Phylogenetic Composition of Angiosperm Diversity in the Cloud Forests of Mexico

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ABSTRACT

Several members of the most ancient living lineages of flowering plants (angiosperms) inhabit humid, woody, mostly tropical habitats. Here we assess whether one of these forest types, the cloud forests of Mexico (CFM), contain a relatively higher proportion of phylogenetically early-diverging angiosperm lineages. The CFM houses an extraordinary plant species diversity, including members of earliest-diverging angiosperm lineages. The phylogenetic composition of CFM angiosperm diversity was evaluated through the relative representation of orders and families with respect to the global flora, and the predominance of phylogenetically early- or late-diverging lineages. Goodness-of-fit tests indicated significant differences in the proportional local and global representation of angiosperm clades. The net difference between the percentage represented by each order and family in the CFM and the global flora allowed identification of clades that are overrepresented and underrepresented in the CFM. Early-diverging angiosperm orders and families were found to be neither over- nor underrepresented in the CFM. A slight predominance of late-diverging phylogenetic levels among overrepresented clades, however, was encountered in the CFM. The resulting pattern suggests that cloud forests provide habitats where the most ancient angiosperm lineages have survived in the face of accumulating species diversity belonging to phylogenetically late-diverging lineages.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp

Key words: angiosperm phylogeny; biodiversity; *G*-test; Mesoamerica; neotropics; phylogenetic level; tropical wet forest.

PLANT DIVERSITY IS DISTRIBUTED UNEQUALLY in different geographical regions, especially along latitudinal and altitudinal gradients (Wiens & Donoghue 2004). Particular biomes have been recognized as biodiversity hotspots given the number of endemic species they harbor, and the degree of threat to their continued existence (Myers *et al*. 2000). Most plant groups are differentially diverse through geographical and ecological landscapes, often showing well-defined environmental preferences (Donoghue 2008). For example, whereas cacti, agaves, and Crassulaceae are frequent in arid biomes, palms, bromeliads, and orchids are more diverse in humid biomes. These examples very likely represent cases in which particular lineages adapted to specific environmental conditions, and subsequently diversified in habitats bearing such conditions. Some of the most ancient lineages of living angiosperms, namely Amborellales, Austrobaileyales, and Chloranthales, tend to inhabit moist, woody, mostly tropical habitats (Judd *et al*. 2002). These environments may represent the original habitats, or may have served as shelters for ancient angiosperm lineages (Feild *et al*. 2004). Wet tropical forests have been considered strongholds of ancestral angiosperms (Feild *et al*. 2004, Soltis *et al*. 2005). These observations raise the question of whether members of the most ancient living lineages, corresponding to the earliest-diverging branches in the angiosperm phylogeny, are significantly more diverse in wet tropical forests.

Substantial progress toward a comprehensive resolution of the relationships among early-diverging lineages and the relationships among angiosperms in general has been achieved (Qiu *et al*. 1999, Soltis *et al*. 1999). Relationships are much better understood at all levels, and there have been recent advances toward the resolution of lingering phylogenetic conflicts (Jansen *et al*. 2007, Moore *et al*. 2007, Burleigh *et al*. 2009, Wang *et al*. 2009). The availability of reliable phylogenetic data, combined with recent methodological advances (*e.g*., relaxed molecular clocks; supertrees) and theoretical models (*e.g*., the unified neutral theory of biodiversity and biogeography; the niche conservatism hypothesis), provide a strong basis for a better understanding of the origin and maintenance of organismal diversity.

Recent studies have investigated some of the evolutionary causes underlying species diversity, composition and structure across communities, biomes, and geographical regions (reviewed by Pennington *et al*. 2006). These include, for example, mechanisms of species generation and diversity (Richardson *et al*. 2001, Fine *et al*. 2005, Goldberg *et al*. 2005, Heard & Cox 2007), geographic and community phylogenetic structure (Webb 2000, Webb *et al*. 2002, Lavin *et al*. 2004, Vamosi *et al*. 2009), and measures of biodiversity for conservation priorities (Faith 1992, Forest *et al*. 2007, Helmus *et al*. 2007). Several relevant studies have investigated the underlying causes and dynamics of clade distribution in disjunct geographical regions (Renner *et al*. 2001, Renner 2004, Lavin *et al*. 2005), or along latitudinal diversity gradients (Hawkins

et al. 2006, Wiens *et al.* 2006, Diniz-Filho *et al.* 2007, Wiens 2007). A complementary component of this research area is the identification of the most influential factors that determine the differential diversity of biological lineages in a particular biome.

In this study, we evaluate the phylogenetic composition of angiosperm species diversity in the cloud forests of Mexico (CFM) by evaluating the relative abundance of angiosperm clades with respect to the global flora. This study provides fundamental information for a better understanding of the main causes of differential lineage diversity and mode of species accumulation. Cloud forests and lowland tropical rain forests house members of the earliest-diverging living angiosperm lineages that occur in Mexico, *i.e.*, Nymphaeales, Austrobaileyales, and Chloranthales. The CFM represents a system within which to assess whether a tropical wet forest contains a relatively higher proportion of early-diverging angiosperm lineages with respect to the global flora. In addition, it allows us to better understand the evolutionary processes underlying the origin and maintenance of plant diversity in a Mesoamerican diversity hotspot (Myers *et al.* 2000).

The CFM represent the northernmost extension of cloud forests in the New World. They occur in environments that combine high relative humidity (mainly 1500–3000 mm), irregular topography, deep litter layer, altitudinal range of 600–3200 m asl, and mild to cool temperatures (Af, Am, Aw, Cw; Rzedowski 1978, Velázquez *et al.* 2000). Cloud forests represent widely scattered patches that are distributed through mountain slopes, gorges, and ravines (Fig. 1). This vegetation is best developed at 1000–1750 m asl (Luna *et al.* 1988). As a result of centuries of intensive logging, the CFM are severely endangered, currently covering < 1 percent of the Mexican territory

(Luna *et al.* 2001). The areas they formerly occupied have been transformed into agricultural lands, coffee plantations, or pastures.

The CFM consist of a dense association of trees 15–30 m tall, although some species can reach 40–60 m (*e.g.*, representatives of *Engelhardtia*, *Fagus*, *Platanus*, and *Ulmus*). The CFM consists of a multistratified canopy where the uppermost layer is formed by deciduous taxa, and understories are formed by evergreens. There are also shrub and herbaceous layers that tend to be poorly developed whenever the arboreal community is undisturbed. Epiphytes and vines are abundant. The structural complexity of cloud forests decreases gradually as altitude increases, and varies from slope to slope. It has been suggested that their floristic composition evolved through the integration of elements from the ancient Boreotropical flora (Wolfe 1975), from Central and South America, and elements that originated *in situ* (Rzedowski 1996). Cloud forests are among the most species-rich biomes in the territory of Mexico (Rzedowski 1991). They contain at least 2500 vascular plant species, and are estimated to include 10–12 percent of the total plant species diversity of the whole country (Rzedowski 1996).

Here we evaluate the phylogenetic composition of angiosperm species diversity in the CFM. Specifically, we (1) test for significant differences between the relative richness of angiosperm orders, families and phylogenetic levels in the CFM and their relative richness in the global flora; (2) identify strongly overrepresented and underrepresented orders and families in the CFM with respect to their relative abundance in the global flora; and (3) evaluate if over- and underrepresented orders and families in the CFM predominantly belong to early-diverging or to late-diverging angiosperm lineages.
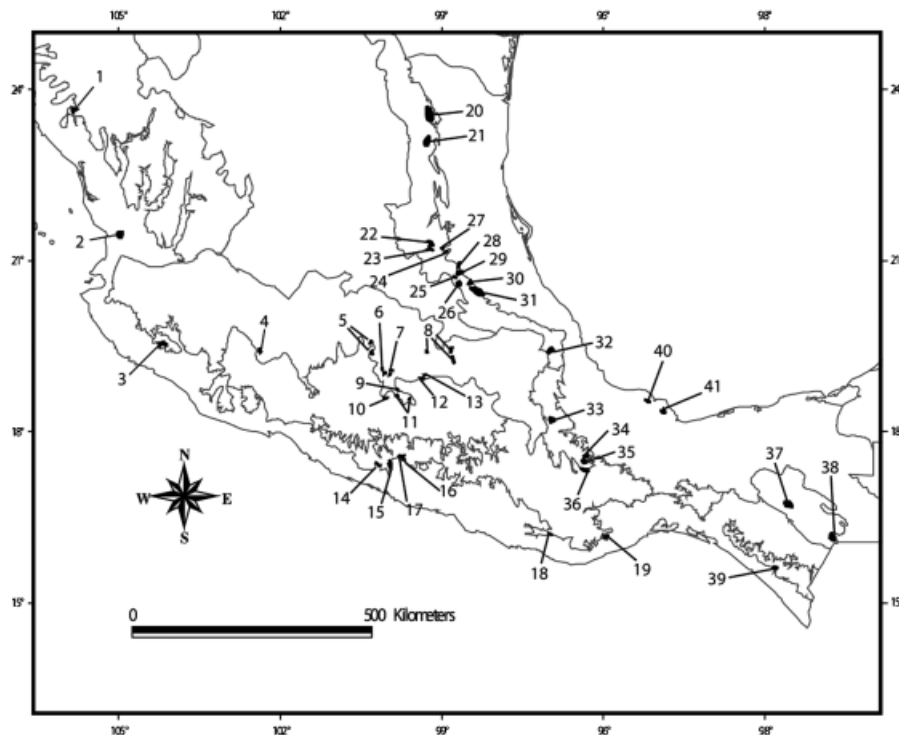

FIGURE 1. Distribution of cloud forests in Mexico. Numbers correspond to localities in Table S3.

METHODS

ANGIOSPERM ORDER-LEVEL AND FAMILY-LEVEL CLADES.—The definition of main angiosperm lineages, and the relationships among them, has led to the proposition of a classification system that reflects evolutionary relationships (APG 1998, APG II 2003). Angiosperm order-level and family-level clades were obtained from the Angiosperm Phylogeny Website (APW; Stevens 2009), complemented with results from recently published phylogenetic analyses (Wang *et al.* 2009). The APG system is explicitly based on phylogenetic trees, hence, APG-defined orders and families are monophyletic entities. Nevertheless, delimitation of taxa in a phylogenetic tree, *i.e.*, which node is chosen as the limit of a taxon, is arbitrary. The APW relies strongly on the APG system, integrates phylogenetic results from independent studies, and is continuously updated. No tree derived from a single phylogenetic analysis yet provides the level of supported resolution found in the independent studies amalgamated in the APW tree. We obtained estimates of the number of species in each order and family from the APW, and used them to (1) identify clades with the greatest species richness within angiosperms and (2) identify the relative percentage of each clade in the global flora.

DELIMITATION AND SPECIES COMPOSITION OF THE MEXICAN CLOUD FORESTS.—The geographic location of cloud forest patches was derived from a revision of published floristic and ecological literature, and mapped in ArcView 3.2 (ESRI 1999; Fig. 1). Additional small and isolated cloud forest patches have been informally reported for different areas in Mexico (*e.g.*, areas within the state of Oaxaca and isolated ravines of the Sierra Madre Occidental). Because no published information about their location or species content is available, they were not included in this study.

The CFM angiosperm species list was obtained through a comprehensive compilation from published floristic literature, and databases from the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO 2007). This list was then revised by taxonomists (see Acknowledgments), who excluded redundant or incorrect reports, and included missing species. Finally, portions of the species list were verified against monographs and herbarium collections. The complete list of sources and species are available in http://www.fciencias.unam.mx/academicos/ilv/index.html.

Each angiosperm species from the CFM was assigned to its family and order according to the APW (Stevens 2009). The total number of species, the number of species in each family and the number of species in each order was then recorded for the CFM. In addition, the relative representation of each family and order with respect to the total number of angiosperm species in the CFM were obtained (Tables S1 and S2).

ANGIOSPERM PHYLOGENETIC LEVELS.—Phylogenetic levels are here defined as the number of nodes (phylogenetic branching events) separating the crown node (*i.e.*, the most recent common ancestor of all living species) of each angiosperm order, from the crown node of the angiosperms, in an order-level tree (*sensu* APW; Fig. 2). All species belonging to an order of phylogenetic level x are assigned to phylogenetic level x, although in reality, each species (except for
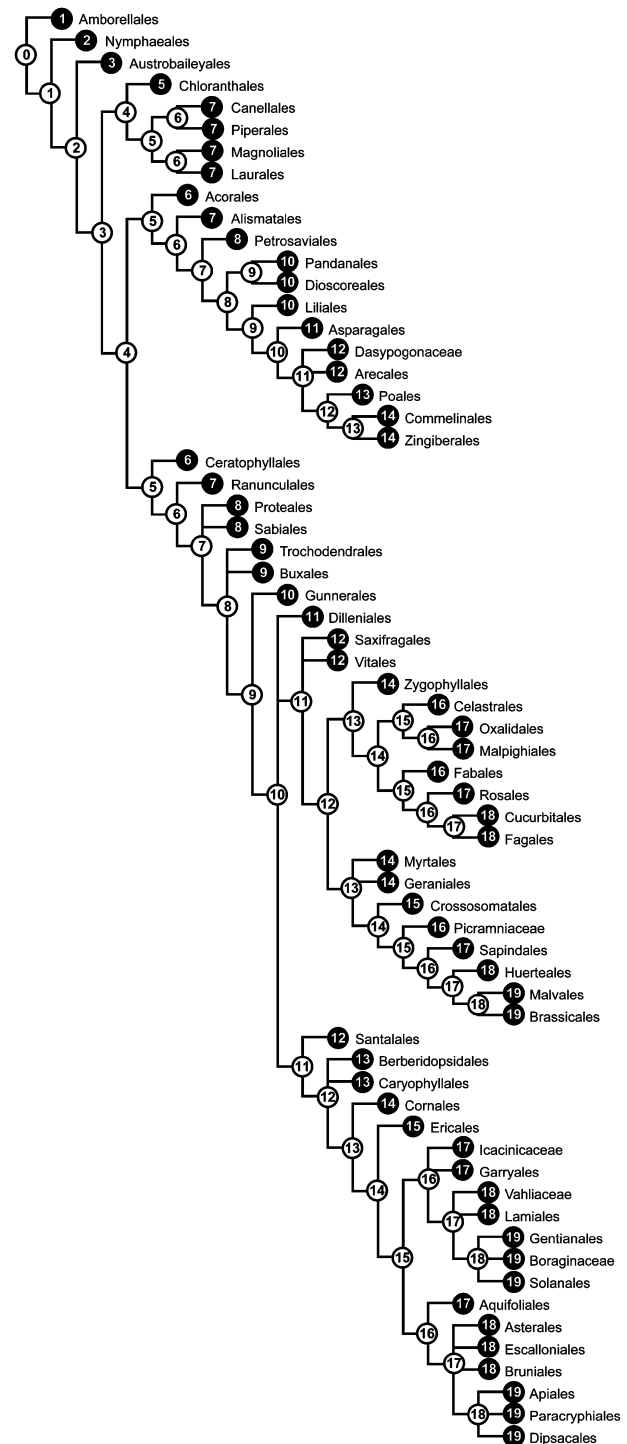

FIGURE 2. Angiosperm phylogenetic levels. Phylogenetic levels were determined by the number of nodes separating the crown node of each order (numbers inside solid circles), from the crown node of angiosperms in an order-level phylogenetic tree (Stevens 2009). Polytomies are considered to result from rapid radiations, and emanating branches are considered to belong to the same phylogenetic level.

members of monotypic orders) is separated by a number of nodes greater than x from the angiosperm crown node. Orders that belong to the same phylogenetic level are equivalent only because they share

the number of nodes separating their crown node from the angiosperm crown node. Because of the nature of the phylogenetic structure, a lower (deeper) phylogenetic level is older than a higher (shallower) nested phylogenetic level (Fig. 2). However, orders that belong to a particular phylogenetic level need not be of the same absolute age (unless a strict molecular clock is in place). Because a phylogenetic level includes orders that may or may not be each others' closest relatives, phylogenetic levels are not necessarily monophyletic. We selected orders to determine phylogenetic levels because the angiosperm phylogenetic tree is acceptably resolved at the order level. We emphasize, however, that because angiosperm orders are arbitrarily delimited clades, phylogenetic levels lack biological reality.

Phylogenetic levels are a type of class ultimately based on node distance to the angiosperm crown node that allow direct comparisons between the CFM and the global flora. Although node distance between an order and the angiosperm crown node provides a quantification that is meaningful only among orders in the same tree, it allows an assessment of their relative phylogenetic position. Specifically, it allows us to determine whether a given clade diversified after few or many phylogenetic branching events since the onset of diversification of the whole group. Recent studies (Prinzing *et al.* 2004, Hawkins *et al.* 2006), have also relied on node distance to the root of the tree to assess 'phylogenetic degree.'

Complications for determining phylogenetic level arise if the phylogenetic tree is incompletely resolved. In spite of substantial advancement resolving angiosperm relations (Jansen *et al.* 2007, Moore *et al.* 2007, Burleigh *et al.* 2009, Wang *et al.* 2009), some portions of the angiosperm tree still remain unresolved. Families of yet unidentified phylogenetic position were retained as isolated clades, and introduced as a polytomy at the root node of the least inclusive clade to which they can be reliably assigned. We considered unresolved portions of the angiosperm order-level tree as resulting from ancient, rapid radiations (*i.e.*, hard polytomies). Hence, lineages involved in polytomies are here considered to belong to the same phylogenetic level. We obtained the order and family content, as well as the total number of species, in each phylogenetic level. The percentage that each phylogenetic level represents in the global flora and in the CFM was quantified.

DIFFERENCES BETWEEN MEXICAN CLOUD FORESTS AND THE GLOBAL FLORA.—The significance of differences between the relative representation of orders, families and phylogenetic levels in the CFM and in the global flora were evaluated with *G*-tests of goodness-of-fit (Sokal & Rohlf 1994)

$$G = 2 \sum f_i \ln \frac{f_{i\text{obs}}}{f_{i\text{exp}}}.$$

The *G* statistic was divided by a correction factor *q* to avoid inflation of Type I error (Williams 1976, in Sokal & Rohlf 1994)

$$q = 1 + \frac{a^2 - 1}{6n(a - 1)}.$$

We conducted tests to evaluate the following null hypotheses:
(1) $H_{0[1]}$: The representation of angiosperm orders in the CFM is proportional to their representation in the world flora.

(2) $H_{0[2]}$: The representation of angiosperm families in the CFM is proportional to their representation in the world flora.
(3) $H_{0[3]}$: The representation of angiosperm phylogenetic levels in the CFM is proportional to their representation in the world flora.

In these tests, classes (*a*) correspond to orders, families and phylogenetic levels, respectively. Sample size (*n*) corresponds to the total number of species in the CFM. Observed frequencies (f_{obs}) are the number of species in each class, and expected frequencies (f_{exp}) are the proportional number of species in the world flora in each class, given a sample of size *n*. Classes with $f_{\text{obs}} = 0$ were excluded and classes with $f_{\text{exp}} \leq 3$ were pooled together (Sokal & Rohlf 1994). Each test statistic *G/q* was compared with single-tailed $\chi^2_{0.05[\text{df} = a - 1]}$ critical values. Although these tests are non-independent, it is appropriate to conduct all three, because we here ascribe importance not on how many of the tests are significant, but on which are.

Overrepresented and underrepresented clades were identified by calculating the difference between the percentage each clade represents in the CFM and in the global flora:

percent represented by clade in CFM−percent represented by clade in global flora.

We considered positive or negative differences to indicate, respectively, a proportionally higher or lower representation in the CFM than in the global flora. The obtained differences were sorted in descending order, to identify the clades with greatest overrepresentation (most extreme positive difference) and greatest underrepresentation (most extreme negative difference) in the CFM. The phylogenetic levels to which the most strongly over- and underrepresented clades belong were identified, to evaluate if each of these categories preferentially corresponds to early-diverging or late-diverging angiosperm lineages.

RESULTS

ANGIOSPERM ORDERS AND FAMILIES.—According to the APW (Stevens 2009), there are *ca* 269,902 living angiosperm species in 13,483 genera, 452 families, and 65 orders. Order- and family-level clades belong to eight major lineages with substantially different species diversity: Amborellales (1 order, 1 family, 1 spp.), Nymphaeales (1 order, 3 families, 74 spp.), Austrobaileyales (1 order, 3 families, 100 spp.), Chloranthales (1 order, 1 family, 75 spp.), Magnoliids (4 orders, 19 families, 9998 spp.), Monocots (12 orders, 92 families, 61,582 spp.), Ceratophyllales (1 order, 1 family, 6 spp.), and Eudicots (or Tricolpates; 44 orders, 332 families, 198,006 spp.). The most speciose orders and families in the world are listed in Tables 1 and 2. As for other biological lineages, sorting angiosperm orders and families in descending order by their world species richness resulted in hollow curves (geometric distributions, *e.g.*, Dial & Marzluff 1989; Figs. 3A and B).

SPECIES DIVERSITY IN THE MEXICAN CLOUD FORESTS.—The revision of angiosperm diversity in the CFM resulted in an estimate of 3785 species belonging to 1066 genera, 182 families, and 52 orders (Tables S1 and S2). Six major angiosperm lineages are represented: Nymphaeales (1 order, 1 family, 1 spp.), Austrobaileyales (1 order,

TABLE 1. *Fifteen most species-rich orders in the world, and in the cloud forests of Mexico (CFM). The absolute number of species in each order and the percentage represented in the global flora and in the CFM are indicated.*

Order	No. spp. global	% spp. global	Order	No. spp. CFM	% spp. CFM
Asparagales	29,275	10.9	Asterales	433	11.4
Asterales	26,869	9.96	Asparagales	354	9.35
Lamiales	23,613	8.75	Lamiales	322	8.51
Fabales	20,351	7.54	Poales	293	7.74
Poales	18,343	6.80	Fabales	270	7.13
Gentianales	17,791	6.59	Gentianales	233	6.16
Malpighiales	16,061	5.95	Malpighiales	195	5.15
Ericales	11,824	4.38	Solanales	185	4.89
Myrtales	11,632	4.31	Myrtales	164	4.33
Caryophyllales	11,387	4.22	Ericales	152	4.02
Rosales	7423	2.75	Rosales	122	3.22
Malvales	6093	2.26	Piperales	104	2.75
Apiales	5469	2.03	Caryophyllales	86	2.27
Sapindales	5288	1.96	Malvales	76	2.01
Brassicales	4753	1.76	Fagales	73	1.93

TABLE 2. *Twenty-five most species-rich families in the world, and in the cloud forests of Mexico (CFM). The absolute number of species in each family and the percentage represented in the global flora and in the CFM are indicated.*

Family	No. spp. global	% spp. global	Family	No. spp. CFM	% spp. CFM
Asteraceae	23,600	8.74	Asteraceae	405	10.7
Orchidaceae	21,950	8.13	Orchidaceae	296	7.82
Fabaceae	19,400	7.19	Fabaceae	255	6.74
Rubiaceae	11,150	4.13	Rubiaceae	163	4.31
Poaceae	10,035	3.72	Poaceae	155	4.10
Lamiaceae	7173	2.66	Solanaceae	147	3.88
Euphorbiaceae	5735	2.12	Lamiaceae	117	3.09
Myrtaceae	4620	1.71	Piperaceae	103	2.72
Melastomataceae	4570	1.69	Euphorbiaceae	86	2.27
Apocynaceae	4555	1.69	Bromeliaceae	69	1.82
Cyperaceae	4350	1.61	Melastomataceae	68	1.80
Malvaceae	4225	1.57	Malvaceae	64	1.69
Araceae	4025	1.49	Cyperaceae	59	1.56
Acanthaceae	4000	1.48	Fagaceae	54	1.43
Ericaceae	3995	1.48	Apocynaceae	54	1.43
Apiaceae	3780	1.40	Apiaceae	51	1.35
Brassicaceae	3710	1.37	Rosaceae	50	1.32
Piperaceae	3615	1.34	Lauraceae	43	1.14
Gesneriaceae	3200	1.19	Myrsinaceae	40	1.06
Boraginaceae	2740	1.01	Plantaginaceae	39	1.03
Urticaceae	2625	0.97	Acanthaceae	39	1.03
Ranunculaceae	2525	0.94	Convolvulaceae	38	1.00
Rosaceae	2520	0.93	Commelinaceae	37	0.98
Lauraceae	2500	0.93	Begoniaceae	35	0.92
Amaranthaceae	2500	0.93	Onagraceae	34	0.90

1 family, 2 spp.), Chloranthales (1 order, 1 family, 1 spp.), Magnoliids (4 orders, 10 families, 172 spp.), Monocots (9 orders, 33 families, 808 spp.), and Eudicots (36 orders, 136 families, 2801 spp.). Amborellales and Ceratophyllales are not represented. The most speciose orders and families in the CFM are nearly the same as in world flora, and are listed in Tables 1 and 2. The distribution of orders and families arranged descendingly by their species richness in the CFM also resulted in hollow curves (Figs. 3C and D).

ANGIOSPERM PHYLOGENETIC LEVELS.—The number of nodes between the crown node of orders and the crown node of angiosperms resulted in 19 phylogenetic levels (Fig. 2). The proportional diversity represented by each phylogenetic level in the CFM and in the global flora is very similar (Fig. 4). The most species-rich phylogenetic levels, and the percentage of the total world and CFM diversity each represents, respectively, are 18 (20.0%, 23.4%), 19 (15.6%, 16.9%), 17 (11.6%, 11.0%), 13 (11.0%, 10.0%), and 11 (10.9%, 9.4%). Together, these phylogenetic levels encompass 69.1 and 70.7 percent of species diversity in the global flora and in the CFM, respectively. Phylogenetic levels 18 and 19 contain a slightly higher proportion of the diversity in the CFM than in global flora (Fig. 4).

DIFFERENCES BETWEEN MEXICAN CLOUD FOREST AND THE GLOBAL FLORA.—The three goodness-of-fit tests to evaluate proportional representation of angiosperm classes in the CFM and the global flora obtained G/q-tests statistics much larger than the critical value of the corresponding χ^2 distribution (Table 3). Therefore, the null hypotheses of no significant differences between the proportional representation of orders ($H_{0[1]}$), families ($H_{0[2]}$), and phylogenetic levels ($H_{0[3]}$) in the CFM and in the global flora were rejected.

Overrepresented clades include a slightly higher representation of high phylogenetic levels, for example, Solanales, Asterales, and Fagales, but also include clades of intermediate and low phylogenetic levels, such as Laurales and Piperales (Table 4; Fig. 5A). Underrepresented clades include members of high (*e.g.*, Brassicales, Gentianales), intermediate (*e.g.*, Caryophyllales, Orchidaceae), and low (*e.g.*, Magnoliales, Araceae) phylogenetic levels (Table 5; Fig. 5B).

The net differences between the percentage represented by the early-diverging angiosperm clades in the CFM and in the global flora are, in all cases, close to zero. The differences for Nymphaeales, Austrobaileyales, and Chloranthales are −0.0011, 0.0157, and −0.0014, respectively, and the differences for Nymphaeaceae, Illiciaceae, and Chloranthaceae are 0.0035, 0.0165, and −0.0032.

DISCUSSION

There is general congruence between the most speciose orders and families in the CFM and the global flora. Nevertheless, some clades
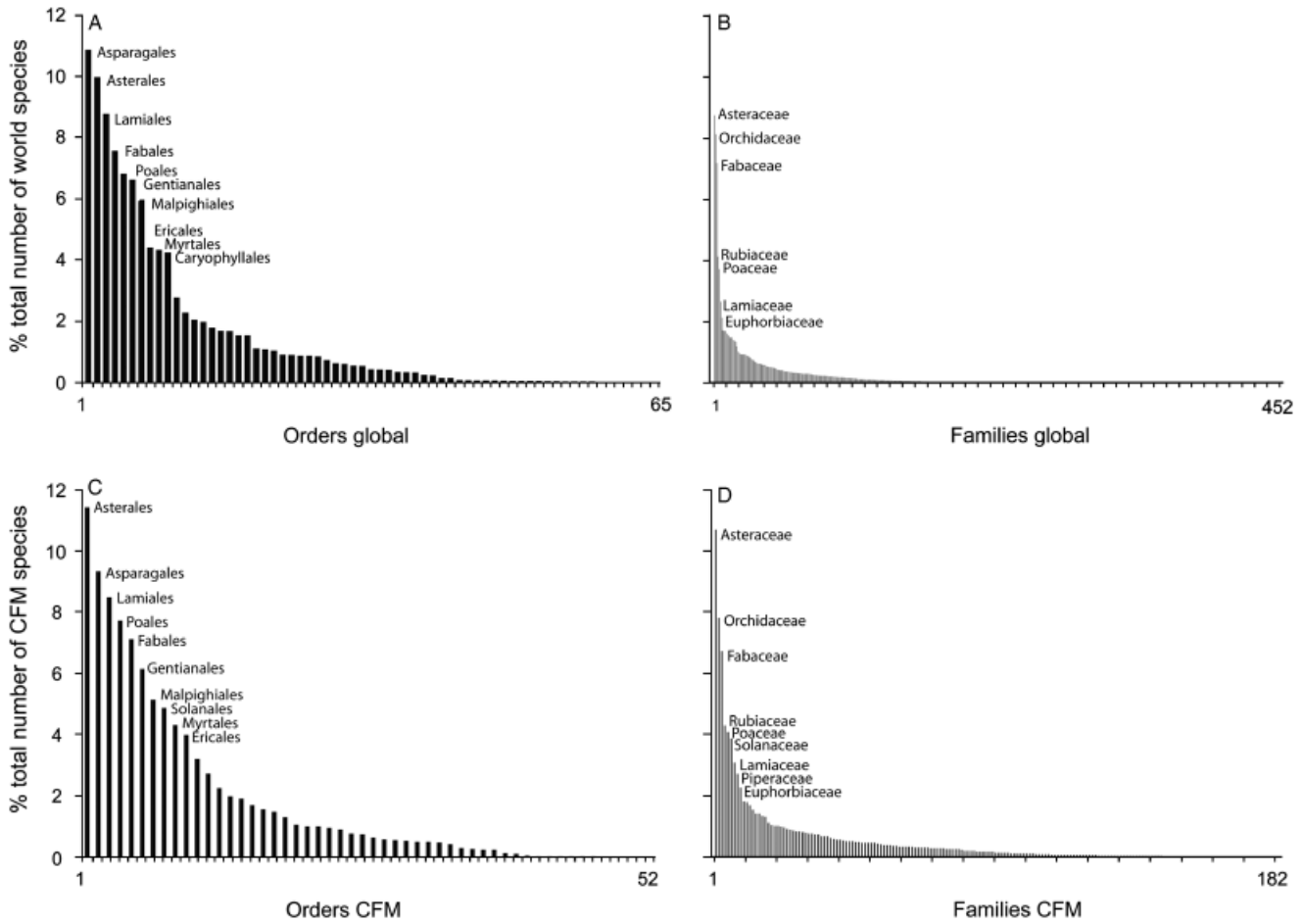
FIGURE 3. Frequency distribution of orders and families sorted by their proportional species richness in the global flora and in the cloud forests of Mexico (CFM). (A) Orders in the global flora, listing orders with highest absolute diversity. (B) Families in the global flora, listing families with highest absolute diversity. (C) Orders in the CFM, listing orders with highest absolute diversity. (D) Families in the CFM, listing families with highest absolute diversity. The four graphs represent hollow curves.

that are speciose in the CFM, for example Fagales, Solanaceae, Bromeliaceae, Myrsinaceae, and Begoniaceae, do not figure among the most speciose worldwide (Tables 1 and 2). It is noteworthy that Fagales, occupying the 35th place in absolute richness in the world, is much more prominent in the CFM, where it occupies the 15th place in absolute richness (Table 1). Similarly, Solanaceae is the 26th richest family in the world, but the 6th in the CFM; and Bromeliaceae is the 46th richest in the world, but 10th in the CFM.

Statistical tests of the proportional representation of angiosperm clades in the CFM and in the global flora indicated significant differences. In the three goodness-of-fit tests, the difference between the G/q statistic and the critical χ^2 value was extremely large (Table 3). Hence, adjustments in the number of species in the global flora and in the CFM are unlikely to revert the significance of differences.

Several clades strongly overrepresented in the CFM are among the richest locally. For example, Asterales, Poales, and Solanales are the first, fourth, and eighth richest orders (Table 1), while Asteraceae, Solanaceae, Lamiaceae, and Piperaceae are the first, sixth, seventh, and eighth richest families (Table 2). Other overrepresented

clades, for example, Passifloraceae, Clethraceae, Juglandaceae and Smilacaceae, contain a moderate absolute number of species in the CFM. Underrepresented clades have high, moderate, or low
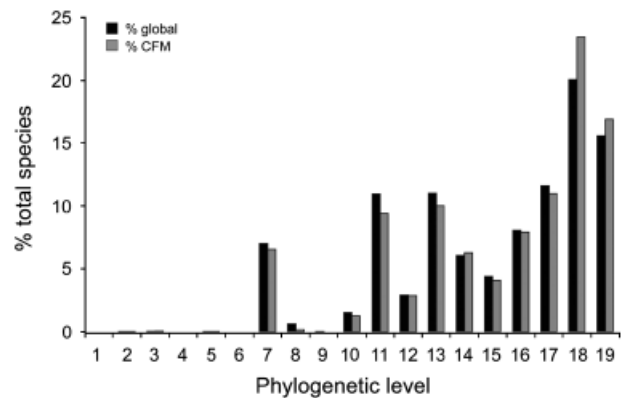

FIGURE 4. Species diversity in phylogenetic levels. Proportional species richness contained in each phylogenetic level in the global flora (black bars) and in the cloud forests of Mexico (CFM; gray bars).

TABLE 3. *Results of* G-*tests of goodness-of-fit.* G-*tests of goodness-of-fit were used to evaluate the null hypotheses of proportional representation of angiosperm orders ($H_{0[1]}$), families ($H_{0[2]}$), and phylogenetic levels ($H_{0[3]}$) in the cloud forest of Mexico (CFM) and in the global flora.*

	Total classes	Excluded classes ($f_{obs} = 0$)	Pooled classes ($f_{exp} \leq 3$)	Included classes (a)	df	n	G/q	$\chi^2_{[\alpha = 0.05]}$	P
$H_{0[1]}$	65	13	11	42	41	3785	667	56.9	3.8×10^{-114}
$H_{0[2]}$	452	270	60	123	122	3785	1240	149	2.5×10^{-184}
$H_{0[3]}$	18	3	3	13	12	3785	100	21.0	4.6×10^{-16}

absolute local species richness. No unambiguous correlation is apparent between over- and underrepresented clades in the CFM and their phylogenetic level. In general, overrepresented clades tend to belong to high phylogenetic levels. Underrepresented clades are a mixture of high to low phylogenetic levels (Tables 4 and 5).

The net differences between the percentage represented by early-diverging orders and families in the CFM and in the global flora are, in all cases, close to zero. This suggests that early-diverging lineages are neither overrepresented nor underrepresented in the CFM.

WHAT DETERMINES DIFFERENTIAL DIVERSITY OF CLADES IN THE MEXICAN CLOUD FOREST?—Clades that are overrepresented in the CFM together encompass a variety of life forms and vegetative habits, including canopy and understory trees (*e.g.*, Lauraceae, Fagaceae, Juglandaceae, Rosaceae, Clethraceae, Adoxaceae), shrubs (*e.g.*, Piperaceae, Rosaceae, Solanaceae, Asteraceae, Myrsinaceae), herbs (*e.g.*, Commelinaceae, Onagraceae, Lythraceae, Begoniaceae, Plantaginaceae, Lamiaceae, Solanaceae, Asteraceae), vines (*e.g.*, Smilacaceae, Rosaceae, Passifloraceae, Convolvulaceae), epiphytes (Bromeliaceae), and parasites (Convolvulaceae). All strongly overrepresented clades belong to the Asterids, Rosids, Monocots, or Magnoliids.

An examination of the general attributes of overrepresented and underrepresented families (Stevens 2009; complemented with Cronquist 1981, Mabberley 1997) suggests several explanatory factors for their differential diversity in the CFM. Several overrepresented families have a strong environmental preference for wet forest biomes. These include Piperaceae, Onagraceae, Lythraceae, Smilacaceae, Verbenaceae, Begoniaceae, and to a certain extent, Juglandaceae. Particularly, Myrsinaceae, and Clethraceae are characteristic elements of the cloud forests, either as diagnostic members of mature and conserved forests, or as dominant or co-dominant members of the understory. Some families are abundantly represented by life forms well developed in wet forests, namely vines (Passifloraceae, Convolvulaceae, and Smilacaceae), and epiphytes (Bromeliaceae and Piperaceae, particularly the genus *Peperomia*). Other overrepresented families, for example, Solanaceae, Bromeliaceae, Onagaraceae, and Passifloraceae, have their main geographical distribution in tropical America. Specifically, the territory of Mexico is a center of diversification of Fagaceae. Clethraceae, Adoxaceae and Juglandaceae have eastern Asian–eastern North American distributions, extending southwards into Mexico and Central or South America through the eastern Sierra Madre (Sierra Madre Oriental). Being speciose does not directly translate into overrepresentation: only 3 of the 20 most globally speciose families, and 9 of the 20 most locally speciose families, are overrepresented in the CFM. A possible exception is Asteraceae. With relatively few species that are forest trees and a general preference for habitats that are not densely forested, this family was found to be overrepresented in the CFM.

Two very clear factors, individually or combined, explain underrepresentation in the CFM: a different environmental preference (*e.g.*, Brassicaceae, Ericaceae, Amaranthaceae, and Balsaminaceae), and a different main geographic distribution (*e.g.*,

TABLE 4. *Ten most overrepresented and underrepresented orders in the cloud forests of Mexico (CFM). The phyogenetic level to which each order belongs, and the magnitude of the difference between percentage represented in the CFM minus percentage represented in the global flora are indicated.*

| Overrepresented orders	Phylogenetic level	% CFM − % global	Underrepresented orders	Phylogenetic level	% CFM − % global
Solanales	19	3.36	Caryophyllales	13	−1.96
Fagales	18	1.54	Asparagales	11	−1.52
Asterales	18	1.46	Brassicales	19	−1.21
Piperales	7	1.22	Malpighiales	17	−0.81
Poales	13	0.93	Alismatales	7	−0.74
Commelinales	14	0.73	Magnoliales	7	−0.64
Cucurbitales	18	0.65	Ranunculales	7	−0.57
Rosales	17	0.47	Proteales	8	−0.55
Dipsacales	19	0.39	Pandanales	10	−0.50
Laurales	7	0.26	Gentianales	19	−0.45
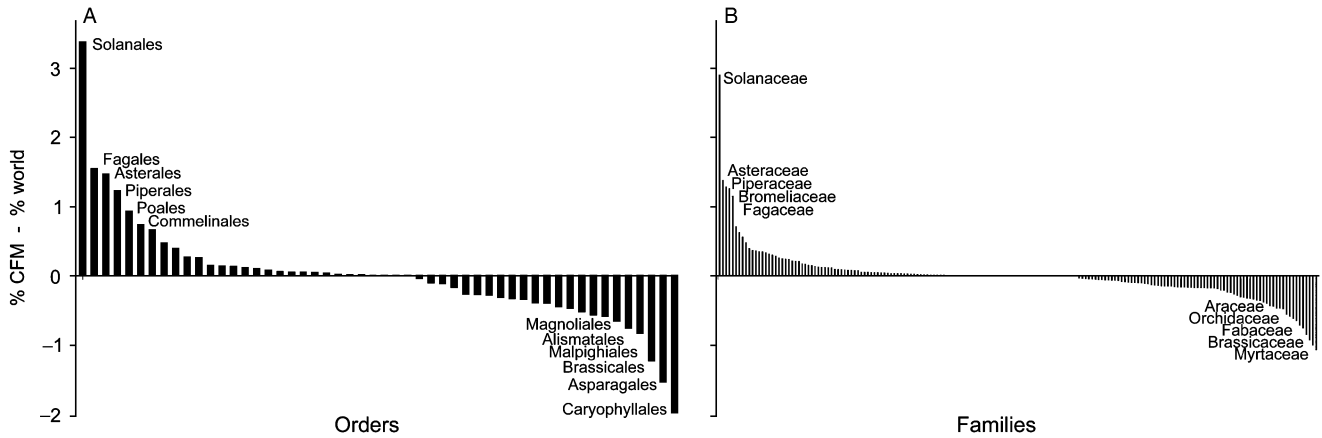
FIGURE 5. Overrepresented and underrepresented clades in the cloud forests of Mexico (CFM). The difference between the proportion represented by each order and family in the CFM minus the proportion in the global flora is used to identify overrepresented (most extreme positive differences) and underrepresented (most extreme negative differences) clades. (A) Most overrepresented and underrepresented orders are indicated on the left and right ends of the graph, respectively. (B) Most overrepresented and underrepresented families are indicated on the left and right ends of the graph, respectively.

Brassicaceae, Ericaceae, Proteaceae, Ranunculaceae, and Zingiberaceae). The finding that Myrtaceae, Fabaceae, Orchidaceae, Araceae, Annonaceae, and Arecaceae are underrepresented is surprising. Myrtaceae is preferentially distributed in tropical and subtropical regions around the world, and subfamily Myrtoideae (*sensu* Cronquist 1981) is best developed in tropical America. Fabaceae is cosmopolitan and diverse in nearly all types of environments. Orchidaceae, Araceae, Annonaceae, and Arecaceae are emblematic components of tropical wet forests: Orchidaceae are the most abundant epiphytic angiosperms in the CFM; Araceae are herbs on the forest floor, or vines; Annonaceae are mostly understory or canopy trees; and Arecaceae are characteristic understory elements. Orchidaceae and Fabaceae, and to a lesser extent Myrtaceae and Araceae, are very speciose in the CFM (Table 2). Perhaps their underrepresentation is a consequence of their high global species richness, which renders their diversity in the CFM comparatively low.

TABLE 5. *Twenty most overrepresented and underrepresented families in the cloud forests of Mexico (CFM). The phylogenetic level to which each family belongs, and the magnitude of the difference between the percentage represented in the CFM minus the percentage represented in the global flora are indicated.*

Overrepresented families	Phylogenetic level	% CFM − % global	Underrepresented families	Phylogenetic level	% CFM − % global
Solanaceae	19	2.91	Myrtaceae	14	− 1.06
Asteraceae	18	1.39	Brassicaceae	19	− 0.99
Piperaceae	7	1.29	Fabaceae	16	− 0.92
Bromeliaceae	13	1.27	Orchidaceae	11	− 0.84
Fagaceae	18	1.16	Araceae	7	− 0.74
Commelinaceae	14	0.72	Ericaceae	15	− 0.70
Onagraceae	14	0.64	Annonaceae	7	− 0.64
Lythraceae	14	0.57	Proteaceae	8	− 0.60
Myrsinaceae	15	0.49	Gesneriaceae	18	− 0.58
Passifloraceae	17	0.41	Acanthaceae	18	− 0.55
Verbenaceae	18	0.38	Ranunculaceae	7	− 0.47
Begoniaceae	18	0.37	Zingiberaceae	14	− 0.46
Convolvulaceae	19	0.36	Amaranthaceae	13	− 0.47
Plantaginaceae	18	0.36	Eriocaulaceae	13	− 0.43
Adoxaceae	19	0.34	Phyllanthaceae	17	− 0.42
Rosaceae	17	0.33	Gentianaceae	19	− 0.39
Clethraceae	15	0.31	Apocynaceae	19	− 0.37
Juglandaceae	18	0.30	Arecaceae	12	− 0.35
Smilacaceae	10	0.27	Balsaminaceae	15	− 0.34
Lamiaceae	18	0.26	Scrophulariaceae	18	− 0.33

How does the choice of units to evaluate floristic composition affect our results?—Comparisons between the CFM and the global flora considered orders, families and phylogenetic levels. Angiosperm orders and families, as circumscribed by APG II (2003), are arbitrarily delimited, non-nested monophyletic groups (*i.e.*, an order is not nested in another order, etc.). Phylogenetic levels are non-monophyletic groupings of orders, explicitly delimited by node distance to the angiosperm crown node. Their reality is ultimately determined by evolutionary processes that govern the rate of species diversification, but in practice, are highly contingent on phylogenetic resolution among major angiosperm lineages, on the fact that only living branches in the phylogenetic tree are accounted for, and importantly, on the choice of order-level clades to establish node distance to the root of the tree. Although lacking biological reality, these three units can nevertheless be unambiguously identified in different floras, and allow meaningful comparison.

It is likely that a different choice of taxa to evaluate proportional representation between the CFM and the global flora would have also resulted in significant differences. The more narrowly circumscribed geographical ranges and environmental preferences of less inclusive taxa (*i.e.*, genera and species) would result in greater compositional differences. Endemic genera and species would represent an extreme example: by having their total diversity concentrated in the CFM, they would be strongly overrepresented with respect to the global flora.

The number and inclusiveness of identified phylogenetic levels depended entirely on the choice of order-level clades to establish node counts. Determining phylogenetic levels on the basis of family-level clades would have resulted in a more precise comparison. However, family-determined phylogenetic levels were unfeasible because of (yet) substantial lack of resolution in the relationships among angiosperm families.

What does the greater representation of higher phylogenetic levels in the Mexican cloud forests mean?—The observation that high phylogenetic levels predominate slightly among overrepresented classes, and that levels 18 and 19 are relatively more abundant in the CFM than in the global flora (Fig. 4) suggest that species diversity in the CFM contains a somewhat higher proportional representation of orders that originated after much phylogenetic branching within angiosperms. Nevertheless, these results cannot provide absolute or relative times of species origin, nor indicate if the species composition of the CFM is preferentially due to *in situ* species generation, or to long-term species preservation. Several studies have estimated the origin, and in many cases the onset of diversification of angiosperm orders in the Upper Cretaceous (Wikström *et al.* 2001, Bremer *et al.* 2004, Janssen & Bremer 2004, Anderson *et al.* 2005, Magallón & Castillo 2009). Species that belong to early-diverging angiosperm lineages may have originated at any time since the differentiation of the lineage they belong to, including the recent past. Alternatively, because many late-diverging lineages began to diversify in the Upper Cretaceous (Magallón & Castillo 2009), species resulting from their initial diversification are quite ancient.

Summary and perspectives.—Major clades are represented differently in the CFM and the global flora at the three levels tested.

Early-diverging lineages are neither over- or underrepresented in the CFM with respect to the global flora. An overwhelming quantitative predominance of early-diverging or of late-diverging lineages in the CFM was not found. Nevertheless, the slight predominance of phylogenetic levels among overrepresented classes, and the slightly greater proportional representation of the highest phylogenetic levels in the CFM than in the global flora, indicate a somewhat higher representation of late-diverging angiosperm clades in the CFM.

Cloud forests are the only biomes in Mexico where members of two of the earliest-diverging angiosperm lineages, namely, Austrobaileyales and Chloranthales, occur. Together with lowland tropical rain forests, cloud forests also house Nymphaeales. Whether the slight preponderance of late-diverging lineages combined with representation of the earliest-diverging lineages is a distinctive feature of the CFM, or an attribute shared by cloud forests or wet tropical forests around the world, requires a comprehensive investigation. If a global pattern, it could perhaps imply that cloud forests, or wet tropical forests in general, provide habitats where the most ancient angiosperm lineages have persisted in the face of accumulating species diversity (whether by origination or by immigration) in phylogenetically derived lineages. This possibility remains to be tested against explicit alternatives. The subtly emerging pattern for the CFM contrasts with the lowland tropical rain forests of Mexico, where a slightly higher proportional representation of early-diverging angiosperm lineages was found (Campos Villanueva 2008). These early-diverging overrepresented lineages contain emblematic structural and epiphytic components of this type of vegetation.

An understanding of the evolutionary origin and maintenance of floristic diversity in a particular biome requires knowledge of what causes differential diversity of lineages in that biome, and how its species diversity has accumulated. Here, we found suggestions that geographic distribution and environmental preference/habitat specialization may be among the most important factors in determining the diversity of particular angiosperm lineages in the CFM and in the global flora. A more focused investigation may test for differential composition, and identify overrepresented and underrepresented clades with respect to the flora of the same biogeographic region (including different biomes), and with respect to the flora of similar biomes around the world.

The identification of specific processes that shaped the species composition of a particular biome represents a major contribution toward a comprehensive understanding of the evolutionary determinants of biodiversity. These processes may include, for example, prolonged species survival resulting from low extinction; within-lineage species replacement driven by (time-homogeneous) speciation and extinction; rapid radiation driven by a (time-delimited) increase in speciation; or immigration of elements adapted to similar biomes from different geographical regions. One possible research strategy is a clade-by-clade approach using dated species-level phylogenies (Sanderson 2002, Drummond & Rambaut 2007) and reconstructed ancestral areas of distribution (Ronquist 1996) to determine the timing, tempo, and place of origin of the species from a focal biome. This information would provide explicit clade-based

information of the diversification dynamics and directions of migration.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Diversity of angiosperm orders in the global flora, and in the cloud forests of Mexico.*
TABLE S2. *Diversity of angiosperm families in the global flora, and in the cloud forests of Mexico.*
TABLE S3. *Distribution of the cloud forests of Mexico.*

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