ANTS

STANDARD METHODS FOR MEASURING AND MONITORING BIODIVERSITY

EDITED BY DONAT AGOSTI, JONATHAN D. MAJER, LEEANNE E. ALONSO, AND TED R. SCHULTZ

FOREWORD BY EDWARD O. WILSON
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STANDARD METHODS FOR MEASURING AND MONITORING BIODIVERSITY
Biological Diversity Handbook Series

Series Editor: Don E. Wilson

This series of manuals details standard field methods for qualitative and quantitative sampling of biological diversity. Volumes focus on different groups of organisms, both plants and animals. The goal of the series is to identify or, where necessary, develop these methods and promote their adoption worldwide, so that biodiversity information will be comparable across study sites, geographic areas, and organisms, and at the same site, through time.
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This book is dedicated to the memory of William L. Brown Jr., with affection, respect, and gratitude. For the inspiration you provided, for the firm foundation you built for ant systematics, and especially for your generous soul and irreverent good humor, we will never forget you, Bill.
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Global Ecology of Rainforest Ants

Functional Groups in Relation to Environmental Stress and Disturbance

Alan N. Andersen

This chapter deals with global ecology—the analysis and synthesis of ecological patterns and processes on a global scale (Cowling and Midgely 1996), referred to by Brown (1995) as *macroecology*. Global ecology does not address details of community composition and dynamics in any particular place, but instead provides a broad framework for doing so.

Study of the global ecology of rainforest ants seeks to understand how the structure and function of ant communities vary between rainforest and other biomes, among different rainforest types, among different strata within rainforest, and in response to disturbance. This approach requires a predictive understanding of the responses of rainforest ants to environmental stress and disturbance, where stress is defined, following Grime (1979), as any factor limiting productivity, and disturbance as any factor removing biomass. A key to such an understanding is the identification of functional groups that transcend taxonomic and biogeographic boundaries and respond predictably to stress and disturbance (Lavorel et al. 1997; Smith et al. 1997).

**Principles of Stress and Disturbance**

The primary stressors for ants are the following:

1. *Low temperature*. I consider low temperature to be the primary stress controlling global patterns of ant productivity and community structure (Andersen 1995). From an ant’s perspective, temperature is a product
of both climate (which controls ambient temperature) and habitat structure (which determines the degree of insolation of the foraging surface and therefore microclimate). Low-temperature stress is high in cool and shaded habitats, moderate in cool and open or warm and shaded habitats, and low in warm and open habitats (Andersen 1995).

2. Nest site availability. The availability of nest sites (the range of types and their abundance) exerts an important influence on ant productivity and community structure. The range of types of nest sites varies with the structural complexity of the habitat, and this range constrains the types of ants that can occur there. Structurally complex habitats, such as lowland tropical rainforests, offer nest sites (e.g., leaf litter, rotting logs, epiphytes, myrmecophytes) that are often not available in other habitats, and therefore they support functional types of ants (e.g., cryptic, myrmecophytic, and other arboreal species) that are often uncommon or absent elsewhere (Wilson 1987; Benson and Harada 1988; Byrne 1994). Herbers (1989) considered the abundance of nest sites such as preformed plant cavities in acorns and twigs to be a key limiting factor in temperate forests of the United States. In structurally simple habitats, where most ant species nest in soil, soil type has a major influence on ant productivity and community structure. Throughout Australia, for example, the highest degree of ant richness and abundance is often found on sandy soils, and the lowest on heavily textured soils (Greenslade 1979; Andersen and Spain 1996), reflecting differences between the substrates as nest sites.

3. Food supply. Food availability is obviously a critical determinant of the distributions of species with specialized diets, such as seed harvesters and specialist predators. However, most ant species are scavengers, generalist predators, collectors of honey-dew, or a combination of these, and the extent to which overall ant productivity is limited by food supply is not clear (Kaspari 1996b). There is no clear global relationship between primary productivity on the one hand and the productivity (reflected in either abundance or species richness) of ants on the other. Food resources often do not appear to be limiting in local ant communities (Byrne 1994), and it appears that factors such as temperature (e.g., insolation of foraging surfaces) and nest site availability (e.g., soil type) are more important (Kaspari 1996b), except in the most unproductive habitats, such as true deserts (Marsh 1986).

4. Microhabitat structure and resource capture. The structural complexity of the foraging surface exerts a major influence on the ability of ant species to capture food resources. For example, leaf litter on the ground reduces the efficiency with which resources can be located, retrieved, and defended by epigaeic ants. This factor has a major effect on ant community structure and possibly also influences overall ant productivity.

Given that disturbance is defined as the removal of biomass, for most animals it is synonymous with mortality. Ants, however, are modular organisms, and many “modules” (individual ants) can be lost without necessarily threatening the reproductive unit (the colony), in a manner analogous to the effects of herbivory on plants (Andersen 1991a). Therefore, combined with the protection provided by nests, especially those in the soil, habitat disturbance is often not much of a disturbance to ants at all, unless it is so severe that it causes widespread destruction of colonies. The major effects of
habitat disturbance are often indirect and stress-related, influencing habitat structure, microclimate, and food supplies (Andersen 1995). The importance of predation as a disturbance of ant communities has been little studied. Despite a wide range of animal species that feed on ants, some exclusively so (Redford 1987; Abensperg-Traun and Steven 1997), predation is not generally regarded as a major force structuring ant communities. However, there is increasing evidence that predation by other insects (Gotelli 1996) and more particularly parasitism by phorid flies (Feener 1981; Orr 1992; Porter et al. 1995c) can be an important factor in regulating foraging in some ant species, with significant effects on community dynamics.

From a global perspective, environments can be classified according to the relative importance of stress and disturbance as factors driving community structure, following the nomenclature of Grime (1979). Environments subject to severe stress or disturbance are characterized by highly specialized stress-tolerant species and unspecialized ruderal species, respectively. At very low levels of stress and disturbance, competition becomes the primary factor regulating community structure, and highly competitive species predominate. Three primary types of communities—stressed-tolerant, ruderal, and competitive—can therefore be recognized in relation to stress and disturbance (Andersen 1991a, 1995). At intermediate levels of stress and disturbance, a variety of secondary community types can also be identified (Fig. 3.1).

Just as the degree of disturbance from a vegetation perspective does not necessarily reflect the level of disturbance to ant communities, the same environmental conditions can represent very different levels of stress from plant and ant perspectives, and can therefore support very different structural types of communities (Andersen 1995). For example, hot and open environments represent low levels of stress for ants and support competitive ant communities. However, these same conditions are stressful for plants (i.e., primary productivity is low), and such environments support stress-tolerant plant communities, dominated by taxa such as cacti in North America and hummock grasses in Australia. Environments support structurally analogous plant and ant communities only when ants and plants respond similarly to limiting factors. An example of this is the ground layer of rainforests, which supports stress-tolerant ant and plant communities because both ants and plants are limited by low levels of sunlight.

Ant Functional Groups

Global community ecology requires the identification of functional groups that transcend taxonomic and biogeographic boundaries and vary predictably in response to stress and disturbance. Such groups have been identified for ants based on Australian studies (Greenslade 1978; Andersen 1995, 1997a). There are seven such ant functional groups, and their major representatives in Australia and the New World are listed in Table 3.1. A generalized model of the relationships of these groups to each other, and to environmental stress and disturbance, is
Table 3.1 Ant Functional Groups in Relation to Stress and Disturbance, with Major Representatives in Australia and the New Worlda

<table>
<thead>
<tr>
<th>Functional Group</th>
<th>Australia</th>
<th>New World</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Dominant Dolichoderinae</td>
<td><em>Anonychomyrma</em>, <em>Froggattella</em>, <em>Iridomyrmex</em>, <em>Papyrius</em>, <em>Philidris</em></td>
<td><em>Azteca</em>, <em>Forelius</em>, <em>Linepithema</em>, <em>Liometopum</em></td>
</tr>
<tr>
<td></td>
<td><em>Polyrhachis</em></td>
<td><em>Camponotus</em></td>
</tr>
<tr>
<td>2. Subordinate Camponotini</td>
<td><em>Calomyrmex</em>, <em>Camponotus</em>, <em>Opisthopsis</em>,</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Camponotus</em></td>
</tr>
<tr>
<td>3. Climate specialists</td>
<td></td>
<td></td>
</tr>
<tr>
<td>a. Hot</td>
<td><em>Melophorus</em>, <em>Meranoplus</em>, <em>Monomorium</em> (part)</td>
<td><em>Pogonomyrmex</em>, <em>Solenopsis s.s.</em>, <em>Myrmecocystus</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Formica</em> (part), <em>Lasius</em>, <em>Leptothorax</em>, <em>Stenamma</em>, <em>Lasiophanes</em></td>
</tr>
<tr>
<td>b. Cold</td>
<td><em>Monomorium</em> (part), <em>Notoncus</em>, <em>Prolasius</em>, <em>Stigmatomorpha</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Many taxa</em></td>
</tr>
<tr>
<td>4. Cryptic species</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Very many small myrmicines and ponerines, including Hypoponera, most Dacetonini, and Solenopsis</em> (Diplorhoptrum)</td>
<td><em>Very many small myrmicines and ponerines, including Hypoponera, most Dacetonini, and Solenopsis</em> (Diplorhoptrum)</td>
</tr>
<tr>
<td>5. Opportunists</td>
<td><em>Paratrechina</em>, <em>Rhytidoponera</em>, <em>Tetramorium</em></td>
<td><em>Dorymyrmex</em>, <em>Formica</em> (fuscus gp.), <em>Myrmica</em>, <em>Paratrechina</em></td>
</tr>
<tr>
<td>6. Generalized Myrmicines</td>
<td><em>Crematogaster</em>, <em>Monomorium</em>, <em>Pheidole</em></td>
<td><em>Crematogaster</em>, <em>Monomorium</em>, <em>Pheidole</em></td>
</tr>
<tr>
<td>7. Specialist Predators</td>
<td><em>Bothroponera</em>, <em>Cerapachys</em>, <em>Leptogenys</em>, <em>Myrmecia</em></td>
<td><em>Dinoponera</em>, <em>Leptogenys</em>, <em>Pachycondyla</em>, <em>Polyergus</em></td>
</tr>
</tbody>
</table>

*aSee text and Table 5.1 for details.*

shown in Fig. 3.2. The seven functional groups are as the following:

1. **Dominant Dolichoderinae.** From a global perspective, competitively dominant taxa are by definition those that predominate in environments experiencing low levels of stress and disturbance. For ants, such environments are hot and open ones, and these are often dominated both numerically and functionally by highly aggressive dolichoderines. This is particularly true in Australia, where *Iridomyrmex* and other dolichoderines dominate the continental ant fauna to an extent unparalleled elsewhere. However, it is also true for warmer regions of the New World, where *Forelius*, *Linepithema*, and *Liometopum* are behaviorally dominant ants in open habitats, and *Azteca* and *Dolichoderus* are highly dominant in the canopies of rainforest. It is important to appreciate that global dominance (where *global* defines the spatial scale on which dominance is considered) does not at all imply universal dominance (Andersen 1997b). Dolichoderines are not at all universally distributed, and they are often absent entirely from even moderately stressful habitats.

2. **Subordinate Camponotini.** Camponotine formicines, especially species of *Camponotus*, are also very often diverse and abundant in rich ant communities. Most are behaviorally submissive to dominant dolichoderines, and many are ecologically segregated from them owing to their large body size and often nocturnal foraging.

3. **Climate specialists.** These taxa have distributions heavily centered on either arid zones (hot climate specialists), the humid tropics
(tropical climate specialists), or cool-temperate regions (cold climate specialists). Both cold and tropical climate specialists are characteristic of habitats where the abundance of dominant dolichoderines is low, and, aside from their habitat tolerances, they are often unspecialized ants (army and fungus-growing ants are obvious exceptions). Hot climate specialists, on the other hand, are characteristic of sites where dominant dolichoderines are most abundant, and they possess a range of physiological, morphological, and behavioral specializations relating to their foraging ecology, which reduce their interaction with other ants. They include thermophilic taxa (such as species of *Cataglyphis*, *Melophorus*, *Myrmecocystus*, and *Ocymyrmex*; Snelling 1976; Marsh 1985; Christian and Morton 1992; Wehner et al. 1992) and specialist seed harvesters (including species of *Messor*, *Monomorium*, and *Pogonomyrmex*; Morton and Davidson 1988; Andersen 1991b; Medel and Vásquez 1994), which feature in virtually all of the world’s desert ant communities. Although species of *Forelius* have been described as dominant dolichoderines (Andersen 1997a), they might also be regarded as hot climate specialists (Bestelmeyer 1997).

4. Cryptic species. These are small to minute species, predominantly myrmicines and ponerines, that nest and forage primarily within soil, litter, and rotted logs. They are most diverse and abundant in forested habitats and are a major component of leaf litter ants in rainforest.

5. Opportunists. These are unspecialized, poorly competitive, ruderal species (Grime 1979), whose distributions appear to be strongly influenced by competition from other ants. They often have very wide habitat distributions, but predominate only at sites where stress or disturbance severely limit ant productivity and diversity, and therefore where behavioral dominance is low.

6. Generalized Myrmicinae. Species of *Crematogaster*, *Monomorium*, and *Pheidole* are ubiquitous members of ant communities throughout the warmer regions of the world, and they are often among the most abundant ants. As will be discussed later in this chapter, there is often competitive tension between them and dominant dolichoderines, including in tropical rainforest.

7. Specialist predators. This group comprises medium-sized to large species that are specialist predators of other arthropods. They include solitary foragers, such as species of *Pachycondyla*, as well as group raiders, such as species of *Leptogenys*. Except for direct predation, they tend to have little interaction with other ants owing to their specialized diets and typically low population densities.
Distribution of Behavioral Dominance

Globally, behavioral dominance becomes increasingly important to community structure with decreasing stress and disturbance. This trend is illustrated by ant behavior at tuna baits along an environmental gradient in southeastern Arizona, where monopolization by large numbers of behaviorally dominant species was greatest in desert (warm and open) habitats and least in forest (cool and shady) habitats (Fig. 3.3; Andersen 1997a).

The behaviorally dominant ants in warm regions are primarily Dominant Dolichoderinae and Generalized Myrmicinae, and, as previously mentioned, in open habitats there is often competitive tension between them. Dominant dolichoderines are strongly associated with hot, open habitats, such as deserts, Mediterranean ecosystems, and the canopies of tropical rainforests. Generalized myrmicines, by comparison, are far more shade tolerant, with *Pheidole* being a numerically dominant genus on the rainforest floor throughout the tropical world (Chapter 8). Globally, I consider Generalized myrmicines to be competitively subdominant ants (Andersen 1995) for the following reasons (Table 3.2):

1. They are considerably more stress tolerant than Dominant dolichoderines.
2. Whereas Dominant dolichoderines typically have large territories and individuals exhibit extremely high rates of activity, territory size tends to be more restricted in

![Graphs showing ant behavior at tuna baits in desert, woodland, and forest sites in southeastern Arizona.](image)

Figure 3.3. Behavior of ants at tuna baits at desert, woodland, and forest sites in southeastern Arizona, illustrating high, moderate, and low levels of behavioral dominance, respectively. Ant abundance (top; solid lines) at desert sites increases rapidly, reaching saturation levels after 30 minutes. Species richness (top; dotted lines), however, levels off after 5 minutes owing to competitive exclusion. Ant abundance is lower at woodland sites, but species richness continues to increase with time (local species richness is similar at desert and woodland sites). Both abundance and richness are very low at forest sites. Ant abundance scores (bottom) were usually either 5 (>20 ants) or 6 (>50 ants) at desert sites, fairly evenly distributed at woodland sites, and usually 0 (no ants) at forest sites. Data from Andersen (1997a).
Table 3.2 Generalized Myrmicines as Subdominant Ants to Dominant Dolichoderines*  

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Dominant Dolichoderinae</th>
<th>Generalized Myrmicinae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primary distribution</td>
<td>Low stress</td>
<td>Moderate stress</td>
</tr>
<tr>
<td>Territory size</td>
<td>Large</td>
<td>Restricted</td>
</tr>
<tr>
<td>Rates of foraging activity</td>
<td>Very high</td>
<td>Moderate</td>
</tr>
<tr>
<td>Resource monopoly</td>
<td>Aggressive displacement</td>
<td>Occupation and defense</td>
</tr>
</tbody>
</table>

*See text for details.

Generalized myrmicines, and rates of activity are more moderate.

3. Dominant dolichoderines actively displace other ants from food sources, whereas Generalized myrmicines often rely more on stout defense of food sources they have initially occupied (Andersen et al. 1991).

In cooler parts of the world, Dominant dolichoderines are mostly absent, and the abundance of Generalized myrmicines is greatly reduced. Throughout the Palearctic and Nearctic, the behaviorally dominant ants of cool-temperate regions are mound-building formicines (Cold climate specialists)—species of Formica and to a lesser extent Lasius (Creighton 1950; Rosengren and Pamilo 1983; Savolainen and Vepsäläinen 1988). It seems likely that their behavioral dominance in such cool climates is related to the thermoregulatory properties of their nests (Hölldobler and Wilson 1990). For example, with air temperature less than 14°C, Formica polyctena can achieve nest temperatures of up to 25°C (Coenen-Stass et al. 1980).

The relative importance of behavioral dominance varies markedly within the rainforest in response to increasing stress. Most behaviorally dominant taxa that occur in the tropics are arboreal, a habitat in which they can exploit direct sunlight. Such taxa include Dominant dolichoderines (e.g., Azteca, Dolichoderus, Philidris; Greenslade 1971; Adis et al. 1984; Tobin 1991; Shattuck 1992b), Generalized myrmicines (e.g., Crematogaster; Greenslade 1971; Majer 1976; Adis et al. 1984), Tropical climate specialists (e.g., Myrmica, Oecophylla; Greenslade 1971; Majer 1976; Stork 1991), and Subordinate camponotines (e.g., Camponotus; Wilson 1987). The canopy is the most productive microhabitat for both ants and plants in tropical rainforest, and there is increasing evidence that behaviorally dominant ants are predominantly primary consumers, being sustained by plant and homopteran exudates (Tobin 1994; Davidson and Patrell-Kim 1996).

The abundance of behaviorally dominant ants in rainforest decreases with increasing latitude and altitude, with Dominant dolichoderines virtually being restricted to the lowland tropics. On the rainforest floor, the heavy shade and litter represent considerable stresses for ants, and, as discussed by Kaspari (Chapter 2), behavioral dominance is relatively poorly developed, even in the lowland tropics.

Functional Group Composition

Consistent patterns of functional group composition can be recognized in relation to climate and vegetation (i.e., environmental stress). Functional group composition varies between climatic zones and, within any particular zone, varies systematically with vegetation type (Andersen 1995, 1997a). For example, in monsoonal northwestern Australia (Fig. 3.4a–c) the
Figure 3.4. Effects of vegetation on functional group composition in the monsoonal tropics of northern Australia (a–c; data from Andersen 1991c; Andersen and Reichel 1994) and in cool-temperate southern Australia (d–f; data from Andersen 1986a, 1986b). Functional groups: CCS, Cold climate specialists; CS, Cryptic species; DD, Dominant Dolichoderinae; GM, Generalized myrmicines; HCS, Hot climate specialists; OPP, Opportunists.

predominant vegetation is savanna, and functional group composition is similar to that in the arid zone (predominantly Dominant dolichoderines, Hot climate specialists, and Generalized myrmicines; Fig. 3.4a). The long-term absence of fire increases the structural complexity of the vegetation (Andersen 1996), thereby markedly reducing insolation at the soil surface. This dramatically reduces the abundance of Dominant dolichoderines and Hot climate specialists, and increases the abundance of Generalized myrmicines (Fig. 3.4b; Andersen 1991c).

In local patches of monsoonal rainforest, where insolation at the soil surface is even lower, Dominant dolichoderines and Hot climate specialists are absent altogether, and most ants are either Generalized myrmicines or Opportunists (Fig. 3.4c; see also Andersen and Majer 1991; Reichel and Andersen 1996). In cool-temperate southern Australia (Fig. 3.4d–f), the abundance of Dominant dolichoderines and Generalized myrmicines is generally low, and Opportunists and Cold climate specialists are usually among the most common ants. Dominant dolichoderines and Generalized myrmicines are usually only abundant in open habitats (Fig. 3.4d), and the relative abundances of cold climate specialists and cryptic species increase with decreasing insolation (Fig. 3.4e,f).

The ground-foraging ant faunas of different rainforest types have distinctive functional group signatures. The lowland tropics feature Generalized myrmicines (particularly Pheidole), Cryptic species, Tropical climate specialists (including army and leaf cutter ants), and Specialist predators (primarily large ponerines; Chapter 8). With increasing elevation or latitude, the diversity and abundance of cryptic species and particularly Generalized myrmicines and Specialist predators declines, and Tropical climate specialists are replaced by Cold climate specialists (including Stenamma in the New World). The faunas of cool-temperate rainforests are composed almost entirely of Cold climate specialists (including Lasius, Leptothorax, Prenolepis, and Stenamma in the
north, and *Lasiothynes, Notoncus, Prolasius*, and certain *Monomorium* in the south), Cryptic species (e.g., *Hypoponera*), and Opportunists (e.g., *Paratrechina, Rhytidoponera*, and the *fusca* group of *Formica*).

Functional group composition responds predictably to habitat disturbance in temperate and semiarid regions (Andersen 1990; Bestelmeyer and Wiens 1996), but the effects of disturbance on functional group composition of tropical rainforest ant communities have been poorly documented. In temperate southeastern Australia, for example, disturbance typically results in the proliferation of Opportunists, especially small species of *Rhytidoponera* (Andersen 1988, 1990; Andersen and McKaige 1987). Such a proliferation of Opportunists, especially species of *Formica* (*fusca* group) and *Myrmica*, following disturbance is also characteristic of cool-temperate regions in the Northern Hemisphere (Brian 1964; Gallé 1991; Andersen 1997a). Results from Queensland (Fig. 3.5) indicate that a proliferation of Opportunists (species of *Paratrechina* and *Rhytidoponera*) is also a characteristic response to severe disturbance in humid tropical Australia. This also appears to be true in the Solomon Islands, where tree clearing favors opportunistic species of *Cardiocondyla, Paratrechina, Tapinoma,* and *Tetramorium* (Greenslade and Greenslade 1977). Aside from arbo-

real taxa, Specialist predators and Cryptic species were especially sensitive to tree clearing in the latter study. Cryptic species also appear to be especially sensitive to tree clearing in the neotropics (Majer et al. 1997), where edge effects can be manifest for up to 200 m into the forest.

Conclusion

In any functional group analysis there is an inevitable trade-off between generality and precision, and the broad-scale predictive power of a global scheme will inevitably be inadequate for a detailed understanding of the dynamics of particular communities (Andersen 1997b). However, a global ecology based on functional groups in relation to stress and disturbance provides a predictive framework for analyzing broad patterns of (1) community composition and behavioral dominance within and between rainforest types, and (2) the responses of rainforest ant communities to disturbance. Unfortunately, even such coarse-scale analyses are highly constrained by a patchy geographic coverage of relevant studies (e.g., very little has been published from Africa) and a paucity of information on the effects of habitat disturbance (other than tree clearing). Nevertheless, there appears to be substantial convergence between biogeographic regions in the distribu-
tion of behavioral dominance within and between rainforest types and in changes in functional group composition in relation to stress (primarily temperature) and disturbance. To the extent that these patterns are confirmed by further studies, global functional groups are a valuable tool for understanding the dynamics of rainforest ant communities.

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