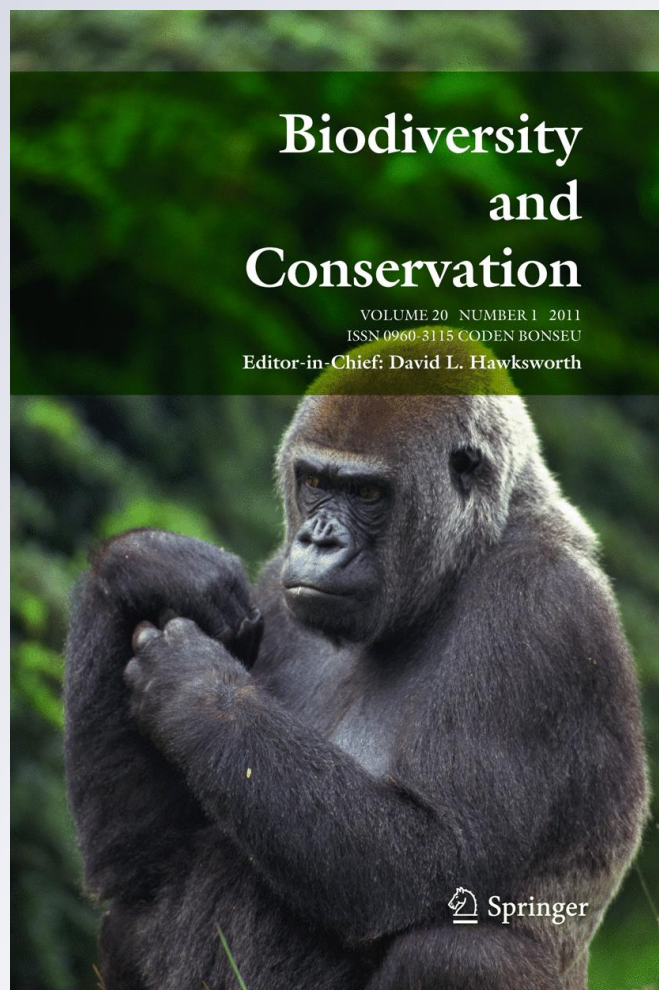


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**Biodiversity and
Conservation**

ISSN 0960-3115
Volume 20
Number 1

Biodivers Conserv (2010)
20:59-72
DOI 10.1007/
s10531-010-9946-2



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Species richness, endemism, and conservation of American tree ferns (Cyatheales)

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Received: 19 February 2010 / Accepted: 18 November 2010 / Published online: 5 December 2010
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Abstract Analyses of richness and endemism of Cyatheales (tree ferns) in tropical America were performed and evidence of a diversity gradient is presented. For this, the occurrence ranges of 239 species were plotted into a $5^\circ \times 5^\circ$ grid-cell map and then analyzed using species richness and endemism indices. Here we show that species richness and endemism are not distributed randomly over the landscape, but do aggregate into defined regions of high diversity in tropical America: the northern Andes, lower Central America, upper Central America and Mexico, the Guyana Highlands, southeastern Brazil, and the Antilles. These distributional patterns are congruent with the geographical distribution of cloud forest, which in turn is determined by topography, high humidity, and persistent cloud immersion. The mountain regions of tropical America, especially the cloud forests, harbour most of the species of American Cyatheales and have high levels of habitat loss and climatic fragility. Conservation policies for Cyatheales are centred on the local use and trade of many tree fern species, but none such policies focus on cloud forest habitat loss. This makes tree ferns a critically endangered group of plants. In the face of the current environmental crisis and global climate change, the presence of Cyatheales in these regions sounds the alarm on their conservation priorities.

Electronic supplementary material The online version of this article (doi:[10.1007/s10531-010-9946-2](https://doi.org/10.1007/s10531-010-9946-2)) contains supplementary material, which is available to authorized users.

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Keywords Cloud forests · Climate change · Deforestation · Hotspots · Montane regions · Tropical America

Introduction

Over the past decades there has been an emphasis on locating ‘centres’ of species richness and endemism in an attempt to optimize conservation strategies (Beentje et al. 1994; Ceballos and Brown 1994; Linder 2001). Most studies are index-based assessments that use endemism and species richness indices as surrogates for the conservation value of a region (Brooks et al. 2006; Kier et al. 2009). For this purpose, broad-scale patterns of plant richness and endemism have been documented, showing that montane tropical regions have the highest levels of plant diversity and thus are considered as highly valuable for conservation (e.g., Davis et al. 1995; Hobohm 2003; Barthlott et al. 2005; Mutke and Barthlott 2005; Kreft and Jetz 2007; Kier et al. 2009).

These studies, however, require detailed distribution data of taxa that are not available for the vast majority of fern groups. Compared to flowering plants, there are relatively few studies focusing on fern diversity (Kramer 1993; Márquez et al. 1997). General distribution patterns have been discussed for some fern taxa at different geographical scales (e.g., Smith 1972; Tryon 1972; Tryon and Tryon 1982; Gómez-P 1985; Barrington 1993; Given 1993; Kato 1993; Kornas 1993; Kramer 1993; Hassler and Swale 2001; Guo et al. 2003; Mutke and Barthlott 2005). As in other vascular plant groups, these studies recognize tropical montane regions as areas with high levels of fern diversity. According to Tryon (1972), most of the tropical regions in America are characterized by species inhabiting montane communities, particularly the cloud forests.

These forests occur in montane regions where there are frequent or persistent ground level clouds (Foster 2001; Mulligan and Burke 2005) (Fig. 1). These unique climatic conditions are restricted to narrow, high-elevation belts, and thus the cloud forests occur in fragmented strips that have been likened to island archipelagos (Foster 2001). The cloud forests are characterized by their high levels of biodiversity and the presence of many endemic taxa (Luna-Vega et al. 2001), but unfortunately these forests are among the most threatened communities in the world, with almost 60% of their original worldwide cover lost due to deforestation (Churchill et al. 1995; Mulligan and Burke 2005).

Although the ferns inhabiting cloud forests represent an important part of global plant diversity, studies on their conservation priorities are still needed (Gómez-P 1985; Given 1993). It has been suggested that Cyatheales A.B. Frank (tree ferns, Korall et al. 2006) are mostly restricted to cloud forests and related types of forest (Conant et al. 1994; Bernabé et al. 1999; Foster 2001; Lehnert 2003, 2006a, b; Mickel and Smith 2004; Velíz and Vargas 2006; Watkins et al. 2006; Mehlreter and García-Franco 2008). However, there are no studies that formally analyze the ecological affinities of tree ferns. The conservation policies for these fern species have been primarily concerned with the commercial trade and use of trunks from several of these ‘tree’ species (CITES 2009), but there are other factors (e.g., deforestation, climate change) that represent serious threats to Cyatheales conservation.

The main goal of this paper is to determine the patterns of richness and endemism of American Cyatheales. In particular, we ask whether these two aspects of diversity are evenly distributed throughout tropical America. For the purpose of highlighting Cyatheales conservation priorities, we compare the patterns of diversity with the cloud forest cover in the region.



Fig. 1 Broad-scale geographical distribution of cloud forests (*green*) in tropical America; adapted from Mulligan and Burke (2005)

Methods

Study group

The order Cyatheales is the second largest group of living ferns, with +660 species (Smith et al. 2008). The group is distributed throughout the tropics and also in some temperate areas such as Japan, New Zealand, and southern Chile. Most Cyatheales are characterised by an arborescent growth form, but this is neither unique to, nor ubiquitous among Cyatheales (Korall et al. 2006; Smith et al. 2008). The taxonomy of Cyatheales is characterised by instability at the generic and species levels.

The eight families within Cyatheales are represented in the New World: Cibotiaceae Korall, Culcitaceae Pic. Serm., Cyatheaceae Kaulf., Dicksoniaceae (C. Presl) Bower, Loxomataceae Christ, Metaxyaceae Pic. Serm., Plagiogyriaceae Bower, and Thyrsopteridaceae Kunze (Kramer and Green 1990; Lehnert 2006a; Lehnert et al. 2001; Lobin 2002; Smith et al. 2001, 2008). Most American species are restricted to the Neotropic (*sensu* Cabrera and Willink 1973; Morrone 2001), which extends from northern Mexico, through Central America and the Antilles, to northern South America, reaching central Argentina (Morrone 2001). Some families are restricted to (i.e., Thyrsopteridaceae) or extend into (i.e., Dicksoniaceae) south temperate America (Antarctic region), and some (i.e., Metaxyaceae) reach north temperate America (Holarctic region).

Distributional data

Following the classification of Smith et al. (2008), a list of 254 species of American Cyatheales was compiled (Table 1S, supporting information), based on information from online databases [i.e., Missouri Botanical Garden's (Tropicos, www.tropicos.org), the Global Biodiversity Information Facility (GBIF, data.gbif.org), and the Red Mundial de Información sobre Biodiversidad (REMIB, www.conabio.gob.mx/remib)], inspection of herbarium specimens from the following collections: MEXU, FCME, and ENCB, and reviews of published monographic, revisionary, and floristic studies (Alcántara and Luna-Vega 2001; Barrington 1978; Colli et al. 2004; Conant 1976, 1983; Figueiredo and Salino 2005; Fontana et al. 2007; Gomes et al. 2006; Kelly et al. 1994; Labiak and Matos 2009; Large and Braggins 2004; Lehnert 2003, 2005, 2006a, b, 2008; Lehnert et al. 2001; Lellinger 1989; León 2006; Lobin 2002; Marticorena 1995; Mickel and Smith 2004; Monterrosa and Monro 2008; Moran 1990; Moran et al. 2003, 2008; Mori 1992; Murillo and Murillo 2003; Øllgard 2000; Pietrobon and Barros 2006; Prado and Labiak 2001; Proctor 1977, 1984, 1985, 1989; Rojas-Alvarado 2001, 2007; Rzedowski 1996; Santiago et al. 2004; Schmitt and Windisch 2005, 2006, 2007; Smith et al. 2001; Tryon 1976, 1986; Tryon and Stolze 1991; Vareschi 1968; Velíz and Vargas 2006; Windisch 1977, 1978; Young and Leon 1989; Zuloaga 1996).

Distributional data for 239 of the species listed were compiled in a database consisting of 6,182 georeferenced localities. With this information occurrence range maps were generated using ArcView GIS ver. 3.2 (ESRI 1999). No geographic references were available for 15 species.

Data analysis

The occurrence range of each species was plotted into a $5^\circ \times 5^\circ$ grid-cell base map (Fig. 1S, supporting information). A presence/absence matrix of areas \times taxa was constructed and the diversity patterns were analyzed with richness and endemism indices.

In order to calculate richness and endemism scores, the distribution of taxa in all areas has to be known, but the lack of Cyatheales collection records in some areas is likely to account for a significant number of absences. However, in many cases scores can be calculated when data are less abundant (Kier and Barthlott 2001).

Species richness

Species richness is a straightforward measure that simply counts the number of species in a particular area. Richness (R) was calculated as the total count of species within each grid-cell unit. However, as the land area within grid-cells is not uniform, because some grid-cells include coastlines and others show a latitudinal change in metric area from the equator to the poles, a corrected richness (CR) index was calculated by: $R/\log A$, where $\log A$ is the logarithm of the land area (km^2) within each grid-cell. This procedure assumes linearity of the $R - \log A$ curve, which has been shown to be significantly high for fern species (Murakami et al. 2005).

Endemism

Endemism, or range-size rarity (Rabinowitz 1981), not only gives information about the percentage of species restricted to a particular area, but evaluates the contribution of the

species not confined to that area (Kier and Barthlott 2001). Endemism was calculated with the endemism richness index (*ER*) (Crisp et al. 2001; Kier and Barthlott 2001; Linder 2001). For this, each species is down-weighted by the number of grid-cells in which it occurs (i.e., occurrence range-size) and then the sum of down-weighted species values (Σs) is calculated for each grid-cell (Linder 2001). To correct for the correlation between species richness and endemism (Crisp et al. 2001), the Σs was divided by the richness of the corresponding grid-cell.

As the land area is not uniform across grid-cells, there is a restriction on the comparison of values from different grids (Kier and Barthlott 2001) and species present in the same number of grids do not necessarily have the same occurrence range-size. To eliminate the effect of the first source of error, *ER* values were divided by the log *A* of each grid-cell. This corresponds to Kier and Barthlott's (2001) specific contribution value (*Cs*), with the additional correction for the species-endemism correlation. To correct for the second source of error, species presence was down-weighted by the logarithm of the sum of the land area (log ΣA) it occupies. As in *ER*, the sum of specific values for each grid-cell was calculated and then divided by the corresponding species richness. This index was termed range corrected endemism (*RCE*).

Results

Floristics

Of the total diversity of American Cyatheales (Table 1), family Cyatheaceae accounts for almost 95% of all species. *Cyathea* Sm. (= *Cnemidaria* Presl = *Trichipteris* Presl = *Hymenophyllopsis* Goebel) alone accounts for almost 80% of the flora, making this genus by far the most important in terms of species richness. *Alsophila* R. Br. and *Sphaeropteris* Bernh., both in Cyatheaceae, are the second and third most diverse genera with 14 and 2% of the total flora, respectively. Dicksoniaceae are the second largest family, with two genera representing only 3% of the total flora: *Dicksonia* L'Hér (4) and *Lophosoria*

Table 1 Total number of species per genera in order Cyatheales A. B. Frank for tropical America

Family	Genus	Species
Cyatheaceae Kaulf.	<i>Cyathea</i> Sm.	197
	<i>Alsophila</i> R. Br.	35
	<i>Sphaeropteris</i> Bernh.	6
Dicksoniaceae (C. Presl) Bower	<i>Dicksonia</i> L'Hér	4
	<i>Lophosoria</i> C. Presl	3
Cibotiaceae Korall	<i>Cibotium</i> Kaulf.	2
Metaxyaceae Pic. Serm.	<i>Metaxya</i> C. Presl	2
Plagiogyriaceae Bower	<i>Plagiogyria</i> (Kunze) Mett.	2
Culcitaceae Pic. Serm.	<i>Culcita</i> C. Presl	1
Loxomataceae Christ	<i>Loxomopsis</i> H. Christ	1
Thyrsopteridaceae Kunze	<i>Thyrsopteris</i> Kunze	1

Author's names with Gray Cardex Index (GCI) and some in Index Filicum (IF). Consulted in IPNM (<http://www.ipni.org/index.html>, accessed 27 August 2009)

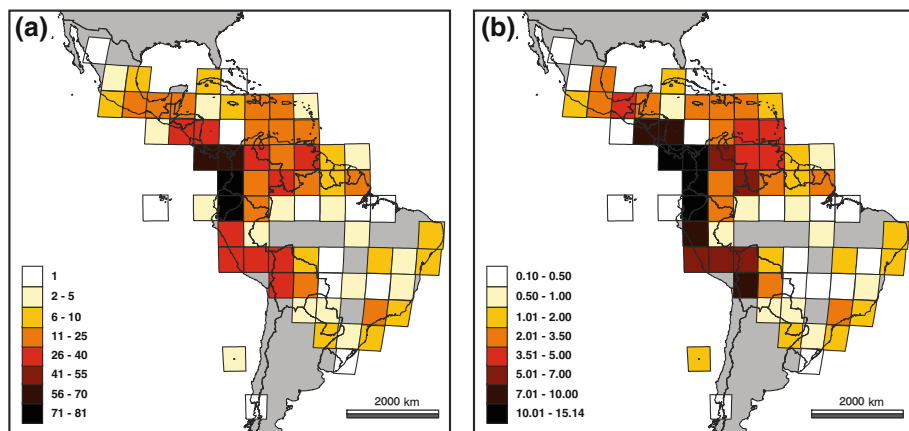


Fig. 2 Map of Cyatheales **a** species richness (R) and **b** corrected richness (CR) for each $5^\circ \times 5^\circ$ grid-cell within the study area. Richness values are given in number of species; these are corrected for grid-cell size (logarithm of the land area in km^2), yielding CR estimates (values per grid-cell in Table 2S, supporting information)

C. Presl (3). The remaining six families are represented by single genera with less than three species each (Table 1).

Most families, except Cibotiaceae, Loxomataceae, and Thyrsopteridaceae, have wide distributions within the study area (i.e., Mexico, Central America, the Antilles, the Andes, the Guyana Shield, and southeastern Brazil). Both American species of *Cibotium* Kaulf. are restricted to upper Central America-Mexico, *Loxsomopsis costaricensis* Christ is distributed in the Andes and lower Central America, and *Thyrsopteris elegans* Kunze is restricted to the Juan Fernandez Islands.

Richness

Species richness indices showed that Cyatheales are concentrated in the northern Andes (i.e., Colombia, Ecuador, and northern Peru) and in lower Central America (i.e., Panama and Costa Rica) (Fig. 2) (Table 2S, supplementary material). Other species rich areas can be found throughout the rest of the Andes, upper Central America-Mexico, and the Guyana Highlands.

Endemism

Endemism patterns differ from the observed distribution of species richness (Fig. 3) (Table 2S, supplementary material). Both the specific contribution (C_s) and range corrected endemism (RCE) show that island systems (i.e., the Antilles, and the Juan Fernandez Islands) have the highest endemism values (Fig. 3a, b). This is expected because the suitable areas for species occurrence are larger on continental areas than on insular areas. If islands are excluded from the analyses, the endemism patterns are similar to that of species richness (Fig. 3c, d).

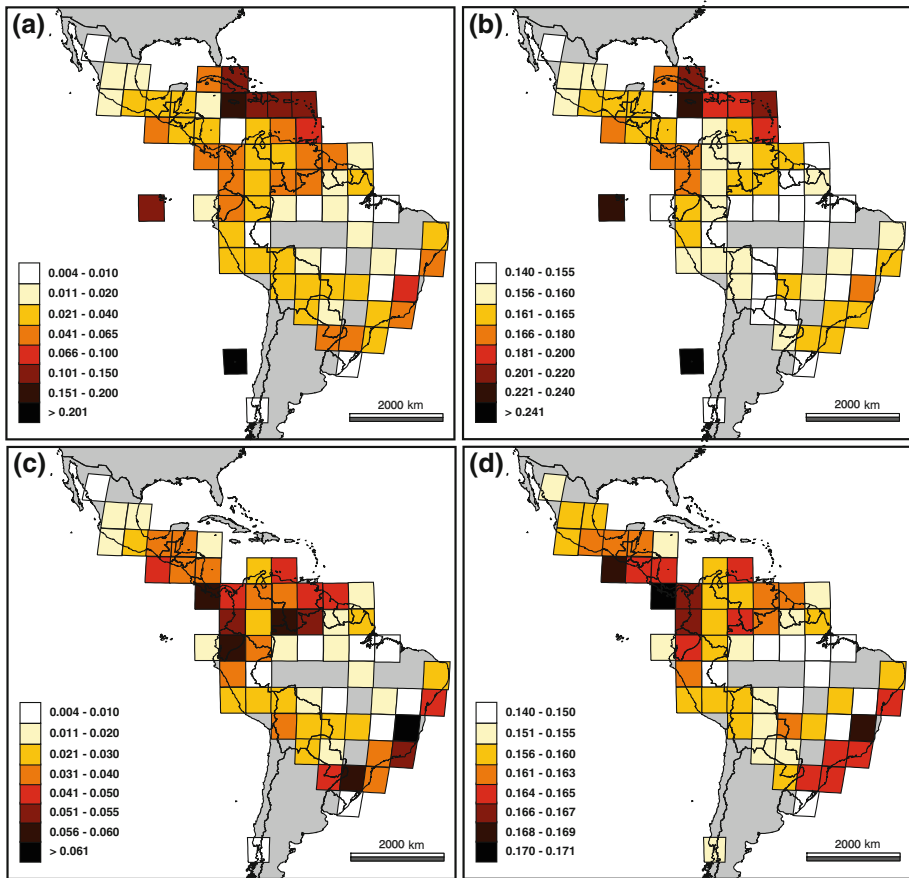


Fig. 3 Map of Cyatheales **a, c** specific contribution (Cs), and **b, d** range corrected endemism (RCE) for each $5^{\circ} \times 5^{\circ}$ grid-cell within the study area; **c, d** exclude island grid-cells. Endemism richness values are corrected for grid-cell size (logarithm of the land area in km^2), yielding Cs; RCE corrects for species range variation (logarithm of the occurrence range in km^2) due to unequal sized areas (values per grid-cell in Table 2S, supporting information)

Discussion

Floristics

The differential taxonomic representation shown by the eight families of Cyatheales in tropical America is expected by looking at the global estimates of species for each family. The Cyatheaceae are the most diverse family of tree ferns, representing 90% of the total diversity in Cyatheales (703 species listed, Hassler and Swale 2001; +660 species, Smith et al. 2008). The second largest family are the Dicksoniaceae with ca. 30 species (5% of the total diversity), of which only seven are distributed in tropical and temperate America. Pooled together, the remaining six families are considerably less diverse with ca. 33 species (5%) (Smith et al. 2008), of which only eight are American species.

The worldwide overrepresentation of Cyatheaceae is evident in the flora of tropical America, but there is a differential representation at the generic level. *Cyathea* are

predominantly New World in distribution (Large and Braggins 2004) with 197 species, but the genus extends across the Pacific Ocean with the members of the *C. decurrens* complex (Large and Braggins 2004; Korall et al. 2007). *Alsophila* shows an inverse diversity gradient, predominating in the Old World with +210 species (Large and Braggins 2004; Mickel and Smith 2004; Korall et al. 2007) and only 35 species in tropical America. *Sphaeropteris* also predominate in the Old World (excluding Africa), with +120 species (Large and Braggins 2004) and only six representatives in tropical America.

The number of species in *Cyathea* presented here differs substantially from previous global estimates of species diversity in the genus (+120 species, Large and Braggins 2004; +115 species, Mickel and Smith 2004). The genus *Alsophila* has been considered, by far, the largest subgroup within Cyatheaceae (Korall et al. 2007) and Australasia as the most diverse 'centre' for tree ferns. Given the present estimates of American tree fern diversity, *Cyathea* should be considered equally diverse than *Alsophila* and tropical America as a main 'centre' of tree fern diversity, having ca. 40% of the total species of Cyatheales.

Richness and endemism

It is clear from this study that species richness and endemism are not distributed randomly over the landscape, but do aggregate into defined regions of high diversity and endemism in tropical America: the northern Andes, lower Central America, upper Central America-Mexico, southeastern Brazil, the Guyana Highlands, and the Antilles. These regions have been recognized as regional centres of plant diversity (Tryon 1972; Mittermeier et al. 1999; Hassler and Swale 2001; Hobohm 2003; Mutke and Barthlott 2005; Kier et al. 2009). The Andean 'centre' is the largest and most diverse region for tree ferns in tropical America, followed by lower Central America (i.e., Costa Rica and Panama). Both these regions are notable for their cloud forest and montane fern species (Tryon 1972).

Tryon (1972) recognized the Mexican 'centre' as most notable for the xeric and semi-xeric ferns of central Mexico, but he also noticed a prominent element of species and endemism in the south of the region. This last region, here referred as upper Central America-Mexico, is distinctive in the ferns of the cloud forests of Guatemala, El Salvador, and northern Nicaragua (Tryon 1972). Although this region shows relatively low levels of tree fern species richness and endemism, compared to lower Central America, it is noteworthy for the presence of Cibotiaceae.

Southeastern Brazil and the Guyana Shield, otherwise considered as having large numbers of fern species (Tryon 1972; Hassler and Swale 2001; Moran 2008), show reduced levels of Cyatheales species richness. This is due to the concentration of Cyatheales in the mountain ranges of the Atlantic coast and in the Guyana Highlands. Both these mountain regions have been often considered distinct biogeographic regions with a strong endemic component in their biota (Tryon 1972; Hobohm 2003; Kier et al. 2009; Löwenberg-Neto and Carvalho 2009). As in other fern genera (Tryon 1972), there are several endemic species in the Guyana Highlands and in the Serra do Mar in southeastern Brazil. For example, the eight species in the *Hymenophyllopsis* group (Table S1, supplementary material) are endemic to the Guyana Highlands (Christenhusz 2009) and are considered as basal to American *Cyathea* (Korall et al. 2007).

Our results identify the Antilles as a 'centre' of endemism, a pattern consistent across other plant groups (Davis et al. 1995; Hobohm 2003; Whittaker and Fernández-Palacios 2007; Kreft et al. 2008; Kier et al. 2009). Cyatheales endemism in this region is considerable and there are several single-island endemic species (e.g., *Alsophila balanocarpa* (D.C. Eaton) D.S. Conant in Cuba, *Cyathea harrisii* Underw. ex Maxon in Jamaica, and

Alsophila portoricensis (Spreng. ex Kuhn) D.S. Conant in Puerto Rico). However, there are some disjunct species from South and Central America (e.g., *Alsophila inrayana* (Hook.) D.S. Conant, *Cyathea horrida* (L.) Sm., *Metaxya rostrata* (Kunth) C. Presl). This pattern of endemism is also evident in the Juan Fernandez Islands, in the Pacific Ocean, which have three restricted species (i.e., *Dicksonia berteriana* Hook., *Dicksonia extensa* Skottsb., and *T. elegans*) and one disjunct species from the mainland (i.e., *Lophosoria quadripinnata* (J.F. Gmel) C. Chr.).

Hotspots, cloud forests, and conservation

Cyatheales species richness and endemism are concentrated within previously accepted biodiversity hotspots (Myers et al. 2000; Brooks et al. 2002, 2006; Hobohm 2003; Mutke and Barthlott 2005; Kier et al. 2009). These hotspots are: Mesoamerica (i.e., Mexico and Central America), the Caribbean, Chocó-Darién-western Ecuador, the tropical Andes, and Brazil's Atlantic forests (Myers et al. 2000). These regions feature high concentrations of endemic vascular plant species and are experiencing elevated habitat loss (Myers et al. 2000). Some of these hotspots have lost a major part of their original primary vegetation (e.g., 75% in the tropical Andes, 80% in Mesoamerica, 89% in the Caribbean, and 92.5% in Brazil's Atlantic forests), and most of the remaining primary vegetation is not currently protected (Myers et al. 2000).

Island systems, with their high density of endemic vascular plant species, including many Cyatheales, are important for global conservation of genetic resources (Kier et al. 2009). In particular, the genus *Alsophila* has 16 species restricted to the Antilles, mostly single-island endemics that represent 46% of the total diversity of the genus in tropical America. Also, the Juan Fernandez Islands harbour a high density of endemic elements in an area of roughly 100 km² (75% for Cyatheales; ca. 40% for other ferns, Hassler and Swale 2001; ca. 60% for other plant species, Davis et al. 1995; Hobohm 2003), with half of the American species of *Dicksonia* and the single species in Thyrsopteridaceae (*T. elegans*).

Much of the original forest cover in American islands has been lost to deforestation and land use-cover change (e.g., 70% in Hispaniola, 60% in Cuba, 55% in Puerto Rico, Mulligan and Burke 2005; 33% in the Juan Fernandez Islands, Dirnbock et al. 2003) and many of these islands are listed as some of the most endangered locations in the world (IUCN 2009).

The global scale of cloud forest deforestation is much less intense compared with the lowland forests, largely because of the difficult environmental conditions in which we find cloud forests, which makes them unsuitable for many agricultural activities (Mulligan and Burke 2005). Nevertheless, the cloud forests are among the most threatened communities in the world, with almost 60% of their original worldwide cover lost to deforestation (Churchill et al. 1995; Mulligan and Burke 2005). According to Mulligan and Burke (2005), intensive cloud forest loss has occurred throughout much of Mexico, western and central Colombia, western Ecuador, Peru, Bolivia, and the Brazilian Atlantic Forests. These regions have the highest levels of Cyatheales species diversity.

Furthermore, the cloud forests appear to be exceptionally vulnerable to climate change and the subsequent changes to the hydrological cycle (Foster 2001). As the climate changes, there will be alterations to the water balance in cloud forests by an increasing loss of humidity through evaporation, due to higher temperatures, and by the increase in the length of the dry season (Hulme and Viner 1998; Foster 2001). Long-term observations (Pounds et al. 1999) and preliminary modelling (Foster 2001) at the Monteverde cloud

forest in Costa Rica suggest that the height of the cloud-bank is already rising, resulting in less cloud immersion and reduced levels of humidity, and thus driving local extinction through enhanced dryness.

Conclusions

Given the present estimates of American tree fern diversity and endemism, tropical America is considered as a major ‘centre’ of tree fern diversity, having ca. 40% of the total species of Cyatheales. The present study shows that Cyatheales diversity is unevenly distributed at a continental scale, with a pattern of richness and endemism that is congruent with the geographical distribution of cloud forest, in areas with complex topography, high humidity, and persistent cloud immersion.

In the absence of greatly increased conservation efforts, these regions all seem likely to lose much if not most of their remaining primary vegetation (Myers et al. 2000). The regions with the highest species richness and endemism of tree ferns coincides with those recognized as the most threatened by deforestation and climate change. This threat is even greater for species inhabiting cloud forests, which are amongst the most threatened types of forests in the world. Conservation policies for Cyatheales have been centred on the local use and trade of many tree fern species (CITES 2009), but none such policies focus on the loss of cloud forest habitat. In the face of the current environmental crisis and global climate change, the concentration of Cyatheales in these regions sounds the alarm on their conservation priorities.

Brooks et al. (2002) confirmed that without urgent conservation intervention, mass extinction would occur in major biodiversity hotspots. This extinction would undoubtedly include most, if not all, Cyatheales species. If we fail in protecting the cloud forests, we must acknowledge Gómez-P (1985) forewarnings and agree with him that ferns were thing of past beauty and that in times not long past humans enjoyed such trivia as ‘cheerful communities of polypodies’.

Acknowledgments We would like to thank Juan J. Morrone, Thomas A. Ranker, Michael Heads, and two anonymous reviewers for their constructive evaluations of a previous version of the manuscript. Alan R. Smith for amendments to the database. Alfn T. Díaz helped with the identification of synonyms. This paper is part of the doctoral research of the first author, who thanks the Doctorado en Ciencias Biomédicas (Universidad Nacional Autónoma de México), CONACyT (Grant no. 229363), and the project DGAPA-PAPIIT IN-215510 for financial support, and the Laboratorio de Evolución Molecular y Experimental (Instituto de Ecología, Universidad Nacional Autónoma de México) for technical support.

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