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FERN SPECIES RICHNESS PATTERNS AND THEIR ENVIRONMENTAL PREFERENCES ACROSS ELEVATIONAL GRADIENT ON MOUNT TRUS MADI, SABAH, MALAYSIA

Suis MAF[1, 2], Majuakim L[2] & Suleiman M[2, *]

[1]*Forest Research Centre, Sabah Forestry Department, Post Office Box 1407, 90715 Sandakan, Malaysia*
[2]*Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Jalan UMS, 88400 Kota Kinabalu, Malaysia*

**monicas@ums.edu.my*

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Elevational species richness studies in Borneo have overlooked Mount Trus Madi even though it is the second highest summit in the island. This study intends to elucidate the pattern of fern species richness along the elevational gradient of Mount Trus Madi. The environmental preferences of ferns in this mountain were studied with sampling efforts along the mountain's north-western slope. The survey recorded 11 species at 1000 m, 18 species at 1400 m, 29 species at 1800 m, 23 species at 2200 m and 14 species at 2600 m above sea level respectively. The study showed ferns species richness was very high at the intermediate elevation and decreased towards the highest and lowest elevation. However, terrestrial ferns showed a deviation from this trend, in which species richness decreased with elevation. The enumerated ferns are largely epiphytic and has shown a strong affinity towards moderate temperature and forest canopy cover at intermediate elevation. Ferns on this mountain are divisible into high-elevation and low-elevation assemblages. New discoveries from this study will enable ecologists to better understand the elevational species richness patterns of ferns in Borneo.

Keywords: Borneo, terrestrial fern, epiphytic fern, forest canopy cover, mid-elevational peak trend, species richness

INTRODUCTION

Biodiversity dynamics along elevational gradients have caught the attention of ecologists since the nineteenth century and many have carried out manipulative studies along the sites (Sanders & Rahbek 2012). As an example, elevational pattern of species richness has been studied at local and regional scales which leads to the variation in species richness patterns. There are many elevational species richness patterns documented and are represented by decreasing, increasing and mid-elevational peak trends (Kessler et al. 2011). Elevational species richness pattern is a reflection of the ecological preferences for a taxonomic group (McCain 2009).

Ferns have received much attention from ecologists, in which many of them concluded that this taxonomic group peaked somewhere between elevational gradient ends (Kromer et al. 2005, Salazar et al. 2013). However, such claims are only true for mountains with extensive elevational gradients from the lowlands up to the treelines (Kessler et al. 2011). Diversity patterns for terrestrial and epiphytic plants are discrete and should be treated separately (Mandl et al. 2010). Ironically, many plant studies across elevational gradients have over-emphasised terrestrial species rather than epiphytes (Watkins et al. 2006).

As a moisture-dependent plant, ferns are not well adapted to harsh conditions. Thus, environmental variables are an example of a limitation on fern communities in mountain ecosystems (Kessler et al. 2011). In Costa Rica, the maximum species richness of pteridophytes is resulted by the optimal combination between moderate temperatures and high humidity at intermediate elevations (Kluge et al. 2006). This herbaceous vegetation when under a closed forest canopy, receives lesser sunlight compared to an open forest canopy. A closed forest canopy is characterized by small canopy gaps with very high coverage by canopies. Sufficient light availability is a vital requirement for most plants; including ferns, to grow at an optimal rate. The low light availability due to an increase in forest canopy cover can reduce herbaceous species richness on forest floors (Liu et al. 2005).

Most elevational species richness studies in Borneo were focused on Mount Kinabalu (4095 m above sea level (asl)) where its treeline is at about 3700 m above sea level (Nor 2001, Kessler et al. 2001). Mount Trus Madi is the second tallest mountain on Borneo but its peak is below the treeline of Mount Kinabalu. Although fern flora on this mountain has been documented botanically (Adam & Muhammad 1989, Sugau & Andi 2014), much is not known about its species richness patterns and environmental preferences along an elevational gradient. There were very few published studies on elevational fern species richness in Borneo. Hence, the addition of replicate studies is deemed necessary to enable ecologists to understand the similarities of the underlying factors that give rise to these patterns.

Through this study, we aimed to investigate the patterns of fern species richness and the environmental preferences of ferns along the elevational gradient on Mount Trus Madi. We expected that this study would shed some light about Bornean fern ecology and thus serve as a baseline information for further ecological studies.

MATERIALS AND METHODS

Study area

Focal area of this study is the north-western slope of Mount Trus Madi between 5° 33'–5° 36' N and 116° 26'–116° 32' E (Figure 1). The mountain (2642 m asl) is located within the Nuluhon Trusmadi Forest Reserve (Class I Protection Forest) in Sabah, Malaysia. The mountain consisted of several high peaks above 2000 m above sea level that spread from the southwest to the northeast. The mountain comprised of five forest types; namely summit scrub (2500–2642 m asl), upper montane (2000–2499 m asl), lower montane (1500–1999 m asl), upland mixed dipterocarp (600–1499 m asl) and lowland mixed dipterocarp (< 600 m asl) (Kitayama et al. 1993). The forest reserve experienced selective logging which lasted until 2002.

Sampling design

A total of five elevational sampling sites were set along the north-western slope of Mount Trus Madi (Figure 1). These sites were selected based on its forest quality and elevation. Historical images of the study area were assessed via the Google Earth Pro programme. Ground verification was conducted to validate the initial assessment. Sites with signs of anthropogenic disturbance, for instances tree stumps, skid trails, large forest canopy gaps and presence of pioneer tree species (i.e. *Macaranga* spp. and *Mallotus* spp.) were excluded. No research plots were established in the lowland mixed dipterocarp forest because this forest is located beyond the forest reserve border; particularly at the north-western slope of the mountain. The lowland mixed dipterocarp forests on other slopes were severely damaged due to previous anthropogenic disturbances while some of them are inaccessible.

The focal area is virtually divided into five elevational bands; which started from the summit scrub to the upland mixed dipterocarp forest. Elevational intervals between each band are fixed at 400 m. Each band has an elevational sampling site. Hence, the sampling sites span localities from an upland mixed dipterocarp forest in the vicinity of Mirad Irad river at 1000 m asl to the summit scrub at 2600 m asl. Three research plots (20 × 20 m) in each elevational sampling site were established (Table 1). Due to the irregular and mountainous topography of the study area, relative distances between research plots ranged between 24–91 m.

Data collection

Fern enumeration and sampling of low-trunk epiphytic (≤ 2 m above ground) and terrestrial ferns was conducted from 8th of April to 25th September 2015. If few individuals of the same species clustered together on one substrate (e.g. a small branch), they were counted as a single individual. Fern specimens were processed and identified at the Institute for Tropical Biology and Conservation (ITBC), Universiti Malaysia Sabah. Specimens were cross-matched with the authentic voucher specimens from BORNEENSIS Herbarium (BORH) of ITBC and Herbarium of Sabah Forestry Department (SAN). The identification process was assisted by Mr. Markus Gubilil of SAN and with the aid of local field guide literature on ferns (Beaman & Edwards 2007). Voucher specimens were deposited at BORH.

Four environmental variables studied were temperature, humidity, elevation and forest canopy cover. The first two parameters were

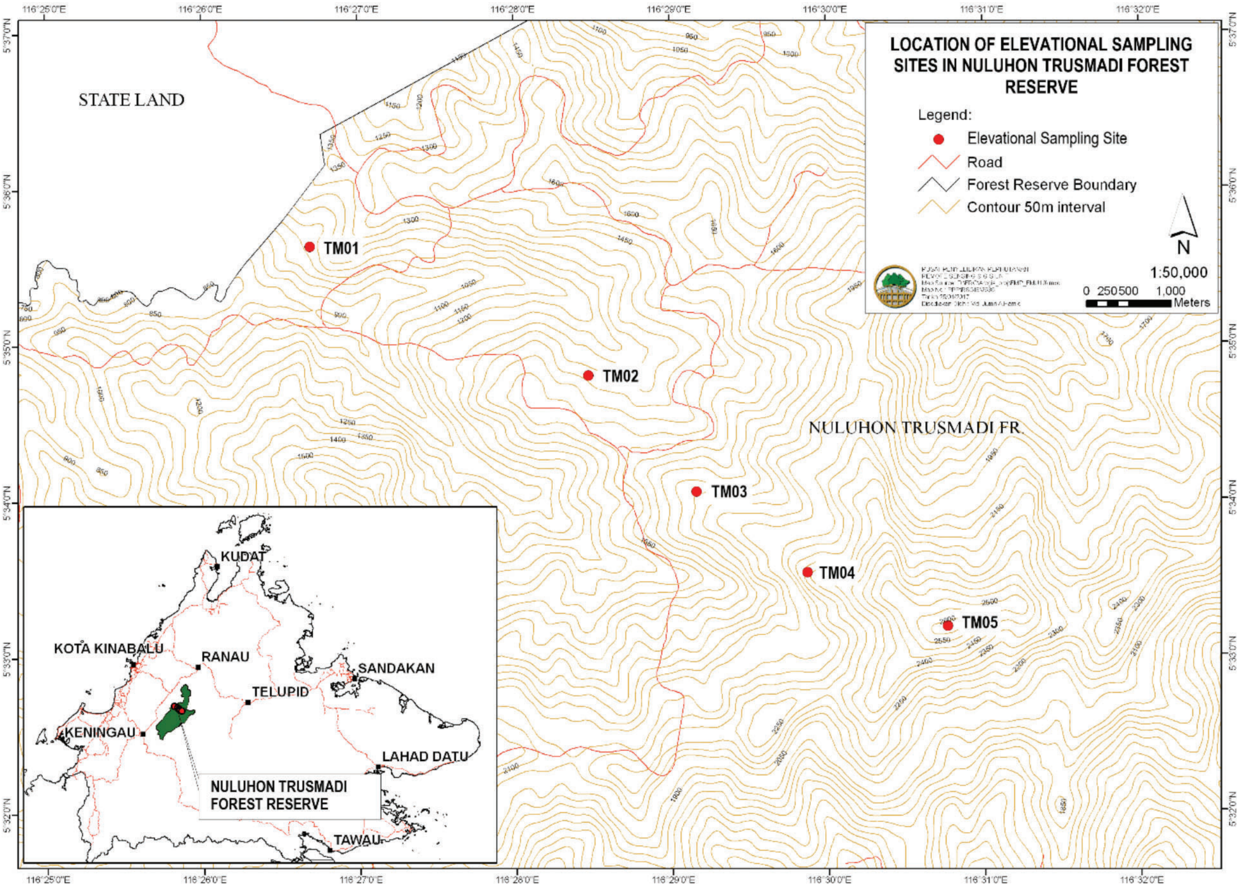

Figure 1 Location of elevational sampling sites and the study area (inset) in Sabah.

Table 1 Research plots elevational sampling sites on Mount Trus Madi, Sabah, Malaysia.

Elevational Sampling Site	Research Plot	Datum: WGS 84	
		Latitude	Longitude
TM01 (1000 m asl)	RP04	05° 35' 31.96"	116° 26' 49.92"
	RP05	05° 35' 34.87"	116° 26' 51.72"
	RP06	05° 35' 35.99"	116° 26' 52.04"
TM02 (1400 m asl)	RP01	05° 34' 46.27"	116° 28' 38.60"
	RP02	05° 34' 44.80"	116° 28' 38.53"
	RP03	05° 34' 46.81"	116° 28' 39.04"
TM03 (1800 m asl)	RP07	05° 34' 00.01"	116° 29' 20.65"
	RP08	05° 33' 59.94"	116° 29' 19.79"
	RP09	05° 33' 59.44"	116° 29' 20.08"
TM04 (2200 m asl)	RP10	05° 33' 28.01"	116° 30' 01.12"
	RP11	05° 33' 28.66"	116° 30' 02.27"
	RP12	05° 33' 27.18"	116° 30' 00.76"
TM05 (2600 m asl)	RP13	05° 33' 08.82"	116° 30' 57.46"
	RP14	05° 33' 07.88"	116° 30' 56.09"
	RP15	05° 33' 07.13"	116° 30' 54.94"

automatically measured using HOBO Data Loggers at each elevational sampling site. Each logger was set to record the environmental variables at every two hours interval. The loggers were left to operate for 12 months (April 2015 to April 2016). The forest canopy cover of each research plot was estimated using a Forestry Suppliers Spherical Crown Densiometer. In order to minimise operating error, the handheld densiometer was operated by the same person. A total of four readings (facing north, east, south and west) were taken at the centre of each 10 × 10 m research subplots. The average readings were used to estimate the forest canopy cover. Elevation was determined using a handheld Garmin GPSmap 60CSx.

Data analysis

Cluster analysis based on Bray Curtis distance was performed to measure the dissimilarity in fern species composition between research plots. Simple linear and polynomial regression models were built to assess the pattern of fern species richness along the elevational gradient. Spearman's Rank-Order Correlation was computed to determine the direction and strength between environmental variables. The multivariate relationship between fern communities and environmental parameters were determined through canonical correspondence analysis (CCA). The dataset has been tested with Detrended Correspondence Analysis (DCA) to check whether the unimodal ordination technique (i.e. CCA) is suitable for multivariate analysis. The length of the first DCA axis is equivalent to a value of 6.56, indicating a heterogeneous dataset where CCA is a preferred method. All statistical analyses were performed using multiple R packages within the RStudio v.1.2.1335.

RESULTS

A total of 15 families, 29 genera and 58 species of ferns were enumerated within the research plots (Table 2). The recorded ferns comprised of 35 epiphytic and 23 terrestrial species. Eleven fern species were recorded at 1000 m asl, 18 species at 1400 m asl, 29 species at 1800 m asl, 23 species at 2200 m asl and 14 species at 2600 m asl. *Hymenophyllum bakeri* is the most abundant fern with 396 individuals, followed by *H. acanthoides* (219), *Selliguea taeniata* (185), *S. enervis* (164) and *Diplazium cordifolium* (159).

The hierarchical cluster indicated that the enumerated ferns can be grouped into two main assemblages based on their occurrences and abundances (Figure 2). These fern communities were of high-elevation and low-elevation assemblages. The dissimilarity value between them is close to the score of 1 (complete dissimilarity). The within-group dissimilarity values are mostly less than 0.5. Elevational sampling sites are well represented by their respective fern communities (e.g. ferns in the RP07, RP08 and RP09 are grouped in the same sub-cluster).

A total of three regression models were chosen to explain and predict the pattern of fern species richness along the elevational gradient on Mount Trus Madi (Table 3). These regression models are considered parsimonious because all of the coefficients are statistically significant. Additionally, the Adjusted R^2 are high except for the terrestrial species.

Both epiphytic and terrestrial ferns presented two contrasting elevational patterns of species richness along the elevational gradient of Mount Trus Madi (Figure 3). The epiphytic fern exhibited a pronounced mid-elevational peak trend. Meanwhile, species richness of terrestrial ferns declined with elevation. When terrestrial and epiphytic ferns are combined, the overall species showed a typical mid-elevational peak trend of species richness.

The mean annual temperature declined with elevation, at an estimated temperature lapse rate of 0.51 °C 100 m^{-1} (Figure 4). The highest mean annual temperature (20.73 °C) is recorded at 1000 m asl while the lowest (12.61 °C) is on the mountain summit. Forest floors at 1000 m asl are well shaded with 93.43 % of forest canopy cover. However, forest floors in the summit scrub are less shaded due to lower forest canopy cover (86.22 %). Based on these environmental data, moderate mean annual temperatures and mean forest canopy cover of Mount Trus Madi are approximately at 16.67 °C and 89.83 % respectively. The mean annual humidity at all elevations are considered high with a range between 96.59–99.00 %. There is no correlation ($S = 8$, $\rho = 0.6$, $p = 0.350$) between mean annual humidity and elevation. On the other hand, strong negative correlations are observed between elevation with mean annual

Table 2 Fern species recorded from the fieldwork on Mount Trus Madi, Sabah, Malaysia.

Family	Species	Abbreviation
Aspleniaceae	*Asplenium normale* D. Don	C4
Aspleniaceae	*Asplenium* sp. 1	B11
Aspleniaceae	*Asplenium tenerum* G. Forst.	B8
Athyriaceae	*Diplazium cordifolium* Bl.	C1
Athyriaceae	*Diplazium porphyrorachis* (Bak.) Diels	B6
Athyriaceae	*Diplazium riparium* Holtt.	B3
Athyriaceae	*Diplazium* sp. 1	C2
Athyriaceae	*Diplazium tomentosum* Bl.	B2
Blechnaceae	*Blechnopsis orientalis* (L.) Presl	A6
Cyatheaceae	*Cyathea* sp. 1	A18
Davalliaceae	*Davallia hymenophylloides* (Bl.) Kuhn	B1
Davalliaceae	*Davallia repens* (L. fil.) Kuhn	A12
Davalliaceae	*Davallodes* sp. 1	C8
Dennstaedtiaceae	*Dennstaedtia ampla* (Bak.) Bedd.	B5
Dryopteridaceae	*Elaphoglossum angulatum* (Bl.) Moore	A1
Dryopteridaceae	*Elaphoglossum stenolepis* Bell ex Holtt.	A7
Hymenophyllaceae	*Abrodictyum obscurum* (Bl.) Ebihara & K. Iwats.	B9
Hymenophyllaceae	*Abrodictyum pluma* (Hook.) Ebihara & K. Iwats.	A32
Hymenophyllaceae	*Hymenophyllum acanthoides* (v. d. Bosch) Rosenst.	A9
Hymenophyllaceae	*Hymenophyllum bakeri* (Copel.) Copel.	A2
Hymenophyllaceae	*Hymenophyllum blandum* Racib.	A15
Hymenophyllaceae	*Hymenophyllum nitidulum* (v. d. Bosch) Ebihara & K. Iwats.	A20
Hymenophyllaceae	*Hymenophyllum pallidum* (Bl.) Ebihara & K. Iwats.	A26
Hymenophyllaceae	*Hymenophyllum pilosissimum* C. Chr.	A11
Hymenophyllaceae	*Hymenophyllum productum* Kze.	A27
Hymenophyllaceae	*Hymenophyllum* sp. 1	B10
Lindsaeaceae	*Lindsaea oblanceolata* Alderw.	A17
Lindsaeaceae	*Lindsaea parallelogramma* Alderw.	B14
Lindsaeaceae	*Lindsaea* sp. 1	A25
Lindsaeaceae	*Lindsaea* sp. 2	A24
Oleandraceae	*Oleandra pistillaris* (Sw.) C. Chr.	A14
Plagiogyriaceae	*Plagiogyria egenolfioides* (Bak.) Copel.	A5
Polypodiaceae	*Calymmodon borneensis* Parris	A3
Polypodiaceae	*Calymmodon cucullatus* (Nees & Bl.) C. Presl	A34
Polypodiaceae	*Calymmodon gracilis* (Fée) Copel.	A21
Polypodiaceae	*Chrysogrammitis* sp. 1	A22
Polypodiaceae	*Dasygrammitis brevivenosa* (Alderw.) Parris	A29
Polypodiaceae	*Dasygrammitis* sp. 1	A13
Polypodiaceae	*Leptochilus decurrens* Bl.	C3
Polypodiaceae	*Oreogrammitis congener* (Bl.) Parris	A30
Polypodiaceae	*Oreogrammitis reinwardtioides* (Copel.) Parris	A33
Polypodiaceae	*Prosaptia alata* (Bl.) Christ	B13
Polypodiaceae	*Pyrrosia* sp. 1	B12
Polypodiaceae	*Selliguea albidosquamata* (Bl.) Parris	B7
Polypodiaceae	*Selliguea enervis* (Cav.) Ching	A35
Polypodiaceae	*Selliguea soridens* (Hook.) Hovenk.	A31
Polypodiaceae	*Selliguea* sp. 1	A4
Polypodiaceae	*Selliguea* sp. 2	A28
Polypodiaceae	*Selliguea taeniata* (Sw.) Parris	A10
Polypodiaceae	*Themelium* sp. 1	A16
Pteridaceae	*Haplopteris* sp. 1	A36
Tectariaceae	*Tectaria beccariana* (Ces.) C. Chr.	C5
Tectariaceae	*Tectaria* sp. 1	C7
Thelypteridaceae	*Coryphopteris gymnopoda* (Bak.) Holtt.	A8
Thelypteridaceae	*Mesophlebion dulitense* Holtt.	B4
Thelypteridaceae	*Pronephrium nitidum* Holtt.	C6
Thelypteridaceae	*Sphaerostephanos heterocarpus* (Bl.) Holtt.	A23
Thelypteridaceae	*Trigonospora* sp. 1	A19

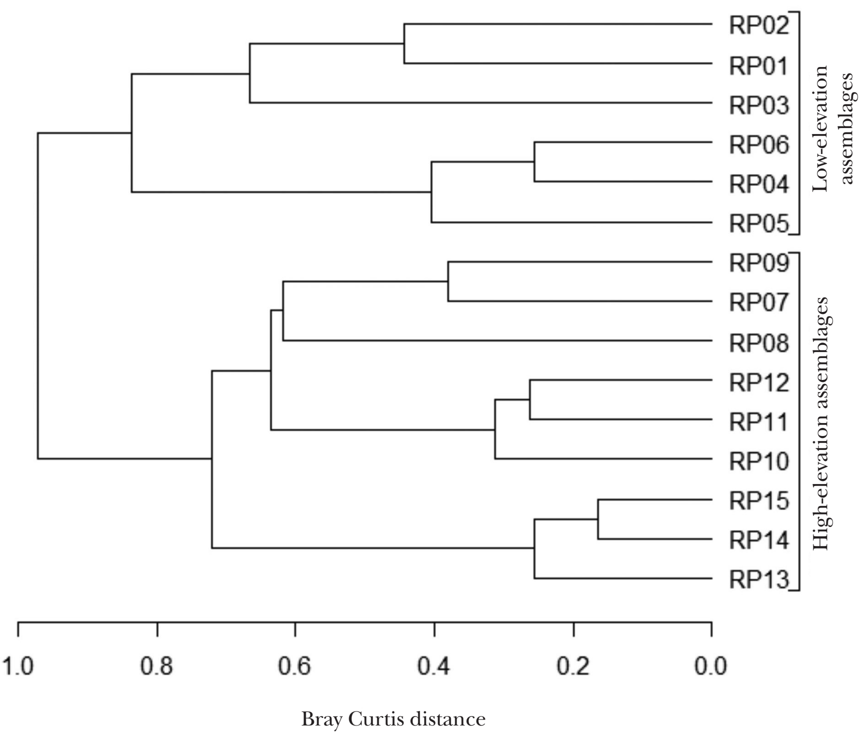

Figure 2 Dendrogram of two main fern assemblages based on their occurrences and abundances.

Table 3 Regression analysis of all species, epiphytes and terrestrial life forms species richness patterns along the elevational gradient on Mount Trus Madi, Sabah, Malaysia.

Life form	Model	Equation	Adjusted R^2
All species	Quadratic	$y = -3.369e + 5.324e^{-2}x - 1.384e^{-5}x^2$	0.59 (p = 0.002)
Epiphytes	Quadratic	$y = -3.834e + 5.124e^{-2}x - 1.280e^{-5}x^2$	0.70 (p = 0.000)
Terrestrial	Linear	$y = 7.683 - 0.002x$	0.37 (p = 0.010)

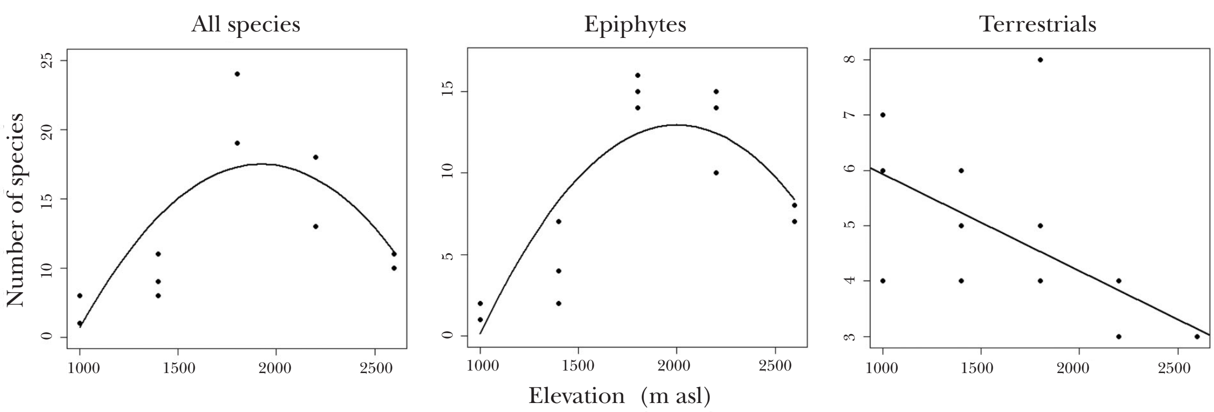

Figure 3 Patterns of fern species richness of all species, epiphytes and terrestrial life forms along the elevational gradient on Mount Trus Madi, Sabah, Malaysia. Solid dots represent the number of fern species recorded within the research plots.

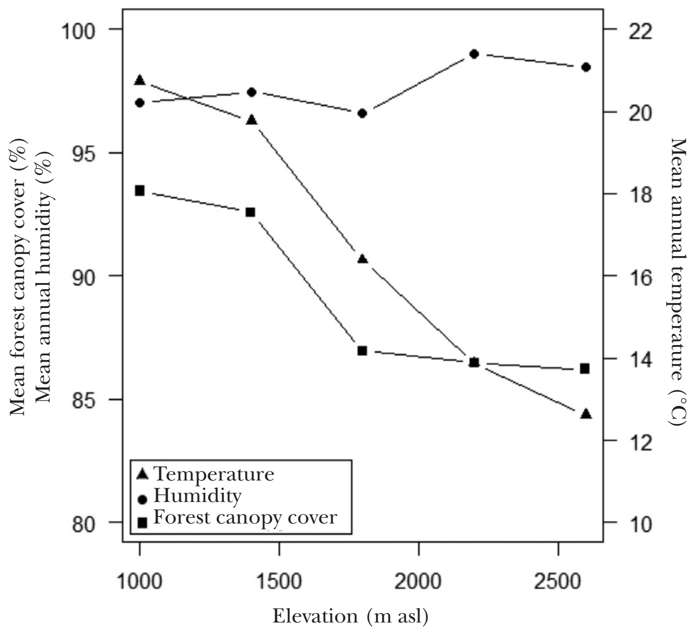

Figure 4 Elevational trends of forest canopy cover, mean annual temperature and humidity on Mount Trus Madi, Sabah, Malaysia.

temperature ($S = 40$, $\rho = -1$, $p = 0.017$) and mean forest canopy cover ($S = 40$, $\rho = -1$, $p = 0.017$).

At least 62 % of the total variability in the relationships between fern communities and environmental variables have been explained by the CCA. The first axis (CCA1) explained 41.97 % of the total constrained variability and it increased up to 71.30 % after the inclusion of the second axis (CCA2) (Table 4). This showed that the two-dimensional CCA biplot is sufficient for the multivariate analysis. The lengths of environmental arrows are not equal. For instance, forest canopy cover has the longest arrow while humidity is the shortest (Figure 5).

The CCA biplot indicated that ferns of Mount Trus Madi can be divided into three groups, namely Group A, Group B and Group C (Figure 5). These groups are based on their environmental preferences. Most members of a group often preferred identical environmental conditions whereas only few species may deviate from the majority. For example, *Diplazium cordifolium* preferred warm temperature and high forest canopy cover but other members in the Group C favoured warmer and higher forest canopy cover. Nevertheless, all members in the Group C showed a strong tendency towards forests in the lower elevations.

Group A comprised of 36 fern species and dominated by epiphytes opposite to Group C. Members of Group A generally preferred humid habitats at upper elevations of Mount Trus Madi. *Dasygrammitis* sp. 1, *Oleandra pistillaris, Hymenophyllum blandum* and *Themelium* sp. 1 are unique from the other members as these species are far from the environmental arrow of elevation. The aforementioned species were recorded only at 1800 m asl and none at 2200 m asl or above. With equal composition of epiphytic and terrestrial species, ferns of Group B favoured habitats at the lower elevations but are associated with slightly low forest canopy

Table 4 Canonical correspondence analysis (CCA) for the relationship between fern communities and environmental variables on Mount Trus Madi, Sabah, Malaysia.

Axis	CCA1	CCA2
Eigenvalue	0.88	0.61
Variance explained (%)	41.97	29.33
Cumulative variance explained (%)	41.97	71.30

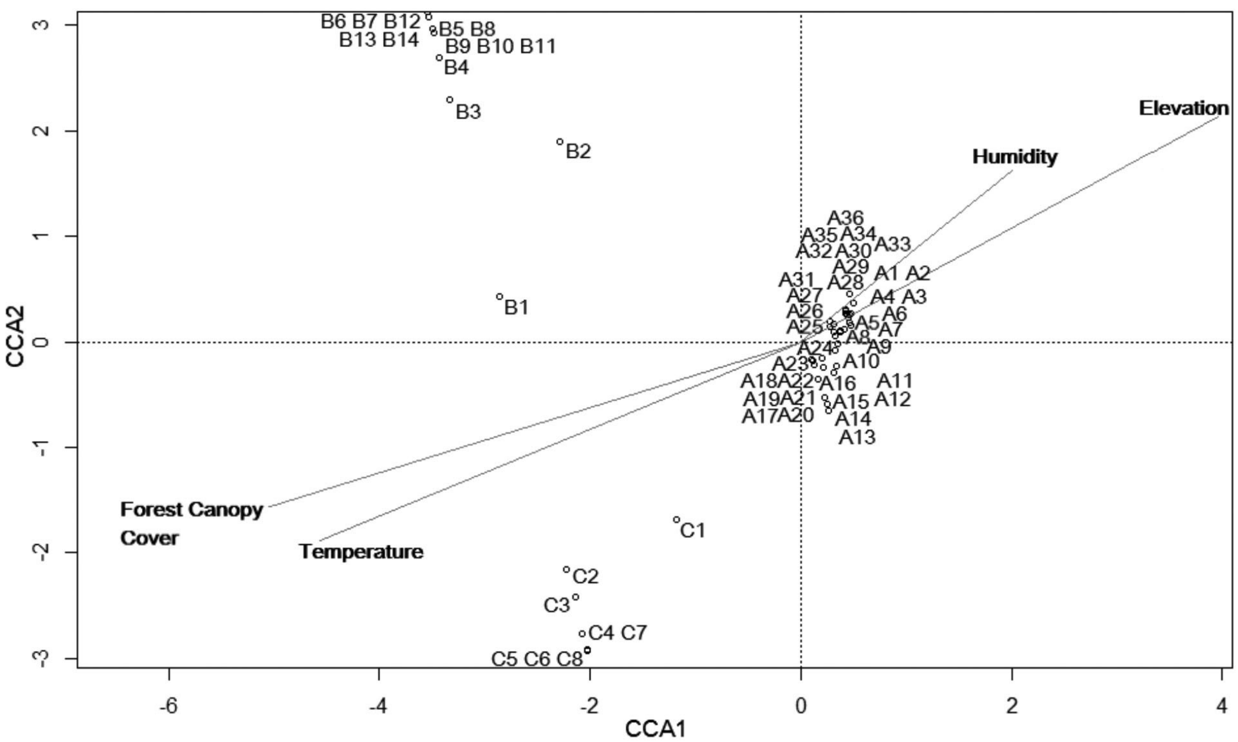

Figure 5 Canonical correspondence analysis (CCA) biplot map of the relationship between fern communities and environmental variables on Mount Trus Madi, Sabah, Malaysia.

cover and temperature. *Diplazium tomentosum* prefered slightly higher elevation compared to other members of Group B.

DISCUSSION

Ferns of Mount Trus Madi attained their maximum species richness somewhere in the middle of the elevation range and decreased towards both extremes of the mountain (Figure 3). The terrestrial ferns deviated from the mid-elevational peak trend of species richness. Linear regression model for terrestrial fern species has relatively low adjusted R^2 value due to the presence of an outlier (Table 3). Epiphytic ferns have more weight on the mid-elevational peak trend compared to the terrestrial species. This is based on the high adjusted R^2 value of quadratic regression model for epiphytic fern species (Table 3). Furthermore, the number of registered epiphytic ferns is greater than their terrestrial counterparts.

The mid-elevational peak trend on Mount Trus Madi bears a resemblance to the species richness pattern of ferns on Mount Kinabalu though the latter maximised at 1500 m asl (Kessler et al. 2001). Despite that, the decreasing trend of terrestrial fern species richness has not been reported on Mount Kinabalu. Terrestrial ferns are known to display weak mid-elevational peak trend of species richness (Salazar et al. 2013). Additionally, pattern of terrestrial fern species richness in Myanmar also showed a deviation from this unimodal pattern (Khine et al. 2017). It is important to note that a decreasing trend in fern species richness is not uncommon and has been documented around the globe (Kessler et al. 2011).

In this study, the mean annual humidity across elevational gradient of Mount Trus Madi is close to the saturation point (100%) and is thus, consistently humid regardless of elevation (Figure 4). This is not surprising for a mountain in a tropical realm (Salazar et al. 2013). The high tree density which subsequently resulted in a contiguous forest canopy might have retained the humid air in the surrounding area. Both mean annual temperature and forest canopy cover are negatively correlated with elevation. The monotonic decreasing trend of mean annual temperature with elevation is expected. In fact, it is estimated that the temperature lapse rate is nearly identical with Mount Kinabalu (-0.55 $^{\circ}C$ 100 m^{-1}) (Kitayama et al. 1999). The upland mixed dipterocarp forest in the study area comprised of big trees with huge crown sizes and hence, has high forest canopy cover. The forest canopy height decreased with elevation in the Amazonian tropical forests (Asner et al. 2014). A similar ecological feature is also observed in montane forests on Mount Trus Madi. At 1500 m asl, trees begin to show stunted growths of which their heights are often less than 30 m. Hence, it is very likely for the under-canopy plants in the montane forests to receive high intensity of sunlight in a day.

The lower montane forest at 1800 m asl hosted high fern species richness (Figure 3). At this elevational band, mean annual temperatures and forest canopy covers are close to the moderate values calculated based on the average of maximum and minimum entries of the data loggers. Furthermore, the maximum fern species richness occurred at an elevation with moderate temperatures and high humidity (Khine et al. 2017). Nevertheless, environmental elements are not the only determinants that lead to mid-elevational peak trend of fern species richness on Mount Trus Madi.

Figure 5 illustrated that the environmental arrow for humidity is the shortest. This can be linked with the uniformity (i.e. no correlation) of mean annual humidity along the elevational gradient (Figure 4). These data implied that the influence of humidity over the fern species richness pattern on Mount Trus Madi is weak. Ferns rely heavily on moisture but when the humidity is very high and unvarying at all elevations, their communities are actually more likely controlled by other environmental parameters.

The mid-elevational peak trend is driven by Group A as members of this group are mostly epiphytic (Figure 5). Many of these epiphytes recorded in the montane forests of Mount Trus Madi are subjected to intense sunlight. The Hymenophyllaceae (filmy fern) is abundant in the cold and humid montane forests of Mount Banahaw, Philippines (Banaticla & Buot 2005). Filmy ferns are generally sensitive to extreme environmental conditions (Proctor, 2012). The fieldwork in April 2016 coincided with the *El Nino* phenomenon that resulted in prolonged hot and dry weather in Sabah. Filmy ferns in the sites with low forest canopy cover were badly impacted. Such adverse effect was not limited to ferns only but also to other moisture-dependant plants in the mountain. *Blechnopsis orientalis* is common along the roadside in a non-forested area (Beaman and Edwards 2007). Interestingly, this study recorded the same species at the undisturbed summit scrub which typically have large canopy gaps but absent in the intermediate elevation. This implied that even though fern is an excellent spore-shedding plant, the establishment of juvenile is determined by environmental conditions.

The decreasing trend is attributed to the high terrestrial fern species richness at the lower elevations of Mount Trus Madi. The majority of ferns that constituted lower elevations belonged to both Group B and Group C (Figure 5). Even though the edaphic factor is not the main focus in this study, it does influence fern communities to some extent. High species richness of terrestrial ferns in lowland tropical forests rather than in montane forests is due to better edaphic conditions in the lower elevations (Nervo et al. 2019). Soils at the upper elevations of Mount Trus Madi are highly acidic and have shallow humus layer (Kitayama et al. 1993). This claim corroborates our field observations of the unusual abundance of multiple pitcher plant species in the upper montane forest and summit scrub. Carnivorous plants have the tendency to adapt in oligotrophic conditions (Millet et al. 2012) but terrestrial ferns attained their highest diversity on nutrient-rich soils (Richardson & Walker 2010). The lower elevations of Mount Trus Madi are primarily mixed dipterocarp forest with many large trees (Adam 2001), indicating fertile edaphic conditions. Thus, the study inferred that the edaphic factor might have a significant contribution to the decreasing trend of terrestrial species richness on this mountain.

The first axis (CCA1) clearly separated the groups into two sides, Group B and Group C on the left whereas Group A on the right (Figure 5). Such division is in agreement with the cluster analysis output (Figure 2). Group A is of the high-elevation assemblages whereas both Group B and Group C are affiliated to the low-elevation assemblages. The species compositions and abundances of these assemblages are almost completely distinct. The epiphytes largely contributed to the total recorded species on Mount Trus Madi. The results are in concordance with Shim et al. (2011) who observed high richness of epiphytic ferns on Mount Kuli in Imbak Canyon Conservation Area, Sabah. Moreover, tropical mountains are hotspots for epiphytic plants (Richter et al. 2009). On the contrary, terrestrial ferns are frequently encountered than epiphytes in the lowland mixed dipterocarp forests in Tawau Hills Park (Bidin & Jaman 1999).

CONCLUSION

The study concluded that ferns of Mount Trus Madi exhibited a mid-elevational peak trend of species richness. Terrestrial ferns displayed a decreasing trend of species richness but epiphytes showed a pronounced mid-elevational peak trend along the north-western slope of the mountain. As the humidity along the elevations is almost constant, fern communities on this mountain are greatly influenced by the temperature and forest canopy cover. However, they are also affected by other factors especially edaphic conditions. The measured environmental parameters are not sufficient to explain the variation in species richness trend because the effect of one factor might be influenced by other determinants. Nonetheless, this study has demonstrated that Mount Trus Madi can be a natural laboratory for fern ecological research in Borneo. Future studies should consider a larger-scaled, as well as greater sampling efforts to fully understand the mechanisms behind the elevational pattern of fern species richness in Borneo.

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