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Ecological drivers of pteridophyte diversity and distribution in Togo (West Africa)

Komla Elikplim Abotsi[a,*], Ruksan Bose[b], Kossi Adjossou[a], Vincent Deblauwe[b,c,d], Germinal Rouhan[e], Kossi Novinyo Segla[a], Komina Honam Atsri[a], Kouami Kokou[a]

[a] Laboratoire de Recherche Forestière, Université de Lomé, 01BP1515 Lomé, Togo
[b] International Institute of Tropical Agriculture, Yaoundé, Cameroon
[c] Herbarium et Bibliothèque de Botanique africaine, Université Libre de Bruxelles, CP 265, Boulevard du Triomphe, B-1050 Brussels, Belgium
[d] Center for Tropical Research, Institute of the Environment and Sustainability, University of California, Los Angeles, Los Angeles, CA 90095, USA
[e] Institut Systématique Evolution Biodiversité (ISYEB), Muséum National d'Histoire Naturelle, CNRS, Sorbonne Université, EPHE, 57 rue Cuvier CP 39, Paris, France

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ABSTRACT

The conservation and sustainable management of biodiversity requires an understanding of the biotic and abiotic factors that condition the presence and survival of organisms in natural habitats. The global distribution and ecological hypersensitivity of pteridophytes have made them ideal candidates for studying the impact of biotic and abiotic factors on levels of biodiversity.

This study aims to determine the effect of vegetation cover, human disturbance, and climatic factors on the distribution and diversity of pteridophytes in Togo with a view to guide conservation efforts. Our data comprises 130 plots of 500 m^2 representing all ecological zones of the country, complemented by several opportunistic collections. After determining the patterns of pteridophyte distribution, multivariate analysis of variance and the calculation of diversity indicators made it possible to determine the influence of the factors studied.

We found that pteridophyte species diversity and distribution in Togo are strongly influenced by climatic variables, with more than 90% of species diversity being concentrated in the submontane forest areas. Humidity related variables, insolation, and human disturbances are the main drivers of their distribution. Species diversity is positively associated with an increase in humidity, but decreases with increasing insolation and human disturbance. Importantly, our results emphasize the association of specific species to particular conditions created by climate, land cover, and human disturbances, highlighting the role of pteridophyte species as indicators of environmental conditions or exposure to stress. Within humid forest areas, our analysis of the impact of disturbance indicates that about a quarter of the pteridophyte flora of humid forests is sensitive to minor disturbances, whereas almost all rainforest species decline in the face of high levels of disturbance. Agroforests are a particular case of moderately disturbed rainforests, and have the potential to harbour at least 30.5% of Togolese rainforest pteridophyte species diversity.

We conclude that the conservation of pteridophytes in Togo requires the protection of submontane rainforests and the adoption of less destructive practices in terrestrial species habitats in coffee/cocoa-based agroforests.

1. Introduction

Current knowledge of vascular plant diversity suggests an unequal distribution across the main biogeographic zones of the terrestrial globe (Barthlott et al., 2007, 1996; Myers et al., 2000). About 44% of vascular plants are concentrated on just 1.4% of the earth's land surface (Myers et al., 2000). In the case of pteridophytes, Europe is home to only 179 species in over 10 million km^2, compared to 1120 species in less than a quarter of that area in the Caribbean (Hassler and Schmitt, 2019). Numerous studies highlight close links between the current distribution of vascular flora and the biotic (viz. interactions with other living organisms) and abiotic (viz. climate, soil, topography) characteristics of their habitat (Currie and Paquin, 1987; Bickford and Laffan, 2006; Kreft and Jetz, 2007; Kreft et al., 2010). Generally, water and energy related variables have been identified as the leading factors that constrain the distribution of species at biogeographic scale while biotic factors define their realized niche at the habitat scale.

Less studied than Spermatophytes (seed plants), pteridophytes

* Corresponding author.
E-mail address: abotsikomlaelikplim@yahoo.fr (K.E. Abotsi).

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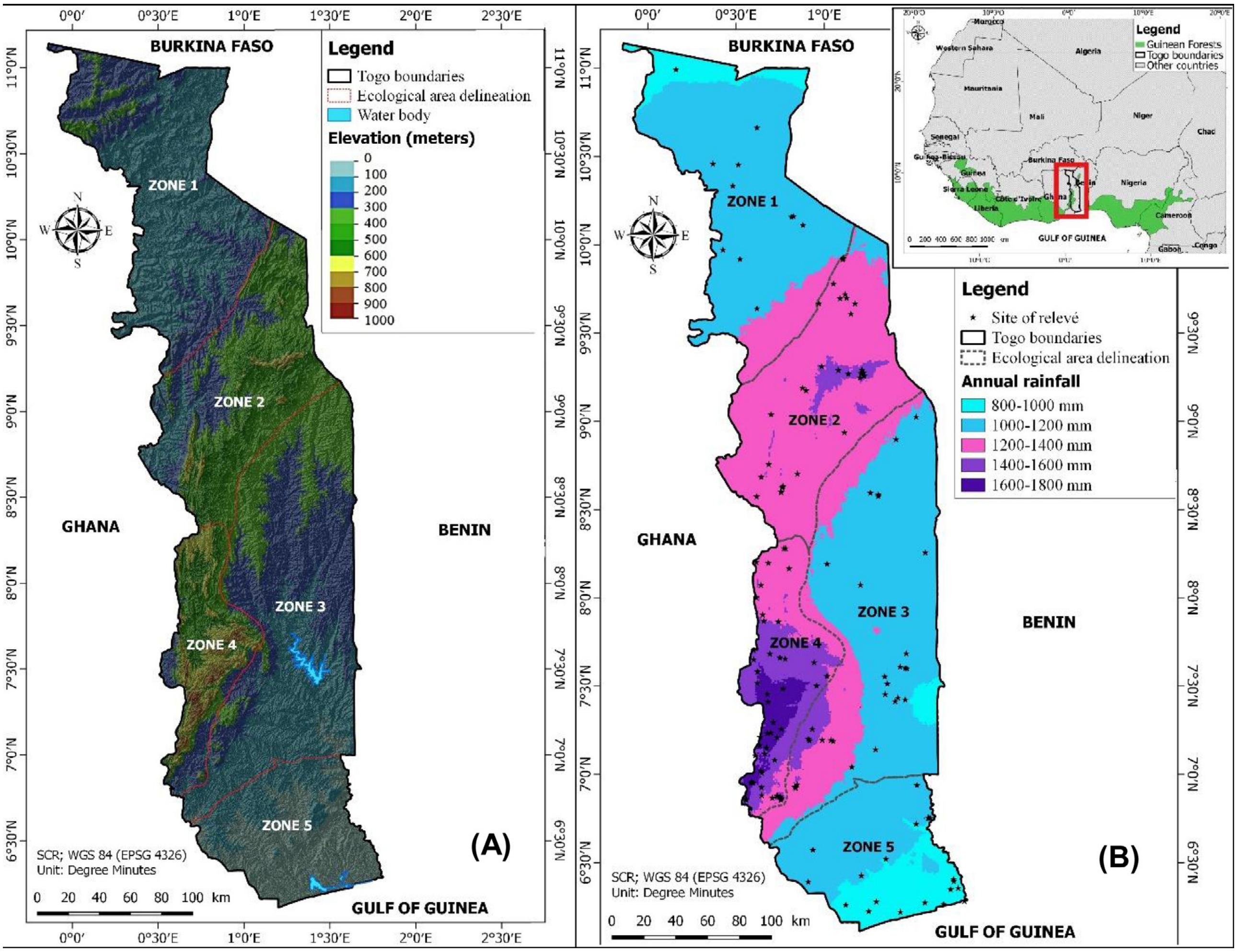

Fig. 1. Study area (A) relief map showing elevation range in the country, (B) annual rainfall map with inventoried sites (B). The delineation of the five ecological zones of Ern (1979) is provided for each map. The insert in the upper right corner indicates the localization of Togo (in the red rectangle) in West Africa and within West African Guinean forest area (green area). Relief derived from SRTM elevation data, and rainfall derived from WorldClim version 2.0 (current climate).

(spore-bearing vascular plants), grouping two distinct evolutionary lineages i.e. ferns and lycophytes (PPG I, 2016), are nevertheless major constituents of the flora of tropical forests (Salazar et al., 2015; Watkins et al., 2006), especially in the undergrowth and as low epiphytes (Acebey et al., 2017; Krömer et al., 2007; Mehltreter et al., 2005). Given their wide distribution, wide range of habitat preferences, hypersensitivity to micro-variations in their environment, and relative independence from herbivores (Barrington, 1993), they are good indicators of the state of habitats on a global scale, thus constituting effective monitoring subjects, especially in the current context of the global biodiversity crisis related to habitat loss (Ceballos et al., 2010; Teyssèdre, 2004).

With a pteridophyte diversity estimated at 765 species (Kornas, 1993), the flora of tropical Africa is less rich than those of other tropical regions of the world such as South America or the Malesia region (respectively 3628 and 2963 species; Tryon, 1989, 1986; Tryon and Tryon, 1982). Kornas (1993) attributes this relative poverty to local extinctions as a result of shifting of vegetation zones due to continental drift and climatic oscillations during the late Tertiary, which also confined the flora to biodiversity refuges (Aldasoro et al., 2004). However, the capacity of the remaining species to recolonize the rest of the continent is governed by current environmental constraints such as humidity and elevation (Aldasoro et al., 2004). Later studies, mainly in the Neotropics, confirmed the major role of habitat constraints (bioclimatic and anthropogenic) in determining the distribution and richness of extant pteridophyte species (Gasper et al., 2015; Karst et al., 2005; Kluge et al., 2008; Kreft et al., 2010; Tuomisto et al., 2014). While a few studies focused on the African continent (Hemp, 2002, 2001), providing insights into the effect of elevation, vegetation and land use on the distribution of pteridophytes in montane zones, much remains to be done to understand the distribution of pteridophytes at local scales, especially in the West African lowlands.

Partly located in the "Dahomey gap" which is an interruption of the West African Guinean forests (White, 1983), Togo is home to a rich vascular flora (4002 plant species and 4019 animal species; SCBD, 2018) including 122 species of native pteridophytes (Abotsi et al., 2018). The country is part of the Gulf of Guinea area of endemism and biodiversity hotspot (Mittermeier et al., 2000; Myers et al., 2000). The alarming degradation and fragmentation of forest habitats underway in Togo in recent decades poses a real threat to the survival of pteridophytes and biodiversity in general (MERF, 2014).

The main objective of this study is to contribute to our knowledge of the diversity and ecology of pteridophytes in Togo with a view to guide conservation efforts. To this end, we addressed the following questions: How is this flora spread over the Togolese territory? What are the ecological factors that best explain this distribution? We hypothesize that favorable ecological conditions, such as humidity, cloudiness and forest cover of the mountains of Togo could be the drivers of this distribution (Aldasoro et al., 2004; Anthelme et al., 2011; Moran, 1995; Moran and Smith, 2001). Also, in the light of recent works which show a close relationship between forest disturbance and degradation and the loss of pteridophyte species diversity (Barthlott et al., 2001; Carvajal-

Hernández et al., 2017; Paciencia and Prado, 2005), it is hypothesized that human activities also impact this group in Togo. We therefore also ask how does human disturbance impact the diversity and distribution of pteridophytes in Togo?

Specifically, this study aims (1) to characterize the pteridophyte flora in the different ecological zones of Togo, (2) to determine the influence of climate related variables on the distribution patterns of pteridophyte species, (3) to determine the influence of land cover types on pteridophyte species diversity and composition, and lastly, (4) to analyze the impact of human disturbance on the species diversity and composition in rainforests. The study is based on the analysis of data gathered between 2013 and 2018 in Togo, including georeferenced occurrences, physical data (elevation), ecological data (land cover types), anthropogenic influences (degree of disturbance of habitat) and climatic data (temperature range, precipitation, cloud cover, climatic water deficit and aridity).

2. Material and methods

2.1. Study area

This study was conducted in Togo (Fig. 1), a country of 56600 km^2 located in the Gulf of Guinea in West Africa. In terms of relief, Togo is characterized by lowlands separated by the Togo Mountains which run diagonally across the country from the south-west to the north-east (highest peak 986 m).

Based in its topography (Fig. 1A) and rainfall (Fig. 1B), Togo can be subdivided into 5 ecological zones (Ern, 1979). Zone 1 is the northern plains area with Sudanian savanna vegetation and patches of dry forest along rivers, and zone 2 (northern part of Togo Mountains) is characterized by submontane dry forests and woodland areas. These northern zones come under the Sudanian climatic and floristic region (Aubréville, 1950) whereas the zones in the south fall in the Guinean climatic and floristic regions. Zone 3 is a Guinean-Sudanian transition area and comprises the central plains with a mosaic of dry forests and Guinean savanna. Zone 4 (southern part of Togo mountains) is mostly covered by rainforests and Guinean savanna vegetation, and zone 5 includes the coastal plains covered by meadows, mangroves, and rainforests. The southern plains areas (zones 3 and 5) are located in the West African Guinean forest discontinuity ("Dahomey Gap", Kokou, 1998; White, 1983). Annual rainfall ranges from 800 mm in zones 1 and 5 to 1800 mm in zone 4 (see Fig. 1B).

2.2. Data collection

The data supporting this study were collected between 2013 and 2018. In the initial stage, ecological data were collected at plot level in order to characterize the flora. A total of 130 plots of 500 m^2 (50 m × 10 m), randomly spread over the country and covering the 5 ecological zones were inventoried and characterized (Fig. 1B). The following stage consisted of the recording of opportunistic species along river banks and forest trails (at a distance of at least 2 km from each plot), to complete species occurrence data for the country.

For each plot, the following information was recorded: land cover type and level of disturbance, tree cover, elevation, longitude and latitude. In addition, we noted the scientific name, the habit (i.e. terrestrial or epiphytic) and calculated the relative abundance-dominance of each pteridophyte species occurring in the plot. The relative abundance-dominance (A-D) of a species was assessed by the Braun-Blanquet approach (Braun-Blanquet, 1932; Westhoff and Van Der Maarel, 1978). It represents the importance (combination of abundance and surface cover) of each species relative to all other pteridophyte species occurring at the plot scale and is expressed on a scale of 0–100%.

For an ecological characterization of the plots, the maximum temperature of the warmest month (BIO5), the minimum temperature of the coldest month (BIO6) and the annual precipitation (BIO12) were obtained for each plot from WorldClim version 2 (Fick and Hijmans, 2017) at a resolution of 30 arc-seconds. Cloud cover was obtained from "Earth Env" (https://www.earthenv.org/cloud) at a resolution of 1 km (Wilson and Jetz, 2016). The humidity index (Middleton and Thomas, 1992) and the climatic water deficit variable were acquired at a resolution of 3 arc-minutes from Deblauwe's data portal (https://vdeblauwe.wordpress.com). The humidity index is an average of the yearly sum of precipitation divided by the annual Potential Evapo-Transpiration (PET). Climatic water deficit is the difference between rainfall and PET (only during dry months, i.e. months where PET exceeds rainfall). It represents the intensity of dry periods and is by definition negative. All the climatic variables were extracted for each plot and occurrence, using R packages "foreach", "raster", "rgdal" and "sp" (R Core Team, 2013). All subsequent statistical analyzes were performed using "vegan", "labdsv" and "indicspecies" packages in R.

Land cover (vegetation and land use) was categorized into 8 classes, namely: (1) Rainforest, (2) Dry forest, (3) Coffee/cocoa-based agroforest, (4) Savannah/Woodland, (5) Mangrove and affiliate ecosystems, (6) Palm grove, (7) Meadow (aquatic) and (8) off-forest areas (farms, dwellings, etc.). Habitat disturbance level was evaluated on a scale of 0 to 3 with 0 denoting an undisturbed forest state, 1 representing minor disturbance (low impact on the floristic composition and physiognomy of the habitat), 2 denoting average disturbance (affecting less than 25% of large trees but not significantly affecting the appearance of the habitat) and 3 applied to disturbed states (more than 25% of large trees and the physiognomy of the habitat affected). Tree cover refers to the estimated percentage of area covered by tree canopy at the plot level. It was expressed in 5 classes namely 0–20%, 20–40%, 40–60%, 60–80% and 80–100%.

All the data supporting this study were deposited on Mendeley and are accessible at doi:https://doi.org/10.17632/sgts85fjfb.1.

2.3. Characterization of the pteridophyte flora of Togo's ecological zones

For our first objective, we compared the species richness (gamma diversity) of the five ecological zones and examined the association between specific pteridophyte species and each of these zones. For each ecological zone, we distinguished, by combining in-plot and out-plot occurrences, the number of species exclusive to the zone and the number of species shared with other zones. The match between a particular pteridophyte flora and a given ecological zone was determined from the matrix of relative abundance-dominance of species in plots, using two association indices: the indicator value and the phi coefficient of association, which is the Pearson correlation for binary variables (De Cáceres and Legendre, 2009). We used the indicator value to identify specific or exclusive links of the species to an ecological zone. A high indicator value is obtained by a combination of high *specificity* (maximal when the species is present only in the targeted habitat) and high *fidelity* (maximal when the species is present in all the plots of the targeted habitat) of the species to a given zone (De Cáceres and Legendre, 2009). In case of the absence of any exclusive links, we used the phi coefficient of association to determine the degree of ecological preference of a species for a specific zone compared to other zones where it may occur.

2.4. Evaluation of the influence of climate on the distribution patterns of pteridophyte species in Togo

In order to evaluate the hypothesis that ecological niches of species shape their geographic distribution, we performed a Canonical Correspondence Analysis (CCA) on the presence/absence table of the species in the plots, constrained by climatic variables. We conducted permutation tests to evaluate the significance of the effects of each climatic variable. This allowed us to identify the main climatic drivers of pteridophyte species distribution in Togo.

2.5. Evaluation of the influence of land cover on the diversity and floristic composition of pteridophytes at local scale

For our third objective, we analyzed the importance of land cover by comparing pteridophyte species diversity and floristic composition (species and habits) for each land cover type. We further identified potential associations between species, land cover type and tree cover.

For diversity comparison, we estimated species diversity in four different ways: Whittaker's alpha diversity (average number of species per plot), gamma diversity (total number of species), Whittaker's species turnover ($T = \left(\frac{gamma\ diversity}{alpha\ diversity}\right) - 1$), and Shannon diversity index ($H^{'} = -\sum_{i=1}^{R} p_i * \ln(p_i)$), where p_i is the proportion of individuals belonging to the i^{th} species, and R is the total number of species).

To compare the floristic composition of different land cover types, we performed an ascending hierarchical classification (AHC), using Bray-Curtis dissimilarity metric (Bray and Curtis, 1957), and Ward's minimum variance, which are clustering methods recommended for vegetation cluster analysis (Borcard et al., 2018). The Bray-Curtis index varies from 0 (same species composition and relative frequencies) to 1 (no shared species) for each pair of land cover type. We also compared the proportion of epiphytes (relative number of epiphytic species per plot) in each land cover type to study the potential impact of land cover on the habit of species.

To evaluate the significance of the role of land cover type and tree cover on species diversity, composition, and habit, we performed a Permutational Multivariate Analysis of Variance (PMAV, McArdle and Anderson, 2001), using distance matrices. Finally, we performed an indicator value analysis to determine if land cover constraints can lead to specific associations to some species.

2.6. Evaluation of the impact of human disturbance on the diversity and floristic composition in rainforests

The impact of disturbance on species diversity (alpha diversity, species turnover, and Shannon diversity index), and composition (proportion of epiphytes) was analyzed on the rainforest plots, considering the three levels of disturbance. A total of 36 plots located in rainforests (with 0 plots for perturbation level 0, 9 plots for level 1, 21 plots for level 2 and 6 plots for level 3) were analyzed. We performed a PMAV to evaluate the significance of the impact of human disturbance on species composition in rainforest plots. An indicator species analysis was performed to identify potential links between species and each disturbance level. The importance and the constancy of the species were then calculated and compared at a minimum abundance/dominance threshold of 25% in order to highlight structural changes. For a set of plots, the importance of a species refers to the mean abundance of the species in a targeted habitat compared to its mean abundance across all the habitats, while the constancy is the proportion of plots where the species is present in the targeted habitat. At the scale of the plot, we considered species with less than 25% abundance-dominance as marginal and others as important species. Coffee/cocoa-based agroforests were further compared with rainforests in order to determine the relative impact of this particular type of forest disturbance on the native flora.

3. Results

3.1. Distribution of pteridophyte species within ecological areas in Togo

Pteridophyte species richness is unequally distributed in Togo (Table 1). The submontane area of Togo Mountains is richer (90.16% of the total diversity) than the lowlands. A majority of species is limited to ecological zone 4. This zone alone shelters 104 species of a total of 122 native recorded species growing in the country, that is 85.25% of the flora of which 81 species are exclusive to it, while the northern lowlands (zone 1) shelter only two species which are also represented in zone 3.

Ecological zones 2, 3, and 5 are each characterized by at least one indicator species, whereas zones 1 and 4 do not have any indicator species (Table 2). The values of the Pearson association coefficient however indicate a significant ecological preference of *Pteris togoensis* Hieron. (φ = 0.414, p-value = 0.013), *Pellaea doniana* (J. Sm.) Hook. (φ = 0.365, p-value = 0.025), *Tectaria fernandensis* (Baker) C. Chr. (φ = 0.365, p-value = 0.037), *Asplenium formosum* Willd. (φ = 0.363, p-value = 0.040) and *Platycerium stemaria* (P. Beauv.) Desv. (φ = 0.343, p-value = 0.042) for ecological zone 4.

3.2. Influence of climate on the distribution patterns of pteridophyte species in Togo

According to the CCA, the first two axes together explained about 48% of the overall variation in the species composition-climate relationship. Permutation tests indicated that altitude (p-value = 0.002), BIO5 (p-value = 0.004), annual precipitation (p-value = 0.002), climatic water deficit (p-value = 0.004), and cloud cover rate (p-value = 0.002) had significant effects (Fig. 2). Axis 1 of the CCA represents variation in humidity, which corresponds to an increase in precipitation coupled with an elevation related decrease in evapotranspiration and temperature. Axis 2 of the CCA reflects the importance of the intensity of dry periods, shading, and temperature maxima in the differentiation of species niches. Variation in annual precipitation (axis 1) and climatic water deficit (axis 2) are the main variables that contribute to differentiating the climatic niches of pteridophyte species in Togo (Table 3). Along CCA axis 1 we observed a fairly clear discrimination between the flora of the lowlands (zones 1, 3, and 5) vs. mountain areas (zones 2 and 4). CCA axis 2 contrasts the Guinean and Guinean-Sudanian transition area (zone 4, 5 and 3) to the Sudanian (zones 1 and 2) flora (Fig. 2).

The ecological zone 4 is characterized by higher annual precipitation, lower climatic water deficit and cloudiness (Fig. 2). The climatic characteristics of this zone are favorable for the presence of species such as *Microgramma mauritiana* (Willd.) Tardieu, *Asplenium biafranum* Alston & F.Ballard ex Ballard Hook., *Asplenium dregeanum* Kunze, *Haplopteris guineensis* (Desv.) E.H. Crane and *Alsophila camerooniana* (Hook.) R.M. Tryon. In contrast, the presence of species such as *Anemia sessilis*, *Palhinhaea cernua* (L.) Carv. Vasc. & Franco, *Selaginella buchholzii* Hieron and *Actiniopteris radiata* (Koenig ex Sw.) Link. is observed in Sudanian submontanous regions (zone 2) which are more deficient in climatic water (positive CCA Axis 2).

Between these two climatic conditions, the Guinean-Sudanian transition region (zone 3) is particularly favorable to *Adiantum incisum*, *Ophioglossum costatum* R.Br., and *Platycerium elephantotis*. *Adiantum soboliferum*, *Selaginella kalbreyeri* Baker and *Nephrolepis cordifolia* are found in both zone 2 and zone 3. *Acrostichum aureum*, *Marsilea minuta*, and *Cyclosorus striatus* (Schum.) Ching. are related to the wetlands of the ecological zone 5, which are characterized by lower annual rainfall, higher temperatures during the warm months and lower elevations (negative CCA Axis 1).

3.3. Influence of land cover on diversity and floristic composition

Pteridophytes are unevenly distributed in the different land cover types in Togo. Indeed, 82 species (representing 67,21% of the local flora) are exclusive to rainforests and only 5 species (*Ophioglossum* spp.), that is 4.1% of the species, are restricted to the savanna zones. Rainforests are clearly richer with 105 species overall and more than 5 species per 500 m^2 plot on average (Table 4), while mangroves shelter only two species, including *Acrostichum aureum*, which is an indicator species (Table 5). Although rainforests shelter a higher number of epiphytic species overall, palm groves comprise only epiphytes (100%), followed by off-forest areas, agroforests, etc. (see Table 4). Mangroves

Table 1
Floristic structure of pteridophytes within Togo ecological zones. Zones 1 to 5 represent the 5 ecological zones defined by Ern (1979).

Ecological zone	Species richness	Exclusive species rate	Species per genus	Species per family	Genera per family	Epiphytic over terrestrial species
Zone 1	2	0 (0.00%)	2/2 (1,00)	2/2 (1,00)	2/2 (1,00)	0/2 (0.00)
Zone 2	22	4 (3.28%)	22/13 (1.69)	22/9 (2,44)	13/9 (1,44)	3/19 (0.16)
Zone 3	17	5 (4.10%)	17/9 (1.89)	17/7 (2,43)	9/7 (1,29)	6/11 (0.55)
Zone 4	104	81 (66.39%)	104/49 (2.12)	104/21 (4,95)	49/21 (2,33)	20/84 (0.24)
Zone 5	10	5 (4.10%)	10/9 (1.11)	10/7 (1.43)	9/7 (1,29)	2/8 (0.25)

Table 2
Indicator species of the ecological zones of Togo. Zone 1–5 are Togo ecological areas.

Ecological zones	Species	Indicator value	P-value
Zone 1	–	–	–
Zone 2	*Anemia sessilis* (Jeanp.) C.Chr.	0.369	0.037
Zone 3	*Platycerium elephantotis* Schweinf.	0.466	0.009
Zones 2 and 3	*Adiantum soboliferum* Wall.	0.749	0.001
Zone 4	–	–	–
Zone 5	*Cyclosorus striatus* (Schum.) Ching	0.555	0.002
	Acrostichum aureum L.	0.480	0.014
	Ceratopteris thalictroides (L.) Brongn.	0.392	0.022
	Marsilea minuta L.	0.392	0.014
	Salvinia auriculata Aubl.	0.392	0.025
	Salvinia nymphellula Desv.	0.392	0.027

and meadows do not shelter epiphytic species.

Salvinia auriculata is an indicator of meadows while palm groves are characterized by the presence of *Nephrolepis bisserata* (Sw.) Schott., *Microsorum scolopendria* (Burm.f.) Copel. and *Nephrolepis undulata* (Afzel. ex Sw.) J. Sm. The open vegetations of savanna/woodland are characterized by *Nephrolepis cordifolia* (L.) Presl. With significant indicator values, *Adiantum soboliferum* is unequivocally the indicator species of dry forests, *Pteris togoensis* of agroforests and *Pellaea doniana* of rainforests. Only agroforests and dense humid forests are similar on the basis of the constancy of *Adiantum philippense* L. and *Pteris togoensis* within them. The most frequent species of each land cover type differs from those of other land cover types.

The dendrogram obtained from the distance matrix of land cover types indicates that there are affinities between the flora within each group (Fig. 3). Indeed, 4 floristic groups are identified for pteridophytes

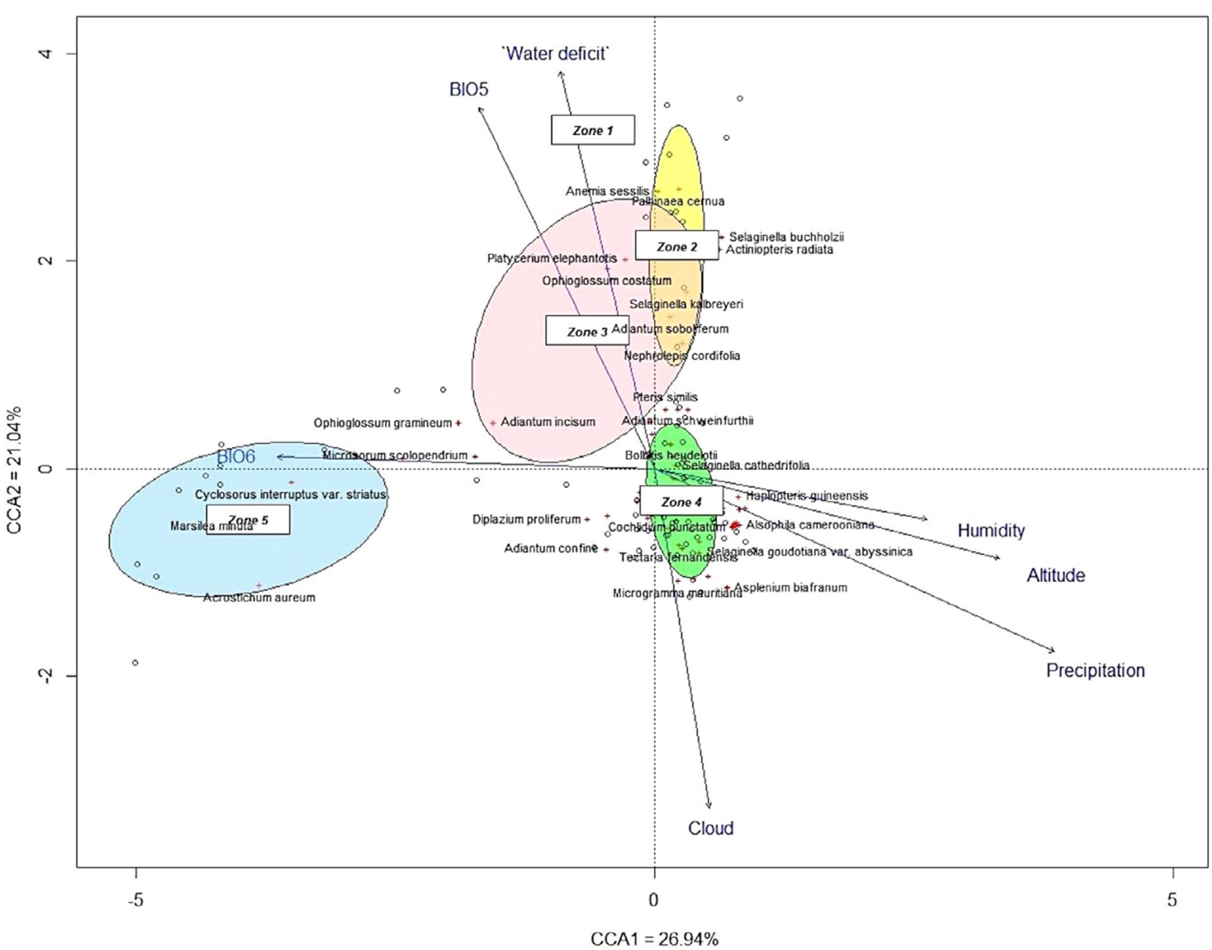

Fig. 2. Canonical Correspondence Analysis (CCA) of pteridophyte species and climatic variables characterizing the plots in which they occur. The five ecological zones of Togo are shown in colour; their position and extents were automatically generated at 95% confidence interval from the centroid of the factorial coordinates of the plots that were inventoried within each zone. The climatic variables are: “BIO5” or the maximum temperature of the warmest month; “BIO6” or the minimum temperature of the coldest month; “Cloud” is the index of nebulosity or cloudiness; “Water deficit” represents the reduction in climatic water deficit; “Humidity” evaluates the annual rate of precipitation over PET.

Table 3
Correlation of climatic variables with the two constrained axes retained after the permutation test on axes.

Tested variables	CCA1	CCA2
Altitude	**0.7235**	−0.18797
Humidity	0.5707	−0.10529
BIO5	−0.3664	**0.75717**
BIO6	**−0.7883**	0.02492
Climatic water deficit	−0.1965	**0.83211**
Cloud coverage	0.1148	**−0.70985**
Precipitation (annual)	**0.8368**	−0.38362

Values in bold indicate the axis to which the climatic variables contribute the most in the model (the maximum contribution of Humidity index is for CCA6, which is not retained by the permutation test); CCA1 and CCA2 are the main constrained axis of the model; BIO5 is the maximum temperature of the warmest month; BIO6 is the minimum temperature of the coldest month.

Table 4
Species diversity and floristic structure of land cover types in Togo.

Land cover	Shannon index	Alpha diversity	Gamma diversity	Terrestrial rate	Epiphyte rate
Rainforest	1.6183	5.6111	105	83.81%	16.19%
Agroforest	1.3590	4.5714	32	78.13%	21.88%
Dry forest	0.8060	2.6250	20	90.00%	10.00%
Palm grove	0.7749	2.4285	10	0.00%	100.00%
Savanna/ Woodland	0.5291	1.8421	21	90.48%	9.52%
Meadow	0.2479	1.4285	9	100.00%	0.00%
Mangrove (rear)	0.2310	1.3333	2	100.00%	0.00%
Off forest	–	–	12	41.67%	58.33%

Table 5
Indicator species of land cover types.

Land cover	Indicator species	Indicator value	P-value
Rainforest	*Pellaea doniana* (J. Sm.) Hook.	0.2500	0.047
Agroforest	*Pteris togoensis* Hieron	0.3522	0.019
Dry forest	*Adiantum soboliferum* Wall.	0.5028	0.006
Palm grove	*Nephrolepis bisserata* (Sw.) Schott.	0.5102	0.007
	Microsorum scolopendria (Burm.f.) Copel.	0.2857	0.050
	Nephrolepis undulata (Afzel. ex Sw.) J. Sm.	0.2481	0.040
Savanna/Woodland	*Nephrolepis cordifolia* (L.) Presl.	0.3254	0.024
Meadow	*Salvinia auriculata* Aubl.	0.2857	0.049
Mangrove (rear)	*Acrostichum aureum* L.	1.0000	0.001
Off forest	–	–	–

in Togo.

Group G1 corresponds to the flora of the open vegetation of coastal wetlands. It can be distinguished by its heliophilic affinity, unlike others which require shade provided by tree cover. The group G2 stands out from the other two ombrophilous groups by its entirely anthropogenic origin. This group, found in farms, inhabited areas and palm groves, is characterized by a low diversity of ligneous species (generally only one tree species), unlike the last two groups, which are almost natural multi-species vegetation types with a dry variant (Group 3) and a wet one (Group 4).

The results of the PMAV showed that land cover type (p-value = 0.0049) and tree cover (p-value = 0.0199), taken separately, have a significant impact on flora. However, significant differences are not observed at different levels of tree cover (p-value = 0.7861) within the same land cover class.

3.4. Impacts of habitat disturbance in rainforests

The multivariate analysis of variance of the matrix of distance between rainforest plots and the values of species constancy and importance, depending on the degree of disturbance, indicate that disturbance has a significant impact on the pteridophyte flora.

Pteridophyte species diversity decreases continuously with increasing disturbance; however, this is mainly due to the reduction in terrestrial species as both the number and proportion of epiphytes are highest at medium disturbance levels (Table 6). The average disturbance level is where we observed the highest species turnover.

In terms of relative abundance-dominance (A-D) representing species importance, *Christella dentata* (Forssk.) Brownsey & Jermy (A-D = 33%), *Pellaea doniana* (A-D = 44%) and *Pteris linearis* Poir. (A-D = 33%) were the most typical species of areas with minor disturbance levels. *Adiantum philippense* L. and *Asplenium formosum* Willd. have good constancy, almost as much at low disturbance levels (present in 33% and 44% of plots, respectively) as at medium disturbance levels (40% and 30% of plots, respectively). Only major disturbances of the habitat lead to their being classified as marginal (A-D < 25%), even if the importance of *Adiantum philippense* decreases considerably from 33.33% to 23.12% at the average level of disturbance. *Pteris togoensis* (A-D = 45%), *Tectaria fernandensis* (Baker) C.Chr. (A-D = 30%), *Nephrolepis bisserata* (A-D = 25%), and *Doryopteris kirkii* (Hook.) Alston (A-D = 25%) characterize the average disturbance level with a constancy of 25% of the plots. The maximum disturbance level is characterized by the constancy of *Blotiella currorii* (Hook.) R.M.Tryon (40% of plots) and *Selaginella myosurus* (Sw.) Alston (60% of plots). The latter is the indicator species for highly disturbed rainforests in the country (p-value = 0.015).

Thus, about 22% of the most important species at the minor disturbance level become marginal (A-D < 25%) at the average disturbance levels, and 97% become marginal at maximum disturbance levels. Only 3% of rainforest species are therefore less sensitive to the disturbance of their environment.

In addition, when the disturbance of rainforests led to their transformation, there were 73 species fewer in coffee/cocoa-based agroforest, representing a loss of 69.5% of the total pteridophyte species richness of these forests. Changes in the structure of the residual flora are also observed. Indeed, there is an increase in the proportion of epiphytes from 16.19% in the rainforest to 21.88% in agroforests. *Adiantum philippense* and *Pteris togoensis*, the only two species with good constancy in these two land cover types, move from marginal species status in terms of their relative abundance in rainforests to important species status in agroforests.

4. Discussion

Our study contributes to a better understanding of climatic and anthropogenic factors that influence the distribution of tropical pteridophytes, with a particular focus on the area of endemism of the Gulf of Guinea. We found that pteridophyte species diversity and distribution in Togo is strongly influenced by climatic variables, with the highest levels of diversity coinciding with areas of higher water availability. While the majority of Togo's pteridophyte species are therefore found in sub-montane humid forest areas, our results point to the presence and adaptation of certain species to other land cover types with lower water availability. Importantly, our results demonstrate that specific species can be associated with particular conditions created by climate, land cover, and human disturbance, highlighting the role of pteridophyte species as indicators of environmental conditions or the exposure to stress. Within humid forest areas, our analysis of the impact of disturbance indicates that about a quarter of the pteridophyte flora of humid forests are sensitive to minor disturbances, whereas almost all rainforest species decline in the face of high levels of disturbance. Agroforests are a particular case of moderate disturbance and retain

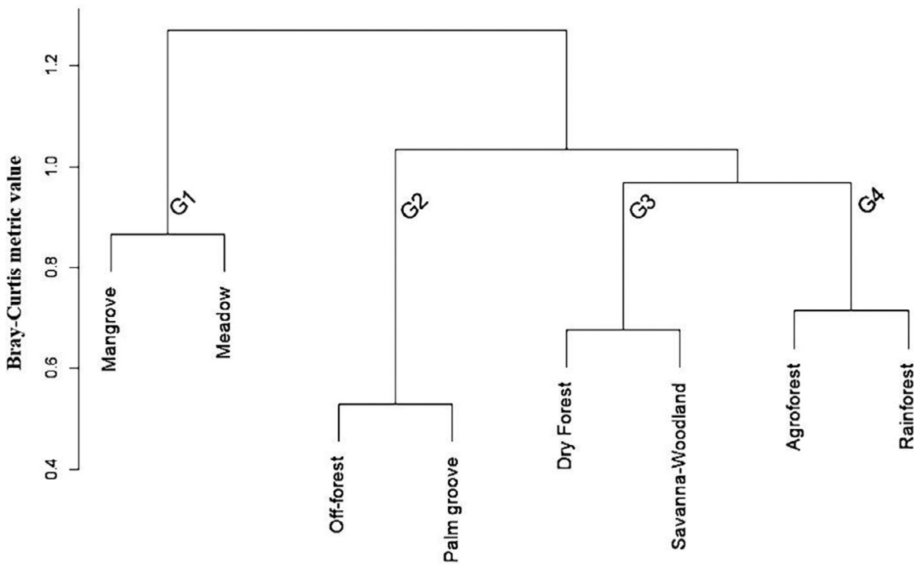

Fig. 3. Floristic affinities of land cover types in Togo based on pteridophyte species composition. The dendrogram is based on floristic dissimilarities between plot data. Y axis shows the Bray-Curtis distance between land cover types. G1 to G4 are the identified floristic groups within the local flora; G1: coastal wetlands heliophilic flora; G2: anthropogenic ombrophilous flora; G3: natural dry vegetations ombrophilous flora; G4: wet vegetations ombrophilous flora.

Table 6
Effect of disturbance on pteridophytes diversity in rain forests.

Disturbance	Alpha diversity			Epiphyte rate	Turnover	Shannon index
	All species	Terrestrial	Epiphyte			
Level 1	6.5555	5.7966	0.7589	11.58%	4.7966	1.8045
Level 2	5.7500	4.4210	1.3289	23.11%	7.0000	1.6589
Level 3	4.8000	3.8571	0.9428	19.64%	3.3750	1.4544

about a third of the species of humid forests that are able to occupy spaces left by less-tolerant species.

4.1. Water availability as the main driver of pteridophyte diversity and distribution

Our results point to the strong influence of humidity related variables and insolation (cloudiness and tree shading) on the floristic composition of plots. In particular, the CCA shows that niche preferences of pteridophyte species in Togo are constrained largely by water availability. As pointed out by Kreft et al. (2010), unlike seed plants, pteridophytes have two independent free-living life stages, one of which are fertilized by motile spermatozoids that need a water film for movement. Given their functional biology therefore, this explains the pronounced relation of pteridophyte presence to water availability (Kreft et al., 2010).

Humidity is generally identified as the main climatic driver of species richness in pteridophytes (Aldasoro et al., 2004; Bystriakova et al., 2015; Kessler et al., 2014; Kreft et al., 2010; Kreft and Jetz, 2007; Tuomisto et al., 2014). In Togo, annual precipitation increases with elevation and the highest diversity of pteridophytes was found in the submontane forest areas of Togo (ecological zones 4 and 2) compared to the low diversity of lowland zones, which predominantly comprise savanna ecosystems (zones 1, 3 and 5). The higher species diversity of pteridophytes in mountainous areas was previously attributed both to the effect of elevation (providing wetter and cooler climatic conditions) and high habitat diversity, which offers a wider range of niches available for the species (Kessler et al., 2001; Salazar et al., 2015). In the submontane zones, despite almost similar annual rainfall levels in zones 4 and 2, the relatively low diversity of zone 2 (Table 1) can be linked to a higher exposure to the Harmattan, a warm and dry continental trade wind, which creates a seasonal gradient of increasing evapotranspiration and temperature from the SW to the NE (Brunel et al., 1984). Within the lowlands, the observed diversity increases from lower rainfall areas of zone 1 to zone 5 to relatively higher rainfall areas in the transition zone 3. Further, the decrease in climatic water deficit could be associated with an increase in cloudiness and a decrease in the maximum temperature of the warmest month, which are also factors that contribute to higher pteridophyte diversity in our study. However, while much of Togo's pteridophyte flora is concentrated in humid high elevations, certain species are adapted to conditions of the lower elevation coastal wetlands of zone 5 and others to the drier conditions of the northern Sudanian climatic zones.

In zone 2, despite sufficient annual rainfall (1200–1600 mm), the water deficit created by high exposure to the Harmattan and the 4–5 month long dry season (Brunel et al., 1984) are major constraints to the presence of pteridophytes. Being exclusively saxicolous (Porembski and Barthlott, 2000), species that are associated with this zone (*Anemia sessilis*, *Palhinhaea cernua*, *Selaginella buchholzii* and *Actiniopteris radiata*) are characterized by a high tolerance to desiccation (poikilohydry strategy, Proctor and Tuba, 2002). Desiccation tolerant species have the ability to lose as much as 95% of the water content of their leaves without dying (Porembski and Barthlott, 2000). This tolerance is generally inferred at the morphological level by a high density of piliform scales protecting the rhizome and apex in *Anemia sessilis*, an absence of foliose lamina in *Palhinhaea cernua*, a very short reproductive cycle in *Selaginella buchholzii*, or the texture and longitudinal curling of the lamina in *Actiniopteris radiata*. The occurrence of the latter species has even been reported in the desert regions of the Sahara (Anthelme et al., 2011). The species associated with semi-arid plains in zones 3 and 5 have for their part adopted a desiccation-avoidance strategy, thanks to (i) their presence in aquatic or semi-aquatic environments such as mangroves (*Acrostichum aureum*), swampy areas (*Cyclosorus striatus, Ceratopteris thalictroides* and *Marsilea minuta*) and water bodies (*Salvinia auriculata* and *S. nymphellula*) or (ii) the establishment of a water-filled tuberous rhizome (*Ophioglossum* spp.). These strategies have been widely documented for pteridophytes in the tropics (Aldasoro et al., 2004; Hemp, 2001; Kornaś, 1977; Proctor and Tuba, 2002).

These results underline the major contribution of climate related variables to the geographic distribution of pteridophyte species across the country.

4.2. Pteridophytes as indicators of habitat conditions

Since pteridophytes are not dependent on pollen and seed vectors, their habitat preferences and hence distribution tend to closely reflect climatic and other environmental factors such as land cover type and anthropogenic disturbances (Barrington, 1993). Indeed, the direct relationship between the environment and the distribution of pteridophyte species is highlighted by our finding of associations between species and particular ecological conditions such as climate, land cover, and human disturbance.

The various land cover types, climatic zones and degrees of habitat disturbance are ecologically contrasted enough in Togo to impact their constituent flora. The floristic groups resulting from the hierarchical clustering analysis reflect the combined influence of land cover characteristics (particularly tree cover in insolation control), climatic factors (humidity related variables), and anthropogenic disturbances. The flora can be broadly grouped into coastal wetland heliophilic flora, which includes those of the mangroves and meadows of zone 5; anthropogenic ombrophilous flora of inhabited areas and palm groves; and the ombrophilous wet- and dry-adapted flora of Guinean humid forests (mainly in zone 4) and Sudanian dry forests (zones 2 and 3).

Almost all the ecological zones and land cover types can be characterized by a single or numerous indicator species. *Anemia sessilis* persists under conditions of relatively higher climatic water deficit (positive CCA Axis 2) and is an indicator species of the Sudanian submontanous zone 2. *Adiantum soboliferum* is an indicator species of both zone 2 and the Guinean-Sudanian transition zone 3 as it is indicative of the dry forest land cover type that is found in both these zones. Ecological zone 5 presents numerous indicator species, possibly indicative of the various unique coastal land cover types it includes. Of these, *Acrostichum aureum* is an indicator of mangrove land cover types, and *Salvinia spp*. of aquatic meadows. The absence of indicator species for ecological zone 4 can be explained by the high habitat heterogeneity of the humid southern Togo mountains. Indeed, given the high specificity (76.92% of observed species are restricted to the zone 4), it is the weak fidelity in species occurrences that leads to low indicator values (species are not present in the majority of plots of the zone). However, a number of species like *Pellaea doniana*, an indicator species of rainforest land cover types, present a significant ecological preference for conditions in zone 4 where most rainforests are found.

Importantly, we found that within rainforests, pteridophyte species are potential indicators of the exposure of the biological components of rainforests to stress caused by disturbance. We identified species that are relatively abundant under minor (e.g. *Pellaea doniana*), moderate (e.g. *Pteris togoensis*) or maximum (e.g. *Selaginella myosurus*) disturbance levels. While *P. doniana* is an indicator of rainforest land cover type, *P. togoensis* is the indicator species of agroforests. Previous works have also demonstrated the role of ferns as indicators of forest integrity (Bergeron and Pellerin, 2014; Page, 1997), soil characteristics (Zuquim et al., 2014), or land cover (Hemp, 2001). Indeed, Carvajal-Hernández et al. (2017) also identified indicator species in natural, disturbed and secondary forests in Mexico. They demonstrate the suitability of using pteridophytes as indicators of the state of conservation of forest habitats, especially in humid areas. In drier areas, pteridophytes are thought to be less sensitive to minor changes in their habitat (Carvajal-Hernández et al., 2017; Werner et al., 2011). This could explain the absence of indicator species at low and medium disturbance levels in Togolese forests which are a drier variants of West African Guinean forests (IUCN, 2015). Since the species still have significantly different relative abundance/relative dominance between the various levels of disturbance, we suggest the use of this parameter in the monitoring of forest disturbance in dry regions.

4.3. Sensitivity of rainforest flora to disturbance linked to angiosperm presence

In Togo, rainforest disturbance usually consists of selective felling for timber or energy production, bush fires, deforestation and conversion into agroforests (MERF, 2014; Nadjombe, 1992). The Togo Mountains being almost entirely a chain of low elevation plateaus (usually 600–800 m, Fig. 1A), their upper flanks and summits are inhabited and generally intensely impacted by human activities, while the lower and mid-elevation flanks are generally less so. These disturbed forests also have the lowest levels of alpha diversity within rainforests. Previous studies have associated forest disturbance with the preponderance of lianas (Kokou et al., 2002; Laurance et al., 2001), as well as with the loss of diversity in both pteridophytes (Barthlott et al., 2001; Kessler, 2001a, 2001b; Paciencia and Prado, 2005) and angiosperms (de la Rosa-Manzano et al., 2014; Hundera et al., 2013; Tabarelli et al., 1999). Indeed, *Selaginella myosurus*, the indicator species of highly disturbed rainforests, is a lianascent species. These two systematic groups interact closely. Studies on the history of Chlorophyllian lineage indicate that, although the lineage of ferns appeared before that of angiosperms, most of the current species diversified following the rise of angiosperms, by occupying the niches created on the forest floor, tree trunks, and canopies of angiosperm-dominated ecosystems (Schneider et al., 2004; Schuettpelz and Pryer, 2009; Testo and Sundue, 2016). As a result, these plants decline and disappear as soon as the support (for epiphytes only), and the protection provided by angiosperms against insolation and evapotranspiration (for both habits) is impacted by human activities (Barthlott et al., 2001; Carvajal-Hernández et al., 2017; Kreft et al., 2010).

In Singapore, epiphytic pteridophyte species appeared particularly prone to extinction (62% loss) due to deforestation (Turner et al., 1994). However, in general, the pteridophyte flora suffered moderate extinction, losing 49 out of 174 species (28%), of which 23 were epiphytes. Unlike the findings in Singapore, terrestrial species are more affected by forest disturbances than epiphytic species in Togo. While Testo and Sundue (2016) concluded that there has been no real difference in diversification rates between epiphytic and terrestrial species since the rise of angiosperms, the current study shows that damage to angiosperm trees do not impact species of the two habits in the same way. Krömer et al. (2013) also observed differential effects of environmental factors on both habits in Mexico for a large spectrum of plant groups, including ferns. Terrestrial species are potentially affected by increasing insolation whereas in the case of epiphytes, it is the impoverishment of the habitat in phorophytes that is fatal. Indeed, close links have been established between availability (Johansson, 1974) and characteristics (de la Rosa-Manzano et al., 2014; Einzmann and Zotz, 2016; Wang et al., 2017) of phorophytes on the one hand and the diversity of vascular epiphyte species on the other hand. In Ecuador, Haro-Carrión et al. (2009) observed significant differences in the vertical distribution and the diversity of epiphytic pteridophytes in both cocoa agroforest and natural forests that they attributed to differences in phorophyte availability, diameter and height. According to Carvajal-Hernández et al. (2017), hygrophilous epiphytic ferns are most affected by disturbances in humid montane forests, whereas fern species of drier habitats are already adapted to low air humidity and high insolation, and thus are less affected by forest disturbance. Thus, as in Bolivian forests (Kessler, 2001a), only major disturbances of the Togolese forests lead to diversity loss in epiphytes. Insofar as the disturbance leads to landscapes where old trees persist at low to moderate densities, epiphyte species are not as vulnerable as terrestrial species (Einzmann and Zotz, 2016), which are directly impacted by agricultural activities, bushfires, roads, houses, etc. The trees that remain standing (mainly non-timber and sacred tree species) continue to host a high number of strict and occasional epiphytic species (a commonly terrestrial species that can also grow as epiphytic in some particular cases) in degraded forests, agroforests, and inhabited areas, as has previously been shown in the Neotropics (Einzmann and Zotz, 2016). The presence of these occasional epiphytic species could explain the high alpha diversity of epiphytes in disturbed forests and agroforests, considering that there is no weeding of epiphytic species in Togolese agroforests and most shade trees are remnant trees from the initial natural forests. In shaded coffee systems in Mexico, the deliberate removal of epiphytes from the shade trees is a common management practice. Elsewhere in Mexico, epiphyte weeding is frequently performed in order to increase light availability for the coffee plants and also because producers generally consider epiphytes to be parasites (Toledo-Aceves et al., 2012).

4.4. Agroforests as a particular case of rainforest disturbance

Considering that agroforests were often preceded by rainforests (Adjossou, 2009), and their species therefore share similar climatic and edaphic conditions, the low pteridophyte diversity in agroforests compared to rainforests could be attributed to agricultural practices, such as weeding and the use of harmful chemicals. In Mexico, Mehltreter (2008) also attributed this lower diversity to intensified management in coffee agroforestry and especially with the use of agrochemicals that can affect up to 88.89% of the original forest diversity. These practices may have a greater destructive impact on terrestrial flora than on epiphyte flora since they primarily involve terrestrial habitats. It results in the loss of most of the rainforest species, which display sensitivities ranging from 22% to 97% of species from low to high levels of habitat disturbance, respectively. However, the transformation of rainforests into agroforests is ecologically comparable to an average level of disturbance. All pteridophyte species in Togolese agroforest plots (about 30.50% of the initial diversity in rainforests) were also recorded in rainforest plots. Our results which show the persistence of forest species in agroforests are consistent with those obtained in Central America. Forest habitats shared about 51.95% of epiphytic species with cocoa agroforests in Ecuador (Haro-Carrión et al., 2009), and 24.60% to 41.50% of their species with coffee agroforests in Mexico (Carvajal-Hernández et al., 2014; Mehltreter, 2008). For example, *Pteris togoensis*, an indicator species of Togolese agroforests, is found fairly consistently in rainforest plots (31%), but less than in agroforests (57%). In rainforests, this species displays a marginal relative abundance (less than 5%), but in agroforests it acquires a major position (32.5%) by occupying the niches left available by the disappearance of the most sensitive species. Moreover, *P. togoensis* is reported as a frequent species (almost half of the sites) only in moderately disturbed rainforests. In addition, the three remaining frequent species in moderately disturbed rainforests (*Tectaria fernandensis*, *Nephrolepis bisserata* and *Doryopteris kirkii*) are also present in agroforests, highlighting the high similarity of both floras (Faria et al., 2007).

These similarities were highlighted in the land cover cluster analysis (Fig. 3), which grouped agroforests and rainforests together, as “wet vegetation ombrophilous flora” in G4. Our results show that all the groups which resulted from the AHC in Fig. 3 reflect the combined effects of land cover characteristics (particularly tree cover which controls insolation), climatic factors (humidity related variables), and anthropogenic drivers of species assembly. The distribution of pteridophyte species in the country cannot therefore be explained by any single studied factor. However, tree cover may be the most important constraint, followed by human disturbances, and humidity.

5. Conclusion

The main issues raised by this study revolve around the determinants of the current distribution of pteridophytes in Togo and their ecological implications.

Most pteridophyte species in Togo occur in submontane humid forest areas. These submontane areas are part of the West African Guinean forest biodiversity hotspot and have played the role of biodiversity refuges for pteridophytes, from which species could spread to the surrounding lowlands. The species are generally constrained in their distribution by the combined effect of humidity, insolation, and human activities. This humidity gradient, which can be linked to precipitation and elevation, is also influenced by the Harmattan, a warm and dry continental trade wind, which increases the climatic water deficit and the temperature of the warmest periods. Human disturbance is a serious threat to Togo’s pteridophyte flora, leading to significant changes in their habitats, ranging from increased insolation on the ground and competition with agricultural crops, to the loss of support for epiphytes provided by large trees. Importantly, our results emphasize the association of specific species to particular conditions created by climate, land cover, and human disturbance, highlighting the role of pteridophyte species as indicators of environmental conditions or the exposure to stress. For better management decision making, it is necessary to characterize the ecology of species by combining all the main ecological factors that could constrain the realized niche of species at the scale of the habitat. This will also help to better identify suitable areas for the sustainable conservation of species.

The transformation of rainforests, the preferred habitat of more than 86% of pteridophyte species, into coffee/cocoa-based agroforests, has consequences for pteridophyte richness, reducing it to less than a third of rainforest species diversity. The impact on pteridophyte diversity in agroforests could be mitigated by maintaining more native tree species, reducing chemical inputs, and prohibiting herbicides and pesticides in local agricultural practices. Together with improved rainforest conservation, it is therefore essential to promote sustainable and environment-friendly practices of agroforestry in order to minimize the devastating effects of the agricultural sector on biodiversity.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.105741.

References

Abotsi, K.E., Kokou, K., Dubuisson, J.-Y., Rouhan, G., 2018. A first checklist of the Pteridophytes of Togo (West Africa). Biodiversity Data J. 6, e24137. https://doi.org/10.3897/BDJ.6.e24137.

Acebey, A.R., Krömer, T., Kessler, M., 2017. Species richness and vertical distribution of ferns and lycophytes along an elevational gradient in Los Tuxtlas, Veracruz, Mexico. Flora 235, 83–91. https://doi.org/10.1016/j.flora.2017.08.003.

Adjossou, K., 2009. Diversité, structure et dynamique de la végétation dans les fragments de forêts humides du Togo: les enjeux pour la conservation de la biodiversité (PhD Thesis). Université de Lomé, Lomé, Togo.

Aldasoro, J.J., Cabezas, F., Aedo, C., 2004. Diversity and distribution of ferns in sub-Saharan Africa, Madagascar and some islands of the South Atlantic: Diversity and distribution of African ferns. J. Biogeogr. 31, 1579–1604. https://doi.org/10.1111/j.1365-2699.2004.01106.x.

Anthelme, F., Abdoulkader, A., Viane, R., 2011. Are ferns in arid environments underestimated? Contribution from the Saharan Mountains. J. Arid Environ. 75, 516–523.

Barrington, D.S., 1993. Ecological and historical factors in fern biogeography. J. Biogeogr. 20, 275. https://doi.org/10.2307/2845635.

Barthlott, W., Hostert, A., Kier, G., Kueper, W., Kreft, H., Mutke, J., Rafiqpoor, M.D., Sommer, J.H., 2007. Geographic patterns of vascular plant diversity at continental to global scales. Erdkunde 61, 305–315. https://doi.org/10.3112/erdkunde.2007.04.01.

Barthlott, W., Lauer, W., Placke, A., 1996. Global distribution of species diversity in vascular plants: Towards a world map of phytodiversity. ERDKUNDE 50. https://doi.org/10.3112/erdkunde.1996.04.03.

Barthlott, W., Schmit-Neuerburg, V., Nieder, J., Engwald, S., 2001. Diversity and abundance of vascular epiphytes: a comparison of secondary vegetation and primary montane rain forest in the Venezuelan Andes. Plant Ecol. 152, 145–156. https://doi.org/10.1023/A:1011483901452.

Bergeron, A., Pellerin, S., 2014. Pteridophytes as indicators of urban forest integrity. Ecol. Ind. 38, 40–49. https://doi.org/10.1016/j.ecolind.2013.10.015.

Bickford, S.A., Laffan, S.W., 2006. Multi-extent analysis of the relationship between pteridophyte species richness and climate. Glob. Ecol. Biogeogr. 15, 588–601. https://doi.org/10.1111/j.1466-8238.2006.00250.x.

Borcard, D., Gillet, F., Legendre, P., 2018. Numerical ecology with R, 2nd ed. Springer, New York, NY.

Braun-Blanquet, J., 1932. Plant Sociology, firstst ed. Mcgraw-Hill Book Company Inc, New York.

Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27, 325–349.

Brunel, J., Hiepko, P., Scholz, H., 1984. Flore analytique du Togo: Phanérogames: Botanischer Garten und Botanisches Museum. Englera, Berlin-Dahlem, Germany.
Bystriakova, N., Peregrym, M., Dragicevic, S., 2015. Effect of environment on distributions of rock ferns in the Mediterranean climate: The case of the genus Asplenium in Montenegro. Flora 215, 84–91. https://doi.org/10.1016/j.flora.2015.07.003.
Carvajal-Hernández, C.I., Krömer, T., López-Acosta, J.C., Gómez-Díaz, J.A., Kessler, M., 2017. Conservation value of disturbed and secondary forests for ferns and lycophytes along an elevational gradient in Mexico. Appl. Veg. Sci. 20, 662–672. https://doi.org/10.1111/avsc.12318.
Carvajal-Hernández, C.I., Krömer, T., Vázquez-Torres, M., 2014. Riqueza y composición florística de pteridobiontes en bosque mesófilo de montaña y ambientes asociados en el centro de Veracruz, México. Revista Mexicana de Biodiversidad 85, 491–501. https://doi.org/10.7550/rmb.41292.
Ceballos, G., García, A., Ehrlich, P.R., 2010. The sixth extinction crisis: loss of animal populations and species. J. Cosmol. 8, 1821–1831.
Currie, D.J., Paquin, V., 1987. Large-scale biogeographical patterns of species richness of trees. Nature 329, 326–327. https://doi.org/10.1038/329326a0.
De Cáceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. Ecology 90, 3566–3574. https://doi.org/10.1890/08-1823.1.
de la Rosa-Manzano, E., Andrade, J.L., Zotz, G., Reyes-García, C., 2014. Epiphytic orchids in tropical dry forests of Yucatan, Mexico – Species occurrence, abundance and correlations with host tree characteristics and environmental conditions. Flora 209, 100–109. https://doi.org/10.1016/j.flora.2013.12.002.
Einzmann, H.J.R., Zotz, G., 2016. How diverse are epiphyte assemblages in plantations and secondary forests in tropical lowlands? Trop. Conserv. Sci. 9, 629–647. https://doi.org/10.1177/194008291600900205.
Ern, H., 1979. Die vegetation Togos. Gliederung, Gefährdung, Erhaltung. Willdenowia 9, 295–312.
Faria, D., Paciencia, M.L.B., Dixo, M., Laps, R.R., Baumgarten, J., 2007. Ferns, frogs, lizards, birds and bats in forest fragments and shade cacao plantations in two contrasting landscapes in the Atlantic forest, Brazil. Biodivers. Conserv. 16, 2335–2357. https://doi.org/10.1007/s10531-007-9189-z.
Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315.
de Gasper, A.L., Eisenlohr, P.V., Salino, A., 2015. Climate-related variables and geographic distance affect fern species composition across a vegetation gradient in a shrinking hotspot. Plant Ecolog. Divers. 8, 25–35. https://doi.org/10.1080/17550874.2013.843604.
Haro-Carrión, X., Lozada, T., Navarrete, H., de Koning, G.H.J., 2009. Conservation of vascular epiphyte diversity in shade cacao plantations in the Chocó region of Ecuador. Biotropica 41, 520–529. https://doi.org/10.1111/j.1744-7429.2009.00510.x.
Hassler, M., Schmitt, B., 2019. Checklist of ferns and lycophytes of the world [WWW Document]. URL https://worldplants.webarchiv.kit.edu/ferns/ (accessed 7.30.19).
Hemp, A., 2002. Ecology of the pteridophytes on the southern slopes of Mt. Kilimanjaro–I. Altitudinal distribution. Plant Ecol. 159, 211–239.
Hemp, A., 2001. Ecology of the pteridophytes on the southern slopes of Mt. Kilimanjaro. Part II: habitat selection. Plant Biol. 3, 493–523. https://doi.org/10.1055/s-2001-17729.
Hundera, K., Aerts, R., Beenhouwer, M.D., Overtveld, K.V., Helsen, K., Muys, B., Honnay, O., 2013. Both forest fragmentation and coffee cultivation negatively affect epiphytic orchid diversity in Ethiopian moist evergreen Afromontane forests. Biol. Conserv. 159, 285–291. https://doi.org/10.1016/j.biocon.2012.10.029.
IUCN, 2015. Ecosystem profile: Guinean forests of West Africa biodiversity hotspot. Critical Ecosystem Partnership Fund.
Johansson, D., 1974. Ecology of vascular epiphytes in West African rain forest. Sv. växtgeografiska sällsk.
Karst, J., Gilbert, B., Lechowicz, M.J., 2005. Fern community assembly: the roles of chance and the environment at local and intermediate scales. Ecology 86, 2473–2486. https://doi.org/10.1890/04-1420.
Kessler, M., 2001a. Maximum plant-community endemism at intermediate intensities of anthropogenic disturbance in Bolivian montane forests. Conserv. Biol. 15, 634–641. https://doi.org/10.1046/j.1523-1739.2001.015003634.x.
Kessler, M., 2001b. Pteridophyte species richness in Andean forests in Bolivia. Biodivers. Conserv. 10, 1473–1495. https://doi.org/10.1023/A:1011811224595.
Kessler, M., Parris, B.S., Kessler, E., 2001. A comparison of the tropical montane pteridophyte floras of Mount Kinabalu, Borneo, and Parque Nacional Carrasco, Bolivia: Comparison of tropical montane pteridophyte floras. J. Biogeogr. 28, 611–622. https://doi.org/10.1046/j.1365-2699.2001.00577.x.
Kessler, M., Salazar, L., Homeier, J., Kluge, J., 2014. Species richness-productivity relationships of tropical terrestrial ferns at regional and local scales. J. Ecol. 102, 1623–1633. https://doi.org/10.1111/1365-2745.12299.
Kluge, J., Bach, K., Kessler, M., 2008. Elevational distribution and zonation of tropical pteridophyte assemblages in Costa Rica. Basic Appl. Ecol. 9, 35–43. https://doi.org/10.1016/j.baae.2006.11.004.
Kokou, K., 1998. Les mosaïques forestières au sud du Togo: biodiversité, dynamique et activités humaines (Thesis). Université de Lomé, Lomé, Togo.
Kokou, K., Couteron, P., Martin, A., Caballe, G., 2002. Taxonomic diversity of lianas and vines in forest fragments of Southern Togo. Revue d'Ecologie (France).
Kornas, J., 1993. The significance of historical factors and ecological preference in the distribution of African pteridophytes. J. Biogeogr. 20, 281. https://doi.org/10.2307/2845636.
Kornaś, J., 1977. Life-forms and seasonal patterns in the pteridophytes in Zambia. Acta Soc. Botan. Poloniae 46, 669.
Kreft, H., Jetz, W., 2007. Global patterns and determinants of vascular plant diversity. PNAS 104, 5925–5930. https://doi.org/10.1073/pnas.0608361104.
Kreft, H., Jetz, W., Mutke, J., Barthlott, W., 2010. Contrasting environmental and regional effects on global pteridophyte and seed plant diversity. Ecography 33, 408–419.
Krömer, T., Acebey, A., Kluge, J., Kessler, M., 2013. Effects of altitude and climate in determining elevational plant species richness patterns: a case study from Los Tuxtlas, Mexico. Flora 208, 197–210. https://doi.org/10.1016/j.flora.2013.03.003.
Krömer, T., Kessler, M., Gradstein, S.R., 2007. Vertical stratification of vascular epiphytes in submontane and montane forest of the Bolivian Andes: the importance of the understory. Plant Ecol. 189, 261–278. https://doi.org/10.1007/s11258-006-9182-8.
Laurance, W.F., Diego, Pérez-Salicrup, Patricia, Delamônica, Fearnside, Philip M., Sammya, D'Angelo, Adriano, Jerozolinski, Luciano, Pohl, Lovejoy, Thomas E., 2001. Rain forest fragmentation and the structure of amazonian liana communities. Ecology 82, 105–116. https://doi.org/10.1890/0012-9658(2001) 082[0105:RFFATS]2.0.CO;2.
McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82, 290–297. https://doi.org/10.1890/0012-9658(2001) 082[0290:FMMTCD]2.0.CO;2.
Mehltreter, K., 2008. Helechos. In: Manson, R.H., Hernandez-Ortiz, V., Gallina, S., Mehltreter, K. (Eds.), Agroecosistemas cafetaleros de Veracruz: biodiversidad, manejo y conservación. Instituto de Ecologıa AC, Instituto Nacional de Ecologıa, Xalapa, MX., pp. 83–93.
Mehltreter, K., Flores-Palacios, A., García-Franco, J.G., 2005. Host preferences of low-trunk vascular epiphytes in a cloud forest of Veracruz. Mexico. J. Trop. Ecol. 21, 651–660. https://doi.org/10.1017/S0266467405002683.
MERF, 2014. In: Cinquième rapport national sur la diversité biologique du Togo: 2009–2014 (Rapport national No. 5). République Togolaise, Lomé, Togo.
Middleton, N.J., Thomas, D.S., 1992. In: UNEP. World atlas of desertification. Edward Arnold Publishers, London, pp. 15–45.
Mittermeier, R.A., Myers, N., Gill, P.C., Mittermeier, C.G., 2000. Hotspots: earth's richest and most endangered terrestrial ecoregions. CEMEX, Mexico City.
Moran, R.C., 1995. The importance of mountains to pteridophytes, with emphasis on neotropical montane forests, in: Churchill, S.P., Balslev, H., Forero, E., Luteyn, J.L. (Eds.), Biodiversity and Conservation of Neotropical Montane Forests, Proceedings of the Neotropical Montane Forest Biodiversity and Conservation Symposium. New York, pp. 359–363.
Moran, R.C., Smith, A.R., 2001. Phytogeographic relationships between neotropical and African-Madagascan pteridophytes. Brittonia 53, 304–351.
Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. https://doi.org/10.1038/35002501.
Nadjombe, O., 1992. La déforestation par l'agriculture itinérante et les feux de brousse, in: Cleaver, K.M. (Ed.), Conservation de la forêt dense en Afrique Centrale et de l'Ouest. pp. 110–116.
Paciencia, M.L.B., Prado, J., 2005. Effects of forest fragmentation on pteridophyte diversity in a tropical rain forest in Brazil. Plant Ecol. 180, 87–104. https://doi.org/10.1007/s11258-005-3025-x.
Page, C.N., 1997. Pteridophytes as field indicators of natural biodiversity restoration in the Scottish flora. Botanic. J. Scotland 49, 405–414. https://doi.org/10.1080/03746609708684885.
Porembski, S., Barthlott, W., 2000. Granitic and gneissic outcrops (inselbergs) as centers of diversity for desiccation-tolerant vascular plants. Plant Ecol. 151, 19–28. https://doi.org/10.1023/A:1026565817218.
PPG I, 2016. A community-derived classification for extant lycophytes and ferns: PPG I. J. System. Evol. 54, 563–603. https://doi.org/10.1111/jse.12229.
Proctor, M.C.F., Tuba, Z., 2002. Poikilohydry and homoihydry: antithesis or spectrum of possibilities? New Phytol. 156, 327–349. https://doi.org/10.1046/j.1469-8137.2002.00526.x.
R Core Team, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Salazar, L., Homeier, J., Kessler, M., Abrahamczyk, S., Lehnert, M., Krömer, T., Kluge, J., 2015. Diversity patterns of ferns along elevational gradients in Andean tropical forests. Plant Ecol. Divers. 8, 13–24. https://doi.org/10.1080/17550874.2013.843036.
SCBD, 2018. Togo - country profile: Biodiversity facts [WWW Document]. accessed 1.12.18. https://www.cbd.int/countries/profile/default.shtml?country=tg#facts.
Schneider, H., Schuettpelz, E., Pryer, K.M., Cranfill, R., Magallón, S., Lupia, R., 2004. Ferns diversified in the shadow of angiosperms. Nature 428, 553–557. https://doi.org/10.1038/nature02361.
Schuettpelz, E., Pryer, K.M., 2009. Evidence for a Cenozoic radiation of ferns in an angiosperm-dominated canopy. PNAS 106, 11200–11205. https://doi.org/10.1073/pnas.0811136106.
Tabarelli, M., Mantovani, W., Peres, C.A., 1999. Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. Biol. Conserv. 91, 119–127. https://doi.org/10.1016/S0006-3207(99)00085-3.
Testo, W., Sundue, M., 2016. A 4000-species dataset provides new insight into the evolution of ferns. Mol. Phylogenet. Evol. 105, 200–211. https://doi.org/10.1016/j.ympev.2016.09.003.
Teyssèdre, A., 2004. Vers une sixième grande crise d'extinctions. Biodiversité et changements globaux : enjeux de société et défis pour la recherche. Ministère des Affaires Etrangères–ADPF, Paris 24–36.
Toledo-Aceves, T., García-Franco, J.G., Hernández-Rojas, A., MacMillan, K., 2012. Recolonization of vascular epiphytes in a shaded coffee agroecosystem. Appl. Veg. Sci. 15, 99–107. https://doi.org/10.1111/j.1654-109X.2011.01140.x.
Tryon, R.M., 1989. Chapter 17 – Pteridophytes. In: Lieth, H., Werger, M.J.A. (Eds.), Tropical rain forest ecosystems, Ecosystems of the World. Elsevier, Amsterdam, pp. 327–338 https://doi.org/10.1016/B978-0-444-42755-7.50023-7.
Tryon, R.M., 1986. The biogeography of species, with special reference to ferns. Bot. Rev.

52, 117–156. https://doi.org/10.1007/BF02860999.
Tryon, R.M., Tryon, A.F., 1982. Ferns and allied plants: with special reference to Tropical. America. Springer Science & Business Media.
Tuomisto, H., Zuquim, G., Cárdenas, G., 2014. Species richness and diversity along edaphic and climatic gradients in Amazonia. Ecography 37, 1034–1046. https://doi.org/10.1111/ecog.00770.
Turner, I.M., Tan, H.T.W., Wee, Y.C., Ibrahim, A.B., Chew, P.T., Corlett, R.T., 1994. A study of plant species extinction in Singapore: lessons for the conservation of tropical biodiversity. Conserv. Biol. 8, 705–712. https://doi.org/10.1046/j.1523-1739.1994.08030705.x.
Wang, Q., Guan, W.-B., Gi Wong, M.H., Ranjitkar, S., Sun, W.-N., Pan, Y., El-Kassaby, Y.A., Shen, L.-X., 2017. Tree size predicts vascular epiphytic richness of traditional cultivated tea plantations in Southwestern China. Global Ecol. Conserv. 10, 147–153. https://doi.org/10.1016/j.gecco.2017.03.002.
Watkins Jr, J.E., Cardelús, C., Colwell, R.K., Moran, R.C., 2006. Species richness and distribution of ferns along an elevational gradient in Costa Rica. Am. J. Bot. 93, 73–83.
Werner, F.A., Köster, N., Kessler, M., Gradstein, S.R., 2011. Is the resilience of epiphyte assemblages to human disturbance a function of local climate. Ecotropica 17, 15–20.
Westhoff, V., Van Der Maarel, E., 1978. The Braun-Blanquet approach. In: Whittaker, R.H. (Ed.), Classification of Plant Communities, Classification of Plant Communities. Springer Netherlands, Dordrecht, pp. 287–399 https://doi.org/10.1007/978-94-009-9183-5_9.
White, F., 1983. The vegetation of Africa: a descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa. UNESCO.
Wilson, A.M., Jetz, W., 2016. Remotely sensed high-resolution global cloud dynamics for predicting ecosystem and biodiversity distributions. PLoS Biol. 14, e1002415. https://doi.org/10.1371/journal.pbio.1002415.
Zuquim, G., Tuomisto, H., Jones, M.M., Prado, J., Figueiredo, F.O.G., Moulatlet, G.M., Costa, F.R.C., Quesada, C.A., Emilio, T., 2014. Predicting environmental gradients with fern species composition in Brazilian Amazonia. J. Veg. Sci. 25, 1195–1207. https://doi.org/10.1111/jvs.12174.