

## 6 Plant Life-Forms and Tropical Ecosystem Functioning

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*Structure without function is a corpse; function sans structure is a ghost.*  
(Vogel 1972)

### 6.1 Introduction

Life-form was said by Warming (1909) to represent the sum of adaptive characters in a species, and thus is an expression of the harmony between a plant and its environment. This colorful perspective, although too broad to be useful in classification, does highlight the essential point that life-form groupings should be ecologically relevant.

With widely accepted phylogenetic classification schemes available, why even seek broad schemes of categorization in which the members of a group share no evolutionary history? The answer, simply put, is that form dictates function, and we contend that, among adults of higher plants adapted to a particular habitat, the smallest unit that exerts major control on mesoscale ecosystem processes is the life-form. Many higher plants are functionally equivalent: they all consume carbon dioxide and water; they all use solar energy of the same wavelengths; and they all require the same suite of 13 mineral nutrients. To be sure, there are some differences (the pigments of some algae have different absorption spectra, some congeners specialize on different chemical species of nitrogen, some plants are symbiotic with microorganisms capable of fixing diatomic nitrogen), but these describe the exceptions: for the most part, all plants feed out of the same trough.

Now the heresy: preoccupation with the consequences of loss of plant species on ecosystem functioning (energy and material fluxes, for example) is probably unwarranted. If, among higher plant species, there is substantial redundancy in nature, then loss of a minor player or substitution of one species for another is likely to have immeasurably small consequences for mesoscale processes such as carbon and oxygen exchange, soil erosion, and water and nutrient budgets. But this is not likely to be the case with loss of life-forms, for if there are significant functional differences among plants, surely these will manifest themselves most dramatically among species of

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strikingly different architecture. It is the assemblage of life-forms that give forests their characteristic structure, and structure, in turn, dictates whole-system functioning.

#### 6.1.1 Functional Significance of Life-Forms

Solbrig (1993) accurately described life-forms as single-character-based functional groups, yet even at this level there are some similarities in life history and resource use that lend coherence to the categories. This is perhaps to be expected if life-forms are the result of evolutionary forces that lead to ecological convergence (Böcher 1977). For example, a restricted set of pollen vectors may be available to plants that flower in any given part of the canopy, eventually leading to convergence on a particular set of breeding mechanisms.

In fact, several studies have shown good correlation between life-form and various life-history traits in tropical forests. Examples: (1) In a study of a Mexican dry forest, Bullock (1985) found that monostylous hermaphroditism was strongly associated with epiphytic and herbaceous life-forms, but less so with trees; (2) within the large, mostly tropical family Rubiaceae, genera that combine particular dispersal systems and life-forms (gravity dispersal in herbs, animal-mediated dispersal in shrubs, and winged seeds in shrubs and trees) tend to have large numbers of species (Eriksson and Bremer 1991); and (3) across a range of forest sites in Venezuela, trees have significantly higher seed, fruit, and flower weight; rates of abortion; and ratios of fruit to flower mass than other life-forms (Ramírez 1993). Thus, even life-form groups as inclusive as "tree" or "herb" may share more characters than is generally appreciated.

#### 6.1.2 Assessing the Consequences of Life-Form Diversity

There are only three ways to predict accurately the consequences of loss of life-form diversity; for convenience we dub them the experimental, natural history, and examination of pattern approaches. The most direct method would consist of performing removal (or perhaps addition) experiments, accompanied by measurement of responses on replicated treatment and control plots. Unfortunately, few such experiments have been performed, and few are underway (e.g., Haggard and Ewel 1994). There are, nevertheless, a number of places where an "experiment" has been performed without benefit of replication, controls, or monitoring of response variables. For example, climber cutting is a common silvicultural prescription in Malaysia (e.g., Fox 1968; Putz 1985), and the Kekchí Maya people have killed (in harvesting its fruits) the dominant understory palm (*Astrocaryum*) throughout much of the eastern Guatemalan lowlands. Some of these situations, though not ideal, might lend themselves to a posteriori analysis.

The second approach consists of using a sound knowledge of natural history to deduce relationships and dependencies among life-forms, and to predict the consequences of life-form loss. The primary effects will undoubtedly be easier to deduce than the secondary effects, for example, loss of red-flowered herbs, probably loss of hummingbirds, and maybe loss of snakes that feed on hummingbirds. But what about the impacts on the peccary that feeds on that snake and 43 other things as well? And what effects might this ultimately have on soil churning and erosion? Could any scholar ever acquire the experience and breadth of knowledge required to make such predictions accurately? Not likely, but the potency of the natural history approach should not be underestimated, for it is our only link to the complexity of the real world and our only check on the models and generalizations of theoreticians.

The third approach consists of examining patterns of life-form distribution across the landscape and seeking differences in ecosystem functioning that accompany those patterns. Such an approach will never reveal cause and effect, except circumstantially, but it is the path most readily amenable to analysis using the plethora of vegetation descriptions available from throughout the tropics. We do not attempt the analysis herein, but we do describe some of the players and patterns.

## 6.2 Classification

The scheme of Christian Raunkiaer, the Danish phytogeographer whose name is synonymous with life-form, is of little help in the tropics, for his system of classifying plants according to the height of over-wintering buds compresses tropical plants into relatively few categories (Raunkiaer 1934). For example, Raunkiaer's system fails to discriminate between two of the most distinct growth habits, self-supporting and climbing. Life-form classification schemes are beset with two classes of problems, both of which impede their use when seeking functional correlates. The first are those that overemphasize a particular trait, often one that is extremely important in the region where the system was developed. Raunkiaer's emphasis on position of the perennating organ is an example: it works well in the Alps and poorly in the Amazon. The other is the tendency to subdivide major groups so finely that the system contains vast numbers of categories, and a manual is required to distinguish one from another; such systems simply do not get used.

Several life-form classifications preserve essential features of Raunkiaer's system while incorporating additional detail likely to be of ecological relevance. One such system, which has the added advantage of having been devised by ecologists exceptionally knowledgeable about the tropics, is the scheme of Mueller-Dombois and Ellenberg (1974). The first tier in their

three-layered hierarchy is based on trophic status, the second on vascularization, and the third on support structures; the result is a manageable 23-category system.

Nevertheless, there is no universal agreement on one system of life-form classification. A minimal description of tropical forest plant life-forms would have to include trees, herbs, epiphytes, and climbers, but this would hardly do justice to the astonishing proliferation of morphologies in most equatorial forests. To be useful, a system would have to include at least the seven most-conspicuous categories: dicotyledonous trees; trees with one or few meristems (e.g., arborescent palms and pandans); treelets; shrubs; giant herbs; vines; and epiphytes. For some purposes one might want more classes (forbs, grasses, and succulents would be essential additions in many tropical environments), but in no case would it be useful to compress these into fewer categories.

Tropical trees are, of course, the background fabric of forest structure, and their great importance and diversity have led to several attempts to make ecologically meaningful classifications based on form. These range from simple stature-based systems such as the treelet-understory-subcanopy-canopy trees of Hartshorn and Poveda (1983) to the elaborate system of models proposed by Hallé et al. (1978). Although stature-based classification systems may have some ecological significance, the same is not necessarily true of the models of Hallé et al. Studies of crown formation have shown that trees are so plastic that different tree architectures can converge on the same crown morphology; conversely, a given model can give rise to quite different crown forms (Fisher 1986). It is during the regeneration phase, when architecture is most clearly expressed, that the models prove their utility. Kohyama (1987), for example, found that architectural models were correlated with crown allometry in saplings, and that these characteristics were sound predictors of performance in gaps.

Environment is, without doubt, the primary driver of life-form evolution. Nevertheless, the very core of every definition of ecology implies two-way interactions between organisms and environment, and just as life-form is a response to environment, the entire *oikos* is influenced by structure. Thus, the product of an evolutionary response to environment becomes a major actor in the interplay among biota, soil, and atmosphere. Two form-linked traits, size (which influences many aspects of resource acquisition) and life span (which affects community turnover), may have special significance.

### 6.2.1 Stature

Plant size is not an inevitable indicator of resource dominance, for it is the leaves that capture radiation and the mycotrophic roots that retrieve nutrients from the soil, regardless of the massiveness of organs such as stems, buttresses, and support roots. Some life-forms invest heavily in resource-

capturing organs (e.g., foliage of some grasses, fine roots of some vines) despite their relatively modest stature overall. Nevertheless, size-class distinctions are important: within a given life form, a plant's ability to gather resources is, in large part, determined by its size. A canopy tree, for example, typically intercepts a far greater proportion of incident light than a sapling; furthermore, this advantage should allow the tree to allocate substantial photosynthate to roots, thus enabling it to explore a greater volume of soil than its shorter neighbors. Domination of the resource base may then influence other life-history traits; Rockwood (1985), for example, examined herbarium specimens from Costa Rica and Panama and found that mean seed weight increased from herbs to shrubs to trees.

The importance of stature, and the functional attributes it imparts, is perhaps best epitomized in the dichotomy between trees and shrubs. Evidence suggests that shrubs and trees are best treated as distinct life-forms and not just part of a continuum that is arbitrarily divided on the basis of size. Compared with trees, shrubs may have proportionally fewer thick, structural roots; a greater fraction of their roots concentrated near the surface; persistent, reproductively active shoots close to the ground; greater ability to reproduce vegetatively (by layering or rooting of crushed or broken branches); and the capacity to return to reproductive mode more quickly following crown damage. Excavation of shrubs and treelets on Barro Colorado Island, Panama, for example, revealed that shrubs have a larger ratio of root-surface area to leaf-surface area than saplings of co-occurring trees (Becker and Castillo 1990). Because shrubs invest in flowers and fruits (which can be major nutrient sinks), whereas saplings of equal height do not, Becker and Castillo hypothesized that shrubs allocate proportionately more carbon to shallow roots. The fact that shrubs have limited need for the thick, belowground anchors required to keep massive trees upright might also contribute to their concentration of roots near the surface.

Species with relatively small lateral branches arranged around a stout trunk grow larger than species with heftier lateral branches; in fact, shrub-like architectures may not even be possible for saplings that will later grow tall (Stevens and Perkins 1992). Most trees shed their lower branches once they no longer make net contributions to carbon balance, but these temporary branches are often relatively short; presumably the structural investment required to produce long branches (thus, a broad crown) is unwarranted unless limbs are to be retained for a long time. Shrubs, in contrast, suffer no future penalty for investing in persistent branches, and they may be more adapted to dominating substantial lateral space relative to their height.

These arguments hold only for dicotyledonous plants, but monocots of all sizes are also prevalent throughout the tropics. Indeed, one reason for the success of arborescent palms may be that they avoid the tradeoff: their unique leaf morphology allows a wide crown on short individuals, without

an investment in branches that will later become a permanent metabolic drain when they become shaded. The fiber-rich tissues of broad, arching palm leaves also impart strength and elasticity which enable them to survive branch falls that would fracture most understory dicots.

Studies of the neotropical understory palm genus *Geonoma* have explored the tradeoffs involved in increasing stature to improve light interception (Chazdon 1991). Low-stature plants of the tropical forest understory have to cope with extremely low light levels, but small increases in stature can lead to greatly increased light interception (Chazdon and Fetcher 1984). It might be expected, therefore, that natural selection would inevitably favor height. Nevertheless, Chazdon (1985) demonstrated that increases in stature are linked to increases in leaf size, number, and morphological complexity; but as these factors increase, efficiency of light interception per unit of biomass decreases. Small plants, therefore, have reduced metabolic costs and can grow and reproduce in more shaded conditions. Thus form, stature, and reproductive status are tightly integrated to determine shade tolerance. By foregoing the ability to grow large, the understory palms effectively exploit the scant light resources available in the understory. The opportunity presented by this habitat is reflected in the group's great diversity and, in some tropical forests, its extraordinarily high density (Kahn 1986).

#### 6.2.2 Longevity

Just as it is useful to break life-forms down into stature classes, it is equally useful to distinguish among members of a life-form that have different life spans. Stand turnover has, in the last 20 years, become recognized as a major controlling agent of species richness (Connell 1978, 1979), resource patchiness (Vitousek 1985), and vegetation pattern (Hubbell 1979; Hubbell and Foster 1983; Weinstein and Shugart 1983). Thanks to the gap-dynamic paradigm, ecologists have finally abandoned their visions of tropical forests as static entities comprised of uniformly ancient trees; instead, most forests are recognized as mosaics comprised of unequal-aged patches, as was suggested decades ago by Aubréville (1938); and if different locales are subjected to disturbance with different frequencies, it is not surprising that the species within each life-form are characterized by many different life spans, making longevity a useful second-tier categorization tool.

Plants, which (unlike some animals) do not transfer information to the next generation except through their DNA, pay a fitness penalty for surviving longer than the reproductive phase (because of occupancy of resources by the parent), just as they pay a penalty for dying early, before their reproductive potential is realized. One would expect, therefore, the frequency of longevity classes within a local flora to reflect the dominant frequencies of disturbance. If stand turnover were caused by a single factor

of predictable long-term frequency, for example, one might expect all plants in an ecosystem to converge on a single life span; likewise, if two forces acted at different frequencies (fire every 20 years and typhoons every 160, for example), one might expect a bimodal distribution of longevity classes, with one class vulnerable to fire and another class capable of withstanding fire but vulnerable to wind. Tolerance to both fire and wind would presumably lead eventually to dominance by one or more still-longer-lived species, according to the inhibition model of succession (Connell and Slatyer 1977).

Such an accommodating relationship between disturbance regimen and life span does not, of course, obtain in nature, where death is probabilistic and comes from many agents. Furthermore, not all disturbances are exogenous, and those that are endogenous expose different life forms to different frequencies of mortality within the same forest. For example, fallen branches kill understory trees (Clark and Clark 1991) and eventually the epiphytes they carry with them (Matelson et al. 1993), whereas some palms (de Castro y Santos 1980) and shrubs survive.

The situation is further complicated because the information required to enable ecologists to analyze plant longevity in tropical forests is hard to obtain due to the difficulty of aging most tropical perennials (Bormann and Berlyn 1981). The only sure option currently available is long-term observation, a grim prospect when one recognizes that mean life spans of some suites of species are likely to be measured in centuries. Nevertheless, the extremes are apparent: some trees live little more than a decade, whereas others are known (e.g., trees long used as African village gathering points; prominent landmarks) to live for centuries. Curiously, some of the fast-growing, low-wood-density pioneer trees (e.g., several Bombacaceae and Dipterocarpaceae) are also long-lived species.

Because the direct aging of long-lived organisms that yield no anatomical clues is extremely difficult, it might be useful to attempt to estimate longevity classes indirectly, using another variable. A good candidate might be growth rate, for there is some evidence, both empirical (see discussion in Ewel 1986) and theoretical (Pearl 1928; Rose 1991), that within a species, individuals with the fastest growth rates come to the end of their allotted life span soonest.

Nevertheless, some life-forms do not lend themselves to such an approach because they couple short-lived (often fast-growing) shoots with an almost irrepressible ability to resprout from a long-lived base. Examples include large woody vines (shoots of which usually die when they tumble out of the canopy) and understory herbs (whose shoots frequently succumb to branch fall). Ecosystem functioning might be affected in one way by the longevity of the ramet and in another by the longevity of the genet, and in such cases it would be useful to make a distinction between the two longevity classes of the same "individual."

One otherwise conspicuous longevity class does seem to be missing, or nearly so, from humid tropical forests: annuals. These short-lived plants are creatures of harsh season and high frequency of disturbance; where they abound in the humid tropics they seem to have tracked human activity. Coincidentally, they also tend to have higher relative growth rates than most longer-lived plants (e.g., Grime and Hunt 1975).

### 6.3 Biogeographical Patterns

There is undeniably a huge increase in species diversity along a gradient from the poles towards the equator, but whether there is a concomitant increase in life-form diversity is debatable. Clearly, life-form diversity depends on the classification system used, but what should be expected in theory? Plants in the tropics operate under relaxed environmental constraints, and the lack of a cold winter may have permitted the proliferation of plant morphologies that would have been selected against in harsher climes. Tree architectural diversity (*sensu* Hallé et al. 1978) reaches its zenith in the tropics, as does the life-form diversity of epiphytes (Gentry 1988). Although this augurs for higher life-form diversity in the tropics, according to Box (1981) tropical regions contain 18 life-forms, whereas the subtropics have 20, and temperate regions no fewer than 25. Raunkiaer predicted that life-form diversity should be highest in the mid-latitudes where the over-wintering season is intermediate in harshness, and his prediction seems to be borne out by Box' analysis.

Life-form spectra are by no means identical in tropical forests on different continents, even in areas of comparable climate. Having sampled some 80 sites, for example, Gentry (1991) reported that climbers (and hemiepiphytes) were more abundant in Africa (> 1000 stems per hectare) than in the Neotropics or Australasia (about 700/ha in each). These data, while intriguing, are based on modest sample sizes (11 plots of 1000 m<sup>2</sup> in continental Africa and Madagascar, 56 in the Neotropics, and 13 in Australasia), and more extensive documentation would be desirable. The distribution and abundance of vines is particularly complex because so many families are involved and because vine abundance is inextricably confounded with site history and climate.

The relative paucity of arborescent palms in Africa and Asia compared to the Neotropics is better documented (Moore 1973), as one might expect easy-to-count members of a single, conspicuous family. Across a broad range of lowland rain forest sites in the Neotropics, arborescent palms accounted for roughly 15% of the trees, whereas they comprised less than 2% of the adult trees in four African sites and were completely absent from two Asian sites (Grubb et al. 1964; Emmons and Gentry 1983).

Island floras are notoriously depauperate. Are they also disharmonic (*sensu* MacArthur and Wilson 1967), i.e., do they lack many of the adaptive types found on their donor continents? It might be reasonable to predict that life-forms with predominantly wind-dispersed seeds (e.g., vines, as demonstrated by Gentry 1983, 1991) or extremely large, mammal-dispersed seeds (e.g., many trees and arborescent palms) would be under-represented in island floras, whereas those with bird-dispersed seeds (e.g., shrubs) would be disproportionately abundant. On the other hand, the life-form spectrum of the Hawaiian Islands is not skewed relative to that of continents, even though the Hawaiian flora is species-poor overall (Mueller-Dombois et al. 1981). Comparisons of islands having disharmonic floras with continents would be potent tools for elucidating relationships between life-form diversity and ecosystem functioning.

### 6.4 Environmental Correlates of Life-Form Diversity

Life-form diversity is correlated with a number of abiotic variables. The most elaborate attempt in recent years to predict life-form distribution as a function of climate was that of Box (1981), who used six climatic variables to define the niche space of each of 77 life-forms. His tropical life-forms include such categories as Tropical Linear-Leaved Trees, Tropical Broad-Evergreen Small Trees, and Tropical Broad-Evergreen Lianas. The impressive agreement between actual and predicted occurrence (based on Box' model) indicates that, at a global scale, life-form distribution is largely controlled by climate.

#### 6.4.1 Rainfall

Within the tropics, precipitation is a major determinant of life-form distribution (Table 6.1). If life-form definitions emphasize the types most important in the tropics, the general trend is one of greater life-form richness with increasing rainfall. If, on the other hand, Raunkiaer's system, with its emphasis on adaptations to harsh environments, is used, life-form richness increases with aridity (e.g., Shreve 1936; Whittaker and Niering 1965).

Different life-forms respond in different ways to increasing availability of water, even in tropical forests. Epiphytes are more affected than any other life-form group, and there is a strong correlation between annual precipitation and contribution of epiphytes to species richness (Table 6.1). Along a gradient from dry forest to wet forest in Ecuador, for example, the abundance of epiphytes increased by a factor of 450 and the number of species increased from 2 to 35 (Gentry and Dodson 1987b). Palms also become increasingly dominant (at least in the Neotropics) as precipitation increases (Table 6.1).

Table 6.1. Life-form composition of selected tropical forests, arranged in order of increasing rainfall. All sites are at elevations lower than 500 m except Mt. Kerigomma, Papua New Guinea, at 2700 m. Values are percentages of species. Blanks indicate that information could not be extracted from data as published

Site Reference (annual rainfall, mm)	Trees >10 cm DBH	Arborescent palms	Small trees, large shrubs	Terrstral herbs, small shrubs	Climbers	Epiphytes	Other
Chamela, Mexico (784)	26	0	23	24	22	4	
Capetra, Ecuador (804)	15	6	52	24	24	2	1
Ibadan Nigeria (1220)	51	16	16	32	32	1	
Santa Rosa, Costa Rica (1550)	21	0.3	10	48	17	4	1
Makou, Gabon (1755)	34	0.4	37	23	23	6	1
Jauneche, Ecuador (1855)	20	11	36	22	22	11	1
Rio Manu, Peru (2000)	27	0.5	28	14	18	12	
Queensland, Australia (2330)	68	10	10	11	11	4	7
Barro Colorado, Panama (2750)	21	1	10	33	20	13	1
Rio Palenque, Ecuador (2980)	15	10	10	36	16	22	1
La Selva, Costa Rica (4000)	21	1	42	12	12	25	1
Horquetas, Costa Rica (4000)	31	1	6	13	24	25	
Mt. Kerigomma, Papua New Guinea (4000)	39	0	14	14	16	16	

1 Bullock (1985); 2,4,5,6,9,10,11; Gentry and Dodson (1987a,b); 3 Hall and Okali (1978); 7 Foster (1990); 8 Stocker (1988); 12 Whitmore et al. (1985); 13 Grubb and Stevens (1985).

For example, Santa Rosa, Costa Rica, (1.6 m mean annual precipitation) has 3 palm species, compared to 18 at La Selva, Costa Rica (4 m). Many palms tolerate anoxic conditions well and become the sole dominants on flooded soils (Myers 1990). The large water storage capacity in the trunks of arborescent palms may play a significant role in enabling survival during times when roots can make little contribution to plant needs (Holbrook and Sinclair 1992). In contrast, the contribution of climbers to species richness may decline slightly as precipitation increases (Table 6.1), and herb richness is often greater in dry forests than in wet forests, perhaps owing to the more open canopy (Gentry and Dodson 1987a).

#### 6.4.2 Altitude

The changes in life-form (as well as forest stature and species composition) that accompany change in elevation are readily observed but hard to assess, in part, at least, because three environmental factors – temperature, rainfall, and mist – tend to change simultaneously with altitude. In the humid tropics, temperature drops more or less predictably, at a rate of 5.5 to 6.0 °C per 1000 m. Atmospheric moisture, on the other hand, is more complex. Orographic uplift of incoming air masses often results in an increase in rainfall with elevation. Furthermore, at the lifting condensation level (often in the range of 600 to 2000 m), forests are bathed in mist. Above the lifting condensation level, once the atmosphere has been sapped of its water, both rainfall and humidity decline, so low temperatures often co-occur with aridity at high elevations.

Epiphytes, both vascular and nonvascular, commonly reach their greatest abundance and diversity in montane cloud forest (Gradstein and Pócs 1989). Along an altitudinal transect in Ecuador, for example, Grubb et al. (1964) found 2555 epiphytes in a 465 m<sup>2</sup> montane plot, compared to only 675 individuals in a similarly sized plot in lowland rain forest. Palm diversity declines with elevation, but many mid- to high-elevation forests contain one (or a few) palms in great abundance. In fact, the tallest palm in the world, *Ceroxylon andicola*, which grows to 60 m, is found as high as 3000 m in the Colombian Andes (Cuatrecasas 1958). Climbers appear to maintain an important place in the biological spectrum, at least up to the transition from upper montane forest to cloud forest (Leigh 1975; Grubb 1977). Nevertheless, there is a shift in relative abundances of different types of climbers with altitude in the Neotropics. Gentry (1988), for example, found that hemiepiphytes reached peak abundance at mid-elevations in the Andes, to be supplanted at lower and higher elevations by free-climbing lianas.

### 6.4.3 Soil Fertility

Climate is not the only environmental factor that influences life-form distribution; the ability of a soil to meet nutritional needs seems to control distribution in some cases. In general, fertile soils support a greater profusion of forms than do impoverished soils in the same climate.

Based on his own extensive surveys and data in the literature, Gentry (1991) concluded that "there is a very slight tendency for greater liana density on richer soils," but within small areas the relationship seems more pronounced (e.g., Grubb and Tanner 1976; Proctor et al. 1983; Putz 1983; Putz and Chai 1987). The giant, perennial herbs (e.g., members of the Heliconiaceae, Zingiberaceae, Marantaceae, Musaceae, etc.) so typical of tropical forests seem to be more abundant and diverse on fertile soils, but data are scarce, as most authors do not segregate them as a life-form. Epiphytes might seem to be nutritionally autonomous, but tank epiphytes (and probably others) depend on inputs of detritus, the quality of which is determined, in part, by soil fertility. Shrubs and understory palm-like plants (Palmae, Pandanaceae, Cyclanthaceae, and similar forms) are more abundant on fertile soils, but whether this is a direct effect of nutrition or an indirect effect of the fast turnover of trees on fertile soils is unknown.

## 6.5 Episodic Impacts on Life-Form Diversity

In addition to the chronic environmental controls of life-form diversity in tropical forests, such as climate and soils, a number of agents intervene locally or aperiodically to affect forest structure. Whether biological or environmental, they do not usually have equal impacts on all life-forms.

### 6.5.1 Wind

Typhoons (cyclones, hurricanes, willy-willies) are common in many parts of the tropics and subtropics, especially the western side of warm ocean basins at latitudes higher than about 10°. Their impacts on life-form diversity can best be illustrated by the response of a single group, arborescent palms. The broad crowns of dicotyledonous trees are architectural marvels at intercepting light and occupying space, but they are almost equally effective in intercepting hurricane-force winds, with the predictable outcome that they topple. Palms, in contrast, have two structural characteristics that enable them to survive wind storms. One is the elasticity and flexibility of their stems (Wainwright 1976), which can bend to a remarkable degree without either breaking or uprooting the palm. The second is that the huge leaves of palms can be blown off, thus reducing the interception of

wind. These traits prompted Beard (1949) to suggest that the extensive, nearly monospecific *Prestoea* forests (palm brakes) on steep slopes of Caribbean islands were a reflection of the differential survival of this life-form to hurricanes, although poorly drained soils in these slopes exposed to the trade winds may be important as well (Frangi and Lugo 1985).

Winds less fierce than typhoons also influence tropical vegetation and the life-forms of which it is composed. Palm brakes (*Livistonia*) in Malaysia may reflect the combined drying effects of strong winds and shallow soil (Wyatt-Smith 1963), and Leigh et al. (1993) concluded that wind was a key factor in practically eliminating huge canopy trees from small, artificially created islands in Gatun Lake, Panama.

### 6.5.2 Fire

Despite their all-or-nothing investment in a single apical bud, palms are also remarkably resistant to fire. Again, the monocotyledonous anatomy plays a role. The vascular strands of palms are embedded throughout a matrix of parenchyma and fibers, which insulates the conducting tissues. The bud is often massive and sheathed in thick scales that similarly provide insulation. When fires sweep through forests dominated by a mix of dicotyledonous trees and palms, the dicots tend to be killed, leading to differential survival and eventual dominance by the palms (together with the hemiepiphytes they support). A remarkable example is the tens of thousands of hectares of monospecific stands of *Orbignya martiana* in southeastern Amazonia, a region blanketed by species-rich deciduous forest less than a century ago (Anderson et al. 1991).

Perhaps the most striking and widespread physiognomic change on tropical landscapes is the human-mediated conversion of forest to grassland. Derived savannas, dominated by grasses such as *Imperata*, *Hyparrhenia*, *Panicum*, and *Saccharum*, occur throughout the tropics and are sustained by fire. Not surprisingly, such a dramatic change in life-form dominance results in major shifts in ecosystem functioning. The fires themselves yield emissions of gases important in climate change, and the retention of nutrients by shallow-rooted grasses is less effective than that of trees.

### 6.5.3 Animals

The changes induced in vegetation structure by animals range from wholesale landscape conversion to minor shifts in composition and individual plant architecture. Among the most dramatic impacts on life-form diversity are those of large African herbivores: the conversion of savanna dominance from tall grass to short grass by hippopotamuses, for example. Perhaps the best known case is the conversion of woodlands to grasslands

by elephants, which destroy trees in the process of consuming bark (e.g., Dublin et al. 1990). Not surprisingly, the dramatic changes in vegetation structure wrought by elephants cascade through the biota: tsetse flies breed in woodlands, and when the trees are killed the flies disappear; in the absence of tsetse flies, *Trypanosoma* (sleeping sickness) loses its vector, and the area becomes habitable by a number of mammals, including domesticated cattle, that would otherwise have been excluded by disease; and grazing potential attracts people, with all the changes their presence implies.

Less dramatic, perhaps, but equally important to ecosystem structure, is the Neotropical example studied by Leigh et al. (1993). They found that the absence of agoutis on small islands resulted in a proliferation of tree species whose seeds would otherwise have been consumed, and this contributed to reduced diversity of trees.

Sometimes the actions of an animal do not lead to replacement of one species or life-form by another, but to more subtle morphological changes in the targeted plant. Consider, for example, the effect of the marine isopod (*Sphaeroma*), whose larvae burrow into the exposed tips of mangrove (*Rhizophora*) prop roots. Death of the apex can lead to dichotomous branching, thus increasing the surface area of prop roots, which in turn serve as substrate for many sessile organisms, both plant and animal (Simberloff et al. 1978; but see Ellison and Farnsworth 1990). Or consider the impacts of white-faced monkeys (*Cebus*) on the architecture of *Gustavia* trees as a result of bud grazing. Consumption of the apex releases lateral buds, leading to a proliferation of new shoots, young leaves, and flowers and fruits (Oppenheimer and Lang 1969). In a dry area of southeastern Sri Lanka, elephant browsing deforms the crowns of the dominant trees, undoubtedly leading to shifts in the competitive balance among species (Mueller-Dombois 1972).

The impacts of one species, *Homo sapiens*, are so pervasive that they merit separate consideration, for there is scarcely a tropical forest in the world in which human activities have not left their mark on life-form diversity (Denslow and Padoch 1988; Goldammer 1992). Nonindustrialized people selectively harvest large dicotyledonous trees for construction of bee hives and canoes (Kahumbu 1992) and vines as a raw material for basketry, tying, and construction. Palms tend to suffer disproportionately at the hands of humans because of singular features that lend themselves to a remarkable variety of uses: the large, fibrous leaves are used as thatch; the main axis of many climbing palms becomes rattan; the bud and starch reserves are sources of food; slats from the trunk are used in house construction; and fruits yield cooking oil, animal fodder, human food, stimulants, fertilizer, analytical-grade charcoal, organic chemicals, soap, ethanol, fuel, and many other products (Anderson et al. 1991).

Epiphytes, which reach their highest diversity and rates of endemism in montane belts, may be the life-form that is most threatened by anthropo-

genic disturbance. Nonvascular epiphytes in particular are less well known floristically than other groups, and there is little doubt that many species are extinguished before they are known to science. Because montane forests tend to be patchily distributed, destruction of relatively small areas can result in extinctions. Epiphyte populations are obviously affected by timber harvesting, even when it does not involve clearing of entire forest patches. More subtly, international demand for rare epiphytic orchids and bromeliads encourages the stripping of untold numbers of these plants from tropical forests. Furthermore, epiphytes, including lichens, are extremely sensitive to air pollution. Although levels of toxic emissions in most tropical regions are nowhere near as high as those that contributed to the decimation of the European bryoflora during the industrial revolution, the fertilization effects of nitrogen deposition due to agricultural practices and biomass burning in tropical regions may be causing insidious changes. The ability of bryophytic epiphytes to take up atmospheric sources of inorganic nitrogen could lead to long-term increases in nitrogen availability in the canopy via feedbacks to decomposition rates (Clark et al., unpubl. ms). In other nutrient-poor plant communities, increases in nitrogen supply have led to declines in species richness, a process possibly being replayed today in the canopies of tropical cloud forests.

#### 6.5.4 Climate Change

The impacts of wind, fire, and wildlife on the life-form composition of tropical forests pale in comparison with the changes induced by swings of climate on a geologic time scale. Paleoecology has long been regarded by most as one of those interesting but esoteric endeavors of little direct relevance to society. Today, however, that perception has changed, as we become increasingly aware of the intimate relationships between human activity and climate.

According to P. Colinvaux (pers. comm.), three statements can now be made with reasonable assurance about the tropical lowlands of ice-age Earth: (1) temperatures were about 6 °C cooler than they are today, (2) atmospheric carbon dioxide concentrations were about two-thirds as high as today's, and (3) rainfall and seasonality were different – it was drier for longer in some places, and wetter in others. Paleoecologists recognize that vegetation types do not respond to climate change by remaining intact and slithering, amoeboid fashion, about the landscape. Rather, species drop in and out of communities, resulting in mixes that would seem incongruous in today's world: *Podocarpus* and *Magnolia* cohabiting with the palms and legumes of the modern lowland flora of the Neotropics, for example. There is no reason to think that the same sorts of recombinations that occurred with species did not also obtain at the level of life-forms, however hard it might be for us to visualize vine-festooned *Dacrydium*, or swards of grass



sprinkled with terrestrial bromeliads, neither employing C<sub>3</sub> carbon fixation. The shifts in life forms that most assuredly will accompany tropical climate change are bound to have profound effects on both primary productivity (through interactions between CO<sub>2</sub> and temperature effects by life-forms that employ different modes of carbon fixation, for example) and secondary productivity (because of the wide range in food supplying powers of different life forms – shrubs compared with treelets, for example). It is less certain that they will exert great effects on processes that are under more direct control of climatic and atmospheric conditions, such as soil development and fluxes of water and nutrients.

### 6.6 Life-Forms and Succession

Drawing on a 5-year study of post-slash-and-burn succession on a fertile soil in Costa Rica, we see that the vegetation undergoes important shifts in life-form composition, even in those early stages of stand development (Fig. 6.1, upper). A marked decrease in herbaceous vines, for example, was accompanied by increases in shrubs and trees. Perhaps the most dramatic change occurred with epiphytes, which underwent a dramatic surge in abundance during the 3rd year, when trees developed sufficient stature to support them (Fig. 6.1, lower). This is a clear case of facilitation, whereby colonization of an entire life-form was made possible by the development of structure provided by a second life-form.

Some life-forms, on the other hand, are major impediments to colonization and stand development. Vine tangles, like the grasses described earlier, sometimes hold sites against all potential invaders for decades. These life-form-poor disclimaxes may have very different functional traits than the richer forests that might otherwise occupy the same sites, but data to support or refute such an inference are scarce.

### 6.7 Implications of Loss of Life-Forms

Just as factors such as environment, episodic phenomena, and community development influence life-forms, the life-forms themselves influence the internal workings of ecosystems. We have illustrated how dominant life-forms influence ecosystem-wide resource availability and stand dynamics. Nevertheless, it is through their impacts on within-community functioning that the mix of life-forms is likely to have its greatest impacts. Some might argue that such within-community processes are bona fide components of ecosystem functioning, some might not; it is easy to imagine situations

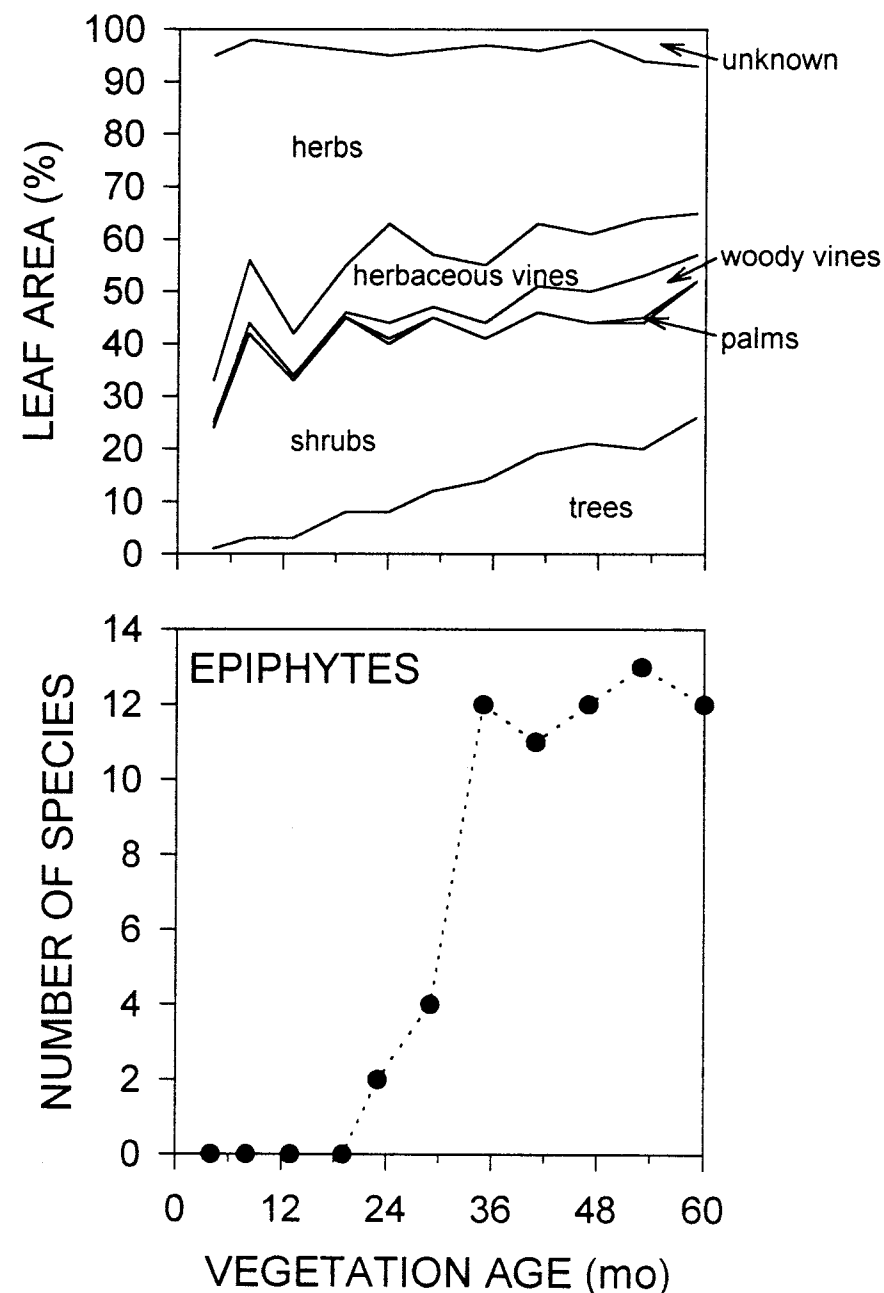


Fig 6.1. Changes in life-form composition during 5 years of post-slash-and-burn succession. The study took place near Turrialba, Costa Rica. Values are derived from species inventories and leaf-area assessments of six 16 x 16 m plots. *Upper* Relative dominance (expressed as proportional contribution of leaf area) by species comprising different life-forms; *lower* epiphyte colonization, facilitated by trees during the 3rd year

when either perspective would have merit. Semantic differences aside, the important point is that life forms do influence processes at many scales (just as different species, and different age classes and size classes within species, have distinct impacts on processes), and loss of a life-form is likely to precipitate changes in both the composition and functioning of the ecosystem of which it was a part.

Life-form diversity creates ecological opportunity, and this positive feedback culminates in the high biotic diversity we find in tropical forests. Rico-Gray (1993, and pers. comm.), for example, examined ant-plant associations in dry forest along the Gulf coast of Mexico. Associations between the 102 plant species and 30 ant species he studied sorted out by life form as follows: shrubs, 31 relationships with ants; trees, 26; herbs, 18; herbaceous vines, 10; woody vines, 9; parasites, 4; epiphytes, 2; cacti, 1; and fungi, 3. Although most of these relationships are nonspecific (one ant species fed on 72 plant species), it is likely that the diversity of relationships provides temporal continuity, and in some cases that continuity of food or defense is undoubtedly crucial to survival. Loss of shrubs, for example, might lead to local extinction of many ant species, whereas loss of cacti might be inconsequential.

Can we predict the consequences of loss of one life-form from a structurally diverse community, or is each situation so unique that we cannot generalize? As is the case with most ecological predictions, robust generalization may prove impossible due to the inherent complexity of interactions in biotic communities. Nonetheless, some life-forms fill certain roles uniquely (or nearly so; Table 6.2), and we can speculate about the consequences of their loss. As examples we choose two life-forms that reach peak abundance and diversity in tropical forests – woody vines and epiphytes.

Vines serve as trellises for arboreal mammals, such as rodents (Malcolm 1991; Langtimm 1992), monkeys (Emmons and Gentry 1983), and sloths (Montgomery and Sunquist 1978). They are also a webbing that binds tree crowns together, perhaps increasing canopy stability against windthrow, or perhaps generating larger openings when trees do fall. In addition to the benefits they impart on other members of the community, vines produce a tremendous amount of foliage which shades their host trees and slows their growth; furthermore, they sometimes add so much mass to a tree's crown that it breaks (Putz 1980). Other things being equal, a vine-free tropical forest might be expected to have fewer (or less mobile) arboreal mammals, faster tree growth, less tree breakage, and smaller gaps.

Table 6.2. Examples of linkages between plant life-forms and processes in tropical forests

Life-form	Role
Dicotyledonous trees, long-lived	<ol style="list-style-type: none"> <li>1. Provide skeletal structure of entire forest</li> <li>2. Dominate primary productivity and material flows</li> <li>3. Influence off-site climate and hydrology</li> <li>4. Provide shelter and roosts in hollow trunks</li> </ol>
Dicotyledonous trees, short-lived	<ol style="list-style-type: none"> <li>1. Reduce nutrient loss in early succession</li> <li>2. Reduce likelihood of site takeover by vines and shrubs</li> </ol>
Rosette trees (e.g., palms)	<ol style="list-style-type: none"> <li>1. Channel rainwater toward stem</li> <li>2. Capture and aggregate litter</li> <li>3. Concentrate calcium</li> <li>4. Roots bore through soil pans, creating channels that can be exploited by other plants</li> <li>5. Root foraging emphasizes scale (rather than precision, sensu Campbell et al. 1991)</li> </ol>
Understory trees	<ol style="list-style-type: none"> <li>1. Scavenge sparse radiation of understory (and have low nitrogen demand)</li> <li>2. Provide platforms (in humid microenvironment) for nitrogen-fixing epiphylls</li> </ol>
Shrubs	<ol style="list-style-type: none"> <li>1. Drive productivity of scansorial rodents and birds that feed on fleshy fruits</li> <li>2. Retard nutrient loss in early succession</li> </ol>
Giant-leaved herbs	<ol style="list-style-type: none"> <li>1. Constitute large, homogeneous patches in otherwise heterogeneous understory</li> <li>2. Foster secondary productivity through nectar and fruit production</li> <li>3. Provide roosting sites for bats and building sites for carton nests of social insects</li> </ol>
Vines	<ol style="list-style-type: none"> <li>1. Provide trellises for movement of arboreal animals</li> <li>2. Act as webbing that ties trees together</li> <li>3. Buffer microclimatic changes by sealing forest edges</li> </ol>
Graminoids	<ol style="list-style-type: none"> <li>1. Constitute readily combustible dry-season fuel</li> <li>2. Provide forage for grazers and food for seed-eating birds, rodents, ants, and fungi</li> </ol>
Hemiepiphytes	<ol style="list-style-type: none"> <li>1. Increase tree mortality rates</li> <li>2. Provide slender vine trellises (aerial roots) in understory of closed canopy forest</li> </ol>
Epiphytes	<ol style="list-style-type: none"> <li>1. Augment leaf area (by colonizing opaque surfaces)</li> <li>2. Slow nitrogen through-flow</li> <li>3. Divert water from soil to atmosphere</li> <li>4. Redistribute through-fall and stem flow</li> <li>5. Provide unique habitats essential for reproduction of other species</li> </ol>

Epiphytes, which scavenge water and nutrients out of the atmosphere, play important roles in stand hydraulics and nutrition. In forests where mist and rain come as pulses interspersed with dry spells, epiphytes act as capacitors, or storage devices. Much of the water that might otherwise plummet directly through the canopy as throughfall is captured by the epiphytes and eventually evaporates directly back to the atmosphere. In some forests this short-circuiting can be beneficial because it reduces water input to the soil, thus reducing leaching; in others, where water may be in short supply between rains, it can be detrimental. In continuously wet tropical forests, such as mist-shrouded cloud forests, bryophytic epiphytes are like permanently soaked sponges. They intercept vast quantities of saturated air, and the water condenses on the epiphytes. Nevertheless, because the epiphytes are already saturated, the water is not absorbed and stored, but drips off the epiphytes onto the forest floor. In one of the few stand-level life-form-removal experiments ever performed, Weaver (1972) found that removal of the epiphytes (dominated, in this case, by bryophytes) from a Puerto Rican dwarf cloud forest did not change the total amount of water reaching the forest floor, but it did produce an important change in its spatial distribution. In plots with epiphytes intact, water dribbled more or less evenly through the canopy, but in epiphyte-free plots, water was channeled down stems in torrents to the forest floor.

Inorganic nitrogen in cloud water, mist, and precipitation is rapidly taken up by epiphytic bryophytes; 70 to 80 % of the inorganic nitrogen in atmospheric deposition was retained by the forest canopy at one mid-elevation site (Clark et al., unpubl. ms). Much of this nitrogen, which is in a highly mobile form and arrives in pulses, is transformed into more recalcitrant forms and may persist for years as part of the mats of dead organic matter that line the limbs of large trees in montane cloud forest (Nadkarni and Matelson 1992). It appears likely, therefore, that nitrogen leaching losses in tropical montane forest ecosystems would be significantly greater in the absence of epiphytic bryophytes (Clark et al., unpubl. ms).

Tank-forming epiphytes are complex microcosms that support detritus-based food chains and are essential habitats for some stages of the life cycles of many organisms. Indeed, the study of these miniature communities, or phytotelmata, is an ecological subdiscipline in itself (Laessle 1961; Fish 1976). To cite one example, the males of a Central American terrestrial, viviparous frog, *Dendrobates pumilio*, transport young on their backs up trees to epiphytes, where the offspring leave the parent and develop into adults (Wells 1977). A second example concerns vectors of human disease. Because the larvae of some species of mosquitoes that spread yellow fever and malaria develop in them (Bates 1952; Pittendrigh 1948), the elimination of tank epiphytes was a major tactic in disease control earlier this century. Unfortunately, the ecological impacts of this landscape-level experiment were not evaluated.

Epiphytes, plus the water they store, add a tremendous mass to tree crowns and there can be no doubt that they promote limb breakage and tree fall. Epiphyte loads likely contribute to the rapid turnover of some tropical forests (e.g., Samper 1992), especially at mid-elevation where, due to orographic rainfall and the lifting condensation level, their abundance reaches its peak. Nevertheless, the contribution of epiphytes to tree fall is difficult to quantify because of the complexity of branching patterns, interspecific differences among trees in their support of epiphytes, and spatial heterogeneity in the epiphyte flora.

Although epiphytes of many taxa form tanks of sorts in all tropical regions, none are as abundant or well-developed as those of the Bromeliaceae, an essentially neotropical family. Thus, biogeography has yielded a giant, unreplicated experiment whose results have yet to be analyzed. Does the absence of bromeliad tanks in the African and Asian tropics, for example, manifest itself in measurable ways in inter-regional forest structure or functioning? Are certain functional groups of amphibians and insects less abundant because the microcosms required for completion of their life cycle are absent, or do they simply have different habitat requirements? Could the Dipterocarpaceae biomechanically support water-filled tank epiphytes, or would their dominance of Asian forests be reduced if bromeliads were present?

## 6.8 Conclusions

Our interpretation of ecosystem functioning as encompassing only fluxes and storages of energy and materials affords two advantages. First, these processes are definable and measurable (though seldom measured), and second, they are the processes whose influence is most likely to extend beyond the bounds of the system in question. From this admittedly narrow perspective, we conclude that it is the mix of life-forms, not the mix of species, that exerts major controls over ecosystem functioning.

Just as taxonomists base their science on phylogenetic relationships among the groups they study, ecologists should ground theirs on functional similarities. Unfortunately, our capacity to recognize architectural types far exceeds our capacity to measure functional differences among them. Nevertheless, categorization of life forms should be based on gross morphology, which in turn must be coupled to measures more directly linked to function – physiology, stature, and longevity; and to be useful in a particular setting, a life-form categorization scheme must be tailored to the appropriate environment, in this case tropical forests.

The consequences of loss of life-form diversity can be predicted through experimentation, natural history observations, or analysis of landscape patterns. Rigorous determination of the relationships between life-form

diversity and ecosystem functioning can come only from ecosystem-level experiments that include manipulation of life-form composition coupled with measurement of the appropriate response variables. Meanwhile, a number of natural "experiments" might yield qualitative insights into the consequences of life-form enrichment or impoverishment. These include biogeographical comparisons (e.g., between islands and mainlands, or between Neotropics and Paleotropics); analysis of patterns along gradients of climate and soil, both past and present; study of episodic and catastrophic events, such as typhoons, rain-forest fires, and imbalances in wildlife populations; and, perhaps most importantly, the disruptions of ecosystem structure and functioning caused by that most disruptive of species, *Homo sapiens*.

**Acknowledgments.** We thank Paul Colinvaux, who contributed everything paleo, plus several other nuggets, to this manuscript; Francis Putz, whose vast knowledge of vines, palms, roots, hemiepiphytes, and forest dynamics was tapped constantly by us; Victor Rico-Gray, who generously provided data on ant-plant relationships; Kenneth Clark, who shared his insights on epiphytes and their relationships to atmospheric chemistry; Ankila Hiremath, whose suggestions improved the clarity and accuracy of the manuscript; and F. Stuart Chapin III, who provided a very useful review. The views expressed herein reflect, in part, data and perspectives developed during work on National Science Foundation awards BSR-8506373, BSR-9000089, and BSR-9004281.

We dedicate this chapter to the memory of Alwyn H. Gentry, in recognition of his courageous devotion and unparalleled contributions to tropical botany, ecology, education, and conservation.

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