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Identification of areas of endemism in the Mexican cloud forests based on the distribution of endemic epiphytic bromeliads and orchids

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Abstract

To identify areas of endemism (AEs) in the Mexican cloud forests based on the distribution of endemic epiphytic bromeliads and orchids species and to propose a hypothesis about the current biogeographical relationship of the Mexican cloud forests. The AEs were identified using 1007 records corresponding to 205 species and the endemicity analysis as is implemented in the NDM/VNDM programs. To obtain the consensus areas a strict consensus analysis was carried out considering 60% of shared species as the lower limit; those that presented an Endemicity Index ≥ 3.0 were recognized as AEs. A parsimony analysis of endemicity was performed with WINCLADA/NONA programs to infer their biogeographical relationships. Five AEs were recognized: 1) Western Mexico (supported by six species), 2) Southern Mexico (eight species), 3) Northern Gulf of Mexico, and 4) Central Gulf of Mexico (with nine species each), and 5) Northern Oaxaca (four species). The spatial homology hypothesis suggests that the areas of endemism from the Pacific Ocean Slope and from the Gulf of Mexico Slope has a different evolutionary history. Each AEs has a different species composition; the greatest species diversity is presented in the Gulf of Mexico slope AEs, while the greatest diversity of exclusive species is presented in the Pacific Ocean slope AEs. There is no a spatial homology hypothesis between the AEs of the Gulf of Mexico and the AEs of the Pacific Ocean, therefore, our results do not support the hypothesis of a cloud forest with continuous distribution in the past. The divergence times of the bromeliads and orchids and ecological succession theory could explain our results.

Keywords: Biogeography, Bromeliaceae, optimality criteria, Orchidaceae

Introduction

The recognition of areas of endemism has been a primary objective of historical biogeography because they represent the basic units of analysis (Linder, 2001). Their identification, however, can be difficult when species are not completely sympatric and there is a minimal overlap of their distribution areas due to evolutionary processes such as dispersal or extinction. These processes can increase or decrease the overlap of the areas of two or more taxa with different evolutionary histories, even in certain cases, when geographic and/or climatic conditions allow different species to extend their distribution areas synchronously. Dispersal should generate patterns of sympatry, such as in the case of islands or the formation of biological corridors (Domínguez *et al.*, 2006; Escalante *et al.*, 2009; Morrone, 2009; Torres-Miranda *et al.*, 2013). The search of coinciding distribution areas of taxa with different characteristics and evolutionary histories increases the reliability of a biogeographical relationship hypothesis, because the common distribution of different groups may indicate common evolutionary processes (Azevedo *et al.*, 2016).

Several definitions of area of endemism have been proposed (see Parenti & Ebach, 2009), as well as some methods for its identification (Dos Santos *et al.*, 2012; Linder, 2001; Szumik *et al.*, 2002; Szumik & Goloboff, 2004; Torres-Miranda *et al.*, 2013). Some authors (Azevedo *et al.*, 2016; Casagranda *et al.*, 2012; Escalante *et al.*, 2009; Gomes-da-Silva *et al.*, 2017; Morrone, 2014; Torres-Miranda *et al.*, 2013) have suggested that the most effective method for delimiting areas of endemism is the endemicity analysis proposed by Szumik *et al.* (2002) and Szumik and Goloboff (2004). It uses an optimality criterion, evaluating how many taxa are and what is their contribution to the delimitation of a given area, that is, identifies areas of endemism considering the spatial distribution of taxa that occur in a given area and evaluates explicitly the congruence between their distributions. It is a method based on the concept of area of endemism proposed by Platnick (1991), that identifies congruent distribution patterns.

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The actual fragmentation and restricted distribution of the Mexican Cloud Forest (MCF) make it an adequate model to analyze and propose hypotheses on its possible origin and current distribution, however, biogeographic studies on MFC are scarce. Luna Vega *et al.* (1999), proposed that current MCFs fragments present in Chiapas, Colima, Guerrero, Hidalgo, Jalisco, Michoacán, Nayarit, Oaxaca, Puebla, Querétaro, Estado de México, Tamaulipas and Veracruz, diverged sequentially from a continuous original forest in Mexico, where ecological and historical factors provided isolation events that induced their fragmentation. Luna Vega *et al.* (2001), found that, from a floristic point of view, the MCFs are closely related to the cloud forests of the Antilles and Central American regions, so they suggested that this type of vegetation represents a natural biogeographical unit.

MCFs biogeographic relationships hypotheses have been proposed mainly based on their trees flora, leaving aside the vascular epiphytes, even though that they are well represented and have a great ecological importance in this type of vegetation. The objectives of this work were to identify the areas of endemism in the MCFs based on the distribution of endemic epiphytic bromeliads and orchids, and to infer their relationship using a parsimony analysis of endemicity and propose a spatial homology hypothesis.

Materials and Methods

Distribution data:—The MCFs area of distribution was delimited by both Uso de Suelo y Vegetación and Vegetación Potencial vector layers (CONABIO, 1999; Rzedowski, 1990), both available on the Portal de Geoinformación, Sistema Nacional de Información sobre Biodiversidad (http://www.conabio.gob.mx/informacion/gis/; Fig. 1a). The Mexican endemic species list was obtained from Espejo Serna (2012). Distribution data from 205 species was included, 170 orchids and 35 bromeliads. Herbarium specimens of 10 national institutional collections were reviewed: AMO, CHAPA, CHIP, CORU, HEM, IBUG, IEB, MEXU, UAMIZ, and XAL (the acronyms correspond to those published in the Index Herbariorum Thiers ([continuously updated]). Only those specimens whose labels indicated that the specimen grew epiphytic and that had been collected in a cloud forest or in any of its synonyms (bosque caducifolio, bosque de niebla, bosque de neblina, bosque mesófilo de montaña, deciduous forest, evergreen rain forest, lower montane rain forest, montane rain forest, mountain rain forest and nubliselva) were included.

The database contained 1007 records and is available on request from I. Estrada. We corroborated identifications and 75% of all records were georeferenced using Google Earth Pro ver. 7.3.1.4507 and Mapa Digital de México V6.3.0 (http://gaia.inegi.org.mx/mdm6/F0OjE5LjM2MDAwLGxvbjotOTkuMDcyNDIsejo5LGw6YzExMXNlcnZpY2lvc3x0YzExMXNlcnZpY2lvcw==). Locality records for individual specimens were checked and corrected when necessary.

Areas of endemism:—To identify the areas of endemism, the endemicity analysis (EA) proposed by Szumik *et al.* (2002) and Szumik and Goloboff (2004) was used as is implemented in the NDM/VNDM programs, ver. 3.0 (Goloboff, 2004). The EA is based on an optimality criterion, and searches for areas that are congruent with the distribution of as many species as possible. To evaluate each area obtained, NDM/VNDM assigns a score to each species, depending on how well the species fits de area; all the areas receive an endemicity index (EI) which is the sum of scores of the supporting species. The EI value improves both with the number of species concordant with the area and with the degree of concordance between the area and those species (Aagensen *et al.*, 2013; Szumik *et al.*, 2006)

We used for the analyses two latitude-longitude cell sizes, 0.5° x 0.5° and 0.7° x 0.7°, as several authors have suggested (Aagensen *et al.*, 2009; do Prado *et al.*, 2015; Szumik *et al.*, 2012). In both cases, for the records inferred parameter (R. fill) and records assumed (R. ass) parameter a zero value was used. For each cell size, a heuristic search was carried out and all areas with an EI ≥ 2.0 and with at least two endemic species were retained. To define the consensus areas based on the percentage of shared species (Aagensen *et al.*, 2013), a strict consensus analysis was carried out considering 60% of shared species as the lower limit; those areas that presented an EI ≥ 3.0 were recognized as areas of endemism. The areas of endemism obtained were converted to shapefile format and then exported to Team Development QGIS (2016) Desktop 2.10.1 to be visualized.

Relationships among the areas of edemism:—To infer the spatial homology hypothesis of the areas of endemism, a parsimony analysis of endemicity (PAE) was performed (Morrone, 2009, 2014). A new presence-absence matrix was conformed by five areas of endemism obtained in the EA (rows) and 154 species (columns) of endemic epiphytic bromeliads and orchids from Mexico that were registered in the MCFs (Appendix 1). The cladistic analysis was carried out in the WINCLADA/NONA program (Goloboff, 1999; Nixon, 2002). Heuristic searches were conducted with Multiple TBR (mult*) option active, retaining 10000 trees and performing 100000 repetitions.

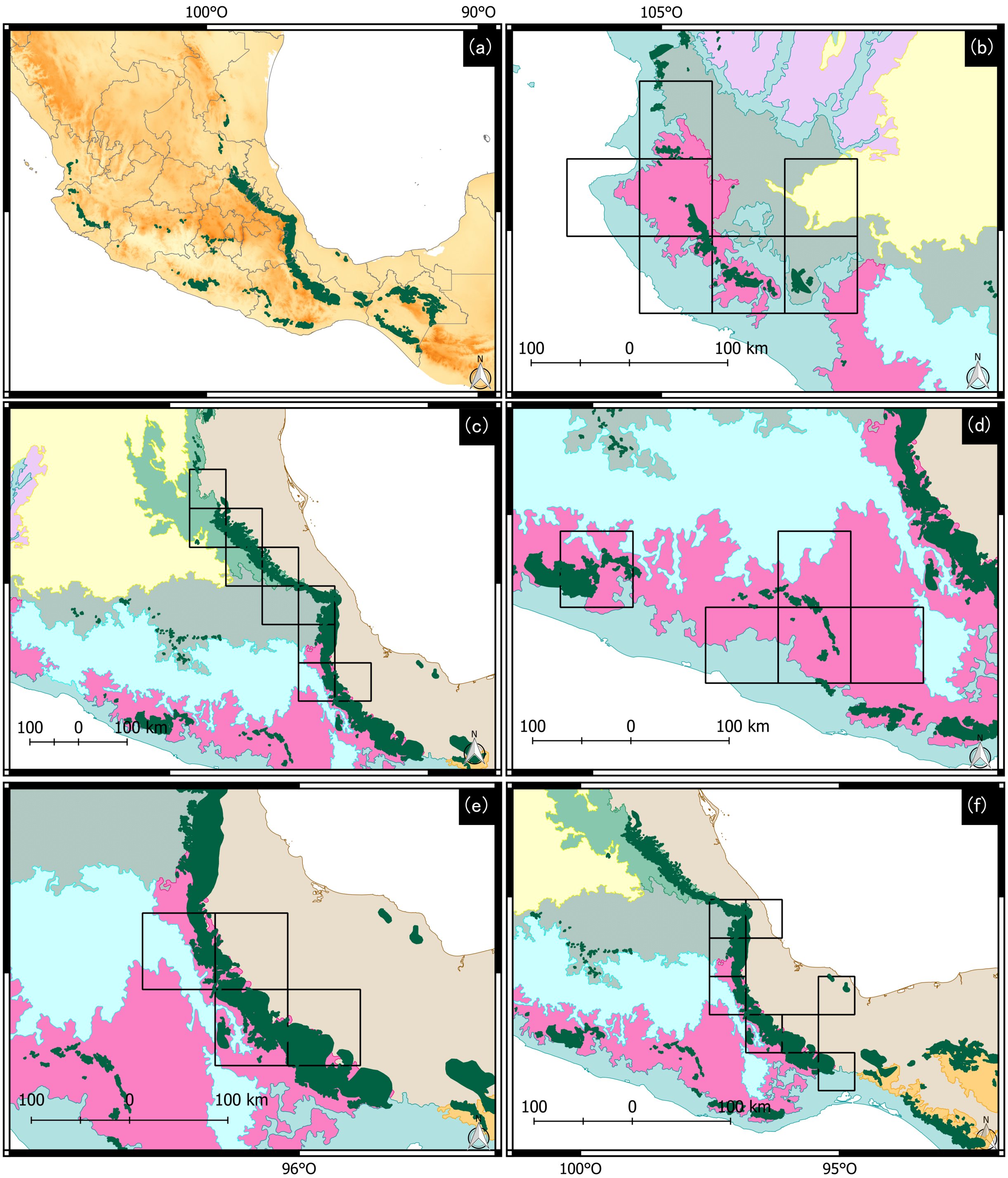

FIGURE 1. Study area and five areas of endemism are shown. (a) Mexican cloud forest; (b) Western Mexico; (c) Northern Gulf of Mexico; (d) Southern Mexico; (e) Northern Oaxaca; (f) Central Gulf of Mexico. Study area and biogeographic provinces names are shown in legend.

Results

Areas of endemism:—The matrix with the latitude-longitude cell size of 0.5° consisted of 30 columns and 18 rows, with a total of 540 cells, of which only 88 (16.3%) were occupied with at least one record. The analysis performed with this matrix recovered five areas, and with the strict consensus analysis four consensus areas (CA) were recognized with 28 endemic species (CA 1 to 4 in Table 1).

The matrix with the latitude-longitude cell size of 0.7° consisted of 22 columns and 13 rows, with a total of 286 cells, of which only 57 (19.9%) were occupied with at least one record. The analysis performed with this matrix recovered 10 areas, and with the strict consensus analysis five CA were identified with 36 endemic species (CA 5 to 9 in Table 1).

TABLE 1. Characteristics of areas of endemism and consensus areas of the Mexican endemic epipthytes bromeliads and orchids species.

Areas of Endemism	Consensus Areas	Cell size (°)	Cells number	EI score	Endemic species (I_{EX} scores)
Western Mexico	1	0.5	7	3.361	*Leochilus crocodiliceps* (0.643), *Meyracillum gemma* (0.556), *Rossioglossum splendes* (0.643), *Stanhopea martiana* (0.714), *Stelis xerophila* (0.556)
	5	0.7	7	3.425	*Laelia crawshayana* (0.75), *Leochilus crocodiliceps* (0.643), *Meiracyllium gemma* (0.611), *Rossioglossum splendens* (0.75), *Stanhopea martiana* (0.875), *Stelis xerophila* (0.714)
Northern Gulf of Mexico	2	0.5	7	3.575	*Encyclia candollei* (0.8), *Epidendrum longipetalum* (0.792), *Laelia anceps* (0.643), *Mormodes maculata* var. *unicolor* (0.65), *Oestlundia cyanocolumna* (0.75), *Stanhopea tigrina* (0.7), *Tillandsia heterophylla* (0.643), *T. imperialis* (0.5), *T. limbata* (0.714)
	6	0.7	10	4.448	*Encyclia candollei* (0.8), *Epidendrum longipetalum* (0.792), *Laelia anceps* (0.643), *Mormodes maculata* var. *unicolor* (0.65), *Oestlundia cyanocolumna* (0.75), *Stanhopea tigrina* (0.7), *Tillandsia imperialis* (0.5), *T. heterophylla* (0.643), *T. limbata* (0.714)
Southern Mexico	3	0.5	4	3.625	*Acianthera chrysantha* (0.75), *Artorima erubescens* (0.75), *Isochilus langlassei* (0.583), *Lepanthes yuvilensis* (0.75), *Oncidium oblongatum* (0.5), *Pachyphyllum mexicanum* (0.75), *Prosthechea obpiribulbon* (0.75), *Rhynchostele candidula* (0.75)
	7	0.7	5	5.25	*Acianthera chrysantha* (0.75), *Artorima erubescens* (0.75), *Isochilus langlassei* (0.583), *Lepanthes yuvilensis* (0.75), *Oncidium oblongatum* (0.5), *Pachyphyllum mexicanum* (0.75), *Prosthechea obpiribulbon* (0.75), *Rhynchostele candidula* (0.75)
Northern Oaxaca	4	0.5	6	4.417	*Lepanthes aprica* (0.75), *L. chiangii* (0.833), *L. erythroxantha* (1), *L. galeottiana* (1), *L. moorei* (0.875), *L. rekoi* (0.667)
	8	0.7	4	3.25	*Lepanthes aprica* (0.75), *L. catlingii* (0.75), *L. chiangii* (0.75), *L. rekoi* (0.75)
Central Gulf of Mexico	9	0.7	8	3.704	*Homalopetalum pumilum* (0.667), *Lepanthes avis* (0.7), *Oestlundia luteorosea* (0.7), *Rhynchostele ehrenbergii* (0.917), *Stelis nagelii* (0.4), *S. oaxacana* (0.75), *S. veracrucencis* (0.429), *Tillandsia kirchhoffiana* (0.571), *Werauhia vanhyningii* (0.65)

Note: Area endemicity index (EI); species endemicity index (I_{EX}).

The species composition of the consensus areas is the same for areas two and six and for areas three and seven; the one and five areas shared five of six species, while areas four and eight shared four of seven species (Table 1). The IE values were higher in all consensus areas obtained with cell size of 0.7° latitude-longitude, except in area eight (Table 1). The geographical location and the number of cells between the CAs obtained with both cell sizes is very similar. We recognized as areas of endemism the five consensus areas obtained with the cell size of 0.7°, namely: Western Mexico, Northern Gulf of Mexico, Southern Mexico, Northern Oaxaca, and Central Gulf of Mexico (Table 1; Fig. 1; Fig. 2).

The Gulf of Mexico slope AEs were supported by species of both families, while those from the Pacific slope were supported only by orchid species. The number of endemic species in each AE varied from four to nine. Both Northern Gulf of Mexico and Central Gulf of Mexico AEs present the highest species number (9), whereas Northern Oaxaca presents the lowest (4; Table 1). The AEs were described according to its endemic species, to its geographical location and the biogeographic region that they occupy. The biogeographic regions follows the biogeographical regionalization proposed by Morrone *et al.* (2017).

Western Mexico AE:—Seven cells constitute this area and is located in western Jalisco and northern Colima; it includes the western end of the Sierra Madre del Sur (Sierra del Tuito, Sierra de Cuale, Sierra de Cacoma y Sierra de Manantlán), and the western end of the Transmexican Volcanic Belt (Colima and Nayarit volcanoes) biogeographic provinces (Fig. 1b) (Morrone, 2017). Its geographical limits are between 19.2° and 21.3° N, and 103.1° and 105.2° W. Forty-four endemic species occur in this area, 43 orchids and only one bromeliad (Appendix 2); it is supported by six orchid species (*Laelia crawshayana* Rchb. f., *Leochilus crocodiliceps* (Rchb. f.) Kraenzl., *Meiracyllum gemma* Rchb. f., *Rossioglossum splendens* (Rchb. f.) Garay & G. C. Kenn, *Stanhopea martiana* Bateman ex Lindl., and *Stelis xerophila* (Schltr.) Soto Arenas) with an EI = 3.425 (Table 1; Fig. 2e). All species occur between 1000–2300 m elev.

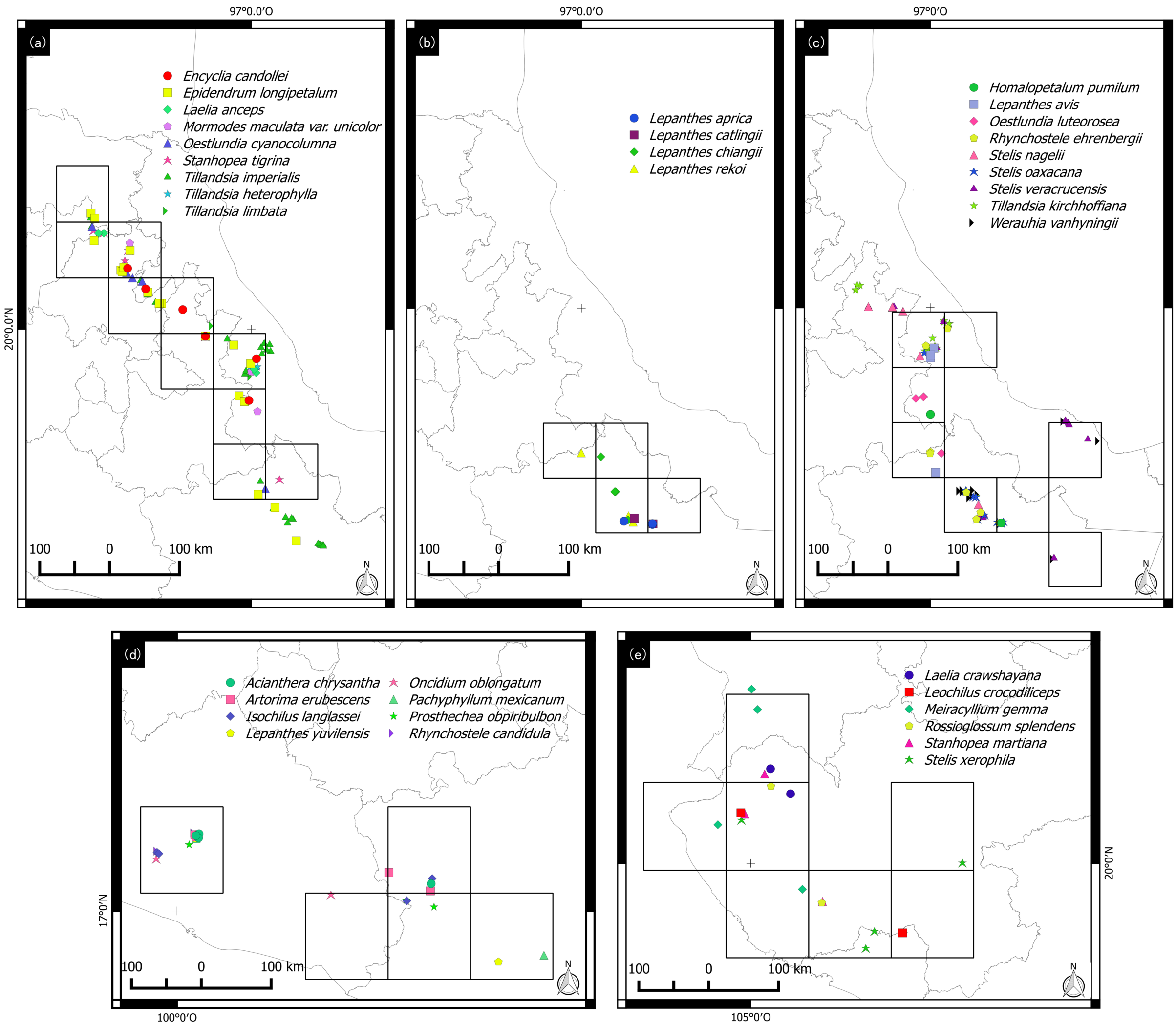

FIGURE 2. Species distributions that support the areas of endemism in the Mexican cloud forest; (a) Northern Gulf of Mexico; (b) Northern Oaxaca; (c) Central Gulf of Mexico; (d) Western Mexico; (e) Southern Mexico.

Northern Gulf of Mexico AE:—This is the largest area, it is formed by ten cells and is located in the Carso Huasteco (Querétaro, Hidalgo and North of Puebla), Sierra Norte de Puebla and Sierra Negra (Puebla), Sierra de Zongolica (Veracruz), and Sierra de Juárez (North of Oaxaca); it is located, mainly, along the Sierra Madre Oriental biogeographic province, but includes portions of the Transmexican Volcanic Belt, Veracruzan, and Sierra Madre del Sur biogeographic provinces (Fig. 1c). Its geographical limits are between 17.8° and 22.0° N, and 96.1° and 99.6° W. Fifthy-two endemic species were registered in this area 36 orchids and 16 bromeliads (Appendix 2); it was supported only by nine species, six orchids (*Encyclia candollei* (Lindl.) Schltr., *Epidendrum longipetalum* A. Rich. & Galeotti, *Laelia anceps* Lindl., *Mormodes maculata var. unicolor* (Hook.) L. O. Williams, *Oestlundia cyanocolumna* (Ames, F. T. Hubb. & C. Schweinf.) W. E. Higgins, and *Stanhopea tigrina* Bateman ex. Lindl.) and three bromeliads (*Tillandsia imperialis* E. Morren ex Mez, *T. heterophylla* E. Morren, and *T. limbata* Schltdl.), with an EI = 4.448 (Table 1; Fig. 2a). The elevational range of all species varied from 800–2800 m.

Southern Mexico AE:—This area is composed by five cells and is located the Guerrero and Oaxaca Highlands in the Sierra Madre del Sur biogeographic province (Fig. 1d); it is a discontinuous area, one cell is located in the surroundings of Cerro Teotepec in the center of the state of Guerrero, the other four cells are located in the Sierra del Sur Oaxaca region. Its geographical limits are located between 16.4° and 17.8° N, and 95.4° and 97.5° W. Fifthy-three endemic species were registered, 43 orchids and 10 bromeliads (Appendix 2); it was supported by eight orchids species: *Acianthera chrysantha* (Lindl.) Pridgeon & M. W. Chase, *Artorima erubescens* (Lindl.) Dressler & G. E. Pollard, *Isochilus langlassei* Schltr., *Lepanthes yuvilensis* Catling, *Oncidium oblongatum* Lindl., *Pachyphyllum mexicanum* Dressler & Hágsater, *Prosthechea obpiribulbon* (Hágsater) W. E. Higgins, and *Rhynchostele candidula* (Rchb. f.) Soto Arenas & Salazar, with an EI = 5.25 (Table 1; Fig. 2d). The elevation where species occurred ranges from 780–2700 m.

Northern Oaxaca AE:—This area is the smallest and is constituted by four cells, two of them are shared with Northern Gulf of Mexico AE and three cells with Central Gulf of Mexico AE. Is placed in the Sierra Mazateca northern Oaxaca and southern Puebla and in the Sierra de Zongolica Veracruz; it is in the Oaxacan Highlands district of the Sierra Madre del Sur biogeographic province (Fig. 1e). Its geographical limits are between 17.1° and 18.5° N, and 95.4° and 97.5° W. Forty-five endemic species occur in this area, 39 orchids and 6 bromeliads (Appenidx 2); it was supported by four orchid species, all of them from *Lepanthes* genus: *L. aprica* Catling & V. R. Catling, *L. catlingii* Salazar, Soto Arenas & O. Suárez, *L. chiangii* Salazar, Soto Arenas & O. Suárez, and *L. rekoi* R. E. Schult. With an EI = 3.25 (Table 1; Fig. 2b). All species occurred between 780–2600 m elev.

Central Gulf of Mexico AE:—This area is composed by eight cells and is located in the Sierra Mazateca northern and central Oaxaca, reaching the Tuxtlas region in Veracruz; it is located in portions of Transmexican Volcanic Belt, Veracruzan, and Sierra Madre del Sur biogeographic provinces (Fig. 1f). Its geographical limits are located between 16.4° and 19.8° N, and 94.6 and 97.4° W. Sixty-seven species were registered in this area, 52 orchids and 15 bromeliads (Appendix 2); it is supported by nine species, seven orchids (*Homalopetalum pumilum* (Ames) Dressler, *Lepanthes avis* Rchb. f., *Oestlundia luteorosea* (A. Rich. & Galeotti) W. E. Higgins, *Rhynchostele ehrenbergii* (Link, Klotzsch & Otto) Soto Arenas & Salazar, *Stelis nagelii* Solano, *S. oaxacana* Solano, and *S. veracrucencis* Solano) and two bromeliads (*Tillandsia kirchhoffiana* Wittm. and *Werauhia vanhyningii* (L. B. Sm.) J. R. Grant), with an EI = 3.704 (Table 1; Fig. 2c). The elevational range of all species varies from 800–2600 m.

Relationships among areas of endemism:—The PAE of the AEs generated a single area cladogram with 177 steps, a consistency index of 0.87 and a retention index of 0.78 (Fig. 3). In the cladogram there are two clades, clade A including the Western and Southern Mexico areas of endemism, and clade B including the Northern Gulf of Mexico, Northern Oaxaca and Central Gulf of Mexico areas of endemism (Fig. 3). Clade A is supported by 11 species, 10 orchids (*Acianthera hartwegiifolia*, *Encyclia adenocaula*, *Gongora galeottiana*, *Oncidium ghiesbreghtianum*, *O. karwinskii*, *O. reichenheimii*, *Prosthechea trulla*, *Rhynchostele cervantesii*, *R. maculata*, and *Stelis rufobrunnea*) and only one bromeliad (*Tillandsia prodigiosa*; Fig. 3). Clade B is supported by 25 species, 21 orchids (*Alamania punicea*, *Arpophyllum laxiflorum*, *Epidendrum longipetalum*, *E. tuxtlense*, *Gongora galeata*, *Homalopetalum pumilum*, *Isochilus unilateralis*, *Lepanthes attenuata*, *L. avis*, *L. chiangii*, *L. mazatlanensis*, *L. rekoi*, *Oestlundia cyanocolumna*, *O. luteorosea*, *Oncidium incurvum*, *Rhynchostele cordata*, *R. ehrenbergii*, *Stanhopea tigrina*, *Stelis nagelii*, *S. oaxacana*,and *S. veracrucensis*) and four bromeliads (*Tillandsia gymnobotrya*, *T. imperialis*, *T. kirchhoffiana*, and *Werauhia vanhyningii*; Fig. 3).

In clade B, the Northern Gulf of Mexico AE is branched out first, and is supported by seven species, four orchids (*Epidendrum lignosum, Habenaria virens, Lepanthes moorei*, and *Prosthechea mariae*) and three bromeliads (*Pitcairnia ringens, Tillandsia bartramii*, and *T. parryi*; Fig. 3). In the next place, there is a dichotomy between Northern Oaxaca and Central Gulf of Mexico. This relationship is supported by 19 species, 17 orchids (*Anathallis greenwoodii*, *Camaridium atratum*, *Lepanthes acuminata* subsp. *acuminata*, *L. aprica*, *L. calopetala*, *L. catlingii*, *L. erythroxantha*, *L. gabriellae*, *L. galeottiana*, *L. greenwoodii*, *L. machorroi*, *L. moorei*, *L. schultesii*, *L. suarezii*, *L. thurstoniorum*, *L. totontepecensis*, and *Ornithidium tonsoniae*) and two bromeliads (*Catopsis compacta* and *Racinaea rothschuhiana*; Fig. 3). The PAE did not support the endemicity of the Northern Oaxaca area of endemism.

According to the PAE, all areas of endemism present exclusive species except the area Northern Oaxaca. Southern Mexico presented the highest number of exclusive species with 38, followed by Western Mexico with 29, both areas localized on the Pacific Ocean slope. The areas of endemism with the lowest number of exclusive species were Northern Gulf of Mexico and Central Gulf of Mexico, with seven and three respectively (Fig. 3; Table 2).

TABLE 2. Exclusive species of the areas of endemism according to the cladogram obtained with PAE.

Clade	Area of Endemism	Exclusive species
A	Western Mexico	*Bulbophyllum cirrhosum, B. nagelii, Cuitlauzina pendula, Encyclia trachycarpa, Epidendrum anisatum, E. chlorops, E. gomezii, E. gonzalez-tamayoi, Erycina hyalinobulbon, Hintonella mexicana, Laelia autumnalis, L. crawshayana, L. speciosa, Leochilus crocodiliceps, Meiracyllium gemma, Oncidium hastatum, O. stelligerum, O. tigrinum, Prosthechea favoris, P. pastoris, P. pterocarpa, Rodriguezia dressleriana, Rossioglossum splendens, Stanhopea hernandezii, S. martiana, S. pseudoradiosa, Stelis retusa, S. sanguinolenta y S. xerophila.*
	Southern Mexico	*Acianthera chrysantha, Aechmea mexicana, Artorima erubescens, Camaridium rhombeum, Elleanthus teotepecensis, Epidendrum gasteriferum, E. magnificum, E. mocinoi, E. rowleyi, E. succulentum, E. tortipetalum, Isochilus langlassei, Laelia furfuracea, Lepanthes guerrerensis, L. hagsateri, L. nagelii, L. yuvilensis, Lockhartia galeottiana, Malaxis hagsateri, Nemaconia longipetala, Oncidium oblongatum, Pachyphyllum mexicanum, Ponera exilis, Prosthechea citrina, P. ghiesbreghtiana, P. mulasii, P. obpiribulbon, Rhynchostele candidula, Rossioglossum insleayi, Stelis desantiagoi, Tillandsia bourgaei, T. langlasseana, T. macdougallii, T. paraisoensis, T. pentasticha, T. quaquaflorifera, T. violacea* y *Viridantha plumosa.*
B	Northern Gulf of Mexico	*Epidendrum lignosum, Habenaria virens, Lepanthes moorei, Pitcairnia ringens, Prosthechea mariae, Tillandsia bartramii* y *T. parryi.*
	Northern Oaxaca	Without exclusive species.
	Central Gulf of Mexico	*Acianthera sotoana, Acineta hagsateri* y *Epidendrum dressleri.*

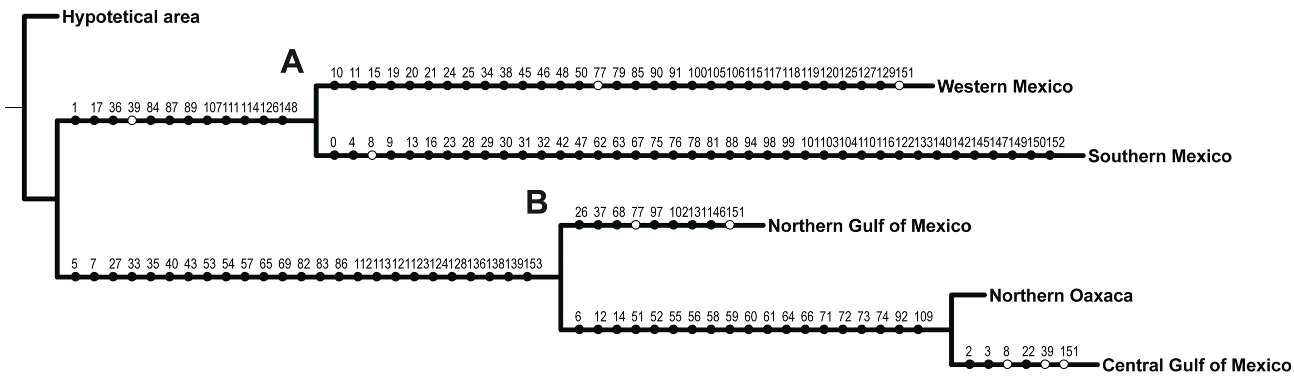

FIGURE 3. Single area cladogram of five areas of endemism of the Mexican endemic bromeliads and orchids. Species supporting the clades are shown (black circles), numbers above lines correspond to the species number as cited in Appendix 1.

Discussion

Areas of endemism:—The endemicity analysis allowed us to identify five AEs in the MCFs, supported by four to nine species, which suggests that the distribution of bromeliads and orchids epiphytic endemic species in the MCFs is not random, and therefore, their distributtion is the result of both ecological and historical factors.

Western Mexico AE: recovered in both analyses. It is supported by six endemic orchid species (Fig. 2e): *Laelia crawshayana* endemic to Jalisco and *Leochilus crocodiliceps* endemic to Jalisco and Colima. According to our data, *Meiracyllium gemma*, *Rossioglossum splendens, Stanhopea martiana*, and *Stelis xerophila* only have been collected in the Jalisco cloud forests. This AE is located in the Western Sierra Madre del Sur biogeographic subprovince, where endemic species from other biological groups have been reported: *Pinus jaliscana* Pérez de la Rosa (Pinaceae) and *Canthon riverain* Halffter & Halffter (Scarabaeideae), and also includes the Jalisciense (*Quercus cualensis* L. M. González and *Q. tuitensis* L. M. González) and Jalisciense-Manantlán (*Beilschmiedia manantlanensis* Cuevas & Cochrane, *Populus guzmanantlanensis* A. Vázquez & Cuevas, *Rhabdias manantlanensis* Martínez-Salazar, *Canthon occidentalis* Halfter & Rivera, and *C. riverain*) districts, each one with various endemic taxa (Morrone, 2017).

Northern Gulf of -Mexico AE: recovered in both analyses. It was supported by nine endemic species, six orchids and three bromeliads (Fig. 2a). The nine species are distributed from the Carso Huasteco (Querétaro, Hidalgo and North of Puebla), Sierra Norte de Puebla and Sierra Negra (Puebla), Sierra de Zongolica (Veracruz), and Sierra de Juárez (North of Oaxaca).

Southern Mexico AE: recovered in both analyses. It is supported by eight endemic orchid species (Fig. 2d); *Acianthera chrysantha, Artorima erubescens*, *Isochilus langlasesei, Lepanthes yuvilensis*, *Oncidium oblongatum*, *Pachyphyllum mexicanum*, *Prosthechea obpiribulbon* and *Rhynchostele candidula,* all endemic to Guerrero and Oaxaca. This area is located in the Guerrero and Oaxacan Highland districts of the Sierra Madre del Sur biogeographic province and a large number of endemisms from other groups (insects, amphibians, reptiles, birds and mammals) have been reported, including: *Elliptoleus whiteheadi* Liebherr*, Petrejoides imbellis* Casey*, Cotinis ibarrai* Deloya & Ratcliffe, *Onthophagus bassariscus* Zunino & Halfter, *O. chevrolati* Bates subsp. *omiltemus, O. semiopacus* Harold*, Gansia flavata* Ashe & Lingafelter*, Cyanolyca mirabilis* Nelson, *Handleyomys guerrerensis* Goodwin*, Megadontomys thomasi* Merriam*, Peromyscus mexicanus* Saussure subsp. *putlaensis* Goodwin*, Reithrodontomys bakeri* Bradely*, Méndez-Harclerode, Hamilton & Ceballos, Anolis dunni* Smith*, A. gadovii* Boulenger*, A. liogaster* Boulenger*, A. omiltemanus* Davis*, A. peucephilus* Cöler, Trejo-Pérez, Petersen & Méndez de la Cruz, *Sylvilagus insonus* Nelson*, Sceloporus adleri* Smith & Savitzky, *Plestiodon brevirostris* Günther*, Eupherusa poliocerca* Elliot, and *Lophornis brachylophus* Moore (Espinosa Organista *et al.*, 2008; Morrone, 2017; Morrone *et al.*, 2017).

Northern Oaxaca AE: recovered in both analyses. It is supported by four endemic orchid species (Fig. 2e); *Lepanthes aprica*, *L. catlingii,* and *L. chiangii*, all endemic to Oaxaca, and *L. rekoi* endemic to Oaxaca and Puebla. This area is placed in the Oaxacan Highlands district of the Sierra Madre del Sur biogeographic province. It is important to mention that this area shares two cells with the Northern Gulf of Mexico AE and three cells with Central Gulf of Mexico AE, in addition, in the PAE this AE was not supported by any species. The restricted distribution of the *Lepanthes* genus species allows us to recognize it as an area of endemism (Fig. 2e). Nevertheless, this could change as the floristic knowledge of the genus increases.

Central Gulf of Mexico AE: recovered only with the analysis of 0.7° cell size. It is supported by nine endemic species, seven orchids and two bromeliads: *Lepanthes avis* and *Stelis oaxacana* are endemic to Oaxaca and Veracruz, while *Stelis nagelii*, *S. veracrucensis* and *Tillandsia kirchhoffiana* are distributed in the three states in which this AE is located. According with our data, *Homalopetalum pumilum*, *Oestlundia luteorosea, Rhynchostele ehrenbergi*, and *Werauhia vanhyningii* only have been collected in the cloud forests of this area, located in the Transmexican Volcanic Belt, Veracruzan and Sierra Madre del Sur biogeographic provinces, including a portion of the Oaxacan Highlands District of the last biogeographic province.

The Oaxacan Highlands district of the Sierra Madre del Sur biogeographic province is an interesting region, because it makes part of three of the AEs recognized in this study (Northern Gulf of Mexico, Central Gulf of Mexico and Northern Oaxaca). Furthermore, Morrone (2017) reported 35 endemic species of plants and animals from this region, suggesting that it is a rich area in endemics.

Munguía-Lino *et al.* (2016) using the Tigridieae plant family species from North America recognized six areas of endemism, four of them (Low and High western Mexico, Southern Mexico and Central-southern Mexico) have a very similar geographic location with three areas of endemism (Western Mexico, Southern Mexico and Northern Oaxaca) recognized in the present work. On the other hand, Escalante *et al.* (2009) using Mexican mammals' data, recognized 16 areas of endemism, unfortunately, some of them overlaps, so that more than one area of endemism coincides, in general, with the geographical position of the five areas recognized here. Although these authors included the entire national territory and used different cell sizes and different biological groups, they recognized areas of endemism with similar geographical location that those reported by our results.

Relationships among areas of edemism:—The cladogram here obtained shows two well-supported clades, clade A formed by both Western Mexico and Southern Mexico AEs and clade B formed by the AEs Northern Gulf of Mexico, Northern Oaxaca and the Central Gulf of Mexico (Fig. 3). Therefore, we have two cloud forest groups with a very different floristic composition. Clade A is supported by 11 species, all of them from the family Orchidaceae with distribution along the Pacific Ocean slope. Clade B is supported by 25 species, five of the Bromeliaceae family, with distribution along Gulf of Mexico slope. These results suggest that it is not possible to propose a hypothesis of primary spatial homology between clades A and B, because they do not share species, what could indicate that the Pacific Ocean Slope AEs and the Gulf of Mexico Slope AEs has a different evolutionary history.

Rzedowski (2006), based on the large number of exclusive families and on the richness of taxa with restricted distribution that inhabit the cloud forests, suggested that this type of vegetation exists in Mexico since the Eocene (56 My) or perhaps earlier. On the other hand, Rzedowski (1996) and Cevallos-Ferriz *et al.* (2012) mentioned that the large proportion of endemic species present in cloud forests is the result of its present fragmented distribution, and therefore, they suggested that the cloud forest distribution should had been continuous during some past geological periods, and its current distribution could be considered relictual. In the same way, Luna Vega *et al.* (1999) agree with the idea that the MCFs distribution was a continuous in the past, and suggested that the MCFs is a natural biogeographic unit that has gradually been fragmented until reaching its current distribution.

Based on the area cladogram presented in this study (Fig. 3), we can propose two hypotheses of primary spatial homology, the first between clade A EAs and the second between clade B AEs. The different floristic composition that exists in both oceanic slopes could be explained by several dispersal and speciation events. Some orchids and bromeliads genera are presented in both oceanic slopes as *Laelia*, *Rhynchostele*, *Lepanthes*, and *Tillandsia*, among others, however, they have species restricted to one or another oceanic slope. Other genera are only present in a single oceanic slope as *Artorima*, *Meyracillum* and *Rossioglossum*, among others. This suggests that the MCFs were already established when the epiphytic groups dispersed.

The divergence times of bromeliads subfamilies and orchids subtribus, represented in this study, are 29 and 14 My, respectively (Givnish *et al.*, 2011, 2015); considering those divergence times, then, the dispersal of these groups is relatively recent with respect to the oldest date of cloud forest establishment (56 My) proposed by Rzedowski (1996); this suggests too, that the cloud forest had already been established when the epiphytes groups arrived.

The ecological succession theory postulates that the floristic composition changes over time until reaching the climax, that is, in an ecological succession process lichens are considered as pioneer elements, then the grasses, the shrubs and finally the arboreal elements are established, reaching, at this point, the vegetation climax that allows the epiphytes establishment (Cuevas-Reyes & Vega-Gutiérrez, 2012; Odum & Barret, 2006). Based on the ecological succession theory, phorophytes had to be established first and then the epiphytic groups, this could be another explanation of why our results do not support the hypothesis that the MCF had a continuous distribution in the past.

Primary biogeographical homology refers to a conjecture about a common biogeographic history, which postulates that different taxa are spatio-temporally integrated into the same biota. As the epiphytic groups studied in the present work did not allow us to propose a hypothesis of primary spatial homology between Gulf Slope EAs and Pacific Slope AEs, this could suggest that the MCF of both slopes does not have a common biogeographic history, as has been suggested by Luna Vega *et al.* (1999), Rzedowski (1996) and Cevallos-Ferriz *et al.* (2012). However, we must not forget that the epiphytic groups are relatively recent groups and that they surely arrived later than the establishment of the MCF.

Areas of endemism and conservation:—The Southern Mexico AE presented the greatest richness of exclusive species with 38 followed by Western Mexico with 29. These areas comprise portions of the Hidalgo, Querétaro, Puebla, Colima, Jalisco, Veracruz, Guerrero and Oaxaca states; the last four, according to Espejo Serna (2012), are among the first five states with highest number of endemic species. The species of both Gulf of Mexico AEs have a wide geographical distribution, while the species of both Pacific AEs have a restricted geographical distribution.

Finally, the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO, 2010) carried out an MCF regionalization, to prioritize its conservation. First, the main threats that put-on risk the permanence of this community were identified: timber resources overexploitation, agricultural activities, ownership land conflicts and climate change negative impacts. Second, three categories of priority conservation were stablished: critical, high and medium. A total of 44 subregions were recognized: 15 in critical category, 17 in high category, 10 in medium category and 3 without data. The five areas of endemism identified in this study are in 30 (68.2%) priority conservation subregions, of which 13 (86.7%) are in the critical category, 12 (70.6%) are in high category and five (50%) are in medium category. The Western Mexico AE includes four priority conservation subregions of high category and Central Gulf of Mexico and Northern Gulf of Mexico AEs include four priority conservation subregions of critical category and three of high category each one. These three AEs host the largest number of subregions with priority conservation (critical and high category), 18 (60%). For this reason, it is urgent to promote their conservation.

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Appendix 1

Data matrix used in the parsimony analysis of endemicity.

	Species	Areas of endemism					
		Hypotetical area	Western Mexico	Northern Gulf of Mexico	Southern Mexico	Northern Oaxaca	Central Gulf of Mexico
0	*Acianthera chrysantha*	0	0	0	1	0	0
1	*Acianthera hartwegiifolia*	0	1	0	1	0	0
2	*Acianthera sotoana*	0	0	0	0	0	1
3	*Acineta hagsateri*	0	0	0	0	0	1
4	*Aechmea mexicana*	0	0	0	1	0	0
5	*Alamania punicea*	0	0	1	0	1	1
6	*Anathallis greenwoodii*	0	0	0	0	1	1
7	*Arpophyllum laxiflorum*	0	0	1	0	1	1
8	*Arpophyllum spicatum*	0	0	0	1	0	1
9	*Artorima erubescens*	0	0	0	1	0	0
10	*Bulbophyllum cirrhosum*	0	1	0	0	0	0
11	*Bulbophyllum nagelii*	0	1	0	0	0	0
12	*Camaridium atratum*	0	0	0	0	1	1
13	*Camaridium rhombeum*	0	0	0	1	0	0
14	*Catopsis compacta*	0	0	0	0	1	1
15	*Cuitlauzina pendula*	0	1	0	0	0	0
16	*Elleanthus teotepecensis*	0	0	0	1	0	0
17	*Encyclia adenocaula*	0	1	0	1	0	0
18	*Encyclia candollei*	0	0	1	0	0	1
19	*Encyclia trachycarpa*	0	1	0	0	0	0
20	*Epidendrum anisatum*	0	1	0	0	0	0
21	*Epidendrum chlorops*	0	1	0	0	0	0
22	*Epidendrum dressleri*	0	0	0	0	0	1
23	*Epidendrum gasteriferum*	0	0	0	1	0	0
24	*Epidendrum gomezii*	0	1	0	0	0	0
25	*Epidendrum gonzalez-tamayoi*	0	1	0	0	0	0
26	*Epidendrum lignosum*	0	0	1	0	0	0
27	*Epidendrum longipetalum*	0	0	1	0	1	1
28	*Epidendrum magnificum*	0	0	0	1	0	0
29	*Epidendrum mocinoi*	0	0	0	1	0	0
30	*Epidendrum rowleyi*	0	0	0	1	0	0
31	*Epidendrum succulentum*	0	0	0	1	0	0
32	*Epidendrum tortipetalum*	0	0	0	1	0	0
33	*Epidendrum tuxtlense*	0	0	1	0	1	1
34	*Erycina hyalinobulbon*	0	1	0	0	0	0
35	*Gongora galeata*	0	0	1	0	1	1
36	*Gongora galeottiana*	0	1	0	1	0	0
37	*Habenaria virens*	0	0	1	0	0	0
38	*Hintonella mexicana*	0	1	0	0	0	0
39	*Homalopetalum pachyphyllum*	0	1	0	1	0	1
40	*Homalopetalum pumilum*	0	0	1	0	1	1
41	*Isochilus bracteatus*	0	1	1	1	0	0
42	*Isochilus langlassei*	0	0	0	1	0	0
43	*Isochilus unilateralis*	0	0	1	0	1	1

...continued on the next page

Appendix 1. (Continued)

	Species	Areas of endemism					
		Hypotetical area	Western Mexico	Northern Gulf of Mexico	Southern Mexico	Northern Oaxaca	Central Gulf of Mexico
45	*Laelia autumnalis*	0	1	0	0	0	0
46	*Laelia crawshayana*	0	1	0	0	0	0
47	*Laelia furfuracea*	0	0	0	1	0	0
48	*Laelia speciosa*	0	1	0	0	0	0
49	*Leochilus carinatus*	0	0	1	0	0	1
50	*Leochilus crocodiliceps*	0	1	0	0	0	0
51	*Lepanthes acuminata* subsp. *acuminata*	0	0	0	0	1	1
52	*Lepanthes aprica*	0	0	0	0	1	1
53	*Lepanthes attenuata*	0	0	1	0	1	1
54	*Lepanthes avis*	0	0	1	0	1	1
55	*Lepanthes calopetala*	0	0	0	0	1	1
56	*Lepanthes catlingii*	0	0	0	0	1	1
57	*Lepanthes chiangii*	0	0	1	0	1	1
58	*Lepanthes erythroxantha*	0	0	0	0	1	1
59	*Lepanthes gabriellae*	0	0	0	0	1	1
60	*Lepanthes galeottiana*	0	0	0	0	1	1
61	*Lepanthes greenwoodii*	0	0	0	0	1	1
62	*Lepanthes guerrerensis*	0	0	0	1	0	0
63	*Lepanthes hagsateri*	0	0	0	1	0	0
64	*Lepanthes machorroi*	0	0	0	0	1	1
65	*Lepanthes mazatlanensis*	0	0	1	0	1	1
66	*Lepanthes moorei*	0	0	0	0	1	1
67	*Lepanthes nagelii*	0	0	0	1	0	0
68	*Lepanthes papilionacea*	0	0	1	0	0	0
69	*Lepanthes rekoi*	0	0	1	0	1	1
70	*Lepanthes schiedei*	0	0	1	0	0	1
71	*Lepanthes schultesii*	0	0	0	0	1	1
72	*Lepanthes suarezii*	0	0	0	0	1	1
73	*Lepanthes thurstoniorum*	0	0	0	0	1	1
74	*Lepanthes totontepecensis*	0	0	0	0	1	1
75	*Lepanthes yuvilensis*	0	0	0	1	0	0
76	*Lockhartia galeottiana*	0	0	0	1	0	0
77	*Lycaste crinita*	0	1	1	0	0	0
78	*Malaxis hagsateri*	0	0	0	1	0	0
79	*Meiracyllium gemma*	0	1	0	0	0	0
80	*Mormodes maculata* var. *unicolor*	0	0	1	0	0	1
81	*Nemaconia longipetala*	0	0	0	1	0	0
82	*Oestlundia cyanocolumna*	0	0	1	0	1	1
83	*Oestlundia luteorosea*	0	0	1	0	1	1
84	*Oncidium ghiesbreghtianum*	0	1	0	1	0	0
85	*Oncidium hastatum*	0	1	0	0	0	0
86	*Oncidium incurvum*	0	0	1	0	1	1
87	*Oncidium karwinskii*	0	1	0	1	0	0
88	*Oncidium oblongatum*	0	0	0	1	0	0

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Appendix 1. (Continued)

	Species	Areas of endemism					
		Hypotetical area	Western Mexico	Northern Gulf of Mexico	Southern Mexico	Northern Oaxaca	Central Gulf of Mexico
90	*Oncidium stelligerum*	0	1	0	0	0	0
91	*Oncidium tigrinum*	0	1	0	0	0	0
92	*Ornithidium tonsoniae*	0	0	0	0	1	1
93	*Ornithocephalus tripterus*	0	0	1	0	0	1
94	*Pachyphyllum* mexicanum	0	0	0	1	0	0
95	*Papperitzia leiboldii*	0	0	1	0	0	1
96	*Pitcairnia densiflora*	0	0	1	0	0	1
97	*Pitcairnia ringens*	0	0	1	0	0	0
98	*Ponera exilis*	0	0	0	1	0	0
99	*Prosthechea citrina*	0	0	0	1	0	0
100	*Prosthechea favoris*	0	1	0	0	0	0
101	*Prosthechea ghiesbreghtiana*	0	0	0	1	0	0
102	*Prosthechea mariae*	0	0	1	0	0	0
103	*Prosthechea mulasii*	0	0	0	1	0	0
104	*Prosthechea obpiribulbon*	0	0	0	1	0	0
105	*Prosthechea pastoris*	0	1	0	0	0	0
106	*Prosthechea pterocarpa*	0	1	0	0	0	0
107	*Prosthechea trulla*	0	1	0	1	0	0
108	*Prosthechea varicosa*	0	0	1	1	1	1
109	*Racinaea rothschuhiana*	0	0	0	0	1	1
110	*Rhynchostele candidula*	0	0	0	1	0	0
111	*Rhynchostele cervantesii*	0	1	0	1	0	0
112	*Rhynchostele cordata*	0	0	1	0	1	1
113	*Rhynchostele ehrenbergii*	0	0	1	0	1	1
114	*Rhynchostele maculata*	0	1	0	1	0	0
115	*Rodriguezia dressleriana*	0	1	0	0	0	0
116	*Rossioglossum insleayi*	0	0	0	1	0	0
117	*Rossioglossum splendens*	0	1	0	0	0	0
118	*Stanhopea hernandezii*	0	1	0	0	0	0
119	*Stanhopea martiana*	0	1	0	0	0	0
120	*Stanhopea pseudoradiosa*	0	1	0	0	0	0
121	*Stanhopea tigrina*	0	0	1	0	1	1
122	*Stelis desantiagoi*	0	0	0	1	0	0
123	*Stelis nagelii*	0	0	1	0	1	1
124	*Stelis oaxacana*	0	0	1	0	1	1
125	*Stelis retusa*	0	1	0	0	0	0
126	*Stelis rufobrunnea*	0	1	0	1	0	0
127	*Stelis sanguinolenta*	0	1	0	0	0	0
128	*Stelis veracrucensis*	0	0	1	0	1	1
129	*Stelis xerophila*	0	1	0	0	0	0
130	*Tillandsia alvareziae*	0	0	1	0	0	1
131	*Tillandsia bartramii*	0	0	1	0	0	0
132	*Tillandsia belloensis*	0	0	1	0	0	1
133	*Tillandsia bourgaei*	0	0	0	1	0	0
134	*Tillandsia deppeana*	0	0	1	0	0	1

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Appendix 1. (Continued)

	Species	Areas of endemism					
		Hypotetical area	Western Mexico	Northern Gulf of Mexico	Southern Mexico	Northern Oaxaca	Central Gulf of Mexico
136	*Tillandsia gymnobotrya*	0	0	1	0	1	1
137	*Tillandsia heterophylla*	0	0	1	0	0	1
138	*Tillandsia imperialis*	0	0	1	0	1	1
139	*Tillandsia kirchhoffiana*	0	0	1	0	1	1
140	*Tillandsia langlasseana*	0	0	0	1	0	0
141	*Tillandsia limbata*	0	0	1	0	0	1
142	*Tillandsia macdougallii*	0	0	0	1	0	0
143	*Tillandsia macrochlamys*	0	0	1	0	0	1
144	*Tillandsia nolleriana*	0	0	1	0	0	1
145	*Tillandsia paraisoensis*	0	0	0	1	0	0
146	*Tillandsia parryi*	0	0	1	0	0	0
147	*Tillandsia pentasticha*	0	0	0	1	0	0
148	*Tillandsia prodigiosa*	0	1	0	1	0	0
149	*Tillandsia quaquaflorifera*	0	0	0	1	0	0
150	*Tillandsia violacea*	0	0	0	1	0	0
151	*Trichocentrum pachyphyllum*	0	1	1	0	0	1
152	*Viridantha plumosa*	0	0	0	1	0	0
153	*Werauhia vanhyningii*	0	0	1	0	1	1

Appendix 2

Mexican endemic epiphytic species registered in the areas of endemism recognized in this work.

Western Mexico: Bromeliaceae: *Tillandsia prodigiosa* (Lem.) Baker. Orchidaceae: *Acianthera hartwegiifolia* (H. Wendl. & Kraenzl.) Solano & Soto Arenas, *Bulbophyllum cirrhosum* L. O. Williams, *B. nagelii* L. O. *Williams, Cuitlauzina pendula* Lex., *Encyclia adenocaula* (Lex.) Schltr., *E. trachycarpa* (Lindl.) Schltr.*, Epidendrum anisatum* Lex., *E. chlorops* Rchb. f., *E. gomezii* Schltr., *E. gonzalez-tamayoi* Hágsater, *Erycina hyalinobulbon* (Lex.) N. H. Williams & M. W. Chase, *Gongora galeottiana* A. Rich. & Galeotti, *Hintonella mexicana* Ames, *Homalopetalum pachyphyllum* (L. O. Williams) Dressler, *Isochilus bracteatus* (Lex.) Espejo & López-Ferr., *Laelia autumnalis* (Lex.) Lindl., *L. crawshayana* Rchb. f., *L. speciosa* (Kunth) Schltr., *Leochilus crocodiliceps* (Rchb. f.) Kraenzl., *Lycaste crinita* Lindl., *Meyracillum gemma* Rchb. f.; *Oncidium ghiesbreghtianum* A. Rich. & Galeotti, *O. hastatum* (Bateman) Lindl., *O. karwinskii* (Lindl.) Lindl., *O. reichenheimii* (Linden & Rchb. f.) Garay & Stacy, *O. stelligerum* Rchb. f., *O. tigrinum* Lex., *Prosthechea favoris* (Rchb. f.) W. E. Higgins, *P. pastoris* (Lex.) Espejo & López-Ferr., *P. pterocarpa* (Lindl.) W. E. Higgins, *P. trulla* (Rchb. f.) W. E. Higgins, *Rhynchostele cervantesii* (Lex.) Soto Arenas & Salazar, *R. maculata* (Lex.) Soto Arenas & Salazar, *Rodriguezia dressleriana* R. González, *Rossioglossum splendes* (Rchb. f.) Garay & G. C. Kenn., *Stanhopea hernandezii* (Kunth) Schltr., *S. martiana* Bateman ex Lindl.; *S. pseudoradiosa* Jenny & R. González, *Stelis retusa* (Lex.) Pridgeon & M. W. Chase, *S. rufobrunnea* (Lindl.) L. O. Williams, *S. sanguinolenta* (Garay & W. Kittr.) Solano, *S. xerophila* (Schltr.) Soto Arenas, *Trichocentrum pachyphyllum* (Hook.) R. Jiménez & Carnevali.

Northern Gulf of Mexico: Bromeliaceae: *Pitcairnia densiflora* Brongn. ex Lem., *P. ringens* Klotzsch, *Tillandsia alvareziae* Rauh, *T. bartramii* Elliott, *T. belloensis* W. Weber, *T. deppeana* Steud., *T. flavobracteata* Matuda, *T. gymnobotrya* Baker, *T. heterophylla* E. Morren, *T. imperialis* E. Morren ex Mez, *T. kirchhoffiana* Wittm., *T. limbata* Schltdl., *T. macrochlamys* Baker, *T. nolleriana* Ehlers, *T. parryi* Baker, *Werauhia vanhyningii* (L. B. Sm.) J. R. Grant. Orchidaceae*: Alamania punicea* Lex., *Arpophyllum laxiflorum* Pfitzer, *Encyclia candollei* (Lindl.) Schltr., *Epidendrum lignosum* Lex., *E. longipetalum* A. Rich. & Galeotti, *E. tuxtlense* Hágsater, García-Cruz & L. Sánchez, *Gongora galeata* (Lindl.) Rchb. f., *Habenaria virens* A. Rich. & Galeotti, *Homalopetalum pumilum* (Ames) Dressler, *Isochilus bracteatus* (Lex.) Espejo & López-Ferr., *I. unilateralis* B. L. Rob., *Laelia anceps* Lindl., *Lepanthes carinatus* (Knowles & Westc.) Lindl., *L. attenuata* Salazar, Soto Arenas & O. Suárez, *L. avis* Rchb. f., *L. chiangii* Salazar, Soto Arenas & O. Suárez, *L. mazatlanensis* R. Solano & Reynaud, *L. papilionacea* Salazar & Soto Arenas, *L. rekoi* R. E. Schult., *L. schiedei* Rchb. f., *Lycaste crinita* Lindl., *Mormodes maculata* var. *unicolor* (Hook.) L. O. Williams, *Oestlundia cyanocolumna* (Ames, F. T. Hubb. & C. Schweinf.) W. E. Higgins, *O. luteorosea* (A. Rich. & Galeotti) W. E. Higgins, *Oncidium incurvum* Barker ex Lindl., *Ornithocephalus tripterus* Schltr., *Papperitzia leiboldii* (Rchb. f.) Rchb. f., *Prosthechea mariae* (Ames) W. E. Higgins, *P. varicosa* (Bateman ex Lindl.) W. E. Higgins, *Rhynchostele cordata* (Lindl.) Soto Arenas & Salazar, *R. ehrenbergii* (Link, Klotzsch & Otto) Soto Arenas & Salazar, *Stanhopea tigrina* Batema ex. Lindl., *Stelis nagelii* Solano, *S. oaxacana* Solano, *S. veracrucensis* Solano, *Trichocentrum pachyphyllum* (Hook.) R. Jiménez & Carnevali.

Southern Mexico: Bromeliaceae: *Aechmea mexicana* Baker, *Tillandsia bourgaei* Baker, *T. langlasseana* Mez, *T. macdougallii* L. B. Sm., *T. paraisoensis* Ehlers, *T. pentasticha* Rauh & Wulfinghoff, *T. prodigiosa* (Lem.) Baker, *T. quaquaflorifera* Matuda, *T. violacea* Baker, *Viridantha plumosa* (Baker) Espejo. Orchidaceae*: Acianthera chrysantha* (Lindl.) Pridgeon & M. W. Chase, *A. hartwegiifolia* (H. Wendl. & Kraenzl.) Solano & Soto Arenas, *Arpophyllum spicatum* Lex., *Artorima erubescens* (Lindl.) Dressler & G. E. Pollard, *Camaridium rhombeum* (Lindl.) M. A. Blanco, *Elleanthus teotepecensis* Soto Arenas, *Encyclia adenocaula* (Lex.) Schltr., *Epidendrum gasteriferum* Scheeren, *E. magnificum* Schltr., *E. mocinoi* Hágsater, *E. rowleyi* Withner & Pollard, *E. succulentum* Hágsater, *E. tortipetalum* Scheeren, *Gongora galeottiana* A. Rich. & Galeotti, *Homalopetalum pachyphyllum* (L. O. Williams) Dressler, *Isochilus bracteatus* (Lex.) Espejo & López-Ferr., *I. langlassei* Schltr., *Laelia furfuracea* Lindl., *Lepanthes guerrerensis* Salazar & Soto Arenas, *L. hagsateri* Salazar & Soto Arenas, *L. nagelii* Salazar & Soto Arenas, *L. yuvilensis* Catling, *Lockhartia galeottiana* A. Rich. ex Soto Arenas, *Malaxis hagsateri* Salazar, *Nemaconia longipetala* (Correll) Van den Berg, Salazar & Soto Arenas, *Oncidium ghiesbreghtianum* A. Rich. & Galeotti, *O. karwinskii* (Lindl.) Lindl.*, O. oblongatum* Lindl., *O. reichenheimii* (Linden & Rchb. f.) Garay & Stacy, *Pachyphyllum mexicanum* Dressler & Hágsater, *Ponera exilis* Dressler, *Prosthechea citrina* (Lex.) W. E. Higgins, *P. ghiesbreghtiana* (A. Rich. & Galeotti) W. E. Higgins, *P. mulasii* Soto Arenas & L. Cerv., *P. obpiribulbon* (Hágsater) W. E. Higgins, *P. trulla* (Rchb. f.) W. E. Higgins, *P. varicosa* (Bateman ex Lindl.) W. E. Higgins, *Rhynchostele candidula* (Rchb. f.) Soto Arenas & Salazar, *R. cervantesii* (Lex.) Soto Arenas & Salazar, *R. maculata* (Lex.) Soto Arenas & Salazar, *Rossioglossum insleayi* (Baker ex Lindl.) Garay & G. C. Kenn., *Stelis desantiagoi* Solano & Salazar, *S. rufobrunnea* (Lindl.) L. O. Williams.

Northern Oaxaca: BROMELIACEAE: *Catopsis compacta* Mez, *Racinaea rothschuhiana* (L. B. Sm.) M. A. Spencer & L. B. Sm., *T. gymnobotrya* Baker, *T. imperialis* E. Morren ex Mez, *T. kirchhoffiana* Wittm., *Werauhia vanhyningii* (L. B. Sm.) J. R. Grant. ORCHIDACEAE*: Alamania punicea* Lex.*, Anathallis greenwoodii* Soto Arenas & Salazar*, Arpophyllum laxiflorum* Pfitzer, *Camaridium atratum* (Lex.) M. A. Blanco*, Epidendrum longipetalum* A. Rich. & Galeotti, *E. tuxtlense* Hágsater, García-Cruz & L. Sánchez, *Gongora galeata* (Lindl.) Rchb. f., *H. pumilum* (Ames) Dressler, *Isochilus unilateralis* B. L. Rob., *Lepanthes aprica* Catling & V. R. Catling, *L. acuminata* Schltr. subsp. *acuminata, L. attenuata* Salazar, Soto Arenas & O. Suárez, *L. avis* Rchb. f., *L. calopetala* Salazar & Soto Arenas, *L. catlingii* Salazar, Soto Arenas & O. Suárez, *L. chiangii* Salazar, Soto Arenas & O. Suárez, *L. erythroxantha* Salazar & Soto Arenas, *L. galeottiana* Salazar & Soto Arenas, *L. gabriellae* Salazar & Soto Arenas, *L. greenwoodii* Salazar & Soto Arenas, *L. machorroi* Salazar & Soto Arenas, *L. mazatlanensis* R. Solano & Reynaud, *L. moorei* C. Schweinf., *L. rekoi* R. E. Schult., *L. schultesii* Salazar & Soto Arenas, *L. suarezii* Salazar & Soto Arenas, *L. thurstoniorum* Salazar & Soto Arenas, *L. totontepecensis* Salazar & Soto Arenas, *Oestlundia cyanocolumna* (Ames, F. T. Hubb. & C. Schweinf.) W. E. Higgins, *O. luteorosea* (A. Rich. & Galeotti) W. E. Higgins, *Oncidium incurvum p*Barker ex Lindl., *Ornithidium tonsoniae* (Soto Arenas) Senghas, *Prosthechea varicosa* (Bateman ex Lindl.) W. E. Higgins, *Rhynchostele cordata* (Lindl.) Soto Arenas & Salazar, *R. ehrenbergii* (Link, Klotzsch & Otto) Soto Arenas & Salazar, *Stanhopea tigrina* Bateman ex. Lindl., *Stelis nagelii* Solano, *S. oaxacana* Solano, *S. veracrucensis* Solano.

Central Gulf of Mexico: BROMELIACEAE: *Catopsis compacta* Mez, *Pitcairnia densiflora* Brongn. ex Lem., *Racinaea rothschuhiana* (L. B. Sm.) M. A. Spencer & L. B. Sm., *Tillandsia alvareziae* Rauh, *T. belloensis* W. Weber, *T. deppeana* Steud., *T. flavobracteata* Matuda, *T. gymnobotrya* Baker, *T. heterophylla* E. Morren, *T. imperialis* E. Morren ex Mez, *T. kirchhoffiana* Wittm., *T. limbata* Schltdl., *T. macrochlamys* Baker, *T. nolleriana* Ehlers, *Werauhia vanhyningii* (L. B. Sm.) J. R. Grant. ORCHIDACEAE*: Acianthera sotoana* Solano, *Acineta hagsateri* Salazar & Soto *Arenas, Alamania punicea* Lex., *Anathallis greenwoodii* Soto Arenas & Salazar, *Arpophyllum laxiflorum* Pfitzer, *A. spicatum* Lex., *Camaridium atratum* (Lex.) M. A. Blanco, *Encyclia candollei* (Lindl.) Schltr., *Epidendrum dressleri* Hágsater, *E. longipetalum* A. Rich. & Galeotti, *E. tuxtlense* Hágsater, García-Cruz & L. Sánchez, *Gongora galeata* (Lindl.) Rchb. f., *Homalopetalum pachyphyllum* (L. O. Williams) Dressler, *H. pumilum* (Ames) Dressler, *Isochilus unilateralis* B. L. Rob., *Laelia anceps* Lindl., *Leochilus carinatus* (Knowles & Westc.) Lindl., *Lepanthes acuminata* Schltr. subsp. *acuminata, L. aprica* Catling & V. R. Catling, *L. attenuata* Salazar, Soto Arenas & O. Suárez, *L. avis* Rchb. f., *L. calopetala* Salazar & Soto Arenas, *L. catlingii* Salazar, Soto Arenas & O. Suárez, *L. chiangii* Salazar, Soto Arenas & O. Suárez, *L. erythroxantha* Salazar & Soto Arenas, *L. gabriellae* Salazar & Soto Arenas, *L. galeottiana* Salazar & Soto Arenas, *L. greenwoodii* Salazar & Soto Arenas, *L. machorroi* Salazar & Soto Arenas, *L. mazatlanensis* R. Solano & Reynaud, *L. moorei* C. Schweinf., *L. rekoi* R. E. Schult., *L. schiedei* Rchb. f., *L. schultesii* Salazar & Soto Arenas, *L. suarezii* Salazar & Soto Arenas, *L. thurstoniorum* Salazar & Soto Arenas, *L. totontepecensis* Salazar & Soto Arenas, *Mormodes maculata var. unicolor* (Hook.) L. O. Williams, *Oestlundia cyanocolumna* (Ames, F. T. Hubb. & C. Schweinf.) W. E. Higgins, *O. luteorosea* (A. Rich. & Galeotti) W. E. Higgins, *Oncidium incurvum* Barker ex Lindl., *Ornithidium tonsoniae* (Soto Arenas) Senghas, *Ornithocephalus tripterus* Schltr., *Papperitzia leiboldii* (Rchb. f.) Rchb. f., *Prosthechea varicosa* (Bateman ex Lindl.) W. E. Higgins, *Rhynchostele cordata* (Lindl.) Soto Arenas & Salazar, *R. ehrenbergii* (Link, Klotzsch & Otto) Soto Arenas & Salazar, *Stanhopea tigrina* Batema ex. Lindl., *Stelis nagelii* Solano, *S. oaxacana* Solano, *S. veracrucencis* Solano, *Trichocentrum pachyphyllum* (Hook.) R. Jiménez & Carnevali.