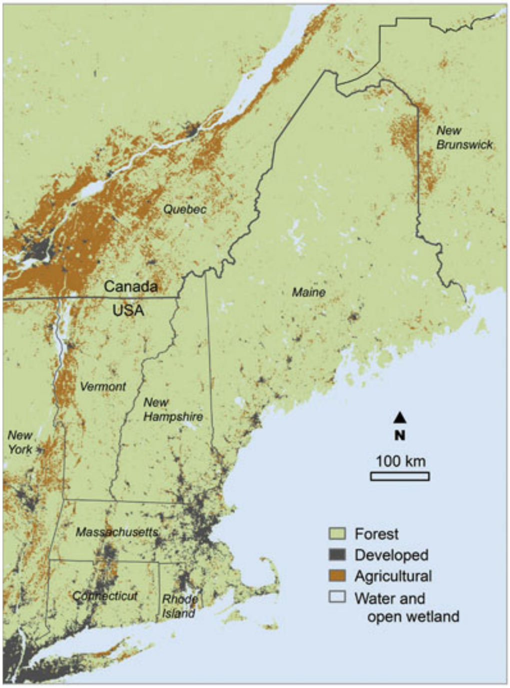

Figure 1.4. The current land cover of New England and adjacent counties of New York and provinces of Canada, based on 2001–2007 data from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) (http://modis.gsfc.nasa.gov/). Map produced by Brian Hall, Harvard Forest.

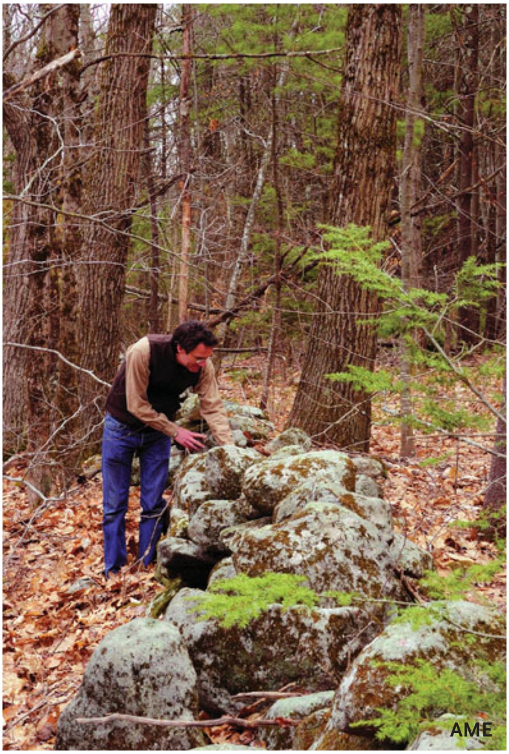

Figure 1.5. The stone walls meandering through New England's forests are good places to look for ants.

Glaciers flowed and receded; New England was colonized, cleared, and in places abandoned; but the forests, pine barrens, grasslands, and wetlands have remained. Their persistence and recovery demonstrate the resilience of New England ecosystems. We will never know all the details of how ants responded to these major historical changes, but we can learn much about these insects, their ecological interactions, and their influences on ecosystems by studying them in the multitude of different habitats in our region.

2.
Ant Basics: Evolution, Ecology, and Behavior

The Life of Ants

Ants are very different from most other animals. They form large colonies of closely related individuals, many of whom have specific tasks required to maintain the colony, and most of whom are unable to reproduce themselves. The ant you see crawling up a tree trunk or along your kitchen counter is almost always a sterile female. She will never reproduce, and she works exclusively for the benefit of the queen and the rest of her colony. An active ant colony consists of one or several queens—the only females that reproduce—and anywhere from a couple of dozen to tens of thousands of female workers. These workers carry out all the activities of the colony other than reproduction. They gather food, care for the young, defend the colony from predators and invaders, maintain the chambers and passageways, remove waste and debris, and even (in some specialized species such as *Prenolepis imparis*) store food. Queens (and their colonies) can live for decades, but workers rarely live longer than a single year or growing season. Males are produced only when the colony is about to undergo sexual reproduction, but they contribute nothing to the care and maintenance of the colony.

How does an ant colony get started? In response to a variety of cues, including day length, temperature, crowding, or stress, the queen lays eggs that develop into special winged (alate) females (virgin queens) or winged males. After rains and during daylight hours, especially early mornings or late afternoons, the virgin queens and males fly out of the nest to mate, after which the males die and the now inseminated queens go on to form new colonies. These nuptial flights can be spectacular, especially in the boreal forests of New England, where huge clouds of winged ants in the genus *Lasius* rise into the air from many different nests (Figure 2.1).

Ant swarms often alarm homeowners because they resemble swarming termites, but a closer look reveals clear differences between termites and ants. Our common termites are small, soft, white, and fat (Figure 2.2). Even though they may be called "white ants," they are more closely related to cockroaches than they are to any insect species in the order Hymenoptera, which includes the ants, along with the bees and wasps. Three important characters (among many others) distinguish Hymenoptera (including the ants) from termites: the front wings of Hymenoptera (present only on alate queen and male ants) are larger than their rear wings, but they are the same size in termites; most Hymenoptera, including the ants, have a "wasp waist" (a narrow constriction in their body; see Chapter 4 for more details), whereas

Figure 2.1. A mating swarm of *Lasius umbratus* emerges from a large hollow oak tree on the flanks of Mount Monadnock in southern New Hampshire.

Figure 2.2. The Eastern Subterranean Termite (*Reticulitermes flavipes*) is more closely related to cockroaches than to ants, bees, or wasps. Unlike ants, termites have bead-like antennae and lack a pedicel, the narrowly constricted "wasp waist" in the middle of ants' or wasps' bodies. These termites were nesting under a rock near a colony of *Lasius flavus* at the High Ridge Wildlife Management Area in central Massachusetts.

termites do not; and the distal ends of the legs (the tarsi; see Chapter 4) of Hymenoptera have five segments, whereas those of termites have only four.

In some ant species, such as *Aphaenogaster rudis,* the alate females will mate with only a single male. In others, such as the European Fire Ant, *Myrmica rubra,* a single female may mate with five or more males. But whether there are single or multiple matings, this is the only point in the life cycle of a colony (Figure 2.3) at which mating occurs. The queen will spend the rest of her life inside her colony, and all her fertilized eggs will be produced with sperm that has been stored from this single mating flight.

The males die immediately after they mate with a queen, but the newly-mated queen lands, sheds her wings, and searches for a patch of soft soil, a hollow twig, an acorn, a rotting log, or a protected place beneath a small stone roof where she can found a new colony. Most queens never make it; the vast majority land on inhospitable terrain and end up as food for birds, other insects, or even the occasional carnivorous plant (Figure 2.4). The lucky females who land in a good spot dig in and quickly lay a first batch of fertilized eggs, converting some of their wing muscle tissue into spitlike salivary secretions to feed their new brood. The female workers that hatch

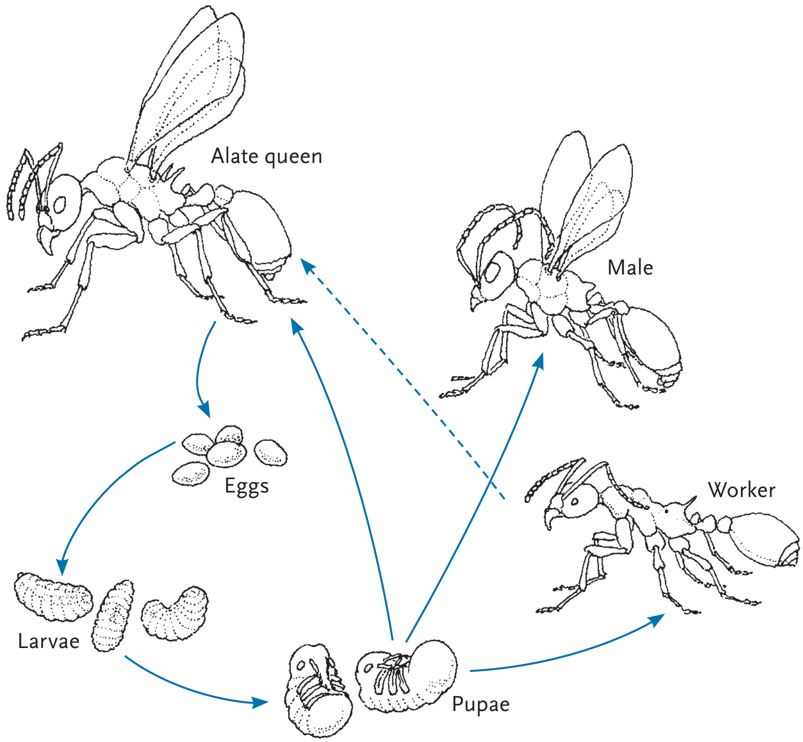

Figure 2.3. The life cycle of an ant colony. Drawings by Elizabeth Farnsworth.

Figure 2.4. A queen New York Carpenter Ant, *Camponotus novaeboracensis,* mistakes an insectivorous pitcher plant for a safe nest site.

from these founding eggs will begin gathering food, enlarging the nest, and tending the queen, helping her to produce more sisters for the colony. This first cohort of workers, called nantic workers, are much smaller than the workers that are produced later in the life of the colony.

The colony now begins an extended growth phase that can last anywhere from several months to several years, depending on the species and the life span of the queen. During this growth phase, the queen continues to produce broods of eggs that will hatch into more sterile (female) workers. In most species, workers take on different tasks as they age. Young workers attend the queen and take care of eggs and pupae. Older workers feed and care for the maturing larvae. The oldest workers forage for prey, maintain and expand the nest, and defend it from predators, competitors, and slave-raiders.

In many genera, the tasks that any individual worker performs change from day to day, depending on the needs of the colony and interactions among the workers. But in a handful of genera, including *Camponotus* and *Pheidole* here in New England, eggs develop directly into different castes of workers with distinct sizes and appearances that fulfill specialized roles in the life of the colony. The smaller, “minor” workers do most of the colony maintenance and foraging, whereas the largest, “major” workers defend the nest and stores of food. The number and types of workers produced by the queen are under delicate chemical and hormonal control, which is mediated by the quantity and quality of food that is brought back to the nest and by the relative numbers of individuals in different castes.

Whether colonies have flexible workers or fixed castes, without the guiding chemical control of the queen, the activity and behavior of the workers can become disorganized or random. If the queen dies or is removed from the nest, the entire colony usually disintegrates and dies. In a few species, however, workers will begin to produce eggs if the queen dies. Because these eggs are unfertilized, they usually develop into males (see the discussion of haplodiploidy and the evolution of eusociality later in this chapter). In rare cases, however, workers can produce new queens either from unfertilized eggs (parthenogenetically) or after mating with a male ant.

An ant colony will continue to grow in size and add workers, but at some point it becomes mature and will begin sexual reproduction by producing virgin queens and males. Many species produce males and reproductive females just before the nuptial flight. Others produce males and reproductive females that stay in the nest for a long time before the nuptial flight. Our largest carpenter ant, *Camponotus herculeanus,* produces males and virgin queens in late summer. They are groomed and fed by workers throughout the fall and winter before they emerge from the colonies for their mating flights in the spring. Finally, some species, including *Monomorium pharaonis* and *Myrmica rubra,* have large colonies with multiple queens that create new colonies asexually by fragmenting the original colony. However, even these polygynous (literally, many queens) and polydomous (literally, many houses, referring to their many nests) ants eventually go through a phase of sexual reproduction in which males and new queens are produced.

The ant colony thus functions as a highly social, organized "superorganism." The queens and most workers are safely hidden below ground or protected within the interstices of rotting wood. But for the ant workers that must go out and forage for food for the colony, life above ground is short and dangerous. The single ant that you see running across the forest floor or your kitchen counter is, in reality, a short-lived, specialized extension of the colony itself, just as an individual leaf is a specialized part of a single living tree.

What Makes an Ant an Ant?

Ants are insects, and insects are arthropods: invertebrates (animals without backbones) within the larger group of animals that includes lobsters, spiders, and lice (Box 2.1). Like all insects, ants have a segmented body consisting of three major regions (head, thorax, and abdomen), compound eyes and antennae on the head, three pairs of jointed legs on the thorax, and an external (outer) skeleton made of chitin (a stiff, starchy compound that feels like fingernails) covering the entire body. Ants are all members of one insect order: the Hymenoptera. This order also includes the sawflies, bees, and wasps. With nearly 150,000 described species, the order Hymenoptera contains more species than any other order of insects except for the beetles (Coleoptera) and the butterflies and moths (Lepidoptera). All Hymenoptera have membranous wings, an egg-laying organ (called an ovipositor) that is frequently modified into a stinger, chewing mouthparts

Box 2.1. Ants in the animal kingdom

Biologists classify organisms in a hierarchy of groups, beginning with their kingdom. Ants are in their own family—a relatively fine division within the animal kingdom.

Kingdom: Animalia—multicellular organisms that have to eat other organisms to survive.

Phylum: Arthropoda—animals without backbones that have an exoskeleton, a segmented body, and jointed appendages (legs, antennae).

Class: Insecta—arthropods with an exoskeleton made of chitin, a body with three major parts (head, thorax, and abdomen), three pairs of jointed legs, compound eyes with multiple reflecting lenses, and two antennae.

Order: Hymenoptera—the ants, bees, wasps, and sawflies.

Family: Formicidae—the ants.

(although the proboscis of bees has been modified for drinking nectar), complete developmental metamorphosis with larval and pupal stages (so-called holometabolous development), segmented antennae, compound eyes, and a narrow "waist" (except for the most ancestral group, the sawflies).

Within the Hymenoptera, the ants are in their own family: the Formicidae. Ants are distinguished from the rest of the Hymenoptera by two key evolutionary innovations: (1) a distinctive metapleural gland that secretes antibiotics that keep the ant exoskeleton free from bacteria and fungal spores that could infect the nest and (2) a morphological modification of the typical hymenopteran narrow waist into a nodelike structure called the pedicel. Although the pedicel appears to separate the thorax from the abdomen, don't be fooled; the pedicel actually consists of the second segment or the fused second and third segments of the abdomen! This evolutionary rearrangement has led myrmecologists to develop specific terms to describe ant anatomy. Some of these terms are different from those used to describe the "typical" insect (see Chapter 4).

The Evolution of Ants

The insect order Hymenoptera originated in the Triassic period (~250 million years ago), and the oldest fossils of antlike creatures look a lot like wasps. In fact, a short-lived side branch of the hymenopteran evolutionary tree had characteristics of both ants and wasps. These insects, which went extinct 45–65 million years ago, are called sphecomyrmines (from the Greek *sphéx,* meaning wasp, + *myrmex,* meaning ant).

The modern ant appears to have evolved between 115 and 135 million years ago; the earliest definitive ant fossil was found in French amber that is about 100 million years old. Ants first evolved in tropical rainforests, but they diversified rapidly and colonized deserts, grasslands, wetlands, and cold northern and high-elevation habitats. Today they occur in all terrestrial habitats on every continent except Antarctica. Even Arctic regions and remote islands that originally had no ant fauna now harbor a few introduced species. In New England, the vestiges of all this evolutionary history are evident in the taxonomic distribution of ant species, genera, and subfamilies (see also Chapter 6). The New England fauna includes species from the "big three" subfamilies of ants—the Myrmicinae, Dolichoderinae, and Formicinae—along with a handful of species in three other subfamilies, the Amblyoponinae, Proceratiinae, and Ponerinae (Figure 2.5).

Ants have been in what is now New England for millions of years, leaving when the glaciers covered the land and returning as the glaciers

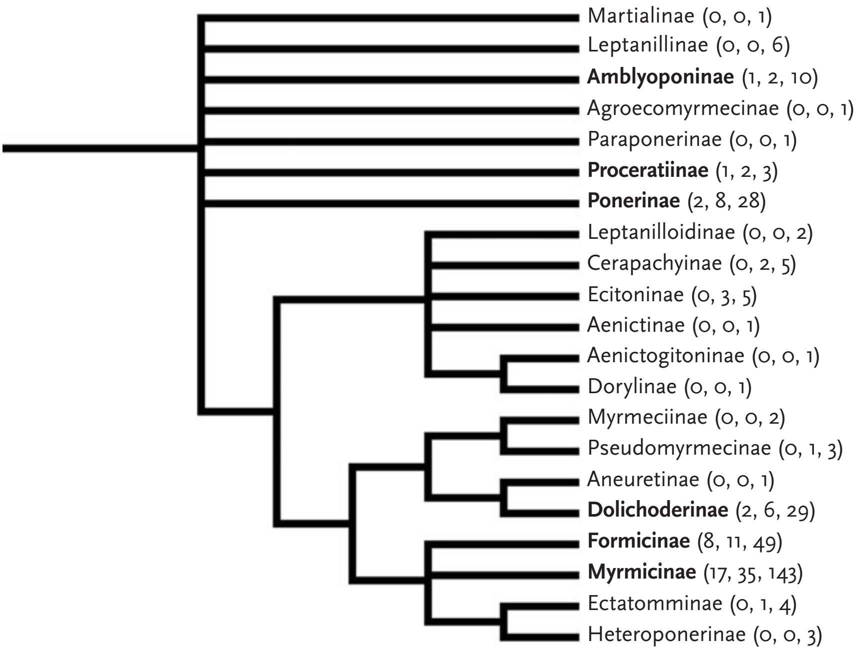

Figure 2.5. The subfamilies of the ants and their evolutionary relationships. Families in **boldface** type include species that nest in New England. The numbers in parentheses after each subfamily are the number of genera in New England, North America, and the entire world, respectively.

melted. Most of the ant species that we find in New England today recolonized our region after the glaciers receded about 10,000 years ago, but others may have evolved and diversified right here. Exotic tropical species, such as army ants and leaf-cutter ants, cannot survive a killing frost or a New England winter. However, some tropical and subtropical tramp species take advantage of global commerce and show up occasionally in New England's hospitals, grocery stores, greenhouses, and warm basements.

Eusociality—The Pinnacle of Social Evolution

Scientists distinguish ants from other insects by their unique morphology. But probably the most important event for ants in their nearly 150-million-year history was the evolution of their complex social behavior. Along with humans, other mammals, and some colonial invertebrates, ants (and the other social insects) represent one of the pinnacles of social evolution. Ants are "eusocial" (truly social); there is a reproductive division of labor, with one (or only a few) reproductive female, a nonreproductive caste of workers, overlapping generations, and cooperative care of young.

Eusociality has evolved repeatedly within the order Hymenoptera. Bees and wasps have several eusocial lineages, but there are also bees and wasps that are solitary or have only a modest degree of social organization. Across the rest of the animal kingdom, eusociality has evolved only in the termites and the naked mole rats, although there is evidence for some elements of eusocial structure in a few species of thrips, gall-making insects, and snapping shrimp. Eusociality is an evolutionary paradox, because classical theories of natural selection (and modern economics) predict that individuals should act in their own selfish reproductive interest. It is hard to understand how evolution would favor the development of sterile castes of workers in which individuals sacrifice their own reproductive potential, caring for the colony and the offspring of the queen instead of reproducing themselves.

The first key to understanding the evolution of eusociality is the observation that all Hymenoptera have a unique genetic system that determines the sex of their offspring. In most animals, males and females are diploid; they each have two sets of chromosomes. One (haploid) set is contributed by each parent in the sperm or the egg. These two haploid sets combine during fertilization so that the offspring is diploid like its parents. But the Hymenoptera are different. Like most other organisms, including humans, all female ants (workers and queens) develop from fertilized eggs produced by uniting an egg and a sperm cell—they are diploid. But male ants develop from *unfertilized* eggs and therefore have only one set of chromosomes—they are haploid. As we described earlier in this chapter, the life cycle of an ant colony consists of repeated production of diploid workers and only occasional production of diploid queens and haploid males. We refer to this as a haplodiploid sex determination, or haplodiploidy for short.

An important consequence of haplodiploidy is that females share more genes with their sisters than they do with their own daughters. The theory of kin selection predicts that eusociality should evolve in haplodiploid organisms. Workers that give up their own reproduction to help the queen produce more sisters are actually behaving selfishly (in an evolutionary sense), because more copies of their genes will spread through their sisters (kin) than through their own production of daughters. This is the concept of inclusive fitness: if you are not going to produce your own offspring, take care of your siblings (and other more distant relatives) with whom you share genes. In contrast, the haploid males are not more closely related to their sisters than to their own offspring. The theory of kin selection correctly predicts that males of eusocial species should spend all their time selfishly reproducing (or trying to reproduce) rather than working to contribute to the success of their sisters' colony.

However, haplodiploidy cannot be the ultimate explanation for the evolution of eusociality. Although all ants are eusocial, many groups of bees and wasps are not, even though they all have haplodiploid sex determination. Eusociality also has evolved in some animal species that have typical diploid males, such as naked mole rats and termites. An alternative hypothesis for the evolution of eusociality is that one female (the queen) can dramatically increase her fitness if she can prevent her offspring from reproducing and instead force them into caring for all her young. Other characteristics of Hymenoptera that may have favored the evolution of eusociality in this order of insects include the habit of group nest-building (which favors cooperative defense) and the repeated occurrence of trophallaxis—the regurgitation of liquid fed to other members of the colony during cooperative care of offspring. But whatever the ultimate forces leading to the evolution of eusociality, it is certainly responsible for much of the evolutionary and ecological success of the ants. The modest ant worker running across the pavement reflects millions of years of successful morphological evolution and social organization that have led to the ecological dominance of ants throughout the world.

Ant Ecology

Ants are the unseen and unrecognized giants of the terrestrial world. Most ant species are small, usually less than 10 mm long, although the largest living ant, Wilverth's Driver Ant (*Dorylus wilverthi*), is a whopping 52 mm long. The largest ant that ever lived is the extinct Lube's Titanic Ant, *Titanomyrma lubei,* whose ~57-mm-long queens roamed the hills of Wyoming nearly 50 million years ago. But despite their small individual size, ants en masse outweigh all other invertebrate groups and may comprise as much as one-third of the mass of all insects on Planet Earth. In one study in a Brazilian rainforest, the total mass of the ants was approximately four times greater than that of all mammals, reptiles, and amphibians combined!

Although ants are everywhere, they are not especially conspicuous because most ant colonies are underground; we see only the actively foraging workers on the surface or the occasional mating swarm. But it is the ants, not the earthworms, that are the prime movers and turners of soil. The classic brown (podzolic) soils of northern New England are created by ants continually digging up soil from deep beneath the surface, leading to a layer of 25–45 centimeters of brown topsoil that accumulated over several thousand years before European colonists began to plow it for agriculture. Indeed, because ants are so abundant and widespread, it is difficult to imagine what Earth's vegetation and soils would look like without them.

Ants are the chief scavengers and garbage collectors of the forest, efficiently consuming and disposing of animal carcasses. Several species of ants that lurk in the dry and decaying leaves littering the forest floor are specialist predators that consume springtails, mites, spiders, and other microfauna. Ants themselves are prey for birds, small mammals, spiders, and other insects.

Ants also compete with one another for limited ecological resources, especially food and nesting sites. Competition among ants occurs directly, when ants engage in coordinated territorial combat and defense of food resources, as well as indirectly, when many species jointly exploit scarce resources. Ants move plants around, too. In New England, the common forest ant *Aphaenogaster rudis* collects the seeds of many different understory herbs, including Wake-robin (*Trillium*), Bloodroot (*Sanguinaria canadensis*), Wild Ginger (*Asarum canadense*), Fringed Polygala (*Polygala paucifolia*), violets (*Viola*), and some species of sedges (*Carex*). Attached to the seeds of these herbs is a fleshy, fat-filled structure called an elaiosome, which is an attractive food for many ants. The ants collect the seeds, eat the elaiosomes, and leave the seeds in or near the nest, where they can germinate in the nutrient-rich soil that the ants have turned over. In many of our forests, *Aphaenogaster rudis* and *A. picea* are the most common and abundant ants to be found, and the more *Aphaenogaster* nests that are present in the forest, the higher the density of understory herbs.

Other ants, including the widespread silvery-colored *Formica subsericea,* tend aphids and scale insects that themselves are feeding on plant juices. As the aphids and scale insects pump fluids from the plant into their bodies, the ants harvest the sugar-rich liquid they excrete. This honeydew can be either a sweet treat or the primary food supply for the ant colony. Other ants are predators: New England's three *Proceratium* species prey only on spider eggs, and our *Pyramica* species stalk centipedes.

Social Parasitism—Guests, Inquilines, Temporary Parasites, and Slave-Makers

Parasites have evolved to exploit almost every kind of organism. The primary characteristic of a parasite is that it is physically dependent on another species (the host) for at least part of its life cycle; the parasite cannot survive and reproduce successfully without the host. For example, parasitic plants attach to roots or other parts of other plants and suck nutrients and carbon from the host. Without this source of essential nutrients and energy, the parasite dies. Parasitic roundworms take up residence inside humans, feeding on blood, tissue, or your last meal. Without the food and shelter provided by your body, these roundworms could not survive. Parasitic protozoa, including the species that cause malaria in humans and birds, have evolved complex life cycles that require multiple species of hosts to house them, feed them, and move them around.

Many kinds of parasitism have evolved among the ants, too. Myrmecologists recognize four different kinds of social parasites (the term *social* refers to the fact that these parasites have evolved in the eusocial insects): guest ants (also called xenobiotics), temporary social parasites, slave-makers (also called permanent social parasites with slavery, dulosis, or pirates), and inquiline social parasites (also called permanent social parasites without slavery). Among the ants, fewer than 2% of species are known to be parasites, but continued exploration and study of ant natural history, especially in the tropics, regularly uncover new parasitic species. And a surprising number of temperate-zone species in the ant subfamilies Myrmicinae and Formicinae are parasitic. In New England alone, we have at least 42 species of social parasites—over one-third of our resident species!

Guest ants are fed by, and live in the same nest as, their host. Unlike the other three kinds of social parasites, guest ants rear all of their own workers. In New England, we know of only one such guest ant: *Formicoxenus provancheri* is a guest of *Myrmica incompleta*. *Formicoxenus* forms small nest chambers within the nest of *M. incompleta,* and the hosts regurgitate food into the mouths of the guests. This behavior co-opts some of the energy from the host colony but does not compromise its existence.

Temporary social parasites depend on their hosts only to found a new colony. After she has mated, the founding parasitic queen enters a host colony and kills or otherwise removes the host queen. As the parasitic queen lays her own eggs, the host workers care for them, rearing her brood as if they were the hosts' sisters. As the host workers age and die, they are replaced by the parasite workers; eventually the colony is made up entirely of the parasite queen and her offspring. In New England, many species of *Lasius* and *Formica* are temporary social parasites.

Slave-makers, on the other hand, depend on one or more host colonies for their entire lives. As with temporary social parasites, the first step in enslaving a colony is for the founding parasitic queen to find a host colony and kill or expel the host queen. In some species, including our own *Harpagoxenus canadensis,* the parasitic queen kills or otherwise removes all the host workers, too. In other species, the host workers start to care for the parasitic queen and her offspring. But in both cases, the offpring of the parasitic queen do not care for their brood or forage for their own food. Rather, the parasite workers raid other colonies of the host species and carry off the captured brood. Once these captives are returned to the parasite's nest, they do all the work required to keep the colony clean and well fed. In New England, species in the *Formica sanguinea* group, our two *Polyergus* species, and *Protomognathus americanus* are the most common slave-making ants.

Finally, inquiline social parasites have dispensed with workers altogether. A founding parasitic queen invades the host's nest but usually does not kill the host queen. Instead, the host queen continues to produce her own workers, who care for the parasites' offspring, which are only males and new queens. In rare cases, the parasite queen can only invade a nest in which the host queen has died; this appears to be the case in New England for *Anergates atratulus,* which is an inquiline social parasite of the Pavement Ant, *Tetramorium caespitum*. Other New England inquiline social parasites are in the genera *Leptothorax, Myrmica, Nylanderia*, and *Tapinoma*.

A key feature uniting all these forms of social parasitism is that the parasite queen co-opts the host's workforce, either by displacing the host queen (temporary social parasites and slave-makers) or by exploiting the workers that the host queen continues to produce (guests and inquilines). How does the parasite queen manage to convince the host colony to care for her (and her offspring)? Ants belonging to a single colony recognize each other by the unique chemical signature of the nest; essentially, they use their antennae to taste and smell each other. If other ants smell right, they're sisters, but if not, they're foreign and must be removed or killed. Parasitic species have to mask their own smell and quickly take on the chemical signature of the host colony, and they do this in a variety of ways. For example, on her way into the host's nest, the parasitic queen might grab a host worker, kill it, chew it up, and smear herself with the unique chemicals from the cadaver's exoskeleton. Alternatively, the parasitic queen does the same thing to the host queen once the parasite enters the brood chamber. Slave-makers that capture foreign broods transfer their own chemical scent to the slave workers as they hatch. There are many variations on these themes, but virtually all of them involve the use of distinctive hydrocarbons —molecules made up only of carbon and hydrogen—that are found on the surface of ants' exoskeletons.

Myrmecophily—Life among the Ants

Socially parasitic ants are not the only species that invade, co-opt, or otherwise take advantage of ants and their nests. Myrmecophiles—literally, ant lovers (from the Greek *myrmex,* meaning ant, + *philos,* meaning loving)—can be found in all corners of the animal kingdom. Mites, flies, beetles, butterflies, crickets, and many other organisms spend part or all of their lives in the warm, dry, and secure nests that ants build. Like the social parasites, the myrmecophiles use chemical deception to insinuate themselves into their hosts' nests.

Myrmecophiles range from parasites that feed on their hosts to mutualists that enhance the survivorship or reproduction of the host colony. In New England, the most common myrmecophiles are scarab beetles in the genus *Cremastocheilus,* clown beetles in the genus *Haeterius,* rove beetles in the genus *Xenodusa,* and hoverflies in the genus *Microdon*. We also have our share of myrmecophilous crickets, in the aptly named genus *Myrmecophilus* (Figure 2.6).

Cremastocheilus beetles live in nests of various species of *Formica,* where the adult beetles feed directly on the larvae or brood of the ants. The beetle grubs (larvae) feed on the accumulated detritus of the nest. Adult *Hetaerius* beetles steal liquid food from ants as they exchange food with each other. A few species of *Hetaerius* also have been observed actively soliciting food from ant workers; the ant responds by regurgitating bits of food into the mouth of the beetle. The immature stages of *Hetaerius* beetles have yet to be found. If the ants ever attack either of these beetles, the victim will play dead—staying perfectly still and holding its legs tight to its body. The ants may then carry the beetle around and taste or smell it with their antennae, but they eventually release it, whereupon it resumes foraging in another chamber of the nest.

Xenodosa beetles have a very interesting life cycle. The larvae spend the summer in nests of *Formica* species, including *F. exsectoides* and *F. incerta*. The beetle larvae are cared for and fed by the host ants; occasionally the larvae will eat some of the host workers. In midsummer, the larvae leave the *Formica* nests and move into nests of carpenter ants, including *Camponotus americanus, C. chromaiodes, C. novaeboracensis,* and *C. pennsylvanicus*. There they overwinter, completing their larval development, pupating, and eventually emerging as adults.

Hoverflies in the genus *Microdon* have a similarly bizarre life history. The fly lays its eggs on the surface of the host ant's nest. As soon as the

Figure 2.6. The most common of New England's myrmecophiles include (clockwise from top left): larvae of the syrphid fly *Microdon ocellaris*, the scarabid beetle *Cremastocheilus variolosus*, crickets in the genus *Myrmecophila*, and the histerid beetle *Haeterius brunnipennis*.

eggs hatch, the larvae burrow down into the nest, making a beeline to the brood chamber. The sluglike larvae develop inside the nest, where they feed on detritus or prey on developing ant larvae. Like ant social parasites, many species of *Microdon* produce chemicals on their exoskeletons that mimic the odor of the ant colony they are inhabiting. In the spring, the pupating *Microdon* larvae move up to the top of the ant nest, where they pupate and then emerge as adults, flying off to lay their eggs in new colonies. Most *Microdon* species are thought to be host specific. In New England, they have been collected from nests of *Camponotus novaeboracensis, Formica exsectoides, F. incerta, F. obscuriventris,* and *F. querquetulana*. To identify *Microdon* species, it is necessary to rear the larvae (or pupae) to adulthood and also to keep a specimen of the host.

Myrmecophilus crickets also live in ant nests, where they feed on secretions regurgitated by worker ants or obtain nourishment by licking the hydrocarbons from the ants' exoskeletons. Why *Myrmecophilus* is tolerated by ants continues to be studied and debated. The currently accepted explanation is that the cricket fools the host ants into thinking it is an ant itself