

Chapter 19

Ant-Plant Symbioses in Africa and the Neotropics: History, Biogeography and Diversity

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I. Introduction

Symbiotic ant-plant relationships afford an excellent opportunity to analyze the effects of both historical and ecological factors on the evolution of mutualisms. Occurring in tropical forests throughout the world, all myrmecophytic plants provide food and permanent housing to ants; the ants, in turn, are known or presumed to protect their hosts from herbivores or competition or to provision them with nutrients. Despite this underlying similarity, ant-plant symbioses differ in diversity and nature on different land-masses. These disparities could have arisen due to either unique features of the separate biotas or to distinctive climatic and other environmental variables that have influenced the net outcome or stability of the inter-

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actions. In contrast, similar selection pressures could have produced strongly parallel or convergent evolution in independent and geographically isolated ant-plant relationships. Cross-continental comparisons of ant-plant symbioses might then reveal the types of selection pressures driving plants and ants into intimate and mutually beneficial associations, as well as the kinds of plant and ant traits that could have facilitated such transitions.

Here we compare radiations of myrmecophytes and specialized plant-ants (ants that regularly live in symbiosis with a comparatively restricted set of host plants) in Africa and the Neotropics. We begin by assessing the extent to which patterns in the representation of ant-plants and plant-ants on different tropical land masses are correlated with trends in the diversity of floras or ant faunas as a whole. For both plants and ants, we then examine existing phylogenetic evidence bearing on the relationships between both ant-plants and plant-ants in Africa and America. Has the evolution of ant-plant associations occurred independently in the two regions, or can associations in Africa and America be traced to a common evolutionary past? Elsewhere (Davidson and McKey 1993), we argue that similar selection pressures may have driven strongly parallel and convergent evolution in ant-plant symbioses on different tropical landmasses and that selection operated on similarly preadapted plants and ants of Africa and the Neotropics. This evidence, weighed in the context of the historical data presented here, allows us to infer how major differences in the climatic and geologic histories of Africa and America may have profoundly influenced contemporary patterns in the number and distribu-

tion of ant-plant associations on the two continents.

Focusing on the more highly specialized participants in *symbiotic* ant-plant relationships of Africa and the Neotropics, we restrict our analyses to trees, shrubs, and hemiepiphytes with ant domatia. Domatia are regularly occurring cavities, either in stems or stem-like structures, or enclosures formed by invagination, by folding, for example, of leaves, stipules, and similar organs. Our discussion frequently includes the Asian and Australian ant-plant symbioses, as these often serve as useful reference points. Throughout our contribution, we use the terms *myrmecophyte*, *myrmecophytic*, and *ant-plant* to describe plants in which ants regularly nest, without implying that plants either benefit from the ants or have traits evolved principally as ant attractants. Existing evidence is often too meager for a convincing assessment of the benefits of particular associations to the plant (Davidson and McKey 1993).

A. The Ecological Diversity of Ant-Plant Symbioses

Janzen's pioneering study of ant-acacias gave us the first clear evidence for the mutualistic nature of an ant-plant symbiosis, by demonstrating conclusively the advantages to the plant of occupancy by specialist *Pseudomyrmex* acacia-ants. These ants protect the host from insect and other herbivores and prune neighboring plants, preventing engulfment of their host by vines (Janzen 1966). Over the past 25 years, studies have generalized these basic findings to a number of other ant-plant systems, while at the same time showing that considerable diversity lurks beneath the surface of these fundamen-

tally similar interactions (see Beattie 1985; McKey 1988; Hölldobler and Wilson 1990). For example, in addition to protection, ant associates of myrmecophytic epiphytes and ant-garden plants can make important contributions to the mineral nutrition of their hosts (Janzen 1974b; Huxley 1980; Rickson 1979; Davidson and Epstein 1989). Even in systems in which the principal benefits to the plant are protection against herbivores and vines, there is substantial diversity in functionally important aspects of the symbiosis. This includes variation in ant traits such as worker size and number, aggressiveness toward different intruders, and distribution of patrolling activity over the plant (McKey 1988). Variation in plant traits occurs in the type of food rewards produced for ants and the rate at which plants supply resources to ants (Davidson et al. 1991; Davidson and Fisher 1991). Plant-ants also vary in the degree to which they are host-specific. Some plant-ants occupy a number of unrelated plants that are morphologically and ecologically similar, though phylogenetically distant. Other plant-ants (e.g., acacia-ants) occupy several related host species. Cases of absolute species-specificity in host relationships appear to be exceptional and usually involve taxonomically depauperate systems (McKey 1989). Patterns of specificity and matches between plant and ant associates appear to be due not simply to pairwise interaction between plant and ant, but to interspecific competition among ants for plant resources (Davidson et al. 1988, 1989; Davidson and McKey 1993).

B. Similarities in Form of Ant-Plant Symbioses between Africa and the Neotropics

Emerging patterns are beginning to define the ecological and functional diversity of

ant-plant symbioses. Recognizable guilds of ant-plants and plant-ants occur on more than one continent. The term *guild* is used here to designate subsets of ant-plants and plant-ants differing in the traits that affect functioning of ant-plant interactions. Such characteristics include competitive abilities, behaviors, colony sizes, and energy requirements of ants, and the habitats, life forms, growth rates, and myrmecophytic attributes of plants. Between Africa and the Neotropics, in particular, remarkable similarities exist in the forms of symbiotic ant-plant relationships (Davidson and McKey 1993). Thus, on both continents, large colonies of active and aggressive ants occupy fast-growing and light-demanding pioneer trees, such as the Neotropical *Cecropia* and the African *Macaranga*. (Hollow stemmed Asian *Macaranga* are even closer analogues of *Cecropia*.) In contrast, timid ants inhabit small, slow-growing understory shrubs or treelets. The domatia of these ant-plants are often leaf-pouches covered with long, erect, and dense trichomes (as in African *Magnistipula*, *Delpydora*, *Cola*, and *Scaphopetalum* and Neotropical *Hirtella*, *Duroia*, and many melastomes). Finally, myrmecophytic trees of secondary forests and forest light gaps (African *Barteria* and Neotropical *Triplaris*) grow in circular clearings made by pseudomyrmecine ants, which attack vegetation in the neighborhood of their hosts.

Elsewhere (Davidson and McKey 1993) we argue that these remarkable similarities are the product of convergence and parallelism on a grand scale in different tropical regions. Both convergent and parallel evolution have been driven by similarities in the organization of arboreal ant communities and have led to similar selective forces on the participants in ant-plant symbioses. On

both continents, competitively dominant ants are associated with plants that provide resources at the high rates required to fuel the energy-intensive life-style that competitive dominance entails. In contrast, competitively subordinate ants of different continents are restricted to plants that supply resources at low rates or to those from which the dominants are excluded by traits of ants (e.g., pruning of neighboring vegetation: Davidson et al. 1988), plants (e.g., long, dense trichomes: Davidson et al. 1989), or both. Leading to further parallels between relationships on different continents, the evolution of these symbioses has also been facilitated by the same set of ant and plant preadaptations in both regions.

However, a simpler hypothesis to account for similarities between ant-plant symbioses in the two regions would be that they (or their participants) share a common origin. Our contribution addresses this alternative hypothesis. We begin by describing the myrmecophyte and plant-ant biotas of the two continents, comparing first their diversity and then the taxonomic composition of their participants in an effort to distinguish between hypotheses of shared and independent origins of African and Neotropical ant-plant symbioses.

II. Diversity of Myrmecophytes and Plant-Ants in Africa and America

A. Plants

1. Myrmecophytes in Relation to Floristic Diversity Patterns in the diversity of myrmecophytes across tropical landmasses mirror the trends for floras as a whole (table 19.1 and the appendix): plants are less diverse in tropical Africa than in tropical

America. The flora of tropical Africa is estimated to include about 2500 genera and 30,000 species, whereas that of tropical America is much richer, with 40,000 species estimated for Brazil alone (Brenan 1978). A total of 4200 genera and perhaps as many as 90,000 species may exist in the Neotropical region (Gentry 1982). As table 19.1 shows, tropical Africa is also poorer in the absolute number of genera of myrmecophytes than is tropical America. However, the *proportion* of plant genera including myrmecophytes is similar on the two continents. This similarity holds whether we compare entire biogeographic regions or mesic tropical forest regions. With the exception of *Acacia* spp., myrmecophytes are virtually restricted to mesic tropical forest habitats in both regions.

On both continents, among genera that have produced ant-plants, there is great variation in the number of myrmecophytes per genus (see the appendix). Both regions offer examples of species-rich genera that contain only one or very few myrmecophytic species, *Cola* (Sterculiaceae), with ca. 140 species (Nkongmeneck 1985), possibly the largest plant genus endemic to Africa, has a single myrmecophytic species (Schnell and Beaufort 1966). The same is true for *Diospyros* (Ebenaceae), with 49 mesic-forest species in Africa (White 1979). In the Neotropics, *Cordia* (Boraginaceae) contains 245–250 species but is represented by only 2 ant-plants (J. Miller, personal communication, 1991). *Besleria* (Gesneriaceae) and *Hoffmannia* (Rubiaceae), both with 100 or more species, each includes only a single myrmecophyte (Benson 1985). Among plant genera with ant-plants, myrmecophytism appears to be restricted to a single species in

Table 19.1. Generic diversity and endemism by biogeographic region for plants as a whole and myrmecophytic plants.

Measure	Region		
	Ethiopian	Neotropical	Oriental and Australian
All Plant Genera			
Total/mesic tropical region	2497 ^a	?	>2178 ^b
Total/biogeographic region	?	4200 ^c	?
Endemic to a biogeographic region	1500 ^d	?	?
Percentage endemic	?	?	?
Ant-Plant Genera			
Total/biogeographic region	31	39	52
Percentage of mesic tropical genera	1.2	?	<2.1
Percentage of regional genera	?	0.9	?
Endemic to a biogeographic region	17	30	32
Percentage endemic	54.8	78.9	61.5

^aTropical Africa: Brenan 1978

^bFigure given is the number of accepted generic names in the area covered by Flora Malesiana: van Steenis 1987

^cGentry 1982

^dTropical Africa, Madagascar, and southern Africa: Thorne 1973

a greater fraction of African genera (18 of 31, or 58%) than of Neotropical genera (12 of 39, or 31%).

Ant-plants from the Oriental and Australian regions are included in our tabulations for comparison (table 19.1 and the appendix). Species of 51 genera have been reported to be frequently or regularly occupied by ants, indicating a rich potential source of material for testing many of the generalizations we will offer from analysis of African and Neotropical cases. Many of the Oriental and Australian examples, however, are very poorly known at present, though work on these systems is accelerating (Fiala and

Maschwitz 1990; Fiala et al. 1989; Maschwitz et al. 1989, 1991).

Sizable radiations of ant-plants within genera are more frequent in the Neotropics than in Africa. When Neotropical genera are compared with closely related or ecologically analogous African genera, the number of congeneric myrmecophytic species is consistently lower in Africa. In part, this simply reflects the smaller size of many African genera. In the *Chrysobalanaceae*, for example, the African genus *Magnistipula* contains only a single ant-plant, whereas closely related *Hirtella* has 6–7 Neotropical myrmecophytes (see the appen-

dix), which Prance (1972, 1989) treats as a separate section of close relatives. The proportions of myrmecophytic species are similar, however, since *Magnistipula* contains only 6 species in all (Letouzey and White 1978), whereas *Hirtella* has 88 species, all but 2 of them Neotropical (Prance 1972). Similarly, the African genus *Musanga* (Cecropiaceae) contains only 2 species (de Ruyter 1976). One of these, *M. cecropioides* (frequently associated with ants [Duviard and Segeren 1974], though probably not a true myrmecophyte), is widely distributed, whereas the other is restricted to montane forest on the eastern fringe of the central African forest zone. In contrast, the closely related and ecologically analogous American genus *Cecropia* has about 75 currently recognized species (Mabberley 1987), though this number is likely to decrease to 60–70 with further revision (C. C. Berg, personal communication, 1992). Probably four-fifths of *Cecropia* spp. are myrmecophytes (Benson 1985; C. C. Berg, personal communication, 1992).

In addition to *Cecropia* and *Hirtella*, several Neotropical genera without obvious taxonomic counterparts in Africa have produced substantial numbers of myrmecophytic species. These radiations include *Tachigali* (Fabaceae), *Triplaris* (Polygonaceae), and *Ocotea* (Lauraceae), as well as *Clidemia*, *Maieta*, and *Tococa* (all Melastomataceae). For some of these we can identify unrelated African plants as ecological analogues. Here too, comparisons show that African genera are smaller and contain fewer myrmecophytic species than do their Neotropical counterparts. Neotropical *Triplaris* spp. (Polygonaceae) and African *Barteria fistulosa* (Passifloraceae) are both trees

of secondary forest and forest light gaps and have evolved associations with vegetation-pruning pseudomyrmecine ants. *Barteria* includes only one other species, *B. nigritana*, a small tree associated with *Crematogaster* ants. With 18 species (Brandbyge and Ollgaard 1984; Brandbyge 1990), *Triplaris* has undergone a much more extensive radiation. All but 1 of these species are myrmecophytes associated with pseudomyrmecines or (1 or 2) with a timid species of *Azteca* (Davidson et al. 1989; Ward 1991). Similarly, ant-plants with hairy domatia (most often in leaf pouches) occur in both African and Neotropical forests. In Africa, this group includes only 8 species in 7 genera of five families, whereas in the Neotropics, more than 80 species from 19 genera and eight families possess such domatia (Davidson and McKey 1993). Together, 3 of these genera in the Melastomataceae, *Clidemia* (*sensu stricto*), *Maieta*, and *Tococa*, contain more than 75 myrmecophytic species (W. Judd, personal communication, 1992).

Comparisons of the number of myrmecophytes in African and Neotropical genera allow two conclusions: (1) On both continents, myrmecophytism usually characterizes only a small proportion of the species of a genus. When radiations of myrmecophytic lineages occur, these are usually modest at best. (2) Exceptions to this general rule are more frequent in the Neotropics than in Africa. The only African genera with sizable numbers (5 or more) of myrmecophytic species are *Canthium*, *Cuviera* (both Rubiaceae), and possibly *Clerodendrum* (Verbenaceae), all poorly studied.

2. *Distributional Ranges in Africa and America* Comparisons of plant diversity in Africa and the Neotropics often emphasize

what seems to be a major disparity in ranges: not only is the tropical African flora less species-rich, but many of its species are also more widely distributed. In African forests, many tree species have very large geographic ranges, sometimes occupying the whole of the forest zone (Brenan 1978; White 1979). Some African myrmecophytes also exhibit this pattern. *Barteria fistulosa*, for example, occurs throughout the Central African forest zone, as do *Musanga cecropioides* and, among ant-plants with leaf-pouch domatia, *Diospyros conocarpa*. In contrast, in the Neotropics, Gentry (1990) has noted that often few plant species are shared between disjunct forests despite much overlap in the dominant genera. Correspondingly, the Neotropical analogues of widespread African myrmecophytes are genera rich in species; many of these species have restricted geographic ranges. For example, most species of *Triplaris* occupy only a small portion of the collective range of the genus, with fully 9 of the 17 myrmecophytic *Triplaris* species confined to western Amazonia (Brandbyge 1986, 1990). Three of 6–7 myrmecophytic *Hirtella* (*dorvalii*, *revillae*, and *vesiculosa*) are restricted to very narrow ranges in central Amazonia (Prance 1972, 1989). Although most *Cecropia* have medium-sized ranges, a number also appear to have small to very narrow endemic ranges, especially in western Amazonia (C. C. Berg, personal communication, 1992).

African myrmecophytes reflect two additional patterns within the African tropical forest zone: the poverty of species in the West African forest block compared to the Central African block (Gentry 1988), and the concentration of diversity in Lower

Guinea, the coastal forest from Nigeria through Cameroon to Gabon in the western part of the Central African block (White 1979). Only a few myrmecophytes are known from African forests west of the Dahomey gap. Those for which information is available (e.g., *Canthium glabriflorum* and other species of *Canthium*, *Cuviera* spp., and *Gardenia imperialis*) are inhabited by *Crematogaster* spp. that are probably not host-specific, suggesting that these may be recently evolved relationships. *Gardenia imperialis* is the only myrmecophyte with leaf-pouch domatia known from the West African forest block. Its pouches are little more than enlarged nectary-bearing pits over which carton-nesting *Crematogaster* build small carton shelters (Schnell and Beaufort 1966). The other possible myrmecophytes from this region are *Stereospermum kunthianum* and *Uncaria africana*. Both are wide-ranging and morphologically highly variable species that have been noted to be associated with ants (probably not host specific) in the Congo basin or further east, but whose biology in West Africa is unknown. With the possible exception of some *Canthium* and *Cuviera* species, none of the West African myrmecophytes is endemic to this forest block.

All other African myrmecophytes (except those found in drier vegetation types: *Acacia* and *Stereospermum*) are restricted to the central African rainforest block extending from Nigeria to the eastern rim of the Congo Basin. A number of these are distributed rather generally throughout this region: *Diospyros conocarpa*, *Macaranga saccifera*, *Buchnerodendron speciosum*, *Barteria fistulosa*, *Bertiera simplicicaulis*, *Nauclea vanderghuchtii*, *Rothmannia macro-*

carpa, *Cola marsupium*, *Scaphopetalum thonneri*, and myrmecophytic *Vitex* lianes. In addition to these, numerous species are found only in the western part of this forest block, the Lower Guinea coastal forest. These include *Magnistipula bimarsupiata*, *Calpocalyx cauliflorus*, *Leonardoxa africana* and other congeneric species soon to be described, *Barteria nigritana*, *Heinsia myrmoeccia*, *Ixora hippoporifera*, *Rothmannia lujae*, and *Delpyora macrophylla*. Thus myrmecophytes belonging to virtually all of the 31 African genera are found in Lower Guinea, and species of at least 8 genera are found only there. This relatively small area harbors a disproportionately large share of African myrmecophytes.

In the Neotropics (Gentry 1986a, 1990), regional endemism is comparatively high, and geographic trends in plant species diversity are closely mimicked by patterns in myrmecophyte diversity. Tree forms in the genera *Cecropia*, *Triplaris*, and *Tachigali* have their centers of diversity in Amazonia, whereas myrmecophytic shrubs and climbers, for example, *Ocotea*, *Piper*, *Acacia*, *Besleria*, *Hoffmannia*, *Clidemia* and *Costonegia*, are best represented in Central America or Andean foothills and ridges, or both (Gentry 1982). Like many endemic plants in tropical communities (Gentry 1986a), narrowly endemic ant-plants of the Neotropics appear to be largely neoendemics, products of perhaps recent and rapid speciation, rather than paleoendemic relicts of formerly widespread taxa. Consistent with Gentry's (1986a) view that habitat specialization has been the "prevalent evolutionary theme in giving rise to local endemics in some Amazonian families," a large component of the species diversity in at least

some myrmecophyte genera accumulates across habitat boundaries. For example, in southeastern Peru, one or more *Cecropia* species are typical of recently building sandy river beaches (*C. membranacea*), oxbow lakes (*C. latiloba*), banks of quebradas or small streams (*C. engleriana* and *C. polystachya*), land-slips along steep riverbanks and ridges (*C. polystachya* and an unidentified species), and aguajals and *Ficus trigona* swamps (provisionally *C. "tessmannii"*; Davidson et al. 1991). Both the narrowly endemic *Hirtella* ant-plants and myrmecophytic *Duroia* species are habitat specialists confined to white sand substrates or other soils of low fertility (Prance 1972, 1989; A. Gentry, personal communication, 1991).

In summary then, not only the diversity but also the distributions of myrmecophytes mirror general differences between African and Neotropical floras. Comparing tropical floras as a whole, African genera usually lack the proliferation of geographically restricted species that characterize radiations of many American genera in both western Amazonia and Central America and northwestern South America (Gentry 1986a). Although wide-ranging myrmecophytes (e.g., *Triplaris americana*, *Cecropia peltata*, and *Cordia alliodora*; Brandbyge 1986; Berg 1978; Gibbs and Taroda 1983) are not lacking in the Neotropics, species-rich Neotropical genera also include many ant-plants that are geographically restricted and often very specialized in their habitat associations.

3. *Local Diversity* Differences in ant-plant diversity on a regional scale are reflected at the level of local diversity (alpha-diversity), which can be two-fold higher in western Amazonia than in Africa. The coastal forests of Cameroon are richer in ant-plants than

any other part of the African forest zone, but even here no more than about 6 or 7 species of ant-plants are usually found in a single site. In the richest site known to us, near Ebodié, about 30 km north of the Cameroon–Equatorial Guinea border in the Campo Forest Reserve, at least 9 myrmecophytes occur sympatrically (i.e., can be found within a radius of ca. 7 km): 2 species of *Barteria*, 1 species each of *Leonardoxa*, *Delpydera*, *Diospyros*, *Ixora*, *Cola*, and *Scaphopetalum*, and 1 or more species of *Cuviera*. Further north, in Korup National Park, where with the exception of *Diospyros conocarpa*, leaf-pouch myrmecophytes appear to be absent, the list would include 1 species each of *Barteria*, *Leonardoxa*, *Diospyros*, *Calpocalyx*, *Vitex*, *Canthium*, and *Cuviera*. In southeastern Cameroon, away from the Lower Guinea coastal forest, frequently encountered myrmecophytes are 1 species each of *Barteria*, *Vitex*, and *Cuviera*. Thus, at a local community level, the number of myrmecophytes at least potentially involved in ecological interactions with arboreal ants, and indirectly with each other, often does not exceed 3 to 6 species in African forests.

In contrast, in western Amazonia the number of co-occurring ant-plants can range to at least 16 species. At or near both Cocha Cashu and Reserva Tambopata, two sites in Madre de Dios, Peru, local myrmecophytes include at least 6 *Cecropia* species (8 at Cocha Cashu), 2 species each of *Cordia* and *Triplaris*, 1 *Pleurothyrium*, 3 melastomes with leaf-pouch domatia (1 *Tococa*, 1 *Maieta*, and 1 *Clidemia*), and at least 11 species of ant-garden epiphytes (Davidson 1988; Davidson et al. 1989, 1991). Nevertheless, as indicated above, many of these

species exhibit strict habitat associations. Only *Cordia nodosa* and *Triplaris americana* are typical of both low-lying floodplain forests and terra firme forests. Thus, it seems that the high local myrmecophyte diversity may be largely a function of the complex mosaic of habitats typical of western Amazonia (Räsänen et al. 1987). Although many of the associated plant-ants are restricted to particular host genera or even species, some are not (Davidson et al. 1989, 1991). Where distinctive habitat types are closely adjacent, as in western Amazonia, there should be considerable potential for myrmecophytes of one habitat to be colonized (at least occasionally) by ants characteristic of other ant-plants in contiguous habitats.

B. Ants

Among specialized plant-ants, generic richness across tropical biogeographic regions does not seem to parallel that for ant faunas as a whole (table 19.2). The greatest contrast is between ants of the Oriental and Australian regions, on the one hand, and ants of the Ethiopian and Neotropical regions, on the other. Although generic richness of the Oriental and Australian ant faunas is greater than that of Africa and comparable to that of the Neotropics, fewer Oriental and Australian genera (apparently only 5–7%) include specialized plant-ants. (This may change with further study of many poorly investigated Oriental and Australian ant-plants and revisionary work on their ant occupants.) In the Ethiopian and Neotropical biogeographic regions, 10 to 12 percent of genera include plant-ants, and the fraction increases to 13 to 15 percent of genera in

Table 19.2. Generic diversity and endemism by biogeographic region (Hölldobler and Wilson 1990) and mesic tropical regions (Brown 1973), for ants as a whole and obligate plant-ants.

Measure	Ethiopian	Neotropical	Oriental	Australian
All Ant Genera				
Total/mesic tropical region	75	94	96	88
Total/biogeographic region	92	120	124	109
Endemic to a biogeographic region	31	57	31	29
Percentage endemic	33.3	47.5	25.0	26.6
Plant-Ant Genera				
Total/biogeographic region	11	12	7	8
Percentage of mesic tropical genera	14.5	12.8	7.3	9.1
Percentage of regional genera	12.0	10.0	5.6	7.3
Endemic to a biogeographic region	5	5	1	2
Percentage endemic	45.5	41.7	14.3	25.0

Note: Australian includes Oceania. Classification of these regions follows Brown (1973) and departs slightly from Hölldobler and Wilson (1990). Endemism is calculated in relation to the seven zoogeographic regions of Darlington (1957) and includes Palearctic, Nearctic, and Madagascan regions, as well as those listed here. Calculations based on genera and distributions given by Brown (1973) and Hölldobler and Wilson (1990) were updated to account for revisionary work by Ward (1990) and Shattuck (1991, 1992a, 1992b). Fractions of regional genera with specialized plant-ants include ants whose specialization remains questionable (see table 19.3).

mesic tropical areas, to which plant-ants are mostly restricted.

Disparities between Africa and the Neotropics in the frequency of plant-ants are less marked. For all ant genera and for endemic genera, richness is greater in the Neotropics than in the Ethiopian region. But although mesic Neotropical forests have 1.2 times the number of ant genera as inhabit mesic tropical forests of Africa, the number of genera known to include specialized plant-ants is almost the same for the two areas. Thus the proportion of ant genera with specialized plant-ants is slightly higher in Africa.

As for myrmecophytic plants, the most striking differences in the diversity of African and American plant-ants occur at the species level (table 19.3). Whereas 5 Neotropical genera, representing 4 different subfamilies, are rich in plant-ants (*Pseudomyrmex*, *Allomerus*, *Pheidole*, *Azteca*, and *Myrmelachista*), this is true in Africa only for the pseudomyrmecine genus *Tetraponera* and probably the dolichoderine genus *Techonomyrmex*. Even in these cases, the number of plant-ant species is markedly lower than in the Neotropical members of the respective subfamilies. For example, in the Pseudo-

Table 19.3. Present-day distributions of (wholly tropical) obligate plant-ants by subfamily, tribe, and genus.

Taxon	Ethiopian	Neotropical	Oriental	Australian	References
Ponerinae					
Ponerini					
<i>Pachycondyla</i>	×	×(3–4+)	×	×	Davidson & Fisher 1991; J. Longino PC
Pseudomyrmecinae					
<i>Myrcidris</i>	—	×(1)	—	—	Ward 1990
<i>Pseudomyrmex</i>	—	×(32)	—	—	Ward 1991; P. Ward PC
<i>Tetraponera</i>	×(5+)	—	×(2)	×(1)	Ward 1991; P. Ward PC
Myrmicinae					
Cephalotini					
<i>Zacryptocerus</i>	—	×(1+)	—	—	Longino 1989a
Crematogastrini					
<i>Crematogaster</i>	×(3+)	×(2+)	×(8+)	×(1+)	Eth = DM; Neo = Davidson et al. 1989; Davidson & Fisher 1991; Vasconcelos 1990; Ori = Fiala & Maschwitz 1990; J. Longino PC; DD; Aus = Hölldobler & Wilson 1990
Leptothoracini					
<i>Leptothorax</i>	×(1)	×	×	×	R. Snelling PC; DM
Pheidolini					
<i>Pheidole</i>	×	×(6+)	×	×(1+)	Neo = Benson 1985; Davidson et al. 1989; Letourneau 1983; Aus = Hölldobler & Wilson 1990
Solenopsidinae					
<i>Allomerus</i>	—	×(8+)	—	—	Wheeler 1942; Benson 1985
<i>Solenopsis</i>	×	×(1+)	×	×	Benson 1985
Tetramoriini					
<i>Tetramorium</i>	×(1+)	×	×	×	R. Snelling PC; DM
Dacetini					
<i>(Strumigenys)</i>	×	×(1+)	×	×	Brown 1962; W. L. Brown, Jr. PC
Tribes unclassified					
<i>Cataulacus</i>	×(1+??)	—	—	—	R. Snelling PC; DM

<i>Podomyrma</i>	—	—	—	×(2+)	G. Monteith & P. Flower PC; DD
<i>Atopomyrmex</i>	×(1)	—	—	—	R. Snelling PC; DM
Dolichoderinae					
Tapinomini					
<i>Anonychomyrma</i> ^a	—	—	—	×(3+)	DD
<i>Axinidris</i>	×(2+??)	—	—	—	R. Snelling PC; DM
<i>Azteca</i>	—	×(20++)	—	—	Wheeler 1942; Benson 1985; Longino 1989a, 1989b, 1991
<i>Philidris</i> ^b	—	—	×(1+)	×(1+)	Ori = Ridley 1910; R. Snelling PC; DD; Aus = DD
(<i>Tapinoma</i>)	×(1?)	×	×(1?)	×	Eth = R. Snelling PC; DM; Ori = T. Musthak Ali PC; DM
<i>Technomyrmex</i> ^c	×(6+??)	×	×(1+)	×(1+)	Eth = R. Snelling PC; DM; Ori = D. Samson PC; R. Snelling PC; Aus = DD
Formicinae					
Plagiolepidini					
(<i>Plagiolepis</i>)	×(1+)	—	×	×	Bequaert 1922
Myrmelachistini					
<i>Aphomyrmex</i>	×(1)	—	—	—	R. Snelling PC; DM
<i>Cladomyrma</i>	—	—	×(4+)	—	Agosti 1991; Maschwitz et al. 1991; DD
<i>Myrmelachista</i>	—	×(6++)	—	—	J. Longino PC; DD
<i>Petalomyrmex</i>	×(1)	—	—	—	Snelling 1979; McKey 1984
Camponotini					
<i>Camponotus</i>	×	×(3+)	×(7+)	×(2+)	Neo = Davidson & Fisher 1991; Ori = Hölldobler & Wilson 1990; DD; Aus = Monteith 1987; Hölldobler & Wilson 1990

Note: Presence (×) or absence (—) by zoogeographic region. Taxonomy and distribution from Hölldobler and Wilson (1990). Obligacy of symbiotic association with plants is uncertain for genera in parentheses. Rough estimates of numbers of plant-ant species are indicated in parentheses; these are likely to increase moderately (+) or substantially (++) with additional collection and taxonomic revision. Abbreviations used in references: Aus = Australian; DD and DM = respective author's observations; Eth = Ethiopian; Neo = Neotropical; Ori = Oriental; PC = personal communication.

^aRecently segregated from *Iridomyrmex* (Shattuck 1992b).

^bRecently segregated from *Iridomyrmex* (Shattuck 1992b). Most or all of these plant-ants occupy ant-epiphytes.

^cIncludes *Engramma* (S. Shattuck 1992a).

myrmecinae, only 3 of 12 hypothesized independent origins of plant-ants in the Pseudomyrmecinae have taken place in Africa, and only 4 of 37 confirmed pseudomyrmecine plant-ants occur there (Ward 1991). All but 1 of the remaining species and origins are Neotropical. (To these published records must be added an undescribed plant-ant species of *Tetraoponera* recorded from *Mimosa* sp. in Madagascar; this apparently represents an additional independent origin of the habit; see P. Ward, personal communication, 1991). *Technomyrmex* appears to have produced a modest number of plant-ants in Africa (table 19.3), and their hosts include 8 genera of 5 plant families (Davidson and McKey 1993). The number of plant-ant species, and the number of independent origins of the plant-ant habit, are unclear in this case. Among Africa's 5 endemic plant-ant genera, both *Aphomyrmex* and *Petalomyrmex* are monotypic, and the other 3 contain only 1 or 2 confirmed plant-ant species. All 5 plant-ant genera endemic to Africa are associated with 1 or very few host genera. In contrast, all 4 genera of Neotropical endemic plant-ants inhabit hosts in multiple plant families (see below) and probably include multiple radiations of plant-ants. Especially in *Pseudomyrmex*, discussed above, but also in *Azteca*, radiations of plant-ants have been explosive, giving rise to specialists on plants in a broad range of wet and even dry forest habitats (Benson 1985; Ward 1991). *Azteca* includes at least 20 plant-ant species (table 19.3), occupying at least 13 plant genera in 8 families (Davidson and McKey 1993). *Allomerus*, *Pheidole*, and *Myrmelachista* each have at least 6 to 8 plant-ant species in the Neotropics (table 19.3) and occupy a diversity of hosts (in

each case at least 6 genera in at least 4 families; Davidson and McKey 1993).

The apparent lower species richness of African plant-ant genera may be due in part to less thorough collecting. Despite some work in the former Belgian Congo (Bequaert 1922), collections of African plant-ants have been much less thorough and more narrow in geographic scope than collections in the Neotropics (Wheeler 1942), and this difference continues today. Further field work and taxonomic revision will probably tend to reduce the gap between the numbers of African and Neotropical plant-ants. An increase in the number of African plant-ant species is likely to be concentrated in the dolichoderine genera *Axinidris* and *Technomyrmex* and to result from both description of new species (especially *Technomyrmex*) and work on the natural history of known species. The dolichoderine genus *Axinidris* is a case in point. Before Shattuck's (1991) revision, this genus was considered monotypic, but it now contains 13 named species. Prior to the collection (in 1989) of 2 species from swollen internodes of *Leonardoxa* in Cameroon, *Axinidris* was not known to include plant-ants, since it had been collected only as stray workers and its habits were undescribed. Despite such indications that the African fauna is poorly studied, we believe that the intercontinental difference in species richness of plant-ant genera is real. New Neotropical plant-ants have also recently been found in the genera *Pachycondyla*, *Crematogaster*, *Myrcidris*, and *Azteca* (Davidson and Fisher 1991; Ward 1990; Longino 1989b; J. Longino, personal communication, 1991). Furthermore, if myrmecophyte species richness gives any indication of plant-ant species richness, the

Neotropical region would be expected to contain more plant-ants. The two continents differ dramatically in myrmecophyte species richness, and this difference is unlikely to be greatly altered by further work.

As in ant-plants, much of the diversity of plant-ants appears to be attributable to habitat specificity. Even a single plant host species often harbors different ant associates in different habitats (Benson 1985; Harada and Benson 1988; Longino 1989b; Davidson et al. 1989, 1991). Similarly, related ant-plants that are specialized on different habitats, like the *Cecropia* spp. discussed above, are occupied by different suites of ants. The ant associates of members of a plant lineage in different habitats are often not closely related, belonging to different species groups, genera, or even subfamilies (Benson 1985; Davidson et al. 1991; Davidson and Fisher 1991; Davidson and McKey 1993). This suggests that habitat-dependent host shifts, and habitat-dependent secondary colonizations of ant-plants by multiple ant lineages, have been important processes. Parallel diversification of associated ant and plant lineages, possibly involving parallel patterns of habitat specialization in ants and plants, seems to have occurred less frequently. Some examples, however, are suggestive. In the genus *Pseudomyrmex*, closely related (sibling) species often have broadly overlapping distributions, and allopatric pairs of sister species are uncommon (Ward 1989). As many as 4 species of *Pseudomyrmex* co-occur locally on both Peruvian *Triplaris* (*P. viduus* group) and Central American *Acacia* (*P. ferrugineus* group). Ward implies that speciation in *Pseudomyrmex* has been largely allopatric, with rapid secondary overlap. Across the three *Azteca* lineages

associated with *Cecropia*, three different distributional patterns are apparent (Longino 1989a, 1989b; J. Longino, personal communication, 1991). The newly separated *A. alfari* and *A. ovaticeps* have broadly overlapping geographic ranges extending throughout most of the Neotropics (Longino 1989b). Also, two species of the *A. constructor* complex are sympatric in the Choco region of Colombia (J. Longino and T. M. Aide, personal communication, 1991). In contrast, closely related *A. xanthochroa* and *A. australis* are allopatric, the former occurring in Central America and the latter in South America. Without additional revisionary work in many ant and plant groups, it is impossible to judge the degree to which the distributional patterns and speciation processes are alike in associated ant and plant taxa.

C. Intercontinental Differences in Ant-Plant and Plant-Ant Diversity

As summarized in table 19.1 and the appendix, the major tropical regions differ in diversity of ant-plant symbioses. The Oriental and Australian regions combined have the largest number of reported ant-plant genera, but only a few have been well studied (e.g., Fiala and Maschwitz 1990; Fiala et al. 1989; Maschwitz et al. 1989, 1991). Among the 52 Oriental and Australian genera, only 25 (48%) have been sufficiently well-documented to establish the presence or absence of specialized structures to house ants (Davidson and McKey 1993). On the whole, a greater proportion of African and Neotropical genera appear to be at least minimally understood. In only 2 African genera (6%) and 10 Neotropical genera (26%) do we judge that uncertainty remains about the

presence or absence of specialized domatia. Future studies may yet reveal that the greater uncertainty about Australian and Oriental ant-plants is merely a consequence of the difficulty of ruling out domatia, where obvious domatia are lacking. Here, however, we restrict our comparisons to Africa and the Neotropics.

What factors account for myrmecophytes and specialized plant-ants radiating more extensively in the Neotropics than in Africa? Are discrepancies in diversity the consequence of regional differences affecting the biology of ants or plants in particular, or are they one manifestation of differences that have had general consequences for rates of species extinction or origination in many taxa on the two continents? We first consider the former possibility.

1. Explanations Specific to Ants and Ant-Plant Interactions Carroll (1979) documented intercontinental differences in diversity of the stem-nesting guild of arboreal ants and proposed a hypothesis to explain his findings. Because most specialized plant-ants are derived from ants in this guild, patterns of diversity in plant-ants may be a reflection of underlying differences in the stem-nesting guild.

Compared to African wet forests (Carroll 1979), Central American forests are richer in both biomass and species of arboreal stem-nesters. Carroll (1979) attributes the lower abundance and diversity of African stem-nesters to greater interference from aggressive dominants (genera *Oecophylla*, *Tetramorium*, and *Crematogaster*), whose construction of nests from leaves or carton frees them from nest-site limitation. Tending of Homoptera by these same ants provides an

abundant resource and funds the aggression that prevents behaviorally subordinate species, including most stem-nesters, from coexisting with dominants. Because aggressive and dominant *Camponotus*, *Azteca*, *Hypoclinea* (= *Dolichoderus*; Shattuck 1992a) and *Crematogaster* of South America are ecologically equivalent to the African dominants, Carroll's hypothesis would prove inadequate if South American stem-nesters exhibited biomass and diversity equivalent to that in Central America. Although exactly comparable data are not available, the remarkable abundance and diversity of arboreal ants in Peruvian rainforests appear to contradict the hypothesis. From two censuses of a single leguminous tree in secondary forest at Reserva Tambopata in Madre de Dios, Peru, Wilson (1987) identified 26 genera and 43 species of arboreal ants. Although not all of the species are stem-nesters, we estimate that at least 26 of the species in this tree nest regularly in twigs and branches. The results of Tobin's (1991) studies in a nearby forest within the Manu National Park suggest that Wilson's figures are not anomalously high. In canopy fogging samples from two isolated rainforest trees, Tobin found 52 ant species (not distinguished by nesting sites), accounting for 70 percent of the arthropod numbers and probably more than 50 percent of arthropod biomass. Four dolichoderine species, together comprising more than 90 percent of ant biomass, might qualify as dominants comparable to those identified from African forests. Considering the abundance of ecologically analogous aggressive dominant ants in both continents, we find little evidence to support the view that more intense interaction with dominant ants has led to lower abundance

and diversity of stem-nesting arboreal ants in Africa. Nevertheless, there may be differences between the two continents in abundance of some groups of small-bodied stem-nesters, most notably those belonging to *Crematogaster*. This genus appears to be an especially important component of arboreal ant faunas in the Old World tropics, and its members are often competitive dominants (Davidson and McKey 1993). If twig-nesting *Crematogaster* are more abundant in Africa, this might have important consequences for other twig-nesters. Canopy fogging samples from African forests might shed further light on this issue.

2. General Explanations of Diversity Differences Intercontinental disparities in the diversity of ant-plants closely mirror those for plants as a whole, as well as for other kinds of organisms (Amadon 1973; Laurent 1973; Roberts 1973; Chapter 9). For ants, the same is true in somewhat lesser degree; the correspondence is more evident at the species level than at the generic level, and is more evident for the Neotropical/Ethiopian pair than for other intercontinental comparisons. We find it difficult to avoid the conclusion that differences in the diversity of these symbiotic associates are just one manifestation of a general trend toward greater species richness in the Neotropics. Such a broad pattern likely has general causal mechanisms, and several have been proposed. As Duellman (Chapter 9) points out, the area of mesic tropical forest habitat in America is approximately 2.8-fold greater than that in Africa. Extinction rates on the two continents might have differed dramatically during past periods of climatic deterioration, due to differential effects of Pleistocene

cooling and drying cycles on habitat reduction in Africa and South America (Raven and Axelrod 1974; Axelrod and Raven 1978; Gentry 1986a, 1988). Unlike Amazonia, which is shielded by the Andes, tropical Africa lacks protection from the drying effect of a cold western ocean current. The climate of tropical Africa is also driven largely by the Asian and African monsoons, which weakened greatly during northern glaciations. Consequently, rainfall in Africa at 18,000 B.P. may have been reduced by half, while Amazonian rainfall, dependent mainly on tropical sea surface temperature, might have been reduced only by 10 to 20 percent (Chapter 15). African forests may then have experienced greater reduction, and persisted in a smaller number of refugia, during the Pleistocene (Maley 1987, 1989; Maley et al. 1990; Chapters 15 and 16). Forest reduction was most extreme in West Africa, where rainfall was highly dependent on the African monsoon, and least in the Lower Guinea coastal forests, where the equatorial counter-current maintained relatively high sea surface temperatures and hence relatively high rainfall even during glacial maxima (Maley 1989). This difference may explain the generally low plant diversity of the West African forest block and the concentration of diversity in Lower Guinea, two patterns reflected in the diversity of ant-plants.

Frequent and severe African droughts might also have taken their toll on ant diversity and on symbiotic species associations. The majority of obligate plant-ants appear to have evolved from ancestors that tended Homoptera inside cavities of live plants, and droughts could have limited the diversification of such ants in Africa. Compatible with this hypothesis are the findings of Terron

(1970), who documented a strong impact of seasonal drought on rates of egg-laying, alate production, and larval death in African *Tetraponera anthracina*, a homopteran-tending stem-nester confined to comparatively mesic rainforests and gallery forests. In addition, since the net effects of species interactions on individual participants are usually context-dependent (Davidson and McKey 1993), the greater range of environmental change in Africa might have been more likely to convert mutualisms to parasitisms and to lead to the dissolution of symbiotic mutualisms, even in the absence of species extinctions.

Most attempts to explain differences in diversity between African and South American tropical forest ecosystems have focused on contemporary and historical differences in climate. Several observations, however, make it seem unlikely that these differences fully account for the intercontinental disparities in floral and faunal richness. First, the case of the Cape Province of southern Africa, with its striking plant diversity and endemism, illustrates that even a relatively small area can accumulate high species richness over comparatively brief intervals of geologic time. Second, climate change here seems to have enhanced rather than reduced diversity. Swarms of endemic plant species in the fynbos and other distinctive communities of the Cape Province have evolved in the last 2 to 5 million years, since the establishment of the cold Benguela current that brought mediterranean climates to the Cape (decimating the existing subtropical flora), and hyperaridity to the Namib (Chapter 3). Although comparisons of African and Neotropical diversity have tended to emphasize the negative effects of climate change, such

fluctuations may have helped to magnify diversity here as well (Chapter 16), as geographic ranges fractionated and organisms encountered new habitats during the range re-expansions that would have occurred in periods of climatic amelioration.

Third, major differences in geologic activity on the two continents, and in correlated rates of habitat disturbance, are likely to have affected both the generation of diversity over evolutionary time (e.g., Vanzolini 1973) and its maintenance in ecological time. We believe that differences between the two continents in the structure of historical and contemporary landscapes, resulting from their contrasting geological histories, are an overlooked and crucial factor in explaining differences in their biological diversity. Africa's less eventful geological history has produced a less diverse mosaic of landforms and habitats than in tropical South America and has presented fewer opportunities for habitat specialization.

As the keystone of Gondwana, Africa was at the interior of a supercontinent that had been exposed to weathering for a very long time and was probably relatively flat, as it is now. According to Wright and co-workers (1985:1), "almost the whole of Africa has been unaffected by major mountain-building (orogenic) earth movements since the end of the Precambrian. . . . Africa is predominantly a continent of plains and plateaux and intervening escarpments, the result of erosion and planation lasting many hundreds of millions of years. Topographic relief is low over vast areas." While most of Africa remained flat during drift, the Andes pushed up along the leading edge of South America, with three important consequences for the subsequent evolution of the biota of

this continent. First, the Andes blocked the drying effects of a cold ocean on tropical South America. Second, in western Amazonia the Andes provided habitat diversity in the form of topographic relief, with its consequences for temperature, rainfall, and cloudiness regimes. Third, by lifting vast amounts of rock of varying composition and producing the orographic rainfall that erodes it, "the rising Andes became an inexhaustible source of vast masses of sediment" (Klammer 1984:77). The tectonic activity associated with the Andes generated a fluvial landscape and an edaphic mosaic whose complexity (Salo et al. 1986, Räsänen et al. 1987; Brown 1987c) is unmatched in geologically relatively stable Africa.

With the conspicuous exception of East African mountains and rift valleys, lying mostly outside the mesic forest zone, most of tropical Africa is a relatively featureless plateau. Elevational relief contributes little to habitat heterogeneity in this region of long-term geologic stability. Africa has little cloud forest habitat, in marked contrast to the expanses of mid-elevation, submontane, and montane forest present in the coastal moist forest zone of the northern Andes, in southern Central America, and in western Amazonia near the base of the Andes. These areas harbor a tremendous diversity of plant species, many of them endemic and apparently produced by relatively recent and explosive speciation (Gentry 1986a). Gentry (1986a:168–169) considers this very active speciation, typical of montane areas throughout the tropics, to be "somehow related to the peculiarities of the broken terrain and/or the complex juxtaposition of different vegetation types." Adding to the effects of elevational habitat heterogeneity per se is

Janzen's (1967) observation that elevational relief creates especially effective barriers and isolating mechanisms for tropical organisms, which tend to have narrow thermal tolerances.

Mountain-building activity also creates habitat diversity far beyond the montane and submontane areas immediately affected by orogeny (Salo et al. 1986). Lack of such activity in Africa has resulted in an edaphic landscape that, at least in the mesic forest zone, is much less complex than that of tropical South America. Missing in Africa are areas of both elevated continental shield (e.g., South America's Guyanan shield), and the expanses of acid white-sand soils created by the erosion of these ancient rocks (as in the Rio Negro basin) (Sombroek 1984), or resulting from former beaches of oceans, inland seas, and rivers (Prance 1987). Lacking as well is the edaphic mosaic produced by Andean orogeny: volcanic soils, soils with peculiar mineral imbalances (Chapter 17), and the great sheets of alluvial soils produced as young Andean rocks have been eroded by prodigious orographic rainfall. Particularly in western Amazonia, long-term fluvial perturbation over the Tertiary and Quaternary has produced a temporally structured and highly complex mosaic of fossil and present floodplains (Räsänen et al. 1987). The scale of riverine disturbance in western Amazonia is illustrated by the finding of Salo and co-workers (1986) that 26.6 percent of the modern lowland forests show evidence of recent erosional and depositional activity and that 12 percent is currently in succession. Like elevational diversity in the Neotropics, this edaphic mosaic contributes to great habitat diversity, which has probably magnified species diversity, es-

pecially in northwestern Amazonia (Gentry 1986a, 1986b, 1988; Salo et al. 1986).

Compared to the Neotropics then, the African forest zone seems to offer relative monotony along many environmental dimensions. Greater habitat diversity may explain why regional species diversity and total species richness is greater in the Neotropical forest flora, even though within-site plant species diversity is fairly similar in African and Neotropical forests with comparable rainfall (Gentry 1988; Chapter 17).

Mounting evidence points to an important role of habitat specialization in the evolution of tropical plant species diversity (Gentry 1986a, 1988). We postulate that the African forest zone offers a lower diversity of habitats and hence fewer opportunities for habitat specialization. If Colinvaux (Chapter 16) is correct in hypothesizing a "speciation pump" primed by range re-expansion into new habitats, rates of species origination during periods of past climatic change may have been higher in the Neotropics. First, the number of refugia from which forest species could re-expand, and the size of refugia, are both postulated to have been greater in the Neotropics than in Africa (compare maps in Brown 1987a and Maley et al. 1990). Thus the number of species "available" for speciation may have been greatly reduced in Africa. Second, as climates warmed and became wetter, and ranges of mesic-forest organisms expanded, plants in the Neotropics were more likely than those in Africa to encounter elevational, climatic, and edaphic conditions sufficiently new to stimulate evolutionary change. They may also have encountered more environmental boundaries sharp enough to allow evolutionary divergence from parent populations. Gentry's

(1986a) argument that many endemic Amazonian plants appear to be neoendemics, rather than paleoendemics of old refugia, lends credence to the view that climatic change and habitat heterogeneity could have been major contributors to evolutionary diversification in the Neotropics. Moreover, contemporary ecological differences in habitat diversity on the two continents may be as important as differences in the amount and seasonal distribution of rainfall (Gentry 1988) in maintaining disparities in species richness.

What is the particular role of habitat specialization in the evolutionary diversification of myrmecophytes and specialized plant-ants? As noted previously, outcomes of interspecies interaction may vary markedly among environments. Consequently, the match between ant and plant associates, largely determined by interspecific competition among ants for plant resources, might be particularly sensitive to habitat differences that affect the rates at which plants supply resources to ants (Davidson et al. 1991; Davidson and Fisher 1991). This topic will be treated in detail elsewhere (Davidson and McKey 1993).

III. Relationships between Plant-Ants and Ant-Plants on Different Landmasses

In a subsequent paper (Davidson and McKey 1993), we argue that intercontinental similarities in ant community organization, and in ant and plant preadaptations, have driven strong parallel and convergent evolution in the ant-plant symbioses of Africa and the Neotropics. The strength of such inferences about evolutionary processes based on

ecological similarities depends on a confident answer to the following question: Have ant-plant symbioses evolved independently on the two continents, or do similarities in their form simply indicate a single common origin?

The first step in understanding these striking commonalities is to determine the extent to which they reflect the descent of plants, ants, or even ant-plant associations, from common ancestors. Two kinds of evidence bear on this issue: the extent to which plant groups, ant groups, and symbiotic relationships are shared between the two continents, and fossil evidence dating the first appearance of genera involved in ant-plant symbioses.

A. Intercontinental Relationships of Ants, Plants, and Symbiotic Associations

In a seminal volume comparing tropical forest ecosystems of Africa and South America, Thorne (1973) and Brown (1973) examined the biological relationships in plants and ants, respectively. They reached similar conclusions: relationships between the biotas of Africa and the Oriental-Australian regions are closer than those between Africa and South America. Although their analyses were not explicitly cladistic-biogeographic (lack of data would have precluded such an analysis), the patterns at lower taxonomic levels such as genera and species-groups are clear enough to deserve our general confidence. The pattern of closer relationships between the biotas of tropical Africa and tropical Asia than between tropical Africa and tropical America is widespread among taxa and accords well with paleogeography as summarized by Raven and Axelrod (1974), Rosen (1978), and Barron and co-

workers (1981). The closer ties between the African and Asian tropics may have two explanations: the separation of Afroindia from the rest of Gondwanaland, and the possibility of biotic exchange between tropical Africa and tropical Laurasia (with India now accreted) until the global cooling and drying of about 50 Ma (Goldblatt 1978; McGowran 1990), and much more recently as well, following reestablishment of direct connection between Africa and Eurasia some 17 Ma (Raven and Axelrod 1974).

Lists of plant genera with myrmecophytes (appendix) and ant genera including obligate plant-ants (table 19.3) follow the general pattern. Thorne (1973) estimated that only 111 plant genera are common to Africa and tropical America and found only there, compared to 4500 genera limited to one of the two continents. Myrmecophytes are represented in only three plant genera shared by Africa and South America (*Bertiera* [Rubiaceae], *Hirtella* [Chrysobalanaceae], and *Ocotea* [Lauraceae]), and none of these has myrmecophytic species in both continents. Each genus has one or more myrmecophytic species only in the continent in which it is more diverse. The only genus with myrmecophytic species in both Africa and the Neotropics is the widespread genus *Acacia*, and here evolutionary radiations of myrmecophytes are clearly independent, though somewhat parallel, in African and Neotropical species (McKey 1989). In contrast, links between Africa and Asia are stronger, for both seed plants in general and myrmecophytes in particular. About 500 genera of seed plants have a distribution limited to Africa, Asia, and associated islands (Thorne 1973). Several of these genera include myrmecophytes, and some of them

(*Macaranga*, *Stereospermum*, *Canthium*, *Clerodendrum*, and *Psychotria*) have myrmecophytic species in both tropical Africa and tropical Asia. In addition, tropical Asia harbors at least one myrmecophytic *Acacia*, a south Indian species apparently closely related to East African ant-acacias (D. McKey, unpublished field notes, 1991). Analysis at the generic level thus yields not a single case in which we might suspect that African and American myrmecophytes share a common myrmecophytic ancestor. In contrast, the existence of several African-Asian genera suggests that some ant-plants in these two continents could either have a common origin or have evolved in parallel from congeneric non-myrmecophytic ancestors.

Analysis only at the generic level may obscure intercontinental relationships. Gentry (Chapter 17) believes that in many cases, an African genus is very closely related to one in America. Is our conclusion that myrmecophytes have evolved independently in Africa and America likely to be altered by progress in understanding phylogenetic relationships of plants in the two continents? We think not, for two reasons. First, only two cases involve African and American ant-plants so closely related that they might conceivably be lumped into a single genus. These are *Hirtella* and *Magnistipula* (Chrysobalanaceae), which Prance (1972) holds to be "good" genera (i.e., monophyletic), and two genera of Cecropiaceae, *Cecropia* and *Musanga* (the latter of which is less consistently associated with ants). Second, as pointed out previously, myrmecophytism often characterizes only one or a few species of a genus. Although cladistic treatments are lacking, our strong impression is that myrmecophytic species usually represent mod-

est, and relatively recent, radiations. Even if a few closely related African-American pairs of genera were to be lumped, we believe that analysis of infrageneric relationships would show that myrmecophytes evolved independently in the two continents. In contrast, taxonomic progress might strengthen the apparent relationships between African and Asian ant-plant symbioses. In addition to the congeneric African and Asian ant-plants listed above, African myrmecophytes in *Nauclea* are closely related to the Asian myrmecophytes placed in *Neonauclea* and *Myrmeconauclea* by Ridsdale (1978). We surmise that many of these are cases of parallel evolution of myrmecophytes in Asia and Africa, but without further taxonomic work the alternative of descent from a myrmecophytic common ancestor cannot be ruled out.

For ants, the patterns of intercontinental relationships are similar (Brown 1973, updated by Hölldobler and Wilson 1990 and recent revisionary work; see tables 19.2 and 19.3). No ant genera are restricted to the Ethiopian plus Neotropical regions, but 27 genera are limited to the Ethiopian plus the Oriental-Australian regions. These include 2 genera that have produced specialized plant-ants (*Tetraponera* and *Plagiolepis*), though only *Tetraponera* is represented by such specialists in more than one region (table 19.3). About the same number of ant genera (31) are "tropicopolitan," including 10 genera that have produced specialized plant-ants. Six of these groups (*Pachycondyla*, *Leptothorax*, *Pheidole*, *Solenopsis*, *Tetramorium*, and *Strumigenys*) contain obligate plant-ants in only one area, but 4 genera (*Crematogaster*, *Tapinoma*, *Technomyrmex*, and *Campenotus*) include such specialists in two or

more zoogeographic regions. Of these, only *Crematogaster* is represented by specialist plant-ants in both Africa and the Neotropics, as well as in the Oriental and Australian regions. Because obligate plant-ants account for such a small fraction of the *Crematogaster* fauna in each tropical region, it seems very likely that specialists have evolved independently in Africa and the Neotropics. There are only two known specialist plant-ant *Crematogaster* in the Neotropics, and taxonomic position of at least one of these appears to confirm its independent evolution of the plant-ant habit. This species, a so-far unnamed specialist on *Cecropia* in north-eastern Peru, is a derivative of the widespread Neotropical *C. curvispinosa*, a generalized stem-nester (J. Longino, personal communication, 1991). Further systematic studies may eventually reveal whether or not African and Asian plant-ants in this genus have had independent origins. *Crematogaster* species occur on *Macaranga* in both continents, as well as on closely related plant genera in the two regions. These taxa include African *Nauclea*, compared with Asian *Myrmeconauclaea* and *Neonauclea*, and perhaps African *Leonardoxa*, compared with Asian *Humboldtia*.

Based strictly on comparisons at the generic level, plant-ants in Africa and America appear to have arisen wholly independently. However, this conclusion must be qualified somewhat in view of the marked concentration of African and Neotropical plant-ants into three ant tribes, each represented on each continent by (usually) endemic genera rich in plant-ants or by monotypic plant-ant genera. With plant-ants representing 16 percent of 230 pseudomyrmecines known to Ward (P. Ward, personal communication,

1991), for example, this subfamily consists of New World *Pseudomyrmex* and *Myrcidris* (a monotypic plant-ant), and Old World *Tetraaponera* (Ward 1990). *Tetraaponera* and *Pseudomyrmex* are a possible example of a sister-group relationship that may reflect an old relationship between tropical Africa and South America (Ward 1990).

The most important tapinomine (Dolichoderinae) plant-ants are either *Technomyrmex* (widespread, with most plant-ant species in Africa) or endemic Neotropical *Azteca*. Although plant-ants contribute substantially to each of these genera, exact percentages of plant-ants are not yet known. The genus *Tapinoma* presents a case that may be suggestive of an old origin of the plant-ant habit. Species of *Tapinoma* have been recorded both from *Leonardoxa* (Detarieae) in Africa and *Humboldtia* (in the closely related caesalpinoid tribe Amherstieae) in Asia. While the record of *Tapinoma* in *H. laurifolia* is suspect because it came from a botanical garden (Ridley 1910), two species of *Tapinoma* have been collected from swollen internodes of *H. brunonis* in evergreen forest of the Western Ghats in south India (McKey, unpublished field notes, 1990, and T. Musthak Ali, personal communication, 1990).

The formicine genera currently recognized as the tribe Myrmelachistini (Hölldobler and Wilson 1990) offer a third example suggestive of a very early origin of specialization on live plant hosts. This tribe includes endemic African *Aphomyrmex* and *Petalomyrmex*, and endemic Neotropical *Myrmelachista*. Both African genera appear to be monotypic plant-ants, and *Myrmelachista* appears to be rich in plant-ant species. A recent phylogenetic study con-

firms the close relationships among these genera, placing them all (along with nine other genera) in the *Pseudolasius* genus-group (Agosti 1991). Asian plant-ants in the genus *Cladomyrma* have also been placed in this tribe (Hölldobler and Wilson 1990). Of five described species of *Cladomyrma* (Agosti 1991), at least four, and possibly all five, are plant-ants (Maschwitz et al. 1989, 1991; see table 19.3 and Davidson and McKey 1993). As in pseudomyrmecines and tapinomines, then, both the general importance and the widespread generic distributions of plant-ants among myrmelachistines suggest that specialization on live plant hosts may have evolved early, and not necessarily independently on different continents. Recent work by Agosti (1991), however, suggests that *Cladomyrma* may in fact not be closely related to the African and Neotropical genera placed in the Myrmelachistini. His classification, placing *Cladomyrma* in a different lineage (the *Lasius* genus-group, with six other genera, none including plant-ants), implies that the plant-ant habit evolved at least twice in "myrmelachistines": at least once in *Cladomyrma* and at least once in the lineage including *Aphomomyrmex*, *Petalomyrmex*, and *Myrmelachista*. If Agosti's (1991) conclusion is correct, we are confronted with yet another striking case of parallel evolution of ant-plant symbioses. The hosts of African *Petalomyrmex* and *Aphomomyrmex* and of two Asian *Cladomyrma* species include legumes of the caesalpinoid tribe Detarieae, and these ant-plants (*Leonardoxa* in Africa and *Saraca* in Asia) present many morphological and ecological similarities. Distinguishing among common origin (homology), parallel

evolution from similar starting material (homoiology), and convergence as explanations for the similarities in this set of symbioses in which both ants and plants are somewhat closely related will be a challenging task.

In all these cases, no firm conclusion can be reached without further phylogenetic study. Nevertheless, outside of the subfamily Pseudomyrmecinae and the tribes Tapinomini and Myrmelachistini, and possibly within these groups as well (Ward 1991), plant-ants have clearly had multiple and independent origins in Africa and the Neotropics. Thus, for both myrmecophytes and their associated plant-ants, evidence from extant taxa strongly supports the hypothesis that symbiotic ant-plant associations arose independently on the two continents.

B. The Fossil Record

The independent evolution of myrmecophytes and plant-ants in Africa and the Neotropics is also supported by the fossil record. This evidence is most clearly interpretable for ants (Davidson and McKey 1993). Ants first appeared in the fossil record in the lower Cretaceous (Brandão et al. 1989), and a major adaptive radiation had taken place by the early Tertiary period (Hölldobler and Wilson 1990), approximately 65 Ma. Although this radiation was eventually explosive, faunas taxonomically and ecologically similar to those of contemporary times are not represented by fossils until the middle Tertiary (e.g., Wilson 1985). Elsewhere (Davidson and McKey 1993) we discuss the earliest fossil records of all ant genera containing one or more specialized plant-ants; these findings will be summarized here. Both widely dis-

tributed genera and the few geographically restricted groups with paleontological data typically first appeared in fossil deposits between the early Oligocene and the late Miocene (35–12 Ma) (Hölldobler and Wilson 1990), long after Africa and South America split apart (130–85 Ma; Chapter 2). For the three ant groups rich in plant-ants, one (Myrmelachistini) has no fossil record, and the others first appeared in fossil deposits of the early Oligocene (*Tetraponera* of the Pseudomyrmecinae) or the Miocene (*Tapinoma* and *Technomyrmex* of the Tapinomini). Tending of Homoptera and of extrafloral nectaries may be similarly recent. The earliest fossil record of homopteran tending is that of *Iridomyrmex* and aphids in the early Oligocene Baltic amber (Wheeler 1914). The first paleontological evidence for extrafloral nectaries comes from leaves of Oligocene *Populus* specimens in Colorado's Florissant shales (Pemberton 1990).

For plants, we know of no direct fossil evidence of structures that regularly housed symbiotic ants. Our conclusions must thus be based on inferences from pollen and other fossils of groups that include extant myrmecophytes. (It is interesting but currently idle to speculate about how many of these symbioses have evolved and disappeared without a trace.) The first records of pollen ascribed to extant angiosperm families are from the period 113–88 Ma (Chapter 4). Thus, flowering plant families were becoming well differentiated during the period when Africa and South America were splitting apart. Considering that radiations of myrmecophytes usually characterize taxa at levels no higher than genera or, more commonly, species groups within genera, it

seems a priori unlikely that any extant myrmecophyte lineages had appeared by this time. In some cases, fossil pollen of great age has been attributed to a genus that includes myrmecophytes. Pollen attributed to *Cupaniopsis* (Sapindaceae), for example, is known from the Upper Cretaceous of South America, Africa, and Asia (Chapter 3). But since this genus includes only one extant myrmecophytic species, which is of limited distribution (appendix), there is little reason to suspect that the age of the myrmecophyte habit even approaches the age of this genus.

Patterns in the distribution of symbiotic plants and ants across continents, taxonomic composition of ant-plants and plant-ants, and the fossil record all have important implications for our analysis. Although some comparisons between Africa and Asia suggest common descent of ant-plants, plant-ants, or both, in Africa and the Neotropics both myrmecophytes and specialist plant-ants evolved largely independently. With the possible exception of pseudomyrmecines, tapinomines, and myrmelachistines, in which the plant-ant habit may be ancient, similarities in symbiotic associations between Africa and the Neotropics are not due to common descent of one or both partners from an association that predated continental separation or other vicariance events or that migrated intact from one continent to the other. Similarities must be due to some combination of (1) parallel evolution of ants, plants, or both from similar starting material, (2) evolutionary convergence, and (3) the matching of symbiotic partners according to some set of rules shared between the two continents. Elsewhere (Davidson and McKey 1993), we summarize strong evidence supporting each of these hypotheses.

IV. Why Are Ant-Plant Systems More Diverse in the Neotropics than in Africa?

At the generic level, both myrmecophytes and specialized plant-ants exhibit comparable diversity in tropical Africa and America. However, within genera of each of these groups, radiations of species living regularly in symbiotic partnerships have been more numerous or more expansive in the Neotropics. To a great extent, these regional discrepancies in diversity mirror general trends in floras and faunas of the two continents, and we suggest that they reflect underlying general causes. According to the view developed here, biological diversity in tropical forest ecosystems is the outcome of complex plant and animal responses to both geological and climatic history, as well as to the structure of the landscape generated by this history. Likely explanations for lower African diversity are greater extinction of tropical rainforest species during periods of past climatic deterioration and lower rates of species origination as species re-expanded into novel habitats. A combination of orogenic activity, riverine disturbance, large expanses of ancient, impoverished shield substrate, and white sand products of erosion have created much more complex habitat mosaics in South America than in Africa. Diversity of both myrmecophytes and their attendant ants appears to accumulate mainly across habitats, rather than across biogeographic regions, and narrow endemics of unique or isolated habitats are more common in America than in Africa.

Because intercontinental differences in geomorphology and habitat diversity are ancient, the forest biota of Africa was probably already poorer than that of Amazonia long

before periods of increased aridity in the Pleistocene. Thus, since drought-associated contraction of mesic forest habitats was greater in Africa than in South America, the Pleistocene probably brought to Africa greater extinction in an already less diverse forest biota. Specialist plant-ants and ant-plants were probably more susceptible to extinction during periods of climatic deterioration than were generalist arboreal ants and plants not dependent on symbionts. If ants and plants of moist, shady forest understory were decimated disproportionately, this might explain why leaf-pouch ant-plants and their typical *Technomyrmex* occupants are absent from the West African forest block (Bequaert 1922). These same historical circumstances may account for the predominance of *Crematogaster* as associates of *Canthium*, *Cuviera*, and some other African ant-plants of forest understory (Davidson and McKey 1993), since the ancestors of these ants probably inhabited more open habitats. Other plant-ants and their hosts may have been restricted to refugia such as the coastal forest of Lower Guinea, where they persist today as endemic monotypic genera (e.g., *Aphomyrmex* and its probable derivative *Petalomyrmex*).

Drought may not have been the only nor the most widespread problem facing African ant-plant symbioses during Pleistocene climatic fluctuations. Current evidence (e.g., Bengo and Maley 1991) indicates that montane forest extended into the central African lowlands during several periods over the last 135,000 years as temperature cooled but conditions remained sufficiently moist to support forest. The resulting cool, moist conditions may not have been conducive to poikilothermic surface foragers such as ants

(e.g., Janzen 1973). The African mesic forest zone occupies a plateau whose mean elevation is probably on the order of 500 m higher than the South American tropical forest zone. African ant-plant symbioses may have been harder hit by this type of climatic shift than were their Neotropical counterparts.

Origination of new plant-ant and ant-plant species may have occurred primarily as ranges re-expanded during periods of climatic amelioration. Speciation rates should have been higher in Amazonia, since range expansion would be more likely to place ants, plants, or both into habitats with soil, rainfall, elevation, or other characteristics sufficiently novel to shift selective regimes. Regardless of whether speciation occurred in refugia or during range re-expansion, the potential for the evolution of new associations via host shifts and secondary colonization depended in part on the size of ant-plant and plant-ant guilds that could interact locally. In Amazonia, this potential was higher for two reasons. First, guilds were less likely to have been decimated by past climatic deterioration. Second, the closely packed, small-scale habitat mosaic of the dynamic fluvial landscape (Salo et al. 1986) meant that much of the higher regional diversity of Amazonia was represented at a local level. Close juxtaposition of diverse habitats has allowed exchange of ants and plants across habitat boundaries (Davidson et al. 1991; Davidson and Fisher 1991; Davidson and McKey 1993). Major differences in landscape structure have been associated with a greater effect of beta-diversity on ecological and evolutionary interactions within each habitat in Amazonia than in Africa. To a greater extent in Amazonia than in Africa,

(beta-)diversity has almost certainly been a major factor in enhancing (alpha-)diversity.

V. Conclusions

The symbiotic ant-plant relationships have evolved independently in Africa and the Neotropics. Specialized plant-ants may have evolved comparatively early in some lineages, and not necessarily independently in the major tropical regions. Nevertheless, such specialists form a minor component of numerous distinct taxa and have certainly evolved independently many times. Extant myrmecophytes in Africa and the Neotropics appear to have had separate origins in every case examined. In view of their independent histories, the similarities in ant-plant symbioses of these two regions are remarkable, and they appear to be due to similar selection regimes acting on similarly preadapted plants and ants to produce parallel and convergent evolution in symbiotic relationships of the two continents (Davidson and McKey 1993).

Our analysis of the evolutionary dynamics of ant-plant symbioses leads us to propose a new hypothesis to explain the much greater diversity of ant-plants and plant-ants in the Neotropics than in Africa, a difference that is also seen in many other groups of organisms. Previous explanations for differences in diversity of continental floras and faunas, and even ant-plants (Benson 1985), have emphasized the contrasting climatic histories of these two regions. Focusing on range contractions during periods of unfavorable climate, these explanations postulate that Africa's lower diversity is due to greater extinction during the Pleistocene, as Africa's climate became drier and refugia

were fewer, than in Amazonia. We propose that differences between the two regions in the rates of species origination may be at least as important as extinction rates. The relatively stable geological history of most of Africa, including the rainforest zone, has created a landscape with relatively little elevational relief (hence few sharp spatial contrasts in temperature and rainfall), relatively little edaphic variation, and relatively infrequent and spatially limited fluvial disturbance. In contrast, the Andean orogeny, and sub-Andean tectonic activity, have helped to create a landscape of great elevational, climatic, and edaphic complexity, especially in western Amazonia. This has resulted in a complex and dynamic mosaic of habitats. Colinvaux (Chapter 16) suggests that species origination usually takes place when ranges are re-expanding during periods of climatic amelioration. If this is so, then in the Neotropics, especially in western Amazonia, range expansion would be much more likely than in the African forest zone to place ants and plants into novel habitats, leading to speciation, the formation of new associations, or both.

This hypothesis will, we hope, contribute to a fruitful resolution of the current debate about the roles of history and contemporary ecology in explaining patterns of diversity. As Brown (1987b) argues, progress is likely to come when these two determinants of diversity are viewed not as simple antithetical alternatives, but as interacting components of a synthetic model. The attention we draw to contrasts in landscape structure between these two tropical regions may have broader implications for understanding intercontinental differences in biological diversity within the tropics. Plate tectonics "is proba-

bly an overriding factor in the geomorphological diversity of the humid tropics," and "tectonic contrasts have produced morphological contrasts" (Douglas 1978:174). The pedological and geomorphological contrasts Douglas (1978) presents between the very young, rapidly evolving landscapes of areas included within the great Tertiary mountain arcs and the old, static landscapes of Gondwanaland remnants may be of great importance to understanding patterns of tropical biological diversity.

Appendix

Present-day distribution of plant genera containing species that are regularly symbiotic with plant-ants (taxonomy, distribution, and order of families from Mabberley 1987). The table lists all plants known to have been reported as regularly occupied by plant-ants and includes plants that possess no obvious adaptations for housing ants, as well as plants with myrmecophytic traits. Elsewhere (Davidson and McKey 1993) we present detailed information on these traits. Presence (×) or absence (–) by biogeographic region. Approximate estimates of the number of ant-plant species are indicated in parentheses. Included in ant-plants of the Ethiopian region is *Mimosa* sp. from Madagascar, the only myrmecophyte so far known from the Madagascan region. Supplemental information on distribution within the Asian tropics was taken from van Steenis and de Wilde (1950–1989). If ant-plants within a genus are restricted to either the Oriental or the Australian region, an "O" or an "A" follows the number in parentheses. If ant-plants are known to be found in both regions, the region with the larger number of ant-plant species is indicated first. If distribution of ant-plant species within the Oriental and Australian tropics is uncertain, no information is given following the number of ant-plant species. Abbreviations used: Aus = Australian; Eth = Ethiopian; Neo = Neotropical; Ori = Oriental. Numbered references refer to the list given at the end of the appendix.

Taxon	Ethiopian	Neotropical	Oriental and Australian	References
Myristicaceae				
<i>Myristica</i>	—	—	× (1–3, A)	3, 26
Monimiaceae				
<i>Kibara</i>	—	—	× (4, A)	45
<i>Steganthera</i> ^a	—	—	× (4, A)	44
Lauraceae				
<i>Cryptocarya</i>	—	—	× (?)	25
<i>Licaria</i>	—	× (> 1)	—	10, 73
<i>Ocotea</i>	×	× (6–10)	—	10, 81
<i>Pleurothyrium</i>	—	× (3–4)	—	81
Piperaceae				
<i>Piper</i>	×	× (3+)	× (1, O)	Neo = 9, 67; Ori = 12
Nyctaginaceae				
<i>Pisonia</i>	×	×	× (1)	25
Polygonaceae				
<i>Ruprechtia</i>	—	× (1–3)	—	4, 8
<i>Triplaris</i>	—	× (17)	—	7
Actinidiaceae				
<i>Saurauia</i>	—	×	× (1?)	28
Elaeocarpaceae				
<i>Elaeocarpus</i>	—	×	× (1?)	11, 28
Sterculiaceae				
<i>Cola</i>	× (1)	—	—	52
<i>Scaphopetalum</i>	× (2–3)	—	—	52
Cecropiaceae				
<i>Cecropia</i>	—	× (45–55)	—	4, 66
<i>Coussapoa</i>	—	× (1–2)	—	4
<i>Musanga</i>	× (1)	—	—	19
<i>Poikilospermum</i>	—	—	× (1, O)	80
<i>Pourouma</i>	—	× (2–4)	—	4, 6
Flacourtiaceae				
<i>Buchnerodendron</i>	× (1?)	—	—	5
<i>Ryparosa</i> ^b	—	—	× (1+, O)	25
<i>Tetrathylacium</i> ^c	—	× (1)	—	55
Passifloraceae				
<i>Barteria</i>	× (2)	—	—	5, 84
Sapotaceae				
<i>Delpyora</i>	× (1)	—	—	84
Ebenaceae				
<i>Diospyros</i>	× (1)	×	×	32, 84
Symplocaceae				
<i>Symplocos</i>	—	×	× (1?, A)	71
Myrsinaceae				
<i>Tapeinosperma</i>	—	—	× (1, A)	25, 54

(continued)

Appendix. *Continued.*

Taxon	Ethiopian	Neotropical	Oriental and Australian	References
Chrysobalanaceae				
<i>Hirtella</i>	×	× (6)	—	46, 47
<i>Magnistipula</i>	× (1)	—	—	33, 34
Fabaceae (Leguminosae)				
<i>Acacia</i>	× (ca. 15)	× (12)	× (1, O)	Eth = 24; Neo = 27; Ori = 78, 84
<i>Archidendron</i>	—	—	× (1, A)	13, 58, 83
<i>Calpocalyx</i>	× (1)	—	—	59, 84
<i>Humboldtia</i>	—	—	× (2+, O)	38, 84
<i>Leonardoxa</i>	× (2)	—	—	37, 84
<i>Millettia</i>	×	—	× (1, O)	1, 40
<i>Mimosa</i> ^d	× (1)	×	×	82
<i>Ormosia</i>	—	× (1)	×	4
<i>Pithecellobium</i>	—	× (1)	—	60, 62, 82
<i>Platymiscium</i>	—	× (2)	—	63
<i>Pterocarpus</i>	×	× (1)	×	51
<i>Saraca</i>	—	—	× (1, O)	1, 41
<i>Tachigali</i> ^e	—	× (ca. 20)	—	4
Crypteroniaceae				
<i>Crypteronia</i>	—	—	× (1?, O)	1, 41
Thymelaeaceae				
<i>Wikstroemia</i>	—	—	× (1, O)	28
Myrtaceae				
<i>Myrcia</i>	—	× (1)	—	61, 62
<i>Syzygium</i>	×	—	× (2, A)	26, 42, 76
Melastomataceae				
<i>Allomaieta</i> ^f	—	× (1)	—	70, 79
<i>Blakea</i>	—	× (1)	—	4
<i>Clidemia</i> s.s. ^g	—	× (15–20)	—	29, 72
<i>Conostegia</i>	—	× (1–2)	—	72, 79
<i>Henriettea</i> ^h	—	× (1?)	—	72, 79
<i>Maieta</i>	—	× (ca. 15)	—	29, 72
<i>Medinilla</i>	×	—	× (1–2, O)	53
<i>Miconia</i> ⁱ	—	× (4)	—	4
<i>Sagraea</i> ^j	—	× (2 + ?)	—	72, 79
<i>Tococa</i> ^k	—	× (ca. 40–45)	—	72, 79
<i>Topobea</i>	—	× (1)	—	79
Euphorbiaceae				
<i>Drypetes</i>	×	×	× (1?, A)	71
<i>Endospermum</i>	—	—	× (2+, A)	2, 5
<i>Glochidion</i>	—	×	× (1?, A)	71
<i>Homalanthus</i>	—	—	× (1?, A)	71
<i>Mabea</i>	—	× (1–2?)	—	4

Taxon	Ethiopian	Neotropical	Oriental and Australian	References
<i>Macaranga</i>	× (2)	—	× (ca. 20, O)	Eth = 5; Ori = 20, 21, 64, 65
<i>Pimelodendron</i>	—	—	× (1?, A)	71
<i>Sapium</i>	×	× (1–2?)	×	4
Sapindaceae				
<i>Cupaniopsis</i>	—	—	× (1, A)	62
<i>Harpullia</i>	—	—	× (3, AO)	31
<i>Mischocarpus</i>	—	—	× (1)	71
Anacardiaceae				
<i>Euroschinus</i>	—	—	× (1, A)	14
<i>Lansea</i>	×	—	× (1, O)	28
<i>Semecarpus</i>	—	—	× (4, A)	14, 25
Simaroubaceae				
<i>Picrolemma</i>	—	× (2–3)	—	4
Meliaceae				
<i>Aglaia</i>	—	—	× (?)	25
<i>Aphanamixis</i>	—	—	× (1, A)	36
<i>Chisocheton</i>	—	—	× (6, OA)	35
<i>Guarea</i>	×	× (3+)	—	43, 73
Rutaceae				
<i>Zanthoxylum</i>	×	×	× (5+, AO)	23, 69, 74
Loganiaceae				
<i>Anthocleista</i>	× (1 + ?)	—	—	84
<i>Fagraea</i>	—	—	× (1+, O)	28, 30
Gentianaceae				
<i>Tachia</i>	—	× (5)	—	4, 39, 84
Boraginaceae				
<i>Cordia</i>	×	× (2)	×	63, 75
Verbenaceae				
<i>Callicarpa</i>	×	×	× (1)	57
<i>Clerodendrum</i>	× (3–5)	—	× (3, O)	Eth = 52; Ori = 3, 26
<i>Vitex</i>	× (4)	×	×	52
Scrophulariaceae				
<i>Wightia</i>	—	—	× (1?, O)	28
Gesneriaceae				
<i>Besleria</i>	—	× (1)	—	4
Bignoniaceae				
<i>Stereospermum</i>	× (1)	—	× (1, O)	5, 28, 84
Rubiaceae				
<i>Bertiera</i>	× (1?)	×	—	52
<i>Canthium</i>	× (3–6+)	—	× (1, A)	Eth = 52; Aus = 77

(continued)

Appendix. Continued.

Taxon	Ethiopian	Neotropical	Oriental and Australian	References
<i>Cuviera</i>	× (8+)	—	—	52
<i>Duroia</i>	—	× (2-3)	—	4, 26
<i>Gardenia</i>	× (1?)	—	×	52
<i>Heinsia</i>	× (1)	—	—	52
<i>Hoffmannia</i>	—	× (1)	—	4
<i>Ixora</i>	× (1)	×	×	83
<i>Myrmeconauclea</i>	—	—	× (2-3, O)	40, 49
<i>Nauclea</i> ¹	× (1)	—	×	40, 49
<i>Neonauclea</i>	—	—	× (4+, O)	40, 49, 83
<i>Patima</i>	—	× (1)	—	63
<i>Psychotria</i> ^m	× (1)	×	× (1, A)	Eth, Aus = 5
<i>Remijia</i>	—	× (1-3)	—	4, 26
<i>Rothmannia</i>	× (2)	—	—	52
<i>Tricalysia</i>	× (2)	—	—	22, 50
<i>Uncaria</i>	× (1)	×	×	5, 52
<i>Vangueriopsis</i>	× (2+)	—	—	25, 52
Palmae				
<i>Calamus</i>	×	—	× (2+, O)	5, 16, 17, 56
<i>Daemonorops</i>	—	—	× (4+, O)	5, 48, 56
<i>Eremospatha</i>	× (1+)	—	—	68
<i>Korthalsia</i>	—	—	× (7+, O)	17, 18, 56
<i>Laccosperma</i>	× (4+)	—	—	56, 68
<i>Pogonotium</i> ⁿ	—	—	× (1+, O)	16, 68
Gramineae				
<i>Gigantochloa</i> ^o	—	—	× (1+, O)	15
<i>Schizostachyum</i> ^o	×	—	× (1+, O)	15

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81. H. van der Werff 1990
82. P. Ward 1991
- C. Personal Observations of the Authors
83. D. W. Davidson
84. D. McKey

^a*Anthobombix hospitans* (Becc.) Perkins, cited by Bequaert (1922) is a synonym of *Steganthera hospitans* (Becc.) Kan. & Hat., cited by Hölldobler and Wilson (1990) (Philipson 1984).

^b*Gertrudia*—*G. amplifolia* of Bequaert (1922) and Hölldobler and Wilson (1990)—is a synonym of *Ryparosa* (Mabberley 1987).

^cTwigs of herbarium specimens of *T. macrophyllum* Poeppig are consistently hollow (DM); all ants so far recorded for the plant are known not to be specialist plant-ants (J. Longino, personal communication, 1991).

^dMadagascar.

^eIncludes *Sclerolobium* (J. Zarucchi, personal communication, 1986).

^fA cloud-forest shrub of Colombia, *Allomaieta* looks like *Maieta* but has poorly developed or no domatia (A. Gentry, personal communication, 1991).

^gIncludes *Myrmidone* (Judd and Skean 1991).

^hS. Renner (see also Benson 1985; Huxley 1986) reports myrmecophytism in *Henriettella*, which Judd (1986) has now placed in *Henriettea*.

ⁱIncludes *Pterocladon sprucei* Hook. f. ex Cogn. (S. Renner, personal communication, 1991), also reported to be myrmecophytic (Forel 1904).

^jIncludes *Ossaea* p.p. (W. Judd, personal communication, 1991).

^kIncludes *Microphysca* (W. Judd, personal communication, 1991).

^lAll Asian myrmecophytic species of *Nauclea* listed by Bequaert (1922) and Hölldobler and Wilson (1990) are treated by Ridsdale (1978) as *Myrmeconuclea* or *Neonuclea*.

^m*Grumilea* (Hölldobler and Wilson 1990) is included in *Psychotria* (Mabberley 1987).

ⁿ*Pogonotium ursinum* (Becc.) J. Dransfield is the current name of *Daemonorops ursina* Becc., for which relationships with ants were described by Dransfield (1978).

^oThese two bamboos apparently lack domatia but are inhabited by host-specific plant-ants that build pavilions on leaf surfaces.

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Note added in proof:

Two additional genera including probable myrmecophytes should be added to the appendix (F. Breteler, personal communication, 1993):

1. *Dichapetalum* (Dichapetalaceae), a pantropical genus of about 150 species best represented in Africa, includes one species, *D. gassitae* Bret. of Gabon, with paired hairy leaf-pouches occupied by undetermined ants. This species is described in the following publication: Breteler, F. J. 1986. The African Dichapetalaceae: A taxonomic revision. IX. Agricultural University of Wageningen Papers 86-3. 74 pp.

2. An undescribed species of *Dactyladenia* (Chrysobalanaceae) from Gabon has paired, inflated stipules apparently occupied by ants. This genus, whose species were formerly placed in *Acioa*, is restricted to tropical Africa and includes 27 named species.

This brings to 33 the number of plant genera with myrmecophytic species in Africa and reinforces two findings developed in this chapter: the concentration of myrmecophyte diversity in the Lower Guinea region of the Central African block of rainforest, and the tendency, most marked in Africa, for myrmecophytism to be restricted to single species of large genera.