Plant life forms in the Golfo Dulce region and other neotropical rainforests

Formas de vida vegetal en la región de Golfo Dulce y en otros bosques lluviosos neotropicales

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Abstract: The spectrum of plant life forms strongly reflects the local climate, and to some extent interactions between plants and biogeography, i.e. the pool of species present in a wider region. The traditional categories distinguishing life forms according to the position of winter buds are of limited applicability in ecosystems with year-round growth such as tropical rainforests. The most species-rich life form in the forest of the Golfo Dulce region are trees, followed by herbs, smaller woody plants and epiphytes. 15% of all vascular plant species are shrubs or pygmy trees generally not exceeding 5 m in height, 10% are small trees reaching 10 m, and 26% are trees growing to > 10 m. Terrestrial herbs account for 19%, woody and herbaceous epiphytes for 12%, hemiepiphytes for 3.3%, lianas for 7%, non-woody vines for 5.4%, and hemiparasites, parasites, and aquatic plants each for less than 1% of the local flora. This survey discusses the adaptive significance of the different life forms and compares the life form spectrum found in the Golfo Dulce area with that of other neotropical forests.

Key words: plant life forms, neotropical rainforest, Costa Rica.

Resumen: La variedad de formas de vida vegetal refleja fuertemente el clima local, y en alguna medida, las interacciones entre plantas y biogeografía, es decir las especies presentes en una región. Las categorías tradicionales de formas de vida, diferenciadas de acuerdo a la posición de las yemas invernales, son de limitada aplicación en los ecosistemas con crecimiento todo el año, como sucede en los bosques lluviosos tropicales. Las formas de vida más ricas en especies en el bosque de la región de Golfo Dulce son los árboles, seguidos por las hierbas, pequeñas plantas leñosas y epífitas. El 15% de todas las especies de plantas vasculares son arbustos o árboles pigmeos, que usualmente no exceden los 5 metros de altura, 10% son pequeños árboles que alcanzan 10m, y 26% son árboles que crecen sobre los 10 m. Las hierbas terrestres alcanzan al 19%, epífitas leñosas y herbáceas al 12%, hemiepífitos el 3,3%, lianas el 7%, enredaderas no leñosas el 5,4% y hemiparásitas, parásitas y plantas acuáticas alcanzan menos del 1% de la flora local. Esta investigación discute el significado adaptativo de las diferentes formas de vida y compara la variedad de formas de vida encontradas en el area de Golfo Dulce con la de otros bosques neotropicales.

Palabras clave: formas de vida vegetal, bosque lluvioso neotropical, Costa Rica.

Introduction

Globally, ecosystems are often defined by the composition of plant life forms present. They characterise the structure of the ecosystem and reflect the adaptations and advantages that individual life forms present. Plant life forms have been popularised by Raunkiaer's classification, which distinguishes plants according to the location of their hibernating buds from megaphanerophytes, with buds well above the snow cover, to therophytes, which survive as seeds. Although rainforest plants need no hibernating buds, most of Raunkiaer's life forms can be readily recognised in rainforests. To account for tropical life forms, Raunkiaer himself later added aerophytes for non-parasitic plants growing on other plants, i.e. epiphytes. Even so, the traditional life-form classification for temperate areas has its limits when applied to tropical vegetation as it groups lianas with trees in megaphanerophytes on the one hand, while on the other hand there are hardly any geophytes and therophytes or biennials in rainforests. ELLENBERG (1979) drew a coarse comparison between the life form spectra of tropical lowland forests, and characterised rainforests by the dominance of evergreen trees, the presence of epiphytes, lianas and chamaephytes, and the absence of all other groups such as therophytes and geophytes. Later authors more commonly distinguished at least trees, shrubs, lianas, epiphytes and terrestrial herbs, as defined below.

Life form spectra are strongly affected by sample size. When sampling is based on forest plots, often 1 ha

or less, trees tend to be underrepresented, if for no other reasons than simply because of the much lower number of individual trees relative to other life forms present in small areas. The relationship between a gradually increasing area and the number of species (the species-area curve) in epiphytes often levels off above an area of ca. 1.000 m², so that one hectare, if sampled intensively, includes most epiphyte species found in a given forest (HIETZ & HIETZ-SEIFERT 1995). By contrast, the number of tree species found in one hectare of a diverse tropical rainforest trees, is nowhere close to including all species (CONDIT et al. 1996). As a consequence, the ratio of epiphytes to ground-rooted plants (particularly trees) tends to decrease with larger plot sizes or areas surveyed (NIEDER et al. 2001), and similar biases are likely to be found for other life forms. Because large plants will always be underrepresented in small or even fairly large plots, local floras of intensively collected locations may be more suitable to analyse life form spectra of forests.

Another bias when comparing larger areas may be found in the degree of disturbance and focus of the collection activities. Open habitats tend to have more herbaceous species and species that are not found in the forest by growing in high light, being weedy, exotic, or simply cultivated plants. The La Selva flora includes 220 exotic species: 197 of these are herbs and the bulk of these are grasses and Asteraceae (HARTSHORN & HAMMEL 1993). Given the number of species in the Poaceae (42) and Asteraceae (47) in the checklist of the Golfo Dulce flora, the list seems not to be strongly affected by exotic species that are not representative of the original vegetation, although a number of non-rainforest species are certainly included and no attempt was made to identify and eliminate these. In addition, the collections include a few cultivated plant species such as *Cinnamomum* or *Citrus*, but annual crops such as wheat, maize, squash or tomatoes that are certainly cultivated in the area have not been sampled (although rice was). Cultivated plants are therefore unlikely to distort the picture of the life form spectrum.

Methods

Information on life forms of all vascular plant species collected from the Golfo Dulce region (WEBER et al. 2001). Apart from the published field guide (WEBER et al. 2001) and personal experience, the most important source was "Tropicos", the online herbarium of Missouri Botanical Gardens (Tropicos.org), which includes the original specimen description of the collectors. For each species where no other information was available, the information on life forms of several specimens at Tropicos was checked, and in cases where dif-

ferent specimens of a species were described with different life forms, cross-checked with other published information or accepted as species that are difficult to assign to a single life form (see discussion below). In the case of woody plants, which were distinguished into three size classes, the largest sizes reported were taken. In most cases this information was unambiguous, but a number of species were difficult to assign to a single life form.

As others have noted (MORI et al. 2002), a comparison of plant life form spectra is complicated by the fact that a part of the flora cannot easily be classified as there are continua from herbs to subshrubs, to shrubs, to trees of various sizes, from vines to lianas, from aquatic to terrestrial and from terrestrial to epiphytes and sometimes also between self-supporting woody plants and climbers or epiphytes. In addition to this, scientists do not always agree on how to define these terms, which complicates comparisons between studies. This problem is acknowledged by others, and MORI et al. (2002) suggested a universal terminology to classify tropical plant life forms, to which this compilation of life forms from the Golfo Dulce area adheres as far as possible. The following classes and sub-groups are used in this paper.

Aerial – describes the habitat of a plant neither aquatic nor terrestrial, whose life cycle is completed wholly or partially without ground contact growing on other plants. MORI et al. (2002) considers this a habitat rather than a life form.

Aquatic – plants with or without anchoring roots, whose life cycle is completed wholly or partially in water.

Epiphyte – a non-terrestrial, non-parasitic plant usually growing upon another plant with no contact to the soil throughout their life cycle (true epiphytes) or at least during parts of their life (hemiepiphytes). According to MORI et al. (2002), the term epiphyte refers to the habit of non-parasitic aerial plants, whereas their life forms can be herbs, shrubs, etc. A number of plants can grow terrestrially or as epiphytes (facultative epiphyte), but in the majority of species the distinction between epiphytic or ground-rooted is clear. Accidental epiphytes, plants that almost invariably grow terrestrially but on rare occasions are found growing on trees, were not included in this group.

Hemiepiphyte – an epiphyte that is attached to the ground at some stage of its life cycle. Hemiepiphytes are classified as either primary or secondary (though see the discussion under the latter term).

Hemiparasite – a chlorophyllous parasitic plant that derives part of its nutrition from its host but obtains carbon mostly through photosynthesis. Plants that may be partially mycotrophic, particularly orchids,

are not included here as the degree of parasitism is generally unknown. All but one known hemiparasites in the area are mistletoes (which are not classified as epiphytes).

Herb – generally a non-woody plant, but here excluding plants already categorised as aquatic, epiphyte, vine, or parasite.

Holoparasite – a plant without chlorophyll that derives all carbohydrates and nutrients from its host, including mycorrhizal fungi.

Liana – a woody climbing plant always rooted in the ground.

Primary hemiepiphyte – a plant that starts its life as an epiphyte but later becomes ground-rooted, usually by extending aerial roots to the ground

Secondary hemiepiphyte – a plant that starts its life rooting in the ground, becomes a climber and subsequently loses soil contact. While SCHIMPER (1898) did not consider plants that may lose their soil contact as hemiepiphytes, later authors (BENZING 1990; PUTZ & HOLBROOK 1986) and many scientists recording epiphytes have used the term secondary hemiepiphytes. MOFFETT (2000) argued against this practice, preferring the term "nomadic vine" for climbers that change their position by growing on the one end and dying off at the other, whereby they can continuously root in the soil, never root in the soil, or contact the soil at some stages during its life. These include particularly Araceae and some Marcgraviaceae, Cyclanthaceae and possibly a few species in other families.

Shrub – generally a woody plant that is branched close to its base (but excluding multi-stemmed trees that branch only at ground level) irrespective of height. Here, shrubs are all ground-rooted, self-supporting woody plants not normally exceeding 5 m in height.

Strangler – a primary hemiepiphyte whose aerial roots anastomose and become tightly encircling the host tree, which may eventually cause the death of its host.

Subshrub – a plant intermediate between an herb and a shrub, and only slightly woody or woody only at the base.

Tree – a woody, erect plant, occasionally with multiple stems, that grows to >10 m (MORI et al. 2002) defined trees as plants with a diameter at breast height (d.b.h.) ≥ 5 cm, others distinguish trees above and below 10 cm d.b.h., but this information is less readily available for all plants listed).

Small tree: a woody, erect plant that reaches > 5 m but rarely > 10 m (according to MORI et al. 2002, a treelet is a small tree < 5 cm d.b.h. and > 2 m tall at maturity); others group trees of different sizes differently.

True epiphyte – an epiphyte that is not attached to the ground at any stage of its life cycle.

Vine – a herbaceous climbing plant continuously rooted in the ground. Since any degree of lignification can be found in climbing plants, some are difficult to assign to either vines or lianas.

To simplify and to compare with other studies, groups were sometimes combined as described below. Also, several groups that may be difficult to allocate to a single life form are discussed.

Lianas, which would fall into the megaphanerophyte category of Raunkiaer, are distinguished from other climbers in being large and woody. As non-woody climbers could be placed either into the herb category or together with lianas into a group of climbers or vines, lianas and vines were distinguished, as far as possible. Some herbs with minor climbing tendencies and climbers with minor lignification were difficult to allocate to one of these three groups. Liana records were also checked with GILBERT et al. (2006), PUTZ & WINDSOR (1987), and NEPSTAD et al. (2007). Many aroids germinate on the ground, become climbers and may eventually lose contact with the soil. In this case, they can be classified as secondary hemiepiphytes, though most individuals will become reproductive before losing soil contact and if soil contact is lost at all depends on species, tree height and light climate. For simplicity, all climbing aroids, except for *Heteropsis*, were classified as secondary hemiepiphytes in so far as they can at least potentially become independent of soil. If one does not want to class these "nomadic vines" hemiepiphytes, all 35 hemiepiphytic aroids would be placed in the vine category as they hardly lignify. Also, monocots do not normally show the secondary growth typical of lianas, but the climbing palm *Desmoncus* was classified as a liana as its stem is distinctly woodier than that of aroids. Also, many primary hemiepiphytes can become fertile and conclude their life cycle before rooting in the ground or will never do so if perched high in the canopy. Here, all that are designed to root in the soil by sending long aerial roots downwards are considered primary hemiepiphytes, irrespective of how often this is seen in the field. Since the distinction between shrubs and subshrubs (subfrutices) is particularly gradual, the ca. 20 subshrubs were also classified as shrubs.

Ultimately, which life form a species is put into also depends on the research question, and scientists with a particular interest in epiphytes (such as the author of this manuscript) tend to see an epiphyte in every plant that may possibly become one, and people interested in climbers, trees or other life forms do likewise. To still be able to compare the life form spectrum of the area with other lists or re-group classes to suit other interests, the main classes have in some cases been subdivided.
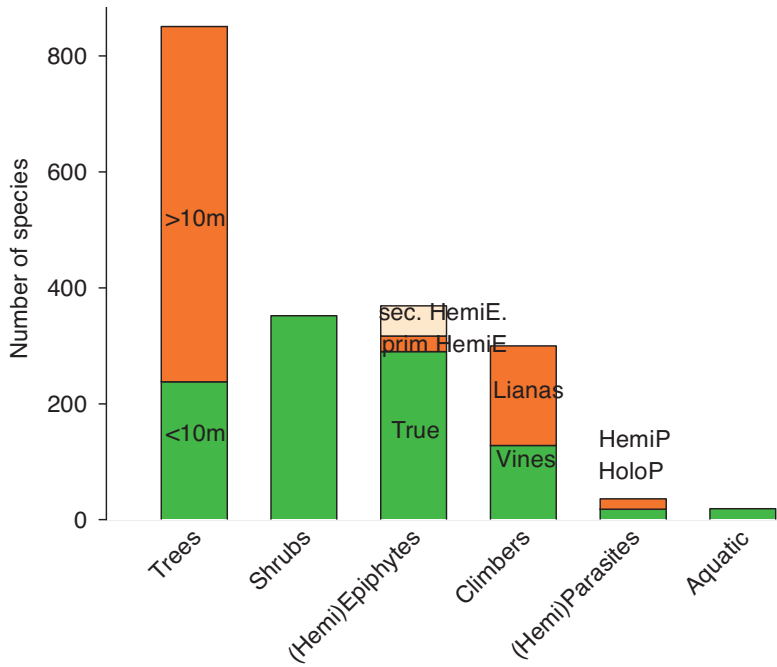
Results

Out of 2.378 vascular plant species reported for the Golfo Dulce region, 851 are trees, including four tree ferns and 238 woody plants that grow between 5 and 10 m tall, but excluding 27 primary hemiepiphytes, more than half of which can also grow into free-standing trees. 352 species are classified as shrubs, woody, free-standing plants < 5 m height, including some 20 sub-shrubs (Fig. 1). Of the 303 climbing plants, 131 were herbaceous (vines) and 172 woody (lianas). In addition, there are 52 climbers (woody or herbaceous) that are classified as secondary hemiepiphytes or nomadic climbers. 290 species are true epiphytes, including a few facultative epiphytes but excluding 27 primary hemiepi-phytes, 17 hemiparasitic mistletoes and one parasitic Rafflesiaceae (*Apodanthes caseariae*). One other hemi-parasite (*Ximenia americana*, Olacaceae) and 17 true parasites are terrestrial, and 19 non-parasitic plants are aquatic. 449 plants are classified as herbs, which are herbaceous plants that do not fall into any of the previ-ous categories of (hemi)epiphyte, climber, aquatic, or (hemi)parasite.

Fig. 1: Life form spectrum of vascular plants from the Golfo Dulce region.

Fig. 2: Families of trees (left) and shrubs (right) with the most species in the Golfo Dulce area. Shrubs are free-standing woody plants <5 m tall, tree species typically reaching a size below or above 10 m are distinguished on the left-hand graph.
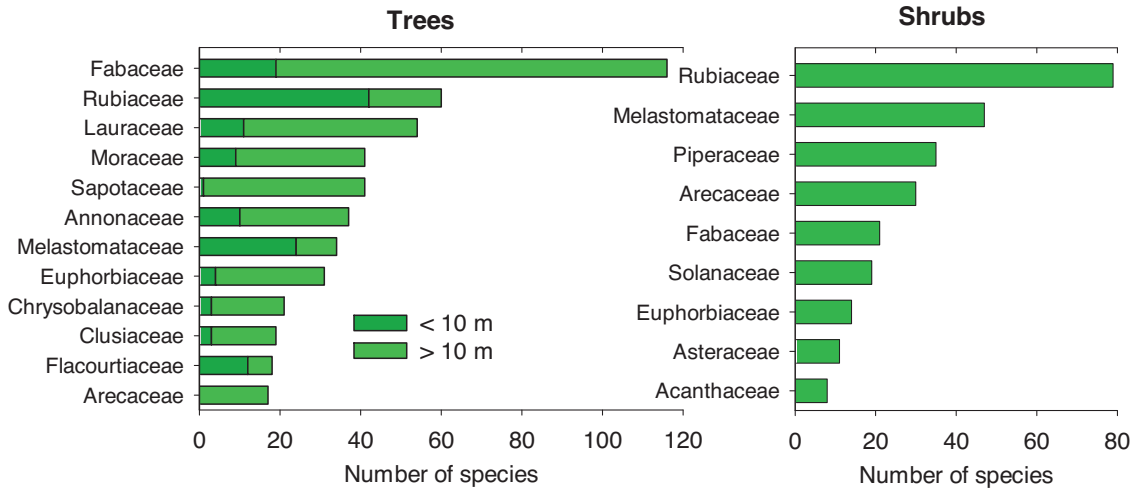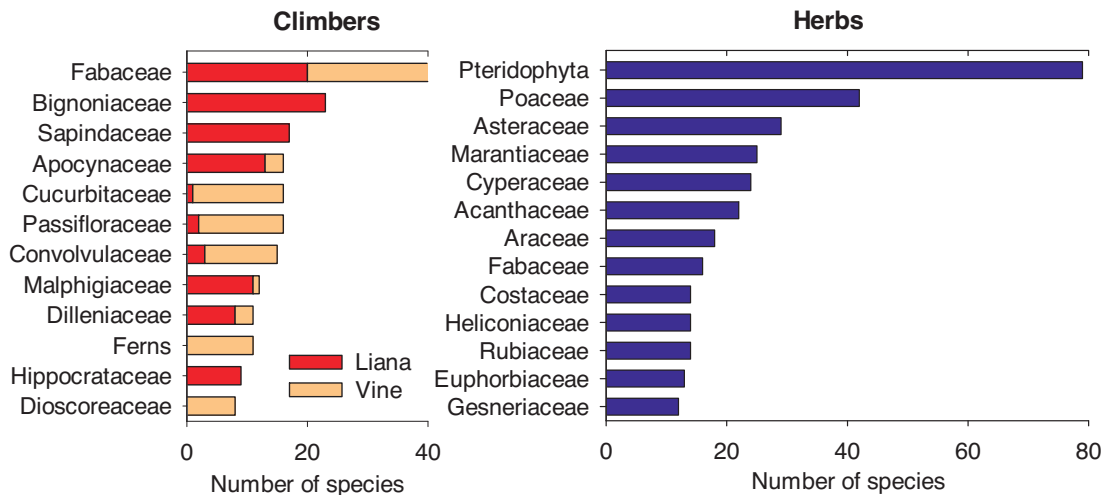

Fig. 3: Families of climbers (left) and herbs (right) with the most species in the Golfo Dulce area. Climbers are divided into woody lianas and non-woody vines.
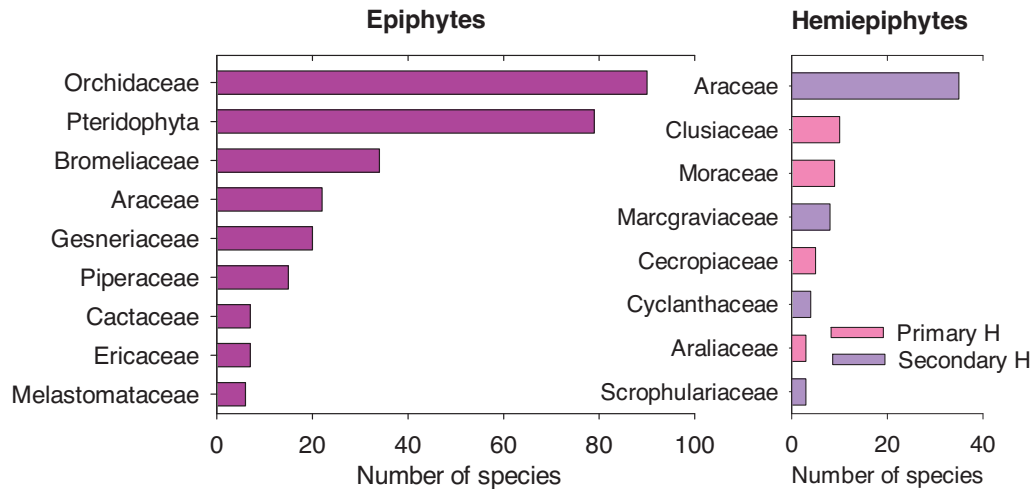
Fig. 4: Families of epiphytes (left) and hemiepiphytes (right) with the most species in the Golfo Dulce area. Primary hemiepiphytes germinate on a tree and later root in the ground soil; secondary hemiepiphytes germinate in the soil, climb a tree, and later lose soil contact.

In addition to trees, shrubs and lianas, all primary hemiepiphytes and all hemiparasites are woody plants, but only about one dozen of the nomadic climbers, most of which are herbaceous aroids. In total, 1.450 species are woody and 928 herbaceous, 1691 species are self-supporting and 687 are dependent, i.e. epiphytic or climbing.

Trees

All forests are dominated by trees, but, in contrast to most other forests, trees may dominate in tropical rainforest not only in terms of biomass but also in terms of diversity. Of the 851 tree species recorded (representing 36% of the entire vascular flora), 238 do not generally grow to > 10 m in height. These small trees were dominated by Rubiaceae and Melastomataceae, followed by Fabaceae, Flacourtiaceae and Lauraceae. Taller trees were strongly dominated by Fabaceae s.l. with 97 species, with *Inga*, the most species-rich genus of trees, comprising 34 species. Of the leguminous trees, 48 belong to the Mimosaceae, 31 to the Fabaceae and 18 to the Caesalpiniaceae. Other tree families dominating the forest are Lauraceae, Sapotaceae (with 23 species in *Pouteria*) and Moraceae (Fig. 2). *Ficus* is present with 23 species, of which 14 were classified as trees and the rest as primary hemiepiphytes. Four small trees are tree ferns and 17 trees are palms.

Many shapes of tropical trees have been described, which are not always easy to recognise in the field (HALLÉ et al. 1978). In the Golfo Dulce area, as in other rainforests, buttresses are common in large trees (Fig. 6). Individual emergent trees in the forest can reach 60 m or even more, typically have large buttresses and a straight, unbranched stem to the upper canopy. Trees of this height and with a d.b.h. substantially over than 1 m are rare and the closed forest canopy reaches a height of 30-40 m in most places.

Trees are the logical and most competitive life form in an environment where neither low temperature nor limited water supply limits the establishment of large woody plants, which explains the dominance of trees over other life forms or at least the higher proportion of trees in rainforests compared to other vegetation types. The high tree diversity in tropical forests is a somewhat different question, since an answer of that must also explain how this high number of species can coexist with-
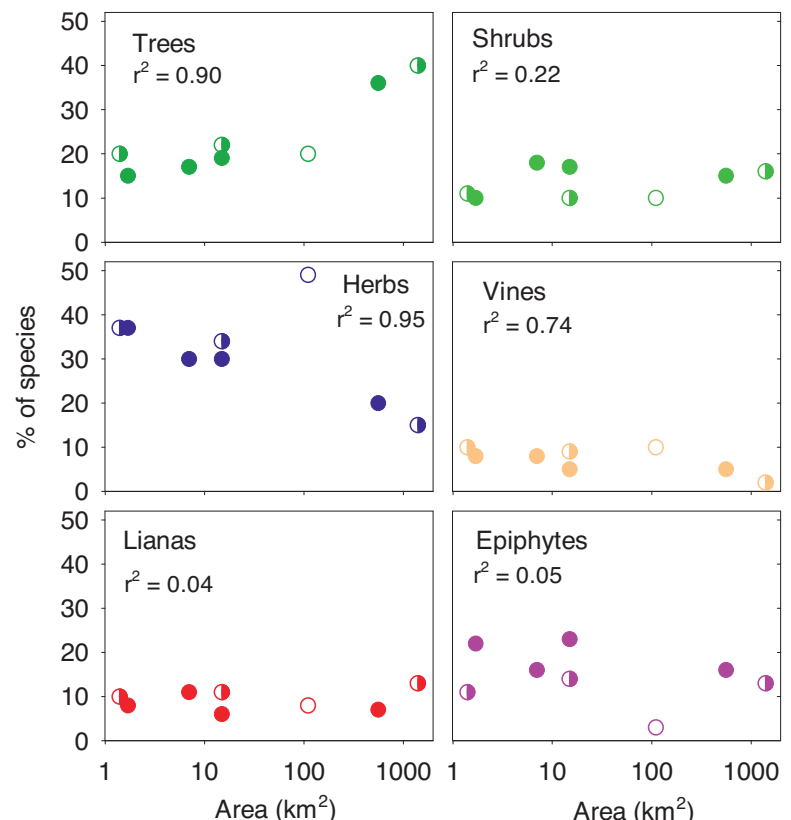

Fig. 5: Contribution of different life forms to vascular plant diversity in neotropical wet forests (filled circles), moist forests (half-filled circle) and a dry forest (empty circle) related to the area sampled for a regional plant list. Indicated is Pearson r^2 for data points on a logarithmic scale, excluding the dry forest. Data are based on Table 1, with the exception of Capeira, for which no area was available and the flora was never fully published. Epiphytes include hemiepiphytes. The wet forest (full symbol) at 560 km² represents the Golfo Dulce forest.

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Fig. 6: Buttresses are common in large rainforest trees, but giants such as this *Ceiba pentandra* are rare.

Fig. 7: Many woody plants in the rainforest understorey are pygmy trees, including small palms such as this *Asterogyne martiana*.

out most being displaced by the most competitive species. This fact has been much discussed and various theories have been brought forward, some by now well-founded in ecological theory and field studies. Parts of the answer appear to be higher rates of speciation in the tropics, a long history of speciation without large-scale extinction, density-dependent mortality driven by pathogens and pests, niche differentiation, intermediate rates of disturbance, non-equilibrium between potentially competing species, and little competition in sup-

pressed understory plants and epiphytes (for reviews see e.g., HARMS et al. 2000, WRIGHT 2002, LEIGH et al. 2004). This question is central in understanding tropical tree and general forest diversity but beyond the present comparison of life forms.

Shrubs

The term shrub generally refers to a woody plant with basal branching, irrespective of plant height. In temperate areas, shrubs are common, sometimes more species-rich than trees and in all but a few cases readily distinguishable from trees (Fig. 7, 8). In tropical rainforests, this life form is less common, mainly because the low light at the ground level makes basal branching and thereby exposing leaves closer to the ground uneconomic. Some small woody plants are thus sometimes called pygmy trees as they have a tree-like habit but remain small. In our area shrubs / pygmy trees are dominated by Rubiaceae with many genera, the most important being *Psychotria*, followed by Melastomataceae (with *Miconia*) and Piperaceae (only *Piper*) and small palms (Fig. 2). It is noteworthy that *Piper*, *Psychotria*, and *Miconia*, with 41, 40 and 35 species, respectively, are the three most species-rich genera of all life forms in the area, which means that almost one in three of the 352 shrub species belongs to one of these three.

Herbs

Among the 449 non-aquatic, non-parasitic and non-epiphytic herbs, pteridophytes are by far the largest group with 76 species (Fig. 3). Pteridophytes (mainly ferns plus a number of clubmosses and two horsetails), of course, comprise several families, and within the terrestrial ferns, the most species-rich families are Pteridiaceae, Thelypteridaceae, Dennstaedtiaceae and Tectariaceae (Fig. 9). Poaceae as well as Cyperaceae are very uncommon in the understorey and sign of natural disturbance or other open habitat such as riverbanks, or were collected from anthropogenic habitats, which to a lesser extent is also true for Asteraceae and Fabaceae. By contrast, most ferns, Gesneriaceae, Acanthaceae and small palms grow in the shady understorey of rainforests. The low light available on the rainforest soil challenges any plant to maintain a positive carbon balance. As an adaptation to very low light, several rainforest herbs and also small shrubs have corrugated upper leaf surfaces and an anthocyanin-rich lower epidermis that collectively maximise the proportion of light absorbed by the leaves which can then be used for photosynthesis (Fig. 10).

Marantiaceae, Costaceae and Heliconiaceae and some Araceae (*Diffenbachia*, *Anthurium*) are monocot herbs with often very large leaf areas. Many, though not all or these, tend to grow abundantly in gaps, forest mar-

gins, steep slopes, rivers margins or other spots where more light reaches the forest floor but where they are less exposed to dry air than in completely open habitats (Fig. 11). Here the abundant sunlight captured by large leaves allows for high rates of photosynthesis. These plants consequently grow fast, but as they invest little in any structure that could help them grow upwards, they are sooner or later outgrown by taller plants when forest succession closes the gap.

The 19 aquatic plants are from 12 different families, the largest with only five species being the Pontederiaceae (Fig. 12).

One life form which is not reported from evergreen tropical regions is annual. For this study, annuals were not classified, among other reasons because this is rarely noted on herbarium vouchers, but quite probably none of the plants recorded classifies as an annual since there is no unfavourable season that a seed might have to survive. Similarly, geophytes and hemicryptophytes are not normally present in tropical rainforests (ELLENBERG 1979). Where rainforest plants have a short live span, this is mostly due to death caused by herbivores, pathogens, competitors or a combination of these factors and these species tend to invest most resources in rapid growth and little in defence. Also rare but not unheard-of are monocarpic rainforest plants, which may be perennial but die after fruiting and thus have a limited life-span. These include some bromeliads and, surprisingly, the tree genus *Tachigalli*.

Climbers

While herbaceous climbers (here, the term vine is limited to herbaceous plants) are also common in temperate areas, lianas (woody climbers) are with a few exceptions limited to tropical zones, though not necessarily to very humid climates. Most of the 128 vine species are found in the Fabaceae and Cucurbitaceae (both also common in temperate zones) and the largely tropical genus *Passiflora*. In addition, 35 climbing aroids at least start their lives as vines. The most important liana families are Bignoniaceae, Fabaceae, Sapindaceae, Apocynaceae and Malpighiaceae (Fig. 4). If secondary hemi-epiphytes or nomadic climbers are counted as climbers, the number of vines increases to 163 and the number of lianas to 189. Many epiphytic ferns have long creeping rhizomes and would thus classify as nomadic vines (sensu MOFFETT 2000), but, being mostly epiphytic and not really changing their position by growing at the one and dying off at the other end, they are all classified as epiphytes. A few ferns in several families (*Bolbitis*, *Danaea*, *Metaxya*, and *Lygodium*) are true climbers with very long, thin rhizomes that can climb many metres up on a tree but do not normally lose soil contact (Fig. 13).

Fig. 8: Rubiaceae (*Psychotria elata*) are the dominant family of shrubs and small trees.

Fig. 9: Filmy ferns (Hymenophyllaceae: *Trichomanes reniforme*) are adapted to very humid and shady environments and found as epiphytes on the lower stem or on the rainforest floor.

Fig. 10: Leaves of rainforest plants in extreme shade are sometimes rich in anthocyans at the abaxial side and have corrugated adaxial surfaces to maximise light capture.

Fig. 11: Megaphyll herbs dominate gaps and other areas where more light reaches the understorey.

Fig. 12: *Eichhornia crassipes*, a free-floating aquatic plant.

Fig. 13: Vines, non-woody climbers, include several ferns such as *Bolbitis nicotianafolium*.

Lianas are perennial, woody plants that have their regeneration buds aboveground and would be classified as phanerophytes in the Raunkiaer system (Fig. 14). While many tree species are able to survive the temperate winter, most lianas apparently are not, and their diversity strongly declines outside the tropics at higher latitudes than ca. 25° (PUTZ & MOONEY 1991). The likely reason is that the water-supply system of lianas is designed for very efficient transport of water through a comparatively thin stem. To do so, they produce very large vessels in which water can be transported fast, but which are vulnerable to freezing in winter. Within the tropics, liana diversity is highest in wet forests with rainfall > 3.000 mm per year and a short or no dry season (CLINEBELL et al. 1995).

Climbers differ in the strategies they employ to move into the canopy and these differences are also reflected in different ecological roles. In twiners either the main stem or branches grows clockwise or anti-clockwise around the support. In tendril climbers, stem or leaf (or rarely root) tendrils show autonomous circular movements and react upon contact by making a few loops around the support. Twiners and tendril climbers can only hold onto relatively thin stems and branches and are therefore not able to climb upwards on a large tree. To reach the canopy they normally establish on young trees and grow upwards with their support. Once there, they can build large crowns, which can span several tree crowns and connect these. Scramblers attach with hooks, thorns, rigid trichomes or simply stiff branches that can find some hold in neighbouring plants. A typical scrambler is the palm *Desmoncus costaricensis*, which scrambles between branches with spiny stems, petioles and rachis, and stiff spreading leaves. *Desmoncus* and some other large woody climbers would be classified as small trees in their juvenile phase when the small stem is more or less self-supporting, but are clearly climbers later. Plants climbing with their roots attaching to the tree stem (root or bole climbers: common in Araceae, Cyclanthaceae, Marcgraviaceae and 11 climbing ferns), are able to climb branchless stems of any diameter, but rarely reach the outer crowns. Some root climbers also have long aerial roots that can grow downwards for many metres and when these grow into the soil, they can provide additional supply of water and nutrients. Twiners have typically higher growth rates than root climbers, which is important for them as they have to keep pace with the upward growth of the tree.

By investing relatively little in their stem, lianas can build a massive leaf biomass, which can represent 10-30% of the entire forest, and become serious competitors with trees. Most lianas have small, wind-dis-

persed seeds that germinate in light as do those of pioneer trees. Others germinate in the shade and are released when a gap forms or grow towards a tree stem in the understorey and start their upward movement from low light conditions. Because most lianas are light-loving, can grow towards light very fast, and usually survive a tree fall, they grow most densely in disturbed sites, particularly in gaps but also forest margins (Fig. 15). Here, they compete with trees and can dominate and determine the succession for many years and thus become important players in the dynamics of rainforests (SCHNITZER & BONGERS 2002).

Epiphytes

The current plant list includes 290 true epiphytes, 27 primary hemiepiphytes, 17 plants that grow as woody climbers but could eventually lose contact with the soil (grouped here are several Marcgraviaceae, Cyclanthaceae, *Schlegelia* in the Scrophulariaceae and a few others) and 35 climbing aroids that are generally in the group of secondary hemiepiphytes (Fig. 4). The most species-rich groups of true epiphytes are Orchidaceae, Pteridophytes (with the main families being Polypodiaceae, Lomariopsidaceae and Grammitidaceae), Bromeliaceae, Araceae (*Anthurium* with 20 species), Gesneriaceae, and Piperaceae (*Peperomia*) (Fig. 4, 16, 17). Primary hemiepiphytes as classified here are all woody plants. Some (particularly *Ficus*, but sometimes also *Coussapoa*) grow into free-standing trees when their host tree dies, others rarely grow to independent trees and remain supported by their host throughout their life cycle. *Ficus*, *Clusia*, *Coussapoa*, *Oreopanax* and possibly others form anastomosing roots that can encircle the stem of their host. If a strangler is a hemiepiphyte that kills its host by restricting lateral growth and ultimately phloem transport, probably only *Ficus* spp. and rarely individuals of other species classify as true stranglers. There are rather few herbaceous plants that are facultative epiphytes (a few aroid species can regularly be found growing either on a tree or the soil or rocks), but there is more ambiguity in the group of woody (hemi)epiphytes. For simplicity, Ericaceae, Gesneriaceae, Melastomataceae, Rubiaceae (*Hillia*) and Solanaceae (*Juanolloa*) were classified as woody epiphytes though some species of *Drymonia* (Gesneriaceae), *Blakea*, *Clidema* (Melastomataceae) and *Juanolloa* can also be found growing as lianas.

Aroids present a particularly diverse group of life forms, growth habits and locations (CROAT 1988). Some are strictly terrestrial (*Diffenbachia*, *Spathiphyllum*, and a few species of *Anthurium*) while others are strictly epiphytic (most *Anthurium* species). Many are climbers, some of which are entirely epiphytic (*Stenospermation*), but more commonly start rooted in the ground (*Philo-*

Fig. 14: *Aristolochia grandiflora*, a liana with large flowers and a dissected xylem typical for many lianas.

Fig. 15: High abundance of lianas in the closed forest often characterises ancient gaps.

dendron, *Syngonium*, Fig. 18). Whether ground-rooted climbers eventually lose soil contact depends on the species, the light climate and water availability. On a well-illuminated stem, plants flower early and the lower parts receive enough sunlight to maintain a positive biomass balance, or at least are useful enough in terms of supplying water to be maintained by the upper leaves. By contrast, plants that escape the shady understory are less likely to maintain the loss-making lower parts, particularly when adventitious roots can absorb sufficient

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Fig. 16: Orchids (*Plerothallis orbiculare*) are the most species-rich group of epiphytes.

Fig. 18: Many aroids are climbers (*Philodendron scandens*) that may lose soil contact as they grow upwards on the stem.

Fig. 17: *Cochliostemma odoratissima*, of a family with few epiphytes (Commelinaceae) has adapted to the epiphytic habitat by arranging its leaves in a rosette that ensures that water and leaf litter is trapped and directed towards the roots.

water from the abundant rainfall and stemflow. Thus, a species that never loses soil contact and remains a climber in a drier forest may well be found as an epiphyte in a wet rainforest. A few climbing aroids (*Philodendron sagittifolium*) will germinate either on the soil or on the tree. If these have become large plants, it is impossible to tell if they started life on the soil (are secondary hemiepiphytes) or in the canopy (true epiphytes). Finally, if an individual that germinated on the tree sends long aerial roots to the soil, it will become a primary hemiepiphyte (Fig. 19).

The diversity of vascular epiphytes is clearly related to the year-round high temperature and water supply in rainforests (BENZING 1990). Without access to soil water, they rely on rain percolating through the canopy and only species with special provisions to survive longer drought can grow in drier forests. Even more than drought, low (freezing) temperatures exclude all but very few epiphytes from temperate forests. The abundance of epiphytes is generally higher in tropical montane forests, where branches can be completely covered with epiphytes and decomposing organic matter builds thick layers of canopy soil. By contrast, in most lowland forests including the one of the Golfo Dulce area, epiphytes may be species rich but their abundance is mostly moderate. The cause of the rather sparse growth of epiphytes in most lowland forests is mainly an effect of water supply and demand. First, though total rainfall is very high, only the rain that remains on the branches or can be readily absorbed or stored by epiphytes is of any use. In lowland rainforests where precipitation comes mainly in strong downpours, the amount intercepted is a small proportion of total rainfall. And second, the higher temperature in lowland

rainforests also results in higher evaporative demand, as a consequence of which wet surfaces dry fast and transpiration is higher than in montane forests. Epiphytes therefore may contribute substantially to the biodiversity of lowland rainforests, but do not play an important role in nutrient or water cycles as in some tropical montane forests (NADKARNI 1984, VENEKLAAS et al. 1989).

Parasites and hemiparasites

Most hemiparasites from the Golfo Dulce area are mistletoes (four Viscaceae and 13 Loranthaceae), a group that is also present, although with many fewer species, in temperate forests. Since mistletoes appear not to be limited by cold temperature, or at least less so than epiphytes, their diversity in tropical forests probably reflects the generally higher plant diversity and specifically the high diversity of their hosts. Temperate and Australian mistletoes are known to differ substantially in their degree of host specificity, but little information is available for mistletoes from rainforests. The only known terrestrial hemiparasite from the Golfo Dulce area is *Ximenia americana* (Olacaceae), a small tree that forms haustoria below ground.

The 18 full parasites include all three genera of the Burmanniaceae, *Wullschlaegelia* in the Orchidaceae, *Voyria* in the Gentianaceae, and one species each in the Triuridaceae, Balanophoraceae and Rafflesiaceae. Except for *Apodanthes caseariae* (Rafflesiaceae), which grows in the stem of the tree *Casearia*, all other parasites emerge from the soil, which means they parasitise roots or fungi. The latter group are plants that obtain their organic compounds from mycorrhizal fungi (the Burmanniaceae, Gentianaceae, Triuridaceae and *Wullschlaegelia* in our area) rather than from other plants are sometimes called saprophytic. However, this is misleading because saprophytes are organisms that obtain their carbon from decomposing dead organic material, whereas in the case of these mycotrophs it is the fungi that are saprophytic and the plants parasitise the fungi.

Golfo Dulce and other neotropical forests

Although there are, by now, fairly detailed plant lists of many neotropical forests, not all of these areas have been sampled intensively, so some groups are likely to be under-represented, and rather few authors have made the effort to compile life-form categories out of these lists or from herbarium collections.

Table 1 compares life forms from Golfo Dulce with available information from other neotropical forests ranging from southern Mexico to Ecuador. All of these have been sampled intensively, typically over several

Fig. 19*: Other aroids can become primary hemiepiphytes be sending long aerial roots to the soil.

years, though unquestionably additional species will be found in all of them and indeed several stations have more recently reported more species than those Table 1 is based on. They also differ in the amount of rainfall and the area covered by a local flora. Golfo Dulce (Costa Rica), Lox Tuxtlas (Mexico), La Selva (Costa Rica), and Rio Palenque (Ecuador) all receive close to 3.000 mm or more of rainfall per year and can be classified as wet forests (sensu HOLDRIDGE 1967), French Guiana, Barro Colorado Island (Panama), and Jauneche (Ecuador) are moist forests with 1800 to 2600 mm of rainfall per year and a distinct dry season. Santa Rosa (Costa Rica) and Capeira (Ecuador) are dry forests with 1.600 and 800 mm per year, respectively.

The total number of species reported is highest for Golfo Dulce and lowest for the drier forests. While this certainly reflects the fact that wetter tropical forests are more species rich than dry forests, the total species numbers reported probably do not permit a more differentiated comparison as areas differ in sampling effort, the number of vegetation types found and substantially in area.

Table 1: Life form spectra of the Golfo Dulce area compared to other neotropical forests. Figures in parentheses are percent of the total vascular flora. Unless stated otherwise, herbs include terrestrial autotrophic and parasitic as well as aquatic herbs, shrubs include subshrubs, trees include small trees, epiphytes include mistletoes, hemiepiphytes include primary and secondary hemiepiphytes. Where no hemiepiphyes are listed, these are included in the epiphytes.1) Trees are > 2 m with d.b.h. > 5cm, 2) difference between trees and shrubs not clearly defined; 3) herbs includes vines and 197 exotic species, 4) shrubs are < 10 cm d.b.h. and < 5 m tall, include 23 exotic species, 5) ca 35% are hemiepiphytes; 6) herbs include subshrubs, 7) trees are ≥ 10 cm d.b.h..

Location	Rainfall	area (km²)	Herbs	Vines	Lianas	Shrubs	Trees	Epiphytes	Hemiepi.	Total
Golfo Dulce, CR present study	4500	560	486 (20)	128 (5)	172 (7)	352 (15)	852 (36)	307 (13)	79 (3)	2376
Los Tuxtlas, Mex GONZÁLEZ et al. 1997	4500	7	283 (30)	179 (19)		170 [2] (18)	160 [2] (17)	151 (16)		943
La Selva, CR HARTSHORN and HAMMEL 1993	4000	15	583 [3] (35)		107 (6)	285 [4] (17)	323 [4] (19)	380 [5] (23)		1678
Rio Palenque, Ecu GENTRY and DODSON 1987	2980	1.7	382 (37)	84 [6] (8)	87 (8)	99 [7] (10)	154 [7] (15)	227 (22)		1033
BCI, Pan GENTRY and DODSON 1987	2600	15	447 (34)	117 [6] (9)	149 (11)	134 [7] (10)	291 [7] (22)	180 (14)		1318
French Guiana MORI et al. 2002	2400	1402	290 (15)	44 (2)	245 (13)	314 (16)	766 [1] (40)	214 (11)	45 (2)	1918
Jauneche, Ecu GENTRY and DODSON 1987	1855	1.4	196 (37)	55 [6] (10)	54 (10)	58 [7] (11)	108 [7] (20)	58 (11)		529
Capeira, Ecu GENTRY and DODSON 1987	804	?	246 (53)	66 [6] (14)	46 (10)	28 [7] (6)	69 [7] (15)	8 (2)		463
Santa Rosa, CR GENTRY and DODSON 1987	1600	100	323 (49)	63 [6] (10)	52 (8)	64 [7] (10)	142 [7] (20)	19 (3)		663

The general pattern of species richness may be better reflected in plots of uniform size, which however, as explained above, tend to produce species lists in which trees are under-represented. Gentry (whose many unpublished plots were compiled by PHILLIPS et al. (2006) and some others sampled a substantial number of 0.1 ha plots (actually 10 transects of 5 x 100 m were sampled), which permits comparisons of diversity on a smaller scale. Overall, the trend is the same as seen in the data compiled in Table 1 with tropical wet forests being the most species rich with an average of 175 species per 0.1 ha, followed by tropical moist forests, premontane wet, premontane moist forests and species number then decreasing towards the subtropics and higher altitude vegetation.

Golfo Dulce also has the highest total number of tree species and, together with French Guiana, the highest proportion of trees (36%). In the Golfo Dulce region, tree diversity on 1-ha plots with between 108 and 179 species >10 cm d.b.h. found in four plots (HUBER 2005) is high for Central American forests (LIEBERMAN et al. 1996), though not for northern South America (GENTRY 1988, ZENT & ZENT 2004). This high representation of terrestrial woody plants also holds true when trees and shrubs, which in many studies were defined differently, are combined and may reflects the geographical position where species of Central American origin mix with those from South America. In addition, the rugged terrain may provide a higher diversity of habitat types from ridge to ravine, and from mangrove

to freshwater forests, and as a consequence a high tree diversity in the area. The proportion of tree species is substantially higher than in five local floras compiled by GENTRY & DODSON (1987), where trees > 10 cm d.b.h. comprise 15-22%. By comparison, though the absolute number of epiphytes found is also high, their proportion (13% true epiphytes and 3% hemiepiphytes) is moderate and lower than in Los Tuxtlas, La Selva and Rio Palenque. It cannot be ruled out that this is also in part an effect of sampling and scale, though epiphyte densities in the Golfo Dulce area appear to be substantially lower than in La Selva or Rio Palenque. Apparently, in spite of the high overall rainfall, the quite distinct dry season on the Pacific side does exclude a number of species that require permanently high humidity or water supply. Lianas, in spite of high species numbers, account for only 7% of vascular plants, the lowest value reported for any of the forests listed, and vines for 5%, the second lowest value. In contrast to epiphytes, climbing plants do not decrease in importance in the drier forests and indeed may become relatively more important in drier forests in terms of species numbers and also biomass. With continuous access to the water stored in the soil, lianas are less limited by rainfall patterns than epiphytes. In dense forests, lianas typically regenerate when gaps permit more light to reach the forest floor. In dry forest, the light level at the ground is generally higher due to the lower leaf area of trees, and, for plants with leaves present during part of the dry season or the beginning of the wet season, the conditions for growing up-

wards from the forest soil are better than in rainforests. Finally, similarly to epiphytes, herbs have high species numbers, though their proportion of the total flora is lower than in all sites except French Guiana.

If plots of 1 ha or smaller are too small to adequately represent the life form spectrum of a forest, is a local florula from a larger area less biased? Only up to a point. A comparison of the proportion of species in individual life forms with the sample area of the local flora shows that up to an area of > 1.000 km^2 the proportion of trees strongly increases with area, the proportion of herbs strongly decreases, the proportion of vines also decreases somewhat, and the importance of epiphytes (including hemiepiphytes), lianas and shrubs is little affected (Fig. 5). Moist forests do not differ much, if at all, from wet forests, and in a given area, dry forests have substantially lower proportions of trees and epiphytes and a higher proportion of herbs.

Acknowledgements

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