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Geographic Differentiation of Tree Ferns (Cyatheales) in Tropical America

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Abstract.—The patterns of geographic differentiation in fern species have been linked to climatic differences across regions and the distribution of available habitat. In this paper, the association between some climatic features and patterns of geographic differentiation in American tree ferns was evaluated. For this, the occurrence ranges of 190 species were plotted and then analysed using track analysis. Here we identify six generalised tracks that span the main highland regions of tropical America: the Andes, the Guyana Highlands, the Brazilian Atlantic coast, lower Central America, the Greater Antilles, and upper Central America-Mexico. We did not find an association between cloud forest habitat and the differentiation pattern revealed by generalised tracks in Central America. Instead, these patterns are congruent with well-documented geological boundaries in the region. Climatic variables associated with cloud forest habitat were extracted from each generalised track and subjected to ANOVA, showing that most tracks have equivalent climates. The Andean track showed significant climatic differences with the Brazilian and Guyanan tracks, which were associated with main habitat discontinuities. From these results, we propose that historical isolation has been important in promoting geographical differentiation in tree ferns and that differentiation by dispersal cannot fully explain the large-scale geographical patterns observed in tree ferns.

Key Words.—cloud forests, dispersal, geology, generalised tracks, historical isolation

The geographic distribution of fern species appears to be mainly affected by dispersal and climate (Brownsey, 2001; Tryon, 1985). In this context, studies of fern biogeography have focused on the dispersal capability of spores to account for the low levels of endemism and reduced geographic differentiation observed in fern species (Barrington, 1993; Kato, 1993; Kramer, 1990, 1993; Shepherd *et al.*, 2009; Smith, 1972; Tryon, 1972, 1986). The high dispersal ability of ferns enables them to colonise distant regions with favourable environments and thus attain wide distributions. Thus, the geographic extent of a fern species appears to be dependent on the capacity for dispersal and the availability of suitable environment (Tryon, 1972, 1986).

It has been suggested that differentiation by long-distance dispersal is a common mechanism leading to geographic differentiation in fern species

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(Barrington, 1993; Brownsey, 2001; Dassler and Farrar, 1999; Gradstein and van Zanten, 1999; Kato, 1993; Moran and Smith, 1999; Page, 2002; Tryon, 1970, 1972, 1985; Wolf *et al.*, 2001). The high dispersal capacity of ferns leads to the dispersal of spores to isolated regions. Subsequently, differentiation in these regions occurs when environmental differences exist or when there is a significant habitat discontinuity impeding further dispersal. Geographic differentiation appears to be dependent on the capacity for long-distance dispersal and the availability of suitable environments (Guo *et al.*, 2003; Shepherd *et al.*, 2009; Tryon, 1972; Wild and Gagnon, 2005).

Historical isolation has also been considered an effective mechanism for differentiation in ferns (Barrington, 1993; Kato, 1993; Moran and Smith, 1999; Page, 2002; Tryon, 1972; Wolf *et al.*, 2001). In this case, differentiation is initiated by the range fragmentation of a formerly widespread species by climatic or geological events. This process divides the species' former range into smaller and isolated patches that eventually become differentiated. However, the probability of differentiation by historical isolation is inversely correlated to the dispersal capacity of species. Thus, even when historical isolation is a possible mechanism of differentiation, it has been considered secondary in fern biogeography (Brownsey, 2001; Kramer, 1993; Perrie and Brownsey, 2007; Tryon, 1970, 1972).

The disregard of historical isolation has been enhanced because this process and differentiation by dispersal generate the same geographical patterns of diversity (Tryon, 1972). Both processes increase the number of species and the endemism of regional floras (Tryon, 1971, 1972). Thus, the study of species richness and endemism cannot fully distinguish the two processes of differentiation. Despite this drawback, patterns of geographical differentiation and their association with climatic and geological features can be used to evaluate the importance of the two processes. The prevalence of long-distance dispersal in ferns predicts that the current distribution of species would be closely linked to the distribution of favourable climates (Shepherd *et al.*, 2009; Wild and Gagnon, 2005). Thus, patterns of geographic differentiation are expected to be associated with major contemporary climatic discontinuities or differences in climate conditions across regions (Page, 2002). On the contrary, historical isolation resulting from geological events would result in patterns of differentiation reflecting the geological history of particular regions (Korall and Pryer, 2014; Rosen, 1975).

Tree ferns (Cyatheales A.B. Frank; Smith *et al.*, 2008) are a favourable group for testing the hypotheses regarding the two processes of differentiation. Cyatheales is the second most diverse group of ferns with 600–660 species in eight families, which are distributed mainly throughout the tropics (Korall *et al.*, 2007; Smith *et al.*, 2008). In tropical America, tree fern diversity and endemism are not randomly distributed, but aggregate into distinct regions (Tryon, 1972). Second, in terms of temperature and humidity, most tree fern species have strict environmental requirements (Bystriakova *et al.*, 2011). This produces distributions that are in close association with mesic, non-seasonal, and humid climates (Conant *et al.*, 1994; Large and Braggins, 2004; Lehnert, 2006a, b; Mickel and Smith, 2004; Véliz and Vargas, 2006; Watkins *et al.*, 2007), which are restricted to discrete mountain regions separated by climatically differing lowlands (Mulligan and Burke, 2005) (Fig. 1-A). These aspects of tree fern distribution generate explicit predictions about their patterns of spatial differentiation.

Recent evidence points to historical isolation as an important mechanism of differentiation, showing that the global distribution patterns of scaly tree ferns (Cyatheaceae) are consistent with the breakup of Gondwana (Korall and Pryer, 2014). In this respect, we expect that the patterns of differentiation in American tree ferns would be a reflection of the geological history of the region, particularly that of the Caribbean region. The most accepted geological history of the Caribbean states that the Antilles and lower Central America originated in the Cretaceous (144–65 Ma) as active volcanic arc systems at the edges of the Caribbean plate during the Cretaceous (Iturralde-Vinent, 2006). As the Caribbean plate drifted eastward into the inter-American gap, these arcs were subsequently displaced giving rise to their present-day configuration (Pindell and Kennan, 2001, 2009). This tectonic history suggests that the parallel development of these two island-arc systems has resulted in the presence of distinct biotic components in the Antilles and in Central America (Rosen, 1975). The Andean orogenesis has been considered as a major factor affecting the patterns and levels of Neotropical species (Gentry, 1982; Young *et al.*, 2002). The Guyana Shield and southeastern Brazil have been considered as distinct biogeographic regions because of their long-standing isolation by the development of broad river valleys and epi-continental marine transgressions (Cracraft and Prum, 1988).

Given the copious dispersal of spores and the strict environmental requirements of most Cyatheales, their distribution patterns have been regarded mainly as the product of differentiation by dispersal (Conant, 1983; Tryon, 1971). Under this hypothesis, climatic differences and habitat discontinuities between the main mountain regions in tropical America would have resulted in a diminished connectivity between regions. Therefore, the distribution patterns in American tree ferns would be expected to be associated with either contemporaneous climatic discontinuities or climatic differences between the main highland regions of tropical America.

In this paper we examine the contribution of dispersal and geological history to geographical differentiation in tree ferns. The aim of the research was to identify patterns of geographical differentiation in American tree ferns using currently available data on their distribution. For this, we implemented a track analysis to identify patterns of distributional congruence between species. The patterns uncovered by this analysis were evaluated for their geographical association with geological and climatic features associated with mesic, non-seasonal, and humid environments.

Materials and Methods

Distributional data.—Data on the distribution of American Cyatheales were obtained from three online databases: the Missouri Botanical Garden's

Tropicos (www.tropicos.org), the Global Biodiversity Information Facility (data.gbif.org), and the Red Mundial de Información sobre Biodiversidad (www.conabio.gob.mx/remib). Possible errors in the data were minimised by checking and complementing the online data with published monographic, biogeographic, and floristic information (Lehnert, 2011; Ramírez-Barahona *et al.*, 2011 and references therein). The resulting list of 254 American species was taxonomically standardised following Smith *et al.* (2008). Distributional data were available for 239 species, which were compiled in a database consisting of 6182 unique records. Distributional data for 15 species were not available.

Track analysis.—Track analysis was originally developed by Croizat (1958, 1964) to identify patterns of distributional congruence between species (Craw *et al.*, 1999; Morrone, 2009). This method requires plotting localities of species and connecting them with line graphs according to their minimal geographical proximity (individual tracks). The geographical overlap of individual tracks determines a generalised track. These tracks estimate the composition and geographical distribution of a biota (Croizat *et al.*, 1974) and thus can be used to detect geographic differentiation (Katinas *et al.*, 1999). If two or more generalised tracks converge they determine a node, which indicates areas where different biotic components interrelate in space (Morrone and Crisci, 1995; Craw *et al.*, 1999).

Following Craw *et al.* (1999), species with only one or two localities were not used in the analysis. Thus, track analysis was conducted for only 190 out of the 239 species. The geographical occurrences of each species were mapped and then connected by their minimal geographical distance using the Trazos2004© extension (Rojas-Parra, 2004) implemented in the ArcView 3.2 software (ESRI, 1999). The 190 individual tracks were superimposed and the generalised tracks were determined from the overlap of two or more individual tracks. It is rarely practical to define generalised tracks by multiple individual tracks sharing the same localities, particularly when detailed distributional data are not available for every species. Thus, a more flexible definition of overlap was used. Overlap was defined when several individual tracks shared the same geometry, but not necessarily were represented by the same localities. Once generalised tracks were obtained, nodes were recognised from the convergence of two or more generalised tracks.

Finally, the generalised tracks and nodes were superimposed on topographical and climatic maps of tropical America. The association of the observed generalised tracks and the climatic discontinuities was assessed by visual inspection.

Climatic analysis.—We used eight bioclimatic layers (Hijmans *et al.*, 2005) to extract data for each generalised track: annual mean temperature (BIO1), temperature seasonality (BIO4), mean temperature of warmest and coldest quarters (BIO10, BIO11), annual precipitation (BIO12), precipitation seasonality (BIO15), and precipitation of wettest and driest quarters (BIO16, BIO17). Environmental data can be extracted directly from generalised tracks, however, this procedure could be strongly biased because tracks have the potential to span through areas where species are not present. To solve this problem, we focused instead on extracting data from the species occurrences defining each generalised track. Climatic data were extracted using the RASTER package in R (R Core Team 2013), and occurrence points were linked with the climatic layers. The climatic variables extracted for the generalised tracks were subjected to a principal component analysis (PCA) using the STATS package in R. Principal components were subjected to an analysis of variance (ANOVA) to compare means between generalised tracks, followed by a Tukey's Honestly Significant Difference (HSD) test for multiple comparisons as implemented in STATS.

Results

Generalised tracks.—A total of 190 individual tracks were used to define six generalised tracks in tropical America. Interestingly, while many tree fern species have wide distributions, most species are restricted to discrete mountain regions. The six tracks were named based on their geographic location: Andean (68 species), Central American (19), Guyanan (14), Antillean (12), Brazilian (10) and Mexican (10) (Table 1). As expected, the distributions of mesic, non-seasonal, and humid climates were associated with the locations of the generalised tracks (Fig. 1). Thus, it appears that the tracks were localised in regions with equivalent climatic conditions.

The Antillean track was associated with the mountains in several islands in the Greater Antilles. This track was evidently separated from the rest by conspicuous oceanic barriers. Apart from this track, all other tracks were associated with continuous mountain regions. The Andean, Guyanan and Brazilian tracks were restricted to discrete highland regions, which are separated by topographical and climatic discontinuities (Fig. 1-A).

The separation of the Mexican and the Central American tracks from others was not associated with cloud forest habitat discontinuities, namely the Isthmuses of Tehuantepec and Panama (Fig. 1A). Accordingly, the Central American track was involved in the definition of two biogeographical nodes (Fig. 1B). This track converged with the Mexican and the Andean tracks, identifying the Nicaraguan (NN) and the Colombian nodes (CN), respectively. Surprisingly, the geographical location of these two nodes was associated with two geological boundaries of the Caribbean plate (Fig. 2).

Climatic differences.—We used PCA to reduce the bioclimatic variables to four principal components, which explained a 97.84% cumulative proportion of climatic variation in the generalised tracks. The most important component of climatic variation (PC1, 50.25%) was associated with mean annual and quarterly temperatures (BIO1, BIO10, BIO 11). The second component (PC2, 22.04%) was mainly determined by precipitation seasonality (BIO 15) and driest quarter precipitation (BIO 17). The third component (PCA3, 14.65%) was dominated by annual and wettest quarter precipitation (BIO 12, BIO16). Finally, the fourth component was strongly associated to temperature seasonality (BIO 4, 10.84%). Using these four components, ANOVA showed significant differences between generalised tracks ($F = 3.93$, $p = 0.002$; Fig. 3). Performing multiple comparisons between tracks, Tukey's HSD test only

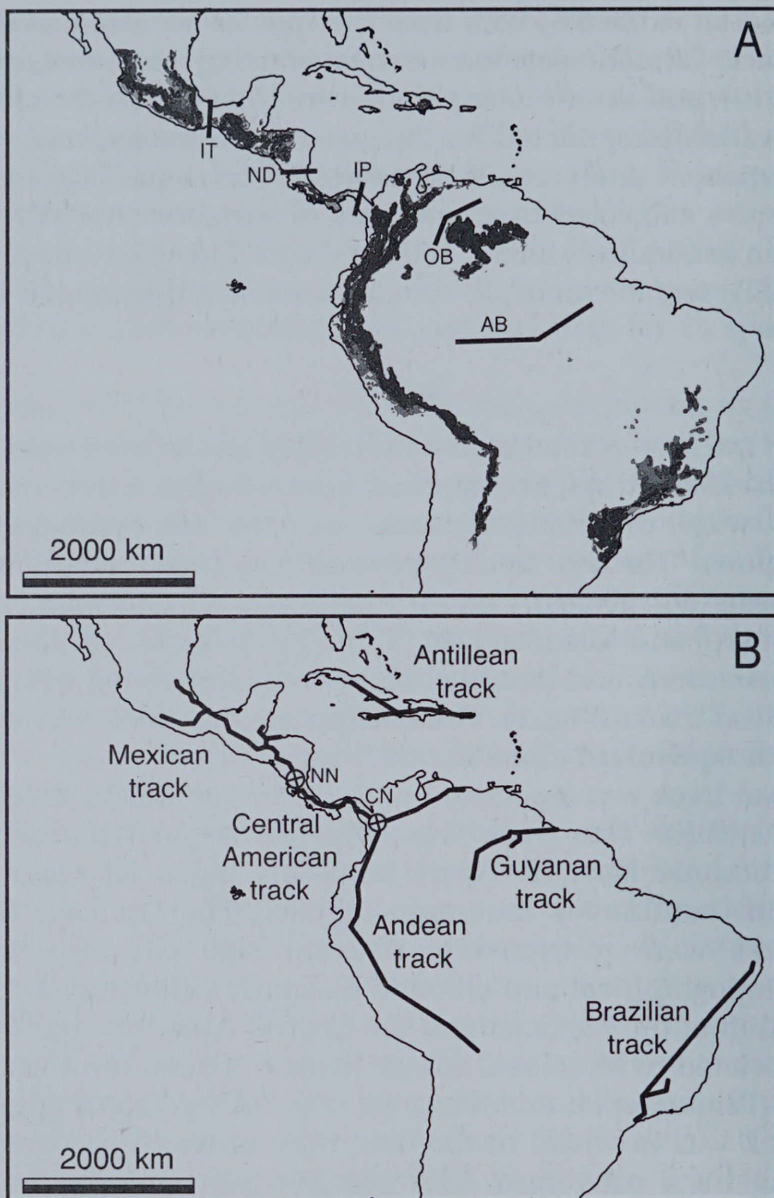

FIG. 1. (A) Geographical distribution of cloud forests (grey) in tropical America (adapted from Mulligan and Burke, 2005) showing the major discontinuities (solid black lines): IT = Isthmus of Tehuantepec; IP = Isthmus of Panama; ND = Nicaraguan depression; OB = Orinoco River basin; AB = Amazon River basin. (B) Generalised tracks (solid black lines) and nodes (crossed circles) uncovered for American Cyatheales. CN: Colombian node; NN: Nicaraguan node (see Table 1 for a list of species supporting each track).

showed significant differences ($p < 0.01$) for the following pairs of tracks: Brazilian-Andean and Guyanan-Andean (Table 2).

Discussion

The main objectives of this study were to recognise patterns of geographical differentiation in tree ferns and evaluate their association with the current climatic features associated with cloud forest habitat. As expected, restricted

TABLE 1. Total number of species of tree ferns (Cyatheales) for each generalised track in tropical America and examples of species defining each track.

Track	Number of species	Examples
Andean	68	*Alsophila incana* (H. Karst.) D.S. Conant
		Cyathea pauciflora (Kuhn) Lellinger
		Sphaeropteris quindiuensis (H. Karst.) R.M. Tryon
Central American	19	*Cnemidaria varians* R.C. Moran
		Cyathea pinnula (Christ) Domin
		Sphaeropteris brunei (Christ) R.M. Tryon
Guyanan	14	*Cyathea cyatheoides* (Desv.) K.U. Kramer
		Hymenophyllopsis dejecta (Baker) K.I. Goebel
		Hymenophyllopsis hymenophylloides L.D. Gómez
Antillean	12	*Alsophila auneae* D.S. Conant
		Cyathea parvula (Jenman) Domin
		Sphaeropteris insignis (D.C. Eaton) R.M. Tryon
Brazilian	10	*Alsophila sternbergii* (Sternb.) D.S. Conant
		Cyathea mexiae Copel.
		Sphaeropteris gardneri (Hook.) R.M. Tryon
Mexican	10	*Cibotium regale* Versch. & Lem.
		Cyathea godmanii (Hook.) Domin
		Sphaeropteris horrida (Liebm.) R.M. Tryon

and coincident species distributions led to the recognition of six generalised tracks, showing clear patterns of differentiation across the main highland regions in tropical America (Bystriakova *et al.*, 2011; Tryon, 1971). In general, these patterns are associated with climatic discontinuities separating highland regions.

Given the environmental preferences of Cyatheales, it is not surprising that most generalised tracks did not show significant climatic differences. With the exception of the Guyanan and Brazilian tracks, all other generalised tracks appear to share similar climatic conditions favourable for tree ferns. However, a number of potential limitations with the data need to be considered. The recognition of the geographical congruence of individual tracks and thus the definition of the generalised tracks is scale-dependent. This has the potential to leave undetected underlying patterns of differentiation within a particular region. Also, the nomenclature and taxonomy of tree ferns, especially Cyatheaceae, are in constant change. Finally, detailed distributional data of many tree fern species are not available and many regions in tropical America remain poorly studied. Therefore, future studies must incorporate new data on the taxonomy and the distribution of tree ferns in tropical America. In spite of these drawbacks, the present results are in agreement with previous biogeographic studies of ferns (Barrington, 1993; Tryon, 1971, 1972).

Differentiation by dispersal can explain some of the patterns of differentiation observed in American tree ferns. Tryon (1972) and Barrington (1993) found that many fern species could be found in forests that develop under stringent environmental conditions, particularly in terms of humidity and temperature (Page 2002; Tryon, 1972; Watkins *et al.*, 2007). This observation

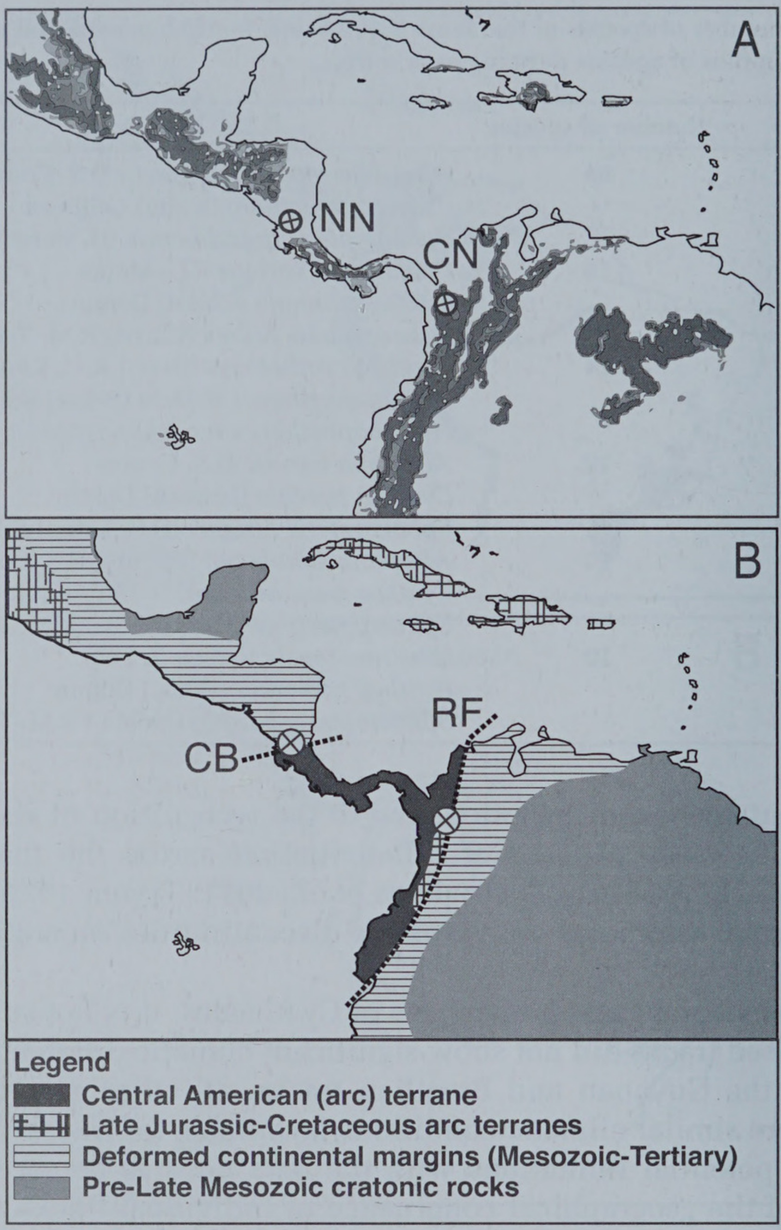

FIG. 2. Panbiogeographical nodes (crossed circles) for American Cyatheales superimposed to (A) the geographical distribution of cloud forests (grey) in tropical America (adapted from Mulligan and Burke, 2005) and (B) a geological map showing distinct terranes (bottom legend) around the Caribbean basin (adapted from Tardy *et al.*, 1994).

has led authors to recognise current climate as the most important factor influencing fern distributions. Consequently, it has been suggested that patterns of differentiation in American tree ferns are predominantly the result of dispersal-coupled differentiation (Conant 1983; Tryon, 1971). After a successful initial dispersal event, environmental discontinuities would impede further dispersal and thus would promote and maintain differentiation of taxa between regions.

On the contrary, the present analysis shows there is no statistical support linking some of the tracks with climatic differences between regions. This does

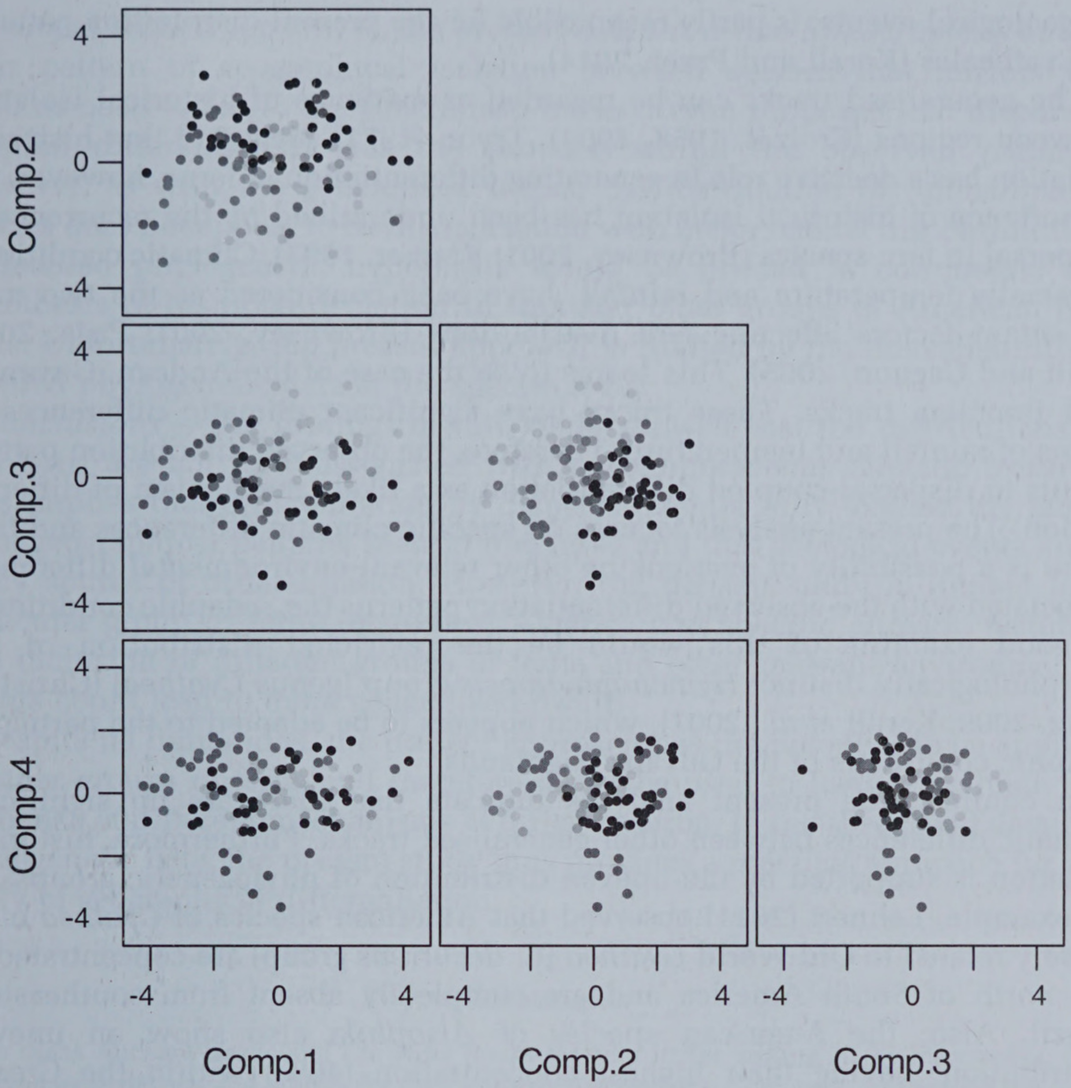

FIG. 3. Principal component analysis of climatic variables associated to cloud forest habitat in tropical America. The first four principal components are shown, representing 50.25%, 22.04%, 14.65% and 10.84% of the total climatic variance between tracks, respectively. Comp1 is positively associated with decreasing mean annual and quarter temperatures. Comp2 is positively associated with increasing seasonality and decreasing driest quarter precipitation. Comp3 is positively associated to increasing annual and wettest quarter precipitation. Comp4 is positively associated with decreasing temperature seasonality. The marker colours indicate points extracted from each generalised track: Mexican (black), Antillean (grey), Andean (yellow), Brazilian (blue), Guyanan (green) and Central American (red).

not support the view that ferns are not limited by dispersal or establishment (Guo *et al.*, 2003; Smith, 1972; Tryon, 1970, 1971). In light of the present results, the stepping-stone mode of differentiation by dispersal proposed for some Cyatheales, where species tend to differentiate as they disperse over the landscape (Conant, 1983; Tryon, 1971), should be reconsidered. In this context, the present analyses indicate that the distribution of tree ferns cannot be fully explained by the distribution and availability of suitable environments. Furthermore, these results indicate that historical isolation, prompted by geological events, is partly responsible for the present distribution patterns of Cyatheales (Korall and Pryer, 2014).

The generalised tracks can be regarded as evidence of historical isolation between regions (Croizat, 1958, 1964). Tryon (1971) suggested that historical isolation has a decisive role in generating differentiation in ferns, however, the importance of historical isolation has been undermined by the recurrence of dispersal in fern species (Brownsey, 2001; Kramer, 1993). Climatic conditions, especially temperature and rainfall, have been considered as the two most important factors affecting fern distributions (Brownsey, 2001; Page, 2002; Wild and Gagnon, 2005). This seems to be the case of the Andean, Guyanan, and Brazilian tracks. These tracks have significant climatic differences in terms of rainfall and temperature. Therefore, the observed distribution pattern points to dispersal-coupled differentiation as a likely mechanism of differentiation. The present analysis focuses on specific climatic differences and thus there is a possibility of overlooking other relevant environmental differences associated with the observed differentiation patterns (*i.e.*, edaphic conditions). A good example of this would be the restricted distribution of the morphologically distinct *Hymenophyllopsis* group (genus *Cyathea*) (Christenhusz, 2009; Korall *et al.*, 2007), which appears to be adapted to the particular edaphic conditions of the Guyana Highlands.

In contrast, the present analyses indicate that there are no significant climatic differences between other generalised tracks. Furthermore, historical isolation is supported by the uneven distribution of phylogenetic groups. As an example, Lehnert (2011) observed that American species of *Cyathea* more closely related to Old World *Cyathea* (*C. decurrens* group) are concentrated in the north of South America and are completely absent from southeastern Brazil. Also, the American species of *Alsophila* also show an uneven distribution, having their highest concentration (46%) within the Greater Antilles (Conant, 1983). This would favour the hypothesis of historical isolation promoting geographical differentiation between these regions.

In this respect, the Antillean and Central American tracks show congruence with the two main island arc systems in the Caribbean (*i.e.*, the Antilles and lower Central America; Tardy *et al.*, 1994). The separation of these tracks is not associated with the geographical location of the main climatic gaps in Central America. Although the separation between the Central American and Mexican tracks is associated with the climatically distinct Nicaraguan Depression, the geographical location of the two nodes is associated with the limits of the volcanic arc terrane of Central America (*i.e.*, the Romeral fault system, the Nicaraguan depression, Tardy *et al.*, 1994). These limits mark the zones of accretion of the lower Central American arc with North and South America (Chicangana, 2005; Coates *et al.*, 2004; Francisco-Ortega *et al.*, 2007; Hedges, 2001; Iturralde-Vinent, 2006; Kerr and Farney, 2005; Mann *et al.*, 2007; Pindell and Kennan, 2001, 2009; Rosen, 1975; Tardy *et al.*, 1994).

Furthermore, there are instances of clear associations between the allopatric distribution of tree fern species and well-documented geological boundaries. A good example of this pattern is the group of New World *Sphaeropteris*. In agreement with Tryon (1971), the present data show that *Sphaeropteris* have a clear pattern of geographical isolation between species that mirrors the patterns observed with the generalised tracks. Tryon proposed that dispersal-coupled differentiation was the process behind the observed patterns. However, as with the generalised tracks, the distribution of *Sphaeropteris* species does not appear to be in association with major habitat discontinuities. A detailed phylogenetic hypothesis would be needed to corroborate the hypothesis of historical isolation in this and other groups of American tree ferns. Unfortunately, the present approach is limited by the unavailability of detailed phylogenetic data at the species level.

Conclusions.—The findings of this study showed that the distributions of tree ferns are not fully associated with contemporaneous climatic features. This implies that differentiation by dispersal cannot fully explain the large-scale geographical patterns seen in tree ferns and that geological events are a likely source of differentiation. However, the present study is limited to a particular group of ferns in tropical America and specific climatic features. The inclusion of different groups of ferns and other relevant environmental factors could lead to more generalised results.

Despite its limitations, the present approach has the potential to be applied to other groups of ferns and therefore it can be used to further evaluate the influence of different mechanisms of differentiation. In the absence of detailed phylogenetic data, the present study thus provides a practical approach for the study of geographical differentiation.

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