Historical biogeography of the Yucatan Peninsula, Mexico: a perspective from ferns (Monilophyta) and lycopods (Lycophyta)

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Based on known data sets and maximum entropy distribution data of fern and lycopod species registered in the Yucatán Peninsula, track and parsimony analyses were undertaken to evaluate the contribution of these groups to the establishment of biogeographical relationships of the peninsula with other areas. The resulting generalized tracks clearly agree with the geological origin of the peninsula and the previously recognized relationship with the Greater Antilles is not supported for ferns and lycopods. Instead, a Central American generalized track connects the Yucatán Peninsula with south-eastern México and Central America. Floristically, the peninsula harbours 66 species of ferns and lycopods. Seven are registered for the first time in the Yucatán Peninsula and one is a new species for México. These species do not follow the latitudinal pattern expected if ecological factors, such as humidity and rainfall, were the most important in determining their distributions. Groups of areas recognized with parsimony analysis of endemicity could not be defined as provinces as a result of the lack of endemic species. Nevertheless, a regionalization scheme based on maximum entropy distribution data and supported by track analyses is proposed. Two separate districts are recognized within the Yucatán Peninsula: arid/dry Yucatán in the north and El Petén (humid) in the south. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, **98**, 775–786.

ADDITIONAL KEYWORDS: floristics – grid-cell analysis – maximum entropy modelling – parsimony analysis of endemicity – regionalization – track analysis.

INTRODUCTION

From a biogeographical viewpoint, the Yucatán Peninsula may be broadly defined as a province comprising the entire territory of the Mexican states of Campeche, Quintana Roo, and Yucatán; adjacent portions of Tabasco and Chiapas; the El Petén department in Guatemala; and the northern half of Belize (Fig. 1) (Lundell, 1934; Miranda, 1958; Morrone, 2006). Accepting small differences in its delimitations (Barrera, 1964); Estrada-Loera, 1991); Espadas-Manrique, Durán & Argáez, 2003)), the peninsula is well accepted as a distinct biological province.

The 'core' of the Yucatán Peninsula (*sensu* Ibarra-Manríquez *et al.*, 2002), entirely comprises the Mexican states of Campeche, Quintana Roo, and Yucatán. This area consists of an unconfined flat lying karst landscape, which is recognized as being quite different from the rest of México in terms of geography, geology, diversity, and biota richness (Lundell, 1934; Smith, 1940; Goldman & Moore, 1946; Miranda, 1958; Barrera, 1964; Rzedowski, 1978; Estrada-Loera, 1991; Ferrusquía-Villafranca, 1993; Morrone, 2006), consequently, highlighting the need for the conservation of this diverse and unique region (Spellerberg & Sawyer, 1999). The region is devoid of surface water and is undergoing rapid change, which has increased concerns with respect to conservation and fresh water

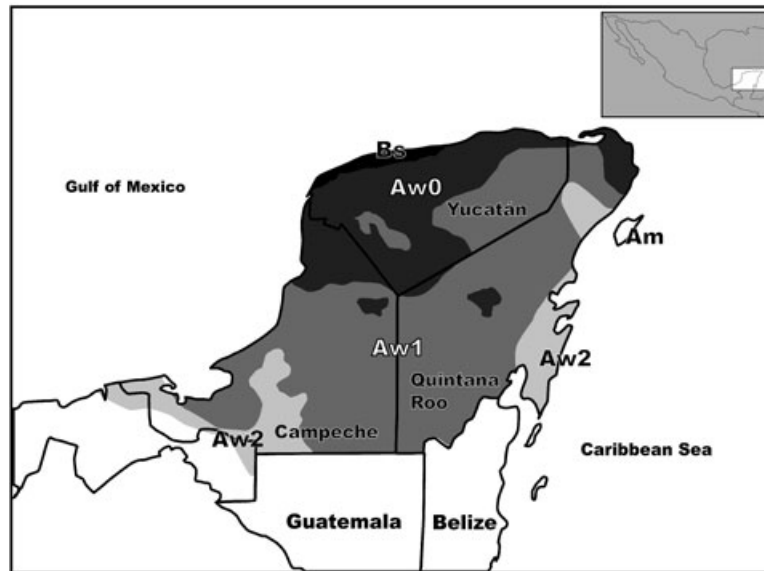*Corresponding author. E-mail: ilv@hp.fciencias.unam.mx

Figure 1. Political limits and prevailing climate (*sensu* García, 1990) of the core area of the Yucatan Peninsula. Am, tropical humid; Aw0, tropical subhumid, Lang's Index < 43.2 mm/m^2/C°; Aw1, tropical subhumid, Lang's Index 43.2 < 55.3 mm/m^2/C°; Aw2, tropical subhumid, Lang's Index > 55.3 mm/m^2/C°; BS, dry (arid and semi-arid).

availability, but sinkholes, locally called 'cenotes' by the Maya people, are widespread in the north, representing the most important hydrological features. It includes tropical dry deciduous forests, comprising ecosystems that are considered as some of the most threatened of the world, with little information on them being available.

Biogeographical examinations of the province's biota have been conducted from three different perspectives: (1) determination of the phytogeographical affinities of the peninsula with neighbouring areas, namely the Antillean flora (Rzedowski, 1978, 1991; Chiappy-Jhones *et al.*, 2001) or other Mesoamerican areas (Ibarra-Manríquez *et al.*, 2002); (2) assessment of endemism in its flora (mainly as a result of edaphic conditions); and (3) production of an intra-peninsular biogeographical regionalization. The latter has resulted in different proposals, as well as the number and extent of biotic units, although all of them coincide in demonstrating biotic differentiation between the northern and southern areas of the peninsula (Ibarra-Manríquez *et al.*, 2002).

The flora and vegetation of the Yucatán Peninsula have been studied from various perspectives (Standley 1939; Souza-Novelo 1945; Pennington & Sarukhán 1968; Rzedowski 1978; Cabrera, Sousa & Téllez, 1982; Thien, Bradburn & Welden 1982; Rico-Gray & García-Franco 1991, 1992; White & Darwin 1995; White & Hood 2004) and the association between climate and vegetation is quite clear.

Ferns (Monilophyta *sensu* Pryer *et al.*, 2004) are the second largest group of vascular plants, with appro-

ximately 9000 living species. Lycopods (Lycophyta *sensu* Pryer *et al.*, 2004) are a clade of spore-bearing plants comprising less than 1% of extant vascular plant species. Both groups have been historically lumped together (e.g. 'pteridophytes' and 'ferns and fern allies'), but are now recognized as distinct groups of vascular plants (Smith *et al.*, 2006), which are ecologically similar. Both groups are most common in wet and seasonally mild-mountains and uplands of tropical and subtropical regions, especially in cloud forests (Johns, 1985; Parris, 1985; Tryon, 1985). There are also secondary centres of diversity in some xeric and semi-xeric regions (Given, 1993), and the Yucatán Peninsula can be regarded as one, with approximately 60 species (approximately 6% of the total fern and lycopod flora of México) (Mickel & Smith, 2004).

Ferns and lycopods of the Yucatán Peninsula are mainly located around 'cenotes' (i.e. sinkholes), 'petenes', 'aguadas' (i.e. underground water sources), and 'oquedades' (i.e. hollows of archaeological ruins) because there are no major lakes and rivers in the peninsula and rainfall quickly infiltrates the ground to form underground run-offs. Species living in such environments would be expected to be highly adapted to the edaphic and hydrological conditions of the peninsula, and species richness should be concentrated in areas where these hydrological features are common (e.g. south-eastern Quintana Roo).

The goal of the present study is two-fold: (1) to evaluate the contribution of the fern and lycopod flora to the establishment of biogeographical relationships

of the Yucatán Peninsula province and (2) to propose a regionalization scheme based on the comparison of the results obtaned versus those from other studies based on different organisms. Accordingly, we performed a track analyses and a parsimony analysis of endemicity, based on known distribution data sets and distribution modelling data.

MATERIAL AND METHODS
STUDY AREA

The 'core' area of the Yucatán Peninsula is located between 17°50′–21°35′N and 86°43′–92°40′W (Fig. 1). The climate type that prevails in the province is Aw (tropical sub-humid, with summer rains and dry winter), but a type Am (tropical humid with summer rains and relatively dry winter) is present in the south-western portions and in Cozumel Island, and a type BS (intermediate between very dry and sub-humid climates, with short rainy season in the summer) prevails in the north-western coastal area (García, 1990) (Fig. 1). The prevailing types of vegetation are sub-humid forests in the north (i.e. tropical deciduous and sub-deciduous forests) and humid forests in the south (i.e. tropical evergreen and semi-evergreen forests). Thorn, palm, and mangrove forests can be found in coastal areas, and other nonforest vegetation types can be found throughout the peninsula (Rzedowski & Calderón de Rzedowski, 1989).

DISTRIBUTIONAL DATA

A list of species was compiled from a first database, based on collections throughout the peninsula and revision of the following herbaria: AAU, B, BM, BR, CAS, CHAPA, CICY, CIHS-UAC, CIQRO, COTE, COCA, CSAT, DS, ENCB, F, FCME, GH, HAC, IEB, ITCH, F, K, MEXU, MICH, MO, NO, NY, P, TEX, UACAM, UADY, UAMIZ, UC, UCR, US, and XAL (Holmgren, Holmgren & Barnett, 1990). This database was georeferenced using topographic maps (scale 1 : 250 000) and information obtained from INEGI (2002). It consisted of 1850 specimens, 711 georeferenced localities, and 56 species. Information for ten more species was retrieved from Mickel & Smith (2004), and validated by one of the authors (M.P.-R.), obtaining a total of 66 species of ferns and lycopods (Table 1). The precise location of two species is unknown (e.g. *Sphenomeris clavata* and *Thelypteris nicaraguensis*) because they are only cited in the work of Mickel & Smith (2004) as being present in the states of Yucatán and Campeche, respectively.

Herbaria records were gathered from the Missouri Botanical Garden's online database (Tropicos, www.tropicos.org) for 57 of the species listed above, as information for nine species could not be retrieved. This second database consisted of 5583 georeferenced localities for México, Central America, Greater and Lesser Antilles, and South America, and was validated with information obtained from Mickel & Smith (2004).

STATISTICAL ANALYSIS
Distribution modelling

Maximum entropy modelling (MaxEnt) was developed by Phillips, Dudik & Schapire (2004) and Phillips, Anderson & Schapire (2006) as an algorithm for predicting species distributions from incomplete presence-only information. MaxEnt uses an algorithm to estimate target probability distribution of maximum entropy (i.e. that is most spread out, or closest to uniform) (Phillips *et al.*, 2006). For this, MaxEnt begins with uniform probability distributions and repeatedly alters the weight of each environmental variable. The model guarantees the convergence on a nonrandom probability distribution (Hernández *et al.*, 2006; Phillips *et al.*, 2006), and produces species distribution raster maps where each pixel represents a maximum entropy value in the range 0–100. As these values approach zero, the resulting probability of finding the species decreases.

Using the first database constructed, the distributions of species with more than five records (28 species) within the peninsula were modelled based on 19 bioclimatic variables, and three additional topographic coverages (see Supporting information, Tables S1 and S2). To remove part of the overestimation error frequently associated with modelling algorithms, we eliminated those pixels with a maximum entropy value of less than 80.

Track analysis

Panbiogeography is a biogeographical approach developed by Croizat (1958, 1964) that emphasizes the importance of the geographical and spatial dimension of biodiversity for understanding evolutionary patterns and processes (Craw, Grehan & Heads, 1999). This method requires mapping localities of taxa and connecting them with line graphs (individual tracks), according to their minimal geographical proximity. The geographical coincidence (overlap) of individual tracks is considered as generalized tracks, which indicates the pre-existence of ancestral biotas that were fragmented in the past as a result of tectonic and/or climatic changes.

Track analyses were conducted using geographical information for 35 species within the peninsula (first database) and for 57 species in México, Central America, Greater and Lesser Antilles, and South America (second database). These analyses were performed using ARCVIEW GIS 3.2 (ESRI, 1999), with TRAZOS2004 (Rojas-Parra, 2004). Species with two

Table 1. List of ferns (Monilophyta) and lycopods (Lycophyta) for the Yucatán Peninsula

Division	Family	Species
Lycophyta		
	Isoëtaceae	*Isoëtes pallida* Hickey†
	Selaginellaceae	*Selaginella convoluta* (Arn.) Spring
		Selaginella harrisii Underw. et Hieron.
Monilophyta		
	Aspleniaceae	*Asplenium dentatum* L.
		Asplenium hoffmannii Hieron.
		Asplenium pumilum Sw.
		Asplenium serratum L.*
	Blechnaceae	*Blechnum serrulatum* Rich.
	Dennstaedtiaceae	*Dennstaedtia bipinnata* (Cav.) Maxon
		Pteridium caudatum (L.) Maxon
	Dryopteridaceae	*Nephrolepis biserrata* (Sw.) Schott
		Nephrolepis hirsutula (G. Forst.) C. Presl
		Tectaria fimbriata (Willd.) Proctor & Lourteig
		Tectaria heracleifolia (Willd.) Underw.
	Hymenophyllaceae	*Trichomanes bucinatum* Mickel et Beitel*†
		Trichomanes reptans Sw.*
	Lindsaeaceae	*Sphenomeris clavata* (L.) Maxon
	Marsileaceae	*Marsilea vestita* var. *vestita* Hook. et Grev.*
	Polypodiaceae	*Campyloneurum phyllitidis* (L.) C. Presl
		Microgramma nitida (J. Sm.) A. R. Sm.
		Pecluma dispersa (A. M. Evans) M. G. Price
		Pecluma plumula (Humb. & Bonpl. ex Willd.) M. G. Price
		Phlebodium aureum (Cav.) Lellinger*
		Phlebodium decumanum (Willd.) J. Sm.
		Pleopeltis astrolepis (Liebm.) E. Fourn.
		Polypodium polypodioides (L.) Watt
		Serpocaulon triseriale (Sw.) A. R. Sm.
	Psilotaceae	*Psilotum nudum* (L.) P. Beauv.
	Pteridaceae	*Acrostichum aureum* L.
		Acrostichum danaeifolium Langsd. et Fisch
		Adiantum amblyopteridium Mickel et Beitel†
		Adiantum decoratum Maxon et Weath.
		Adiantum pulverulentum L.
		Adiantum tenerum Sw.
		Adiantum tricholepis Fée
		Adiantum villosum L.
		Cheilanthes fimbriata (A. R. Sm.) Mickel et Beitel
		C. microphylla (Sw.) Sw.
		Hemionitis palmata L.
		Pityrogramma calomelanos (L.) Link
		Pteris grandifolia L.
		Pteris longifolia L.
		Pteris vittata L.*
		Vittaria lineata (L.) Sm.
	Salviniaceae	*Salvinia auriculata* Aubl.
		Salvinia minima Baker
	Schizaeaceae	*Actinostachys pennula* (Sw.) Hook.
		Anemia adiantifolia (L.) Sw.
		Anemia cicutaria Poepp. ex Spreng.
		Lygodium venustum Sw.

Table 1. *Continued*

Division	Family	Species
	Thelypteridaceae	*Thelypteris augescens* (Link) Munz et I. M. Johnst.
		Thelypteris dentata (Forssk.) E. P. St John
		Thelypteris guadalupensis (Wikstr.) Proctor
		Thelypteris interrupta (Willd.) K. Iwats.
		Thelypteris kunthii (Desv.) C. V. Morton
		Thelypteris leptocladia (Fée) Proctor
		Thelypteris martinezii A. R. Sm.
		Thelypteris nicaraguensis (E. Fourn.) C. V. Morton
		Thelypteris obliterata (Sw.) Proctor
		Thelypteris ovata R. P. St John var. *lindheimeri* (C. Chr.) A. R. Sm.
		Thelypteris patens (Sw.) Small
		Thelypteris poiteana (Bory) Proctor
		Thelypteris reptans (J. F. Gmel.) C. V. Morton
		Thelypteris reticulata (L.) Proctor
		Thelypteris serrata (Cav.) Alston
		Thelypteris tetragona (Sw.) Small

*Species not previously reported for the core portion of the Yucatán Peninsula; †endemic species *sensu* Riba (1998).

localities were not used in the analysis because the resulting tree is the only possibility and is uninformative about biogeographic relationships (Craw *et al.*, 1999). When individual tracks coincided, the resulting summary lines were considered as generalized tracks. A third track analysis was performed utilizing maximum entropy distribution in the same way as that described above.

Parsimony analysis of endemicity
Rosen (1988) developed parsimony analysis of endemicity (PAE) to assess relationships of fossil or recent assemblages from different areas. Grid cells as unit areas have been applied several times for Mexican organisms, such as mammals (Morrone & Escalante, 2002), birds (Rojas-Soto, Alcántara & Navarro, 2003), and flowering plants (Méndez-Larios *et al.*, 2005), among others. This method classifies areas or localities according to their shared taxa to obtain a parsimonious cladogram (Morrone, 1994; Morrone & Crisci, 1995). It takes, as a starting point, the presence/absence of species for a set of sample localities. With this, a data matrix or areas × taxa is constructed and analysed with a parsimony algorithm (Luna *et al.*, 1999).

Maximum entropy distributions were plotted into a 0.5° × 0.5° grid cell map of the Yucatán Peninsula, obtaining 61 grid cells with the presence of one or more species (Fig. 2) (see Supporting information, Table S3). With this information, PAE was performed using Nona (Goloboff, 1999) through WinClada, version 1.00.24 (Nixon, 2002). Data were submitted to a multiple tree bisection–reconnection algorithm,

searching on 100 initial trees (mult*100), and holding ten trees per replicate (h/10). PAE was also conducted using 64 species with distributional data for México, Central America, Greater and Lesser Antilles, and South America. This additional analysis was performed using political entities (countries/states) as unit areas.

RESULTS
DISTRIBUTIONAL DATA
Our database cites seven fern species not previously reported for the study area, namely *Adiantum amblyopteridium*, *Asplenium serratum*, *Marsilea vestita* var. *vestita* (Duno-de-Stefano *et al.* 2005), *Phlebodium aureum*, *Pteris vittata*, *Trichomanes bucinatum*, and *Trichomanes reptans*. Three of these species (i.e. *A. amblyopteridium*, *A. serratum* and *T. reptans*) are reported for the adjacent states of Chiapas, Oaxaca, Tabasco, and Veracruz by Mickel & Smith (2004) and Riba (1998); three other species are reported for other Mexican states not adjacent to the peninsula province (i.e. *P. vittata* is the north-eastern states of Tamaulipas and Nuevo León; *M. vestita* var. *vestita* in the northern states of Baja California, Baja California Sur, Coahuila, Nuevo León, San Luis Potosí, Sonora, Tamaulipas, and Zacatecas; and *T. bucinatum* in Hidalgo and Oaxaca. *Phlebodium aureum* is reported for the first time in México. Riba (1998) considers two species as being endemic for México: *A. amblyopteridium* in Oaxaca, and *T. bucinatum* in Hidalgo and Oaxaca.
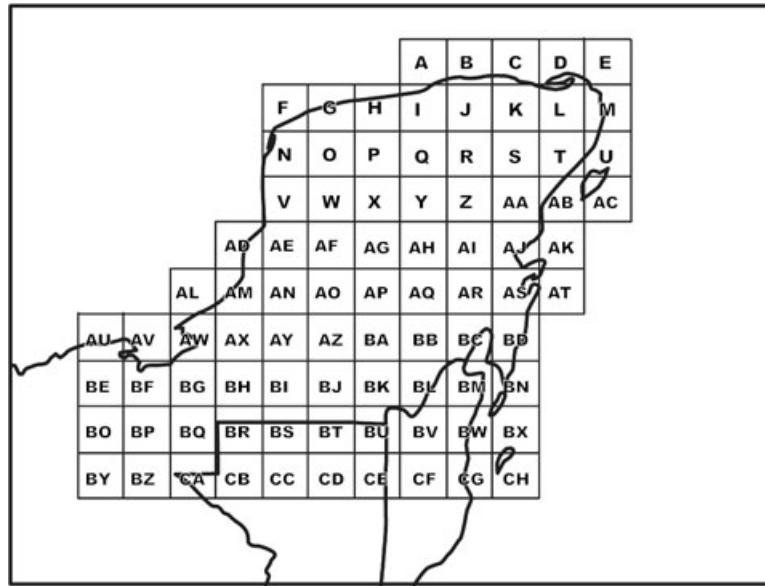
Figure 2. Core portion of the Yucatán Peninsula divided into 0.5° × 0.5° grid cells (names of grid-cells in the Supporting information, Table S2).

TRACK ANALYSIS

The track analysis from distributional data for the peninsula (first database) resulted in two generalized tracks for ferns and lycopods within the peninsula (Fig. 3A). The first track (Northwestern) extends through the west and northern parts of the peninsula, from Isla del Carmen, Campeche in the south, until the eastern municipality of Tizimín in Yucatán. Two components can be recognized within the second track (South-central). The first component (Central) includes overlapping individual tracks that extend in a west-east course throughout the central portion of Yucatán. The second component (Southeastern) includes overlapping individual tracks that run throughout the southern part of Campeche and Quintana Roo in a west-east direction.

The track analysis performed with maximum entropy distributions resulted in two generalized tracks (Fig. 3B). The first track (Northern) runs throughout the northern extreme of the peninsula in a west–east direction. The second track (Southeastern) runs throughout the eastern portion of the peninsula (Quintana Roo) in a north–south direction, branching in two: one branch extending into Guatemala, Belize, and northern Honduras, and the other into south-east México.

The track analysis for the whole American continent (including the Antilles) resulted in two generalized tracks: Central American and Yucatán. The first track runs throughout Central America, from southeastern México to South America, and extends into the Antilles from South America (Fig. 4). In its north-

ern portion, this track forks in two branches: one extending into south-eastern México, and the other reaching the south-central portion of the peninsula. This track also bifurcates upon reaching South America: one branch running south into the Andean region, and another branch extending west into the Guyana Shield. This last branch reaches into the Lesser and Greater Antilles. The Yucatán track is confined to the peninsula, running in an east–west direction throughout the north-central portion, from northern Quintana Roo to north-western Yucatán.

PARSIMONY ANALYSIS OF ENDEMICITY

PAE from MaxEnt distribution data produced 26 739 equally parsimonious trees with 172 steps, consistency index (CI) = 16, and retention index (RI) = 71. A consensus tree was obtained with 311 steps, CI = 09, and RI = 44. This consensus tree shows a large polytomy of 31 grid cells mostly comprising the central portion of the peninsula, and six distinct clades (Fig. 5A, B). The presence of the large polytomy indicates that the central portion of the peninsula shows an ambiguous relationship with both the northern and southern portions of the peninsula.

DISCUSSION

FLORISTICS

Of the 66 species of ferns ($N = 63$) and lycopods ($N = 3$) for the peninsula, 26 belong to three genera: *Thelypteris* ($N = 16$), *Adiantum* ($N = 6$), and *Asple-*
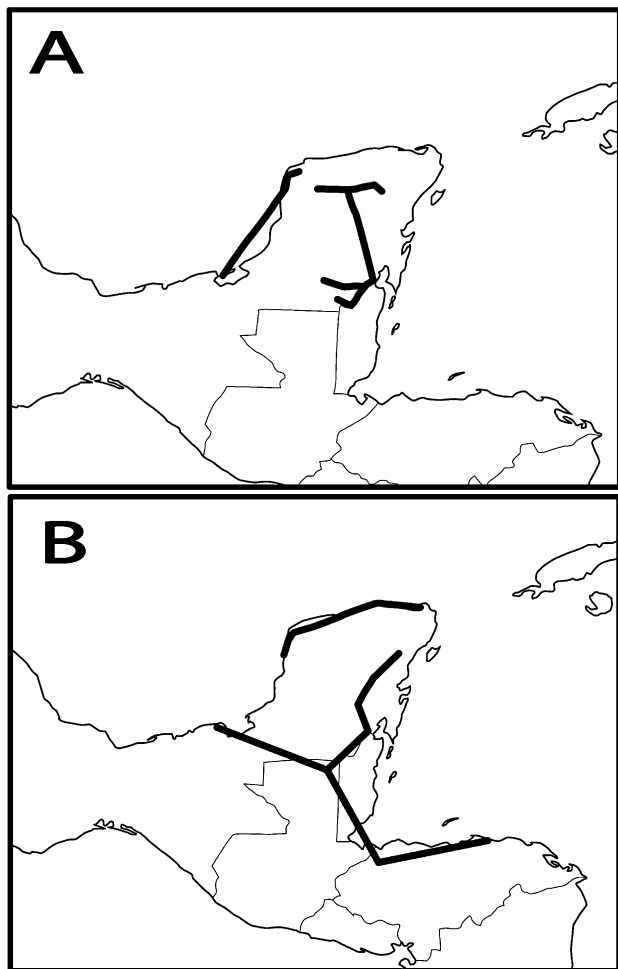
Figure 4. Generalized tracks obtained with known distribution data outside the Yucatán Peninsula province (data gathered from the Missouri Botanical Garden's online database; Tropicos, www.tropicos.org).

Figure 3. Generalized tracks obtained with (A) known distributions within the peninsula and (B) maximum entropy distributions of fern and lycopod species.

nium ($N = 4$), accounting for almost 40% of the total fern and lycopod flora for the peninsula. *Thelypteris* alone accounts for almost 25% of the flora, making this genus by far the most important in terms of species richness. This genus is over-represented in the peninsula because only 69 species occur in México (Mickel & Smith, 2004), which account for less than 7% of the total flora for the country.

Species registered in a single locality encompass almost 30% ($N = 19$) of the total number of species listed, but only one, namely *Isoëtes pallida*, can be regarded as endemic to the peninsula (Mickel & Smith, 2004). These results are in accordance with previous observations on the lack of endemic elements in the fern, lycopod (Riba, 1998), and moss flora of the peninsula (Delgadillo, 1984). This can be explained by the recent geological origin of the peninsula, which results in low diversity with few endemics (Espadas-Manrique *et al.*, 2003).
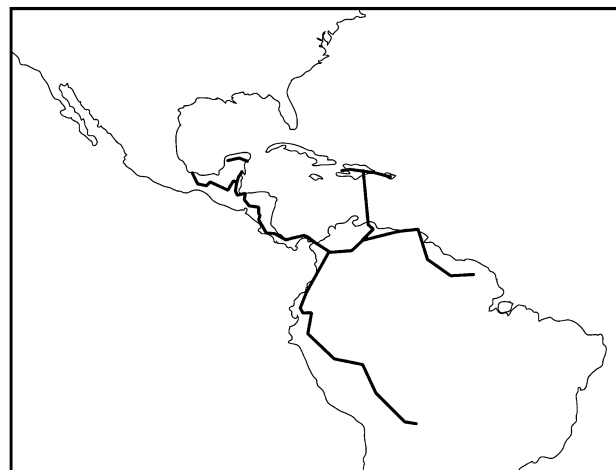
The low number of species is the result of surface waterways absence and presence of calcium carbonate soils with rapid drainage. Delgadillo (1984) reported only 64 species of mosses for the peninsula, a group of plants ecologically similar to ferns and lycopods. As in mosses, fern and lycopod species richness is greater in the southern part of the Peninsula, which is more humid (García, 1990), but there is another species-rich area in the northern portion of the peninsula, which is particularly dry.

Species richness does not show a marked latitudinal pattern and does not follow the northward increase in humidity and rainfall (Fig. 1), which has been proposed for other groups of plants (i.e. mosses; Delgadillo, 1984). Fern and lycopod species are concentrated in two geographically and climatically distinct areas (i.e. north-west and south-east) showing an increase in richness from the centre to the tip and base of the peninsula.

HISTORICAL BIOGEOGRAPHY

The maximum entropy track analysis shows great efficiency in recovering biogeographical patterns because its results coincide with more classical approaches to track delimitation (i.e. complete distribution data). Therefore, maximum entropy distributions could be used to recover patterns in spite of distributional data absence. However, these results should be taken with caution because distribution-modelling algorithms have several methodological complications. Distribution modelling algorithms are generally used as predictors of additional localities
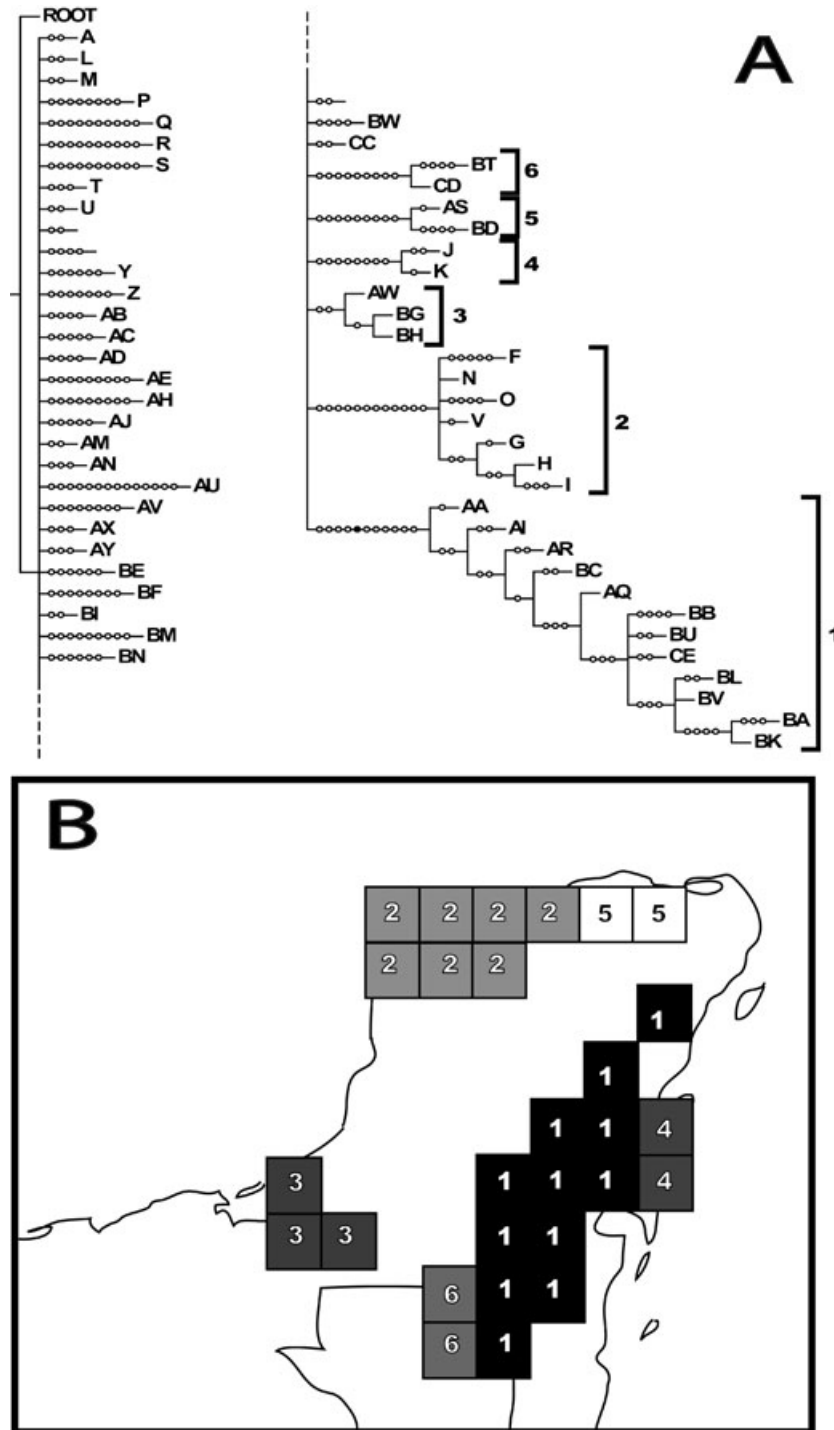
Figure 5. Grid cell groupings recognized within the Yucatán Peninsula with maximum entropy distribution parsimony analysis of endemicity. A, strict consensus tree. B, mapped grid-cell groupings.

that require corroboration or falsification. Therefore, predicted localities should be verified with species distributional data.

Maximum entropy track analysis recovers a pattern that closely resembles the pattern of sequen-

tial genesis of the peninsula. It has been proposed that the Yucatán Peninsula consists of a large calcium carbonate platform that originated in the Cenozoic and continued to develop through the Tertiary and the Quaternary. The southern parts of the peninsula

are the oldest, and the northern region is of Pleistocene or Holocene age (Padilla & Aceves-Quezada, 1990; Ferrusquía-Villafranca, 1993).

Nevertheless, historical biogeographic relationships within the peninsula are obscured by important ecological factors that mimic the sequential geological origins of the region. Generalized tracks obtained in the present study also agree with the climatic zonation of the peninsula (Fig. 1). The Northern track broadly corresponds to the driest part of the peninsula, where a BS climate (García, 1990) and mangrove forests prevail (Rzedowski, 1990). Southeastern track shows correspondence with the more humid portion of the peninsula, where Aw climate (García, 1990) and tropical evergreen forests prevail (Rzedowski, 1990).

Ecological factors such as these do not appear to be as important in establishing distributional patterns of ferns and lycopods as historical factors. Species richness in the peninsula does not follow a latitudinal pattern similar to the one reported for mosses (Delgadillo, 1984) because two distinct species-rich areas are recognized in both ends of the peninsula. This last pattern should be expected if ecological factors (e.g. humidity and rainfall) were the most important in determining the distributional pattern of ferns and lycopods. In this respect, the peninsula is characterized by a flat relief, where main exceptions are the Sierrita de Ticul and the Zoh-Laguna Plateau, reaching heights of approximately 275 and 400 m, respectively (Ibarra-Manríquez *et al.*, 2002). Hence, the wind mediated dispersal of ferns and lycopods across the peninsula is not hindered by any obvious topographic characteristic.

Pertaining relationships of the Yucatán Peninsula with other American areas, Southeastern track (Fig. 3B) and Central American track (Fig. 4), show that the south-eastern portion of the peninsula, which is the oldest, has a closer relationship with Mesoamerica, as supported by Estrada-Loera (1991) and Ibarra-Manríquez *et al.* (2002), rather than with the Antilles as contended by Chiappy-Jhones *et al.* (2001) and Delgadillo (1984). As noted in earlier studies (Miranda, 1958; Rzedowski, 1965; Estrada-Loera, 1991; Ibarra-Manríquez *et al.*, 2002), the ties between the Yucatán Peninsula and the Antilles are weak for several groups of plants. On the other hand, the northern portion of the peninsula shows no such relationship with areas outside the peninsula. Track analyses demonstrated one generalized track confined to the peninsula, extending throughout the northern portion with a more recent origin. Distribution data sets do not include georeferenced localities for Cuba, which obscures relationships of the peninsula with this area.

The Central American track has a marked correspondence with the Caribbean Region plant zone recognized by Rzedowski (1978), which includes portions of México and extends to Central America, the northern end of South America, and the Antilles. This generalized track, as it extends into the Andean region, shows an interesting, previously recognized relationship between the Yucatán Peninsula and this South American area (Chiappy-Jhones *et al.*, 2001).

PAE performed with known distributions for the whole American continent (including the Antilles) showed a major group of areas, comprising the whole of Central America, the Antilles (Greater and Lesser), South America (except Argentina and Paraguay that group together), and almost all of México. Thus, this analysis could not be used to establish the relationship of the Yucatán Peninsula with other areas.

REGIONALIZATION

Despite the absence of areas of endemism (*sensu* Morrone, 1994), maximum entropy PAE recognizes six clades that are in accordance with generalized tracks, and clearly distinguishes between a north-western and a south-eastern area (Figs. 3B, 5A, B). These areas match two of the four areas of endemism identified by Espadas-Manrique *et al.* (2003).

A regionalization scheme is proposed here, which broadly agrees with the intra-peninsular regionalization proposed by others; for example, Lundell (1934) based on climate, physiography, and plants; Goldman & Moore (1946) based on birds, mammals, and plants; and Lee (1980) based on snakes. Two districts are recognized: (1) El Petén and (2) arid/dry Yucatán (Fig. 6).

El Petén district is mainly located in the southern region of the peninsula, and is composed of four sub-districts: (1) Campeche, located west of the

Figure 6. Regionalization scheme for the Yucatán Peninsula based on parsimony analysis of endemicity and track analysis for known and maximum entropy distributions of fern and lycopod species.

Zoh-Laguna Plateau; (2) Calakmul, corresponding to Zoh-Laguna Plateau; (3) Quintana Roo, being the largest of the four, extending from northern Belize (east of the Zoh-Laguna Plateau) to the north-eastern portion of the peninsula; and (4) Sian Ka'an, located east of the Chetumal Bay. This last sub-district has distinctly different soil and vegetation, namely thorn forest and mangrove (Rzedowski, 1990), and molic gleysol (INIFAP-CONABIO, 1995).

The arid/dry Yucatán district is localized in the north-western portion of the peninsula, where a dryer type of climate prevails (Fig. 1), and is composed of two sub-districts: (1) Central, localized in north-central Yucatán (San Felipe and Ría Lagartos National Parks) and (2) Northwestern, localized in the extreme north-western portion of the peninsula. Within this last sub-district, Espadas-Manrique *et al.* (2003) previously recognized an area of endemism.

Although the main division of the peninsula was made earlier by Arriaga *et al.* (1997), who recognized both Yucatán and El Petén areas, the exact placement of the division between the two districts could not be resolved. This division can be located either to the north (Ibarra-Manríquez *et al.*, 2002) or south (Lundell, 1934; Goldman & Moore, 1946) of the central area (Fig. 6).

With the present analyses, it was possible to differentiate these areas but, according to Morrone, Espinosa-Organista & Llorente (2002), it is not appropriate to rank them as two separate provinces based on these information alone because there are no endemic elements in the fern and lycopod flora of the peninsula. We agree with the proposal of Morrone *et al.* (2002) that the basic distinction between these two areas is mainly ecological.

Conclusions

In the present study, ferns and lycopods are included for the first time in biogeographic analyses for the province. The peninsula does not present a high species richness for these groups, but the information provided by the few species inhabiting the area proves useful with respect to asserting historical and ecological hypotheses. Of the total number of fern and lycopod species, six are registered for the first time in the peninsula (i.e. *A. amblyopteridium*, *A. serratum*, *M. vestita* var. *vestita*, *P. vittata*, *T. bucinatum*, and *T. reptans*), and one is a new species for México (i.e. *P. aureum*).

Results of track analysis and PAE using maximum entropy distributions were taken into account to remove the bias generated by incomplete distributions and to uncover the historical relationships of the peninsula. Maximum entropy track analysis shows great efficiency in revealing biogeographical patterns from incomplete distribution data.

Historically, the Yucatán Peninsula shows a closer tie with Central and South America because its southern portion has a close affinity with these areas and the northern portion shows no relationship with other areas. Previously suggested ties with the Antilles are not supported by analyses of fern and lycopod distributions. Despite the fact that track analysis clearly agrees with the sequential geological origin of the peninsula, variation in rainfall shows a similar pattern.

Ecologically, fern and lycopod distributions do not follow the latitudinal pattern registered for other organisms because a species-rich area is recognized in the northern portion of the peninsula. In this case, species richness is the result of both the geographic location, as well as some environmental variables that deserve further analysis (e.g. vegetation and soil type).

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SUPPORTING INFORMATION

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

Table S1. List of species modelled using maximum entropy algorithm (MaxEnt), with their potential distribution in México (states), the Antilles, Central, North, and South America.
Table S2. Bioclimatic variables and topographic coverages used to model the maximum entropy distributions of fern and lycopods.
Table S3. Names of grid cells from the Yucatán Peninsula; *Added grid-cells for the maximum entropy PAE.

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