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Differences in pteridophyte diversity between limestone forests and non-limestone forests in the monsoonal tropics of southwestern China

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Abstract Compared with non-limestone forests, limestone forests tend to show lower pteridophyte diversity, yet they are known to harbor a unique set of species due to their substrate conditions and naturally fragmented habitat areas. Pteridophyte assemblage composition, however, has not been quantitatively investigated in Xishuangbanna, southwestern China, known as one of the most species-rich areas of China. Using a fully standardized sampling protocol, we tested the following hypotheses: (1) pteridophyte species composition is different between limestone forests (LF) and non-limestone forests (NLF); and the differences are attributable to (2) lower species richness in LF; (3) greater spatial and temporal turnovers (beta diversity) in LF; and (4) higher proportion of pteridophyte species restricted to LF. We found significant differences in pteridophyte assemblage compositions between LF and NLF. Average species richness per transect (alpha diversity) was lower in LF than in NLF, but we found no difference in overall species richness (gamma diversity) between LF and NLF at the scale of this study, because species turnover among samples (beta diversity) was higher in LF than in NLF. A total of 23 species were restricted to LF and 32 species restricted to NLF; however, geographic distribution of LF species was limited to certain habitat patches within this habitat. Our results suggest that LF pteridophyte biodiversity cannot be protected by conserving a limited number of habitat patches, because loss of one LF habitat patch may result in local extinction of species or extinction of endemic species that are yet to be discovered.

Keywords Karst forest · Indicator species · Local endemism · Pteridophyte · Species turnover · Tropical rainforest · Xishuangbanna

Introduction

Pteridophytes (an informal grouping which generally includes both Polypodiopsida and Lycopodiopsid including *Selaginella*) are the second largest group

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of vascular plants, with about 11,000 described species (PPG I 2016). They are generally found in shady, moist environments such as the rainforest understory, but some of them can be found in rocky habitats and as epiphytes in the forest canopies (Aldasoro et al. 2004; Karst et al. 2005; Page 2002; Saldaña et al. 2006). Pteridophytes and are often also dominant in newly exposed surfaces such as burns, clear-cut areas, or landslides areas (Sharpe et al. 2010). The distribution patterns of pteridophyte species and their community structures are largely dependent on factors such as climate, soil, and evolutionary history (Kessler 2010).

Southeast Asia (including southern Yunnan and Hainan Province, China) contains four biodiversity hotspots (Indo-Burma, Sundaland, Wallacea, and the Philippines) with the original extent of primary vegetation covering over 4,000,000 km^2 (Myers et al. 2000). The region is topographically and climatically complex, harboring great biodiversity including many endemic species (Corlett 2009). The estimated 4500 pteridophyte species found in Southeast Asia represent more than one-third of the world species, richer than other regions where diverse pteridophyte species are also known to occur (e.g., Andes, southern Mexico, Bolivia, south-eastern Brazil, and Madagascar) (Ebihara et al. 2012; Moran 2008; Winter and Amoroso 2003).

Pteridophyte diversity is concentrated within the wet tropical regions, which is thought to have served as source of expansion into more arid areas (Sharpe et al. 2010). It is therefore not surprising that rainforests support a large proportion of tropical forest diversity (Corlett 2009). Compared with non-limestone forests, the pteridophyte diversity is lower in limestone forests where the porous substrate and thin soil layers cannot hold moisture (Nie et al. 2011). Furthermore, higher pH and lower soil nutrient concentration in limestone habitats may reduce the diversity of pteridophyte species (Clements et al. 2006; Zhang et al. 2011).

In contrast to the total forest area of Southeast Asia (approximately 2 million km^2, most of which is rainforest) (Corlett 2005), limestone karst in this region covers a relatively small area of about 400,000 km^2 (Clements et al. 2006; Day and Urich 2000). Despite its small area and generally lower floristic diversity, plant species on limestone are distinctive, containing numerous calcicolous species unique to limestone habitats (Clements et al. 2006). The Limestone karst ecosystem is generally considered "islands within islands" (Clements et al. 2006). That is, karst ecosystems represent isolated habitats within the matrix of lowland and mountain tropical forests (which are also highly fragmented and isolated due to recent human activities). Unlike non-limestone forests, limestone forests have been naturally fragmented over long periods of time (Clements et al. 2006; Zhu et al. 2004), which have assisted the development of locally endemic species in different locations of limestone forests. Endemic plant species are generally concentrated in isolated habitat (e.g., mountain ridges and oceanic islands) and they are not randomly distributed (Damschen et al. 2012; Gillespie et al. 2008). Pteridophytes are no exception—high levels of pteridophyte endemism are found in isolated islands (Kreft et al. 2010; Palmer 2003). Similarly, high endemism and high species turnover among habitats (i.e., high beta diversity) are found in limestone habitats (Pérez-García et al. 2009). Despite their conservation significance, biodiversity of limestone habitats has not been explored extensively due to limited accessibility (e.g., karst cliff faces), which may have resulted in underestimation of their biodiversity (Sodhi et al. 2010).

The majority of limestone karst is covered by trees except for the mountain outcrops where karst is exposed. Such outcrop areas are generally covered with shrubs and other non-woody plants (Pérez-García et al. 2009). Due to the unique topography and isolation of habitats, karst outcrops are recognized as local diversity hotspots, with high diversity of endemic plants (e.g., begonias, gesneriads, impatiens, orchids, pteridophytes, and bryophytes) and animals (e.g., land snails and other arthropods) (Clements et al. 2008, 2006; Pérez-García et al. 2009). The pteridophyte diversity of karst outcrops, however, has not been quantitatively compared with other surrounding habitats (but see Pérez-García et al. 2009).

Xishuangbanna Dai Autonomous Prefecture is located at the southernmost end of Yunnan Province, southwestern China. This region is located at the northern edges of Asian tropics and is characterized by the monsoonal climate where, unlike other tropical areas, the tropical plants are subjected to prolonged dry seasons (Cao et al. 2006; Zhu 2017). The vegetation on limestone in this region is generally classified as tropical seasonal rainforest, tropical seasonal moist forest, and tropical montane dwarf forest (Zhu et al. 2003, 2015). The limestone substrate covers approximately 3600 km^2, accounting for 19% of the total land area of this region (Tang et al. 2011). The region has been subject to several botanical investigations (Cao et al. 2006; Zhu et al. 2006) including studies of the limestone flora (Li et al. 1996a; Zhu et al. 1998, 2003). Li et al. (1996a) reported a preliminary study of pteridophytes in Xishuangbanna limestone forests, showing that the tropical elements accounted for 80% of the total at the generic level, of which tropical Asian elements made up to 33%. Although Li et al. (1996a) did not report any endemic species in Xishuangbanna, many species are likely to be local endemics as was reported from other locations of limestone forests within China (Lu 1994; Yan et al. 2002; Zhou et al. 1999) and elsewhere (Amoroso et al. 2016).

The local studies mentioned above are, however, based primarily on observation without fully standardized sampling protocols and spatial replications, making it difficult to quantitatively examine and compare pteridophyte species richness and composition in this region. Here we employ standardized sampling and spatial replications to investigate the differences in pteridophyte species diversity and composition between limestone and non-limestone forests in Xishuangbanna. Specifically, we hypothesized that (1) pteridophyte species composition is different between limestone forests and non-limestone forests; and that the differences are attributable to (2) lower species richness in limestone forests than non-limestone forests; (3) greater spatial and temporal turnover (beta diversity) in limestone forests than non-limestone forests; and (4) higher proportion of pteridophytes species restricted to limestone forests.

Methods

Study sites

Xishuangbanna Prefecture is in the southwest of Yunnan Province, bordering Laos and Myanmar. The region has a mountainous topography with mountain ridges running from north to south (Zhang and Cao 1995; Zhu et al. 2006). This area is located in the transition between temperate and tropical Asia and recognized as the northern edge of tropical Southeast Asia (Cao and Zhang 1997; Wu 1980; Wu et al. 1987). Consequently, the biotic groups are mainly composed of tropical and some temperate elements (Cao and Zhang 1997; Zhu et al. 2006). Due to agricultural expansion, large tracts of forests are now highly fragmented (Cao et al. 2017; Jiang et al. 2011), which may have resulted in a loss of pteridophyte species diversity. This region contains limestone forests and non-limestone forests, both of which are scattered across the landscape as fragmented forest patches. The local climate is characterized as monsoon climate with two distinct seasons: wet season (May–October) and dry season (November–April). The average annual temperature is 21.7 °C, average annual precipitation is around 1500 mm, and the average relative humidity is 87% (Cao et al. 2006; Lü et al. 2010). The hottest month is June with a mean temperature of 25.3 °C, and the coldest month is January with a mean temperature of 15.6 °C (Liu et al. 2004). During the early months of the dry season, fog occurs almost every day from midnight to mid-morning. Two types of limestone habitats are found in this region: limestone outcrops, which typically occur at the peaks of limestone mountains with little soil at the top and the slopes partially covered by thin soil; and limestone forests on relatively flat areas with few rocky outcrops with thicker soil covering the forest floor (Tang et al. 2011; Zhu et al. 1998).

Sampling design

Sampling sites were selected at six locations in Xishuangbanna. Three locations were within limestone forests, all of which included both limestone forests (hereafter referred to as LF) and limestone outcrop habitats (LO). Elevations of LF and LO ranged 567–1318 m, and 694–1440 m asl., respectively. Dominant tree species of LF included *Tetrameles nudiflora, Cleistanthus sumatranus, Celtis philippensis* var. *wightii, Alphonsea mollis, Sumbaviopsis albican, Garruga floribunda* var. *gamblei, Mallotus paniculatus, Lasiococca comberi* var. *pseudoverticillata, Cleidion spiciflorum,* and *Sterculia lanceolata.* Dominant shrubs and tree species of LO included *Osmanthus menglaensis, Dracaena cochinchinensis, Tarenna sylvestris, Sterculia villosa, Schefflera glomerulata, Mitrephora calcarea, Mallotus philippinensis, Garcinia bracteata, Celtis timorensis, Ficus curtipes, Garuga pinnata, Eriolaena kwangsiensis,* and *Diospyros yunnanensis* (Zhu

2006; Zhu et al. 1998). Another three locations were located within non-limestone forests (hereafter referred to as NLF) with elevations in the range of 520–887 m asl. Dominant tree species of NLF included *Parashorea chinensis, Garcinia cowa, Castanopsis echidnocarpa, Sloanea tomentosa, Knema furfuracea, Pometia pinnata, Nephelium chryseum, Cinnamomum bejolghota, Diospyros hasseltii, Semecarpus reticulata, Alseodaphne petiolaris, Antiaris toxicaria, Barringtonia macrostachya,* and *Tetrameles nudiflora* (Cao et al. 2008; Zhu 2006).

Fieldwork was carried out in the dry (January–April, 2017) and wet (June–October, 2017) seasons. At each of the three limestone locations, we established three transects in LF and one in LO. At each of the three NLF locations, we established three transects. These transects were at least 200 m apart and approximately 90 m long, along which we established three quadrats of 10 × 10 m separated by an interval of 30 m (totaling 300 m^2 of surveyed area per transect, Fig. 1). The shape and length of the transect were modified and shortened to fit within a small area of LO. In each quadrat, we recorded the abundance of pteridophyte species. The number of individuals of epiphytic and lithophyte species (rhizomes of which are visible on substrates) was counted directly. For terrestrial species, we either counted the number of caudices (for larger ferns with erect stems which are not connected by rhizomes, namely *Alsophila*, *Allantodia*, and *Cibotium*) or estimated the number of rhizomes by counting the number of leaves that were considered to have developed from individual rhizomes based on the biology of each species. All terrestrial and epiphytic pteridophyte species up to a height of 8 m above the ground were included. GPS coordinates, elevation, slope, and aspect were measured in each quadrat. The canopy openness was estimated in percentage using a digital camera (Nikon Coolpix 4500, Nikon Corporation, Japan) with a fisheye lens (Nikon FC E8 Fisheye Converter, Nikon Corporation, Japan). Hemispherical photographs were taken in the center of each quadrat at 1.3 m height with a tripod. In addition, the light intensity was assessed with the Gap Light Analyzer software (Version 2.0). Pteridophyte specimens were collected in three duplicates per species as dry specimens for taxonomic identification. The identification was done using relevant references including the *Flora of China* (Lin et al. 2013), and *Native Ferns and Fern Allies of Yunnan, China* (Cheng and Jiao 2007). For nomenclature comparisons, we used *the List of Plants in Xishuangbanna* (Li et al. 1996b), and *A Community-Derived Classification for Extant Lycophytes and Ferns* (PPG I 2016).

Analyses

Abundance (the number of individuals per area) of pteridophyte species in the three quadrats of each transect were pooled before analysis, and individual transects were used as replicates in the analyses.

The summary of LO samples are represented in figures and tables, but they were not included in the statistical analysis as the sampling design was not the same (length of the transects were shortened), and sampling intensity was not balanced (*n* = 1 in each location). Statistical analyses therefore included *n* = 36 samples (3 transects × 3 locations × 2 habitats (LF and NLF) × 2 seasons). All univariate

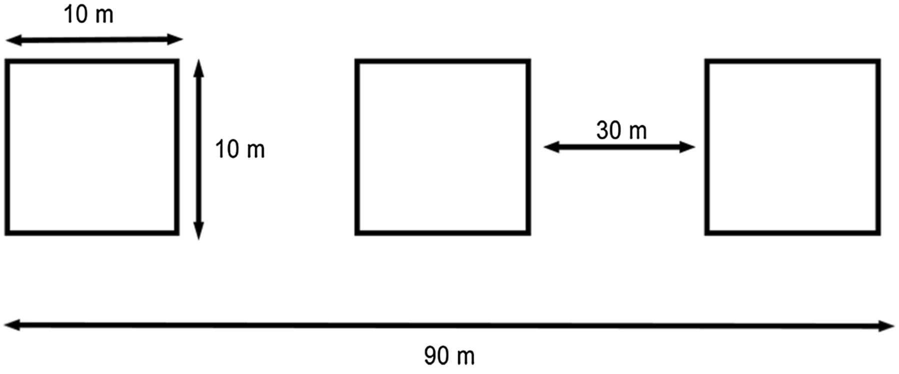

Fig. 1 Schematic diagram of a survey site (not to scale), showing three quadrats where pteridophytes were comprehensively surveyed

analyses were implemented by R version 3.4.4. (R development core team 2015).

We used sample-based and coverage-based rarefaction curves (Chao and Jost 2012) to test the sampling sufficiency and to estimate the total number of pteridophyte species (gamma diversity) in LF and NLF. Instead of the number of individuals, we used the number of samples to generate the rarefaction curves, as pteridophyte abundances may or may not represent the true number of individuals (i.e., some pteridophytes were connected by underground rhizomes). The sample-based rarefaction curves were plotted against the number of species in a given habitat (Colwell et al. 2012). The coverage-based rarefaction curves show the estimated proportion of the total number of individuals in a given habitat, represented by the species collected by a given number of samples (Chao and Jost 2012). We used 100 replicate bootstrapping to generate the rarefaction curves with 95% confidence intervals. We also extrapolated the number of samples from $n = 9$ (the number of observed samples in each habitat and season) to $n = 18$. Rarefaction curves were generated using the *iNEXT* package (ver. 1.0) available in *R*.

Some pteridophyte species showed dormancy (i.e., wilting leaves and stems while the rhizomes stay alive) during dry season. We therefore analyzed species richness and total abundances of pteridophytes using ‘all pteridophytes’ and ‘dormant pteridophytes’ in wet and dry seasons. We tested the effects of habitat (LF and NLF), season (wet and dry) and their interactions (habitat × season) on pteridophyte species richness and total abundances, while controlling for the effect of spatial autocorrelation. To this end, we used generalized least squares (GLS) which allows us to incorporate the spatial autocorrelation in the error terms (Carsten 2007; Pinheiro and Bates 2000). Unlike mixed effects models which account for the spatial relationships by grouping spatially closer samples (i.e., using locations as a random factor), GLS models effectively control for spatial autocorrelation of the individual transects by allowing for a nondiagonal error covariance matrix (Zuur et al. 2007). We first generated a semi-variogram without incorporating spatial autocorrelation in the model (i.e., the model only included the habitat as an explanatory variable). Based on the shape of the semi-variogram (Pinheiro and Bates 2000), we determined the presence of spatial autocorrelation. Different correlation structures (i.e., corRatio, corSpher, corExp, corGaus, and corLin, see Pinheiro and Bates 2000) were tested, and the best fitting model was determined by the Akaike Information Criterion (AIC) (Selmi and Boulinier 2001). As correlation structures in GLS models cannot have zero distance between samples (i.e., wet and dry samples from the same transect had the same GPS coordinates), we added very small numbers to the GPS coordinates of dry season samples (0.00001 for decimal and 0.0001 for decimal). The added values are smaller than the precision of a GPS unit, and did not change the overall spatial structures among the transects. Abundance data were log-transformed before analysis. The same GLS analysis was applied to investigate the differences in elevation and canopy openness between LF and NLF.

We conducted additional analyses to check whether pteridophyte species richness and abundance increased with the increasing habitat area. Size (area) of the habitat (LF or NLF) surrounding each transect was obtained from (Liu and Slik 2014) who calculated forest fragment sizes using GLS-2010 and GLS-2005 images downloaded from International Science Data Service Platform. Habitat size was obtained in square meters and log-transformed before analysis. Simple linear regression was used to test the effects of habitat type, habitat area and their interactions.

Assemblage composition of pteridophyte species was analyzed using Bray–Curtis similarity index (Bray and Curtis 1975) based on log-transformed abundances. Similarity indices were visually examined using nonmetric multiscaling dimensional (NMDS) ordinations (with 25 random restarts to find the lowest stress values). The differences in assemblage composition among the two habitats and two seasons were tested using permutational multivariate ANOVA (PERMANOVA), in which we calculated pseudo-*F* values using Type III sums of squares, and *P* values using 4999 permutations of residuals. We set habitats (LF and NLF) and seasons (wet and dry) as fixed factors, and their interactions were also incorporated in the analysis. We also tested the differences in beta diversity (species turnover) among habitats and seasons using permutational analysis of multivariate dispersions (PERMDISP). Beta diversity was calculated as the distances (deviations) from the centroids of each treatment, and *P* values using 4999 permutations. All multivariate analyses were implemented using PRIMER6 and PERMANOVA+ add-on software (Anderson et al. 2008).

To quantitatively identify pteridophyte species restricted to, and characteristic of LF or NLF habitat, we used indicator value protocol developed by Dufrêne and Legendre (1997), using the *labdsv* package available in *R*. The indicator values are a combination of a measurement of relative abundance (specificity) and relative frequency to a given habitat (fidelity), to calculate percentage indicator values (IndVals) for each species. Indicator value of 100% can be attained when a species is found in all samples from a given habitat and season (maximum fidelity), and none from the other habitat (maximum specificity). We selected species whose IndVal was significant based on 4999 permutations of the samples. McGeoch et al. (2000) have recommended a benchmark of 70% IndVal as a 'strong' indicator species.

Results

We recorded a total of 96 species, belonging to 43 genera and 17 families of which 23 species were restricted to LF, 32 to NLF and 14 to LO. We found a total of 43 species in LF, 47 in NLF, and 24 species in LO (Tables 1, 5).

Elevation and canopy openness

Average elevation was lower in NLF (685 m asl.) than LF (877 m asl.), but the GLS model which incorporated spherical spatial correlation showed only marginally significant differences ($t_{1,16} = -\ 1.98$, $P = 0.065$). Average canopy openness was similar between NLF (7.5%) and LF (7.2%), and the best GLS model (which did not incorporate spatial autocorrelation) showed no significance difference ($t_{1,16} = 0.41$, $P = 0.687$).

Gamma diversity and sample sufficiency

Sample-based rarefaction curves showed no differences in the total number of species (gamma diversity) between LF and NLF in both wet and dry seasons. The number of species in LF was slightly lower during the dry season, but 95% confidence intervals overlapped between the two habitats, even after the extrapolation of samples (Fig. 2a, b). Coverage-based rarefaction curves showed that more than 90% coverage was attained for NLF habitats in both dry and wet seasons, whereas significantly lower coverage was attained for LF, suggesting that LF may have been under-sampled. Extrapolation of the sample numbers suggested that the increased sampling intensity in LF may have attained similar coverage to that of NLF (Fig. 2c, d).

Species richness and total abundance

We first tested habitat, season, and their interaction effects on species richness and total abundance of all pteridophyte species (Fig. 3). The best GLS model for species richness incorporated rational quadratic spatial correlation. The effects of both habitat and season had significant influence, but not their interaction (Table 2). Species richness was higher in NLF than LF, and slightly higher in the wet than in the dry season (Fig. 3a). The best GLS model for total abundance incorporated exponential spatial correlation. The effects of all habitats, season, and their interactions had significant influence (Table 2). Total abundance was higher in NLF than LF and higher in the wet than in the dry season (Fig. 3b). The same analysis was applied to the subset of data consisting of dormant species only. For both species richness and total abundance, the best GLS models included no spatial correlation. Habitat was not significant for both species richness and total abundance, but both season and the interaction effects were significant (Table 2). Both species richness and abundance of dormant species were higher in the wet than in the dry season, but this was only found in LF (dormant species were absent in NLF) (Fig. 3c, d).

We also tested for the effects of habitat, area and their interaction effects on species richness and total abundance. For both species richness and total abundance, all effects, including the interactions, were significant (Table 3). In NLF, both species richness and total abundance were positively correlated with habitat area (Fig. 4). In LF, however, such a relationship was not found.

Species composition and species turnover

The NMDS ordination showed clear difference in assemblage composition between LF and NLF. The PERMANOVA demonstrated significant difference between the two habitats (pseudo-$F_{1,32} = 15.04$,

Table 1 List of the ten most abundant pteridophyte species found in each of the three habitats (+ present in a given habitat)

Family	Species	NLF	LF	LO
Antrophyaceae	*Antrophyllum callifolium*		+	+
Aspleniaceae	*Asplenium obscurum*		+	
Aspleniaceae	*Hymenasplenium apogamum*	+		
Davalliaceae	*Davallodes membranulosum*			+
Dryopteridaceae	*Bolbitis heteroclita*	+		
Dryopteridaceae	*Lomagramma matthewii*	+		
Lygodiaceae	*Lygodium conforme*		+	
Polypodiaceae	*Drynaria bonii*			+
Polypodiaceae	*Lemmaphyllum carnosum*			+
Polypodiaceae	*Lepisorus contortus*			+
Polypodiaceae	*Leptochilus pothifolius*	+	+	
Polypodiaceae	*Microsorum membranaceum*			+
Polypodiaceae	*Phymatosorus cuspidatus*			+
Polypodiaceae	*Pyrrosia assimilis*		+	+
Pteridaceae	*Adiantum caudatum*			+
Pteridaceae	*Adiantum edgeworthii*		+	
Selaginellaceae	*Selaginella doederleinii*		+	+
Selaginellaceae	*Selaginella picta*	+		
Selaginellaceae	*Selaginella stauntoniana*			+
Tectariaceae	*Ctenitopsis devexa*		+	
Tectariaceae	*Pteridrys australis*	+		
Tectariaceae	*Tectaria impressa*	+	+	
Tectariaceae	*Tectaria polymorpha*		+	
Tectariaceae	*Tectaria vasta*	+		
Thelypteridaceae	*Cyclosorus dentatus*		+	
Thelypteridaceae	*Cyclosorus parasiticus*	+	+	
Thelypteridaceae	*Pronephrium gymnopteridifrons*	+		
Thelypteridaceae	*Pronephrium triphyllum*	+	+	

NLF Non-limestone forest, *LF* limestone forest, *LO* limestone outcrop

$P = \; < 0.001$) whereas the seasonal variations (pseudo-$F_{1,32} = 0.09$, $P = 0.999$) and interactions between habitat and season (pseudo-$F_{1,32} = 0.08$, $P = 0.999$) were not significant. Although not included in the statistical analysis, the LO habitat was clearly different from both LF and NLF. Species turnover (beta diversity) was greater in LF (PERMDISP average distance to the centroid = 58.01 and 58.54 for wet and dry seasons, respectively) than NLF (33.01 and 34.10), and the differences were significant ($F_{3,32} = 46.46$, $P = \; < 0.001$) (Fig. 5).

Indicator species

The indicator-values protocol identified 14 significant pteridophyte species indicative of the NLF habitat (Table 4). All but one species (*Pteridrys cnemidaria*) were consistently selected as indicator species of NLF in both wet and dry seasons. Eight indicator species attained IndVals greater than 70%. Unlike NLF indicator species, only one species, *Lygodium flexuosum*, was selected as LF indicator, showed an IndVal less than 70%, and was not a significant indicator in the dry season.

Discussion

Our results demonstrate that pteridophyte species composition was different between limestone forest (LF) and non-limestone forest (NLF), supporting the first hypothesis of our study. Although not

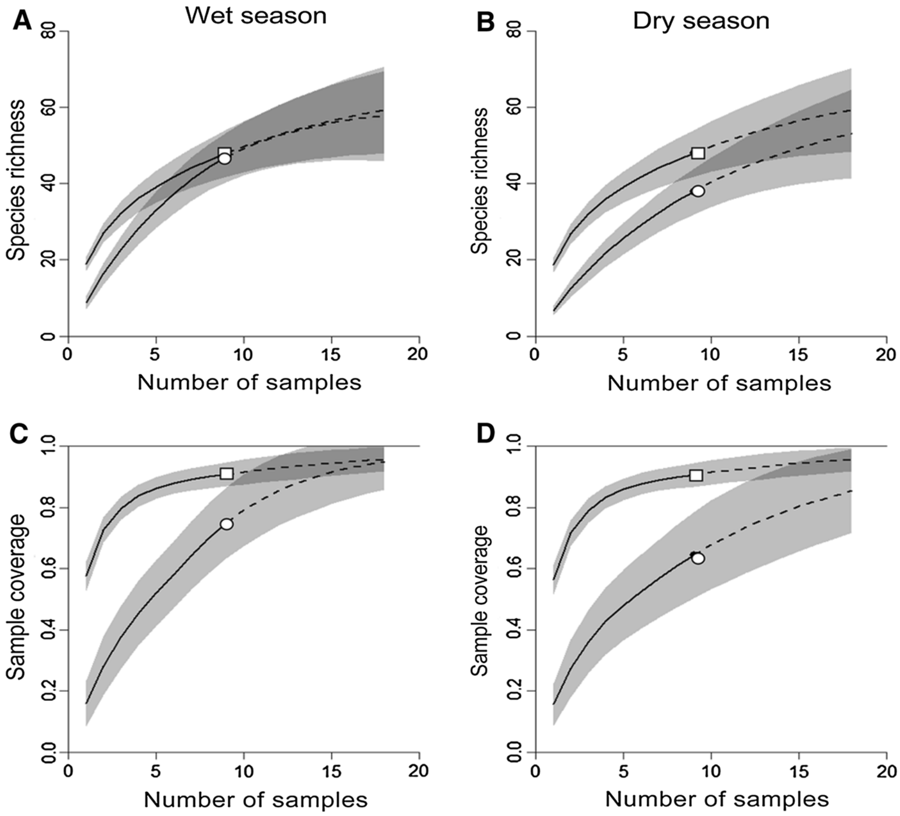

Fig. 2 Species richness (**a**, **b**) and sample coverage (**c**, **d**) rarefaction curves based on the number of samples ($N = 9$) from NLF (square) and LF (circle). Rarefaction curves are made for wet (**a**, **c**) and dry (**b**, **d**) seasons. Shaded areas represent 95% confidence intervals. Extrapolation to the twice the number of observed samples ($N = 18$) is shown by dashed lines

systematically investigated, Li and his colleagues (Li 2015; Li et al. 1996a) also found that species typically found in LF did not occur in NLF (and vice versa). In fact, their list of pteridophyte species in the respective habitats matches with ours (*Adiantum edgeworthii*, *Lygodium flexuosum*, and *Pyrrosia assimilis* in LF; *Bolbitis heteroclite, Pteridrys cnemidaria*, and *Tectaria polymorpha* in NLF, see Table 5). Our results are consistent with those of other groups of organisms which generally have species unique and endemic to LF (Corlett 2005), and show species compositions distinctively different from the surrounding NLF. Our study, however, did not find any species that are locally endemic to Xishuangbanna—all species found in our LF transects are known from other limestone regions. For example, genera commonly found in LF, namely *Adiantum*, *Asplenium*, *Lepisorus*, *Drynaria*, *Lemmaphyllum*, *Phymatosorus*, *Microsorum*, and *Selaginella*, are known from other provinces of southern China and other neighboring Southeast Asian counties (Lin et al. 2013). In contrast to Xishuangbanna, many pteridophyte species have been reported to be locally endemic to particular provinces such as Guanxi (Zhou et al. 1999) and Hainan (Qin et al. 2005). Of the 3000 or more seeded species known to occur in Xishuangbanna, approximately 3–7% are estimated to be endemic to this regions (Zhu 1994). Furthermore, the new fern species recently described in Xishuangbanna (*Leptochilus mengsongensis* (Zhao et al. 2017) is likely to be endemic to this region. It is therefore very likely that Xishuangbanna would contain many endemic pteridophyte species, but our study did not detect such species as we employed fully standardized sampling which did not allow us to survey large areas and specialized microhabitats such as canopies (i.e., epiphytic pteridophytes) and cliff faces.

Pteridophyte species composition is known to be affected by soil substrate conditions (Jones et al. 2013; Tuomisto et al. 2002). Compared with NLF, LF is characterized by harsh habitat conditions, such as higher soil pH, porous substrate, and thin soil layers with little capacity to hold moisture (Liu et al. 2014; Zhang et al. 2011). As tropical pteridophyte species prefer mid-elevations (i.e., about 1500–2000 m with high cloud cover) where humidity is generally high (Khine et al. 2019; Kluge et al. 2006), lower elevations

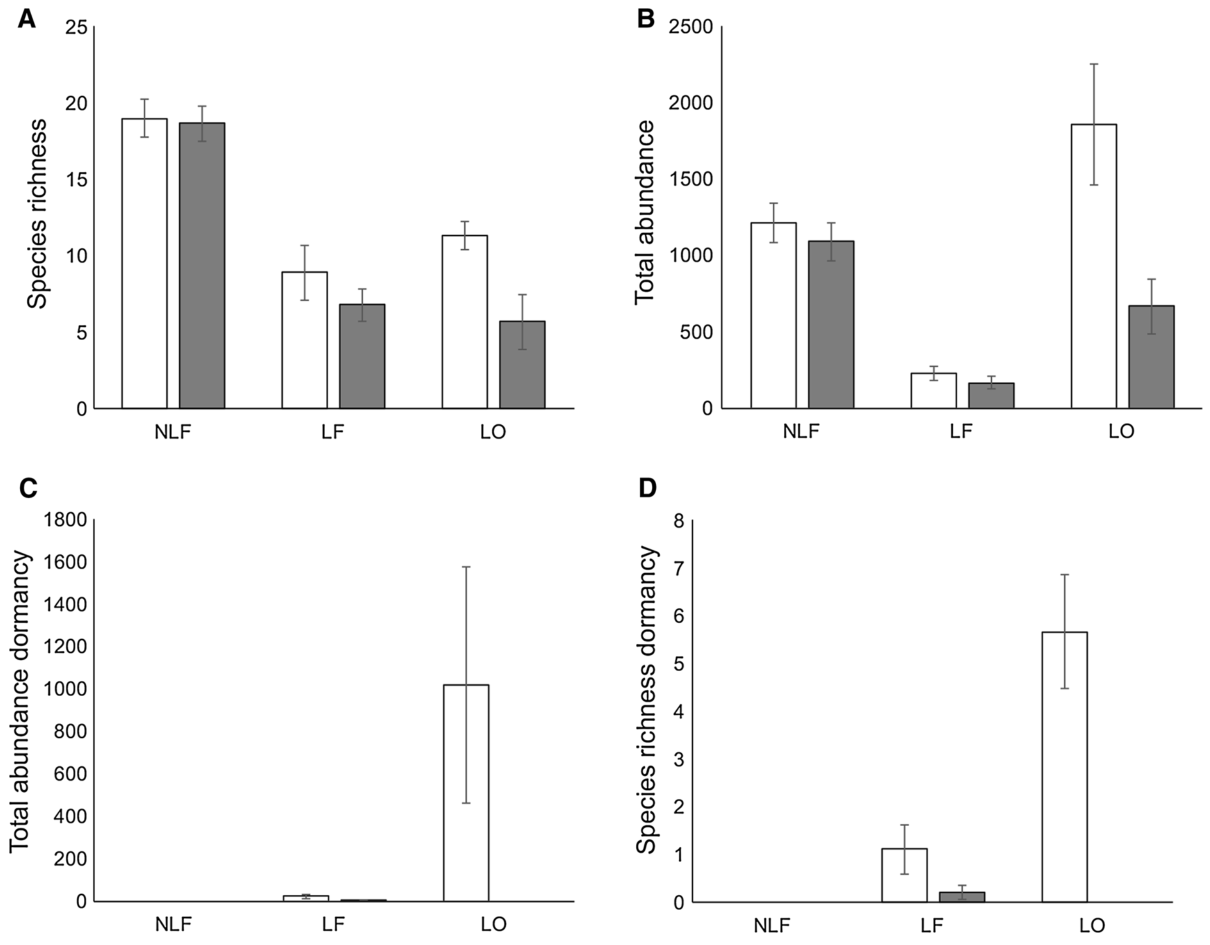

Fig. 3 Mean (± SE) species richness and abundance of pteridophytes in NLF, LF, and LO sampled in the wet (open bars) and dry (closed bars) seasons. The upper graphs (**a**, **b**) include all of the pteridophyte species sampled, whereas the lower graphs (**c**, **d**) include pteridophyte species that become dormant in the dry season (see the Methods section for the definition of dormant species)

at our LF may present harsher habitat conditions and may be less favorable for many pteridophyte species. This was supported in our study where we found a lower number of species (alpha diversity) in LF than NLF. Studies conducted in other tropical regions also found that the pteridophyte species richness was lower in LF compared with lowland NLF (Karst et al. 2005; Lu 2001). Similar results were found for woody plants which showed not only different species composition but lower species diversity and richness in LF than NLF (Tang et al. 2011; Zhu et al. 1998). Unlike pteridophytes and woody plants, moth species richness was comparable between LF and NLF, although assemblage composition was significantly different (Kitching et al. 2014).

Unlike average species richness per transect (alpha diversity), we found no difference in overall species richness (gamma diversity) between LF and NLF at the scale of this study, because species turnover among sample (beta diversity) was higher in LF than NLF. The results of PERMDISP (average distance to the centroid) showed significantly higher beta diversity in LF than NLF. Distribution of LF is limited by the presence of limestone substrate which generally occurs patchily within a given landscape (Gillieson 2005). In other words, LF are naturally fragmented even at a geological time scale. Unique habitat characteristics and isolation of LF patches may therefore have facilitated species being restricted to each LF fragments (Clements et al. 2006; Kessler

Table 2 Summary results of the best GLS models with (or without) spatial correlation, showing *t* (with degrees of freedom in parentheses) and *P* values of habitat, season, and their interaction effects (significant values shown in bold)

	Factor	*t*	*P*
All pteridophyte species			
Species richness	**Habitat**	**$4.64_{(1,32)}$**	**< 0.001**
Spatial correlation: rational quadratic correlation	**Season**	**$2.74_{(1,32)}$**	**0.010**
	Habitat × Season	$-1.66_{(1,32)}$	0.106
Total abundance	**Habitat**	**$4.99_{(1,32)}$**	**< 0.001**
Spatial correlation: exponential correlation	**Season**	**$5.97_{(1,32)}$**	**< 0.001**
	Habitat × Season	**$-3.01_{(1,32)}$**	**0.005**
Dormant pteridophyte species only			
Species richness	Habitat	$0.00_{(1,32)}$	1.000
Spatial correlation: no correlation	**Season**	**$3.42_{(1,32)}$**	**0.002**
	Habitat × Season	**$-2.20_{(1,32)}$**	**0.036**
Total abundance	Habitat	$0.00_{(1,32)}$	1.000
Spatial correlation: no correlation	**Season**	**$3.51_{(1,32)}$**	**0.001**
	Habitat × Season	**$-2.21_{(1,32)}$**	**0.035**

Pteridophytes species richness and total abundance were analyzed using all pteridophyte species and a subset data consisting of dormant pteridophyte species only

Table 3 Summary results of the GLS models without spatial correlation, showing *t* (with degrees of freedom in parentheses) and *P* values of habitat, area and their interaction effects (significant values shown in bold)

	Factor	*t*	*P*
All pteridophyte species			
Species richness	**Habitat**	**$-3.33_{(1,32)}$**	**0.002**
	Area	**$-2.90_{(1,32)}$**	**0.006**
	Area × habitat	**$4.25_{(1,32)}$**	**< 0.001**
Total abundance	**Habitat**	**$-2.32_{(1,32)}$**	**0.027**
	Area	**$-2.91_{(1,32)}$**	**0.006**
	Area × habitat	**$3.19_{(1,32)}$**	**0.003**

2010). Furthermore, the monsoonal climate in Xishuangbanna causes longer drought with higher temperature and precipitation seasonality than other tropical forests at lower latitudes. Under such conditions, small changes such as elevation may result in distinctively different pteridophyte species compositions among the LF patches (Gabriela et al. 2014).

Lack of indicator species in LF is attributable to the high species turnover, which resulted in low fidelity of the LF species (Dufrêne and Legendre 1997). Many pteridophyte species are known to occur only within LF (Clements et al. 2006; Kessler 2010), but their occurrences were patchy and found in one location or transect only, resulting in only one indicator species of LF in our study. In addition, LF species are known to show locally restricted distributions (Clements et al. 2006). In contrast, occurrences of NLF species were more widespread (within their preferred habitats) across locations with high fidelity, resulting in larger number of habitat indicators (Table 3).

Our study showed that species richness and abundance of the NLF were positively correlated with habitat area, whereas LF species did not (Fig. 4a, b). Recent human activities caused fragmentation and reduced habitat size of NLF in this region and elsewhere (Cao et al. 2017; Jiang et al. 2011; Pasion et al. 2018). A previous study observed that some shade-tolerant pteridophyte species disappeared from a fragmented NLF patch in Xishuangbanna, whereas more heliophytic pteridophyte species increased from

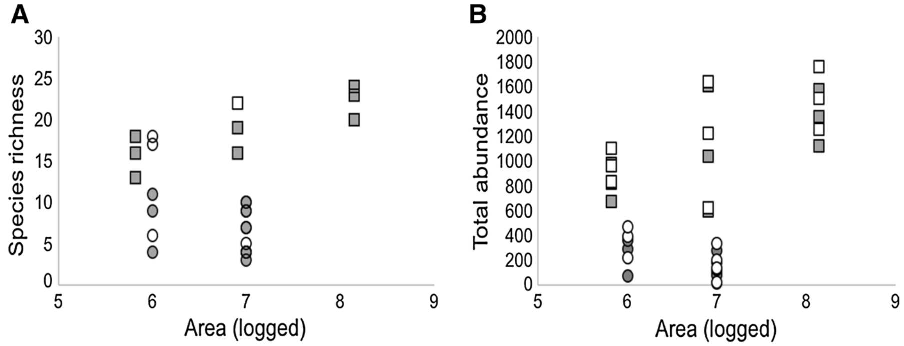

Fig. 4 Habitat area effect on species richness (**a**) and total abundance (**b**) of pteridophytes in NLF (squares) and LF (circles) sampled in the wet (open bars) and dry (closed bars) seasons

Fig. 5 NMDS ordination of pteridophyte assemblages based on Bray–Curtis similarity values of log-transformed abundances. Pteridophytes were surveyed in NLF (circles), LF (squares) and LO (diamonds), in the wet (open symbols) and dry seasons (closed). LO was not included in the statistical analysis

1959 to 1997 (Li et al. 2000). This was attributed to increasingly drier NLF under the canopy owing to forest fragmentation (Li et al. 2000). Unlike NLF, LF is naturally small and fragmented, and pteridophytes may have adapted to habitat conditions in such landscapes. A recent study by Pasion et al. (2018) found that the habitat area of the fragmented forests was a weak predictor of species richness of four life forms (trees, lianas, herbs and ferns) in Xishuangbanna. Ecological impacts of forest fragmentation are difficult to explicitly assess as many factors such as forest physiognomy, habitat isolation, age of fragmented forests and perimeter to area ratio all potentially influence the diversity of forest biota (Fahrig 2017).

As the areas of LO were small, we were unable to conduct fully standardized sampling and hence statistical analyses were not carried out. Despite such shortcomings, our study showed that species composition of LO habitats was distinctively different from LF and NLF, having species only found in LO (Table 1). LO generally occur at isolated mountain tops where the habitat is exposed to highly variable climatic conditions. These unique microhabitat conditions filtered the species that are adapted to such habitat condition (Clements et al. 2006). The presence of dormant species was characteristics of LF, but this was especially true in LO with larger proportions of dormant species (Fig. 3c, d). It is highly likely that dormancy was one of the ecological traits required to survive dry season in such habitat conditions.

It is well known that LF present unique pteridophyte species composition (Clements et al. 2006; Zhou et al. 1999). Our study is in line with this general pattern, showing that species compositions of LF was different from that found in surrounding NLF. Unlike other botanical surveys conducted in this region, we employed fully standardized sampling technique and found that overall species richness (gamma diversity) was similar between these two habitats at the scale of this study, but local species richness (alpha diversity) was lower in LF due to high species turnover (beta diversity) among the locations and, even transects. The results of our study showed that even small patches of LF can contain unique species and thus small LF fragments are disproportionately important to the conservation of pteridophytes in this region. Although we did not find any locally endemic species, it is likely that many new and endemic species are waiting to be discovered especially in LF, as was described by Zhao et al. (2017). We suggest that the true biodiversity values of LF are not fully known, and

Table 4 Pteridophyte species found as significant indicators of either LF (not including LO) or NLF in wet and dry seasons, showing average abundance (± SE) in NLF and LF habitats, and indicator values (IndVals)

	Wet season			Dry season		
	NLF	LF	IndVal (%)	NLF	LF	IndVal (%)
NLF species						
Selaginella picta	318.0 (110.1)	0	100	347.7 (103.56)	0	100
Bolbitis heteroclita	259.8 (58.3)	0	100	216.6 (50.6)	0	100
Allantodia dilatata	26.1 (12.8)	0	100	25.4 (12.8)	0	100
Hymenasplenium apogamum	76.3 (17.7)	0	89	53.6 (14.6)	0	89
Angiopteris caudatiformis	9.6 (3.2)	0	89	9.5 (3.2)	0	89
Tectaria subtriphylla	15.7 (5.4)	0.7 (0.7)	82	14.2 (5.6)	0.4 (0.4)	72
Cyclosorus paralatipinnus	13.0 (9.1)	0	78	11 (7.6)	0	78
Tectaria impressa	34.3 (18.7)	15.4 (11.4)	72	34.7 (20.16)	13.4 (10.1)	73
Lomagramma matthewii	138.6 (60.0)	0	67	145 (68.89)	0	67
Microsorum insigne	13.3 (5.5)	0	67	13 (5.6)	0	67
Asplenium phyllitidis	13.6 (5.2)	0	67	7.5 (2.6)	0	67
Tectaria vasta	30.2 (17.9)	0	56	30.22 (16.97)	0	56
Diplazium donianum	4.1 (2.2)	0	56	4.11 (2.21)	0	56
Pteridrys cnemidaria[a]	11.8 (10.0)	3.0 (3.0)	51	11.6 (10.07)	2.5 (2.5)	–
LF species						
Lygodium flexuosum[a]	0	2.0 (1.0)	56	0	1.4 (1.1)	–

[a] Species were significant indicators only in the wet season

protection of the limited number of LF habitat patches would not effectively conserve the pteridophyte biodiversity. Loss of one LF habitat patch may result in local extinction of species or extinction of endemic species that are yet to be discovered.

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Appendix

See Table 5.

Table 5 List of pteridophyte families and species collected in three NLF locations (“55” plot, Bubeng, XTBG) and three LF locations (Green Stone Forest, Cuipingfeng, Yin Chang)

Family and species	NLF									LF									LO		
	“55” Plot			Bubeng			XTBG			Green Stone Forest			Cuipingfeng			Yin Chang			Green Stone Forest (1), Cuipingfeng (2), Yin Chang (3)		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Antrophyaceae																					
Antrophyllum callifolium													+			+			+		
Aspleniaceae																					
Asplenium austrochinense																					+
Asplenium crinicaule																			+		
Asplenium neolaserpitiifolium	+																				
Asplenium obscurum										+											
Asplenium phyllitidis	+	+	+	+	+	+															
Asplenium saxicola																			+	+	+
Asplenium simonsianum																			+		
Asplenium subtoramanum																+		+	+		
Hymenasplenium apogamum	+	+	+	+	+	+		+	+												
Athyriaceae																					
Allantodia dilatata	+	+	+	+	+	+	+	+	+												
Allantodia pinnatifido-pinnata				+	+			+													
Allantodia squamigera		+																			
Allantodia viridissima	+	+	+		+																
Athyrium dissitifolium																	+	+			
Athyrium sp.		+								+		+									
Deparia boryana							+														
Diplazium donianum			+		+	+	+		+												
Kuniwatzukia cuspidata																		+			
Blechnaceae																					
Blechnum orientale							+														
Woodwardia magnifica																	+	+			
Cibotiaceae																					
Cibotium barometz							+										+	+			
Cyatheaceae																					
Alsophila articulata		+						+													
Davalliaceae																					
Araiostegia imbricata																					+
Davallia griffithiana																	+			+	+
Davallodes membranulosum																					+
Dennstaedtiaceae																					
Microlepia herbacea																	+	+			
Microlepia khasiyana																	+				
Microlepia neostrigosa																	+				
Microlepia pseudostrigosa	+	+		+	+												+				

Table 5 continued

Family and species	NLF									LF									LO		
	"55" Plot			Bubeng			XTBG			Green Stone Forest			Cuipingfeng			Yin Chang			Green Stone Forest (1), Cuipingfeng (2), Yin Chang (3)		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Dryopteridaceae																					
Arachniodes pseudoaristata	+	+																			
Bolbitis heteroclita	+	+	+	+	+	+	+	+	+												
Dryopteris sp.		+																			
Hypodematium crenatum																				+	
Lomagramma matthewii	+	+	+	+	+	+															
Polystichum acutidens		+																			
Hymenophyllaceae																					
Vandenboschia naseana			+	+																	
Lygodiaceae																					
Lygodium conforme							+					+									
Lygodium flexuosum											+		+		+		+	+			
Lygodium scandens																		+			
Marattiaceae																					
Angiopteris caudatiformis	+	+	+		+	+	+	+	+												
Archangiopteris subrotundata							+														
Polypodiaceae																					
Drynaria bonii						+													+	+	
Lemmaphyllum carnosum																+			+		+
Lepisorus contortus																					+
Leptochilus decurrens	+		+		+	+															
Leptochilus pothifolius	+		+	+		+				+			+	+	+	+					
Microsorum insigne	+	+	+	+	+	+															
Microsorum membranaceum																					+
Microsorum punctatum				+																	
Phymatosorus cuspidatus																	+	+	+	+	+
Pyrrosia assimilis																	+	+		+	
Pyrrosia beddomeana																	+				
Pyrrosia calvata																					
Pyrrosia gralla																					+
Pyrrosia mollis																		+			
Pyrrosia nuda																	+		+		
Pyrrosia nummulariifolia																				+	
Pyrrosia piloselloides																			+		
Pteridaceae																					
Adiantum caudatum													+	+					+	+	
Adiantum edgeworthii											+	+	+	+							
Adiantum philippense																		+	+		
Pteris ensiformis											+				+						

Table 5 continued

Family and species	NLF									LF									LO		
	"55" Plot			Bubeng			XTBG			Green Stone Forest			Cuipingfeng			Yin Chang			Green Stone Forest (1), Cuipingfeng (2), Yin Chang (3)		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Pteris esquirolii											+					+					
Pteris fauriei	+																				
Pteris grevilleana																		+			
Pteris linearis																				+	
Pteris semipinnata	+	+																			
Pteris venusta																	+	+			
Selaginellaceae																					
Selaginella delicatula							+	+	+												
Selaginella doederleinii											+	+							+	+	
Selaginella involvens											+										
Selaginella picta	+	+	+	+	+	+	+	+	+												
Selaginella stauntoniana																					+
Tectariaceae																					
Arthropteris palisotii						+															
Ctenitopsis devexa												+		+							
Pleocnemia winitii		+					+														
Pteridrys australis	+	+	+																		
Pteridrys cnemidaria		+	+		+	+		+	+	+											
Tectaria decurrens				+		+		+													
Tectaria impressa	+	+	+	+	+	+	+	+	+	+		+									
Tectaria phaeocaulis							+								+		+				
Tectaria polymorpha	+		+		+	+				+	+	+				+					
Tectaria simonsii											+										
Tectaria subtriphylla	+	+	+		+	+	+	+	+	+											
Tectaria vasta				+	+	+		+	+												
Vittaria linearifolia	+																				
Thelypteridaceae																					
Cyclosorus dentatus											+						+				
Cyclosorus gustavi	+						+	+									+	+			
Cyclosorus paralatipinnus	+	+	+			+	+	+	+												
Cyclosorus parasiticus																		+			
Cyclosorus siamensis			+							+											
Cyclosorus sp.										+											
Cyclosorus subelatus																		+			
Pronephrium gymnopteridifrons		+		+	+			+	+	+											
Pronephrium triphyllum						+	+										+				

The presence of pteridophyte species is indicated by plus (+) sign in each transect (1, 2, 3). Only one transect was established in the LO habitat per limestone locations

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