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Altitudinal distribution patterns of Mexican cloud forests based upon preferential characteristic genera

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Abstract

Mexican cloud forest vegetation has been recorded in temperate humid conditions at rather different elevations ranging from 600 to 3000 m. They are characterised by high biodiversity under continuous foggy situations. Some authors state that many genera are quantitatively important to depict cloud forest conditions. Detailed quantitative studies comprising most of the localities of Mexican cloud forests to depict altidudinal distribution ranges on basis of preferential genera have not been previously conducted. The aim of this study is (1) to recognise characteristic preferential genera of Mexican cloud forest conditions, and (2) to determine quantitatively the current altitudinal distribution pattern of this vegetation type. From a database composed by 995 genera inhabiting in the Mexican cloud forests, six genera were chosen preliminary as preferential characteristics. These were *Clethra, Magnolia, Meliosma, Styrax, Symplocos*, and *Ternstroemia*. These genera include 70 species that occur at over 70% of the current Mexican cloud forest fragments. The mean elevation of these genera records were 1853 m (±600 at 95% confidence interval). The results showed that Mexican cloud forests occur optimally between 1250 and 2450 m. Additionally, Mexican cloud forest is the best distributed within some provinces of the "Región Mesoamericana de Montaña", chiefly at "Serranías Meridionales", "Sierra Madre Oriental", and "Serranías Transístmicas". The results are discussed in light of the importance of these regions as diversification centres.

Introduction

Current vegetation distribution patterns have been related to mesoclimatic conditions as the major attribute explaining such archetypes (Walter 1996). Climatic situations, in practice, have been associated with elevational gradients, along which vegetation types follow restricted distributions (Whittaker 1978; Holdridge 1987). Mesophyllous vegetation types, nonetheless, follow complex distribution patterns along elevation, depending on other factors (Luna et al. 1999). This is most evident in Mexico where several authors (e.g. Rzedowski (1969); Puig (1976); Luna et al. (1994)) recorded cloud forests in different altitudinal belts. This subject, has not been thoroughly investigated and most reports based their distribution patterns on field observations from regional surveys (Challenger 1998).

In Mexico, cloud forests ("bosque mesófilo de montaña" *sensu* Rzedowski (1978)) occur within a relatively narrow altitudinal zone on humid temperate climates, distributed between 600 and 3000 m elevation (Luna et al. 1988). It is composed by distinctive floristic and structural forms (Rzedowski 1978) and is characterised by a high diversity and remarkable predominance of vascular epiphytes and lianas, this is due to the presence of abundant fog (Puig 1976). Its current geographic distribution follows an archipelago-like pattern across Mexico in each of the patches there is a particular biotic composition (Luna et al. 2001).

Rzedowski (1978) states that the Mexican territory can be divided into 17 floristic provinces, clustered into four major regions: “Pacífica Norteamericana”, “Mesoamericana de Montaña”, “Xerofítica Mexicana”, and “Caribea”. This regionalization was based upon a national floristic analysis, phytogeographic affinities and endemicity in the different areas. Within these floristic provinces, Challenger (1998) shows in his map (page 448) that Mexican cloud forest distributes mainly in the next four provinces: “Serranías Transístmicas”, “Serranías Meridionales”, “Sierra Madre Oriental”, and “Sierra Madre Occidental”.

Mexican cloud forest have been considered to be one of the vegetation types that better expresses transitional conditions between tropical and temperate biogeographic realms. It shows close floristic affinities to deciduous forests of North America (Miranda and Sharp 1950), equivalent forests of the east of Asia (Sharp 1966), and similar plant communities present in the Andean region of South America (Gentry 1995; Joergensen et al. 1995; Brown 1995). This transitional condition has been explained, in part, as a result of cooling during the Tertiary and Quaternary. This favoured migration of numerous arboreal genera towards the south, statement that has been supported by the common presence of a number of genera in two or more of these areas (e.g. *Alnus* Miller, *Juglans* L., and *Myrica* L., among others) (Graham 1987).

Rzedowski (1996) considers that some genera that inhabit Mexican cloud forests are quantitatively important to characterise cloud forest conditions. Some of the important genera that he considers as characteristic are *Alfaroa* Standl., *Carpinus* L., *Chiranthodendron* Larréat., *Cinnamomum* Schaeffner, *Clethra* L., *Liquidambar* L., *Magnolia* L., *Matudaea* Lundell, *Meliosma* Blume, *Nyssa* L., *Oreomunnea* Oersted., *Styrax* L., *Symplocos* Jacq., and *Ternstroemia* Mutis ex L.f.,

Detailed quantitative studies comprising most localities of Mexican cloud forest to depict altitudinal distribution ranges have not yet been conducted. Hence, the aims of the present study are to recognise characteristic preferential genera of Mexican cloud forest conditions to determine quantitatively the current altitudinal distribution pattern of this vegetation type on basis of preferential characteristic genera. The way these genera occur at the floristic provinces is also discussed, since this is, relevant to identify priority areas for conservation purposes of this remarkable vegetation type considered as a seriously threatened ecosystem (Hamilton et al. 1995).

Methods

To select the preferential characteristic genera, these criteria were considered: (1) species well-represented in the current Mexican cloud forest patches, especially those genera with vicarious species present in most cloud forest fragments; (2) species belonging to these genera must be closely related to humid mountain environmental conditions; (3) to have significantly large frequency values of species presence at cloud forest conditions; (4) the genera selected ought to be ancient elements, principally woody, (5) they must be important as dominants or co-dominants in Mexican cloud forests. In addition, genera must have been reported as typical elements of the Mexican cloud forests (Miranda and Sharp 1950; Rzedowski 1969, 1996; Luna et al. 1994).

A database comprising 995 genera was compiled from literature, plant collections (MEXU, XAL and FCME), and technical reports of projects funded by “Comisión Nacional Para el Estudio y Uso de la Biodiversidad, CONABIO” (projects F019, H304, A004, P083, P026, P011, B201, P092, and A007). From all the genera reported, only six fulfill the criteria. From these six genera, data of locality of collection, elevation and vegetation type where the collection took place of all species known were gathered.

We avoided double records by only using a single exemplar with the same collection number in the final database information. This implies that our final database comprised species belonging to the selected genera found at distinctive localities.

The frequency values of the records of each species of the genera selected and collected at the different vegetation types were plotted. The vegetation types used in the analysis were those proposed by Rzedowski (1978), with the exception of the pine-oak forest, due that this author considers the *Pinus* and *Quercus* forests separately; in this case we followed Leopold (1950). Frequency values > 50 records of one species present in cloud forest conditions were considered as the threshold to depict genera as potential preferential characteristic. The frequency value of the total number of species of each genus at different vegetation types was plotted. This was needed to detect preferences of species distribution of the selected genera per vegetation type.

The frequency value of the records of each species of the preferential characteristic genera grouped by floristic province *sensu* Rzedowski (1978) were also compared. These permitted the comparison among genera and among floristic provinces. This comparison included the number of species per genus present in each floristic province.

Average altitude of the cloud forest conditions as obtained by the preferential characteristic genera in each floristic province was calculated. The data obtained were pooled into a database, from which the number of records per genera along altitude were plotted, in order to detect the elevations where these genera are best distributed. The distribution curves of the species records of the preferential genera were plotted simultaneously in order to depict elevations where the cloud forest conditions are best represented.

Results

From a final database composed of 995 genera inhabiting in the Mexican cloud forests these, six genera fulfilled the criteria as preferential characteristics, *Clethra, Magnolia, Meliosma, Styrax, Symplocos*, and *Ternstroemia*.

These genera comprised 70 species (Appendix 1). These species, in turn, have been recorded at 1156 sites covering over 70% of the current Mexican cloud forest fragments. The total number of records per species and localities resulted in 1290 scores in the final database.

Many of the species of these genera (five or more of them) occur principally in temperate conditions, for instance, cloud forest, pine-oak forest, oak forest, or coniferous forest (Figure 1a). Notwithstanding, all these species are better distributed in Mexican cloud forest than in any other vegetation type of Mexico (Figure 1b). Pine-oak forest also comprised a large number of records, but substantially fewer than cloud forest. Some species of these genera, however, are also represented in tropical humid vegetation types, such as tropical rain forest ("selva alta perennifolia" *sensu* Rzedowski (1978)). As a whole, many species from these preferential characteristic genera may be considered exclusive of cloud forest conditions (e.g., *Clethra kenoyeri* Lundell, *C. rosei* Britton, *C. vicentina* Standl., *Meliosma dives* Standl. et Steyerm., *M. matudai* Lundell, *M. oaxacana* Standl., *Symplocos excelsa* L.O. Williams, *S. flavifolia* Lundell, and *S. jurgensenii* Standl).

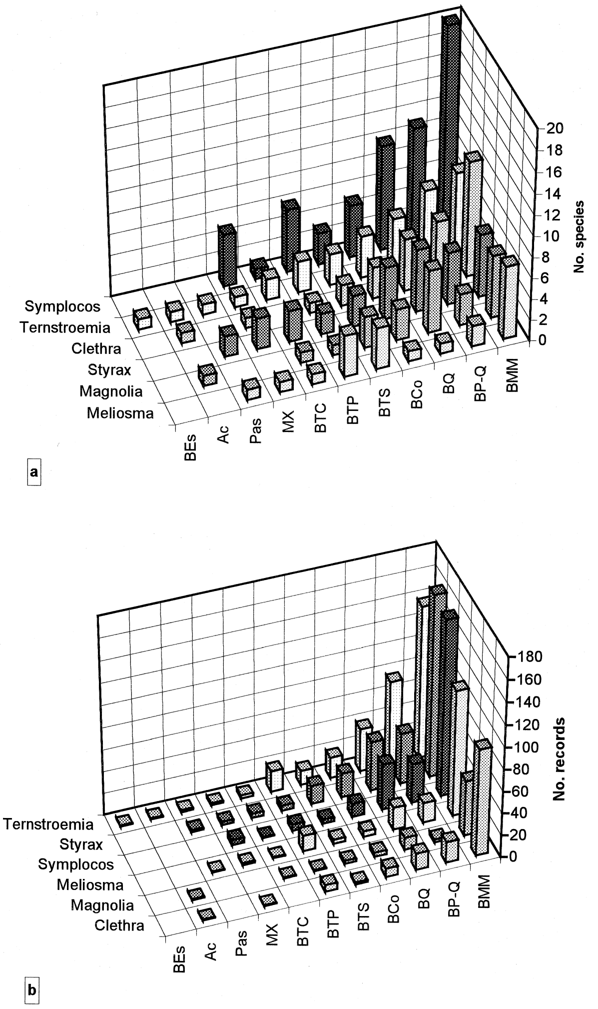

Figure 1. Number of species (a) and records (b) presented in different Mexican vegetation types. The abbreviations state for: BMM = "bosque mesófilo de montaña"; BP-Q = "bosque de *Pinus-Quercus*", BQ = "bosque de *Quercus*", BCo = "bosque de coníferas", BTS = "bosque tropical subcaducifolio", BTP = "bosque tropical perennifolio", BTC = "bosque tropical caducifolio", MX = "matorral xerófilo", Pas = "pastizal", Ac = "acuática y subacuática" and BEs = "bosque espinoso".

The analysis of the records per floristic province also showed restricted distribution patterns. Most of the species belonging to the six preferential genera are best distributed in the floristic province of "Serranías Meridionales"; in descending order, the "Sierra Madre Oriental", "Serranías Transístmicas", and "Sierra Madre Occidental" harbour species that belong to genera of cloud forest conditions. In minor proportion, the "Costa del Golfo de México", "Altiplano",

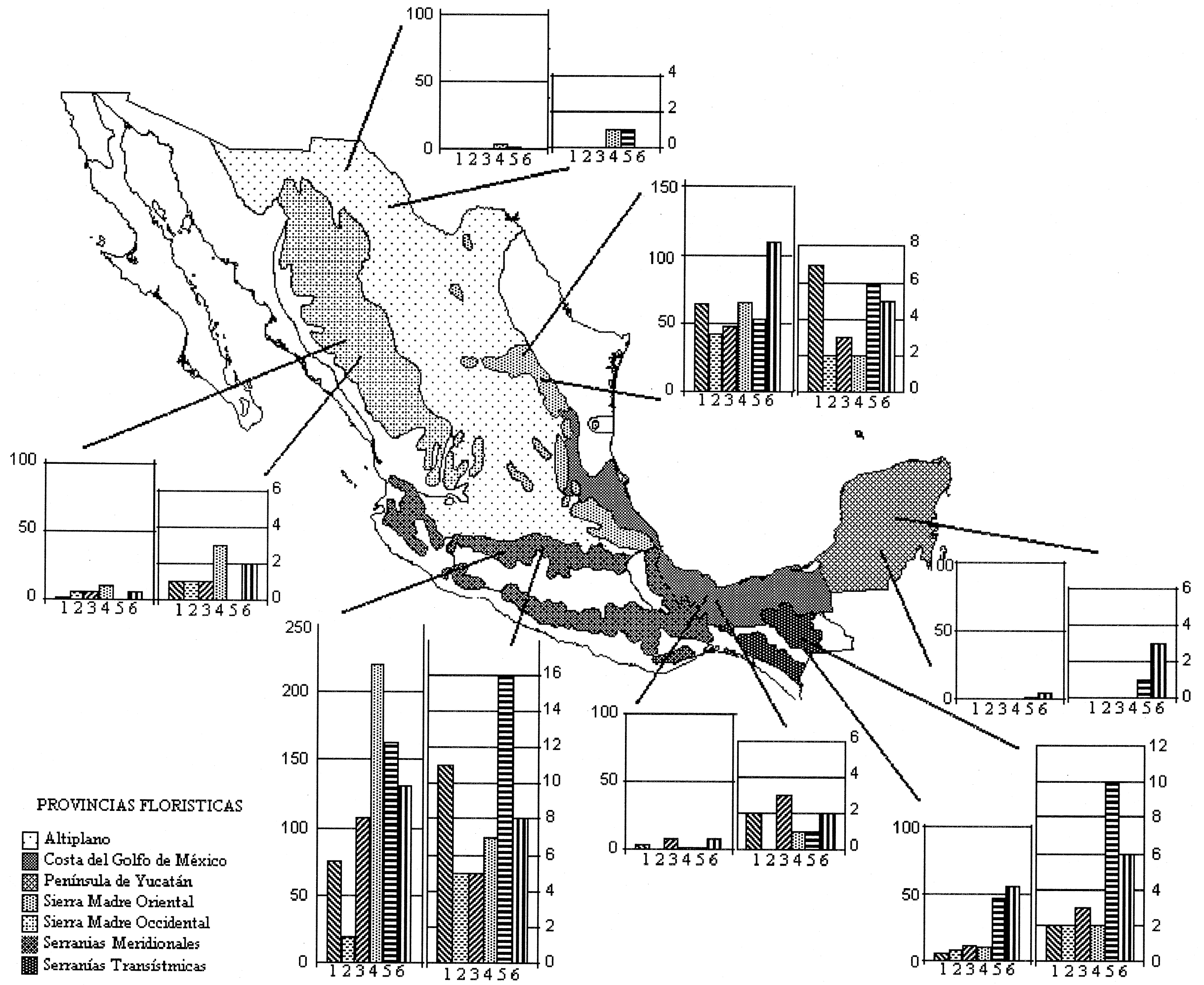

Figure 2. Number of records (left bar graphs) and species (right bar graphs) from the six characteristic preferential genera of Mexican cloud forest per Mexican floristic province. Most records and species are present within "Serranías Meridionales" province. The numbers state for: 1 = *Clethra*, 2 = *Magnolia*, 3 = *Meliosma*, 4 = *Styrax*, 5 = *Symplocos*, and 6 = *Ternstroemia*.

and "Península de Yucatán" provinces also comprised a few records of these genera (Figure 2); only the first harbours cloud forest environments, e.g. Volcán San Martín, Veracruz.

Records of selected species per genera showed an unimodal distribution pattern along elevation. All genera distributed along a large elevational gradient were significantly restricted to elevations between 600 and 2800 m. The mean elevation of all records was 1853 m (±600 places at 95% confidence interval). These data suggest that Mexican cloud forests, typified by the occurrence of the six genera selected as preferential characteristics, are found optimally between 1250 and 2450 m (Figure 3a). This elevational range is broader than others suggested in previous studies (e.g. Luna (1984)), which document that this vegetation type is best developed between 1700 and 2000 m. Many of the species of the selected genera are distributed principally above 1000 m of altitude, with the exception of some species of *Meliosma* (Figure 3b).

Distribution of Mexican cloud forests along elevation intervals, suggested by these characteristic genera, varied among floristic provinces (Figure 4). At the "Sierra Madre Oriental" the most common elevation ranges were between 1200–2000 m. In the "Sierra Madre Occidental" it was more frequent between 1600 and 2200 m. In the "Serranías Meridionales" it distributed between 1800 and 2600 m, whereas in the "Serranías Transístmicas" among 2400 and 2800 m. Mexican cloud forest was also recorded at 1100–1300 m at the "Costa del Golfo" province; notwithstand-

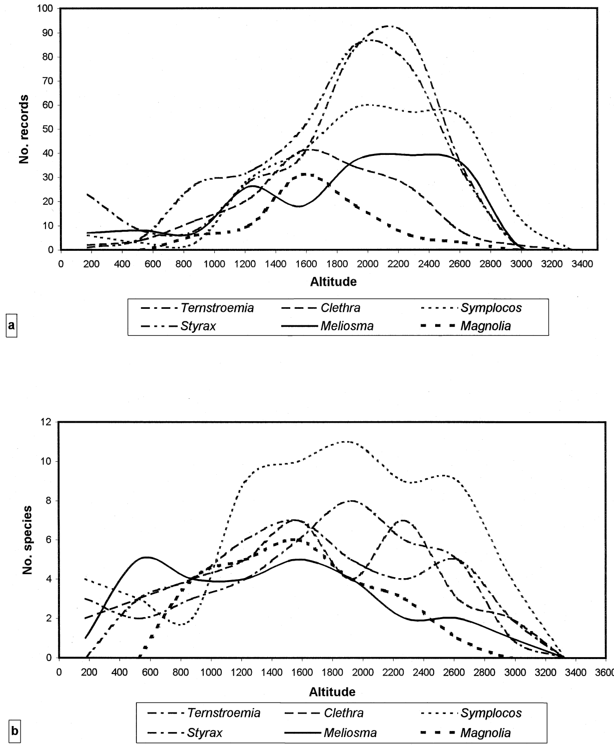

Figure 3. Number of records (a) and species (b) per genera distributed along elevation.

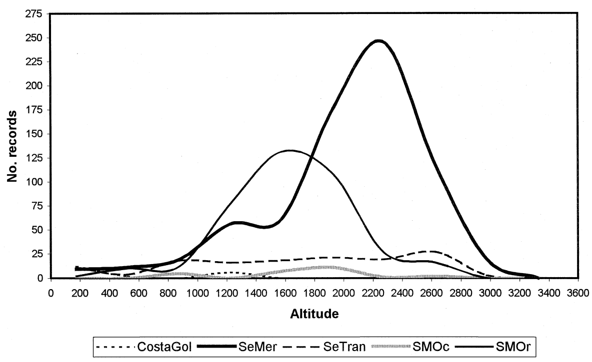

Figure 4. Frequency values of all species records per Mexican floristic province along elevation. Clear peaks are observed between 1000 and 2800 m of altitude.

ing, some species of these genera were recorded at lower altitudes within this province (200 m). Finally, a few species records of the selected genera in the "Altiplano" province occurred, but were neglected in the plots.

The majority of the species of the six genera selected as preferential characteristic were best distributed in Mexican cloud forest (Figure 1). *Clethra* prevailed at the "Serranías Meridionales" and "Sierra Madre Oriental" provinces, whereas no records were found at "Altiplano" and "Península de Yucatán" provinces. *Clethra* was commonly found in oak and pine-oak forest too. *Magnolia* distributed proportionally in Mexican cloud forest and oak forest. Its presence prevailed at "Serranías Meridionales", "Sierra Madre Oriental" and "Serranías Transístmicas" provinces. *Meliosma*, in turn, was common at "Serranías Meridionales", "Sierra Madre Oriental" and "Serranías Transístmicas" provinces, within patches of Mexican cloud forest. It was also frequent in tropical rain forest. *Styrax* and *Symplocos* showed similar distribution patterns, and were more frequent in the cloud forest of the "Serranías Meridionales" and "Sierra Madre Oriental". These taxa are also frequent in oak forest and coniferous forest. *Symplocos* is also abundant in the cloud forests of the "Serranías Meridionales", "Serranías Transístmicas", and "Sierra Madre Oriental", being totally absent in the "Sierra Madre Occidental" floristic province. The species of *Ternstroemia* are very frequent in the cloud forest, oak forest and pine-oak forest of the "Sierra Madre Oriental", "Serranías Meridionales", and "Serranías Transístmicas" (Figures 1 and 2).

Discussion

Previous studies listed some genera as quantitatively important to depict cloud forest conditions (Rzedowski 1969, 1996; Puig 1976, 1989); many of these studies based their outputs upon local or regional studies. Recently Rzedowski (1996) stated that about 650 genera have at least one exclusive or preferential species to this vegetation type in Mexico. Specific genera, however, had not been previously detected and proved as important in this vegetation type, due, in part, to the lack of detailed systematic studies. In the present paper, many species records that belong to six preferential characteristic genera fulfilled the conditions to depict Mexican cloud forest. The number of preferential characteristic genera to these conditions may increase in the near future, as long as we have more studies in systematics, biogeography, and ecology.

The data included into the distribution analysis comprised over 1150 localities covering the majority of the current patches of Mexican cloud forest. The archipelago-like distribution pattern enhanced the biogeographic importance of the Mexican cloud forest. These patches harbour an extraordinary mixture of plants and animals associated with diverse biogeographic zones and display a high degree of local and regional endemism. The current 107 fragments distributed across Mexico cover about 14,119 km^2 (Challenger 1998). Detailed data, at species level, of all these areas are scanty, which makes comparisons among patches difficult. Our results suggests that *Clethra, Magnolia, Meliosma, Styrax, Symplocos*, and *Ternstroemia* are best distributed in the cloud forests of the "Serranías Meridionales", "Sierra Madre Oriental", and "Serranías Transístmicas" provinces. Only a few species from these genera occur in oak forest and coniferous forest, where humid-cool conditions in deep valleys dominate and in tropical rain forest.

The majority of the species of these genera were distributed in elevations above 1000 m within the "Región Mesoamericana de Montaña". Hence, it was here considered that this mountainous zones can be suggested as diversification areas of these genera, as many of these zones of Mexico have been proposed as diversification centres of many other taxa of vascular plants, such as *Quercus* (Nixon 1998), and *Pinus* (Styles 1998). Some authors (*e.g.* Rzedowki (1965); Toledo (1982)) have explained the disjunct distribution of many of these taxa as consecuence of paleoclimatic changes, that create the necesary conditions for the origin of plant and animal groups. Nothwithstanding, Luna et al. (1999) and Luna et al. (2000) concluded that this pattern, in the case of the Mexican cloud forest, is rather the consequence of vicariant events, without proposing any particular process. The refuge model (Haffer 1987) is only a particular case of vicariance.

These diversification areas are characterised by a high percentage of endemism of other living groups such as reptiles (Flores 1998), and birds (Challenger 1998). Cracraft and Prum (1988), in addition, sustained that the speciation rate is incremented in areas of high topographic complexity. This is the case of this region, which turned out to be of extreme importance for conservation purposes (Luna et al. 1999, 2001).

Altitudinal ranges of the cloud forest are difficult to define due to several conditions. To illustrate this further, natural and man-made disturbance, influence of adjacent vegetation, latitudinal effect, different rainfall patterns, and "Massenerhebungseffekt" (Grubb 1971; Webster 1995; Luna et al. 2001) modify current distribution patterns. The records of the "Sierra Madre Occidental" and "Sierra Madre Oriental" are located at lower mean elevation that the ones in the "Serranías Transístmicas" and "Serranías Meridionales" due to the effect of latitude: the higher is latitude, the lower is the mean elevation of the records of the cloud forest. From our results, six genera are recommended as preferential characteristics of cloud forest conditions. Based on these results, preferent elevational ranges of Mexican cloud forests can be established.

Suitable conditions for the development of mountain cloud forest in Mexico are restricted to a few floristic provinces. This, nonetheless, demonstrates that efforts to preserve the current biodiversity harboured in this complex vegetation type requires a network of patches distributed at different floristic provinces and altitudes. Up to now, there are only a few protected areas that include this vegetation type (Challenger 1998). The number of endemic taxa inhabiting in these forests is overwhelming, so official protection must be a priority Mexican cloud forests are a relictual habitat worth conserving. The data presented in this paper illustrate an alternative path to detect most suitable cloud forest conditions on basis of characteristic preferential genera. Further floristic studies using complementary genera are still to be conducted.

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Appendix 1

Table A1. Species included into the present analysis.

Clethraceae
Clethra alcoceri Greenm.
C. hartwegii Britton
C. kenoyeri Lundell
C. aff. *lanata* M. Martens et Galeotti
C. lanata M. Martens et Galeotti
C. aff. *macrophylla* M. Martens et Galeottii
C. macrophylla M. Martens et Galeotti
C. aff. *mexicana* DC.
C. mexicana DC.
C. pringlei S. Watson
C. rosei Britton
C. suaveolens Turcz.
C. vicentina Standl.

Magnoliaceae
Magnolia dealbata Zucc.
M. iltisiana A. Vazquez
M. pacifica ssp. *pacifica* A. Vazquez
M. pacifica ssp. *pugana* A. Vazquez
M. pacifica ssp. *tarahuamara* A. Vazquez
M. schiedeana Schltdl.
M. sharpii Miranda

Sabiaceae
Meliosma alba (Schltdl.) Walp.
M. dentata Urb.
M. dives Standl. et Steyerm.
M. aff. *glabrata* Urb.
M. grandifolia (Liebmn.) Urb.
M. matudai Lundell
M. nesites I.M. Johnst.
M. oaxacana Standl.
M. occidentalis Cuatrec.

Styracaceae
Styrax argenteus Presl.
S. glabrescens Benth.
S. jaliscanus S. Watson
S. lanceolatus P. Fritsch
S. platanifolius Engelm. ex Torr. ssp. *youniae* (Cory) P. Fritsch
S. radians P. Fritsch
S. ramirezii Greenm.
S. warscewiczii Perk

Symplocaceae
Symplocos austromexicana Almeda
S. breedlovei Lundell
S. citrea La Llave et 0Lex.
S. coccinea Humb. et Bonpl.
S. aff. *excelsa* L.O. Williams
S. excelsa L.O. Williams
S. flavifolia Lundell
S. hartwegii A. DC.
S. aff. *johnsonii* Standl.
S. johnsonii Standl.
S. jurgensenii Hemsl.
S. aff. *matudai* Lundell
S. matudai Lundell
S. aff. *limoncillo* Bonpl.
S. limoncillo Bonpl.
S. longipes Lundell
S. aff. *prionophylla* Hemsl.
S. prionophylla Hemsl.
S. aff. *pycnantha* Hemsl.
S. pycnantha Hemsl.
S. sousae Almeda
S. speciosa Hemsl.
S. aff. *vernicosa* L.O. Williams
S. vernicosa L.O. Williams

Theaceae
Ternstroemia dentisepala B.M. Barthol.
T. huasteca B.M. Barthol.
T. impressa Lundell
T. lineata DC. ssp. *chalicophila* (Loes.) B.M. Barthol.
T. lineata DC. ssp. *lineata*
T. maltbyi Rose
T. seemannii Triana et Planch.
T. sylvatica Schltdl. et Cham.
T. tepezapote Schltdl. et Cham.

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