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TOPOGRAPHY, CLIMATE AND FOREST COVER DETERMINE THE GLOBAL SPECIES RICHNESS PATTERNS OF FILMY FERNS (HYMENOPHYLLACEAE)

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Species richness patterns are essential for understanding how species diversity has evolved. The filmy ferns (Hymenophyllaceae) are one of the largest families of epiphytic ferns; however, a comprehensive global overview of their species diversity and distribution is lacking. In the present study, we identified the regions of greatest species diversity as Central America, South America and Southeast Asia (including Taiwan Island), followed by the Brazilian Atlantic Forest and Madagascar. North America and Europe are low in species richness. Global species richness data based on 100 × 100 km grid cells were analysed to investigate the correlation between species richness and ecological factors. Our results show that filmy ferns have a strong preference for moist and warm habitats, and that current species richness patterns are codetermined by topography, climate and forest cover. Our results also indicate that, as expected, the relationship between soil and epiphytic ferns is minimal, and that there is weak support for the use of solar radiation levels to predict global patterns of diversity for filmy ferns, which primarily occur in deep shade. We highlight potential ecological differences between the two lineages of the Hymenophyllaceae: hymenophylloids and trichomanoids. The unusually low species diversity of filmy ferns in some areas (e.g. the Pan-Himalayan region) is potentially explained by historical ecological adaptation and lack of suitable habitats.

Keywords. Climate adaptation, filmy ferns, global diversity, species richness, topographical variation.
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Introduction

Understanding patterns of biodiversity is fundamental to research on evolution, ecology and conservation (Tietje *et al.*, 2023). Over the past few decades, global species richness patterns of different biological groups, for example vascular plants (Kreft & Jetz, 2007), insects (Gaston, 1991) and mammals (Stein *et al.*, 2015), have been explored. Synthesising these patterns, Myers *et al.* (2000) first proposed 25 global biodiversity hotspots, and this number has since been increased to 34 (Mittermeier *et al.*, 2011).

Ferns have existed on Earth since the middle Devonian (383–393 Ma) as a significant component of global biodiversity and ecosystems (Wang *et al.*, 2015). Fern richness patterns at different geographical scales have been investigated (e.g. Dittrich *et al.*, 2005;

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Suissa *et al.*, 2021), as have the drivers of these patterns, mainly climate (Qian *et al.*, 2023), elevation (Kessler *et al.*, 2016), soil (Cicuzza & Mammides, 2022) and ecological preferences (Weigand *et al.*, 2020). It is clear that different fern groups have different specific distributions, diversity hotspots, and adaptation preferences. For example, the epiphytic genus *Platycerium* Desv. (Polypodiaceae) is mainly distributed in Africa, Southeast Asia and Australia (Kreier & Schneider, 2006) and not within the recognised fern hotspots of Mesoamerica and the Himalayas (Suissa *et al.*, 2021). Until now, studies of global fern species richness have rarely been conducted on a whole family, or at a larger-genus level, to explore the distribution patterns within and across specific lineages.

Hymenophyllaceae, the 'filmy fern' family, is a distinct and diverse lineage of globally distributed leptosporangiate ferns (Dubuisson, 1997). Traditionally, Hymenophyllaceae were partitioned into two genera: *Trichomanes sensu lato* and *Hymenophyllum sensu lato* (Pryer *et al.*, 2001). Ebihara *et al.* (2006) recognised nine genera with an estimated 434 species, and the current *World Ferns* database (https://www.worldplants.de/ferns/) accepts 557 species and nine genera.

As indicated by the name of the family, plants of Hymenophyllaceae have thin fronds; these are usually composed of a single layer of cells. They also lack stomata, are highly dependent on environmental humidity, and are strongly associating with tropical forests (Dubuisson *et al.*, 2003). Nonetheless, Hymenophyllaceae includes all the major growth forms that occur in ferns (e.g. epiphytic, terrestrial, climbing). Because of its extremely high morphological and ecological diversity, Hymenophyllaceae was once considered an excellent model group for studying ecological evolution and environmental adaptation (Dubuisson *et al.*, 2003, 2009; Lehnert & Krug, 2019). Existing studies on the diversity of Hymenophyllaceae have mainly focused on patterns linked to local-scale changes in elevational gradient within a mountain or an island (e.g. Nitta, 2006). The authors of these studies regarded temperature, precipitation and solar radiation levels as the most important factors affecting species richness variables along elevational gradients (Nitta, 2006; Parra *et al.*, 2009; Gehrig-Downie *et al.*, 2012). Canopy structure (e.g. canopy light environment) has been repeatedly highlighted as important in determining fern species richness, with a probable negative correlation (Watkins *et al.*, 2006). However, the results of previous studies have suggested that tree canopy height may have a weaker explanatory power at the global scale (Roll *et al.*, 2015). This means that the findings of current studies on local-scale Hymenophyllaceae diversity may not be representative of global patterns, and that a large-scale perspective on diversity and ecological preferences is still lacking.

In the present study, global distribution data for all Hymenophyllaceae species were used to map patterns of species richness, and correlations with potential ecological factors were investigated to provide new insights into the diversification and evolutionary history of this family.

Materials and methods

Hymenophyllaceae global distribution

More than 360,000 occurrence records of Hymenophyllaceae were extracted from the Global Biodiversity Information Facility (GBIF) (https://www.gbif.org/) and Chinese Virtual Herbarium database (CVH) (https://www.cvh.ac.cn/). To improve the quality of the distribution data, cleaning steps were carried out using the R package *CoordinateCleaner* (Zizka *et al.*, 2019) and by manual checking. Only herbarium specimen records were included. Correction and standardisation of Hymenophyllaceae taxa names were mainly based on the latest version of PPG I (Pteridophyte Phylogeny Group, 2016) and *World Ferns* (Hassler, 1994–2025).

In total, 60,323 valid coordinate-level occurrences were included in the raw dataset for the family (**Supplementary file 1**), with 552 accepted names across nine genera. To further explore potential differences between the two major lineages within Hymenophyllaceae, two data subsets were produced: (i) hymenophylloids (i.e. *Hymenophyllum*), and (ii) trichomanoids (i.e. *Abrodictyum*, *Callistopteris*, *Cephalomanes*, *Crepidomanes*, *Didymoglossum*, *Polyphlebium*, *Trichomanes*, *Vandenboschia*).

Environmental factors

In total, 30 environmental variables were investigated as potential determinants of global Hymenophyllaceae species richness: 22 climatic variables, two topographical indices, two soil factors, two forest indices, elevation and latitude. Data for all variables except latitude are listed in Table S1 (**Supplementary file 2**). Mean data for 30 continuous variables were extracted for each 100 × 100 km grid cell and summarised by species richness level (corresponding numerical ranges are provided in Tables S2 and S3, **Supplementary file 2**).

To remove the correlation among all variables, the 30 environmental variables were reduced to 14 (Table S4, **Supplementary file 2**; Figure S1, **Supplementary file 3**). Weak pairwise correlation ($|r| < 0.7$) was shown for the Pearson correlation test using the R package *Hmisc* (Harrell & Harrell, 2019), and for principal component analysis using R packages *factoextra* (Kassambara & Mundt, 2017) and *RStoolbox* (Leutner *et al.*, 2017). We further applied collinearity and stepwise variance inflation factor (VIF) selection (VIF < 5), using R package *CAR* (Fox & Weisberg, 2019), and derived a minimum adequate model by stepwise regression based on the Akaike information criterion (AIC) (Whittingham *et al.*, 2006).

Ten significant environmental variables (Table S5, **Supplementary file 2**) were finally used for multiple regression: (i) mean diurnal range (BIO2), (ii) maximum temperature of warmest month (BIO5), (iii) minimum temperature of coldest month (BIO6), (iv) precipitation of driest month (BIO14), (v) precipitation of wettest quarter (BIO16), (vi) precipitation of warmest

quarter (BIO18), (vii) terrain roughness index (TR), (viii) forest canopy height (FCH), (ix) solar radiation (SRad), and (x) top soil pH (T-SpH).

Data analyses

To explore potential determinants, we counted the numbers of species in each 100 × 100 km grid cell, based on the Behrmann coordinate reference system. For the whole family, grids with fewer than 20 species were considered to have low richness; those with 21 to 40 species, high richness; and those with at least 41 species, high richness (indicating hotspots). The results of normality testing showed that richness data conform to a normal distribution ($p < 0.005$).

Generalised linear models (GLMs) (R *glm*) and the simultaneous autoregressive model (SAR) (R package *spdep*, Bivand & Wong, 2018) were fitted to the variation of global Hymenophyllaceae species richness. Species richness was selected as the response variable, and climate, topography and canopy height as predictors. We further used the reduction of Moran's *I* (residual spatial autocorrelation) and minimisation of AIC values to quantify the goodness of fit. The importance of environmental variables in determining species richness was estimated by generalised boosted regression models (GBMs) in R package *gbm* (Greenwell *et al.*, 2019) and *caret* (Kuhn, 2022), with 100 GBMs run for stochasticity in the internal cross-validation procedure, 80% for training, 20% for testing.

Variation of Hymenophyllaceae species richness (in terms of mean data for each grid) and number of species were determined, and elevation and latitude (recorded in units of 100 m and 2°, respectively) recorded. The variation statistics are displayed as line graphs with smoothed curves. These analyses were repeated for the hymenophylloid and trichomanoid datasets.

Results

Distribution and global species richness pattern

Our data (Figure S2, Supplementary file 3) confirm that Hymenophyllaceae are distributed across all major continents. The Neotropics, East Asia (especially Japan), Southeast Asia, and Oceania (New Zealand, East Australia) contributed the most occurrence records, and Africa, North America and Europe contributed the fewest.

Regarding data for the whole family, a total of 2226 grids had a record of at least one species, but only 29 had records of 40 or more (Table S2, Supplementary file 2). Species richness statistics (Figure 1**A**) indicate that Central America (Costa Rica, Panama, Caribbean), the Andes Mountains (Colombia, Ecuador) and Southeast Asia (North Borneo, Seram Island, East New Guinea Highlands, Java) are world hotspots of Hymenophyllaceae. Taiwan Island, South Luzon Island, the coast of the Brazilian Atlantic Forest, the Guiana Highlands and eastern coast of Madagascar, tropical North Australia, and New Zealand

have medium species richness. East Asia and the African continent have generally low Hymenophyllaceae species richness, although higher levels are found in some scattered regions, such as the southwestern Hengduan Mountains, the eastern and southern foothills of the Qinghai–Tibet Plateau, the area south of the Yunnan–Guizhou Plateau, Hainan Island, the Qinling Mountains, the Nanling Mountains, the Eastern Arc Mountains, and the Gulf of Guinea coastal mountains. Species richness is very low throughout North America and Europe. Hymenophylloids (Figure 1**B**) and trichomanoids (Figure 1**C**) have similar species richness patterns.

Determinants of environmental variables underlying species richness patterns

Because the correlations between each environmental variable and species richness were consistent for the results of GLM and SAR (Tables S5–S7, Supplementary file 2), we excluded the impact of spatial autocorrelation, which may increase the effect of type I errors in the models. Regarding the results for the whole family, our spatial multiple regression analysis identified eight environmental variables with a significant correlation (R^2 = 0.16, p < 0.0001) (Table). Only two variables, TR and BIO6, showed a positive correlation at the p < 0.001 level. For BIO18, the positive correlation with species richness was less significant but still strong (p < 0.01). The BIO2, SRad and FCH variables were moderately (p < 0.05) positively correlated with species richness. BIO5 showed a strong negative correlation with species richness (p < 0.001), whereas T-SpH showed a moderate negative correlation (p < 0.05).

The positive and negative correlation trends observed for hymenophylloids and trichomanoids were generally consistent with those at the family level but with noteworthy differences (Table). For example, for hymenophylloids, BIO18, SRad and FCH did not show significant correlations with species richness, whereas BIO16 did (p < 0.05). The correlations for trichomanoids were more similar to those for the entire family, with the major difference being that BIO2 and T-SpH showed no significant correlations with species richness.

According to the results of the GBMs, the Hymenophyllaceae (Figure 2**A**) and trichomanoids (Figure 2**C**) have significant similarity in terms of the hierarchy of the importance of environmental variables in determining species patterns. TR was the most important variable for the Hymenophyllaceae (40%) and trichomanoid (30%) species, followed by temperature-related (e.g. BIO5) variables and FCH (≥ 15%). Precipitation-related variables (BIO18) were less than temperature in terms of level of importance for Hymenophyllaceae species richness (c.10% for the entire family; c.17% for trichomanoids), and the level for T-SpH was 2% lower than that for BIO18. Compared with other significant environmental variables, SRad showed minimal importance for either Hymenophyllaceae or trichomanoid species richness. By contrast, for hymenophylloids (Figure 2**B**) BIO5 was the most influential variable (44% importance), followed by TR, at 24%, with T-SpH and BIO2 having low importance.

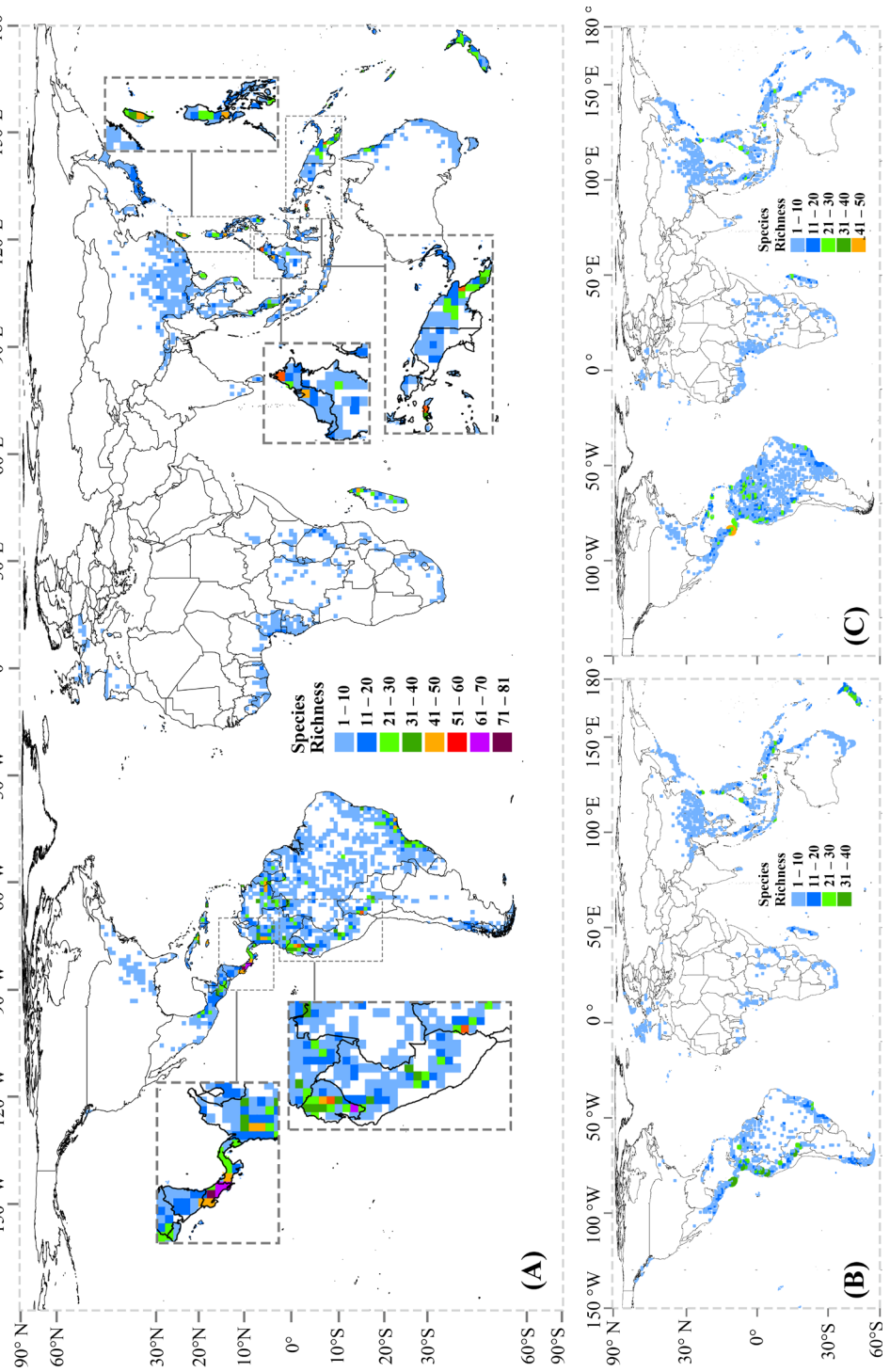


Figure 1. Hymenophyllaceae global species richness patterns: A, Hymenophyllaceae; B, hymenophylloids; C, trichomanoids.

Table. Results of simultaneous autoregressive multipredictor regression models used to investigate Hymenophyllaceae species richness within 100 km × 100 km grid cells[a]

Environmental variable	Hymenophyllaceae	Hymenophylloids	Trichomanoids
BIO2	(+)*	(+)***	
BIO5	(−)***	(−)***	(−)***
BIO6	(+)***	(+)*	(+)***
BIO14			
BIO16		(+)*	
BIO18	(+)**		(+)***
SRad	(+)*		(+)**
TR	(+)***	(+)**	(+)***
T-SpH	(−)*	(−)*	
FCH	(+)*		(+)**

[a](+) and (−) indicate, respectively, a positive or negative correlation between species richness and the predictor. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

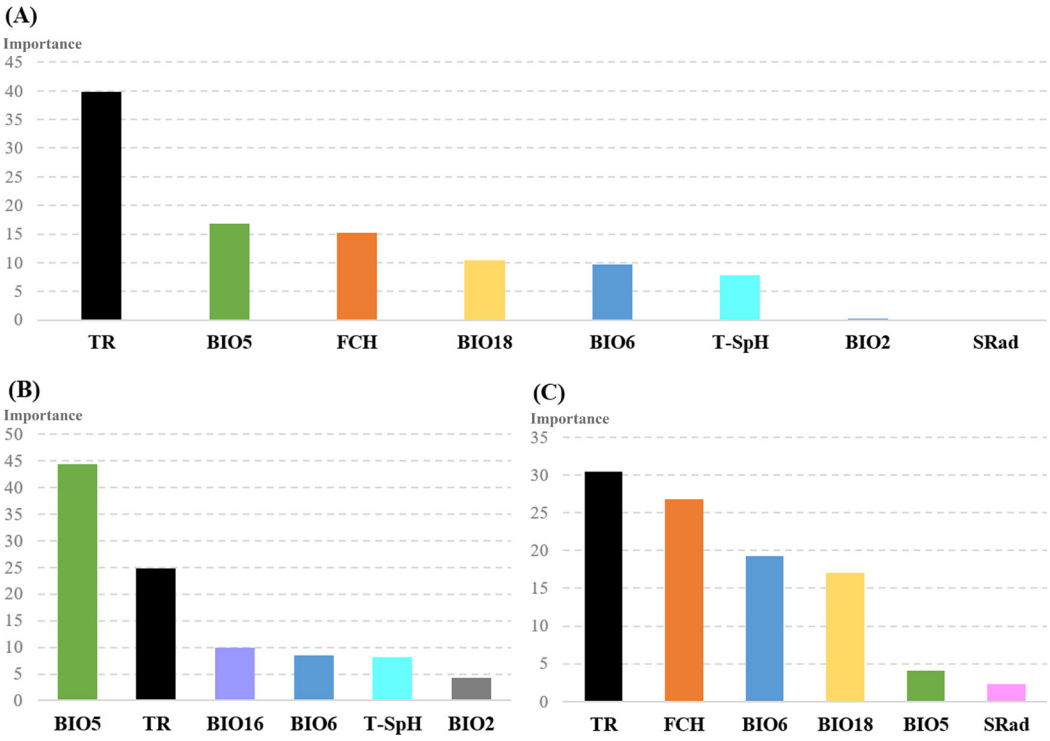


Figure 2. The relative importance of environmental variables in explaining species richness at the global scale: **A**, Hymenophyllaceae; **B**, hymenophylloids; **C**, trichomanoids. BIO2, Mean diurnal range; BIO5, maximum temperature of warmest month; BIO6, minimum temperature of coldest month; BIO16, precipitation of wettest quarter; BIO18, precipitation of warmest quarter; FCH, forest canopy height; SRad, solar radiation; TR, terrain roughness index; T-SpH, topsoil pH.

Our results show that the areas of higher species richness (including for the hymenophylloids and trichomanoids) occur at low to medium latitudes (Figure 3). Notably, both the highest species richness and the quantity of species are mainly found at lower latitudes in the northern hemisphere. We also noted that at middle latitudes (c.30–40°), species richness in the southern hemisphere surpasses that of the northern hemisphere. Our statistics for species richness along elevations showed a trend across the family: higher species richness was typically concentrated in low to middle elevation ranges (Figure 4), with species richness between 2000 and 3000 m exceeding that below 1500 m (Figure 4A). For hymenophylloids, species richness showed a distinct mid-elevational peak at 2500–4000 m, higher than that of trichomanoids in the same range (Figure 4C). Conversely, trichomanoids have a higher richness concentrated at lower elevations, with a significant decrease above approximately 3000 m (Figure 4C). Species count showed a downward trend with rising elevation, a pattern that was consistent across the entire family (Figure 3B) and both lineages (Figure 3D).

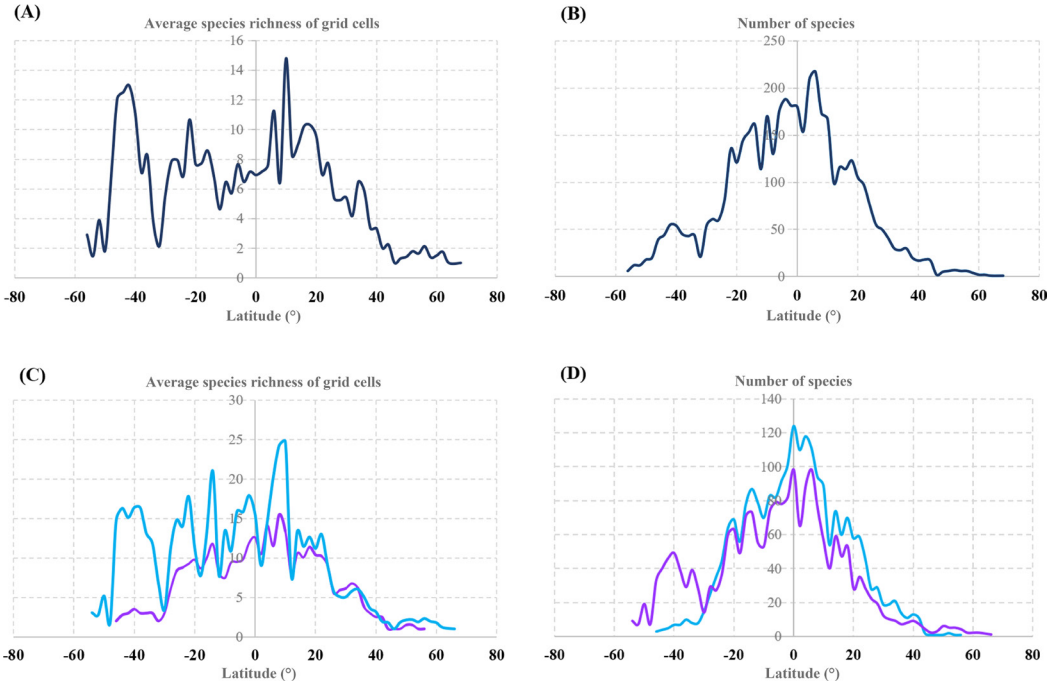


Figure 3. Latitudinal patterns of global Hymenophyllaceae in terms of **A**, mean number of species in grid cells; **B**, total species numbers; **C**, species richness of hymenophylloids (blue line) and trichomanoids (purple line); and **D**, number of species of hymenophylloids (blue line) and trichomanoids (purple line).

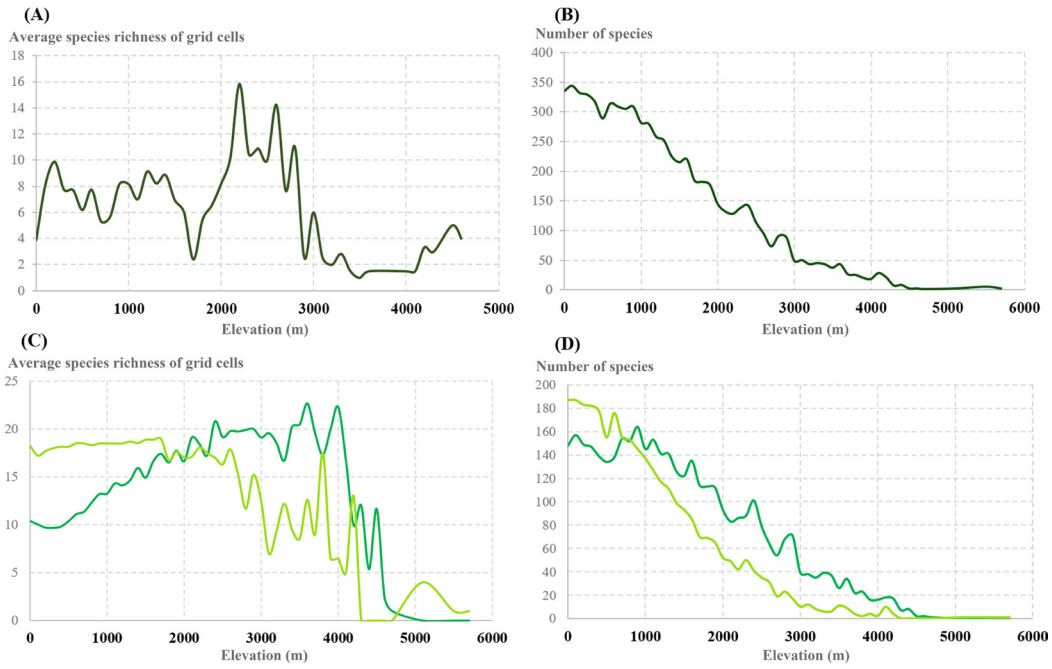


Figure 4. Elevational patterns of global Hymenophyllaceae in terms of **A**, mean number of species in grid cells; **B**, total species numbers; **C**, species richness of hymenophylloids (emerald line) and trichomanoids (light green line); and **D**, number of species of hymenophylloids (emerald line) and trichomanoids (light green line).

Discussion

Hymenophyllaceae have been regarded as a common lineage in the wet tropics since the previous century (Morton, 1968). Fundamentally, its global distribution and species richness patterns support this expectation. An overview of the distribution and the range of high–species richness areas highlights the Neotropics and tropical Asia as centres of species diversity for Hymenophyllaceae, with other regions having slightly lower species richness. Here, we discuss the ecological factors that significantly correlate with species richness and how they affect diversity in Hymenophyllaceae, especially the epiphytic species which dominate the group, with the aim of understanding and explaining the formation of species richness patterns.

Species richness determinants

Topography: terrain roughness index and elevation. It is well known that biodiversity is enriched in areas with complex terrain (Badgley *et al.*, 2017) and environmental

heterogeneity (Dufour *et al.*, 2006; Tukiainen *et al.*, 2023). Previous studies have indicated that the extensive niche space available in (sub)tropical mountains, facilitated by variable elevational gradients, contributes positively to the high species richness of ferns in local areas (Suissa *et al.*, 2021). Our species richness mapping indicates that areas of high species diversity within the Hymenophyllaceae family generally coincide with mountain regions, such as Central America (Marshall, 2007), the North Andes (Josse *et al.*, 2011), Taiwan (Liao & Chen, 2021) and North Borneo (De Bruyn *et al.*, 2014). These regions feature diverse topographies and habitats, and clearly contribute to the observed pattern. Notably, the areas with the highest richness of Hymenophyllaceae typically range in elevation from 2000 to 3000 m on a global scale. Terrain ruggedness is significantly positively correlated with species richness, showing the greatest influence in the analysis. These results support the hypothesis that the abundance of Hymenophyllaceae species is primarily driven by variations in habitat and environment along mountainous regions. Considering its long evolution and dispersal history (Rio *et al.*, 2017), the considerable terrain roughness in these areas might also suggest a correlation between historical habitat (landscape) changes (Rahbek *et al.*, 2019) and subsequent species diversification.

We found that hymenophylloids show greater diversity than the trichomanoids at mid to high elevations at a global scale. Similar patterns have been reported at a local scale in Bolivia, where *Trichomanes sensu lato* is typically found in lowlands, whereas *Hymenophyllum sensu lato* dominates montane forests at relatively higher elevations (Kessler *et al*., 2001; Krömer & Kessler, 2006). However, it is essential to note the absence of a pronounced mid-elevation peak for Hymenophyllaceae, in contrast to the trend observed across all fern species (Kessler *et al.*, 2016). We speculate that this phenomenon may be because the different peak richness elevation ranges between lineages weaken this tendency from low to mid and high elevation.

Climate: *temperature and precipitation*. Temperature is a critical climate variable affecting the distribution of Hymenophyllaceae, a topic not extensively explored in the previous literature, and is generally summarised for these species as “warm” (Iwatsuki, 1990). Although this summary holds, it is more precise to note that Hymenophyllaceae species diversity does not thrive at high temperatures. These plants inhabit areas with a broad spectrum of temperature conditions (annual mean temperature, c.−3°C to −29°C); however, in areas of high species richness (more than 40 species), the temperature range is restricted to approximately 15–23°C (**Supplementary file 2**). The negative correlation with maximum temperature (BIO5) and the positive correlation with minimum temperature (BIO6) indicate that Hymenophyllaceae are particularly tolerant of neither warm nor cold temperatures. These findings align with the findings of previous studies from Malaysia, which showed that temperature favoured by Hymenophyllaceae varies between 19.8°C and 23.8°C (Nurul *et al.*, 2014). Another study on the growth of *Vandenboschia speciosa* (Willd.) G.Kunkel

gametophytes suggested a temperature preference of 24°C, where they achieve optimal growth (based on the highest number of photosynthetic cells) (Makgomol & Sheffield, 2005). However, growth significantly decreases when temperature rise to 28°C (Makgomol & Sheffield, 2005).

The sensitivity of Hymenophyllaceae to temperature variations may partly explain why the highest species richness is found at lower latitudes north of the equator. There is no significant difference in response to species diversity between the two lineages. Notably, the minimum temperature of the coldest month was shown to have slightly higher importance for the species richness of trichomanoids compared with that of hymenophylloids (**Supplementary file 2**), which suggests that compared with hymenophylloids, trichomanoids are more sensitive to low temperatures.

Hymenophyllaceae are regarded as a typical group of poikilohydric plants, whose physiological functions and life stages are determined by environmental moisture conditions (Raven, 1999; Nitta *et al.*, 2021). Accordingly, the results of our analyses showed a significant positive correlation between species richness and environmental humidity for each of our three datasets. Notably, annual precipitation in high–species richness regions typically exceeds 1200 mm (**Supplementary file 2**), as observed in Costa Rica (> 3000 mm; https://www.worldbank.org) and Borneo (2000–4000 mm; https://www.panda.org).

Host microhabitat: forest canopy height. In the present study, the epiphytic niche of filmy ferns is shown by a positive correlation with forest canopy height, which at a global scale is second in importance to temperature. Previous researchers interpreted the diversification of epiphytic ferns as stemming from the new ecological niches created by the expansion of angiosperm-dominated modern forests (Schneider *et al.*, 2004; Schuettpelz & Pryer, 2009). Trees generate microenvironmental variations for epiphytes that vary significantly with increasing height above ground, thereby offering a range of ecological niches within the area (Cardelús & Chazdon, 2005).

This variation necessitates corresponding physiological adaptations (Proctor, 2012; Watkins & Cardelús, 2012; Nitta *et al.*, 2020). For instance, compared with other growth forms, the epiphytic habit usually results in more frequent and prolonged desiccation stress (Alejo-Jacuinde & Herrera-Estrella, 2022). In fact, desiccation-tolerant mechanisms are widespread in epiphytic Hymenophyllaceae, enabling their survival in water-deficient and unstable host environments; they include formation of gametophytic gemmae (Nitta *et al.*, 2020), reduction in size (typical in *Didymoglossum*) (Dubuisson *et al.*, 2009) and photosynthesis protection mechanisms (Cea *et al.*, 2014; Charuvi *et al.*, 2019). These are likely determinants in their diversification and also reflect the adaptive significance of forest canopy height.

Growing from the trunk base to the upper canopy, epiphytes are subject to varying gradients of light and drought (Saldaña *et al.*, 2014; Niinemets *et al.*, 2018). For example,

Niinemets *et al.* (2018) observed that during photosynthetic recovery, methanol emissions due to oxidative stress in *Hymenophyllum dentatum* Cav. situated higher in the canopy significantly exceed those from species lower on the trunk, such as *Hymenophyllum cruentum* Cav. Long periods of desiccation ultimately constrain the growth of Hymenophyllaceae, because they are not true hygrophytes (Dubuisson *et al.*, 2009; Proctor, 2012). Although existing studies have shown that the morphology (e.g. frond size, root system) varies in different growth forms (Dubuisson *et al.*, 2003, 2013), the understanding of morphological variations across filmy ferns species (e.g. in terms of body size, stomatal density) at varying epiphytic heights remains limited.

Soil: organic carbon content and pH value. We have shown that soil (i.e. soil organic carbon content, soil pH) has relatively weak explanatory power regarding Hymenophyllaceae species richness. The species richness of trichomanoids does not appear to reflect specific soil preferences, because no significant correlation with soil organic content and soil pH was found. These results are probably due to the high number of epiphyte and lithophytic species in filmy ferns, as discussed by previous researchers (Dubuisson *et al.*, 2009, 2013).

Light condition: solar radiation level. Our analyses indicate that solar radiation levels do not have high correlation with species richness; this finding was contrary to expectations, given its recognised role in influencing plant distribution in mountainous regions (Barry, 2008; Winkler *et al.*, 2016). Generally, Hymenophyllaceae show varied responses to different light energy levels (Proctor, 2012; Parra *et al.*, 2015). This may relate to the fact that many Hymenophyllaceae live in microhabitats that are protected from direct sunlight.

Global species richness patterns

Taken together, our results support the hypothesis that Hymenophyllaceae occur at low to medium elevation in warm and humid tropical or subtropical forests, typically located in mountains regions or on islands at low latitudes. These patterns align closely with those observed for fern diversity in general (Weigand *et al.*, 2020; Suissa *et al.*, 2021). The humidity, coupled with restricted warm temperatures, constrains the Hymenophyllaceae from achieving high species richness in other regions. For example, despite the southern Chilean wet forests often serving as research sites for physiological and ecological studies of Hymenophyllaceae (Saldaña *et al.*, 2014), the average annual temperature there rarely exceeds 20°C (Parra *et al.*, 2009), probably limiting species richness in these regions. Another example is the comparison between New Zealand and Japan, both mid-latitude islands near 40°, where the species diversity in New Zealand is marginally higher. This difference can be attributed to the colder winter temperatures in Japan, often reaching below zero, which are suboptimal for Hymenophyllaceae.

The model showing mountains as drivers of biodiversity (Antonelli *et al.*, 2018) is particularly evident among Hymenophyllaceae species and elucidates the more dispersed

biodiversity hotspots in tropical Asia compared with the Neotropics, mirroring the mountain distribution. Furthermore, the prevalence of epiphytes in Hymenophyllaceae underscores the considerable explanatory power of forest related factors for high species richness at a global scale. This suggests that further research on epiphyte diversification should thoroughly consider the effects of host diversification and the heterogeneity of habitats provided by hosts.

Unexpectedly, the Pan-Himalayan region was not recognised as a hotspot, and even showed low species richness. It is well known that this region is one of the most geographically heterogeneous mountainous regions, with high terrain ruggedness and many tropical mountain vertical vegetation zones, and it is traditionally considered a biodiversity hotspot and high-diversity region for ferns (Myers *et al.*, 2000; Weigand *et al.*, 2020; Suissa *et al.*, 2021; Wambulwa *et al.*, 2021). Although there are currently few publications focusing on Pan-Himalayan fern diversity, previous molecular dating studies and geographical reconstructions of Hymenophyllaceae (Hennequin *et al.*, 2008; Dubuisson *et al.*, 2022) may provide some explanations from the perspective of ecological adaption in evolutionary history. Hymenophyllaceae is reported to have its origin in the tropical southern hemisphere (Neotropics, Afro-Malagasy, Australia) no later than the Triassic period (Rio *et al.*, 2017). Unsuitable paleo-habitats and the geographical barrier caused by Himalayan uplift may have blocked the dispersal and diversification of this family in the Pan-Himalayan region.

The species diversity of Hymenophyllaceae in the African continent is low (even in rain forest) and largely concentrated in Madagascar. However, biodiversity in Africa (and India) is likely to be underestimated (Farooq *et al.*, 2021). More field studies are required to conclude whether the low species richness reported for these areas is accurate or instead reflects a lack of research.

Conclusions

In the present study, we mapped global species richness patterns for Hymenophyllaceae, showing that the montane tropical rain forests of Central America, the North Andes and Southeast Asia are its major centres of species diversity. Our results indicate that the current pattern is driven by environmental heterogeneity, including topography, climate, and the diversity of host forest microhabitat. We found that Hymenophyllaceae species richness is weakly correlated with soil factors, reflecting their special epiphyte growth form. Furthermore, hymenophylloids and trichomanoids showed some differences in ecological preferences (e.g. elevation and temperature) in our analysis. Future research on physiological mechanisms may help elucidate these differences.

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Supplementary material

Supplementary material is available from the *Edinburgh Journal of Botany* online portal.
Supplementary file 1. Data used in the present study, environmental variables, numerical range of every species richness level, and the results of multivariate regression analysis.
Supplementary file 2. Tables S1–S7.
Supplementary file 3. Figures S1 and S2.

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