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DIVERSITY AND VERTICAL DISTRIBUTION OF FILMY FERNS AS A TOOL FOR IDENTIFYING THE NOVEL FOREST TYPE "TROPICAL LOWLAND CLOUD FOREST"

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Abstract. Recent studies on bryophyte and macrolichen diversity in lowland forests of northern South America have shown the existence of a novel forest type, the "tropical lowland cloud forest" (LCF). LCF is very rich in epiphytes and occurs in lowland river valleys where radiation fog in the morning provides an additional input of liquid water. Because of their dependence on frequent precipitation and low evaporation, Hymenophyllaceae (filmy ferns) are a suitable group for studying moisture availability. We sampled epiphytic Hymenophyllaceae on 32 trees in French Guiana, 16 in LCF and 16 in adjacent rain forest (LRF). Abundance of Hymenophyllaceae was significantly higher in LCF than in LRF. Only 10% of trees in LRF were inhabited by filmy ferns, in contrast to 70% in LCF. Moreover, the number of species recorded in LCF (9) was more than twice as high than in LRF (4), and the mean number per tree 8 times higher. Species restricted to the understory of LRF occurred in the canopy of LCF. We attribute the detected differences in diversity and vertical distribution of Hymenophyllaceae in the two forest types to the occurrence of fog in LCF, enhancing the availability of liquid water and thus facilitating the establishment and growth of the filmy ferns. Also, radiation protection against evaporative loss seems to play a crucial role in the vertical distribution of filmy fern diversity. The observed differences in filmy fern diversity and distribution in LCF and LRF represent novel traits separating the two forest types, and indicate that Hymenophyllaceae species are sensitive indicators of lowland cloud forest.

Key words: Epiphytes, fog, Hymenophyllaceae, indicator, rain forest, species diversity, tropical lowland cloud forest.

INTRODUCTION

Recent work on bryophyte and lichen diversity in French Guiana has demonstrated the existence of a new type of tropical forest, the "tropical lowland cloud forest" (LCF) (Gradstein 2006, Normann *et al.* 2010, Gradstein *et al.* 2010, Gehrig-Downie *et al.* 2011, Obregón *et al.* 2011). LCF occurs in lowland river valleys with high air humidity and radiation fog. The process of fog formation in LCF is different from that in montane cloud forests (MCF). While in MCF, fog formation is mainly due to advective orographic clouds touching the ground, canopy fog formation in valleys characterized by LCF is a result of nocturnal radiation processes (radiation fog). The formation of this type of fog is catalyzed by the nocturnal cold air drainage flow from small hills and crests bordering the river valleys, causing saturation of air humidity during the night and early morning in situations of low air turbulence. Heavy rainfall the day before and waterlogging of valley-bottom soils are additional factors fostering condensation in the valleys. Fog in LCF gradually lifts during early morning hours and clears well before noon by solar heating (Obregón *et al.* 2011). Botanically, LCF resembles lowland rain forest but differs by higher species richness and biomass of epiphytes, especially bryophytes (Gradstein 2006, Gehrig-Downie *et al.* 2011).

Microenvironmental conditions within the tropical rain forest are very heterogenic. Air temperature, light availability and wind speed generally increase from understory towards outer canopy while air moisture and nutrient availability decrease (Johans-

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son 1974, Meinzer & Goldstein 1996, Parra *et al.* 2009). The vertical distribution of epiphytes depends on their physiological requirements and is related to microclimatic conditions and branch characteristics (ter Steege & Cornelissen 1989, Hietz & Hietz-Seifert 1995, Freiberg 1997, Cardelús & Chazdon 2005, Cardelús 2007, Krömer *et al.* 2007). For vascular epiphytes species richness usually increases from lower trunk to inner crown before decreasing again towards the periphery of the canopy (ter Steege & Cornelissen 1989, Acebey *et al.* 2003, Krömer *et al.* 2007, Pos & Sleegers 2010).

This study focuses on the filmy ferns (Hymenophyllaceae) of LCF. Hymenophyllaceae are a large and speciose family of leptosporangiate ferns, containing more than 600 species and occurring commonly as epiphytes in humid lowland to montane forests throughout the tropics (Lellinger 1994, Dubuisson *et al.* 2003). Due to the lack of a well-developed cuticle and stomata, filmy ferns are sensitive to water loss and hence dependent on moist habitats characterized by frequent precipitation and low evaporation (Proctor 2003). Because of their drought-intolerance, filmy ferns are good indicators of high atmospheric humidity (Hietz & Hietz-Seifert 1995). Even though physiologically perceived as shade plants (Gessner 1940, Evans 1964, Richards & Evans 1972, Johnson *et al.* 2000, Proctor 2003), shady conditions are not obligatory for all filmy ferns and some are even desiccation-tolerant (Benzing 1990, Iwatsuki 1990).

Recent molecular work on Hymenophyllaceae (Pryer *et al.* 2001) has shown the existence of two major lineages: the Hymenophyllum clade (= genus *Hymenophyllum* s.l.) and the Trichomanes clade (genus *Trichomanes* s.l.). The two clades differ somewhat in elevational distribution, *Trichomanes* s.l. occurring mainly in lowland and submontane forests whereas *Hymenophyllum* s.l prevails in montane forests, with a wide elevational overlap between the two groups (Kessler *et al.* 2001, Krömer & Kessler 2006). The species primarily grow in the forest understory (Kelly 1985, Hietz & Hietz-Seifert 1995) except in the mountains where species of *Hymenophyllum* may occur in all forest strata, with a high relative abundance in the canopy (Krömer *et al.* 2007). Indeed, some species in these forests may be considered canopy specialists (Krömer & Kessler 2006). In contrast, *Trichomanes* species seem to be largely restricted to the lower portions of the tree trunks.

The aim of this study is to analyze the diversity of Hymenophyllaceae in LCF. By comparing species richness, composition, and vertical distribution in LCF and nearby LRF, we explore the usefulness of filmy ferns as indicators of tropical lowland cloud forest.

METHODS

Study area. Fieldwork was conducted in central French Guiana in the vicinity of the village of Saül (3°37’20”N, 53°12’31”W), about 200 km southwest of the Atlantic coast, and in the Nouragues Natural Reserve (4°02’30”N, 52°40’30”W), *ca.* 100 km inland from the Atlantic coast. Annual rainfall is *ca.* 2500 mm in Saül and *ca.* 3000 mm in Nouragues; there is a distinct dry season from late July to November and a less pronounced dry period for several weeks in February and March. Average temperature is 27°C (Mori *et al.* 1997, Grimaldi & Riéra 2001). For more detailed climate data see Obregón *et al.* (2011). The area is very undulated, with small river valleys at about 100-250 m and hills to about 400 m a.s.l. Other than a zone of minor disturbance surrounding the village, the area is covered by mixed lowland rain forest (e.g. De Granville 1986, 2001; Mori & Boom 1987). The flora is very rich, with about 5000 recorded species of vascular plants and over 300 of bryophytes (Mori *et al.* 1997, 2002; Buck 2003, Gradstein & Ilkiu-Borges 2009). Lowland cloud forest (LCF) is common in the area and occurs in valleys where fog develops during the night but clears well before noon (Gradstein 2006); LRF occurs higher up the slopes. The two forest types are very similar in overall stature (tree height, tree diameter) but emergent trees and gaps were more frequent in LCF.

Epiphyte sampling. Twelve plots of 1 ha each (Gradstein *et al.* 2003) were laid out in almost undisturbed, non-flooded old growth forest in a 6 x 2 km area in the vicinity of Saül. Four plots were situated on the slope of a small hill adjacent to the valley of the Pelée creek (“Crique Pelée”), two in LCF at the bottom of the slope at *ca.* 250 m elevation, the other two in LRF on the upper portion of the slope at *ca.* 325 m. The remaining eight plots were laid out randomly as replicates in LCF and LRF at similar elevations on slopes of small hills adjacent to the valleys of “Crique Roche” and the two smaller tributaries of “Crique Grand Fosseé” and “Crique Popote”. Distance between LCF and LRF plots was about 250 m. In order to explore the occurrence of LCF over a wider area, four additional plots (2 in LCF, 2 in LRF) were laid out in the Nouragues Natural Reserve, 80 km northeast of Saül. A total of 32 mature canopy trees, two in each plot, were climbed using the single rope technique (ter Steege & Cornelissen 1988). Sampled trees were selected randomly, standing (15)20-30 m apart, and were 20 to 45 m in height; diameter at breast height (dbh) was 30-300 cm (Table 1). We collected all epiphytic Hymenophyllaceae from trunk base to outer canopy and subdivided the samples according to location in six tree-height zones (Johansson 1974, Cornelissen & ter Steege 1989): trunk base (zone 1), lower trunk (zone 2), upper trunk to first ramification (zone 3), lower canopy (zone 4), middle canopy (zone 5), and outer canopy (zone 6). For safety reasons, thin canopy branches (zone 6) were cut and carefully lowered to the ground for sampling.

The collected Hymenophyllaceae were identified with relevant taxonomic literature (e.g. Lellinger 1994, Cremers 1997) and using reference collections from the Herbarium of the University of Göttingen (GOET). Vouchers were deposited in GOET. Nomenclature follows Lellinger (1994) and Cremers (1997), using the traditional subdivision of the filmy ferns into two broad genera *Hymenophyllum* and *Trichomanes*.

Microclimate measurements. Air temperature and relative humidity were measured for 60 days during September and October 2007 using data-loggers (HOBO ProV2 RH/Temp, Onset). The sensors were installed in the middle of the crowns (zone 4) of seven canopy trees per site in Saül (for detailed description of study design see Gehrig-Downie *et al.* 2011). Additional meteorological stations were placed in the inner crown (zone 4) and outer canopy (zone 6) of two representative trees in LCF and LRF during 33 days in September and October. The stations encompassed: (i) temperature and relative humidity probes (CS215, Campbell Sci.), (ii) pyranometer sensors (CS300, Campbell Sci.), and (iii) 2D-sonic anemometers (Windsonic4, Gill). The latter were installed in the outer canopy (zone 6), while temperature, relative humidity, and radiation sensors were installed in height zones 4 and 6.

Statistical analysis. The Nouragues plots were pooled with the Saül plots because they shared the same Hymenophyllaceae species and similar levels of diversity. Species richness of height zones and plots was compared using the Shannon Index and by calculating evenness (Magurran 2004, Chao *et al.* 2005). Differences in species number between plots were analyzed with unpaired t-tests. Floristic similarity between epiphytic Hymenophyllaceae in LRF and LCF was tested with the Sørensen coefficient (Banaticla & Buot Jr. 2005). We analyzed the relation between average relative humidity and diversity of Hymenophyllaceae by correlating a species inventory of epiphytes on 14 trees on the Pelée hill with the microclimate data derived by the HOBO loggers. The pyranometer measurements were used to calculate daily global radiation (MJ m^{-2} d^{-1}) by summation over each respective day. Evaporation was estimated using a simplified version of the Penman equation provided by Valiantzas (2006), incorporating daily global radiation, relative humidity, air temperature, and the latitude of the site. Mean diurnal courses were computed for relative humidity and global radiation.

RESULTS

Species richness. On 32 trees we collected in total 9 species of Hymenophyllaceae (2 genera), 9 in LCF and 4 in LRF (Table 2). *Trichomanes* was the largest genus with 6 species; 3 species belonged to *Hymenophyllum*. The latter species were relatively rare and represented only 7% of all specimens collected. *Trichomanes punctatum* was the most abundant species, followed by *T. angustifrons*; together these two species represented more than half (58%) of all Hymenophyllaceae samples. The mean number of species per tree was 8 times higher in LCF than in LRF, with 2.4 ± 2.2 species in LCF (max. = 6, min. = 0) and 0.3 ± 1.0 in LRF (max. = 4, min. = 0) ($P<0.01$). The Shannon Index of α-diversity was higher in LCF (H' = 1.90) than in LRF (H' = 1.33) whereas evenness was slightly higher in LRF (E = 0.96) than in LCF (E = 0.87).

Species composition. Floristic similarity of the two forest types in terms of filmy ferns was low (Ss = 0.33). *Trichomanes angustifrons*, *T. krausii*, *T. pinnatinervium* and *T. punctatum* subsp. *labiatum* occurred in both forest types, while *T. diaphanum*, *T. kapplerianum*, *Hymenophyllum decurrens*, *H. hirsutum* and *H. polyanthos* were exclusive to LCF. The abundance of Hymenophyllaceae was much lower in LRF than in LCF. In LRF only 10% of trees were inhabited by filmy ferns in contrast to 70% in LCF.

Vertical distribution. The vertical distribution of the species on trees in the two forest types was remarkably different (Fig. 1). In LRF, Hymenophyllaceae

TABLE 1. Tree height and diameter at breast height (dbh) of trees sampled in lowland cloud forest (LCF) and lowland rain forest (LRF) in central French Guiana. Tree species name and family are provided where available.

Forest type	Height (m)	Dbh (cm)	Species	Family
LCF	30	61	*Schefflera* sp.	Araliaceae
	32	47	*Jacaranda* sp.	Bignoniaceae
	45	313	*Eriotheca* cf. *globosa*	Bombacaceae
	17	50	*Dimorphandra* sp.	Caesalpiniaceae
	25	40	*Eperua falcata*	Caesalpiniaceae
	25	65	*Eperua falcata*	Caesalpiniaceae
	45	95	*Goupia glabra*	Celastraceae
	30	50	*Licania heteromorpha*	Chrysobalanaceae
	35	69	*Inga paraensis*	Mimosaceae
	25	96	*Ficus insipida scabra*	Moraceae
	30	32	Unidentified 1	
	30	50	Unidentified 2	
	33	48	Unidentified 3	
	35	56	Unidentified 4	
	35	76	Unidentified 5	
	35	42	Unidentified 6	
LRF	40	60	*Thyrsodium spruceanum*	Anacardiaceae
	25	32	*Jacaranda copaia*	Bignoniaceae
	40	92	*Dimorphandra multiflorum*	Caesalpiniaceae
	33	67	*Eperua falcata*	Caesalpiniaceae
	25	60	*Tachigali amplifolia*	Caesalpiniaceae
	30	55	*Caryocar glabrum*	Caryocaraceae
	22	35	*Inga* cf. *alata*	Mimosaceae
	30	26	*Inga* sp.	Mimosaceae
	25	65	*Sterculia* sp.	Sterculiaceae
	25	41	Unidentified 7	
	25	53	Unidentified 8	
	28	45	Unidentified 9	
	30	80	Unidentified 10	
	30	35	Unidentified 11	
	35	65	Unidentified 12	
	40	75	Unidentified 13	

TABLE 2. Occurrence and vertical distribution of Hymenophyllaceae in lowland cloud forest (LCF) and lowland rain forest (LRF) in central French Guiana. Numbers refer to the number of samples in which the species was recorded. For further explanation see text. z1 = trunk base, z2 = lower trunk, z3 = upper trunk, z4 = lower canopy, z5 = middle canopy, z6 = outer canopy. Nomenclature of taxa follows Lellinger (1994) and Cremers (1997).

		LCF							LRF						
Taxa	Height zone	z1	z2	z3	z4	z5	z6	n	z1	z2	z3	z4	z5	z6	n
Hymenophyllum decurrens		1	-	-	1	1	-	3	-	-	-	-	-	-	0
Hymenophyllum hirsutum		-	-	1	-	1	-	2	-	-	-	-	-	-	0
Hymenophyllum polyanthos		-	-	-	-	1	-	1	-	-	-	-	-	-	0
Trichomanes angustifrons		4	6	3	4	4	-	21	-	1	-	-	-	-	1
Trichomanes diaphanum		1	-	-	-	1	-	2	-	-	-	-	-	-	0
Trichomanes kapplerianum		6	1	-	-	-	-	7	-	-	-	-	-	-	0
Trichomanes krausii		-	-	1	3	4	3	11	-	1	1	1	-	-	3
Trichomanes pinnatinervium		-	-	-	2	1	1	4	1	1	-	-	-	-	2
Trichomanes punctatum subsp. *labiatum*		6	6	3	6	2	2	25	1	1	-	-	-	-	2
Hymenophyllaceae total		18	13	8	16	15	6	77	2	4	1	1	-	-	8

were only found up to the inner tree crown (zones 1-4). The trunk base (zone 1) was inhabited by two species (*T. pinnatinervium* and *T. punctatum* subsp. *labiatum*), the lower trunk (zone 2) by four species (*T. angustifrons*, *T. krausii*, *T. pinnatinervium*, *T. punctatum* subsp. *labiatum*) and the upper trunk and

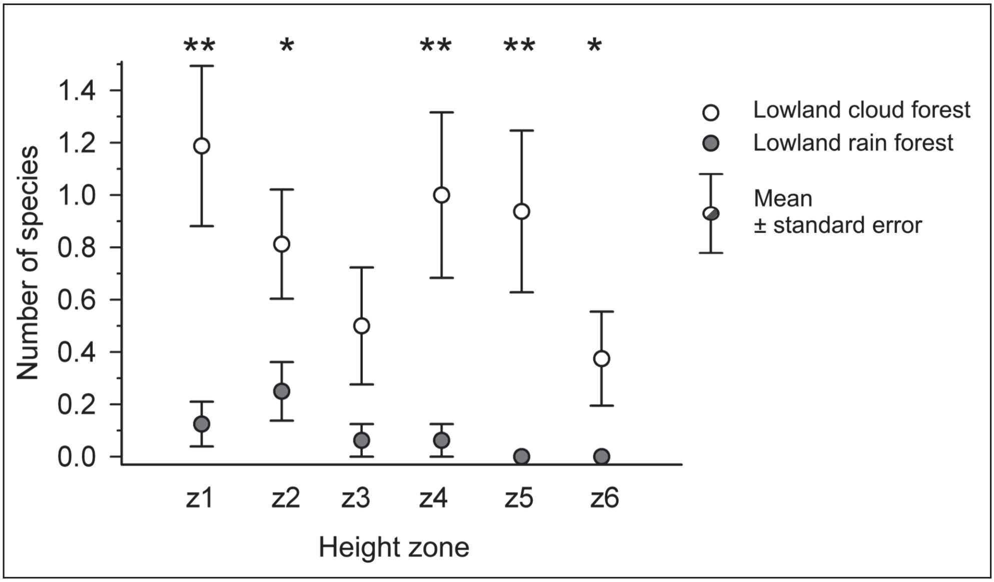

FIG. 1. Number of epiphytic Hymenophyllaceae species per height zone in lowland cloud forest and lowland rain forest; n = 16 trees per forest type. Asterisks indicate level of probability calculated with unpaired t-test (* $p<0.05$, ** $p<0.01$). z1 = trunk base, z2 = lower trunk, z3 = upper trunk, z4 = lower canopy, z5 = middle canopy, z6 = outer canopy.

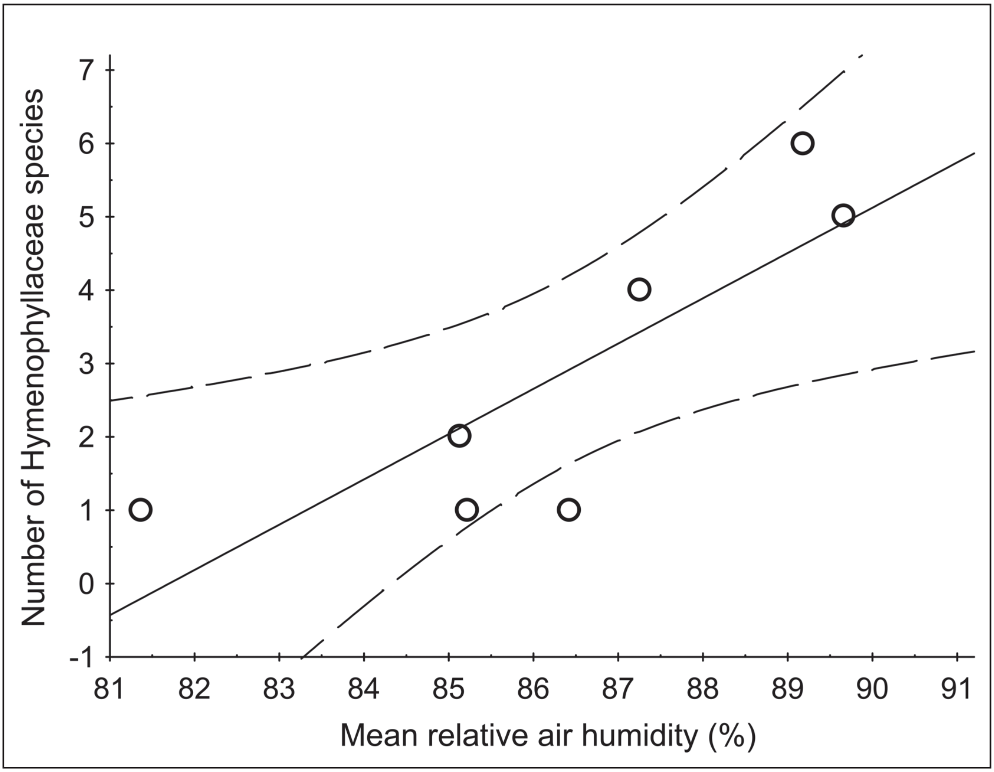

FIG. 2. Correlation between number of Hymenophyllaceae species per tree and mean diurnal relative air humidity for 60 days of the dry season in the canopy of 7 trees in lowland cloud forest. Unbroken line indicates the regression, dotted line the 0.95 confidence interval. R = 0.82, P<0.05.

inner crown (zones 3 and 4) only by *T. krausii*. In contrast, in LCF filmy ferns were present in all height zones, and number of species per height zone was higher and more constant (3-8 species). Within-tree distributions of the species differed, however, some species being restricted to the trunk base (e.g. *T. kaplerianum*), others being crown-centred (e.g. *T. polyanthos*) or occurring evenly throughout the tree (e.g. *T. punctatum*).

Canopy microclimate. During 60 days in the dry season the diurnal mean relative humidity (RH) was positively correlated with species diversity of filmy ferns (Fig. 2; r^2 = 0.81, P<0.001). Estimated mean daily evaporation was highest in the outer canopy in LRF, while smallest values were related to the inner crown in LCF (Fig. 3). Global radiation was clearly reduced in the canopy of LCF as compared with LRF. Interestingly, the diurnal course of global radiation showed a strong decrease in the early afternoon in LCF, coinciding with a sharp increase in relative humidity. At the LRF site, this transition is delayed for some hours. The inner crown zones showed a similar diurnal course of global radiation at both LCF and LRF sites (Fig. 4). Average daily wind speed was 0.65 m s^{-1} in LRF and 0.17 m s^{-1} in LCF.

DISCUSSION

Because they lack a well-developed cuticle and stomata, Hymenophyllaceae are sensitive to water loss and so are dependent on moist habitats (Proctor 2003). Since humidity is a key driver of filmy fern diversity, Hymenophyllaceae are considered good indicators of high atmospheric humidity (Hietz & Hietz-Seifert 1995). With 9 species of filmy ferns recorded on 16 trees in LCF, the lowland cloud forests

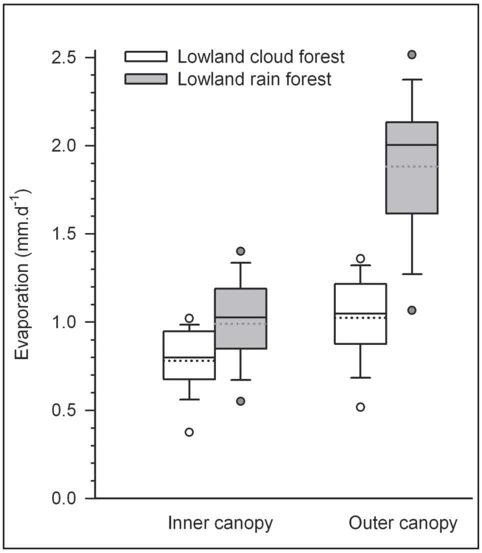

FIG. 3. Evaporation per day in the inner and outer canopy of lowland cloud forest and lowland rain forest, calculated using a simplified version of the Penman equation provided by Valiantzas (2006), incorporating daily global radiation, relative humidity, air temperature and the latitude of the site. Boxes indicate upper and lower quartile of data, unbroken line indicates the median, dotted line the mean, whiskers 5th/95th percentile, and circles mark outliers.

of central French Guiana are a rich habitat for Hymenophyllaceae. In comparison, only a single species was found on 25 trees in LRF of Guyana (ter Steege & Cornelissen 1989) and in 1.5 ha of LRF in Venezuela (Nieder *et al.* 2000). In Amazonian Brazil only 3 species were found on 10 trees (Pos & Sleegers 2010). These data agree with our findings, even though the number recorded in LRF of French Guiana was higher. The highest species number hitherto recorded in moist lowland forest is from Amazonian Ecuador, where an inventory of about 650 ha of forest yielded 12 species of filmy ferns (Kreft *et al.* 2004), or only a few more than recorded for LCF in this study.

Not only the total number of species but also their number per height zone was higher in LCF than in LRF (Fig. 1). The scarce occurrence of Hymenophyllaceae in LRF agrees with the observations of Zotz & Büche (2000), Köster (2002), and Pérez Peña & Krömer (2011), who found that filmy ferns were primarily restricted to the lower strata of LRF. By contrast, in LCF filmy ferns frequently occur in the forest canopy, even in the outer periphery of tree crowns (Table 1).

Within the tropical rain forest, air temperature, light availability, and wind speed generally increase with tree height while air moisture and nutrient availability decrease (Johansson 1974, Meinzer & Goldstein 1996, Parra *et al.* 2009). The sharp decrease of filmy fern diversity towards the canopy in LRF can readily be explained by the vertical changes of the microclimate in this forest type. The high frequency of filmy ferns in LCF crowns, on the other hand, is suggestive of the moister microclimate in this forest type and the availability of surplus water in the canopy attributable to fog events (Obregón *et al.* 2011). Further, radiation protection against evaporative loss seems to play a crucial role in the vertical distribution of filmy fern diversity. The

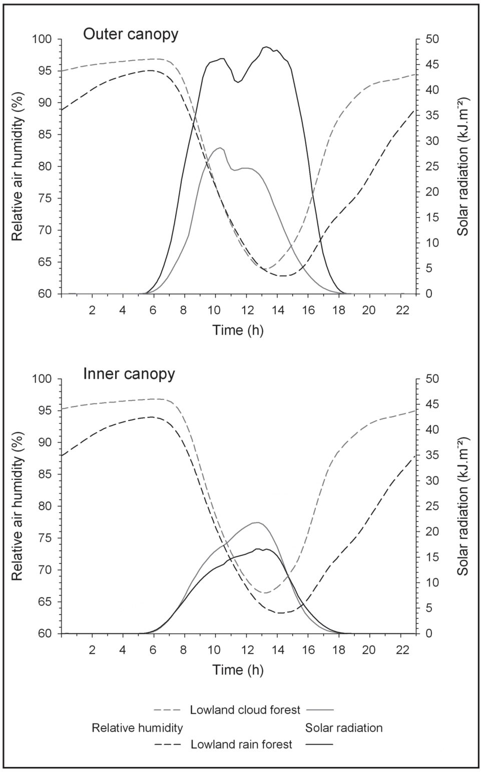

FIG. 4. Mean diurnal course of global radiation and relative humidity in lowland cloud forest and lowland rain forest in the inner and outer canopy during 22 September – 24 October 2007.

relative maximum of diversity in the inner crown (zone 4) in LCF coincides with low values of daily evaporation, which is clearly reduced compared with the canopy. In LCF, epiphytes also benefit from throughfall in the inner crown (zone 4) and in particular from fog events in the outer canopy (zone 6). However, because the highest values of global radiation and hence evaporative loss are in the outer canopy, the inner crown seems to be the most favorable region for filmy ferns in the upper forest stratum (see also Krömer & Kessler 2006). This pattern is also well reflected in the abundance of some filmy fern species. For the lower stratum, the high diversity of filmy ferns in the trunk zone (z1) in LCF may be explained by both radiation protection and high soil moisture. Microclimatic conditions on the hill sites (LRF) are generally less suitable for epiphytes due to higher wind speed, higher evaporation caused by more open canopies, and the lack of fog events. The strong correlation between mean diurnal RH and number of Hymenophyllaceae species per tree reveals the dependence of filmy ferns on humidity (Fig. 2).

Interestingly, we found that species restricted to trunks in the understory of LRF occurred in the canopy of LCF (Table 1; Fig. 5). Shifts in vertical distribution between climatically different habitats have also been observed in epiphytic bryophytes by Acebey *et al.* (2003). Moreover, a similar upward shift in distribution in LCF has been observed in epiphytic macrolichens (Normann *et al.* 2010). The latter study also found that lichens with cyanobacteria as photobionts ("cyanolichens") are sensitive indicators of LCF. Based on our observations, we suggest that species with upwards-shifting distributions (*Trichomanes krausii*, *T. pinnatinervium*, *T.punctatum* subsp. *labiatum*) as well as those exclusive to LCF (*Hymenophyllum decurrens*, *H. hirsutum*, *H. polyanthos*, *T. diaphanum*, *T. kapplerianum*) may be used as indicators of LCF. Furthermore, the upward shift of *T. krausii* and *T. punctatum* is remarkable, as Krömer & Kessler (2006) have classified both species as trunk epiphytes. *Trichomanes kapplerianum* seems to be the best indicator species of LCF based on our study. The species is readily recognized by its simple fronds with glabrous margins and uniformly-colored involucres, and can be easily collected due to its occurrence on tree bases.

LCF and LRF are two different types of tropical lowland forest that were traditionally viewed as a single formation (Gehrig-Downie *et al.* 2011). Discrimination of the two forest types had long been overlooked by the absence of traditional traits separating them, such as differences in tree composition. We present evidence indicating that the presence of morning fog in forest valleys favors the establishment of hygrophilous epiphytes such as filmy ferns. The observed high diversity of filmy ferns in the canopy of LCF and their occurrence in the outer crowns of the trees correlates with the presence of a surplus of liquid water resulting from episodes of fog. The scarcity of Hymenophyllaceae in LRF, in contrast, reflects the drier microclimate in this forest type. The observed differences in filmy fern diversity and verti-

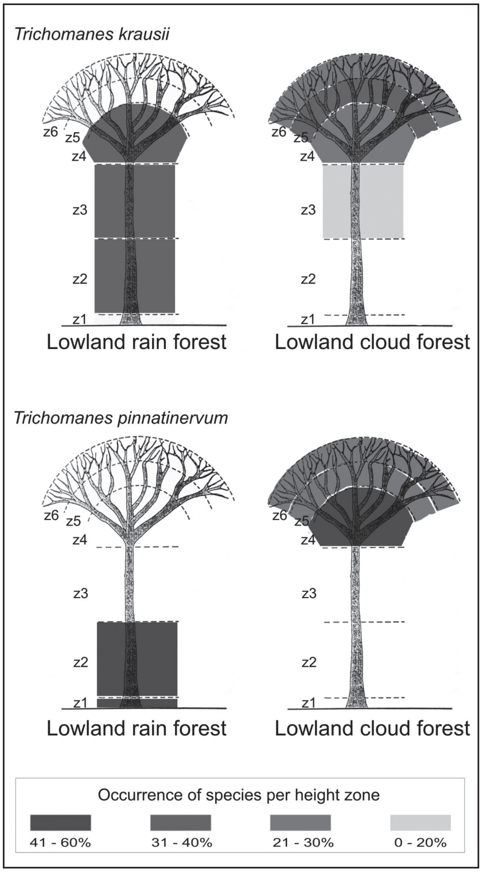

FIG. 5. Vertical distribution of two Hymenophyllaceae species in lowland rain forest and lowland cloud forest, expressed by percent occurrence per zone as compared with occurrence on whole trees. z2 = lower trunk, z3 = upper trunk, z4 = lower canopy, z5 = middle canopy, z6 = outer canopy.

cal distribution in LCF and LRF represent novel traits separating the two forest types and indicate that Hymenophyllaceae are sensitive indicators of lowland cloud forest. Further studies in other sites should verify our observations, and should further explore the usefulness of filmy fern species as indicators of LCF.

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