Biogeographical transect studies in the high elevation mountain areas of Myanmar

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Preface

This study is part of an interdisciplinary research project in one of the least known mountain areas of Asia. Only the recent opening of Myanmar offered the unique possibility to conduct species diversity and mountain ecology research in an area, which harbors the last remaining virtually untouched forests of the Himalayas and possibly of Southeast Asia. Although three extensive expeditions were able to collect a unique dataset, I am fully aware that our results are preliminary and this area offers more to explore. However, I hope that this thesis can contribute to a better understanding of mountain biodiversity patterns and may provide enough incentives for future projects. This cumulative thesis submitted here includes first evaluations of datasets from the expedition areas in northern Myanmar, and connects these data with those from other mountain areas of East and Southeast Asia (see the list below).

Chapter 2	Nowak P, Khine PK, Homeier J, Miehe G, Leuschner C, Kluge J (2018) A first complete plot-based elevational assessment of richness, life forms and leaf traits of seed plants in the Southeast Himalayan Biodiversity Hotspot, North Myanmar. *Plant Ecology & Diversity* (*in review*).	Nowak P (40 %) **Khine PK (20 %)** Homeier J (10 %) Miehe G (5 %) Leuschner C (5 %) Kluge J (20 %)
Chapter 3	Khine PK, Fraser-Jenkins C, Lindsay S, Middleton D, Miehe G, Thomas P, Miehe G, Kluge J (2017) A contribution toward the knowledge of ferns and lycophytes from northern and northwestern Myanmar. *American Fern Journal* 107: 219-256. doi: 10.1640/0002-8444-107.4.219	**Khine PK (60 %)** Fraser-Jenkins C (10 %) Lindsay S (10 %) Middleton D (5 %) Miehe G (5 %) Thomas P (5 %) Kluge J (5 %)
Chapter 4	Khine PK, Lindsay S, Fraser-Jenkins C, Kluge J, Kyaw M, Hovenkamp P (2016) Selliguea kachinensis (Polypodiaceae), a new fern species of uncertain affinity from Northern Myanmar. *PhytoKeys* 25(62):73-81. doi: 10.3897/phytokeys.62.8101.	**Khine PK (40 %)** Lindsay S (9 %) Fraser-Jenkins C (5 %) Kluge J (5 %) Kyaw M (1 %) Hovenkamp P (40 %)
Chapter 5	Khine PK, Kluge J, Miehe G, Opgenoorth L (2018) Phylogenetic structure of fern assemblages along an elevational gradient in the southern Himalaya. (in preparation)	**Khine PK (50 %)** Kluge J (15 %) Miehe G (5 %) Opgenoorth L (30 %)
Chapter 6	Khine PK, Kluge J, Kessler M, Miehe G, Karger DN (2018) Elevational richness pattern of ferns and lycophytes within the context of the latitudinal diversity gradient in East and Southeast Asia: Climate tells just half the story. *Journal of Biogeography* (submitted)	**Khine PK (50 %)** Kluge J (20 %) Kessler M (5 %) Miehe G (5 %) Karger DN (20%)

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CHAPTER 1

General introduction

1 General introduction

1.1 Mountain biodiversity: state of the art

The elevational changes of plant life had been in the focus of biogeography since the first attempts to describe and to compare plant distribution patterns on a regional and worldwide scale. It has been recognized that species richness decrease with increasing latitude and with increasing altitude (e.g. Gentry 1988). Among the known patterns of unevenly distributed species richness, the most conspicuous pattern is the concentration of the greatest number of species in mountain areas: all mountains are richer in species that the surrounding lowlands. This is even the case in areas of highest richness of lowlands, in the equatorial lowland forests of Amazonia or New Guinea. The seminal maps of Barthlott et al (1996) for vascular plants and in Kreft et al (2010) for pteridophytes have conspicuously shown the high importance of especially tropical and subtropical mountains for global biodiversity.

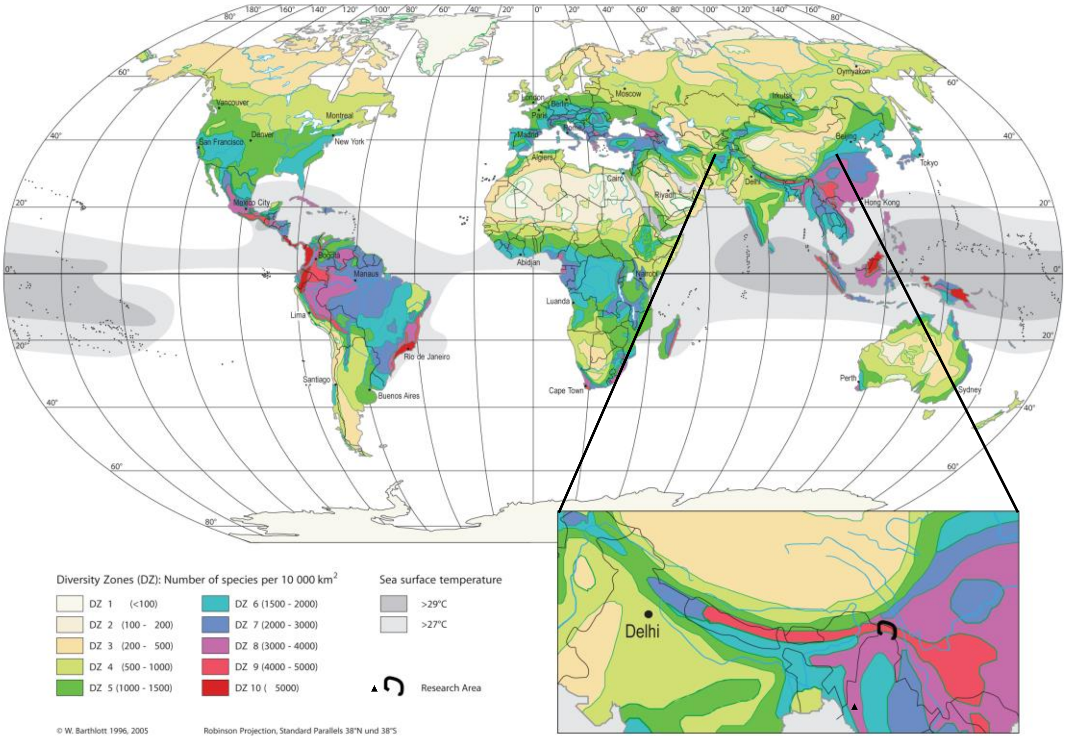
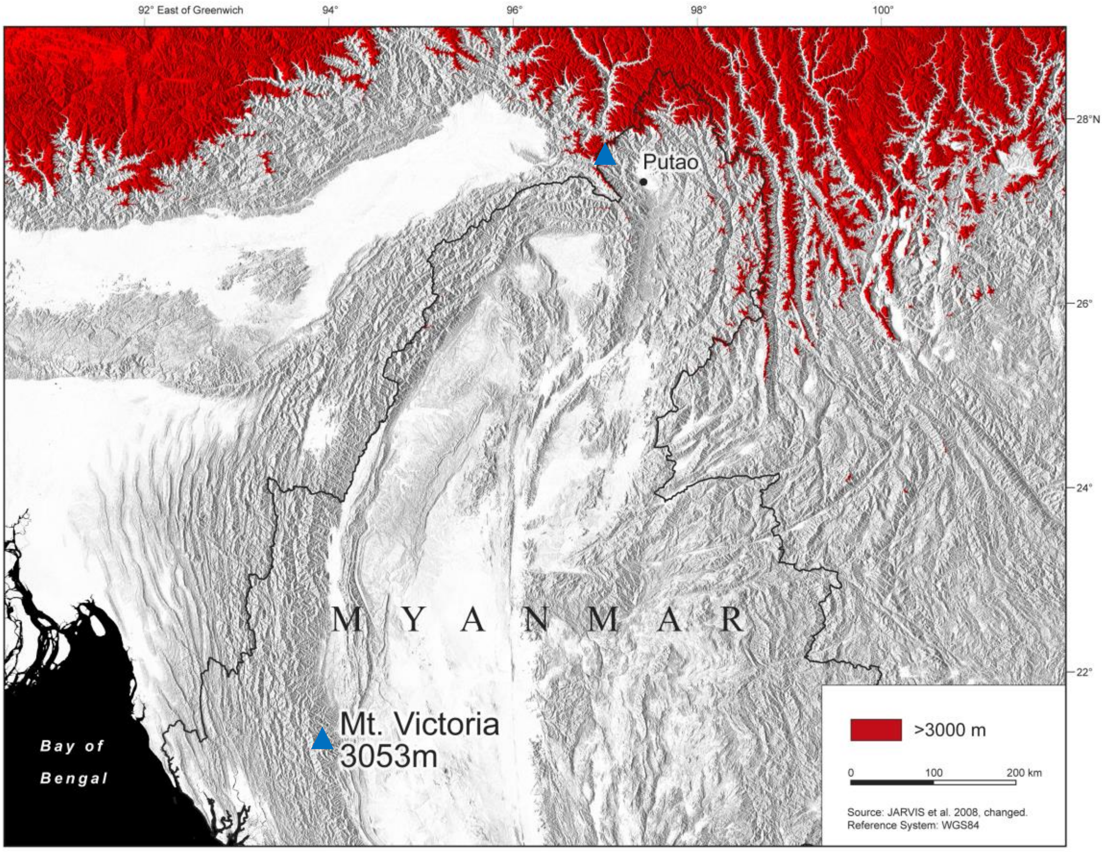


Figure 1-1 World map of vascular plant diversity (Barthlott et al 1996) and close up of DZ9: Himalaya Center and Yunnan Sub-centre.

A striking, yet rarely articulated contradiction is the coincidence of the greatest (modelled) biodiversity in the centres of greatest species diversity, commonly known as "Biodiversity Hotspots" (Myers et al 2000) or "Diversity Zone" on one hand and scarce knowledge of the distribution of species richness throughout those mountain regions, i.e. the altitudinal distribution in these centres of species richness on the other hand. It has to be simply admitted that we do not know the biodiversity structure along elevational gradients in total. This holds even true for the immensely rich tropical mountain areas of the humid Andes of South America (Bendix et al 2013), where only selected taxonomic groups, e.g. vascular plants (e.g. Sklenář et al 2008), trees (e.g. Tiede et al 2016), or plant life forms (e.g. trees Homeier et al 2010) had been recorded by their elevational distributions.

Following the global diversity map of Barthlott et al (1996), the only non-equatorial centre of high biodiversity stretches from Yunnan and Vietnam towards the central Himalaya of Nepal. In contrast to its southeastern part in China (Wen et al 2014) and its western margin in Nepal and Bhutan (Acharya et al 2011, Bhattarai et al 2004, Grau et al 2007, Grytnes & Vetaas 2002, Homeier et al 2017, Kluge et al 2017, Oommen & Shanker 2005, Vetaas & Grytnes 2002, Wang et al 2007), virtually nothing is known from its centre, stretching through northern Myanmar. Thus, in contrast to its global importance and its supposed richness in species, the mountains of northern Myanmar are still one of the last blank spots in mountain biodiversity research.



Source: JARVIS et al. 2008, changed.
Reference System: WGS84

Figure 1-2 Topography of Myanmar and elevation above 3000 m are displayed in red and study sites are marked with blue triangles.

Contrary to its presumably rich biological diversity and supra-regional importance, there is no thorough floristic assessment (Frodin 2001), except of the since long outdated Hooker's "Flora of British India" (1872 - 1897). First floristic surveys were conducted in the late19th and early 20th century by European botanists and foresters

(Fischer 1926, Hundley & Ko 1961, Kingdon-Ward 1945, Kurz 1877, Lace & Hundley 1987, Nath Nair 1960). Their collections were integrated by Kress et al (2003) into a plant list of Myanmar, including 11,800 taxa, yet without ferns and lycophytes. However, the knowledge of the upper montane forest and alpine flora in Northern Myanmar is yet indebted to the first botanical exploration of Frank Kingdon-Ward during 1926 and 1939. In contrast to the scarcity of data from the North, flora and fauna of the Natma Taung area (vulgo “Mt. Victoria”) is far better known since colonial times due to its better accessibility (Kingdon-Ward 1958). Recently teams from Japan and Korea have published results about flowering plants (e.g. Kang et al 2017, Tanaka 2005, Tanaka et al 2010a, Tanaka et al 2015), medicinal plants (e.g. Fujikawa et al 2009), orchids (e.g. Tanaka et al 2010b) and mosses (e.g. Tanaka 2003).

Ferns in general had been neglected by research, except the list of Dickason (1946) with 460 species. Since then the only reports for pteridophytes are Nwe (2009) for southeastern Myanmar with 68 species, of which 12 were new records, Nwe et al (2016) for Natma Taung with four new species and Thet (2003) for the Hkakaborazi National Park in the far north of Myanmar. His list is included in a management plant, contains 53 species of ferns and lycophytesof which 14 species new to Myanmar. Only these three additional surveys of several decades after Dickason’s list show that the fern flora in Myanmar is under-investigated.

1.2 The importance of elevational gradients and a systematic sampling design

The distribution of species richness and the factors responsible for richness patterns along elevational gradients are the main topics of recent biodiversity research (Körner 2007). Several attempts have been emerged to understand the species richness pattern along the geographic and climatic gradients. Climatic variables have been suggested as prominent drivers of species richness patterns, as especially formulated by the water-energy dynamic model (e.g. O'Brien 1998, 2006).

The elevational diversity patterns were long believed as monotonic declines toward the higher elevation (Gentry 1988, Stevens 1992, Yoda 1968) due to the underlying mechanism of climatic gradient from high to low temperatures. However, Rahbek (2005) showed that the majority of elevational gradients show hump-shaped richness patterns with highest richness somewhere in the middle of the gradient, depending on the specific ecological and climatic requirements of the plant or animal groups as well as their life forms (Krömer et al 2005). For example ferns are mainly present at humid elevations in and above the condensation layers of the cloud forest, thus despite different elevational peak positions between regions, the highest richness regularly occurred at temperature levels of 15–17°C. Higher temperatures were therefore presumed to lower the ambient humidity. However, trees show elevational peaks in lowland forests (Lieberman et al 1996) and palms mainly exhibit a linear decline with elevation (Bachman et al 2004).

In contrast to plot-based studies in the Andes (Kessler et al 2011) or the Kilimanjaro (Hemp 2002), the elevational richness patterns in the Himalaya and adjacent mountain ranges are based on interpolated regional occurrence data from local floras or plant lists (e.g. Enumeration of the Flowering Plants of Nepal) especially for vascular plant (Grau et al 2007, Kluge et al 2017, Oommen & Shanker 2005, Vetaas & Grytnes 2002), angiosperms (Grytnes & Vetaas 2002, Wang et al 2007), orchids (Acharya et al 2011), pteridophytes (Bhattarai et al 2004, Grau et al 2007) and bryophytes (Grau et al 2007) and the environmental factors that influence these patterns (Mao et al 2013). The value of these studies is hampered by the fact that interpolation includes species which in fact may not be present at sites between documented occurrences, thus inflating alpha diversity especially at centers of gradients. So the need of local data from plot-based sampling has been demanded to allow direct comparisons between regions and studies, and to justify model building. The very few plot-based studies from Nepal however are of limited value, because their elevational gradient is short (Bhatta et al 2018) and in the other case records plots of a heavily used mountain farming area (Bhattarai & Vetaas 2003).

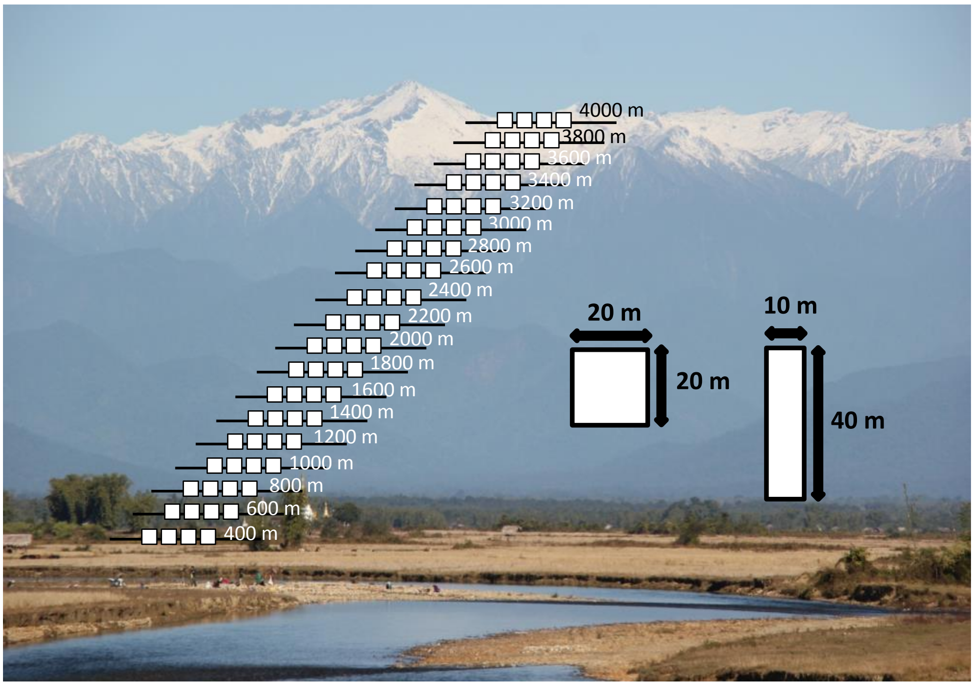


Figure 1-3 Systematic sampling design of elevational gradient by 200 m steps and four plots in each elevation. A white square represents the major plot design and white rectangle design is applied in an area with special relief situation.

As the elevational diversity of plants is in the focus of this project, it is necessary to give an outline specifically about studies dealing with the elevational diversity patterns. We used a plot size of 400 m^2, which is small enough to keep environmental factors and forest structure more or less homogeneous within the plots, and is the minimum area required for representative fern and lycophyte surveys in humid tropical forests (Kessler & Bach 1999). The plots were usually square

(20 m x 20 m) or rectangular (10 m x 40 m) in special relief situations. The minimum distance between the plots was kept to at least 20 m to ensure each plot is independent of the others. The plots were placed at every 200 m of elevation, with four plots established at every elevational level where in areas that showed the least possible anthropogenic disturbance (Figure 1-3). The vegetation sampling was conducted in zonal forest, therefore extraordinarily wet sites near running water in deep valleys, and frequently disturbed steep slopes and ridges were not selected to avoid unrepresentative contributions of azonal vegetation.

1.3 Project introduction, objectives, hypothesis, and outline of the study

This Ph.D. study is a part of two projects supported through funds of the German Research Council (DFG) and the German Academic Exchange Service (DAAD) carried out between 2012 and 2018 under the principle investigators: Prof. Dr. Georg Miehe, Dr. Jürgen Kluge, Prof. Dr. Thomas Nauss, and Dr. Lars Opgenoorth (all from the University of Marburg). An international collaborative project team undertook the first plot-based inventory of pteridophytes, mosses, and vascular plant species recording their elevational distribution in northern and northwestern Myanmar in 2012, 2013 and 2014 in three mountain areas (Natma Taung ("Mt. Victoria"), Hponyinrazi and Hponkanrazi).

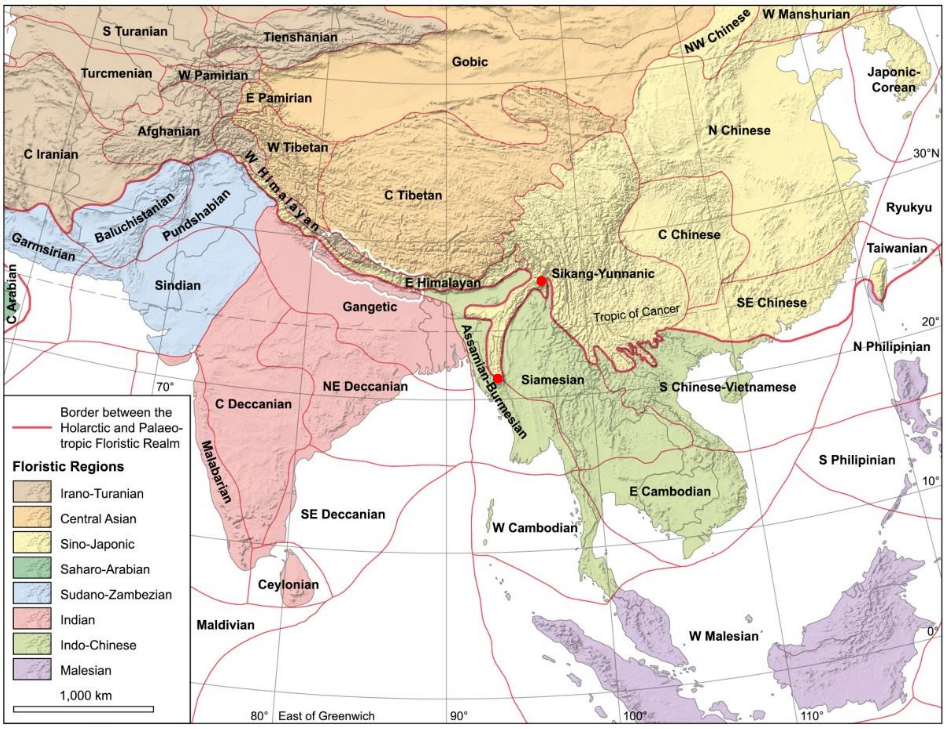


Figure 1-4 Floristic regions of the South, East and Southeast Asia (Welk 2015). The research areas of Myanmar are marked in red dots.

Here, the southeastern periphery of the Himalayan arc disintegrates into narrow mountain ranges such as Hponyinrazi (4,057 m, 27°56'N, 96°96'E) and Hponkanrazi (3603 m, 27°50'N, 96°93'E), and finally into island-like mountain outpost in

Myanmar like Natma Taung (3053 m, 27°50'N, 96°93'E). Regardless of the dataset used, Northern Myanmar with those three mountain areas is (1) supposed to be part of a center of worldwide unique diversity richness "Himalaya-Yunnan (sub) Center of Diversity" after (Barthlott et al 1996, Zhao et al 2016)", Indo-Burma hotspot" (Myers et al 2000) (2) lies at the junction of two floristic regions, the Sino-Japonic and the Indo-Chinese (Welk 2015) and hosts the least undisturbed forest areas in whole Himalaya. Moreover its mountains connect the world's greatest highlands, the Tibetan Plateau, with longitudinal river gorges and sky islands with the lowland forests of Southeast Asia. This unique set was recognized as of outstanding universal value, allowing to propose the area as UNESCO World Heritage Site.

The **overarching research goals** of the two DFG projects were to record and analyze (1) species richness and assembly patterns along elevational gradients at the interface of the Palaeotropic and Holarctic floristic realm, leading to (2) the detection of distribution patterns which may mirror the impact of Quaternary climate dynamics, allowing finally (3) the reconstruction of Quaternary climates.

Within this project horizon, the main task of this Ph.D. study was the assessment of the fern diversity along elevational gradients and their environmental envelope. Additionally, it was my task (1) to fully organize the extensive field campaigns (in total 33 weeks) to these rather remote areas of Myanmar inclusive hiring and guiding about 45 porters and 10 local scientific assistants from the countries organizations, (2) to establish nine climate stations along two transects between 400 and 3200 m, (3) to prepare the expedition collections of a total of 3,978 pteridophyte, 11,500 angiosperm and 160 bryophyte specimens for export (in total 11 weeks), and (4) to organize all sorts of permits and cooperation documents with the partner institutions in Myanmar.

Pteridophytes have been selected for my Ph.D. project, because they are the second largest group of vascular plants and make up a significant part of the non-tree vegetation at almost all elevations; moreover, they occupy a wide range of life forms from terrestrial to epiphytic. They are proposed as indicators for macroclimate conditions because of their preference of moist and shady habitats as a result of their low water use efficiency (Brodribb & McAdam 2011, Brodribb et al 2009). In contrast to angiosperms, taxonomic knowledge and opportunity for ferns specimen being named is relatively good due to the availability of regional fern experts for the Himalaya and Southeast Asia. In order to achieve a broader view on pteridophytes distribution patterns, additional data from New Guinea, Philippines, Taiwan and Japan, which were kindly provided by another DFG project of Dr. Jürgen Kluge and colleagues from the Swiss working group around Dr. Michael Kessler were used in Chapter 5 and 6.

Specifically, the following objectives have been defined to assess the flora and diversity of ferns in an ecological and phylogenetical context. According to the nature of this project and the study area where next to nothing is known about, the first project goal was to lay foundations about the flora of the area. This is selfexplaining not hypothesis-driven. In a second step, three work packages (WP) with underlying hypotheses have been implemented:

(1) Contribution to the knowledge of current pteridophytic flora of Myanmar
(2) Assessment of species richness patterns of angiosperms and ferns along the elevational and climatic gradients (→ WP1)
(3) Evaluation of phylogenetic and trait variation regarding to factors that control the diversity over space and time (→ WP2)
(4) Development of a richness model based on climatic variables and application of the model in a broader spatial scale (→ WP3)

The first objective is crucial to accomplish, unless a hypothesis-driven objective, for the first step filling the flora knowledge gap of the country.

WP 1 Assessment of species richness patterns of angiosperms and ferns along the elevational and climatic gradients

Central question: Two major elevational richness patterns have been discussed in section (1.2) and Himalayan studies presented hump-shaped patterns. However these are results of interpolation causing two major issues:

- It disrupts the crucial control of sampling area and intensity as species are added where they were in fact not present.
- Gaps are filled only between lower and upper recorded range limits, assuming no individuals of a species have been missed beyond the observed range limits, but that individuals have been missed at sampling points within the range limits.

The plot based sampling design overcomes those obstacles, however there are existing results only for ferns from South and Central America showing the hump-shaped patterns. Climatic variables have been suggested as prominent drivers of richness patterns, especially energy availability driven by temperature and water availability. However, the richness patterns and influence factors of angiosperms and ferns in the Himalaya in local scale are yet unknown.

Hypothesis: (1) Angiosperm species richness patterns in Myanmar differ from other gradients within the Himalaya although ferns present hump shaped pattern as in other tropical mountains. (2) Water- energy related climate variable influence the local species richness and drives the diversity pattern.

Method of evaluation: Ferns were sampled in 132 plots from Natma Taung, Hponyinrazi and Hponkanrazi. Angiosperm diversity was evaluated at present only for the Hponyinrazi and Hponkanrazi area and is based on morphospecies only due to taxanomic problems and an unexpected richness of the flora. Seed plant species were recorded on 80 plots between 400 and 4000 m with preferably northern exposure. However the plot size of 400 m² remained and detail sampling design were mentioned in section (1.2). Multiple regression models were used to identify the climatic and topographic variables with highest predictive power for the species richness (different life forms and leaf traits for angiosperms) using generalized linear model.

WP 2 Evaluation of phylogenetic and trait variation regarding to factors that control the diversity over space and time

Central question: Neutral stochastic and niche deterministic are major processes that structure the community. The trophically similar species are demographically identical, therefore under the identical ecological condition and in the same habitat range, closely related species with the same food habits does not likely occur. (1) When the competitive interaction is stronger, co-occurring species are phylogenetically less related than expected by chance, (2) when the species have been influenced more by convergence and adaptation in an assemblage, the local filtering creates the species set more similar than expected by chance. Otherwise the competition interaction and environmental filtering neutralize the community composition. The phylogenetic diversity pattern of seed plants, although the patterns differ with the regions, reflects more to deterministic processes. However, the phylogenetic and trait diversity pattern for pteridophytes has not been well observed, only apart from the Neotropical fern patterns by Kluge and Kessler (2011b).

Hypothesis: (1) Unlike in angiosperms, pteridophytes with large populations reflect more to the stochastic events that give the priority to the random genetic heredity due to the absence of spatial barriers for spores and their reproductive behavior. (2) Traits are dropped off from the assemblage due to the extreme environmental conditions.

Method of evaluation: We used six empirical datasets in total from Japan (Hokkaido, Nishikoma and Kyushu), Taiwan, and Myanmar (Hponyinrazi+Hponkanrazi, Natma Taung). The quantitative pattern of species occurrences and individual numbers of ferns within 315 plots along three tropical and three temperate elevational gradients were tested for phylogenetic structure and ecological sorting of trait patterns. Mean pairwise distances of species based on phylogenetic and trait properties were compared with two different sets of null assemblages, one maintaining species frequency distributions (constrained) with “independent swamp” algorithm of 3000 iterations and one not (unconstrained).

WP 3 Development of a richness model based on climatic variables and application of the model in a broader spatial scale

Central question: Several attempts have been emerged assessing the species richness pattern and relationship between species richness and climate variables, however the model were fitted for the certain locality, as different locality includes the differ set of environmental variables, therefore coefficient values for a local gradient were not applicable to predict the species richness of different localities. Combining both, the elevational and latitudinal richness trend, suggests a strong influence of a temperature regime on the richness of ferns and lycophytes in general, and would support the 'water-energy-dynamics' model (e.g., O'Brien 1998, 2006). Setting this main study gradient in context to other up to now not yet published gradient studies from East and Southeast Asia could show that climatic variables of energy input, for instance temperature and humidity are the decisive factors in predicting species richness. If these temperature and humidity related macroclimatic factors are important for fern species richness, they should be generally applicable for a broader spatial scale.

Hypothesis: (1) A congruence of species richness and temperature isoclines with latitude would predict a decrease of total species richness of each gradient and a shift of the mid-elevation richness peak towards lower elevations, with a gradually turning from complex, unimodal patterns to simple, linear patterns (as hypothetically depicted in Figure 1-5).

(2) The parameters of the climate-richness relationship derived from a subset of elevational gradients should be able to describe the climate-richness relationship at any point along the latitudinal gradient.

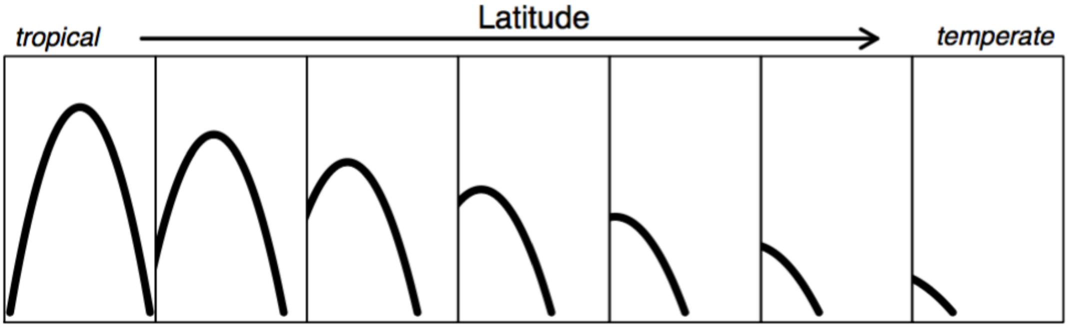


Figure 1-5 Hypothetical curve of elevational richness pattern in the context of latitudinal gradient (Khine et al 2018; submitted).

Method of evaluation: We use eight elevation gradients from East and Southeast Asia between 4°S to 43.3 °N to assess richness patterns of ferns and lycophytes in relation to climatic factors. Ferns and lycophytes were recorded in 480 plots of 400 m2 in total. We related macroclimatic factors to local fern species richness using generalized linear models (GLM). Model evaluation was based on leave-one-gradient-out cross-validation (LOOCV) excluding up to seven gradients and tested the predictive power of each model using Spearman's rank correlation. We tested the predictive power of macroclimatic variables by a leave-one-variable-out cross validation. We assigned our result into broader spatial scale and displayed the predicted models spatially stacking respective variable layers and model parameters.

Model residuals were related to two available local (plot scale) factors, terrain inclination, and terrain heterogeneity using simple linear regression.

The structure shown in Figure 1-6 has been applied to fulfill the aim of this study.

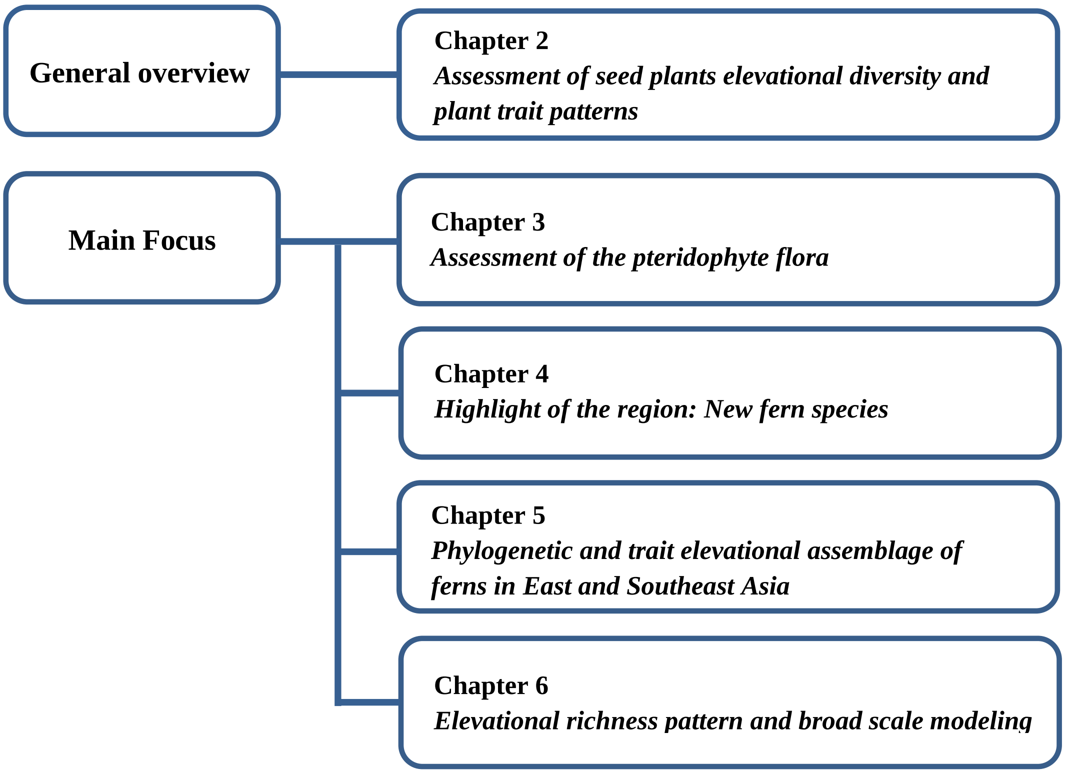


Figure 1-6 The outline of this PhD project; Chapter 2 focus on angiosperms and Chapter 3, 4, 5, and 6 are dealing with pteridophytes.

The **general overview** about plot based vegetation assemblages along the major elevational gradient in Northern Myanmar including all sampled and recorded seed plant species is based on an ambitious Master thesis by Pauline Nowak (→Chapter 2). Since the heavy load of about 11,670 sampled specimens is far from being determined, this study rests on morphotype assessment (traits) and lifeforms. Since these traits and lifeforms occupy different realms within the vegetation assemblages dependent on their specific biological requirements, compositions of plot vegetation is supposed to markedly change with elevation and to show strong relationships to climatic variables.

Chapters 3 to 6 are the main focus of the PhD study on pteridophytes. Sampling sites are located in Natma Taung, Hponyinrazi and Hponkanrazi and data source for broad scale analysis are mentioned in section (1.3).

The first step to close the above mentioned knowledge gap of fern flora and vegetation in one of the pteridologically least known parts of the world was to compile the most comprehensive species list of ferns for North Myanmar and to provide additional data such as elevational range, rareness and substrate preferences (→ Chapter 3). This enumeration is intended as a first step towards a Flora of Myanmar, which is highly needed as a database for further ecological research and nature conservation. As mentioned in general introduction, Hooker's 19th century "Flora of British India" is out-of-date and this recent insight into the pteridophyte diversity is provided as a valuable contribution not only to Myanmar but also to Asian ferns and lycophytes.

As a first result, one sampled species was new to science and the description of this species is presented (→ Chapter 4).

To set fern assemblages not only in a simple taxon richness context, we assessed the phylogenetic and trait relationships between species and set results into an environmental context. Although fully resolved cladograms are rare, the taxonomy based phylogenetic approach is applicable to bridge between ecology and evolution. Variations of phylogenetic and trait distance in the phenotypic space within a community may shed light on processes, whether these assemblages are a result of niche differentiation or environmental filtering (→ Chapter 5).

The relationships between species richness and macroecological patterns as one the most interesting questions in biogeography was finally addressed in Chapter 6. However, in the analyses of the respective patterns from Myanmar, I did not want to simply add another fern elevational gradient study to what we know mainly from Neotropical regions, although this would have been rather new for the Himalaya. Rather, the data from Myanmar were set into a broader spatial scale with a focus on the quality of richness model performance. In total eight elevation gradients along a latitudinal gradient from East and Southeast Asia between 4°S and 43.3°N have been combined for a general model precision testing. Generalized linear models have been applied for assessing richness–macroclimate relationships. In order to predict the species richness for other regions in East Asia, we applied leave one out cross validation analyses (LOOCV) to test the general predictability of a model and uncovering the most influential macroecological variables for species richness distributions at a broad spatial scale (→ Chapter 6).

CHAPTER 2

Assessment of seed plants elevational diversity and plant trait patterns

Pauline Nowak submitted to *plant ecology and diversity*

with **Phyo Kay Khine**, Jürgen Homeier, Georg Miehe, Christoph Leuschner and Jürgen Kluge

A first plot-based complete elevational assessment of richness, life forms and leaf traits of seed plants in the Southeast Himalayan Biodiversity Hotspot, North Myanmar

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Abstract Elevational species richness often shows hump-shaped patterns, but data from the Himalayas are rare. We present the first study on plot-based data to detect the elevational patterns of plant life forms and tree leaf traits, and their relation to environmental factors in northern Myanmar. All seed plant species were recorded on 80 plots (400 m²) between 400-4000 m. Multiple glm-regression models were used to identify the climatic and topographic variables with highest predictive power for the species richness of different life forms and leaf traits. Species richness shows a linear decline towards higher elevations except grasses (increase) and epiphytes (hump). Regression models show that temperature and precipitation play a key role for explaining the species richness patterns of all considered life forms. Tree leaf size reduces with elevation, the proportion of species with simple leaves and leaves with drip tips decreases, while the proportion of toothed leaves increases with elevation.Our data only partly confirm some widely held assumptions about elevational species richness and leaf traits in mountains. Although comparable data from other mountain are rare, it can be supposed that the mountain forests of northern Myanmar belong to the species richest mountain forests.

Keywords species richness, seed plants, Myanmar, life forms, leaf traits, climatic drivers

2 Assessment of seed plants elevational diversity and plant trait patterns

2.1 Introduction

The distribution of species richness and the factors responsible for richness patterns along elevational gradients are main topics of recent biodiversity research (Körner 2007). It was assumed for a long time that species richness is decreasing towards high elevations just as it is decreasing towards high latitudes (Gentry 1988, Stevens 1992, Yoda 1968). Rahbek (1995) revealed that richness often shows unimodal patterns along elevational gradients with highest richness at mid-elevations (Grytnes & McCain 2007), with about 50 % of the studies on elevational gradients showing hump-shaped richness patterns, whereas 25 % showed a monotonic decrease (Rahbek 2005). Among the possible explanations which address spatial configurations such as the "mid-domain"-effect (Colwell & Lees 2000, Colwell et al 2004), species-area relationships (Rosenzweig 1995), landscape heterogeneity (Ricklefs 1977), and dispersal constraints such as "source-sink"-effects (Grytnes 2003, Kessler 2009, Lomolino 2001), the most prominent drivers are assumed to be environmental site characteristics, such as climate variables, and within these predominately energy availability driven by temperature and humidity (Currie et al 2004, Hawkins et al 2003, Kessler et al 2011), or soil properties (Homeier et al 2010, Unger et al 2010). Following these argumentations, the elevational peak of richness should differ between groups of organisms with respect to their individual biological constitutions and occupied niches. For example, palms mainly exhibit a linear decline with elevation (Bachman et al 2004), trees show elevational peaks in lowland forests (Lieberman et al 1996), while ferns are mainly present at humid elevations in and above the condensation layers. Similar, the epiphytic life-form, including groups like e.g., ferns, orchids, aroids, ericads, and peperomiads, as an important component of tropical mountain forests (Gentry & Dodson 1987, Gradstein 2008, Nieder et al 1999) depend, due to their often exposed positions on host trees, on permanently moist environments and the lack of frosts, and are therefore found to be most species-rich at mid elevations (Cardelús et al 2006, Gentry & Dodson 1987, Hietz & Hietz - Seifert 1995, Ibisch et al 1996, Kessler 2001, Krömer 2003, Krömer et al 2005, Küper et al 2004, Muñoz & Küper 2001, Sugden & Robins 1979, Wolf 1994, Wolf & Alejandro 2003).

Beyond the level of plant species richness, morphological traits like e.g., leaf size, leaf shape and thickness are directly coupled to environmental conditions (Peppe et al 2011) and thus studying the composition of plant life forms and traits within homogenous habitats along a elevational gradients may help to reveal specific adaptations of the different plant groups in response to environmental change along the slope.

A large body of literature dealing with species richness patterns in the Himalaya from Nepal (Acharya et al 2011, Baniya et al 2010, Bhattarai et al 2004, Grau et al 2007, Oommen & Shanker 2005, Vetaas & Grytnes 2002) and Bhutan (Kluge et al 2017) does exist. These studies have analyzed species richness patterns by interpolating elevational ranges from published floras. However, interpolation faces two major problems. (1) It disrupts the crucial control of sampling area and intensity as species are added where they were in fact not present. (2) Gaps are filled only between lower and upper recorded range limits, which assumes that no individuals of a species have been missed beyond the observed range limits, but that individuals have been missed at sampling points within the range limits. A simulation study on the Himalayan elevational gradient in Nepal (Grytnes & Vetaas 2002) already showed that interpolation may underestimate species numbers at the lower and upper ends of the gradient due to the assumption that species are present in all elevations between the extremes at which they were observed. Thus the species richness may be overestimated at mid-altitudes. To explore the richness patterns of real assemblages along elevation gradients it is necessary to use plot-based data.

This study reports the composition of life forms and leaf characteristics within a full plot-based inventory of seed plants along an extensive elevational gradient between 400m and 4200m at the southern declivities of the Eastern Himalaya in Northern Myanmar. Despite its supra-regional importance, situated at the transition between two floristic realms, Palaeotropis and Holarctis, and at the junction of the two biodiversity hotspots of Indo-Burma and Eastern Himalaya (Barthlott et al 1996, Myers et al 2000), Northern Myanmar is still one of the last widely unknown areas in mountain biodiversity research. The reports of the early naturalists and plant hunters (Handel-Mazzetti 1927, Kingdon-Ward 1930, Kingdon-Ward 1945, Kingdon-Ward 1957) summarized by Schweinfurth (1957) are still largely the only vegetation records of the area. Specifically we address the following research questions:

(1) What is the elevational trend of seed plant richness and life forms?
(2) What are the elevational trends of major tree leaf traits?
(3) What are the most important environmental variables explaining these species richness and tree leaf trait patterns?

2.2 Materials and Methods

2.2.1 Study area

The study area is located at the northwest border of Myanmar to India located between the Central Himalaya in the West and mountains of Yunnan in the East (Figure 2-1). Study plots were established between 400 m and 4000 m in regular intervals of 200 m. The ridge to Hponyinrazi (4,057 m, 27°56'N, 96°96'E), was assessed in October to December 2013, covering most of the elevational bands. Due to some inadequate areas for vegetation sampling in this study area, the remaining elevational bands were investigated at the neighboring mountain ridge to Hponkanrazi (3608 m, 27°30'N, 96°56'E), in October to November 2014 (Figure 2-1b).

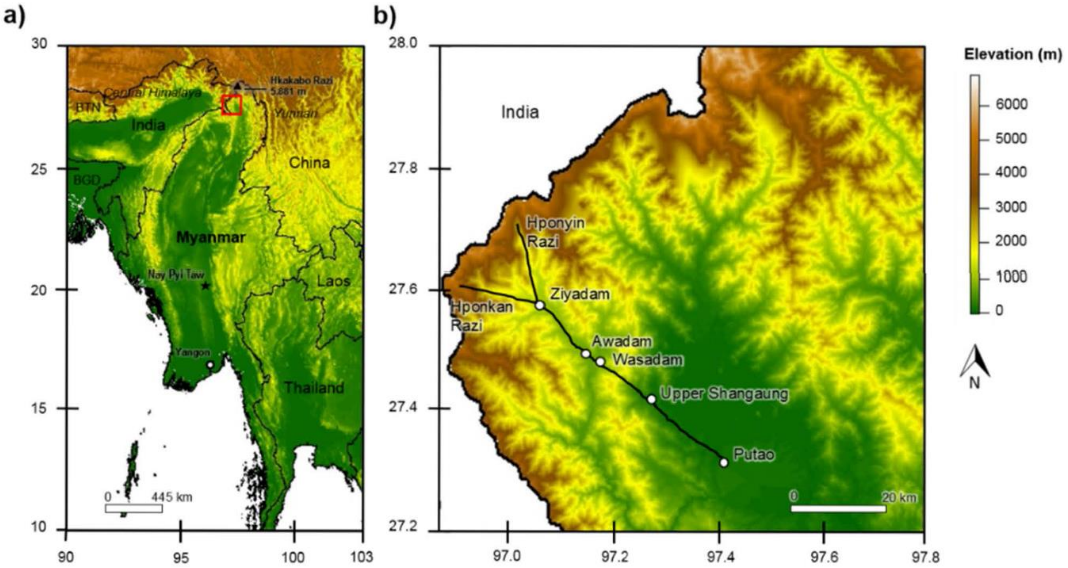

Figure 2-1 Study area in North Myanmar and its surrounding countries shown with topography. The red box in a) represents the position of the study area. b) The study area in detail and the elevational gradient split into two mountain ridges (Hponyin Razi and Hponkan Razi)

The transect stretches from the intramontane basin of Putao at 400 m a.s.l. with *Castanopsis*-Dipterocarp forest, containing mainly lowland tropical evergreen rainforest taxa, up to the treeline ecotone with Himalayan bamboo thickets and scattered *Abies georgei* at 3600 m (Hponkanrazi) and alpine *Rhododendron* dwarf scrub at 4000 m (Hponyinrazi) (see vegetation images in Appendix F 1, Appendix F 2, Appendix F 3, Appendix F 4). In between, subtropical mountain forest at 700–1500 m can be found, followed by the warm temperate rain forest at 1500–2000 m, temperate forest at 2000–2500 m, *Quercus*-*Magnolia* forest at 2500–3000 m and silver fir forest at 3000–3700 m (Kingdon-Ward 1945, Kurz 1877, Stamp 1924). The forests above 1000 m are mostly undisturbed and only weakly used for the collection of medicinal plants or hunting. The area is located between two floristic realms, the Holarctis and Palaeotropis, and the Indo-Chinese Floristic Region of the Palaeotropical Floristic Realm merges into the Sino-Japonic Floristic Region of the Holarctic Floristic Realm (Welk 2015). Myanmar is influenced by the Asian summer monsoon appearing from May to October (Sein et al 2015) with a long period of seasonal drought. The rapid rise of temperature starts right after the monsoon period, especially in the central basins, while other parts of the country receive rainfall throughout the year, mostly in the lowlands along coastlines and at high elevations. The mountains in North Myanmar are orographic barriers for the monsoon and obtain the highest rainfall between June and September. The slopes of Hponyinrazi and Hponkanrazi possibly belong to the wettest slopes of the Himalayan arc. Both areas have cold-air ponding effects with night fog in their intramontane basins at the foot of the slopes.

2.2.2 Vegetation sampling

Vegetation plots were installed every 200 m along the elevational gradient ranging between 400 and 4000 m. At each elevational band, four plots of 20 x 20 m with a minimum distance of at least 50 m between the plots were chosen, at 1000 m and 4000 m two additional plots were recorded resulting in 80 plots in total. The plot locations were selected in virtually untouched or old growth forests with as low anthropogenic disturbances as possible, like single tree cutting or small-scale understorey grazing. These kinds of slight disturbances may have been present at lower elevations, because up to 1200 m the region is, however very sparsely, populated, and even in larger distances from settlements, timber collection or occasional forest grazing is possible.

Within each plot, vegetation structure and vegetation cover of tree, shrub and herb layers as well as stem bryophyte cover were noted. Furthermore, all seed plant species were recorded including their life form.

Samples of all seed plants were collected, including epiphytes in tree crowns up to 45 m by trained local tree climbers (Appendix F 5). All samples were pressed and preserved with ethanol, except of specimens with flowers, which were just pressed and sun dried. Samples were sent to the University of Marburg for further evaluation. The resulting collection counts more than 11,670 seed plant specimens in total.

2.2.3 Life forms and tree leaf trait data

All plant specimens were sorted to life forms and plant family or genus as far as possible. All species per plot were recorded in a database with their respective life form (tree, shrub, herb, grass, climber, epiphyte, bamboo and palm). Furthermore, all specimens were photo-documented for further analyses of morphological leaf traits, especially leaf size and leaf shape. This study is dealing with leaf traits of tree specimens, in total 3,136 tree specimens were evaluated for four different leaf traits. Based on Raunkiaer (1934) and Vareschi (1980), we chose leaf size (four classes: megalophyll (> 1500 cm²), macrophyll (180-1500 cm²), mesophyll (20-180 cm²), microphyll (2-20 cm²)), leaf shape (simple / compound), leaf margin (entire / not entire) and leaf tip (drip tip present / not present). Examples of the photo-documentation of tree leaves can be seen in Appendix (Appendix F 7, Appendix F 8, Appendix F 9, Appendix F 10, Appendix F 11, Appendix F 12).

2.2.4 Environmental and spatial data

To assess climate relationships with elevational trends of life forms and leaf traits, we used a high-resolution (30 arc seconds) climate data set (CHELSA), performed by Karger et al (2017). Since species richness is stated to depend on climatic factors related to energy and humidity, we used mean annual temperature (TEMP) and mean annual precipitation (PREC) as predictor variables as well as temperature seasonality (TEMPs) and precipitation seasonality (PRECs). Average air humidity levels are notoriously difficult to measure, so we used the cover of bryophytes (BRYO) within the tree canopies as a proxy (Karger et al 2012). All other possible climate variables, especially from the CHELSA dataset, were restricted from analyses because of multi-collinearity between the variables (Spearman’s rank correlation R>0.6, p<0.001).

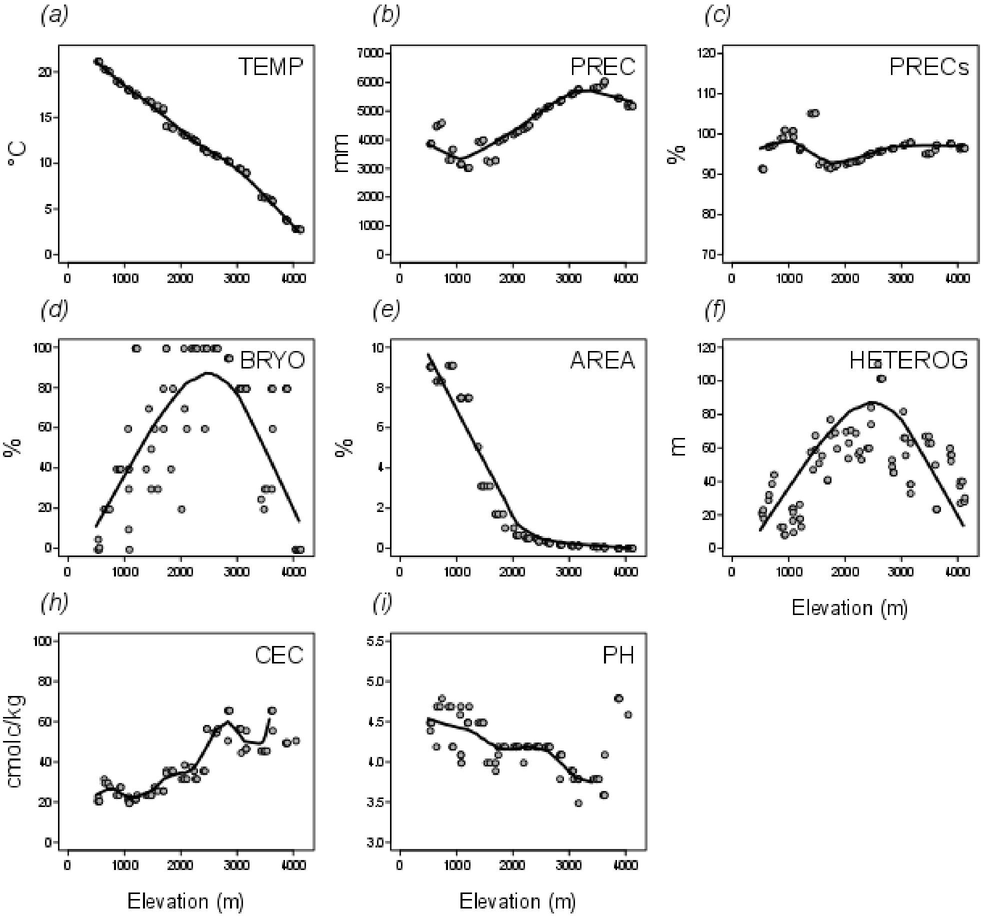

Figure 2-2 Elevational trend of climatic, topographic and soil variables along the gradient in North Myanmar. (a) TEMP = Mean annual temperature [°C]; (b) PREC = Annual precipitation [mm]; (c) PRECs = Seasonality of precipitation (Coefficient of variation) [%]; (d) BRYO = Cover of bryophytes [%]; (e); AREA = percentage of land cover with elevational band; (f) HETEROG = Elevational heterogeneity [m]; (h) cation exchange capacity CEC [cmolc/kg]; (i) Soil pH (KCl). Climatic and topographic data from or derived from Karger et al (2017), data on soil properties from *Soils Grids* (https://www.soilgrids.org, date of download: October 25, 2017). Trend lines were set with distance weighted least square smoothing using the function *lowess* in *R*.

To account for spatial variables hypothesized to influence patterns of species richness, we included the area and landscape heterogeneity in our analyses. The area of elevational bands was calculated for the whole country with data obtained from Jarvis et al (Jarvis et al 2008) (AREA) at a resolution of 90 x 90m, and derived from these data as well the topographic heterogeneity (standard deviation of elevations of all 25 surrounding cells of a 5 x 5 grid) as a proxy for landscape heterogeneity

(HETEROG). Since AREA was strongly related to temperature ($R=0.85$, $p<0.001$), only HETEROG remained as spatial variable in the model.

Among soil variables, we chose the cation exchange capacity (CEC) and soil pH in KCl (PH) at a depth of 10 cm, derived from the public databank *Soils Grids* (https://www.soilgrids.org, date of download: October 25, 2017).

The elevational trends of all variables are shown in Figure 2-2.

2.2.5 Data analysis

In order to examine the relationships between species richness patterns and environmental variables, simple and multiple regression models including all explanatory variables were performed. Since the response variables (different measures of species richness) are count data (i.e., integers: *[0, 1, 2, ..., n]*), which neither have negative values nor constant variances, the errors are not normally distributed. To deal with this issue, we run generalized linear models (*glm*) with a *poisson*-error distribution. In contrast to linear models, which estimate the goodness of model fit by the proportion of explained variances, the goodness of the *glm* model fit is the amount of *deviance* accounted for (D^2; Guisan & Zimmermann 2000). The significance of *glm*s was estimated with ANOVA against the NULL-model (*response~1*).

The availability of energy in an ecosystem is hypothesized to be one of the major drivers of species richness; it shows complex relationships of temperature and precipitation (called *'water-energy-dynamics'* by O'Brien (1998, 2006)). We added the interaction of both variables to the global model (species richness ~ TEMP + PREC + TEMP:PREC + PRECs + BRYO + HETEROG+CEC+PH). The best (final) models were obtained by eliminating the least significant term from the global model (backward elimination) until all model variables were significant and the AIC (Akaike’s information criterion, Turkheimer et al 2003) reached the lowest value. In order to allow direct comparisons of model coefficients, we standardized all predictor variables to *[0, 1]* prior to analyses, resulting in *beta*-coefficients, whereby higher *beta*-coefficients within the final model indicate higher influence of the respective variable within the model.

For the analysis of leaf traits, mean leaf size per plot was calculated by averaging class midpoints across all tree species within a plot. Elevational trends of leaf morphology (shape, margin, drip tip) were calculated as percentages of tree species within a plot, which showed the respective leaf trait.

All analyses were carried out with *R* (Version 3.4.1), standardizing data was performed with package *vegan* (Oksanen et al 2017).

2.3 Results

2.3.1 Elevational species richness pattern

The species richness pattern along the elevational gradient showed a linear decline with highest values between 400 and 600 m, and the number of plant species per 400 m^2 plot ranged between about 350 at low elevations and 25 species at high elevations (Figure 2-3a).

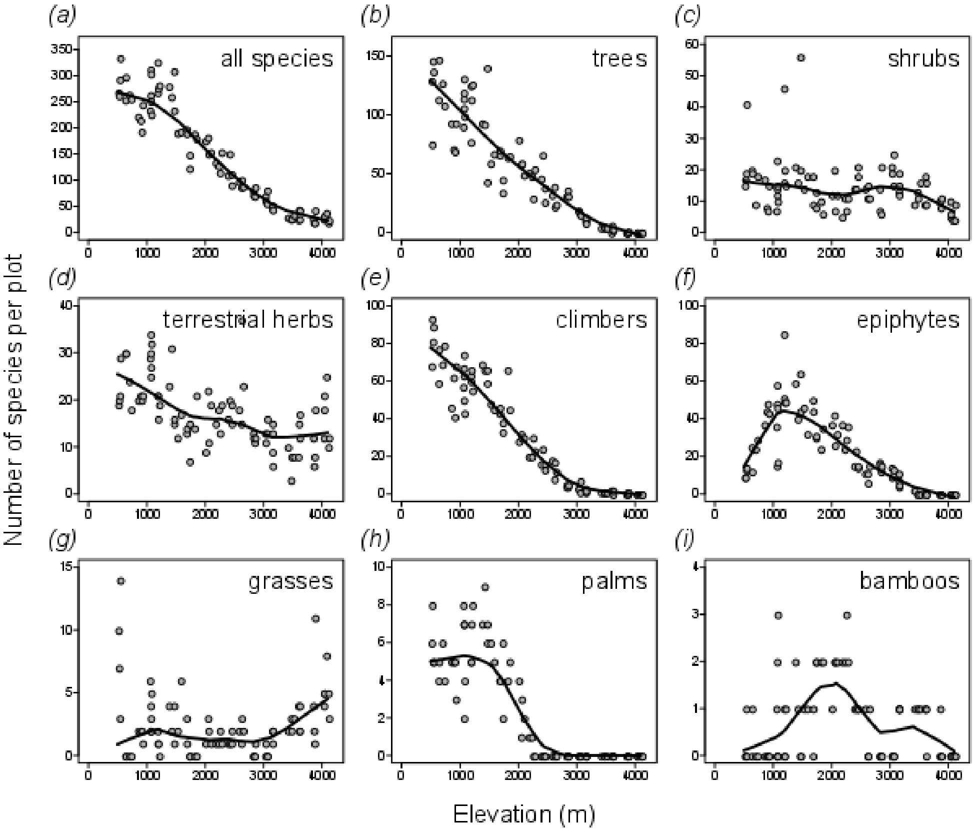

Figure 2-3 Elevational trend of the species number per plot (dots) of different life forms along the gradient in North Myanmar. *(a) all* species, *(b)* trees, *(c)* shrubs, *(d)* herbs, *(e)* climbers (plants rooting in the ground soil as distinction to epiphytes), *(f)* epiphytes (plants rooting on host as distinction to climbers), *(g)* grasses, *(h)* palms, and *(i)* bamboo. Trend lines were set with distance-weighted least square smoothing using the function *lowess* in *R*.

Species richness of trees and climbers, the most species-rich life forms, followed the same pattern (Figure 2-3b, e) and showed richness values of up to 150 and 90 species per 400 m^2, respectively, in lowland plots. Both life forms occurred up to 3600 m. Shrubs, herbs, grasses were present along the entire elevational gradient from 400 to 4000 m (Figure 2-4c, d, g). The richness of shrubs and herbs decreased slightly towards high elevations reaching species numbers of five to more than 50 (for shrubs) and two to 35 (for herbs). Palms occurred up to 2200 m and their species numbers showed a lowland plateau with an abrupt decline at about mid elevations (Figure 2-3h). The elevational pattern of grass diversity is quite different (Figure

2-3g): Their number of species increases with elevation, especially from 3000 m upwards, with the exception of some species-rich plots in the lowlands. Bamboo species did not show a clear pattern (Figure 2-3). The number of species ranged between zero and three species, with occurrence along the whole gradient and a slight hump at about mid elevations.

Unlike the other life forms, vascular epiphyte richness showed a clear hump-shaped pattern along the gradient (Figure 2-3f). The richness of epiphyte species peaked between 1200 m and 1400 m with almost 90 species per plot. It declined to zero close to the alpine tree line at 3600 m.

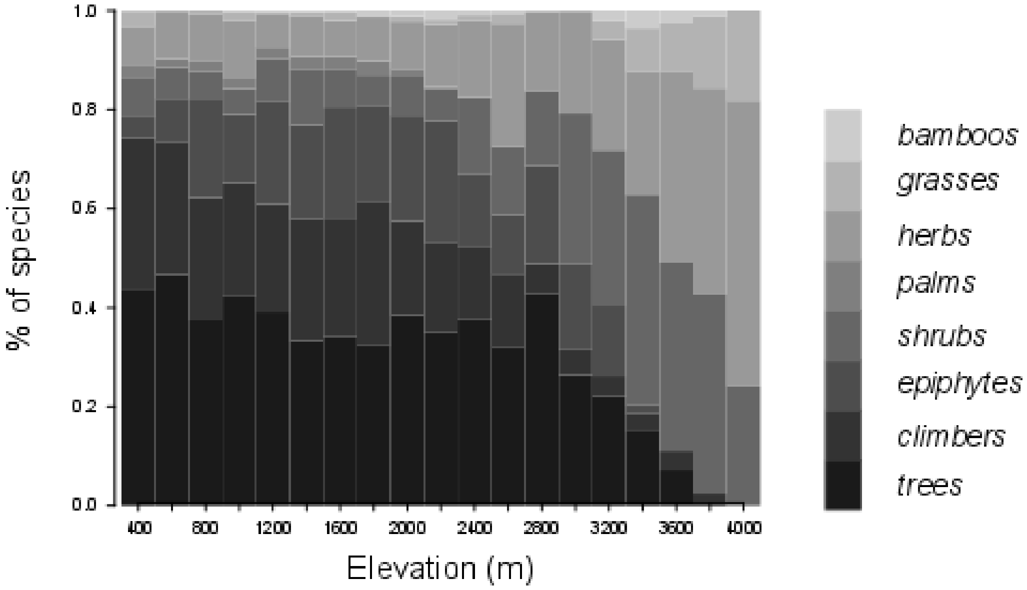

Figure 2-4 Elevational trend of the major life forms shown as percent of all species at every elevational step of 200 m. Mean species numbers of life forms per elevational step were used for figure clarity.

With respect to percental life form composition across the elevation gradient (Figure 2-4), trees and climbers were dominant at lower elevation up to around 2800 m. The percentage of trees varied between 40 and 50 %, the percentage of climbers between 20 and 30 % below 2800 m. The percentages of shrubs, herbs and grasses increased with elevation, especially above 2800 m. Above 4000 m, herbs dominated with more than 60 %, whereas trees and climbers were missing. Epiphytes had the highest relative species number of 20 % at mid-elevations and occurred up to 3600 m, just like the trees and climbers.

2.3.2 Species richness and environmental factors

With regard to the dependence of species richness on environmental variables, in most cases the final models include multiple significant variables (Table 2-1). All models are highly significant ($P < 0.001$) but vary in explanatory power (D^2). For all species together, and trees, climbers, palms and epiphytes, the explanatory power of the final model is high ($D^2 > 0.85$), whereas for shrubs, herbs, grasses and bamboo, the final models were less powerful ($D^2 \leq 0.35$). In almost all model runs, temperature, precipitation and /or their interaction term had the highest standardized (beta) coefficients, except for herbs (precipitation seasonality). In turn, landscape heterogeneity, bryophyte cover (as a proxy of humidity) and soil characteristics were of minor or no importance in all runs.

Table 2-1 Results of the final (best) multiple *glm* models with all species and all life forms as response variables and environmental predictors along the North Myanmar vegetation gradient. Environmental predictors are: *TEMP* mean annual temperature [°C]; *PREC* annual precipitation [mm]; PRECs seasonality of precipitation [%]; BRYO cover of bryophytes [%]; HETEROG elevational heterogeneity as a proxy for environmental heterogeneity [m]; CEC cation exchange capacity [cmolc/kg]; ph soil pH (KCl). The final models are shown with standardized *(beta)* coefficients, adjusted D^2 and significances. *** $P < 0.001$.

	TEMP	**PREC**	**TEMP: PREC**	**PRECs**	**HETEROG**	**BRYO**	**CEC**	**PH**	**D^2**
Life form									
All species	-2.52	**-5.00**	**5.88**	1.45		0.09	-0.49		0.95***
Trees	-5.37	**-9.19**	**11.11**	1.31					0.88***
Shrubs	**7.46**	**5.75**	**-7.26**	2.64	0.65	0.26			0.24***
Palms	**-17.22**	**-30.49**	**30.71**		1.84			3.59	0.88***
Climbers	-5.67	**-10.68**	**12.05**		0.73		-0.88	1.05	0.95***
Epiphytes	**-12.85**	**-16.83**	**18.92**	7.14		0.85		-2.55	0.85***
Herbs		-0.97	0.82	**2.82**					0.35***
Grasses	**20.51**	**15.56**	**-26.17**	-5.48	1.58	-0.88		3.40	0.35***
Bamboo	**-18.36**	**-14.40**	**18.94**				-3.13	-6.81	0.26**
Tree leaf trait									
Leaf shape	**-1.90**	**-2.29**	**2.81**						0.42***
Leaf margin	**-2.02**	**-2.39**	**3.29**						0.45***
Leaf tip	**3.61**	**3.95**	**-5.03**						0.51***
Leaf size	**-1.79**	**-2.14**	**2.61**						0.34***

2.3.3 Leaf morphological traits along the elevational gradient

The mean leaf size of the tree species decreased with elevation, especially above 2800 m (Figure 2-5a). Mean leaf size ranged between 360 cm² at lower elevations and 50 cm² at higher elevations. The three traits concerning shape, margin and tip showed a rather congruent trend with a slight or no trend up to 2000 m and higher up a strong decrease (Figure 2-5b-d), indicating a decreasing dominance of simple leaves with entire margin and drip tip at upper elevation.

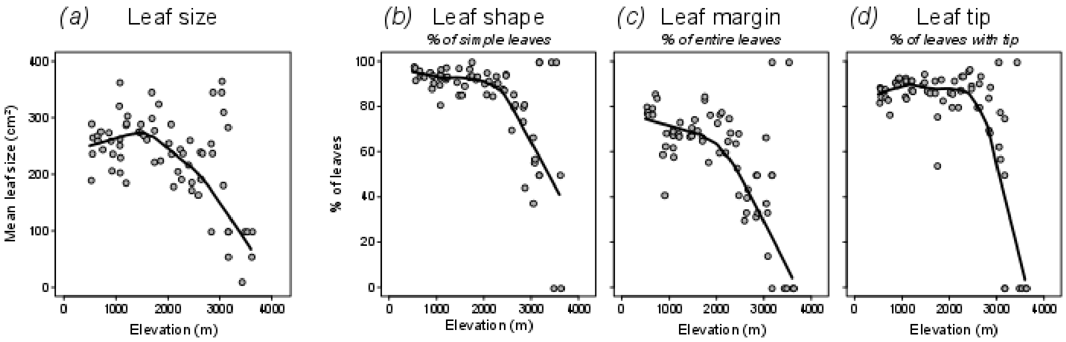

Figure 2-5 Elevational trend of *(a)* mean leaf size (cm²) and *(b, c, d)* three leaf characteristics of the tree species: *(b)* leaf shape (simple/compound), *(c)* leaf edge (smooth/dentate), and *(d)* leaf tip (with tip/without tip). Data of (*b, c, d*) shown as percentage of tree species per plot with the particular characteristic. Trend lines were set with distance-weighted least square smoothing using the function *lowess* in *R*.

2.4 Discussion

2.4.1 Species richness and species trait patterns and their environmental relations

The multiple regression models showed that in almost all cases the variables related to energy and moisture and their interaction terms dominated the results of the most restricted models. This is not surprising, as the large majority of recent papers reporting studies that analyze elevational richness patterns and the underlying mechanistic explanations tend to convergeincide. Temperature controls biological activity and therefore also ecosystem productivity under varying moisture regimes. Thus, temperature strongly affects the importance of the water resource for plants (O'Brien 1998, O'Brien 2006).

Towards high elevations and low-temperature environments, species richness may simply be reduced due to the occurrence of frost and a shorter growing period. Towards low elevations, temperature may enhance species richness, but only in humid climates, i.e. when potential transpiration is not surpassing precipitation. The annual precipitation recorded for this transect amounts to 4000-4500 mm at low elevations, resulting in perhumid climate conditions without drought stress.

Beyond the pattern found for the complete species sample (all life forms), the different life forms as well as tree leaf traits show similar elevational trends and thus similar environmental drivers were identified in the models. This suggests that the different life forms and leaf traits do not require individual analyses, and so we interpret the observed trends jointly in comparison to earlier published findings.

2.4.2 Species richness and elevation

The species richness pattern derived by plot-based data along the elevational gradient shows a linear decrease rather than a hump-shaped pattern. This linear pattern does not match the results of several other recent studies in subtropical and tropical mountains, especially in the Himalayas, where unimodal patterns were most often found (Kluge et al 2017, Li & Feng 2015, Rahbek 1995, Vetaas & Grytnes 2002). As already stated above, unimodal patterns may emerge just by interpolating range data, and with respect to the studies from Nepal and Bhutan, the low species numbers at lower elevation could have been caused by the fact, that both countries have a rather small land surface area at this elevation. A low gamma-diversity would be the outcome (Rosenzweig 1995).

Taking a closer look at the life forms, it is clearly visible that the observed vegetation gradient is largely dominated by tree species. Tree species richness decreases with elevation and reflects also the results of various previous studies in tropical montane forests (Gentry 1988, Homeier et al 2010, Homeier et al 2017, Lieberman et al 1996). An identical elevational richness pattern was found for climbers, which is not surprising, as they depend on trees as hosts, and a high diversity of trees presumably is providing a high niche diversity for climbers as well (Kluge et al 2017). In the same manner, epiphytes also rely on the tall life-form tree, which is providing a large variety of microhabitats along the gradient from the trunk base to the upper canopy (Johansson 1974). Interestingly, the elevational pattern of species richness of this life form is clearly unimodal with highest values at about mid elevations. In this group, thus, not only the available microhabitat diversity may be influential, but also climatic conditions. Low atmospheric saturation deficits in the condensation layer likely are playing a crucial role (Gentry & Dodson 1987, Kessler 2001, Kluge et al 2017, Krömer 2003, Krömer et al 2005, Küper et al 2004).

The species richness of palms is sharply decreasing above 1800 m, revealing that they are mainly distributed at lower elevations. Other studies already showed that the distribution of palms, especially at landscape and continent-wide scales, is largely dependent on the warmth of the climate (Eiserhardt et al 2011). Palms are characteristic for tropical and sub-tropical regions and only a few are occurring in warm-temperate regions or higher elevations (Dransfield et al 2008). Due to their stem tissue with low dry mass density and high water content, they are not capable of dormancy and lack frost adaptation, which restricts them largely to tropical climates (Tomlinson 2006).

All other life forms (shrubs, herbs, grasses and bamboo) show certain diversity patterns along the slope, but the variance around the trends is very high in all cases, rendering interpretation difficult. Shrub species richness shows only a slight decreasing elevational trend, predominately driven by just three datapoints below 1500 m. Herbs and grasses as well have a high variability at lower elevations. In the absence of measurements, it is likely that these pattern are caused by anthropogenic disturbance. The study plots up to 1200 m have small settlements in the vicinity, and although no plot location showed traces of logging, we cannot exclude that earlier small-scale intervention may have favored smaller life forms, which are otherwise negligible in lowland forests with a dense canopy. In turn, in the upper part of the gradient, the increase of grasses was expected as mountain forest close to the treeline is typically of smaller stature and of lower canopy closure, which should favor light-demanding grasses and herbs.

The trend of bamboo is unimodal with highest species richness around mid-elevation. Without overinterpreting this pattern too much (as richness varies just between 0 and 3), this may show a relation to a typical situation along this gradient: overall the topographic energy is high along the whole gradient due to steep valley flanks from the lowlands upwards, with the highest topographic heterogeneity (see variable HETEROG in Figure 2-2) also around mid-elevations. For bamboo it is known that low-frequency disturbances like landslides promote the establishment of bamboo thickets, which can rapidly colonize open spaces and suppress the growth of trees (Miehe et al 2015).

2.4.3 Leaf traits and elevation

Earlier studies on the elevational change of leaf traits of trees have produced mixed results. As expected, the leaf size of tree species was generally found to decrease with increasing elevation (Dkhar & Pareek 2014, Dolph & Dilcher 1980, Leigh 1975, Tanner & Kapos 1982, Velázquez-Rosas et al 2002, Wright et al 2017). The leaf size decrease may be primarily related to the temperature reduction, which lowers meristem activity (Dolph & Dilcher 1980, Tang & Ohsawa 1999).

A second and more complex environmental factor might a decrease in soil fertility, in particular of nitrogen supply, along elevational gradients in tropical mountains (Grubb 1977, Moser et al 2008, Tanner & Kapos 1982) which could negatively affect leaf growth. Ordoñez et al (2009) showed in a global data set that leaf traits such as specific leaf area in general can be better explained by nutrient supply than by climate, whereas, in contrast, plant productivity is primarily controlled by climate.

Regarding leaf shape, the results differ from those of other studies. The frequency of simple leaves normally tends to increase with elevation, while compound leaves decrease with elevation due to the less favorable climatic conditions at high elevation (Velázquez-Rosas et al 2002). Simple or undivided leaves can be regarded as an adaptation to low temperatures and drought events, as well as facilitating water drainage from wet leaves in perhumid environments (Kluge & Kessler 2007). In this study, the ratio between simple and compound leaves narrowed towards high elevations, contrary to expectation. At lower elevations, simple leaves prevail with more than 90 % among the species, while from 2400 m upwards, the fraction of compound leaves increases reaching 40 %. Nevertheless, the total number of tree species with simple leaves is still higher than those with compound leaves at higher elevations. Species, that raise the percentage of compound leaves at higher elevations, are mostly species of Araliaceae, which still occur at high elevations as well as *Sorbus* species, namely *Sorbus harrowiana* and *Sorbus hypoglauca*, especially from 3000 m upwards in the *Abies-Rhododendron* forest (Appendix F 1, Appendix F 2).

In contrast, the elevational increase of dentate leaf margins is in line with findings from other studies. Especially studies dealing with climate history state that dentate leaf margins are more common at sites with lower temperatures, prompting several authors to use the number of fossil leaf teeth for estimating continental palaeo-temperatures (Peppe et al 2011, Royer et al 2009, Wolfe 1971). According to Wolfe (1971) leaves with dentate margins reduce the leaf boundary layer, thus increasing turbulent air movement close the leaf surface and with it transpiration.

The presence of elongated tips on the distal end of the leaves strongly decreases with elevation, especially from 2800 m upwards, rendering leaf tips a characteristic of the trees of lower elevation forests. Our results are in agreement with recent studies which show that the proportion of tree species with drip tips increases with temperature in a forest transect in the Peruvian Andes (Goldsmith et al 2017), and that they are especially frequent in lowland rain forests with high precipitation (Malhado et al 2012). These so-called ‘drip-tips’ were considered as an adaptation to high rainfall by enabling a rapid drainage of the leaf surface, but their functional significance is still debated (Ellenberg 1985, Goldsmith et al 2017, Malhado et al 2012).

2.5 Conclusion

Here, we present data from a complete elevational gradient study from lowland to alpine elevation in northern Myanmar, which is not based on interpolated data from published floras, but explores the results of complete plant specimen sampling of 80 evenly spaced vegetation plots along the gradient. A main outcome is that the often stated elevational hump in species richness distribution along mountain slopes is not a universal phenomenon in the different plant life forms. Thus, the predictive power of various environmental factors with respect to richness patterns does vary with region. Nevertheless, our data confirm that primarily temperature and precipitation and their combination exert the largest influence on diversity patterns. A mechanistic understanding of the climate dependence of leaf morphological traits and life form abundance along elevation gradients has to be based on physiological in-depth studies. An assessment of vegetation across all vascular plant groups in tropical forests on definite plots is rather rare, which is striking given the general perception of the value of tropical forests, but however not striking given the amount of work to realize this, as known to all working in this type of vegetation. Hence, a direct comparison of our results with scattered published data is unfortunately hampered for several reasons:

1. the studies investigated just woody species including different size classes (e.g., > 2,5cm dbh: Gentry (1988); > 5cm dbh: Homeier et al (2010)) or life forms (trees, shrubs, climbers), so including or not including especially younger tree individuals gives a lot of noise to absolute species richness values;

2. studies were performed on different plot sizes (0.01 ha Whitmore et al (1985); 0.1ha Gentry (1988); 0.1ha Hemp (2001)), and in different continents with deviating biogeographical contexts;

3. there are, at least to our knowledge, too few studies to reliable estimate an as regular accepted range of plot based species richness across many life forms. Additionally, we sorted our field samplings up to now to morphospecies, and do therefore not like for all reasons dwelling too much on absolute numbers, since we are aware that a high load of field sampling may cause double notations of species, thus overestimating species numbers.

However, in turn we are pretty sure that such a possible overestimation is within this study constant across plots and life forms, and that therefore our results towards relative contributions of life forms and elevational trends are indeed reliable.

Acknowldgements

We are grateful for the cooperation of Dr Nyi Nyi Kyaw, Win Naing Thaw, Dr Naing Zaw Htun, Myint Kyaw, Law Shein and staff members of the Forest Department, Ministry of Natural Resources and Environmental Conservation, Nay Pyi Taw, Myanmar. Field work was supported through grants of the German Research Council (DFG) and a scholarship financed by the German Academic Exchange Service (DAAD) and the Marburg University Research Academy (MARA).

CHAPTER 3

Assessment of the pteridophyte flora

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with Christopher Fraser-Jenkins, Stuart Lindsay, David Middleton,
Georg Miehe, Philip Thomas and Jürgen Kluge

A contribution toward the knowledge of ferns and lycophytes from northern and northwestern Myanmar

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Abstract.—Although the montane forests of northern Myanmar are part of one of the most biodiverse areas of the world, our knowledge of species richness and elevational distribution of species within these forests is poor and scattered at both spatial and temporal scales. Over the last five decades, very few floristic assessments have been undertaken. This is especially true for ferns and lycophytes. An international collaborative project team undertook the first plot-based inventory of vascular plant species' elevational distribution in northern and northwestern Myanmar in 2012, 2013 and 2014. At elevational gradients in northern and north-western Myanmar, four 400 m2 plots were sampled at intervals of 200 m in natural or little-disturbed forests and alpine thickets. We recorded all ferns and lycophytes from 132 plots, producing a total of 3,978 specimens. Based on these collections we present a list of fern and lycophyte species. A total of 299 species from 72 genera and 24 families were identified. This pilot project is a contribution to the upcoming Flora of Myanmar and provides a baseline dataset of the region to set priorities for conservation and the gazetting of protected areas.

Keywords.— elevational transects; flora; pilot project; plot-based; species distribution pattern

3 Assessment of the pteridophyte flora

3.1 Introduction

Indo-Burma is one of the biodiversity hotspots highlighted by Myers et al (Myers et al 2000), and the northern area of Myanmar covered by this study lies at the junction of three floristic regions: Sino-Himalayan, Indo-Chinese and India (Welk 2015). It is located between the eastern Himalaya and the mountains of Southwest China and is a region of great species richness, with 4,000–5,000 species of vascular plants per 10,000 km2 (Barthlott et al 2007, Zhao et al 2016). However, the flora, vegetation and species distribution patterns are almost unknown. In contrast to most Himalayan countries, Myanmar lacks a national flora and thus a thorough floristic assessment (Frodin 2001).

The earliest floristic accounts from Myanmar were produced when Myanmar was part of British India. These were published in the late 19th century and focused primarily on the timber resources. The most comprehensive of these early publications was Kurz’s 'Forest Flora of British Burma' (Kurz 1877) which included about 2,000 woody plant species. Its focus was to produce an inventory of forest trees, but it did include a few herbaceous plants and the first fern records for Myanmar: species of Cyathea, Alsophila and Brainea insignis (Hook.) J.Sm.. Kurz’s original work was updated and republished by Lace (Lace 1915), Fischer (1926), Nath Nair (1960) and Hundley and Ko (1987). The most recent checklist (Kress et al 2003), primarily derived from these earlier works, includes 11,800 taxa but does not include ferns and lycophytes. The field work for the collections that underpinned these checklists was carried out mostly in western and southern Myanmar. The floristic knowledge of upper Myanmar and especially northern Myanmar is, consequently, much more limited.

The collections of Frank Kingdon-Ward from 1938/39 were published by Merrill (1941) with nine fern species from the Vernay-Cutting expedition. Frederick Dickason compiled his collection of 325 fern species during the period from 1930 to 1942 from the southern Tanintharyi coastline, Chin State, and the Shan Plateau, including a limited number of collections made by Harold Young from northern Myanmar up to the Assam-Burma border in 1943 (Dickason 1946). The most up-to-date and comprehensive list of ferns was published by Dickason (1946) with 460 species belonging to 104 genera. He continued collecting until 1970 in Myitkyina, eastern and southern Shan State, Bago, Yangon (Rangoon), and Myeik (collections deposited in Yangon University herbarium RANG). In (1953), P.S. Bell published 46 species of the wild and cultivated “ferns and fern allies” from Yangon-Insein Region, contributing 15 new ferns and 4 new lycophytes to the existing national list. Since then the only reports on collections of ferns from Myanmar are Nwe (2009), Nwe et al (2016) and Thet (2003). At a regional level, fern collections have been published for Yunnan (Kato et al 1992), for parts of the central Himalaya of Nepal (Fraser-Jenkins et al 2015, Iwatsuki 1988, Miehe 1990, Miehe et al 2015), for Bhutan (Fraser-Jenkins et al 2009), for India (Fraser-Jenkins et al 2016), and in a work mainly on India but also including some records from Nepal and Bhutan (Fraser-Jenkins 2008).

A reason for the striking contrast between northern Myanmar being a potential center of species diversity due to its locality as a transition between two floristic realms, yet being very poorly known floristically, may be due to the remoteness and the relatively unstable political situation in this region. However, the recent opening of Myanmar and the receptiveness of the political administration to nature conservation offered a unique possibility to launch an inventory and systematic assessment of the plant diversity of this mountainous region. With this paper, we present, as a first step, a contribution towards the “Pteridophyte checklist of Myanmar” (Fraser-Jenkins and Khine in prep.) and upcoming "Flora of Myanmar". This is a preliminary checklist in the suspected most species-rich part of the country, part of the “East Himalayas-Yunnan Biodiversity Hotspot”. We present basic data on elevational ranges, frequencies, and life forms of ferns, together with a first outline on richness distribution patterns. The results will be compared to our current knowledge on fern and lycophyte occurrence and distribution patterns worldwide.

3.2 Material and Methods

3.2.1 Study areas

Fern collections were made along elevational gradients in two areas in order to cover diverse altitudinal vegetation zones and thus habitat heterogeneity. In 2012 we sampled an elevational gradient on Natma Taung/Mt. Victoria, Chin State (3,053 m, 21°22'N, 93°90'E, study gradient 400 m to 3000 m) and in both 2013 and 2014 we collected the second gradient in two adjoining areas NW of Putao in Kachin State (Hponyinrazi 4,057 m, 27°56'N, 96°96'E, and Hponkanrazi 3,603 m; 27°50'N, 96°93'E, study gradient 400 m to 4000 m) (Figure 3-1). As these mountainous areas are characterized by frequent land-slides, and the topography is very rugged with narrow ridges, some parts of the Hponyinrazi transect is covered by abundant azonal vegetation, disrupting the possibility of a continuous line of plots in virgin and zonal forests. These gaps were, therefore, sampled from the adjacent mountain, Hponkanrazi. The maps were produced based on CHELSA datasets (Karger et al 2017). Field work was undertaken during the post-monsoon season (October to December) in each year. The northwestern transect, Natma Taung, stretched between 400 m in tropical Southeast Asian Dipterocarp lowland forest to temperate evergreen broadleaved Himalayan Quercus semecarpifolia-Rhododendron arboreum forest on the summit area of Mt. Victoria (3,003 m). The northern area covered a transect from the intramontane basin of near Putao at 490 m, with Castanopsis-Dipterocarp forest, up to the treeline ecotone along with Himalayan bamboo thickets and scattered Abies delavayi at 3600 m (Hponkanrazi) and alpine Rhododendron dwarf scrub at 4,057 m (Hponyinrazi). Both areas are at least partly under the nature conservation administration of the Forest Department, Ministry of Natural Resources and Environmental Conservation. The forests below 2,000 m in the Natma Taung area and below 1,000 m in northern Myanmar are partly managed by a slash and burn agriculture system known as “Taungya”. However, in both areas the forests were relatively well preserved compared to other Himalayan forests. Whereas forest fires during the dry season may occur in the cloud forests of Natma Taung above 2,000 m, maintaining a savannah-like structure between forest patches and grassland, the forests of the northern area are untouched above 1,000 m and only lightly used for the collecting of medicinal plants or for hunting. The forest structure and the height of the canopy is however not homogenous, but mirrors succession stages after rockfall or landslides. Bamboo thickets cover wide areas of those mostly very steep slopes.

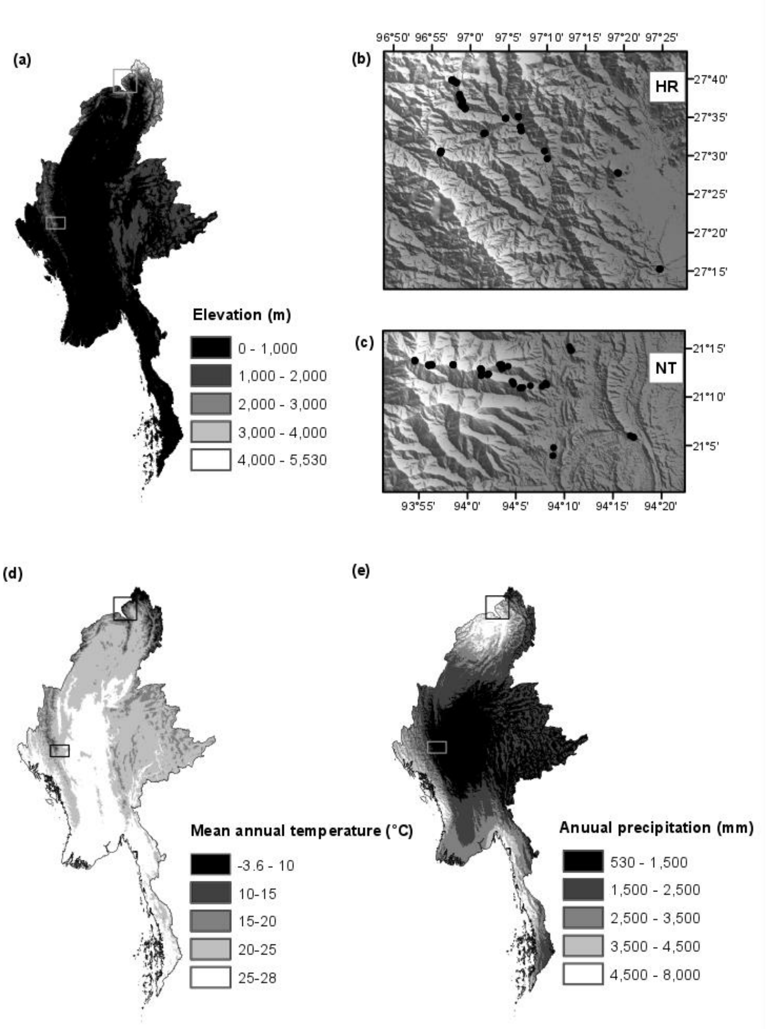

Figure 3-1 (a) Elevational pattern of Myanmar as a whole and with close-ups for both elevational gradients; (b) the northern transect, HR (Hponkanrazi + Hponyinrazi), and (c) the northwestern transect, NT (Natma Taung). Within each close-up, the black dots are the sites of the plots that were sampled over elevational distances of about 200 m. (d) Mean annual temperature and (e) annual precipitation from CHELSA datasets.

Both areas merge from the Indo-Chinese Floristic Region of the Palaeotropical Floristic Realm into the Sino-Himalayan Floristic Region of the Holarctic Floristic Realm (Welk 2015). The transition between the tropical Southeast Asian Dipterocarp forests and the temperate evergreen-broadleaved Himalayan Magnolia-Oak forests stretches between 1,500 m and 2,000 m. The summit area of Mt. Victoria, with its open grasslands and Himalayan oak forests, has attracted the attention of botanists and ornithologists since colonial times due to records of Himalayan species isolated from the Himalayan arc by a distance of 900 km (Kingdon-Ward 1958, Stresemann & Heinrich 1939).

3.2.2 Climate

Myanmar experiences the Asian Summer monsoon, and most parts of the country receive South-West monsoon rains from May to October (Sein et al 2015). A long period of seasonal drought with a rapid rise of temperature starts right after the monsoon period, especially in the central basins, while other parts of the country receive rainfall throughout the year, mostly in the lowlands along coastlines and at high elevations. Mountains in Chin State and Northern Myanmar are the orographic barriers for monsoon and the highest rainfall occurs between June and September. Annual precipitation amounts vary from 500 mm in the Central Dry Zone, 2,300 mm in the Chin Hills (gradient Natma Taung), and about 4,000 mm (Thet 2003) in northern Myanmar (gradient Hponyinrazi / Hponkanrazi, Figure 3-1Figure 3-1). The northwestern area, located at the margin of the country’s dry zone, receives 1,300 mm annual rainfall at the foot of the slope at 400 m, and 2,300 mm at 3,000 m. The amount of fog precipitation has not been measured, but abundant epiphytic mosses and lichens show that evapotranspiration is hampered due to mountain fog during the rainy season and for most of the year at elevations above 2,000 m. In the north, annual rainfall of more than 4,000 mm has been recorded in the center of an intramontane basin (Putao) at 450 m asl. The CHELSA datasets provide extrapolations of decreasing rainfall with altitude; however the humidity conditions as mirrored by the bryophyte coverage in the tree canopy (Karger et al 2012) suggest that rainfall increases considerably with altitude. Fog is an important ecological factor, reducing evapotranspiration and reducing the effects of the dry season. The slopes of Hponyinrazi / Hponkanrazi are possibly the wettest slopes in the whole of the Himalayan arc (Miehe et al 2001). Both areas have cold-air ponding effects with night fog in their intramontane basins at the foot of the slopes; at 1,200 m night frosts regularly occur. Snowfall in the summit area of Mt. Victoria occurs, but is rare, whereas the upper montane Abies forests and alpine shrubberies above 3,000 m remain snow-covered between October and May. In total, the Natma Taung gradient is warmer and dryer at same elevations compared to Hponyinrazi / Hponkanrazi (Figure 3-2).

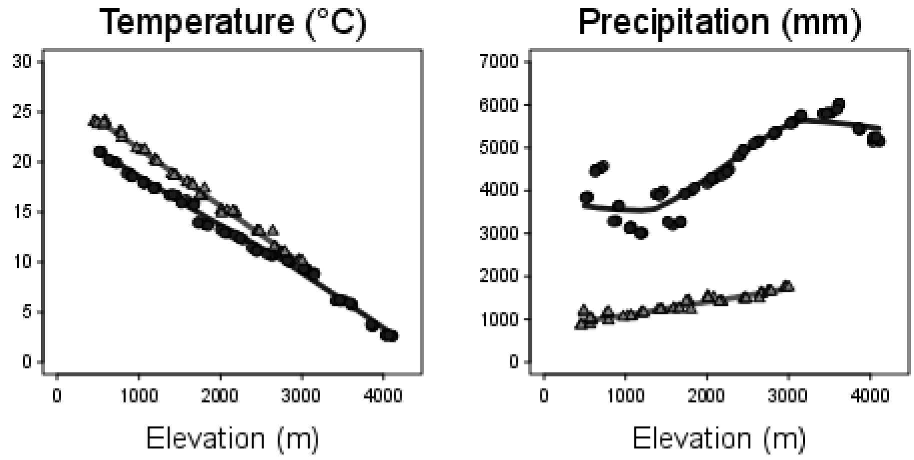

Figure 3-2 Patterns of mean annual temperature (left) and annual precipitation (right) along elevational gradients at Natma Taung (NT; grey lines, triangles) and Hponkanrazi + Hponyinrazi (HR; black lines, circles).

3.2.3 Vegetation records

We used a plot size of 400 m2, which is small enough to keep environmental factors and forest structure more or less homogeneous within the plots, and is the minimum area required for representative fern and lycophyte surveys in humid tropical forests (Kessler and Bach, 1999). The plots were usually square (20 m x 20 m) or rectangular (10 m x 40 m) in special relief situations. The minimum distance between the plots was kept to at least 20 m to ensure each plot is independent of the others. The plots were placed at every 200 m of elevation, with four plots established at every elevational level. The plots were located in areas that showed the least possible anthropogenic disturbance. The vegetation sampling was conducted in zonal forest. Extraordinarily wet sites near running water in deep valleys, and frequently disturbed steep slopes and ridges, were not selected to avoid unrepresentative contributions of azonal vegetation. In total we studied 132 vegetation plots, 56 plots at Natma Taung in 14 elevational steps, and 76 plots at Hponkanrazi / Hponyinrazi in 19 elevational steps.

All species were recorded with their substrate and abundance. Discrete clumps of long-creeping rhizomatous plants were assigned as single individuals. Substrates were noted as terrestrial (soil, rocks, and dead wood) and epiphytic. The microhabitat on a tree was recorded for epiphytes, ranging from low trunk (<2 m), high trunk up to first ramification of tree, lower canopy, inner crown, and outer crown (i.e., 'Johansson's zones', Johansson 1974). Canopy species were checked with binoculars to record individual numbers. Collection and sampling of upper canopy epiphytes on trees up to 50 m tall was done by botanically trained local tree climbers. Additionally, we searched for recently fallen trees and branches inside or in close proximity to the plots for trunk and canopy epiphytes. We also recorded the fertility status of each species. Three sets of specimen vouchers were collected for all putative species at each elevational step, hence 3,978 vouchers in total.

3.2.4 Plant determination and data analysis

The determination of the specimens was undertaken by the authors and by taxonomists thanked in the acknowledgements. The species list follows the nomenclature of (Schneider et al 2016), though this does not imply that the taxonomy put forward in that paper is accepted by all authors, notably by CRFJ. The specimens are deposited in the Forest Research Institute herbarium (RAF) in Yezin, Myanmar; Naturalis Biodiversity Center (L) in Leiden, the Netherlands; the Project Herbarium of the Faculty of Geography, Philipps University of Marburg (PHMR) in Germany; Singapore Botanic Gardens (SING) in Singapore; the University of Bonn (BONN) in Germany and the University and Jepson herbaria (UC) in Berkeley, the United States of America. Two transects from northern Myanmar, the Hponkanrazi and Hponyinrazi transects were combined as one elevational gradient and cited as “HR” for simplicity. The Natma Taung transect will be described as “NT” from now onward. The highest and lowest elevations of each species’ occurrence, their locality and abundance, as well as their life form, are also included as part of the species list. The total number of species, as well as the number of epiphytic and terrestrial species, was plotted against the elevation to visualize the species richness pattern along the elevational gradient.

3.3 Results and Discussion

3.3.1 Taxonomic composition

In 132 survey plots from both transects (56 plots in NT, and 76 plots in HR) 299 species belonging to 72 genera and 24 families were recorded (Table 3-1). Polypodiaceae was the most species-rich family (81 species, 27% of the species recorded) followed by Dryopteridaceae (47 species, 15.7%) and Athyriaceae (32 species, 10.7%). This pattern strikingly coincides with family-level species lists from other regions worldwide. For example, in Costa Rica, one of the global 'fern hot spots' (Kreft et al 2010), with a similar number of plots along an elevational gradient, almost 21% of the species recorded belonged to Polypodiacae (incl. Grammitidaceae), and about 20% Dryopteridaceae (incl. Elaphoglossum) (Kluge & Kessler 2005). The same picture emerged in a study in Indonesia (Kessler, Kluge, Karger, unpublished data) and Borneo (Kessler 2001). However, the most species rich family in the South American Bolivian Andes is Dryopteridaceae at 27%, followed by Polypodiaceae at 18% of the total (Kessler 2001). A regional study from Nepal has listed Dryopteridaceae and Athyriaceae as the most species-rich families (Bhattarai et al 2004). The similarity of the percentage contribution of the families in species lists may be attributed to the fact that ferns in general are more widespread than seed plants, mainly because of their greater age and thus a longer dispersal period (but see Schneider et al 2004) and/or because of a higher dispersability (small size of diaspores) and thus because of a high chance of long distance dispersal (Kramer 1993, Smith 1972).

Certain similarities also emerged at the genus level. For example, Dryopteris and Polystichum within Dryopteridaceae both have large numbers of species and comprise 22% of the total fern species occurrence in the Holarctic floral region and, due to their preference for colder and more extreme habitats in general, also occur in high numbers at elevations above 3,800 m in this study. In neighbouring countries such as China, Polystichum is the most species-rich genus and occurs mostly in subtropical and temperate mountainous regions (Li et al 2008). The genera Athyrium, Acystopteris, Huperzia and Hymenophyllum, distributed mainly in the northern hemisphere and southern temperate regions, have been observed above 3,100 m, which corresponds to the elevation of the lower reaches of evergreen Abies forest in northern Myanmar. Spinulum is found only above 3,500 m in northern Myanmar, while the other genera can be found down to around 850 m in the subtropical moist hardwood forest. Tomophyllum and Arthromeris have been recorded in the Evergreen Fagaceae Forest and Abies-Rhododendron Forest between 1,000 m and 3,000 m in this study; those genera have a wide range of distribution and are known from regions mostly in tropical Asia and the west Pacific Islands as well as some in China and the Himalaya.

When compared to the previous records of ferns for Myanmar by Dickason (1946) and Nwe et al (2016), and Indian pteridophytes checklist by Fraser-Jenkins et al (2016), 125 additional fern species are recorded in this study (Table 3-1). We are aware that an accurate statement of which of these are new records for Myanmar would involve a much more comprehensive assessment of fern literature from neighboring regions, taxonomic monographs, and a more thorough assessment of the accuracy of the identifications of the ferns in the previous literature. This is beyond the scope of this study. In addition, Selliguea kachinensis Hovenkamp, S.Linds., Fraser-Jenk. (Polypodiaceae) has recently been described (Khine et al 2016). It was found in Northern Myanmar at an elevation between 1300 m and 1700 m in evergreen broadleaved forest. A new combination for this species as Arthromeris kachinensis (Hovenkamp, S.Linds. & Fraser-Jenk.) Fraser-Jenk., Odyuo & D.K.Roy in (Mao et al 2017) has also been published. Phylogenetic research to investigate whether Arthromeris should be recognized as distinct from Selliguea is ongoing (Hovenkamp, pers. comm.).

3.3.2 Patterns of species richness

Species richness by elevation for the two areas declines at both lower and higher altitudes showing an unimodal pattern (Figure 3-3). This same pattern has been found in the central Himalayas in Nepal (Bhattarai & Vetaas 2006) and in plot-based sampling from numerous other tropical mountain areas (Grytnes & Beaman 2006 in Borneo, Hemp 2002 in Tanzania, seeKessler et al 2011 for a worldwide comparison, Kluge et al 2006 in Costa Rica, Krömer et al 2005 in Bolivia). The prominent climatic factors for fern and lycophyte species richness are temperature and water availability (O'Brien 1998), hence the richness peak occurs at the elevation with moderate temperature and high humidity, thus differ between the gradients. Hence, the elevational position of richness peaks, as well as the maximum number of species per plot, strongly differs between the two areas in this study. Species richness per plot at NT did not exceed 22 species, while at HR we recorded more than double that number (N=49, Figure 3-3). In addition, the total number of species recorded along each gradient at HR was far higher (262 species) than at NT (85 species). At first glance this pattern may seem surprising as, in general, species richness should decline towards higher latitudes, i.e., with increasing distance from the tropics. This is explained by the climatic setting of both gradients: the NT transect stretches down to the exceptionally dry intramontane basin of central Myanmar, and it receives less rainfall in Monsoon periods reflecting low annual precipitation and thus less ambient humidity (Figure 3-2). Moreover, the elevation with maximum species richness strongly differs between both gradients (in NT 2,200 m, in HR 1,200 m), This difference may be explained by a mountain mass effect (see e.g., Leuschner, 1996): in the higher mountain ranges in the north, to which the HR gradient belongs, the temperature belts shift upwards, which may be the decisive factor influencing the elevation of the maximum species richness. Thus, when aligned to temperature rather than elevation, both peaks of species-richness lie at 15°C–17°C of mean annual temperature (Figure 3-4), consistent with the findings from multiple fern elevational gradients worldwide (Kessler et al., 2011).

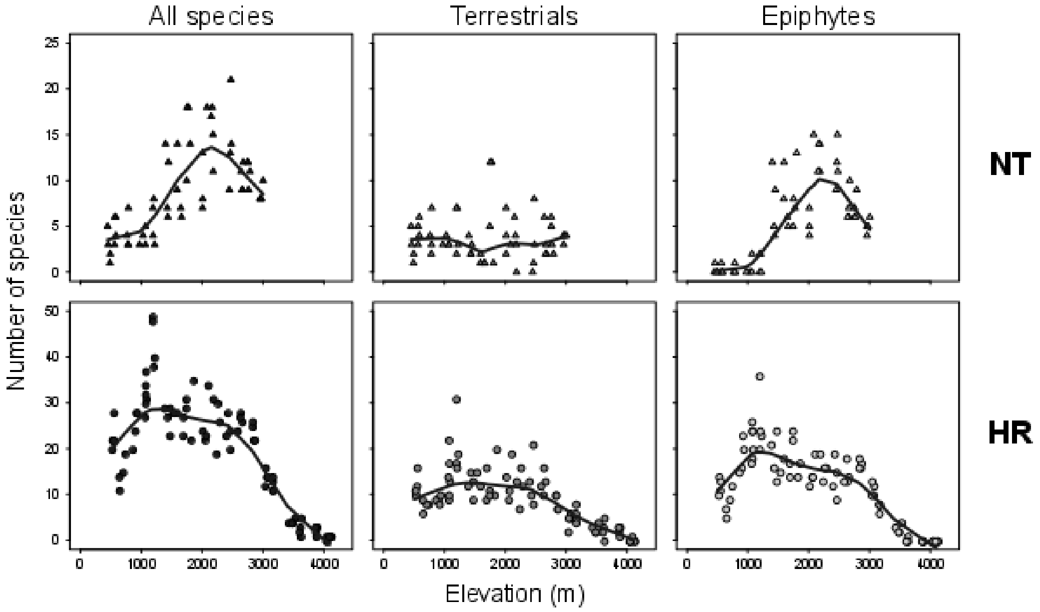

Figure 3-3 Elevational patterns of fern species richness for all species, terrestrial and epiphytic life forms in the northwestern transect (Natma Taung; NT) and northern transect (Hponkanrazi + Hponyinrazi; HR). The trend lines were set by distance weighted least square smoothing (LOWESS).

As found in other elevational fern richness studies, the pattern found in this study is driven by the epiphytic life form (Figure 3-3). Their elevational richness trend was more pronounced than for terrestrial species, rendering them more susceptible to the steep change of environmental condition along the elevational gradient, especially with respect to temperature and humidity (Ding et al 2016, Kluge et al 2006). The richness of epiphytic species per plot was higher than terrestrial species, reaching up to 34 species per 400 m2, at mid elevations at about 1,200 m in the HR transect, and 16 species at about 2,400 m elevation. However, in total 199 species from both transects were terrestrial species, whereas 162 were epiphytic species, thus overall more terrestrial species were recorded across the gradient. This is due to microhabitat variability, which is spatially much coarser for terrestrial species, thus capturing less variability per plot, in contrast to epiphytic microhabitats, which are more variable within one plot due to the complex morphological structure of host trees (Kluge & Kessler 2011a)(Kluge and Kessler, 2011). Thus, epiphytic species should be more evenly distributed than terrestrial species, resulting in a higher number of occupied plots per species for epiphytes. This has been tested with the distribution data of this study by counting the mean number of plots occupied by terrestrial and epiphytic species, and indeed epiphytic species on average were present in a significantly higher number of plots than terrestrials (6.8 vs. 4.0, Wilcoxon rank sum test: $p<0.001$).

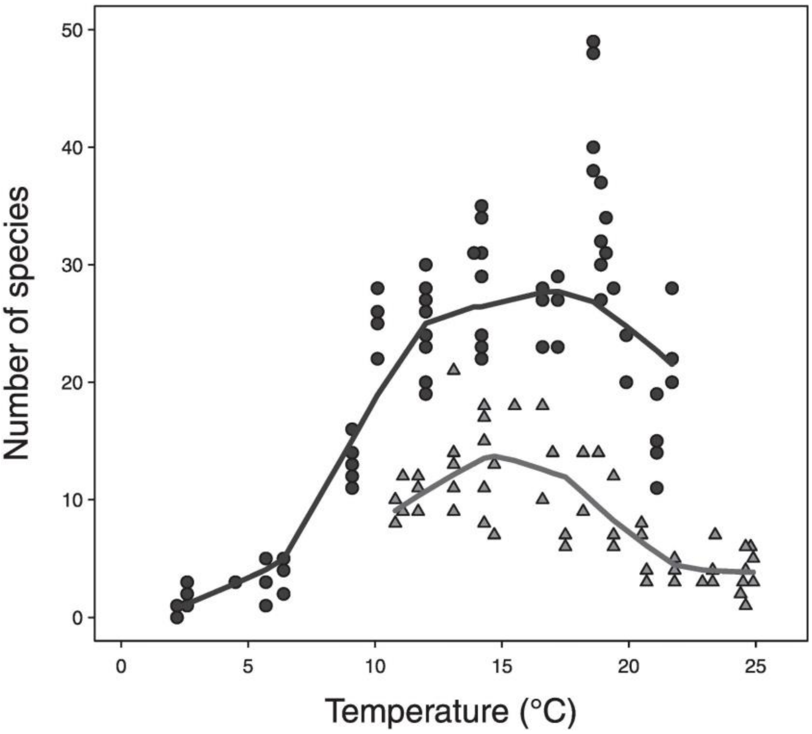

Figure 3-4 Species richness pattern against mean annual temperature; Natma Taung (NT in triangles) and Hponkanrazi + Hponyinrazi (HR in circles). The trend lines were set by distance weighted least square smoothing (LOWESS).

At low elevations, high humidity and its potential benefits for fern and lycophyte richness were offset by high temperatures and therefore high evapotranspiration, whereas towards the upper part of the gradient fern and lycophyte species richness may be limited by low temperatures, especially frost events (Bhattarai et al 2004).

3.4 Conclusion

This first and most comprehensive list of ferns from the mountain forests of northern Myanmar is a contribution to the upcoming Flora of Myanmar and a first contribution to the Myanmar element in aiding our understanding of the “East Himalaya-Yunnan biodiversity hotspot”. On comparing this study to fern floras of other mountainous areas of South East Asia and other tropical mountains, the pattern of lower diversity at lower and higher elevations and of epiphytes dominant in cloud forests is confirmed. As ferns, and especially epiphytic ferns, are well-established indicators of habitat status and landscape fragmentation, this list may support any attempts for a better nature conservation policy in Myanmar. Clearly, this is just the first step towards a country 'Flora', which already exist or are in production for all neighboring countries within the Himalayan region. This work may help to induce further research on species richness and composition, especially in the still largely untouched mountain forest ecosystems bordering the Himalaya, the Tibetan highlands, and Yunnan.

Acknowledgements

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Table 3-1 List of species found within this study with data on elevational range, substrates occupied and herbaria. Family order follows PPG1 (2016), within each family, genera and species are listed alphabetically. Species not listed for Myanmar in Dickason (1946) (excluding lycophytes that were not included in that work), Nwe et al. (2016) and Indian pteridophytes checklist in Fraser-Jenkins et al. (2016) are marked with *. Abbreviations for transects are NT= Natma Taung, HK= Hponkanrazi and HY= Hponyinrazi (both latter combined = HR). The substrate is abbreviated as ground (g), dead wood (w), rock (r), tree trunk below 2 m (t1), 2m to first ramification of the tree (t2), lower crown (t3), inner crown (t4) and outer crown (t5). Collection numbers (ID) and the herbarium where the voucher is deposited is given as b=BONN, l=L, p=PMHR, s=SING, u=UC.

	Transect	**Elevation Range (m)**	**Substrate**	**ID & Herbaria**
Lycopodiaceae				
Huperzia bucahwangensis Ching	HY	2400–3016	t1,t2	13-070-050^{s}, 13-072-054^{p}, 13-075-002^{p}, 13-076-093^{p}, 13-080-111^{p}
Huperzia delavayi (Christ & Herter) Ching*	HY	3840–3840	g	13-057-025^{u}
Huperzia herteriana (Kümmerle) T.Sen & U.Sen	NT&HY	1593–2839	t1,t2,t3,t4	12-012-001^{u}, 13-073-010^{p}, 13-073-011^{s}, 13-075-011^{s}
Huperzia javanica (Sw.) Fraser-Jenk.	HY	1988–2400	g	13-080-112^{p}, 13-090-001^{s}
Phlegmariurus fordii (Baker) Ching*	NT	1595–1803	t1,t2,t4	12-051-001^{u}, 12-096-026^{s}
Phlegmariurus hamiltonii (Spreng.) Á.Löve & D.Löve	NT, HK&HY	1051–2607	t1,t2,t3,t4	12-012-002^{s}, 12-074-003^{s}, 12-095-028^{s}, 13-077-102^{p}, 13-079-083^{p}, 13-084-022^{p}, 13-086-020^{p}, 13-089-114^{s}, 13-106-012^{s}, 14-032-017^{s}, 14-050-001^{u}
Phlegmariurus phlegmaria (L.) Holub	HK&HY	892–1168	w,t1,t4,t5	13-098-256^{p}, 14-054-020^{u}, 14-055-009^{s}, 14-060-002^{u}
Phlegmariurus pulcherrimus (Wall. ex Hook. & Grev.) Á.Löve & D.Löve*	HK&HY	833–2029	r,t1,t3,t4,t5	13-089-113^{p}, 13-094-146^{p}, 13-095-125^{s}, 13-098-233^{p}, 13-099-020^{p}, 13-106-024^{p}, 14-031-028^{s}, 14-041-008^{u}, 14-042-005^{u}, 14-047-019^{u}, 14-057-

				011^{u}
Phlegmariurus squarrosus (G.Forst.) Á.Löve & D.Löve*	HK&HY	621–1048	t1,t4	13-105-019^{s}, 14-054-021^{u}, 14-069-002^{u}
Spinulum annotinum (L.) A.Haines*	HK	3588–3588	g	14-026-001^{s}
Selaginellaceae				
Selaginella biformis A.Braun ex Kuhn	HK	1508–1665	g	14-032-010^{u}
Selaginella braunii Baker*	NT	564–1031	g	12-082-060^{u}, 12-082-063^{u}, 12-082-064^{u}, 12-087-001^{u}
Selaginella chrysocaulos (Hook. & Grev.) Spring	NT	2011–2011	r,t1	12-074-005^{s}
Selaginella doederleinii Hieron. *	HY	1447–2162	g,t1	13-086-017^{s}, 13-088-034^{u}, 13-089-112^{u}, 14-048-011^{s}
Selaginella helferi Warb.	HY	1036–1177	g,w	13-098-240^{p}, 13-101-289^{p}, 13-102-264^{s}, 13-103-245^{p}, 13-104-003^{s}, 14-054-027^{s}
Selaginella involvens (Sw.) Spring	NT&HY	1492–2162	g,w,r,t1,t2	12-046-005^{u}, 12-048-012^{s}, 12-074-006^{u}, 12-077-005^{u}, 13-086-012^{s}, 13-088-044^{s}
Selaginella minutifolia Spring	NT	790–790	g,r	12-016-002^{s}
Selaginella monospora Spring	HY	2011–2807	g,r,t1	13-074-071^{p}, 13-076-082^{s}, 13-076-083^{p}, 13-077-091^{s}, 13-078-012^{p}, 13-080-104^{p}, 13-085-112^{p}
Selaginella picta A.Braun ex Baker	HK	614–715	g	14-066-237^{s}, 14-067-146^{s}
Selaginella repanda (Desv. ex Poir.) Spring	NT	450–790	g,r	12-016-001^{u}, 12-022-003^{u}, 12-082-062^{u}
Selaginella wallichii (Hook. & Grev.) Spring	HK	497–614	g	13-115-009^{p}, 13-116-007^{s}, 13-118-011^{s}, 13-118-012^{s}, 14-070-002^{s}
Ophioglossaceae				
Botrychium formosanum	HY	1036–1197	g	13-098-231^{p}, 13-

Tagawa (perhaps merely a form of B. daucifolium Wall. ex Hook. & Grev) *				103-247^{s}
Japanobotrychium lanuginosum (Wall. ex Hook. & Grev.) Nishida ex Tagawa	NT	2200–2473	g,t1	12-007-001^{s}, 12-073-019^{u}
Marattiaceae				
Angiopteris helferiana C.Presl	HY	497–614	g	13-116-015^{s}, 13-118-007^{u}
Hymenophyllaceae				
Crepidomanes campanulatum (Roxb.) Panigrahi & Sarn. Singh	HY	1046–2400	t1,t2,t3,t4,t5	13-093-002^{p}, 13-094-143^{s}, 13-095-002^{u}, 13-101-293^{p}, 13-101-297^{p}, 13-103-251^{p}, 13-104-014^{p}, 13-104-009^{p}
Crepidomanes cf. minutum (Blume) K.Iwats.*	NT	2480–2480	r	12-066-023^{s}
Crepidomanes latealatum (Bosch.) Copel.	NT, HK&HY	715–3016	g,w,r,t1,t2,t3,t4,t5	12-007-003^{u}, 12-012-003^{u}, 12-048-006^{s}, 12-077-004^{u}, 12-077-006^{s}, 13-088-056^{s}, 13-098-219^{p}, 13-098-226^{s}, 13-099-025^{p}, 13-101-271^{s}, 13-101-292^{s}, 13-103-276^{s}, 13-103-279^{p}, 13-103-252^{p}, 13-103-277^{p}, 13-104-007^{s}, 13-104-014^{s}, 13-105-027^{s}, 13-105-028^{s}, 13-106-003^{p}, 14-031-013^{u}, 14-047-007^{u}, 14-047-227^{p}, 14-047-228^{p}, 14-048-004^{p}, 14-050-003^{p}, 14-050-004^{s}, 14-051-003^{p}, 14-051-004^{u}, 14-054-007^{u}, 14-054-008^{u}, 14-055-002^{u}, 14-057-005^{p}, 14-059-006^{p}, 14-060-011^{u}, 14-061-006^{s}, 14-066-240^{s}
Didymoglossum	HK	614–909	w,t1	14-061-007^{s}, 14-

sublimbatum (Müll.Berol.) Ebihara & K.Iwats.				066-246^{u}, 14-070-005^{s}
Hymenophyllum badium Hook. & Grev.	NT&HY	1168–2632	g,r,t1,t2,t3,t4	12-077-007^{u}, 13-076-079^{s}, 13-098-236^{p}, 13-102-262^{s}
Hymenophyllum barbatum (Bosch) Baker	HK&HY	1404–2600	w,t1,t2,t3,t4,t5	13-078-011^{s}, 13-085-119^{p}, 14-031-014^{u}, 14-042-009^{u}, 14-047-229^{u}, 14-048-005^{u}, 14-051-010^{s}
Hymenophyllum corrugatum Christ*	HK&HY	2676–3502	t1,t2,t3	14-015-002^{u}, 14-015-005^{s}
Hymenophyllum exsertum Wall. ex Hook.	NT, HK&HY	1168–2807	g,t1,t2,t3,t4	12-012-004^{p}, 12-035-001^{u}, 12-035-002^{s}, 12-074-011^{s}, 12-092-056^{u}, 12-097-025^{s}, 12-097-027^{s}, 13-074-065^{s}, 13-075-008^{p}, 13-102-260^{s}, 14-042-003^{u}
Hymenophyllum polyanthos (Sw.) Sw.	NT	1803–2959	t1,t2,t3,t4	12-003-009^{s}, 12-007-005^{su}, 12-035-003^{u}, 12-074-010^{s}, 12-097-024^{u}, 12-097-026^{s}
Hymenophyllum simonsianum Hook.*	HY	2371–3047	g,r,t1,t2,t3,t4	13-069-010^{p}, 13-072-057^{p}, 13-073-006^{p}, 13-077-093^{s}
Hymenophyllum tenellum D.Don	HK&HY	892–3138	g,w,r,t1,t2,t3,t4	13-064-043^{p}, 13-064-044^{p}, 13-064-047^{p}, 13-064-052^{p}, 13-064-053^{p}, 13-064-054^{p}, 13-064-055^{p}, 13-065-040^{p}, 13-066-036^{s}, 13-066-038b^{p}, 13-066-039^{p}, 13-067-034^{p}, 13-067-035^{p}, 13-068-045^{p}, 13-068-047^{p}, 13-068-051^{p}, 13-069-011^{p}, 13-070-053^{p}, 13-075-012^{p}, 13-075-013^{p}, 13-076-080^{p}, 13-076-089^{p}, 13-077-101^{s}, 13-102-298^{s}, 14-060-009^{p}

Vandenboschia auriculata (Blume) Copel.	HY	1047–2078	r,t1,t2	13-088-045^{s}, 13-088-046^{s}, 13-088-047^{s}, 13-093-005^{s}, 13-094-160^{p}, 13-105-017^{p}
Vandenboschia maxima (Blume) Copel. *	HY	1051–1197	t1	13-098-216^{p}, 13-098-218^{p}, 13-101-290^{s}, 13-101-291^{p}
Vandenboschia striata (D.Don) Ebihara	HY	1047–1833	t1,t2	13-093-001^{s}, 13-098-222^{p}, 13-105-003^{u}
Gleicheniaceae				
Dicranopteris taiwanensis Ching & P.S.Chiu*	HY	497–497	g	13-118-009^{s}
Lygodiaceae				
Lygodium flexuosum (L.) Sw.	NT	450–1194	g,t1	12-016-011^{u}, 12-022-002^{u}, 12-082-067^{s}
Plagiogyriaceae				
Plagiogyria glauca (Blume) Mett.	HY	2804–3138	g,w,t1	13-070-052^{s}, 13-074-069^{s}
Plagiogyria pycnophylla (Kunze) Mett.	HY	2029–2839	g,w	13-074-066^{s}, 13-078-001^{p}, 13-079-082^{p}
Cibotiaceae				
Cibotium barometz (L.) J.Sm.	HY	505–519	g	13-115-010^{s}
Cyatheaceae				
Alsophila andersonii J.Scott ex Bedd.	HK&HY	497–1168	g	13-098-230^{b}, 13-103-269^{b}, 13-106-001^{b}, 13-118-013^{p}, 14-057-007^{b}, 14-069-004^{b}
Alsophila costularis Baker*	HY	527–1715	g	13-094-153^{b}
Alsophila gigantea Wall. ex Hook.	HK&HY	519–3047	g,t1	13-117-006^{p}, 14-069-003^{b}
Alsophila khasyana T.Moore ex Kuhn	HY	2078–2078	g	13-088-037^{b}
Alsophila latebrosa Wall. ex Hook.	HY	1168–1360	g	13-101-284^{b}, 14-050-011^{b}
Alsophila spinulosa (Wall. ex Hook.) R.M.Tryon	HK&HY	833–2039	g,t1	13-098-211^{p}, 13-098-239^{p}, 13-102-265^{p}, 14-031-011^{b}
Sphaeropteris brunoniana (Hook.) R.M.Tryon	HY	1168–2029	g,t1,t2	13-089-117^{p}, 13-099-014^{b}

Pteridaceae				
Adiantum philippense L.	NT	450–1209	g,t1	12-015-099^{s}, 12-016-005^{u}, 12-022-004^{u}, 12-022-005^{s}, 12-022-005^{s}, 12-057-003^{u}, 12-082-066^{u}
Adiantum cf. incisum C.Presl*	NT	566–788	g	12-082-065^{u}
Antrophyum henryi Hieron.*	HY	1047–1047	t1	13-105-013^{s}
Antrophyum obovatum Backer	HY	1714–1714	t1	13-095-007^{s}
Antrophyum reticulatum (G.Forst.) Kaulf.	HK&HY	909–1565	t1,t2,t3	13-098-229^{s}, 13-102-280^{p}, 13-103-267^{s}, 13-103-273^{p}, 13-105-002^{s}, 14-031-012^{s}, 14-054-022^{s}, 14-061-012^{u}
Antrophyum wallichianum M.G.Gilbert & X.C.Zhang	HK	892–1508	t1,t2,t3,t4	14-041-002^{u}, 14-048-009^{u}, 14-060-004^{u}
Cerosora microphylla (Hook.) R.M.Tryon	HY	2400–2607	g,r,t1	13-077-103^{p}, 13-078-005^{p}, 13-079-085^{p}, 13-080-113^{s}
Coniogramme fraxinea (Don) Diels	HY	1797–1988	g	13-090-012^{p}, 13-093-032^{p}
Coniogramme petelotii Tardieu	HK	1508–1508	g	14-041-013^{u}
Coniogramme serrulata (Blume) Fée	HY	2233–2600	g	13-078-004^{s}, 13-084-019^{s}, 13-087-108^{p}
Haplopteris doniana (Mett. ex Hieron.) E.H.Crane	HY	2233–2807	r,t1,t2,t3	13-075-004^{s}, 13-080-108^{p}
Haplopteris elongata (Sw.) E.H.Crane	HY	497–909	t1,t2,t3,t4	13-115-004^{p}, 13-118-006^{s}, 14-057-017^{s}, 14-059-005^{s}
Haplopteris flexuosa (Fée) E.H.Crane	NT, HK&HY	874–2632	w,t1,t2,t3, t4,t5	12-051-002^{u}, 12-051-003^{u}, 12-092-055^{u}, 12-096-025^{u}, 13-088-043^{s}, 13-091-002^{s}, 13-091-006^{p}, 13-092-096^{s}, 13-094-141^{p}, 13-095-014^{s}, 13-095-127^{p}, 13-095-128^{p}, 13-098-242^{s}, 13-101-295^{p}, 13-102-

				277^{s}, 13-104-015^{s}, 14-031-017^{p}, 14-032-007^{s}, 14-032-014^{s}, 14-032-016^{s}, 14-041-016^{s}, 14-047-021^{s}, 14-051-005^{s}, 14-051-006^{s}, 14-051-011^{s}, 14-055-010^{s}, 14-057-008^{s}, 14-057-014^{s}
Haplopteris mediosora (Hayata) X.C.Zhang	HY	2632–3136	t1,t2,t3	13-066-035^{s}, 13-067-042^{p}, 13-072-055^{p}, 13-073-009^{s}, 13-076-092^{s}
Haplopteris sikkimensis (Kuhn) E.H.Crane	HY	1168–1168	t1	13-102-288^{s}
Haplopteris taeniophylla (Copel.) E.H.Crane	NT&HY	2151–3003	r,t1,t2,t3,t4,t5	12-005-004^{s}, 12-007-014^{s}, 12-007-016^{s}, 13-076-091^{s}
Pteris alata Lam.	HY	497–527	g	13-116-005^{p}
Pteris arisanensis Tagawa*	HK&HY	892–1168	g	13-098-225^{p}, 13-102-263^{p}, 13-105-005^{p}
Pteris aspericaulis Wall. ex J. Agardh	NT, HK &HY	1036–3003	g,t1	12-005-003^{s}, 13-088-060^{s}, 13-090-011^{s}, 13-090-014^{s}, 13-093-018^{s}, 13-103-243^{s}, 13-104-017^{s}, 13-106-005^{s}, 14-041-014^{s}, 14-054-015^{p}
Pteris biaurita L.	NT&HY	519–1209	g	12-015-098^{s}, 12-057-004^{s}, 13-116-013^{p}, 14-054-003^{s}
Pteris cretica L.	NT&HK	1508–2471	g	12-069-001^{s}, 12-048-014^{p}, 14-031-023^{s}
Pteris fauriei Hieron.	HY	1051–2233	g	13-085-117^{s}, 13-106-022^{s}
Pteris khasiana (C.B.Clarke) Hieron.	HK&HY	1565–1833	g	13-092-001^{su}, 14-031-003^{u}
Pteris longipes D.Don	NT&HY	1168–1776	g	12-048-004^{u}, 12-077-002^{s}, 13-094-158^{s}
Pteris pellucens J.Agardh	HY	1168–1168	g	13-098-266^{p}
Pteris puberula Ching	HY	1715–2607	g	13-077-096^{s}
Pteris spinescens C.Presl	HY	1797–1833	g	13-092-007^{p}, 13-093-018^{s}
Dennstaedtiaceae				

Dennstaedtia zeylanica (Sw.) Zink ex Fraser-Jenk. & Kandel	HY	3138–3138	t1	13-064-060^{s}
Histiopteris incisa (Thunb.) J.Sm.	HY	1168–1168	g	13-102-286^{p}
Microlepia x *bipinnata* (Maxino) Shimura*	HK	1404–1448	g	14-047-009^{u}, 14-047-010^{u}
Microlepia calvescens (Wall. ex Hook.) C.Presl	HK	1404–1404	g	14-051-002^{u}
Microlepia intramarginalis (Tagawa) Seriz. *	HY	1168–1168	g	13-102-258^{s}
Microlepia rhomboidea (Wall. ex Kunze) Prantl	HY	527–1177	g	13-101-286^{u}, 13-106-028^{s}, 13-116-009^{s}, 14-061-009^{u}
Microlepia strigosa (Thunb.) C.Presl	HK&HY	1168–1665	g	13-098-234^{s}, 13-101-296^{u}, 13-102-284^{s}, 14-031-009^{u}, 14-041-006^{u}
Monachosorum henryi Christ	HY	2607–2839	g,r	13-072-064^{p}, 13-073-007^{p}, 13-074-074^{p}, 13-076-090^{p}
Cystopteridaceae				
Acystopteris tenuisecta (Blume) Tagawa	HY	2078–2078	g	13-088-055^{p}
Aspleniaceae				
Asplenium aethiopicum (Burm.f.) Bech.	NT	2011–2020	t1,t2,t3,t4	12-074-004^{u}
Asplenium crinicaule Hance	HY	874–1197	t1,t2	13-098-251^{s}, 14-057-012^{s}
Asplenium ensiforme Wall. ex Hook. & Grev.	NT&HY	892–3041	w,r,t1,t2,t3,t4	12-003-007^{u}, 12-005-005^{p}, 13-068-048^{p}, 13-070-049^{p}, 13-075-003^{p}, 13-077-100^{p}, 13-080-109^{p}, 13-102-261^{p}, 13-102-290^{p}, 14-060-008^{p}
Asplenium falcatum Lam.	HY	892–909	g,w,r	14-061-004^{s}
Asplenium finlaysonianum Wall. ex Hook	HY	1168–1168	g	13-102-276^{p}
Asplenium griffithianum Hook.	HY	678–1197	g,t1,t2	13-098-215^{p}, 13-101-273^{p}, 14-067-147^{p}
Asplenium indicum Sledge	HY	1036–2262	g,w,t1,t2,t3,t4	13-084-023^{p}

Asplenium lacinioides Fraser-Jenk., Pangtey & Khullar	HY	1714–2262	t1,t2	13-084-008^{s}, 13-085-116^{s}, 13-088-049^{p}, 13-088-059^{p}, 13-093-017^{p}, 13-094-147^{p}
Asplenium nidoides Fraser-Jenk. & Kandel	HK&HY	505–1833	w,t1,t2,t3,t4,t5	13-098-209^{p}, 13-105-009^{p}, 14-047-020^{u}, 14-066-242^{u}
Asplenium nitidum Sw.	HY	1059–1059	t1	13-104-005^{p}
Asplenium normale D.Don	HK&HY	715–1661	g,w,r,t1	13-098-223^{p}, 13-101-302^{p}, 13-102-269^{p}, 13-105-001^{p}, 13-105-030^{p}, 14-041-011^{s}, 14-047-005^{p}, 14-054-009^{u}, 14-059-009^{s}, 14-066-243^{s}
Asplenium paucivenosum (Ching) Bir	HY	2607–2632	r	13-076-076^{p}, 13-077-094^{s}
Asplenium phyllitidis D.Don	HK&HY	497–909	t1,t2,t3,t4	13-117-004a^{s}, 13-118-014^{u}, 14-061-014^{u}
Asplenium prolongatum Hook.	HK&HY	892–1197	t1,t2	13-098-207^{p}, 13-099-001^{p}, 13-101-280^{p}, 13-105-004^{p}, 14-054-023^{u}
Asplenium sikkimbirii Fraser-Jenk.*	HY	1168–1168	t1	13-098-232^{s}
Asplenium simonsianum Hook.*	HY	527–527	t1,t2,t3	13-116-017^{p}
Asplenium tenuifolium D.Don	NT	1753–2789	g,r,t1	12-007-002^{u}, 12-066-022^{u}
Asplenium varians Wall. ex Hook. & Grev.*	HK	1565–1665	t1,t2	14-032-019^{s}
Asplenium yoshinagae Makino	NT, HK&HY	678–2789	g,w,t1,t2,t3,t4	12-007-009^{s}, 12-048-005a^{s}, 12-097-023^{s}, 13-085-126^{s}, 13-090-013^{s}, 14-048-008^{s}, 14-050-006^{u}, 14-066-254^{s}
Hymenasplenium cheilosorum (Kunze ex Mett.) Tagawa	HY	1168–1833	g,t1	13-093-009^{p}, 13-101-285^{p}
Hymenasplenium excisum (C.Presl) S.Linds.	HY	1168–1168	r	13-098-221^{p}
Blechnaceae				
Blechnopsis orientalis (L.) C.Presl	HY	497–505	g	13-115-011^{s}

Athyriaceae				
Athyrium aff. *vermae* Fraser-Jenk. *	HY	1051–1059	g	13-104-016^{s}, 13-106-008^{p}
Athyrium anisopterum Christ*	NT	2151–2151	g	12-073-051^{s}
Athyrium atkinsonii Bedd.	NT	1745–3003	g	12-003-004^{u}
Athyrium cumingianum (C.Presl) Ching*	NT	450–585	g	12-022-001^{u}
Athyrium davidii (Franch.) Christ*	HY	3853–3853	g	13-055-016^{s}
Athyrium decurrenti-alatum (Hook.) Copel.*	HY	1168–2162	g	13-086-013^{s}, 13-098-238^{p}, 13-098-261^{p}, 13-102-268^{s}
Athyrium dissitifolium (Baker) C.Chr.	NT&HY	1492–3450	g,t1	12-012-018^{u}, 12-046-001^{s}, 12-046-006^{u}, 12-046-010^{s}, 13-065-045^{s}
Athyrium drepanopterum (Kunze) A.Braun ex Milde	NT&HY	1168–2151	g	12-015-094^{s}, 12-035-004^{s}, 13-102-294^{s}, 13-102-297^{s}
Athyrium fimbriatum (Wall.) T.Moore*	HY	3016–3502	g	13-067-040^{s}, 13-069-012^{p}, 14-015-006^{u}
Athyrium foliolosum T.Moore ex R.Sim*	HY	2029–2632	g,t1	13-076-087^{p}, 13-077-092^{p}, 13-077-104^{p}, 13-078-002^{s}, 13-078-006^{p}, 13-078-013^{p}, 13-079-088^{s}, 13-079-089^{p}, 13-088-053^{u}, 13-089-107^{u}
Athyrium himalaicum Ching ex Mehra & Bir*	HK	3603–3603	g,r	14-027-004^{s}
Athyrium imbricatum Christ*	HY	1036–1177	g	13-101-278^{s}, 14-054-002^{s}
Athyrium mearnsianum (Copel.) Alderw.*	HY	1168–1197	g	13-099-023^{u}, 13-102-295^{u}
Athyrium nakanoi Makino*	HY	2433–2433	g	13-083-081^{p}
*Athyrium opacum (*D.Don) Copel.	HY	1051–1197	g	13-099-002^{p}, 13-099-015^{s}, 13-101-301^{s}
Athyrium puncticaule (Blume) T.Moore*	HY	2162–2807	g	13-074-070^{p}, 13-074-072^{p}, 13-074-073^{p}, 13-075-009^{p}, 13-076-086^{s}, 13-086-005^{p}, 13-086-022^{p}, 13-086-026^{p}

Athyrium quadripinnatifidum (M.Kato) Seriz. (basionym of : Cornopteris badia Ching f. quadripinnatifida (M.Kato) W.M.Chu)*	HY	1168–2262	g	13-084-011^{s}, 13-098-208^{p}
Athyrium roseum Christ*	NT	2753–2753	g	12-041-005^{u}
Athyrium rupicola (Edgew. ex C.Hope) C.Chr.*	HY	3136–3863	g	13-054-016^{s}, 13-056-031^{s}, 13-067-044^{s}
Athyrium setiferum C.Chr.	HY	2433–3136	g,t1	13-065-043^{p}, 13-067-043^{s}, 13-077-099^{p}, 13-083-080^{p}
Deparia boryana (Willd.) M.Kato*	HY	1168–1833	g	13-093-011^{p}, 13-095-010^{s}, 13-102-274^{p}, 13-102-2964^{p}
Diplazium bellum Bir*	HY	1197–2433	g	13-088-054^{s}
Diplazium chattagramicum Ching*	HY	519–519	g	13-117-005^{s}
Diplazium dilatatum Blume	HK&HY	497–2162	g	13-086-027^{p}, 13-098-250^{s}, 13-099-010^{p}, 13-101-298^{s}, 13-115-005^{p}, 13-115-008^{s}, 14-047-008^{s}, 14-054-018^{s}, 14-061-008^{u}, 14-066-250^{s}, 14-067-143^{u}
Diplazium doederleinii (Luerss.) Makino*	HY	1051–1168	g	13-098-264^{p}, 13-102-285^{s}, 13-106-019^{p}
Diplazium donianum (Mett.) Tardieu*	HK&HY	497–1448	g	13-115-006^{s}, 13-117-001^{p}, 14-047-016^{u}, 14-066-238^{u}
Diplazium forrestii (Ching ex Z.R.Wang) Fraser-Jenk. *	HK&HY	1051–2209	g	13-085-120^{p}, 13-090-003^{s}, 13-106-025^{s}, 14-032-015^{u}
Diplazium kawakamii Hayata*	HY	2078–2078	g	13-088-041^{s}
Diplazium laxifrons Rosenst.*	HY	1059–2557	g,w	13-079-084^{s}, 13-081-096^{p}, 13-104-004^{s}
Diplazium spectabile (Wall. ex Mett.) Ching	HY	1047–1988	g	13-102-275^{s}, 13-105-011^{p}
Diplazium stoliczkae Bedd.*	HY	2262–2632	g	13-076-081^{s}, 13-077-090^{p}, 13-084-002^{p}
Diplazium succulentum	NT&HY	1776–2262	g	12-048-011^{s}, 13-

(C.B.Clarke) C.Chr.*				084-001^{s}
Thelypteridaceae				
Christella crinipes (Hook.) Holttum	HY	1197–1197	g	13-099-022^{s}
Christella dentata (Forssk.) Brownsey & Jermy	NT	1753–2011	g	12-048-013^{s}, 12-074-012^{s}
Christella procera (D.Don) Mazumdar	NT&HY	497–1665	g	12-046-009^{s}, 13-103-242^{u}, 13-116-006^{p}, 13-116-008^{s}, 14-055-005^{u}
Christella siamensis (Tagawa & K.Iwats.) Holttum*	HY	1046–1051	g	13-103-260^{s}
Cyclogramma auriculata (J.Sm.) Ching*	HY	2433–2433	g	13-083-084^{u}
Glaphyropteridopsis erubescens (Wall. ex Hook.) Ching	NT	2011–2011	g	12-074-002^{u}
Metathelypteris decipiens (C.B.Clarke) Ching	HY	1168–1988	g	13-090-006^{s}, 13-102-271^{s}
Metathelypteris flaccida (Blume) Ching	HY	1168–1168	g	13-102-273^{p}
Pronephrium articulatum (Houlston & T.Moore) Holttum*	HY	527–527	g	13-116-014^{p}
Pronephrium lakhimpurense (Rosenst.) Holttum	HY	1797–1833	g	13-092-005^{s}
Pronephrium triphyllum (Sw.) Holttum	HY	505–527	g	13-115-016^{p}, 13-116-010^{s}
Sphaerostephanos validus (Christ) Holttum*	NT	790–1197	g	12-016-012^{s}, 12-057-002^{u}
Thelypteris loyalii Fraser-Jenk.*	HY	1047–1168	g	13-102-266^{s}, 13-105-012^{p}
Thelypteris ornatipes Fraser-Jenk.*	HY	1177–1197	g	13-099-003^{s}
Hypodematiaceae				
Leucostegia truncata (D.Don) Fraser-Jenk.*	NT&HY	1429–2789	g,w,t1,t2,t3,t4,t5	12-007-020^{s}, 12-012-011^{u} , 13-093-025^{p}, 13-093-030^{p}
Dryopteridaceae				
Arachniodes assamica (Kuhn) Ohwi	HY	1833–1833	g	13-093-008^{s}
Arachniodes henryi (Christ) Ching	HY	1833–1833	g	13-093-004^{p}, 13-093-016^{p}

Arachniodes spectabilis (Ching) Ching*	NT, HK&HY	527–2433	g	12-048-008^{s}, 13-081-098^{u}, 13-083-082^{u}, 13-086-004^{u}, 13-090-002^{u}, 13-093-015^{u}, 13-101-287^{u}, 14-032-036^{u}, 14-041-004^{u}, 14-048-003^{u}, 14-050-008^{u}
Arachniodes superba Fraser-Jenk.*	HY	2557–2804	g,r	13-074-064^{s}
Bolbitis appendiculata (Willd.) K.Iwats.	HY	678–715	g,t1	14-066-245^{u}, 14-067-145^{s}
Bolbitis crispatula (Wall.) Ching*	NT	1209–1209	g	12-015-101^{s}
Bolbitis heteroclita (C.Presl) Ching	HY	497–1197	g,w,r,t1,t2	13-098-248^{p}, 13-099-019^{s}, 13-103-259^{p}, 13-118-008^{p}, 14-054-019^{u}, 14-066-239^{u}
Bolbitis sinensis K.Iwats.	NT&HY	715–1776	g	12-048-002^{s}, 14-066-244^{s}
Ctenitis apiciflora (Wall. ex Mett.) Ching*	HY	2262–2839	g,w	13-072-060^{p}, 13-074-067^{p}, 13-075-067^{p}, 13-079-081^{p}
Ctenitis clarkei (Baker) Ching	HY	1715–3138	g,w,t1,t2	13-064-050^{p}, 13-072-056^{p}
Ctenitis dumrongii Tagawa & K.Iwats.*	HY	2233–2262	g	13-084-021^{u}
Dryopteris acutodentata Ching*	HK	3575–3603	g,r	14-027-012^{s}
Dryopteris alpestris Tagawa*	HY	3834–4057	g	13-049-010^{p}, 13-056-030^{p}
Dryopteris caroli-hopei Fraser-Jenk*	NT	1492–2473	g	12-007-015^{s}, 12-012-006^{p}, 12-012-015^{s}
Dryopteris cochleata (Buch.-Ham. ex D.Don) C.Chr.	NT	450–2011	g,r,t1	12-015-095^{u}, 12-015-096^{p}, 12-015-100^{p}, 12-016-008^{s}, 12-016-015^{p}, 12-017-101^{p}, 12-017-102^{p}, 12-017-103^{p}, 12-017-104^{u}, 12-017-105^{u}, 12-017-106^{p}, 12-017-107^{u}, 12-017-108^{p}, 12-017-109^{s}, 12-017-110^{p}, 12-074-001^{u}, 12-087-004^{s}
Dryopteris diffracta	HY	1177–1197	g	13-099-026^{s}, 13-

(Baker) C. Chr.				101-300^{u}
Dryopteris hirtipes (Blume) Kuntze subsp. *atrata* (Wall. ex Kunze) Fraser-Jenk.	NT, HK&HY	1508–1988	g,t1	12-048-007^{u}, 13-090-008^{s}, 14-031-004^{u}
Dryopteris neoassamensis Ching*	HK	1404–2078	g	14-051-008^{s}
Dryopteris paleolata (Pic.Serm.) Li Bing Zhang*	HY	2162–3138	g,w	13-064-049^{s}, 13-068-050^{p}, 13-072-062^{s}, 13-073-004^{p}, 13-078-009^{p}, 13-081-100^{p}, 13-084-013^{p}, 13-086-002^{p}, 13-087-101^{p}
Dryopteris peranema Li Bing Zhang*	NT	2957–2957	g	12-003-003^{s}
Dryopteris pseudocaenopteris (Kunze) Li Bing Zhang*	NT, HK&HY	1168–2632	g,t1	12-007-023^{u}, 12-073-053^{s}, 13-076-085^{p}, 13-076-088^{p}, 13-077-089^{p}, 13-077-105^{s}, 13-080-114^{p}, 13-085-113^{p}, 13-085-114^{p}, 13-085-115^{p}, 13-085-125^{p}, 13-086-010^{p}, 13-088-033^{p}, 13-092-003^{p}, 13-102-293^{s}, 14-031-015^{u}, 14-032-004^{u}, 14-041-012^{p}, 14-042-006^{u}, 14-048-006^{s}, 14-051-007^{s}
Dryopteris rubrobrunnea W.M.Chu*	HY	2233–2607	g	13-077-098^{s}, 13-083-085^{p}, 13-084-017^{p}, 13-084-018^{p}
Dryopteris scottii (Bedd.) Ching	NT, HK&HY	892–1833	g,w	13-093-010^{s}, 13-098-213^{p}, 13-099-004^{p}, 13-101-282^{p}, 13-102-278^{p}, 14-060-003^{u}, 14-061-002^{u}
Dryopteris sikkimensis (Bedd.) Kuntze*	HY	2807–3138	g,t1	13-064-051^{s}, 13-065-044^{p}, 13-066-037^{p}, 13-067-037^{p}, 13-072-061^{p}, 13-075-061^{p}
Dryopteris sparsa (D.Don) Kuntze	HK&HY	497–1665	g,w,t1	13-102-292^{p}, 13-103-261^{u}, 13-105-007^{p}, 13-106-021^{u}, 13-118-005^{p}, 14-

				031-018^{u}, 14-032-009^{u}, 14-054-004^{u}, 14-054-016^{p}, 14-055-006^{u}, 14-057-002^{u}
Dryopteris stenolepis (Baker) C.Chr.	HY	1833–1833	g	13-093-022^{p}
Dryopteris vidyae Fraser-Jenk.*	HY	1046–1046	g	13-103-263^{u}
Dryopteris wallichiana (Spreng.) Hyl.	NT&HY	2557–3003	g	12-003-002^{u}, 13-079-086^{p}
Dryopteris woodsiisora Hayata*	HK	3400–3603	g,t1	14-015-004^{u}, 14-027-003^{s}
Dryopteris pseudosparsa Ching*	HY	833–909	g,w	14-057-003^{u}, 14-059-004^{u}
Elaphoglossum marginatum (Wall. ex Fée) T.Moore*	NT, HK&HY	1360–2471	w,t1,t2,t3, t4,t5	12-097-028^{s}, 13-085-123^{p}, 13-086-009^{p}, 13-088-035^{s}, 13-090-005^{p}, 14-050-013^{s}
Elaphoglossum stelligerum (Wall. ex Baker) T.Moore ex Salomon*	NT, HK&HY	1168–1803	w,t1,t2,t3, t4	12-046-007^{u}, 12-051-005^{u}, 12-078-001^{u}, 13-098-243^{p}, 13-098-262^{s}, 14-031-026^{u}, 14-032-011^{u}, 14-032-012^{s}, 14-048-007^{u}
Elaphoglossum yoshinagae (Yatabe) Makino*	HY	874–874	t1	14-057-010^{s}
Lomagramma sorbifolia (Willd.) Ching	HY	519–527	t1	13-116-020^{s}, 13-117-010^{p}
Pleocnemia cf. submembrancea (Hayata) Tagawa & K.Iwats.*	HY	614–678	g	14-067-178^{s}
Polystichum atkinsonii Bedd.*	HY	3136–3136	r	13-067-039^{s}
Polystichum discretum (D.Don) J.Sm.*	NT&HY	1168–2480	g	12-066-021^{u}, 13-102-272^{s}, 13-102-287^{s}
Polystichum hookerianum (C.Presl) C.Chr.	HY	2039–2233	g	13-086-003^{p}, 13-088-036^{p}
Polystichum lentum (D.Don) T.Moore*	NT&HY	1833–2480	g,r	12-073-052^{s}, 13-090-015^{p}, 13-093-023^{s}
Polystichum longipaleatum Christ*	HY	2371–2829	g	13-072-065^{s}, 13-075-007^{p}, 13-077-088^{p}, 13-083-078^{p}
Polystichum manmeiense	NT&HY	2433–2789	g,r	12-041-006^{s}, 13-

(Christ) Nakaike*				076-077s, 13-083-076^{s}
Polystichum moupinense (Franch.) Bedd.*	HK	3603–3603	g	14-027-002^{u}
Polystichum scariosum (Roxb.) C.V.Morton*	HY	892–1833	g	13-093-020^{u}, 13-095-004^{s}, 14-060-005^{u}, 14-061-010^{u}
Polystichum semifertile (C.B.Clarke) Ching*	NT, HK&HY	1447–3003	g,w,r,t2	12-007-011^{u}, 12-037-001^{u}, 12-037-003^{u}, 12-041-001^{u}, 12-048-003^{u}, 12-066-020^{u}, 12-069-003^{u}, 12-073-054^{u}, 12-076-049^{u}, 12-076-050^{u}, 12-077-001^{u}, 12-077-003^{u}, 13-081-097^{p}, 13-083-075^{s}, 13-083-083^{p}, 13-087-100^{p}, 13-090-010^{s}, 14-031-002^{u}, 14-042-002^{u}, 14-048-002^{u}
Polystichum squarrosum (D.Don) Fée*	NT	2471–2789	g	12-037-002^{u}
Polystichum woodsioides Christ*	HK&HY	3588–3863	g,r	13-054-017^{p}, 13-057-001^{s}, 13-057-002^{p}, 13-057-003^{s}, 13-057-004^{p}, 14-026-002^{s}
Polystichum pseudotsus-simense Ching	NT	2665–2959	g	12-003-001^{su}, 12-041-002^{u}, 12-041-003^{u}, 12-041-007^{u}
Nephrolepidaceae				
Nephrolepis cordifolia (L.) C.Presl	HY	497–1197	w,t1,t2,t4, t5	13-098-224^{p}, 13-098-249^{p}, 13-099-009^{p}, 13-099-017^{p}, 13-101-281^{p}, 13-101-288^{p}, 13-102-291^{p}, 13-104-008^{p}, 13-106-020^{p}, 13-118-010^{p}, 14-061-005^{s}
Tectariaceae				
Tectaria coadunata (J.Sm.) C.Chr.	NT	790–1449	g,t1	12-016-009^{u}, 12-016-010^{u}
Tectaria dubia (C.B.Clarke & Baker) Ching*	HY	678–715	g	14-067-142^{s}
Tectaria fuscipes (Wall. ex Bedd.) C.Chr.	HY	519–519	g	13-117-009^{s}

Tectaria ingens (Atk. ex C.B.Clarke) Holttum*	HY	1168–1833	g	13-093-007^{s}, 13-102-267^{p}
Tectaria polymorpha (Wall. ex Hook.) Copel.	HK	1360–1665	g	14-032-002^{s}
Oleandraceae				
Oleandra musifolia (Blume) C.Presl	NT	1492–1492	t2,t3	12-046-008^{s}
Oleandra neriiformis Cav.	HK&HY	1197–1797	t1,t2,t3,t4,t5	13-099-005^{s}, 14-031-024^{u}
Oleandra wallichii (Hook.) C.Presl	NT, HK&HY	1508–3047	t1,t2,t3,t4,t5	12-007-007^{s}, 13-069-006^{p}, 13-073-002^{p}, 13-076-078^{p}, 13-084-015^{p}, 14-041-017^{s}
Davalliaceae				
Davallia assamica (Bedd.) Baker	HK&HY	1036–2807	g,w,t1,t2,t3,t4,t5	13-092-095^{p}, 13-093-027^{p}, 13-094-154^{p}, 13-094-149^{p}, 13-095-001^{s}, 13-095-009^{s}, 13-098-220^{p}, 13-098-237^{p}, 13-099-018^{p}, 13-099-024^{p}, 13-101-272^{p}, 13-101-276^{p}, 13-102-270^{p}, 13-103-244^{b}, 13-105-010^{p}, 13-105-018^{p}, 13-106-006^{s}, 13-106-013^{p}, 13-106-014^{p}, 14-031-025^{u}, 14-032-005^{u}, 14-041-015^{u}, 14-047-004^{u}, 14-054-012^{u}, 14-055-008^{u}
Davallia denticulata (Burm.f.) Mett. ex Kuhn	HY	527–527	t1	13-116-001^{s}
Davallia griffithiana Hook.	HY	519–1197	g,t3,t4,t5	13-106-017^{p}, 13-117-007^{s}
Davallia multidentata Hook.*	HY	1714–2078	w,t1,t2,t3,t4,t5	13-088-052^{p}, 13-089-111^{p}, 13-090-009^{s}, 13-095-011^{p}
Davallia perdurans Christ	HY	2600–2600	t2	13-078-007^{s}
Davallia pulchra D.Don	NT, HK&HY	847–3003	w,t1,t2,t3,t4,t5	12-003-005^{s}, 12-005-001^{s}, 12-094-001^{u}, 14-041-003^{u}, 14-042-007^{u}, 14-047-002^{u}, 14-050-007^{s}

Davallia trichomanoides Blume	NT&HY	505–1492	t1,t2,t3,t4,t5	12-092-057^u, 12-092-058^u, 13-103-262^s, 13-115-020^p, 14-057-018^u, 14-059-007^u, 14-066-241^u, 14-067-144^u
Polypodiaceae				
Aglaomorpha coronans (Wall. ex Mett.) Copel.	HY	497–1168	g,w,t1,t2,t3,t4,t5	13-098-246^p, 13-102-279^p, 13-103-257^p, 13-106-015^p, 13-115-021^p, 13-115-023^u, 14-055-003^u
Aglaomorpha delavayi (Christ) Hovenkamp & S.Linds.*	NT	2082–2184	t1,t2,t3,t4,t5	12-012-014^s
Aglaomorpha parishii (Bedd.) Hovenkamp & S.Linds*	HY	1046–1046	t1	13-103-275^s
Aglaomorpha propinqua (Wall. ex Mett.) Hovenkamp & S.Linds.	NT, HK&HY	892–1665	g,w,t1,t2,t3,t4,t5	12-046-004^p, 13-098-214^p, 13-101-274^p, 13-101-294^p, 13-102-259^p, 13-106-007^p, 13-106-026^p, 14-031-008^p, 14-032-008^s, 14-041-007^s, 14-054-006^u, 14-061-013^s
Aglaomorpha quercifolia (L.) Hovenkamp & S.Linds.	HY	505–505	t4	13-115-002^p
Arthromeris amplexifolia Ching*	NT	1595–1745	t1,t2,t3,t4	12-051-004^s
Arthromeris cyrtomioides S.G.Lu & C.D.Xu*	HY	1988–2233	t2,t3,t4,t5	13-086-016^p, 13-087-104^p, 13-088-058^u
Arthromeris elegans Ching*	HY	1051–2078	t2,t3,t4,t5	13-088-050^u, 13-106-016^u
Arthromeris himalovata Fraser-Jenk. & Kandel*	HY	2804–3133	t1,t2,t3,t4	13-066-040^s, 13-070-047^p, 13-072-059^p
Arthromeris lehmannii (Mett.) Ching	NT&HY	1168–3136	g,t1,t2,t3,t4,t5	12-007-017^{su}, 12-012-005^u, 12-057-001^u, 12-069-002^s, 13-065-042^p, 13-068-049^p, 13-069-001^p, 13-070-051^p, 13-081-099^s, 13-084-010^p, 13-084-

				012^{s}, 13-098-245a^{p}
Arthromeris tomentosa W.M.Chu*	HY	2162–2400	t1,t2,t3,t4,t5	13-080-102^{s}, 13-086-028^{p}, 13-087-105^{p}
Arthromeris wallichiana (Spreng.) Ching	HY	1797–2434	t2,t3,t4,t5	13-080-115^{p}, 13-082-080^{p}, 13-085-121^{p}
Arthromeris wardii (C.B.Clarke)	HY	2371–3047	t1	13-069-008^{s}, 13-081-102^{p}
Goniophlebium amoenum (Wall. ex Mett.) Bedd.	HK&HY	678–3047	g,w,r,t1,t2,t3,t4,t5	13-069-004^{p}, 13-069-005^{p}, 13-069-009^{p}, 13-070-048^{p}, 13-071-002^{p}, 13-080-110^{p}, 13-081-101^{p}, 13-081-103^{p}, 13-084-007^{p}, 13-084-020^{s}, 13-086-011^{p}, 13-086-015^{u}, 13-086-023^{p}, 13-087-102^{p}, 13-088-040^{p}, 13-088-051^{p}, 13-091-005^{p}, 13-093-029^{p}, 13-093-035^{s}, 13-093-031^{p}, 13-094-155^{p}, 13-095-137^{p}, 13-098-258^{u}, 13-099-007^{p}, 13-101-275^{p}, 13-101-299^{s}, 13-103-265^{p}, 13-103-282^{p}, 13-104-001^{s}, 14-031-006^{u}, 14-032-034^{u}, 14-047-018^{s}, 14-054-017^{u}, 14-057-004^{u}, 14-060-007^{p}
Goniophlebium argutum (Wall. ex Hook.) J.Sm. ex Hook.	NT&HY	1492–2839	g,t1,t2,t3,t4,t5	12-007-018^{ps}, 12-048-010^{u}, 12-065-045^{s}, 13-072-063^{s}, 13-078-008^{p}, 13-084-009^{p}, 13-085-118^{s}
Goniophlebium bourretii (C.Chr. & Tardieu) X.C.Zhang*	HY	1046–1046	t2,t3	13-103-255^{s}
Goniophlebium lachnopus (Wall. ex Hook.) J.Sm.*	NT	2082–2765	t1,t2,t3,t4,t5	12-007-019^{s}

Goniophlebium manmeiense (Christ) Rödl-Linder	NT, HK&HY	1404–2480	w,t1,t2,t3,t4,t5	12-007-021^{u}, 12-012-012^{s}, 12-012-013^{s}, 13-085-122^{s}, 13-087-099^{s}, 14-047-011^{u}
Goniophlebium mengtzeense (Christ) Rödl-Linder*	NT&HY	2029–3003	t1,t3,t4,t5	12-005-002^{s}, 13-089-110^{s}
Goniophlebium niponicum (Mett.) Bedd.*	HK&HY	892–1565	w,t1,t2,t3,t4,t5	13-098-227^{p}, 13-102-283^{s}, 13-104-011^{s}, 13-105-014^{s}, 13-106-027^{p}, 14-031-016^{u}, 14-055-004^{u}
Goniophlebium subauriculatum (Blume) C.Presl	HY	505–527	t1,t3	13-115-015^{u}, 13-116-004^{s}
Gymnogrammitis dareiformis (Hook.) Ching ex Tardieu & C.Chr.	NT	2082–2473	g,t1,t2,t3,t4	12-007-006^{u}
Lemmaphyllum carnosum (Wall. ex J.Sm.) C.Presl	HK&HY	497–2078	w,t1,t2,t3,t4,t5	13-088-039^{p}, 13-088-064^{s}, 13-094-162^{p}, 13-094-163^{p}, 13-095-008^{p}, 13-095-126^{p}, 13-098-210^{p}, 13-098-235^{p}, 13-098-263^{p}, 13-098-267^{p}, 13-099-008^{s}, 13-099-011^{s}, 13-099-012^{s}, 13-099-013^{s}, 13-101-279^{p}, 13-103-241^{p}, 13-103-256^{p}, 13-103-266^{p}, 13-103-271^{p}, 13-104-010^{p}, 13-104-012^{p}, 13-105-008^{p}, 13-105-023^{p}, 13-105-027^{p}, 13-105-025^{p}, 13-106-018^{p}, 13-115-013^{s}, 13-117-002^{p}, 13-117-003^{p}, 13-118-001^{p}, 14-031-014a^{u}, 14-050-010^{s}, 14-054-011^{s}, 14-054-024^{p}, 14-055-007^{u}
Lemmaphyllum microphyllum C.Presl*	HY	833–909	t1,t3	14-057-006^{u}, 14-059-008^{u}, 14-060-006^{s}

Lemmaphyllum rostratum (Bedd.) Tagawa	HY	1715–2162	t1,t2,t3,t4	13-086-008^{p}, 13-088-038^{p}, 13-089-108^{p}, 13-092-009^{p}, 13-093-021^{p}, 13-094-150^{p}
Lepidomicrosorium superficiale (Blume) Li Wang	HK&HY	1360–2162	g,r,t1,t2	13-086-006^{p}, 13-092-004^{p}, 13-093-003^{u}, 13-093-033^{p}, 13-094-142^{p}, 14-031-005^{p}, 14-031-007^{u}
Lepisorus bicolor (Takeda) Ching*	NT&HY	2082–3047	t1,t2,t3,t4, t5	12-003-008^{u}, 13-068-046^{p}, 13-069-013^{p}, 13-069-014^{p}
Lepisorus contortus (Christ) Ching	HY	497–2233	t1,t2,t3,t4, t5	13-086-018^{s}, 13-087-109^{p}, 13-088-065^{p}, 13-094-161^{p}, 13-098-244^{s}, 13-103-280^{p}, 13-105-026^{p}, 13-106-023^{s}, 13-118-003^{p}
Lepisorus henryi (Hieron. ex C.Chr.) Li Wang	HK&HY	1046–1714	w,t1,t2,t3, t4	13-095-015^{s}, 13-102-282^{s}, 13-103-270^{s}, 13-104-006^{s}, 13-105-020^{s}, 13-106-030^{s}, 14-050-002^{s}
Lepisorus loriformis (Wall. ex Mett.) Ching*	HY	2029–2839	t1,t2,t3,t4, t5	13-073-001^{p}, 13-073-008^{p}, 13-074-068^{p}, 13-077-095^{p}, 13-087-103^{p}, 13-087-110^{p}, 13-089-115^{p,} 13-089-116^{s}
Lepisorus macrosphaerus (Baker) Ching	HY	1177–2433	t1,t2,t3,t4, t5	13-086-019^{p}, 13-087-111^{p}, 13-095-135^{s}
Lepisorus mehrae Fraser-Jenk.*	NT&HY	2167–2807	w,t1,t2,t3, t4	12-012-009^{u}, 13-075-001^{s}
Lepisorus mucronatus (Fée) Li Wang*	HY	497–1715	w,t1,t2,t3, t4	13-094-148^{s}, 13-098-247^{s}, 13-098-252^{s}, 13-098-253^{s}, 13-101-277^{s}, 13-103-272^{s}, 13-105-006^{s}, 13-105-021^{s}, 13-105-029^{s}, 13-106-009^{s}, 13-106-010^{s}, 13-106-011^{s}, 13-106-031^{s}, 13-106-032^{s}, 13-118-002^{s}, 14-059-002^{s}

Lepisorus nudus (Hook.) Ching*	NT, HK&HY	1046–2233	g,w,t1,t2,t3,t4,t5	12-046-003a^{s}, 12-071-001^{u}, 12-074-007^{u}, 13-095-012^{s}, 13-098-254^{u}, 13-103-278^{s}, 14-032-013^{u}, 14-041-009^{p}
Lepisorus scolopendrium (Ching) Mehra & Bir	NT	1194–2789	g,t1,t2,t3,t4,t5	12-012-010^{u}, 12-046-002^{u}, 12-046-003^{u}, 12-071-002^{u}
Lepisorus spicatus (L.f.) Li Wang*	HY	874–1197	w,t1,t4	14-054-013^{u}, 14-057-009^{p}
Lepisorus subconfluens Ching	HK&HY	715–1833	w,t1,t2,t3,t4	13-093-026^{p}, 13-098-255^{s}, 13-104-002^{p}, 14-032-018^{u}, 14-048-012^{u}, 14-066-253^{s}
Lepisorus sublinearis (Baker ex Takeda) Ching	NT, HK&HY	1168–2839	t1,t2,t3,t4,t5	12-076-051^{s}, 13-072-058^{p}, 13-073-005^{p}, 13-075-005^{p}, 13-076-091^{bs}, 13-077-097^{p}, 13-079-087^{p}, 13-081-104^{p}, 13-084-014^{s}, 13-086-021^{u}, 13-089-109^{p}, 13-090-016^{p}, 13-091-003^{p}, 13-093-019^{p}, 13-094-145^{p}, 13-095-130^{s}, 13-098-255(b)^{s}, 13-102-281^{p}, 14-042-008^{u}
Leptochilus chittagongensis Fraser-Jenk. & Gias*	HY	1051–1051	w,t1,t2	13-106-004^{u}
Leptochilus ellipticus (Thunb.) Noot.	HY	1448–1833	g	13-093-024^{p}, 14-047-017^{s}
Leptochilus hemionitideus (C.Presl) Noot.	NT&HY	833–1776	g,w,r,t1,t2	12-048-001^{u}, 13-098-212^{p}, 13-098-259^{u}, 13-103-240^{s}, 13-105-022^{s}, 13-106-002^{u}, 14-054-026^{u}
Leptochilus insignis (Blume) Fraser-Jenk.	HY	1714–2078	g,r,t1	13-088-042^{p}, 13-093-006^{p}
Leptochilus macrophyllus (Blume) Noot.*	HY	614–614	t1	14-070-004^{s}
Leptochilus minor Fée*	HY	497–1047	t1	13-105-031^{p}, 13-118-004^{s}

Leptochilus pedunculatus (Hook. & Grev.) Fraser-Jenk.	HY	497–2162	g,w,r,t1,t2	13-086-007^{p}, 13-086-024^{p}, 13-088-032^{p}, 13-089-105^{p}, 13-090-004^{p}, 13-092-006^{p}, 13-094-144^{p}, 13-103-249^{p}, 13-103-258^{p}, 13-105-015^{p}, 13-115-007^{u}, 13-116-018^{s}, 14-047-003^{s}, 14-059-003^{u}
Loxogramme chinensis Ching	NT	1753–2753	r,t1,t2,t3,t4	12-007-012^{s}
Loxogramme porcata M.G. Price*	HK&HY	678–1797	t1,t2,t3,t4	13-094-156^{p}, 13-095-006^{p}, 13-095-013^{p}, 13-098-241^{p}, 13-099-021^{p}, 13-103-248^{s}, 13-103-274^{p}, 13-103-283^{p}, 14-032-006^{s}, 14-066-252^{s}
Loxogramme subecostata (Hook.) C.Chr.*	NT	2181–2181	t1,t2	12-012-007^{s}
Micropolypodium sikkimense (Hieron.) X.C.Zhang*	HY	2400–3138	t1,t2,t3	13-064-045^{p}
Microsorum aichmophyllum (Alston) Fraser-Jenk.	HY	2078–2262	g,t1,t2	13-084-003^{s}
Microsorum cuspidatum (D. Don) Tagawa	HK&HY	909–1447	t1,t2,t3,t4,t5	13-098-257^{p}, 13-099-016^{p}, 14-048-010^{u}, 14-050-009^{s}
Microsorum membranaceum (D.Don) Ching	NT&HY	1073–1776	g,w,t1,t2,t3,t4,t5	12-015-093^{s}, 12-048-005^{s}, 13-095-003^{u}
Microsorum punctatum (L.) Copel.	HK&HY	505–1059	t1,t2,t3,t4	13-104-013^{p}, 13-115-003^{p}, 13-116-002^{p}, 13-117-004^{p}, 14-066-249^{u}
Neolepisorus zippelii (Blume) Li Wang	HK&HY	833–1197	g,t1,t3,t4	13-098-260^{p}, 13-099-006^{p}, 13-103-253^{u}, 13-103-246^{p}, 14-054-005^{u}, 14-061-003^{u}
Platycerium wallichii Hook.	NT	566–1073	t1,t2,t3,t4	12-028-001^{p}
Prosaptia khasyana (Hook.) C.Chr. & Tardieu	HY	909–909	t3	14-061-011^{u}

Pyrrosia costata (Wall. ex C.Presl) Tagawa & K.Iwats.*	HY	678–1197	t1,t2,t3,t4, t5	13-098-228^{p}, 13-101-283^{p}, 13-102-289^{p}, 13-103-250^{p}, 13-103-254^{p}, 13-105-016^{p}, 13-105-032^{p}, 13-106-029^{p}, 14-054-010^{p}, 14-054-025^{u}, 14-060-012^{p}, 14-060-013^{s}, 14-066-247^{u}
Pyrrosia heteractis (Mett. ex Kuhn) Ching	HK&HY	1508–2078	t1,t2,t3,t4, t5	13-088-061^{s}, 13-094-151^{p}, 14-031-022^{s}, 14-041-005^{u}
Pyrrosia laevis (J.Sm. ex Bedd.) Ching*	HY	833–874	t1,t2	14-057-013^{s}
Pyrrosia lanceolata (L.) Farw.	HY	505–715	t1,t2,t3,t4	13-115-014^{p}, 13-115-018^{p}, 13-116-011^{p}, 13-116-016^{p}, 13-117-008^{s}, 14-066-248^{s}, 14-070-003^{s}
Pyrrosia lingua (Thunb.) Farw.	HY	833–909	t2,t3,t4	14-057-016^{u}, 14-060-010^{p}
Pyrrosia mannii (Giesenh.) Ching*	HY	715–715	t1	14-066-251^{u}
Pyrrosia nummulariifolia (Sw.) Ching	HY	505–505	t3	13-115-019^{s}
Pyrrosia tonkinensis (Giesenh.) Ching*	HK	1565–1565	t3,t4	14-031-019^{s}
Pyrrosia flocculosa (D.D on) Ching	HY	1833–1833	t1	13-093-028^{s}
Pyrrosia subfurfuracea (Hook.) Ching	HK&HY	1508–1715	t1,t3,t4,t5	13-094-164^{p}, 13-095-134^{u}, 14-041-018^{u}
Selliguea ebenipes (Hook.) S.Linds.	NT&HY	1197–3138	t1,t2,t3,t4, t5	12-003-006^{u}, 13-064-057^{p}, 13-066-041^{p}, 13-067-041^{p}, 13-069-002^{p}, 13-069-003^{p}, 13-071-003^{p}
Selliguea griffithiana (Hook.) Fraser-Jenk.	HY	1046–3016	w,t1,t2,t3, t4,t5	13-070-046^{p}, 13-071-001^{p}, 13-073-003^{p}, 13-076-084^{s}, 13-077-106^{p}, 13-086-025^{p}, 13-088-048^{p}, 13-091-004^{p}
Selliguea incisocrenata (Ching ex W.M.Chu & S.G.Lu) S.G.Lu, Hovenkamp &	NT	2957–3003	t1,t2,t3,t4	12-005-006^{s}

M.G.Gilbert*				
*Selliguea kachinensis (*Hovenkamp, S.Linds. & Fraser-Jenk.) (treated as *Arthromeris kachinensis* (Hovenkamp, S.Linds. & Fraser-Jenk.) Fraser-Jenk., Odyuo & D.K.Roy (Mao *et al.*, 2017)).*	HK&HY	1404–1715	t3,t4,t5	13-094-159^{l,s}, 14-031-020^{l}, 14-047-022^{l,s}
Selliguea majoensis (C. Chr.) Fraser-Jenk.*	HK	1661–1665	t3	14-032-208^{s}
Selliguea malacodon (Hook.) S.G.Lu, Hovenkamp & M.G.Gilbert*	HK	3400–3601	g,w,r,t1,t2,t3	14-015-001^{s}
Selliguea nigropaleacea (Ching) S.G.Lu, Hovenkamp & M.G.Gilbert*	HY	2078–3138	t1,t2,t3,t4,t5	13-064-048^{p}, 13-064-056b^{u}, 13-064-058^{s}, 13-064-059^{p}, 13-066-033^{p}, 13-069-016^{u}
Selliguea oxyloba (Wall. ex Kunze) Fraser-Jenk.	NT&HK	1404–2659	t1,t2,t3,t4,t5	12-012-008^{u}, 14-031-021^{u}
Selliguea quasidivaricata (Hayata) H.Ohashi & K.Ohashi*	HY	2804–3138	t1,t2,t3,t4,t5	13-064-046^{p}, 13-065-041^{s}, 13-066-042^{p}, 13-067-038^{s}, 13-075-006^{s}
Selliguea rhynchophylla (Hook.) Fraser-Jenk.	HK&HY	1360–3047	t1,t2,t4,t5	13-085-124^{s}, 14-051-009^{u}
Selliguea stewartii (Bedd.) S.G.Lu, Hovenkamp & M.G.Gilbert*	HY	3133–3138	t1,t2,t3,t4	13-064-056^{p}, 13-066-038^{p}, 13-067-036^{p}
Selliguea tibetana (Ching & S.K.Wu) S.G.Lu , Hovenkamp & M.G.Gilbert*	HY	2400–2400	t2,t3,t4,t5	13-080-103^{s}
Tomophyllum donianum (Spreng.) Fraser-Jenk. & Parris	NT&HY	2181–3133	r,t1	12-007-004^{s}, 13-066-034^{p}, 13-075-010^{s}, 13-083-079^{p}
Tricholepidium normale (D.Don) Ching	HK&HY	1046–2434	g,w,r,t1,t2,t3	13-080-106^{p}, 13-080-107^{u}, 13-082-079^{s}, 13-084-004^{p}, 13-084-005^{u}, 13-084-006^{u}, 13-085-111^{s}, 13-086-001^{s}, 13-086-014^{p}, 13-087-097^{s}, 13-087-098^{p}, 13-087-107^{u}, 13-088-031^{s}, 13-088-063^{s}, 13-088-

				062^{s}, 13-088-066^{s}, 13-089-106^{u}, 13-090-007^{s}, 13-091-001^{u}, 13-092-002^{u}, 13-092-008^{p}, 13-093-012^{s}, 13-093-013^{p}, 13-093-014^{p}, 13-103-264^{s}, 13-103-268^{s}, 14-032-003^{p}, 14-047-012^{s}, 14-047-014^{s}
Tricholepidium venosum Ching*	HY	2233–2600	r,t1,t2,t3	13-078-010^{p}, 13-080-105^{p}, 13-083-077^{p}, 13-087-106^{p}

CHAPTER 4

Highlight of the region: New fern species

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with Stuart Lindsay, Christopher Fraser-Jenkins, Jürgen Kluge,
Myint Kyaw and Peter Hovenkamp

Selliguea kachinensis (Polypodiaceae), a new fern species of uncertain affinity from Northern Myanmar

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Abstract.—We describe *Selliguea kachinensis* as a new species from Northern Myanmar and discuss its generic placement in either *Selliguea* or *Arthromeris*. The conservation status is assessed as Data Deficient. In addition, we make the new combination *Selliguea erythrocarpa* (Mett. ex Kuhn) Hovenkamp, S. Linds., Fraser-Jenk.

Keywords.— New species, new combination, generic placement, conservation status, taxonomy, morphology, Arthromeris, Southeastern Himalaya

4 Highlight of the region: New fern species

4.1 Introduction

During exploration of the “northern forest complex” on the eastern slope of the Myanmar-India watershed (Kachin State, Myanmar), between November 2013 and October 2014, Khine et al. and Miehe et al. collected an epiphytic fern that could be assigned to the Polypodiaceae but not be to any known species, or even easily placed in an existing genus of Polypodiaceae. After comparing it with all known species of the morphologically closest genera *Selliguea* Bory and *Arthromeris* (T. Moore) J. Sm. we have come to the conclusion that it represents a new species, but we have decided not to erect a new genus to accommodate it. The new species is here described in the genus *Selliguea*.

4.2 Material and Methods

Morphological characters were examined in the field and on herbarium specimens, and using Light (LM) and Scanning Electron microscopy (SEM). For LM, small parts of rhizome and lamina were boiled in water until they sank, and then either sectioned on a Reichert slide microtome or mounted whole without staining in glycerine jelly, and photographed using a Zeiss V20 or a Zeiss AxioImager M2 with an MRc5 digital camera and AxioVision software (Zeiss). For SEM spores were sputter-coated with 10 nm Platinum/Palladium (80/20) in a Quorum Q150TS sputter-coater, and observed with a Jeol JSM 7600F FEG-SEM. For the conservation assessment, Area of Occupancy (AOO) and Extent of Occurrence (EOO) were estimated using GeoCAT (Bachman et al 2011), with default settings for grid size. The specimens collected by Khine et al and Miehe et al are kept at the Faculty of Geography, Philipps University of Marburg, with duplicates distributed to L, RAF and SING (abbreviations according to Thiers, continuously updated).

4.3 Results

Selliguea kachinensis **Hovenkamp, S. Linds., Fraser-Jenk., sp. nov.**
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4.3.1 Type

Myanmar, Kachin State, Hponyinrazi, Quercus-Magnolia-Araliaceae forest, epiphyte. 27.601421°N, 96.988873°E, 1715 m, G. Miehe, P.K. Khine [“Kine”], L. Shein, M. Kyaw, P. Ma, S. Lan Wan 13-094-159, 19 Nov. 2013 (holotype: L; isotype: SING).

4.3.2 Epiphytic

Rhizome long-creeping, branched, 3.2–4.5 mm diam. when dry (c. 6 mm diam. after soaking in boiling water), black and shiny when dry with a glaucous waxy layer, the younger parts densely covered with scales, irregularly rooting from the ventral side, in cross-section with scattered sclerification in the peripheral, epidermal and subepidermal region; phyllopodia c. 2 cm distant, c. 1–3 mm high. Scales deciduous, mostly absent from older parts of the rhizome, basifixed and slightly to strongly auriculate, or pseudopeltate, or sometimes fully peltate, c. 0.5 × 2.0–3.5(–4.0) mm, gradually narrowed from the base to a long narrow acumen, brown or blackish near the attachment, central region brown and thick, the margin and acumen thinner and lighter, margin irregularly dentate, more strongly so towards the base. Fronds pendent, simple, monomorphic, stipitate, all parts densely hairy with multicellular, uniseriate, soft hairs to 1.5(–1.7) mm long, the longest hairs inserted on midrib and veins; sparse, long narrow pale strongly toothed scales present among the hairs on the abaxial midrib (particularly towards the base of the lamina), stipe 0.8–5.0 cm long, c. 1 mm thick; lamina 18–58 × 3.3–7.2 cm, oblong – narrowly elliptic, the basal 1-6 cm often narrowed, base truncate to cordate, apex acuminate, texture thin-herbaceous, glaucous when fresh, translucent when dry, margin very narrowly hyaline, without notches. Venation anastomosing, primary veins straight or slightly curved, at 60–90 degrees to the midrib, secondary veins hardly distinct, delimiting c. 5–6 rows of rectangular areoles with anastomosing tertiary veins and free veins in all directions, ending in hydathodes. Sori in a single row between each pair of primary veins, usually one per areole, but sometimes absent from the first one or two areolae closest to the midrib and occasionally two in areolae closest to the margin, c. 2 mm in diameter when ripe. Sporangia long-stalked, capsules c. 0.2 mm long, bearing 2–6 uniseriate, c. 0.4–0.8 mm long hairs, annulus with 14–16 indurated cells. Spores 29–46 × 25–34 µm in lateral view, perispore with a 0.1–0.3 µm thick, finely colliculate basal layer, rather densely set with narrow, fragile spines, spines c. 2 µm long by 0.5 µm thick at the base, somewhat narrowed to a blunt apex, apparently easily breaking off at the base leaving a low round scar.

4.3.3 Additional specimens seen

Myanmar, Kachin State. Hponyinrazi: G. Miehe, P.K. Khine [“Kine”], L. Shein, M. Kyaw, P. Ma, S. Lan Wan 13-096-034, 23 Nov. 2013, above 1300 m, road site (L); G. Miehe, P.K. Khine [“Kine”], L. Shein, M. Kyaw, P. Ma, S. Lan Wan 13-131-013, 11 Nov. 2013, 1600 m, road site (SING).

Hponkanrazi: P.K. Khine [“Kine”], J. Kluge, A.S. Lanwan, D.R. Lanwan, P. Lanwan 14-031-020, 14 Oct. 2014, 27.548702 N, 97.032742 E, 1565 m, evergreen broadleaved (L). Above Ziadam: P.K. Khine [“Kine”], J. Kluge, A.S. Lanwan, D.R. Lanwan, P. Lanwan 14-047-022, 21 Oct. 2014, 27.585061°N, 97.104085°E, 1448 m, evergreen broadleaved (L, SING). Pisa District: Wang Jun & Zhou Lian Xuan 5431, 18 Apr. 2009, Pangjia (26°31.589'N, 98°18.473'E, 717 m) to Wuru (26°31.589'N, 98°18.473'E), in forest on a tree (CDBI). Ridan: Xia Nianhe, Deng Yunfei, Zhou Wei & Wu Linfang 1519, 20 Mar. 2009, around the Waqkure village, c. 2 miles from Ridan, E. side of Namai Kha river, 27°11.876'N, 98°15.165'E, 1400 m., in forest (CDBI).

4.3.4 Etymology

The name derives from Kachin State, where the species is found.

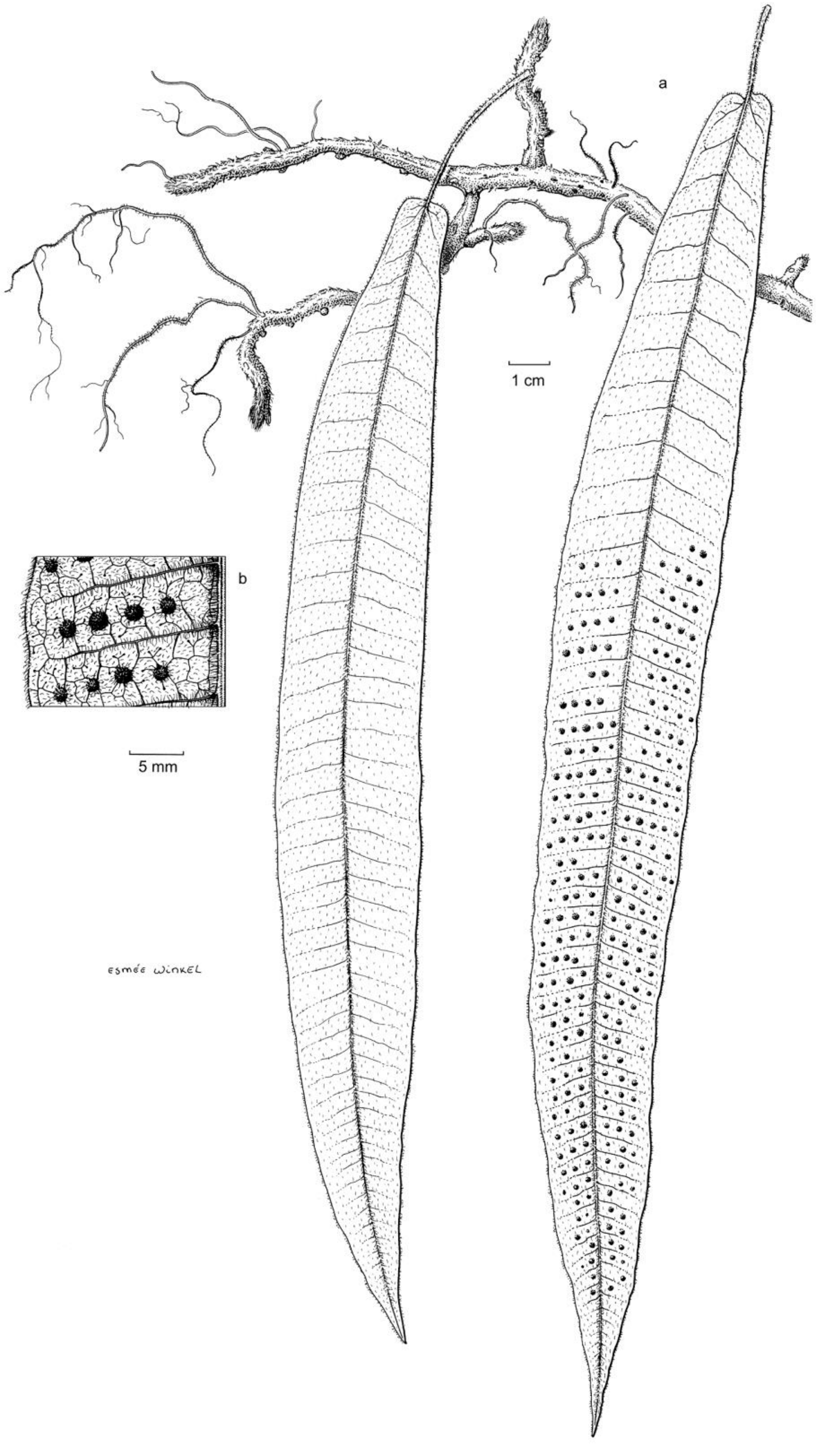

Figure 4-1 *Selliguea kachinensis*. A habit B detail showing venation pattern. After Kine *et al* 14-047-022 (L). Drawing by Esmée Winkel.

4.3.5 Ecology

Based on the specimens collected in the “northern forest complex”, *Selliguea kachinensis* grows on heavily moss-covered trees in primary evergreen broadleaved forest (dominated by *Fagaceae*, *Lauraceae*, *Araliaceae*, and *Magnoliaceae*) between 1300 m and 1715 m. It was found occasionally on trunks at 4 m from the ground (Figure 3), more frequently in the moss cover of trunks and thicker branches above 8 m and in the tree crowns, but is absent in the outer canopy. It is locally abundant together with *Drynaria propinqua* (Wall. ex Mett.) J.Sm. (Figure 4-4). It was not found growing on steep rock cliffs or open banks along trails. During our visits in November 2013, and October 2014 we did not observe any wilting of the fronds (in contrast to *Oleandra neriiformis* Cav. and *O. wallichii* C.Presl which are lithophytes/epiphytes with a somewhat similar habit) and so could not assess whether it is deciduous or evergreen, but the herbaceous texture suggests that it is deciduous.

4.3.6 Climate

The climate station nearest to the collection sites is Putao (450 m a.s.l) in an intramontane basin 50 km to the southeast. It records approximately 4000 mm rainfall between May and October with a pronounced dry season from November to January. We expect that the annual rainfall at altitudes between 1400 and 1800 m a.s.l. exceeds 5000 mm plus an unknown amount of fog precipitation from clouds shrouding the mountains between April and November.

4.3.7 Distribution, conservation and threats

Selliguea kachinensis is currently known from five locations, all in the north of Kachin State, Myanmar. On the basis of these occurrences, the Extent of Occurrence is 4738 km2, while the known Area of Occupancy is 20 km^2. However, as exploration of the area has been very fragmentary, we have little information on the actual occurrence of this species, which could well be more widely distributed along the rim of the Mali Kha / Irawaddy River basin. To date, forests where *S. kachinensis* is found are among the least disturbed submontane evergreen broadleaved forests of the Southeastern Himalaya. Drastically increased population could extend swidden farming and might lead to a reduction of the population, but we have no information on any concrete and current threats to the habitat of the species. Accordingly, we propose a status of Data Deficient (IUCN 2014).

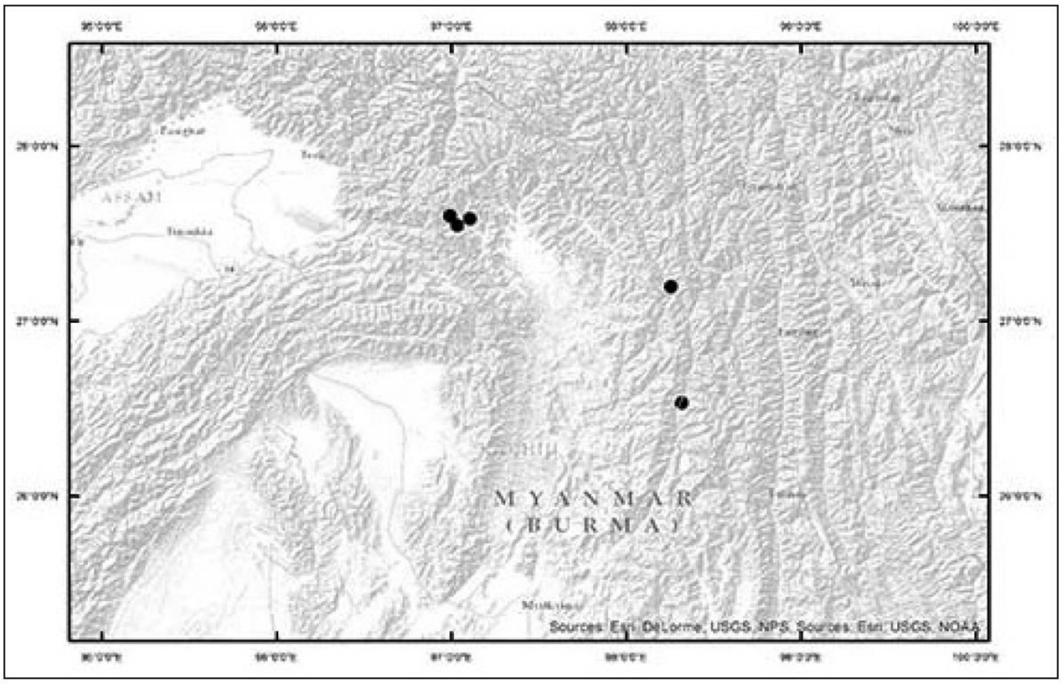

Figure 4-2 *Selliguea kachinensis* – Distribution.

Figure 4-3 Habitat of *Selliguea kachinensis*: a thick bryophyte covered trunk in Hponyin Razi at about 1,700 m (photograph by P. K. Khine).

Figure 4-4 Habitat of *Selliguea kachinensis*: a thick branch covered with other Polypodiaceae such as *Drynaria propinqua*, and Orchidaceae in Hponkan Razi at 1,600 m (photograph by P. K. Khine).

4.4 Discussion

4.4.1 Generic placement

Selliguea kachinensis does not fit easily into the genus *Selliguea*, which contains mostly species with a more coriaceous texture and a distinctly cartilaginous, often notched, margin (although a thin-herbaceous texture is notably present in *S. pui* Hovenkamp). An alternative position would be in the related genus *Arthromeris*. This would agree with the rather distinctive, glabrescent rhizome, which is similar to that of *A. lehmanii* (Mett.) Ching or *A. tomentosa* W.M.Chu, and with a number of other characters (Table 4-1) but it would seriously weaken the diagnostic value of that genus, as all species so far placed in *Arthromeris* have imparipinnate fronds with articulate pinnae (Lu & Hovenkamp 2013, Tagawa & Iwatsuki 1989). There are several distinctive characters in *Selliguea kachinensis* that argue against placement in either of these genera, and for the erection of a new genus. The often somewhat lyrate base of the lamina of *Selliguea kachinensis* is distinctive and not encountered in any other species of either *Selliguea* or *Arthromeris*. The rhizome of *Selliguea kachinensis* is also distinct in that the cross-section shows sclerification only in the peripheral, subepidermal region (Figure 4-5a). Sclerification occurs frequently in *Selliguea*, rarely in *Arthromeris*, but in both cases takes the form of sclerified strands in the central part of the rhizome, or a continuous, sclerified band well below the epidermis. The rhizome scales (Figure 4-5b) do not show any distinctive characters. A dense indument of long hairs similar to the indument of *S. kachinensis* (Figure 5c,

d) occurs in some species of *Arthromeris*, but in *Selliguea*, *S. trisecta* (Baker) Fraser-Jenk. and *S. erythrocarpa* (Mett. ex Kuhn) Hovenkamp, S. Linds., Fraser-Jenk. *comb. nov.* (basionym: *Polypodium erythrocarpum* Mett. ex Kuhn, Linnaea 36: 135. 1869) are also hairy, while *S. chrysotricha* (C.Chr.) Fraser-Jenk. also has hairs (albeit short and stiff ones) on the capsules of the sporangia. The spore ornamentation (Figure 4-5e, f) is matched in *Selliguea* by e.g. *S. quasidivaricata* (Hayata) H.Ohashi & K.Ohashi and *S. yakushimensis* (Makino) Fraser-Jenk. and in *Arthromeris* by e.g. *A. tenuicauda* (Hook.) Ching and *A. lehmannii* (Mett.) Ching (Tryon & Lugardon 1991). Thus, there are arguments both for and against placement in *Selliguea* or in *Arthromeris* and there are arguments in favour of erecting a new genus. We have decided not to do the latter, as the generic taxonomy of the Selligueoid ferns is at the moment unsettled, has been burdened already by the erection of numerous small genera (Hovenkamp 1998), and it is beginning to become clear that the best option to avoid paraphyletic groups may be to accept a large genus *Selliguea* (He et al in prec.). As alternative to a monotypic genus, we prefer a placement in the genus *Selliguea* over one in *Arthromeris* in anticipation of a generic reorganization along these lines.

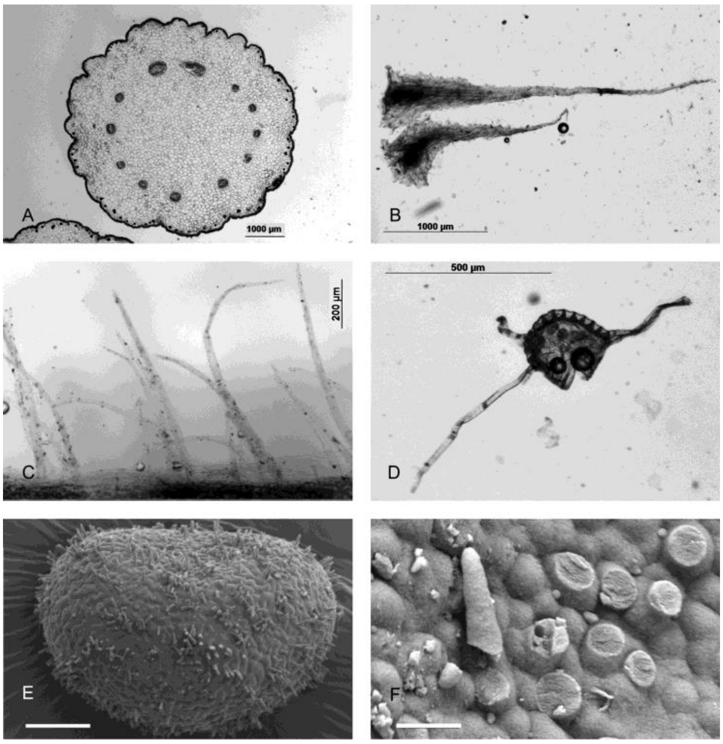

Figure 4-5 *Selliguea kachinensis*. A cross section of rhizome B rhizome scales C lamina margin D sporangium E spore F detail of spore, scale bar. All from the holotype, Miehe *et al*. 13-094-159 (L). Scale bar: 10 µm (A–E); 1 µm (F).

Table 4-1 Comparison of morphological characteristics of *S. kachinensis* with *Selliguea* and *Arthromeris*.

	Selliguea	***S. kachinensis***	***Arthromeris***
Rhizome with scattered sclerification	Absent or central	Peripheral	Absent or central
Rhizome with continuous sclerified band	Often	No	No
Lamina shape	Simple to pinnate	Simple	Pinnate, pinnae articulate
Lamina texture	Mostly coriaceous	Thin-herbaceous	Thin-herbaceous to herbaceous
Lamina indument	Glabrous to short-hairy	Soft hairy	Glabrous to densely soft-hairy
Lamina margin	Mostly cartilaginous, often notched	Not differentiated	Often distinctly flat-cartilaginous, not notched
Sporangial indument	Rarely present, short stiff hairs	Soft long hairs	Absent

Acknowledgments

Fieldwork and collecting was carried out in cooperation with the Forest Dept. of the Ministry of Environmental Conservation and Forestry, Myanmar, Philipps University of Marburg, Germany and the Royal Botanic Garden Edinburgh, Scotland supported by the German Research Council (DFG) and the German Academic Exchange Service (DAAD). Our heartfelt thanks go to Dr. Nyi Nyi Kyaw (Director General, Forest Dept.), Mr. Win Naing Thaw (Director, Nature and Wildlife Conservation Division), Mr. Thein Lwin and Mr. Aung Maung (Park Warden, Hkakaborazi National Park. We thank Singapore Botanic Gardens for allowing SL access to their specimens and facilities. We thank Esmée Winkel for the fine illustration.

CHAPTER 5

Phylogenetic and trait elevational assemblage of ferns in East and Southeast Asia

In preparation

with Jürgen Kluge, Georg Miehe and Lars Opgenoorth

No consistent trait and phylogenetic diversity patterns in fern and lycophyte community assemblies along six elevational gradients in East Asia

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Abstract.— A previous study on a Costa Rican elevational fern gradient found phylogenetic and trait diversity were relatively independent from one another in epiphytic fern assemblages. We hypothesize that this disparity should be expected in pteridophytes due to the practical absence of spatial barriers for their spores. We argue that the resulting massive gene flow should lead to a dominance of convergent evolution in pteridophyte lineages. Consequently, environmental filtering should act on trait assemblages but not phylogenetic assemblages. Furthermore, increasingly steep environmental gradients should lead to stronger disparity. We here investigated ferns and lycophytes assemblages in six additional elevational gradients to test the generality of this pattern. We used six empirical datasets of the quantitative pattern of species occurrences and individual numbers of ferns within 315 plots along three tropical and three temperate elevational gradients to test for phylogenetic structure and ecological sorting of trait patterns. Mean pairwise distances of species based on phylogenetic and trait properties were compared with two different sets of null assemblages, one maintaining species frequency distributions (constrained) and one not (unconstrained). Applying different null models resulted in varying degrees of overdispersion and clustering, but overall patterns of deviation from random expectations remained the same. In line with our theoretical predictions, no phylogenetic structuring emerged along the elevational transects while trait diversity showed significant trends for overdispersion in low elevation and clustering in high elevation in Natma Taung, Hponyinrazi and Nishikoma gradients, and reverse pattern was found in Taiwan. Pteridophyte dispersal strength seems to override any phylogenetic structuring along elevational gradients. In contrast, environmental divergence in most of these gradients is strong enough to lead to clustered assemblages with respect to trait characteristics reflecting environmental filtering. In conclusion, adaptations in ferns occur convergently in diverse phylogenetic lineages.

Keywords.— elevational gradients, ferns and lycophytes, phylogenetic diversity, trait diversity, species diversity

5 Phylogenetic and trait elevational assemblage of ferns in East and Southeast Asia

5.1 Introduction

A huge body of literature deals with community phylogenetics in plant and animal species (e.g. Ackerly 2003, Cavender-Bares et al 2004, Cavender-Bares et al 2009, Floeter et al 2018, Gillespie 2004, Hawkins et al 2014, Webb et al 2002). The general goal of these studies is to disentangle the ecological and evolutionary factors that govern the assembly of communities, and how the interactions among species within them ultimately influence evolutionary and ecosystem processes. Generally speaking three general processes can influence community assembly, namely niche-related (Ackerly 2003, MacArthur & Levins 1967, Webb 2000, Webb et al 2002), neutral (Hubbell 2001, Hubbell 1979, Hubbell 1997) and historical processes (Cavender-Bares et al. 2009). Among taxonomic groups, these different processes have been well investigated in seed plants especially along elevational gradients. Although patterns vary, numerous studies have demonstrated phylogenetic overdispersion of interspecific competition at higher elevation and phylogenetic clustering of environmental filtering at lower elevations. Examples include angiosperms in the Colorado Rocky Mountains and trees on Malesia (angiosperm on Colorado Rocky Mountain: Bryant et al 2008, tree on Malesia: Culmsee & Leuschner 2013). Also, evidence for a clustering of closely related species due to extreme temperature regimes has been gathered for alpine plants in the Hengudan mountains and for woody plants in the Changbaishan and Taibai mountains (tree species on Barro Colorado Island: Kembel & Hubbell 2006, alpine plants on Hengduan mountain: Li et al 2014, woody plant on Changbaishan mountain: Qian et al 2014, woody plants on Taibai mountain: Xu et al 2017).

Surprisingly, to our knowledge there is currently only one study that deals with the phylogenetic diversity in community assemblages in ferns and lycophytes (hereafter called ferns for simplicity). In their study Kluge and Kessler (Kluge & Kessler 2011b) compare phylogenetic diversity and trait diversity in Neotropical fern assemblages from 156 plots along an elevational gradient with a neutral model of random assemblage. They found that niche based processes shape trait diversity but not phylogenetic diversity for epiphytic ferns. Specifically, their study indicates stronger interspecific competition and character displacement of the species rich assemblage under less extreme environmental condition at the lower parts of the gradient, and more influence of environmental filtering in species poor assemblage under extreme climate conditions, i.e. drought at the lowest and cold at the higher plots. Terrestrial fern assemblages in turn are structured by neutral processes alone. Given the singularity of their study, nothing is known yet about the generality of their findings. Several life history traits of ferns make it plausible that fern assembly patterns could deviate from Angiosperm assembly rules. First, in the life cycle of ferns, the gametophyte phase does not rely on sporophyte in contrast to seed plants. A wide range of regular reproduction mechanisms (e.g. bisexuality, selfing, cross fertilization etc.) help to deal with various ecological conditions. Secondly, and in this context maybe more importantly, the small and comparatively light spores enhance the dispersal ability and thus increase gene flow distances greatly. Also, due to the possibility of single spore migration ferns are capable to create a new population with one diaspor, even though the success rate for this might be low due to selfing of homosporous ferns (Haufler et al 2016). Thus, geographic barrier such as dispersal limitation and, seasonal and temporal barrier for fertilization disregards to a certain extent in contrast with angiosperms. As in the community structure of species-neutral interactions (Hubbell 2001), the wider distribution of specie combined with slow speciation and extinction rates in ferns (Smith 1972) could create the equilibrium with environmental filtering processes. Consequently we suggest that fern species assemblies will be governed largely by stochastic events and that convergent evolution will allow for trait clustering but not phylogenetic clustering as a rule.

Thus, in order to test the generality of the patterns found in Kluge and Kessler (2011) we here analysed phylogenetic and trait diversity patterns of fern assemblages along six elevational gradients from tropical to temperate regions in East and Southeast Asia. Specifically we wanted to test the following predictions. Epiphytic and terrestrial fern assemblages show i) a strong correlation of species richness with phylodiversity, ii) phylogenetic and trait overdispersion in the lower elevation plots of the tropical gradients to forego competitive adversity; iii) assemblies ruled by random processes in the mid-elevation plots of the tropical gradients, and in the entire temperate gradients; iv) trait clustering, but no phylogenetic clustering in the upper elevation plots of the tropical gradients.

5.2 Methods

5.2.1 Study sites and sampling

The ferns inventory was conducted in 315 plots from six elevational gradients in Japan: Hokkaido (43°34'N, 142°62'E), Nishikoma (35°81'N, 137°82'E), Kyushu (32°36'N, 131°07'E); Taiwan (24°04'N, 121°21'E) and Myanmar: Hponyinrazi (27°56'N, 96°96'E) and Hponkanrazi (27°56'N, 96°96'E), and Natma Taung (21°22'N, 93°90'E). Two study sites in northern Myanmar were merged as some elevational steps in Hponyinrazi coincided with with azonal vegetation due to the extreme topography. Replacement plots were recorded in Hponkanrazi, the neighbouring transect. Due to the absence of epiphytic species occurrence, Nishikoma and Hokkaido gradients were excluded from the epiphytic life form analysis. We used a plot size of 400 m^2. At each plot species occurrence, abundance and life forms categorizing terrestrial and epiphytes were recorded. High trunk and canopy epiphytes were sampled from fallen branches and also checked with binoculars.

5.2.2 Phylogenetic data

Due to the absence of fully resolved cladograms for the species set of this study we used the taxonomy data of the PPGI classification (Schneider et al 2016) to do a distance matrix calculation. First, the 514 species from the six gradients were assigned to regional species pools. Then the taxonomy data was used to compute a phylogenetic tree with branch lengths using the R-packages picante (Kembel et al 2010) and ape (Paradis et al 2004) according to the method of Grafen (Grafen 1989).

5.2.3 Trait data

The selection of morphological traits was based on functional importance. Specifically, laminar morphology such as dimorphism can be used as indicator for dispersal strength (Halloy & Mark 1996) while laminar dissection indicates the ability to adapt to harsh environments such as temperature and humidity oscillation (Halloy & Mark 1996). Laminar thickness, as well as the presence of scales and hairs, existing indusium and vegetative buds is related to climatic conditions (Dubuisson et al 2003, Halloy & Mark 1996, Koptur & Lee 1993). Finally, rhizome types are an indicator for space and light competition in dense communities (Kluge & Kessler 2007). Morphological characteristics of the species were classified as in Kluge & Kessler (2007). The trait values were standardized using the vegan package (Oksanen et al 2017) as some traits were classified as present and absent whereas others were classified as categorical data.

5.2.4 Statistical analyses

In every gradient, the richness of phylogenetic alpha diversity for each plot was calculated using Faith’s PD. Community phylogenetic and trait structure for both terrestrial and epiphytic life forms were assessed on plot level assemblages, where assemblages were defined as the species co-occurring in each study plot. Distance matrices for phylogeny and traits were calculated based on the Euclidean distances of similarity and cophenetic distances of hierarchical clustering as implemented in the picante package (Kembel et al 2010). The diversity measurement such as mean phylogenetic distance (MPD) and mean trait distance (MTD) were calculated using abundance weighted pair wise distance in an assemblage of the individual gradient. The correlation between those diversities has been tested with Pearson correlation. The explanatory power of species richness to MPD and MTD and significant difference from randomness was assessed with linear regression. The standard effect size of mean phylogenetic diversity and trait diversity (MPD stand and MTD stand) were used to assess the relationship of observed and estimated phylogenetic/trait distances from the null assemblages. MPD stand is defined as the difference between empirical and null assemblage that are then averaged by the standard deviation of the null assemblage (Gotelli & Rode 2002).

To test whether the phylogenetic and trait structure of the community assemblages are different from random assemblies, we compared the abundance weighted trait mean and the mean nearest taxon distance of the phylogeny (MNDT) to randomly computed null communities of 999 assemblages each. Standard effect size of MNDT was -1 time of Nearest Taxon Index (NTI). Thus a positive value indicates phylogenetic overdispersion (to reduce competition), a negative value represents phylogenetic clustering (lineage nested adaptation to specific ecological conditions), and a value close to zero indicates a random assemblage. Regarding traits similar approaches and interpretations were used. All statistical analyses were performed with R programming version 3.1.0 (Team 2017).

5.3 Results

The three tropical gradients showed the highest phylogenetic richness in the mid-elevations decreasing towards both ends of the gradients whereas temperate gradients exhibited decreasing patterns toward higher elevations. Although the overall phylogenetic richness behaved as species richness, the patterns were not identical (Figure 5-1). The two most pronounced differences are a relatively sharp peak of phylogenetic diversity in Taiwan in the mid-elevation compared to species richness, and a sharper decline of phylodiversity compared to species richness in the Hopnyinrazi gradient.

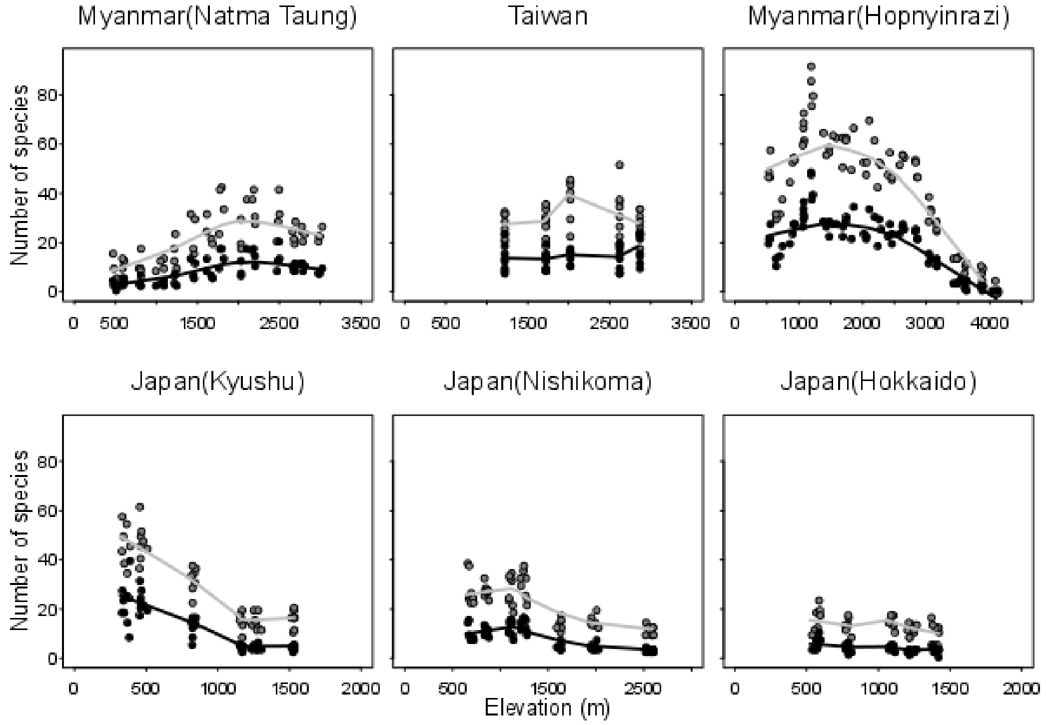

Figure 5-1 Phylogenetic richness (in open circles and grey lines) and species richness (in solid circles) along the elevational gradient. Trend lines are fitted with LOWESS function.

The accumulation of phylogenetic diversity and trait diversity with respect to the species richness was best modelled with an asymptotic curve with a steep slope of rapid change at the beginning (Figure 5-2). Correlations and significant levels were relatively high in all but the Hokkaido gradient for terrestrial ferns and explained between 19 and 44 % of the variance (Hokkaido MPD n.s., and 16 % explained variance for MTD). For epiphytic ferns, only all correlations in the two Myanmar gradients and the species ~ MTD correlation in the Taiwan gradient were statistically significant. The explained variance ranged between nine and 39 % (Figure 5-3).

Among terrestrial species the correlation between MPD and MTD was strong with significant levels between $p < 0.01$ and 0.001, apart from Hokkaido. The terrestrial MPD and MTD correlation were R= 0.87 for Natma Taung and Taiwan, and R= 0.87 for Kyushu and Nishikoma, and R=0.9 for Hokkaido. Taiwan and for epiphytic species were then again strong, performing R= 0.73, 0.84 and 0.90 in Natma Taung, Taiwan and Kyushu respectively. All correlations were found to be statically highly significant $p < 0.001$.

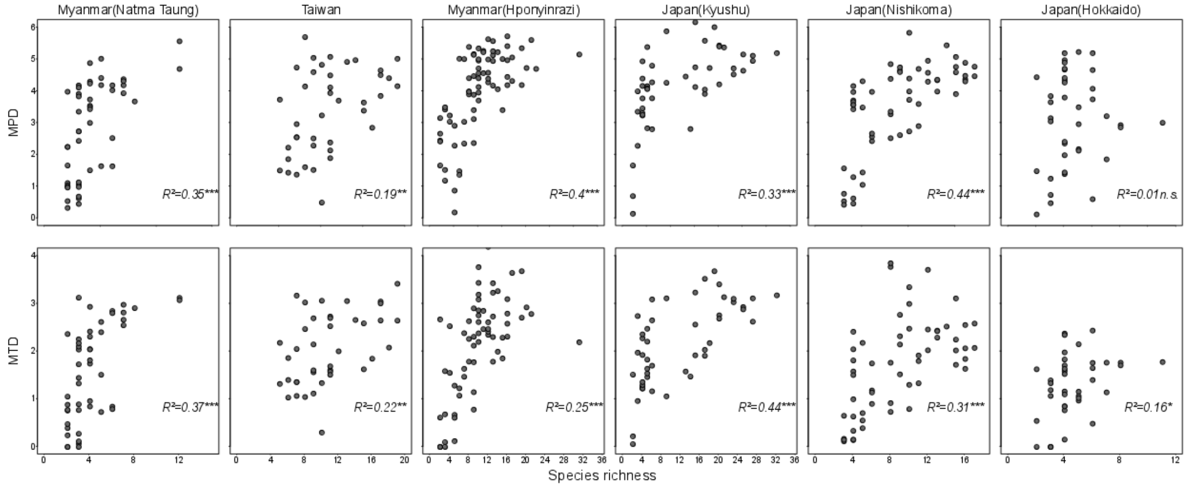

Figure 5-2 Mean phylogenetic diversity (MPD) and mean trait diversity (MTD) of terrestrial ferns assemblage along six elevation gradients and each dot marked the individual plot. The significant levels are *** =p<0.001, **=p<0.01, *=p<0.05

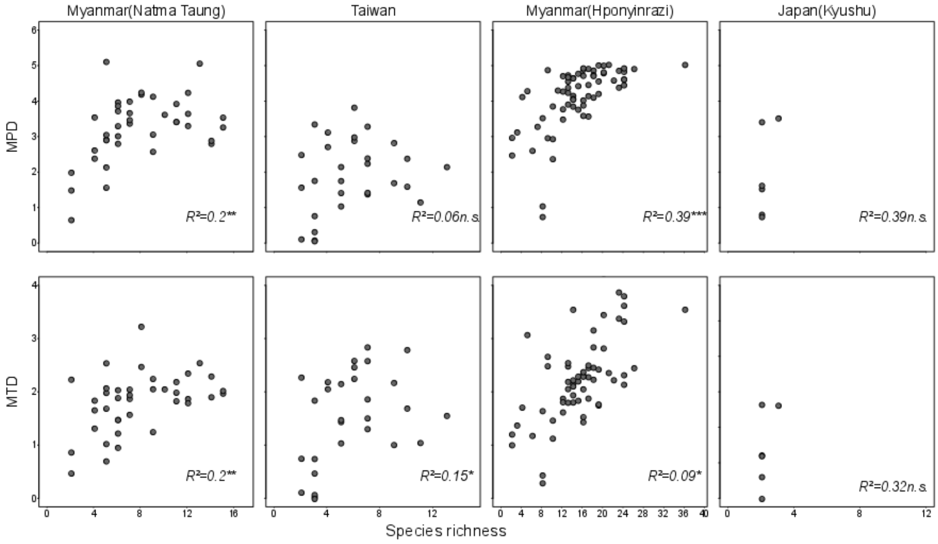

Figure 5-3 Mean phylogenetic diversity (MPD) and mean trait diversity (MTD) of epiphyte ferns assemblage along four elevation gradients and each dot marked the individual plot. The significant levels are *** =p<0.001, **=p<0.01, *=p<0.05

The standardized effect size of mean nearest taxon distance against null communities (equivalent to negative net relatedness index) for phylogenetic and trait diversity patterns for *constraint* and *unconstraint* models for terrestrial species with respect to the elevation showed vastly varying trends even within the tropical and temperate gradients (figure 4). At Natma Taung in Myanmar and Nishikoma in Japan all trends were decreasing with elevation, though in the latter case only the trait diversity correlations were significant. In contrast, Kyushu gradient in Japan as well as the Taiwanese gradient showed increasing MTD_{stand} and MPD_{stand} values with elevation or were not significant, while the Hokkaido gradient did not produce any significant correlation. Finally, at the Hponyinrazi gradient trait diversity also showed significantly decreasing trends while phylogenetic diversity was either slightly increasing (constraint) or not significant (unconstraint). For epiphytic ferns only trait diversity at the Myanmar gradients showed a significant decreasing trend (Figure 5-5).

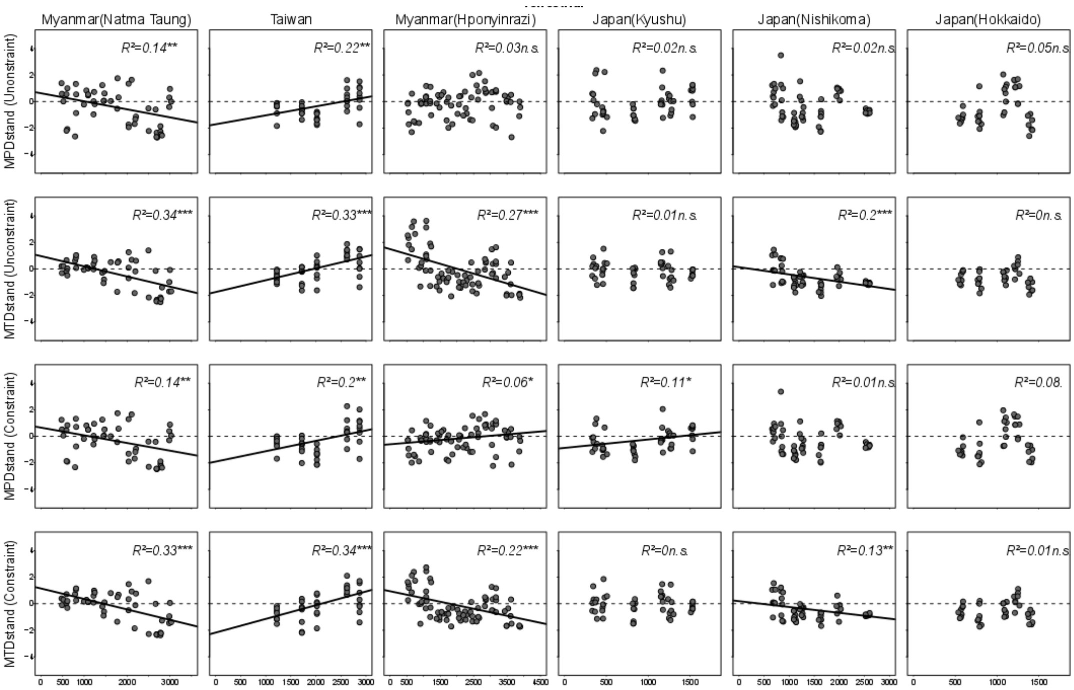

Figure 5-4 The standardized effect size of mean nearest taxon distance against null communities (equivalent to negative net relatedness index) for phylogenetic and trait diversity patterns for *constraint* and *unconstraint* models for terrestrial species are presented with respect to the elevation for all elevational gradient. Trend lines are produced with glm fit and the significant levels are *** =p<0.001, **=p<0.01, *=p<0.05.

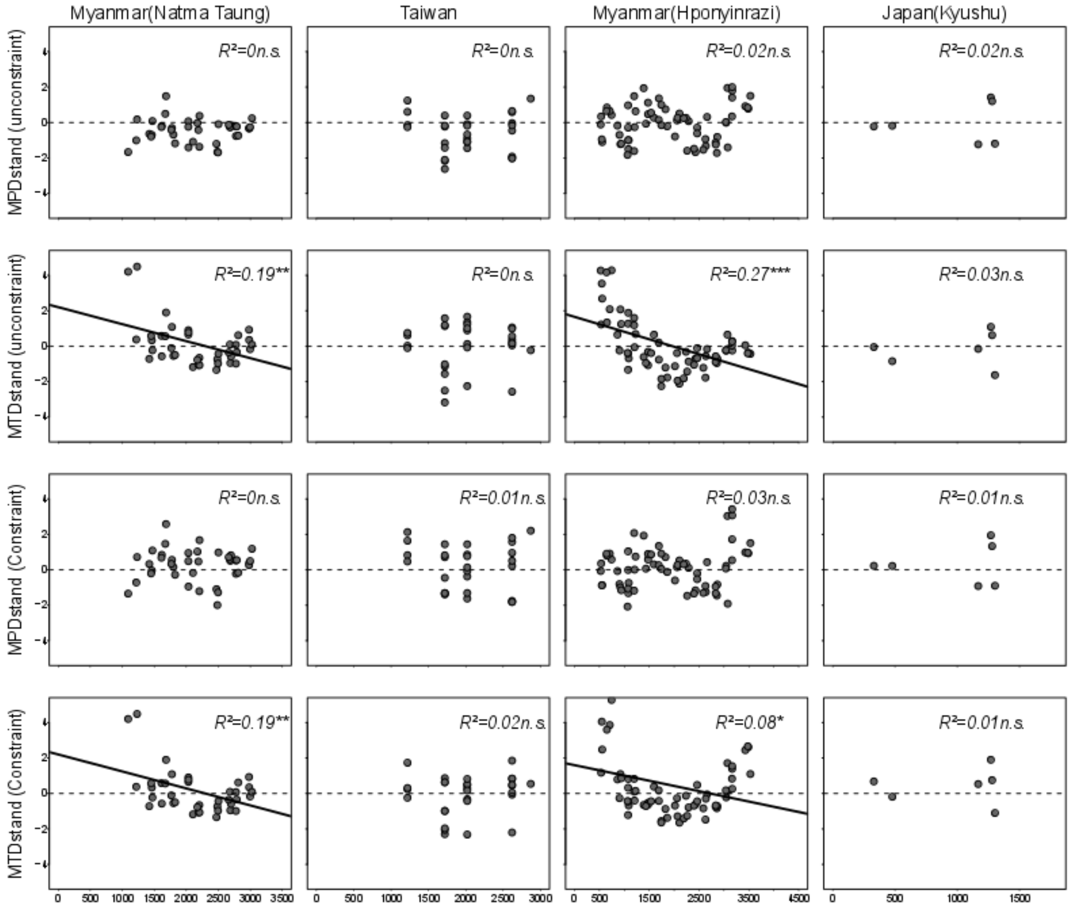

Figure 5-5 The standardized effect size of mean nearest taxon distance against null communities (equivalent to negative net relatedness index) for phylogenetic and trait diversity patterns for *constraint* and *unconstraint* models for epiphytic species are presented with respect to the elevation for all elevational gradient. Trend lines are produced with glm fit and the significant levels are *** =p<0.001, **=p<0.01, *=p<0.05

5.4 Discussion

Our study is only the second to investigate the phylogenetic diversity and trait diversity of fern assemblages along elevational gradients with the intention to contrast ecological sorting of species based on their traits to their evolutionary legacies. We found no coherent pattern in six elevational gradients, three of which were recorded in the tropics and temperate regions of Asia, respectively. Based on the life history, traits of pteridophytes in general and dependent on terrestrial vs. epiphytic life forms, we hypothesized to find consistent patterns of clustering, neutral processes and overdispersion in relation to the strength of environmental cues. Consistent with theory and the only previous study in an elevational gradient of ferns (Kluge & Kessler 2011b), most assemblages were governed by neutral processes (Appendix F 15, Appendix F 16, Appendix F 17, Appendix F 18). However, in relation to our four specific predictions regarding phylogenetic and trait diversity patterns and underlying processes we found varying results.

First, we predicted a strong correlation of species richness with phylodiversity. As predicted, we found phylodiversity to be strongly dependent upon species richness in all gradients. Both, species richness and phylogenetic diversity were highest in the mid-elevation plots conforming with the mid-domain effect Colwell et al (2004). In the Hopnyinrazi gradient there was a relatively pronounced decoupling of phylodiversity from species richness that we interpret as an indication for environmental filtering given relatively dry site conditions there that likely are a significant stress for ferns. Second, we predicted that we would find phylogenetic and trait overdispersion in the lower elevation plots of the tropical gradients as a reaction to optimal and long-term stable site conditions. These site conditions usually are seen as the most important reason why tropical lowlands are known as a museum of species. As a consequence, competition is one of the driving adversities in such systems (Weiher & Keddy 1995) leading to overdispersion as a consequence of niche differentiation between the species (Stubbs and Wilson 2004). Our results are in line with these predictions only partly. Though our tropical gradients did show a decline of MTD and MPD values along elevation, only in the case of Hponyinrazi we found $\mathrm{MTD}_{\mathrm{stand}}$ values well above 2 indicating overdispersion. Given that this gradient is the longest of the 6 and reaches well into the tropical realm it is plausible to find the only signal there. Thus, most assemblies seem to have been governed by neutral processes which confirm and extend our third prediction. The mid-elevations of the mountains mostly have mild temperature and ambient humidity, thus promote the ferns' richness pattern in the context of water-energy dynamics (O' Brien 1996, Hawkins et al. 2003). This is also in line with our findings that temperature and cloud cover alone could explain more than 60% of the species richness of our study site (Khine et al 2018, submitted). Therefore species richness in addition to the high relative abundance reflects neither environmental sorting nor competition interaction that but neutral processes. Finally, we predicted to find trait clustering but no phylogenetic clustering in the upper elevation plots of the tropical gradients as a consequence of environmental filtering on traits that due to high gene flow is not picked up by evolution but instead provokes convergent evolution. As with overdispersion, our data did not clearly support this prediction. Though we did find a general trend in the Natma Taung gradient MPD_{stand} and a weak one at Hponyinrazi, values were not above two and thus are considered to be in the range of neutral processes. Thus, in contrast to the previous study by Kluge and Kessler (2011) we do not confirm that environmental filtering drives phylogenetic diversity in epiphytic ferns. However, we argue that both data sets are well in line showing a dominance of neutral processes in pterydophyte phylogenetic diversity. In contrast the ecological and environmental sorting reflected the differences of the functional traits (Petchey et al 2004). Thus, even though in study showed that the phylogenetic and trait diversity are strongly related, there is decoupling of trait evolution from the species evolution.

In conclusion, the phylogenetic and trait assemblages on a broad scale with different climate zonation could point out the need of extreme climate conditions to test whether phylogenetic clustering can play a significant role in fern assembly rule which would have to be investigated in additional gradient studies in the future. Moreover, the absence of a well resolved cladogram still prohibits a better resolved handling of phylodiversity. We therefore call for more in-depth phylogenetic research in ferns and lycophytes. Finally, we conclude that it is well worth to further study community phylogenetics in plants that propagate by spores as our study shows that assembly rules probably follow different trajectories and certainly have other thresholds than in other taxonomic lineages.

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CHAPTER 6

Elevational richness pattern and broad scale modeling

submitted to *journal of Biogeography*

with Jürgen Kluge, Michael Kessler, Georg Miehe and Dirk N. Karger

Elevational and latitudinal richness pattern of ferns and lycophytes in East and Southeast Asia: Climate tells just half the story

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Abstract.—To assess richness patterns of ferns and lycophytes in relation to climatic factors in Eastern Asia, analyzing eight elevational gradients, situated along a latitudinal gradient. Ferns and lycophytes were recorded in 480 plots of 400 m^2 along eight elevational gradients. We related macroclimatic factors to local fern species richness using generalized linear models. We tested the predictive power of macroclimatic variables by a leave-one-gradient-out cross-validation (LOOCV) and tested the predictive power of each model using Spearman's rank correlation, and predicted the respective models spatially. Model residuals were related to two available local (plot scale) factors, terrain inclination, and terrain heterogeneity using simple linear regression. Local fern species richness declined linearly towards higher latitudes, and simultaneously the elevational richness peaks shifted towards the lowlands with increasing distance from the equator, transitioning from unimodal to linear patterns. Temperature was the macroclimatic factor with the highest predictive power for fern species richness. In combination with other variables, especially cloud cover, macroclimatic factors could only explain up to about 60% of species richness distributions. Macroclimatic factors, such as temperature and cloud cover, are only able to predict a little bit more than half of the variation in local fern species richness in East and Southeast Asia. Although specific climatic factors can show high correlations along a single gradient, they do not necessarily predict fern species richness accurately. Remaining variation in local fern species richness is most likely due to small scale factors, which are hardly accounted for by macroclimatic factors.

Keywords.— elevational gradients, ferns and lycophytes, environmental variables, latitudinal gradient, species diversity, spatial prediction model

6 Elevational richness pattern and broad scale modeling

6.1 Introduction

Understanding the drivers of species diversity and distribution patterns is a major goal of ecology and biogeography, and within this research field, latitudinal and elevational patterns have been widely studied (McCain 2010, Rohde 1992, Rosenzweig & Abramsky 1993, Whittaker 1960). Latitudinal and elevational gradients have long been considered to mirror each other because they were considered to have the same underlying mechanisms along a climatic gradient from high to low temperatures (Rahbek 1995, Terborgh 1977). The decreasing number of species from the equator towards the poles is a well-known pattern and elevational diversity patterns were long believed also to show monotonic declines. However, Rahbek (2005) showed that the majority of elevational gradients show hump-shaped richness patterns with highest richness somewhere in the middle of the gradient, depending on the specific ecological requirements of the plant or animal groups. On the other hand, monotonic elevational declines of species richness are also well documented, and different types of patterns have been found even within a given taxonomic group (Grytnes & McCain 2007, Kessler et al 2011, McCain 2005, McCain 2009, McCain 2010).

Elevational gradients represent excellent natural experimental settings to study drivers of species richness as they span the full environmental range from hot lowlands at sea level to cold and harsh habitats at the vegetation limit, within short horizontal distances. At such distances dispersal limitation does not play a major role, so that distribution patterns reflect environmental drivers for species assemblages. In addition, the complex geographical configuration of mountains leads to high climatic diversity (Kottek et al 2006). Besides climatic restrictions, elevational richness patterns have also been considered to be influenced by topographical effects, where simply the size of a region may limit species richness (species–area relationship, e.g. Rosenzweig 1995). Because in mountains, as area typically declines with elevation (Körner 2000), species numbers decline with elevation (Karger et al 2011, Rohde 1992). In addition, the structure of surface area plays a role, as steep and rugged terrains offer a higher variability of habitats and niches (landscape heterogeneity), and thus provides space for more species(Ricklefs 1987).

Climatic variables have been suggested as prominent drivers of richness patterns, especially energy availability driven by temperature and water availability (Currie et al 2004, Hawkins et al 2003). Recent suggestions point towards an effect of energy on species richness via increased speciation rates and ecosystem productivity (Brown 2014). One of the most prominent models regarding this issue, the ‘water-energy-dynamics’ model, proposes that energetic variables (e.g., temperature) and water availability are not independent, but rather interact so that under sufficient and stable moisture regimes, temperature is the most influential factor (Hawkins et al 2003), whereas water availability in turn is also regulated by temperature in that at high temperatures actual evapotranspiration exceeds precipitation and thus induces drought stress (O'Brien 1998, Vetaas 2006).

Ferns and lycophytes (hereafter called 'ferns' for simplicity) are considered to be good climate indicators, because of their preference of moist and shady habitats as a result of their low water use efficiency (Brodribb & McAdam 2011, Brodribb et al 2009). Moving away from the equator towards higher latitudes, species richness in general decreases across most groups of organisms(Hawkins et al 2004, Hillebrand 2004) and so too for ferns (Karger et al 2011). Highest species richness is found in humid tropical mountainous regions at mid elevations (Bhattarai et al 2004, Grytnes & Beaman 2006, Hemp 2002, Kessler et al 2011, Tanaka & Sato 2013, Tang et al 2014) and declines toward more arid, as well as high alpine, arctic regions (Kreft et al 2010).

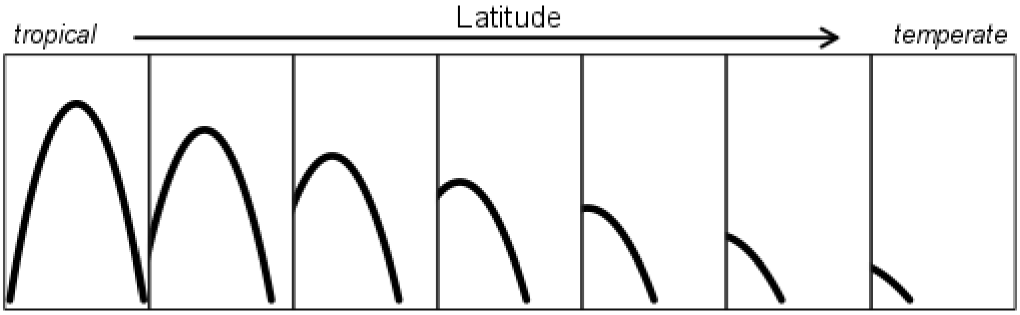

Figure 6-1 Hypothetical trend of elevational fern richness pattern from tropical to temperate latitudes (left to right). The x-axis for each panel shows the elevational ranges, the y-axis species richness per standardized plot. Maximum species richness (Height of curves) and position of maximum species richness are assumed to decline towards higher latitudes, resulting in the perception of different species richness-elevation trends: a hump in the tropics and linear decrease in temperate regions.

Combining both, the elevational and latitudinal richness trend, suggests a strong influence of a temperature regime on the richness of ferns and lycophytes in general, and would support the ‘water-energy-dynamics’ model. A congruence of species richness and temperature isoclines with latitude would predict a decrease of total species richness of each gradient and a shift of the mid-elevation richness peak towards lower elevations, with a gradually turning from complex, unimodal patterns to simple, linear patterns **(H1)** (as hypothetically depicted in Figure 6-1).

If these temperature and humidity related macroclimatic factors are important for fern species richness, they should be generally applicable. Therefore the parameters of the climate-richness relationship derived from a subset of elevational gradients should be able to describe the climate-richness relationship at any point along the latitudinal gradient **(H2)**.

Here we test these hypothesized relationships between macroclimatic variables and fern species richness, by combining elevational richness data from eight elevational gradients between the equator (2.5°S in New Guinea) and the temperate zones (43.3°N in Japan), each ranging from sea-level to above treeline wherever possible. We test if the hypothesized relationship between temperature and species richness changes the shape of fern richness patterns along elevational gradients and evaluate the importance of a set of environmental factors at a macroecological scale. With the use of several elevational gradients, sampled with the same strategy, we use each gradient as independent test to assess if conclusions on climatic drivers of fern species richness drawn from a set of elevational gradients are actually transferable.

6.2 Materials and Methods

6.2.1 Vegetation sampling

The vegetation sampling took place along eight elevational gradients, from New Guinea (4°S and 1.3°S) across the Philippines (8.1°N), Taiwan (24.0°N), Myanmar (21.2°N and 27.6°N) to Japan (32.4°N, 35.8°N, and 43.3°N) (see additional information in Appendix T 1). Along these gradients, we sampled the fern vegetation in a total 480 vegetation plots, which were selected with respect to the least possible anthropogenic disturbance (primary and old growth forest). In Myanmar, the elevational steps were separated by 200 m and four plots were sampled in every step. All other gradients were sampled, wherever possible, at four or eight plots per elevational step at more or less regular elevational intervals based on the accessibility of primary or old growth forest. Plot size was 400 m^2 throughout, mostly of square shape (20 m x 20 m). This plot size was based on previous surveys as representing an optimal compromise between habitat homogeneity and small-scale ecological variability of the plots, while optimizing labor-intensity (Karger et al 2015, Karger et al 2014, Kessler & Bach 1999). Species occurrence, abundance, and life forms were noted for each species. Life forms were categorized into terrestrial and epiphytes, where high trunk and canopy epiphytes were sampled from fallen branches, with trimming poles, and by using binoculars.

6.2.2 Environmental variables

To assess the climatic conditions of sampling plots, we used the climate data set from CHELSA V.1.2. (Karger et al 2017). This climate dataset provides climatic variables such as mean annual temperature (bio1), temperature seasonality (bio4), annual precipitation (bio12), precipitation seasonality (bio15). From this dataset we additionally derive annual evapotranspiration (evapo), frost frequency (frost), snow covered days (snow), and aridity (arid) at a ~1 km resolution (30 arc-seconds). CHELSA is based on a statistical downscaling of a global circulation model and thus integrates global wind systems and gives a much more realistic climate pattern especially in mountainous areas than models based on climate station interpolation. Mean annual cloud cover (cloud) is from global 1-km cloud cover datasets (Wilson & Jetz 2016).

To identify possible predictors on a spatial scale lower than 1km, we additionally used non-climatic variables, such as inclination and landscape heterogeneity (heterog). Heterogeneity was calculated based on the global multi-resolution terrain elevation data 2010 (Danielson & Gesch 2011) of ~225 m resolution (7.5 arc seconds) as the standard deviation of elevations of all 25 surrounding cells (5 x 5 km^2 grid), so that high standard deviations indicate a variable landscape relief. Inclination was based on inclinometer measurements in individual plots.

We applied Spearman's rank correlations for all pairs of variables to check for multicollinearity ($R > 0.8$), which may disrupt multiple regression models, and excluded 'frost' and 'evapo' for their high correlations with temperature at the macroscale. Moreover, an ANOVA test of linear and second ordered polynomial regression showed that there were curvilinear relationships between species richness and climatic variables, thus we used the quadratic terms of climate variables for the regression models.

The elevational trends of climatic and non-climatic variables used within this study are shown in Appendix F 13.

6.2.3 Statistical analyses

To test if the shape of the fern species richness elevation relationship changes as predicted by **H1**, we summed the total species richness for each gradient and estimated, since gradients are composed of different number of plots, total species richness additionally by applying the Chao estimator (Colwell & Coddington 1995). To assess the changes in the shape of elevational richness pattern from near equator to high latitudes, that is, whether the mid- elevation hump disappears with increasing latitude, we calculated the complexity of the species richness–elevation relationship by comparing generalized linear (glm) with general additive models (gam with minimum possible smoothing; k=3) (Peters et al 2016). The assumption is that in case of a strict monotonic relationship, both models explain the same, whereas for an increasing unimodal (humped) relationship, the higher complexity should result in a higher deviance of gam models and lower deviance of glm models and thus higher complexity (complexity index = 1-(glm/gam) (Peters et al 2016).

The relation of species richness and climatic variables was analysed with generalized linear regression models (*glm*) with Poisson distribution. In order to evaluate the relative contribution of explanatory variables on species richness measures, we started with a full model including all climatic variables and their quadratic term and stepwise reduced all non-significant predictors from the model. We report on model deviances D^2 (Guisan & Zimmermann 2000), p-values were derived by comparing the models to a Null-model (*response ~ 1*) by applying ANOVA.

In order to assess the predictive power of the calculated models (**H2**), i.e., to test whether results from a set of gradients can be used to predict another gradient, we iteratively left one gradient out, repeated the glm calculations with the remaining gradients ('training dataset") and predicted the species richness on the left out gradient (*LOOCV, leave-one-out-cross-validation*). The predictive power was calculated with Spearman's *rho* (correlation between predicted and observed species richness between test and training dataset). *Rho* values range between *[-1; 1*] with values close to 1/-1 indicating strong correlation and 0 indicating weak relationships. This procedure was applied on all possible models with iteratively leaving 1 to 7 gradients out. We report D^2, p-value and *LOOCV*-results (mean *rho* values across all model combinations) for the following models: (1) full model with all variables included, (2) best model with no non-significant climatic variables, and (3) best model based on highest *rho* value.

In order to assess the importance of each climatic variable, in a further step we used the same procedure of *LOOCV*: we repeated the steps of leaving out *one* gradient and step by step leaving out *one* climatic variable from the full model. We took the *rho* difference of the full model and the model with the subtracted climatic variable as an indicator for the variance explained by the respective variable. A greater difference between the full model and the model without the respective variable indicates higher variable importance in this case. We report the mean *rho* value for each climatic variable left out.

To further check the robustness of the calculated climate-richness relationship, we predicted the three models mentioned above spatially within the domain from 10°S to 50°N and 90°E to 150°E, to check if areas exist in which these models would predict unusual species richness numbers. In addition to the D^2, p-value and *rho* values for the three models, we report on the estimated maximum species richness per plot in the whole area as an indicator for model plausibility.

To account for species richness variability not captured by macroscale climatic variables, we related model residuals to two local habitat characteristics that were assessed at the plot scale, namely slope inclination and heterogeneity, with linear regressions. We report on R^2 and p-value of these regressions as indicators whether there is additional explained variance not captured by the climatic models.

All analyses were performed with the statistical platform R (Team 2017) using the packages *mgcv* for performing the gam (Wood & Wood 2015), *vegan* (Oksanen et al 2017) for species richness estimation, and *raster* (Hijmans et al 2017) and ArcMap (10.3.1) for spatial projection of the models.

6.3 Results

6.3.1 Elevational and latitudinal species richness patterns

All gradients, both absolute and estimated species richness varied considerably along the latitudinal gradient from in total 20 (estimated 24.4) species recorded in 40 plots in Hokkaido to 361 (506.2) species in 80 plots in New Guinea (Figure 6-2a). Likewise, the maximum number of species per plot of each gradient varied in the same direction (from 11 to 73, Figure 6-2b). The elevational richness patterns at tropical localities in New Guinea, the Philippines, and Myanmar were hump-shaped with highest richness at mid elevations, while turning to linear trends towards higher latitudes (Figure 6-2d) and therefore, resulting in a shift from a complex to a simple relation, as expressed by the complexity index (Figure 6-2c).

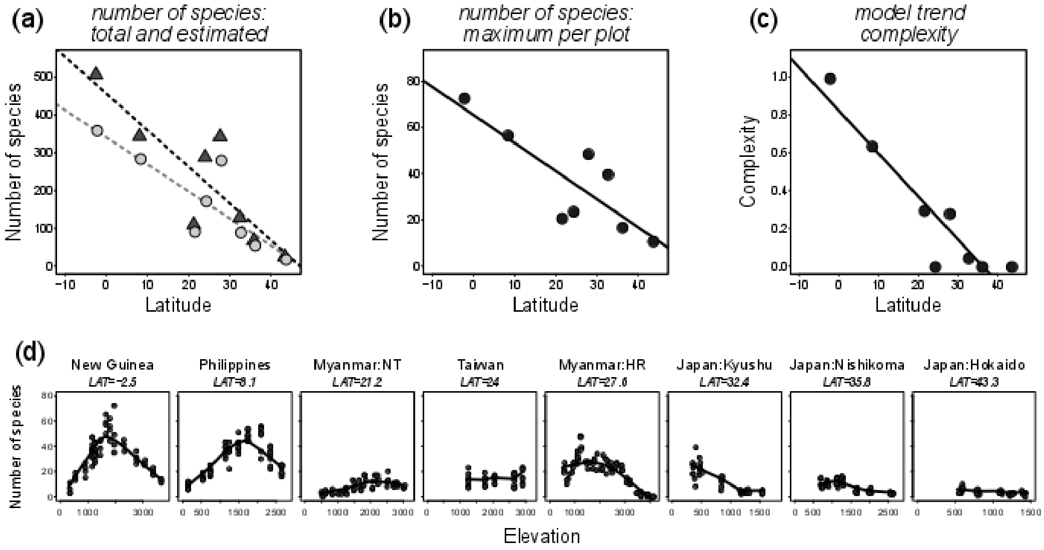

Figure 6-2 Latitudinal trend of (a) the total observed (gray circles and line) and estimated (black triangles and line) species numbers within each gradient; (b) the highest number of species per plot found within each gradient; (c) complexity values of elevational richness model trends for each gradient. Complexity values range between 0 (lowest complexity = linear trend) and 1 (highest complexity = complete unimodal trend). For detailed information on the complexity calculation, see the Methods section. (d) Elevational trends of species richness of tropical and temperate gradients in East and Southeast Asia, ordered by increasing distance from equator; latitudes are given for each gradient. Trend lines were calculated by locally weighted scatterplot smoothing (LOWESS).

6.3.2 Species richness-environment relationships

The full model across all gradients and climatic variables showed a D^2 value of 0.78 (Mod1 in Table 6-1). When leaving out non-significant climate variables, the reduced model with only significant climatic variables had the same D^2 as in Mod1. When applying LOOCV, the best predictive model showed a highly reduced set of variables and included just mean annual temperature (bio1) and cloud cover (cloud) and their quadratic terms. Although it showed, in contrast to Mod1 and Mod2 models, a lower D^2 of 0.72, it had in turn the highest overall mean *rho* (0.61 *vs.* 0.26 (Mod1) and 0.38 (Mod2), respectively) (Table 6-1).

Relating residuals from this model to non-climatic variables showed very low, albeit significant relationships (R^2-values 0 to 0.12, Figure 6-5). When correlating between observed and predicted richness by iteratively leaving random gradients out, all three models performed quite stably, and the mean rho value only dropped when just one gradient was left (Figure 6-3).

Table 6-1 Results of generalized linear models (glm) of environmental variables against species richness for pooled data of all elevational gradients. Significant levels of the variables are *** p< 0.001, ** p<0.01, * p<0.05. D² values, average Spearman's rho from LOOCV (Leave-one-out-cross-validation), and maximum predicted species number are given. Climatic variables are: bio1: mean annual temperature; bio4: temperature seasonality; bio12: annual precipitation; bio15: precipitation seasonality; arid: aridity; cloud: mean annual cloud cover; snow: snow covered days.

Model	Included climatic variables	D²	rho (mean)	predicted S_{max}
Mod1: Full model	bio1***+ $bio1^2$***+bio12+ $bio12^2$**+ bio4+ $bio4^2$+ bio15***+ $bio15^2$***+ arid**+ $arid^2$***+ cloud+$cloud^2$+ snow+$snow^2$**	0.78***	0.26	305
Mod2: Variable reduction model	bio1***+$bio1^2$***+bio12***+ bio4***+bio15***+$bio15^2$*** +cloud***+arid***+ $arid^2$***+snow***	0.78***	0.38	324
Mod3: Best predictive model	bio1***+ $bio1^2$***+cloud***+$cloud^2$*	0.72***	0.61	49

The contribution of individual variables to the full model was not pronounced except for mean annual temperature. When repeating LOOCV with step-by-step approach leaving out one climatic variable, the *rho* difference from Mod1 was highest for temperature (mean Δ*rho* = 0.25), followed by temperature seasonality (mean Δ*rho* = 0.07) (Figure 6-3).

Predicting the models to East Asia showed similar spatial distributions of species rich and species poor areas (Figure 6-4), but with rather different maximum modelled species richness per plot (Mod1: 305 species, Mod2: 324, Mod 3: 49 species; Table 1).

6.4 Discussion

The results of this study, comparing fern richness trends of Southeast and East Asia along elevational gradients within a latitudinal context show that (1) hump shaped relationships dominate in tropical moist gradients (as previously shown by, e.g., Hemp, 2002 for Africa, and Kessler, 2000, 2001; Kluge et al., 2006; Salazar et al., 2015 for Central and South America), and that (2) towards the outer tropics this hump gradually vanishes and increasingly shows a linear trend. The emerging linear trends may be interpreted as the right hand branch of a full hump, most of which is 'hidden' below sea level. Thus, this interpretation suggests that the elevation at which the species richness peak follows a temperature isocline, and therefore decreases in elevation with increasing latitude, as expressed by our hypothetical model in Figure 1, confirming **H1**.

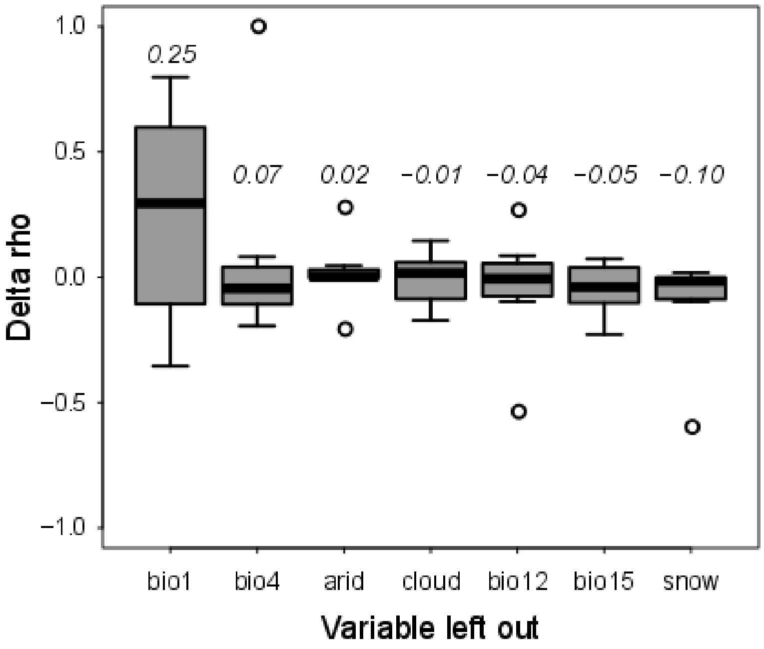

Figure 6-3 The delta rho i. e. the differences of Spearman's correlation of a full model (Mod1) and one variable left out models are presented based on leave one gradient out cross validation (LOOCV)Mean delta rho values are displayed for each model above the respective box plots. Individual variable that is excluded from model are bio1: mean annual temperature (°C); bio4: temperature seasonality (%); arid: aridity (%); cloud: mean annual cloud cover; bio12: annual precipitation (mm); bio15: precipitation seasonality (%); snow: snow covered (days).

By using a number of elevational gradients with a wide latitudinal range, we can show that local fern diversity can only be explained by about 60% by the macroclimatic factors included in the models. Although many environmental factors show correlations along a set of elevational gradients, only temperature and cloud cover emerge as being universally important for fern species richness along the whole latitudinal gradient. This could be understood as evidence for the water-energy-dynamics model (e.g., O'Brien 2006). In general, energy input and water as essential elements for life often appear most prominent in ecological explanations of richness gradients (e.g. Allen et al 2002, Currie 1991), and here especially with their interdependent character: at sites with high temperatures, a certain amount of precipitation does not necessarily constitute high humidity within the plant layer.

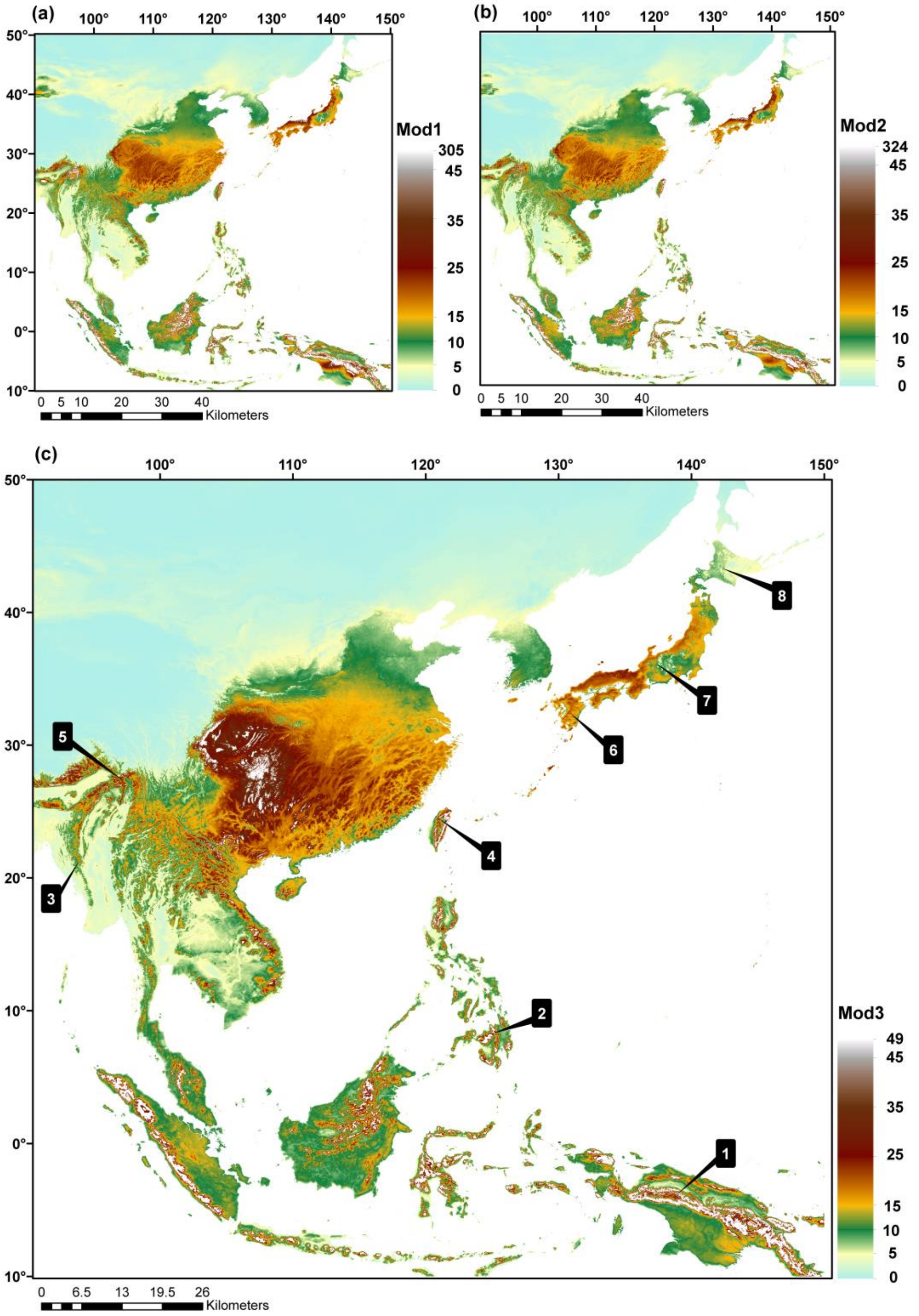

Figure 6-4 Spatial model predictions of plot based species richness for the whole study region spanned by our study gradients. These predictions are based on: Full model (Mod1, a), best model based on just keeping significant terms (Mod2, b) and best model based on LOOCV (leave-one-our-cross-validation) (Mod3, c). Sampling locations are: New Guinea (1), Philippines (2), Myanmar (3, Natma Taung; 5, Hponyinrazi), Taiwan (4) and Japan (6, Kyushu; 7, Nishikoma; 8, Hokkaido).

This has the respective effect especially on plants with a high demand on humidity, especially air humidity. With this line of reasoning, plants may face the least climatic stress at certain levels of temperature–precipitation relations, and this relation is certainly different between plant groups. For ferns, Kessler et al. (2011) found that despite different elevational peak positions between gradients, highest richness regularly occurred at temperature levels of 15–17°C, and higher temperatures were thus assumed to lower the ambient humidity. Trees, in turn, which show their maximum richness in tropical lowlands (e.g. Lieberman et al 1996), may, as deep rooting organisms, be less sensitive to this balance of temperature and precipitation. Consequently, in our models, beside temperature, cloud cover (i.e., a water related variable) showed up to be the most important, in congruence with the line of reasoning mentioned above. The fact that cloud cover emerges as being more important than precipitation could stem from the physiological capacities of ferns. Ferns need constant high humidity as they cannot actively regulate their stomata (Brodribb & McAdam 2011). Moreover, clouds are especially effective for contributing humidity when getting in direct contact with the vegetation layer, i.e., when condensing in complex tree crown structures and producing a persistent water layer, which in turn benefits organisms living here. This is especially true in tropical mountains with stable condensation layers, where the wettest elevational bands may be supposed to be situated above the elevations with highest precipitation values, but we still lack in-depth microclimatic measurements to assess the relative contributions of cloud-driven air moisture and precipitation. However, an assessment Costa Rica showed that although the precipitation peak was situated at about 1000 m, data-logger air humidity measurements revealed highest humidity at about 2000 m (Kluge et al 2006), supported by assessments of tree bryophyte cover as a proxy of air humidity (Karger et al 2015). As a huge amount of fern diversity is actually epiphytic (up to 62 % especially in our tropical and subtropical gradients), water is supplied to them by air moisture rather than through surface precipitation accumulations.

The model with highest fit to species richness (Mod2) contained a wide range of climatic variables, which all are commonly assumed to drive richness patterns, above all temperature (as surrogate for energy input) and humidity related variables (precipitation, snow, aridity). However, this model did not only show relatively low *rho* values, but also seemed to overestimate local fern species richness in some areas (e.g., up to highly unrealistic 324 species per plot in regions of northwestern China). Comparable plot based studies of ferns showed a maximum of 80 species in South and Central America (Kessler et al 2011, Kluge et al 2006).

With regard to what we know from recent studies, species richness models for individual gradients from different regions regularly show high statistical fits to climatic variables (Bhattarai et al 2004, Kessler et al 2011, Kluge et al 2006, Tang et al 2014). However, these models normally include different sets of variables and/or variables with different model estimators. This means that for a particular site such relationships may be well known and as such show a positive result ('high fit'), but they may not necessarily be transferable to a neighboring region, where different variables with different model estimates lead to a similar high fits. Therefore, species richness prediction of a random region using coefficient estimates from a single gradient model may not be useful, because the model presents a species-environment relationship only for the site in which the parameters are estimated. Adding multiple gradients to a more universal model principally reduces model deviance. Such a universal model behaves differently from the individual gradient models, as it has various combinations of regions as well as variables, and thus it could provide a better fit for a broader spatial scale. However, in general a model presenting high correlations between species richness and environmental variables (i.e., being *precise*) does not necessarily imply that a vast amount of species richness has been 'explained' by the environmental factors (i.e, being *general*), therefore model-selection "should not depend solely on statistical considerations" (Guisan & Zimmermann 2000, p. 147) when trying to extrapolate modeling results to unknown regions. Integrating the technique of leave-one-out-cross-validation allows the model to represent the relation of predicted and observed species richness and provides information about the model accuracy in a broader spatial scale. In our case, model performance did not increase much anymore after using more than two gradients in the cross validations, indicating that models derived from a few elevational gradients were already quite robust. The difference in this case can be up to 10% in variance explained, showing that if inference is drawn from single gradients, it is prone to be subject of overfitting environmental factors (e.g. sacrificing generality for precision, Guisan & Zimmermann 2000).

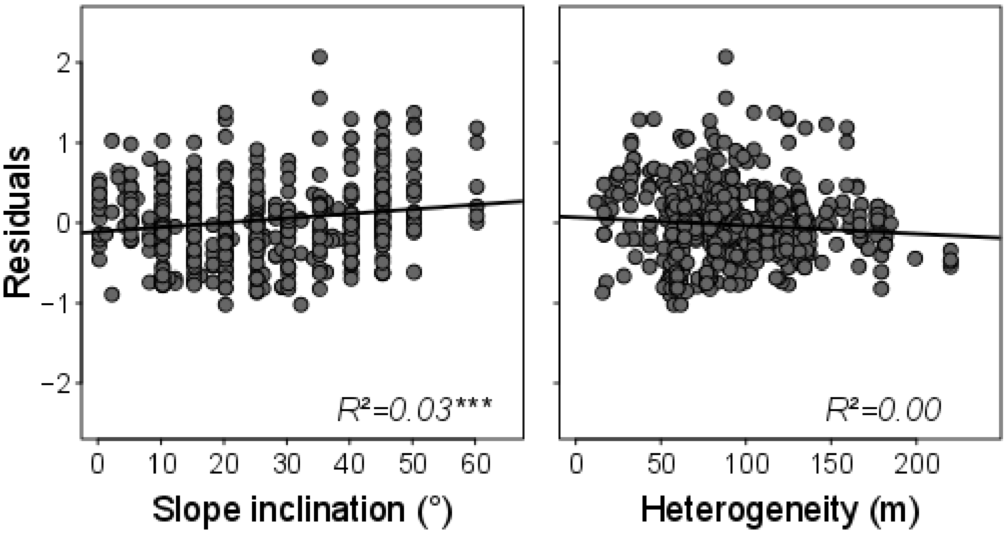

Figure 6-5 The residual of the best rho model plotted against local non-climatic variables such as slope inclination and landscape heterogeneity. Regression R^2 and p (*** = p<0.001) are given.

Macroclimatic factors tell just half the story and certainly other, more local factors could at least partly explain the remaining residuals. The set of local scale environmental factors in our study is limited, and we cannot find any connection between the model residuals and the local factors. Additional factors which are known to be prominent drivers of fern diversity are soil types and moisture (Tuomisto & Ruokolainen 1994, Tuomisto et al 2002), as well as surface radiation (Lehmann et al 2002, Richard et al 2000). Additionally, the species evolutionary history (in-situ-speciation within mountain stocks locally promoting species richness), long-term climate shifts (erasing species without later re-migration), competitive interactions, disturbance and local topographic factors at a small scale could be responsible for the remaining residuals in the simple richness-climate relationships.

In conclusion, we can show that, by combining eight different elevational gradients with a wide latitudinal range, a simple ‘water-energy-dynamics’ model can already explain half of the variance in fern species richness in East- and Southeast Asia. A rather simple model based on temperature and cloud cover shows the best performance of all models. Increasing the number of macroclimatic variables, e.g. including more, and more predictors on the macroscale might not necessarily improve our understanding of fern biodiversity. We rather stress that a full explanation for fern species richness can only be found by a combination of a few macroclimatic, local factors, and increasing integration of the evolutionary history of ferns (Kessler et al 2016).

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SUMMARY

Summary

This study has its focus on elevational biodiversity patterns of ferns and fern allies in three mountain areas of the southeastern periphery of the Himalayan arc in northern Myanmar where the two large floristic realms of Eurasia meet, the Holarctic realm in the north and the Palaeotropic realm in the south. Because complex geographical configuration of mountains leads to high biological and climatic diversity, thus the elevational gradient represents a model system to assess the underlying mechanism of larger scale species richness and diversity patterns. Moreover, diversity pattern represents the regional evolutionary process of species and their ecological sorting, the following **hypotheses** are underlined to meet the objectives of this study to link species diversity patterns on geographical space and evolutionary time connecting with environmental influences.

- Species richness pattern in Myanmar differs from other gradient within Himalaya and climate variables are the influencing factors for elevational richness pattern.
- The absence of phylogenetic diversity pattern is typical for ferns in accordance with lack of spatial barrier with respect to their long distance dispersal rate and reproductive behavior
- Complexity of hump shaped pattern gradually turning to linear pattern along latitudinal gradients and the parameters of the climate-richness relationship derived from a subset of those elevational gradients should be able to describe the climate-richness relationship at any point along the latitudinal gradient

Data collection was carried out during three expeditions of together 33 weeks in the field, with support of up to 45 local helpers and team members of the Myanmar partner institutions. For the first time ever worldwide, aiming at a complete inventory of all species of seed-plants, pteridophytes and bryophytes, samples were recorded plot-based in three transects of four plots of 400 m² at every 200 meters in elevation between the foot of the slopes and summit of mountain up to 4200 m. In total, 14,485 seed plant specimens, 3,978 pteridophyte specimens and 160 gross samples of bryophytes were collected; most of them in three sets. Additionally, two transects of nine automatically recording climate stations were established between 400 and 3200 m.

This first plot based inventory of ferns of in total 132 vegetation plots revealed 299 species from 72 genera and 24 families from Hponyinrazi and Hponkanrazi and Natma Taung gradient. Out of 299 species, 125 are new to Myanmar, in other words the species were previously only known from neighboring countries. The taxonomic composition is strikingly similar to what is known from the very well-known Neotropical regions (Kluge et al 2006), which may be explained by the ability of long distance dispersal of fern spores and the relatively old age of major fern lineages (Smith 1972). One species is new to science, which was found only five times along the gradient in Northern Myanmar, *Selliguea kachinensis* Hovenkamp, S.

Linds., Fraser-Jenk., sp. nov. Additionally a new combination *Selliguea erythrocarpa* (Mett. ex Kuhn) Hovenkamp was described, based on the specimens from our collection. With respect to the new species it is important to mention that the generic placement of this species is rather unclear, because morphological characteristics are close to either *Selliguea* Bory or *Arthromeris* (T. Moore) J. Sm. However, an erection of a new genus was avoided due to the general taxonomic uncertainty of this group of polpodial ferns. These data contribute to the upcoming Flora of Myanmar, but also set the basis for further taxonomic research in one of the least known areas worldwide (Chapter → 3, 4). Another groundbreaking contribution to the diversity knowledge of the mountain forests of northern Myanmar is the unexpected great richness of angiosperm species with maximum morphospecies counts of nearly 400 on plots of the submontane belt. It seems probable, but has to be tested based on determined species sets, that these forests are among the richest worldwide.

Testing of above-mentioned main hypotheses was accomplished within three work packages (WP).

(WP 1) The assessment of elevational richness showed that angiosperm patterns differ not only from other groups such as ferns and epiphytes but also from the interpolated result of other studies of the central Himalaya.

In contrast to plant-list based distribution graphs, the real distribution of angiosperms do not show the widely known hump-shaped diversity, but have a more or less linear decline with increasing elevation. This pattern was mainly driven by trees, shrubs, and palms, whereas especially epiphytes clearly peaked around 1200 m a.s.l., and grasses peaked at the high elevations above treeline. Climatic variables and especially temperature and precipitation play a key role for explaining the species richness patterns of all considered life forms and underpin the climatic dependence of lifeforms. Also for traits there was a clear finding: tree leaf size reduces with elevation, and so did other leaf properties as well. All these patterns can be related to climatic adaptations, especially to frost and drought stress.

Not surprisingly, elevational fern species richness showed along both study gradients a hump shaped richness pattern. This pattern was mainly driven by the epiphytic lifeform, their elevational richness trend was more pronounced than for terrestrial species. This is especially due to the higher sensitivity to the steep change of environmental conditions and their exposed position especially in the upper tree layer. Comparing both gradients, the elevational peak of richness was situated at the northern gradient at a considerably lower elevation, and moreover, the absolute species richness was higher at the northern gradient. This last finding is especially counterintuitive on the first glance, as species richness should increase when coming closer to the equator. However, both results can be explained by the climatic setting of the gradient: (1) Along the northern gradient, temperature levels are situated at lower elevations at the southern gradients, thus peak of richness is at about 16°C mean annual temperature at both gradients. (2) The higher temperature was assumed to lower the ambient humidity that the highest species occurred under the environmental condition with moderate temperature and high humidity. Additionally, due to the close vicinity of the southern gradient to the dry zones of Central Myanmar, species richness is generally lower here, showing the strong demand of humidity for maintenance and lifecycle of ferns. These first findings show the strong environmental relationships of species richness of ferns and confirm what is known from other tropical mountains in the Americas and Africa (Chapter → 2, 3).

(WP 2) Phylogenetic diversity pattern present a certain degree of variation in phylogenetic overdispersion and environmental clustering; however the overall pattern does not deviate from the random assemblage.

Additional four gradients, i.e. Taiwan and Japan: Kyushu, Nishikoma and Hokkaido were added to the study to have a wide range of climate and geographic variations. Phylogenetic richness among the species presents similar pattern with species richness in general, however they are not identical, for instance the decreasing in phylogenetic richness in a species rich assemblage could be a consequence of the less phylogenetic distances between assigned species. In accordance with their reproductive behavior and long distance dispersal rate, the relationship between phylogenetic diversity and species richness might not be different from the randomness in contrast with the angiosperms. In contrast with angiosperms from the previous studies, the phylogenetic diversity of pteridophytes reflects more to stochastic events as the deterministic processes limit the regional species pool in general, however for ferns, the geographic barrier such as dispersal limitation and, seasonal and temporal barrier for fertilization disregards to a certain extent. Thus the equilibrium of competitive interaction and environmental filtering represent the species-neutral interactions and the pteridophytes dispersal might have been overriden the vicariance rate. However the trait patterns of some gradients such as Natma Taung and Hponyinrazi from Myanmar, and Nishikoma from Japan have uncoupled with the phylogenetic pattern, thus the environmental divergence of those gradients are strong to lead the trait having clustered assemblage. Therefore, adaptations in ferns occur convergently in diverse phylogenetic assemblage (Chapter → 5).

(WP 3) The best species richness model was developed with a set few climatic variables such as temperature and cloud cover. However the climate variables explain more than 60% of the local variation and combinations of small scale local factors could enhance the model prediction power.

Putting the local results from Myanmar in a wider context, it is generally accepted that the total richness within each gradient should decline towards high latitudes as reported for most groups of organisms due to the general temperature driven nature of species richness. Second, for the same reason the frequently reported and for Myanmar confirmed hump shape pattern of species richness (mentioned above), the peak of richness should shift towards lower elevations for gradients at increasing latitude. Both trends combined should result in a pattern, where the symmetric hump in tropical regions gradually turned into a linear trend in temperate regions, which

means the respective models were reduced in complexity. Relating species richness patterns to macroclimatic conditions along both gradients types, elevation and latitude, respectively, hypothesize main trends, which were tested on eight elevation gradients between 4°S and 43.3°N.

The combination of eight full elevational gradients in East Asia from Indonesia at the equator via Taiwan and Myanmar to temperate Japan, all sampled with the same standardized sampling protocol, offer the unique possibility to test this hypothesized interlinked trend. Additionally, by applying general additive models, the best fitting climatic variables could be assessed together with their relative contribution. Moreover, since 'best fitting' does not necessarily mean 'good predicting', we applied the technique of leave-one-out-cross-validation (LOOCV) to find the best combination of climatic variables, which predicted the left out gradients. A reasonable result from these analyses can be extrapolated into the whole region covered by the analyzed gradients (East Asia).

As a result we could confirm the simple model of a shift in species richness trends from unimodal to linear towards temperate regions and suggest that over this broad spatial scale temperature is the most decisive factor. Confirming this, the highest predictability following our macroclimatic models was indeed temperature in combination with cloud cover as humidity related variable, together predicting about 60% of species richness variation. It is interesting in this regard that explained variance is rather similar for the model based on generalized linear model result (GLM- model) and best model based on leave one out cross validation result (LOOCV-model) (also somewhat lower for the latter ones), but that absolute numbers of species were more realistically modelled by LOOCV, since GLM predicted up to 380 species per plot, which is by far nonsense.

There are two interesting conclusions to be drawn: First, not precipitation as a humidity variable is included in the models, as most frequently used in species richness-climate models, but rather cloud cover. This indeed better reflects the physiological specifications of ferns, since not absolute water input, but balanced humidity is crucial. Second: In contrast to a large bulk of publications, which regularly report higher fits for richness–climate relationships, our best model is only able to predict a little bit more than half of the variation in local fern species richness in East and Southeast Asia. The remaining variation in local fern species richness is most likely due to small scale factors, which are hardly accounted for by macroclimatic factors (Chapter 6).

The outcome of this study has contributed to comprehensive national conservation plans; (1) the preparation of the national biodiversity strategy and action plan, (2) the nomination dossier of UNESCO neutral heritage site in northern Myanmar.

ZUSAMMENFASSUNG

Zusammenfassung

Die kumulative Dissertation wurde im Rahmen von drei? deutsch-burmesischen Gemeinschaftsprojekten zwischen 2012 und 2018 durchgeführt. Die Arbeiten wurden finanziert durch die Deutsche Forschungsgemeinschaft (DFG) und den Deutschen Akademischen Austauschdienst (DAAD).

Der Norden Myanmars gehört zu den artenreichsten Regionen der Erde („Biodiversity Hotspots“) und bildet, wie die Weltkarten der Biodiversität von Barthlott et al. (1996, 2005) zeigen, die artenreichste Region in ganz Eurasien. Außerdem ist diese Region das einzige Diversitätszentrum, das in zwei Florenreichen liegt, der Holarktis im Norden und der Paläotropis im Süden. Die Bergwälder sind weitgehend ungestört von Landwirtschaft, Forstwirtschaft oder Bergbau. Die Bergwälder im Norden Myanmars liegen zwar im Zentrum des „East Himalaya-Yunnan Diversity Center“ (Barthlott et al., 1996, 2005), sie waren bisher aber, außer dem Mt. Victoria, aufgrund politischer Umstände, praktisch unerforscht.

Der Nordwesten Myanmars zeichnet sich durch longitudinale Gebirgsketten aus. Sie bilden die südöstliche Peripherie des Himalaya und des tibetischen Plateaus (Hochland von Tibet) und lösen sich im Süden in isolierte Bergkuppen („Sky Islands“) auf. Die umgebenden Tiefländer liegen in 400 m Meereshöhe und haben teilimmergrünen tropischen Dipterocarpaceen- und Teakwald, oberhalb 2000 m Meereshöhe sind immergrüne Eichenwälder des Himalaya dominant, oberhalb von 3000 m folgen Rhododendron-Tannenwälder. Die Gipfel im Norden des Untersuchungsgebiets erreichen Meereshöhen von mehr als 4000 m (Hponyinrazi and Hponkanrazi) und sind von alpiner Vegetation bedeckt. Das südlichste Teilgebiet („Natma Taung/ Mt. Victoria“) erreicht nur 3000 m, hat aber an seinem Gipfel auch alpine Vegetation. Die vorhandenen Klimadaten und die kurzen Messreihen der Projektstationen zeigen, dass das Untersuchungsgebiet zu den feuchtesten Bergregionen des Himalaya gehört.

Das Untersuchungsgebiet bietet 1) durch sein Relief (400 – 3000/4200 m), 2) seine intermediäre Position zwischen zwei Florenreichen, 3) seine hohen Niederschläge, 4) seine weitgehend ungestörte Vegetation, und 4) durch seine Lage im artenreichsten Gebiet der Nordhemisphäre gute Voraussetzungen, zentrale Fragen der Biogeographie zu untersuchen.

Aus dem Umstand, dass die Bergwälder im Norden Myanmars so gut wie unbekannt sind ergeben sich zwangsläufig andere Prioritäten als bei Untersuchungen in Regionen, deren Flora und Vegetation wenigstens in Grundzügen bekannt ist. Übergeordnetes Ziel der Studie ist deshalb, erste Grundlagen unseres Wissens über Flora und Vegetation zu schaffen. Darüber hinaus wird mit folgenden Hypothesen ein Beitrag zu übergeordneten Fragen der Biodiversität in Gebirgsregionen geleistet:

Es wurden folgende Hypothesen aufgestellt:

- Die plot-basierte Höhenverteilung von Blütenpflanzenarten in Bergwäldern Myanmars unterscheidet sich von altitudinalen Mustern auf Grundlage von Florenlisten für diverse Pflanzengruppen im Himalaya
- Die plot-basierte Höhenverteilung von Farnen und Farnverwandten zeigt das weltweit aus humiden tropischen Hochgebirgen bekannte Artmaximum in mittleren Höhenlagen
- Klimavariablen bestimmen die Höhenverteilung des Artenreichtums bei Farnen
- Aufgrund ihrer Verbreitungsmittel haben Farnpflanzen keine Ausbreitungsschranken; Morphotypen und genetische Assemblages sind sich ähnlicher unter adversen Standortbedingungen; sie divergieren dagegen unter Optimalbedingungen.

Die Untersuchungen wurden ermöglicht durch Projektverhandlungen und Unterzeichnung eines Memorandum of Understanding (2011/2012) mit der burmesischen Partnerinstitution, dem Forest Department des Ministry of Environmental Conservation and Forestry, the Republic of the Union of Myanmar. Auf drei Expeditionen (2012, 2013, 2014, insgesamt 33 Wochen) wurden 11.670 Blütenpflanzen-, 3978 Farn-Belege und Farnverwandte sowie Moose in dreifachem Satz gesammelt. Dies ist das bisher umfangreichste Herbar, das bisher in ganz Myanmar gesammelt wurde.

In drei Höhentransekten zwischen 400 und 4200 m Meereshöhe wurden auf 132 Flächen (plots?) von je 400 m² alle Blütenpflanzen und alle Farne gesammelt, zur Bestimmung gepresst und in Äthanol konserviert. Epiphyten wurden durch Baumkletterer beschafft. Sammelproben von Moosen im unteren Stammbereich ergänzen die Sammlung.

Die beiden wichtigsten Ergebnisse der Floreninventur sind:

1) 299 Arten an Farnpflanzen und –verwandten wurden gesammelt. Dies ist die bislang umfangreichste Sammlung für ganz Myanmar. 125 Arten sind erstmals für Myanmar nachgewiesen worden. Ein Farn erwies sich als neu und wurde erstmals wissenschaftlich beschrieben.
2) Mit 300 bis knapp 400 Gefäßpflanzenarten pro 400 m² gehören die submontanen Bergwälder des Untersuchungsgebiets wahrscheinlich zu den artenreichsten weltweit, ganz sicher sind sie die artenreichsten des Himalaya. Der Mangel an vergleichbaren Erhebungsmethoden in anderen Gebirgen und der Umstand, dass wir bislang meist nur Morphospecies unterschieden haben, machen weitere Bestimmungsarbeiten notwendig.

Die Ergebnisse der Diversitätsuntersuchungen haben die o.g. Hypothesen bestätigt und sind wie folgt zusammenzufassen:

- Die Höhenverteilung von Blütenpflanzen zeigt nur für Epiphyten das aus Pflanzenlisten bekannte Artmaximum in mittleren Höhen. Die Artenzahlen nehmen mehr oder weniger linear mit der Meereshöhe ab.
- Farne und Farnverwandte haben auch plot-basiert das aus anderen tropisch-humiden Gebirgen bekannte Artmaximum in mittleren Höhenlagen
- Unter den Klimavariablen erwies sich die Bewölkungsdauer als ausschlaggebend für die Artenverteilung
- An ihren Höhengrenzen liegen Morphotypen und genetische Assemblages näher beieinander als unter Optimalbedingungen.

Drei wichtige Ergebnisse der Untersuchung sind auch für den Vorschlag der UNESCO verwendet worden, den nördlichen Teil des Untersuchungsgebiet („Northern Forest Complex“) als World Heritage Site unter Schutz zu stellen: 1) das Vorkommen neuer Arten, 2) der ungewöhnlich große Artenreichtum der Bergwälder und 3) die im Himalaya und seiner Peripherie ungewöhnlich geringe Nutzung durch den Menschen.

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APPENDIX

Appendix

Appendix T 1 Locality of East and Southeast Asia transects along the latitudinal gradients together with number of plots and elevational range.

Transect	No. of plots	Elevational range	LAT	LONG
New Guinea: Wamena Central Valley	36	1100-3600	-4	139
New Guinea: Arfak Mountains	44	300-1900	-1.3	134.1
Phillippines	80	100-2600	8.1	125.3
Myanmar: Natmataung	56	450-3000	21.2	94
Taiwan	40	1200-2850	24.0	121.2
Myanmar: Hponyinrazi	80	500-4100	27.6	97
Japan: Kyushu	48	320-1520	32.4	131
Japan: Nishikoma	56	640-2580	35.8	137.9
Japan: Hokkaido	40	530-1410	43.3	142.6

Appendix F 1 *Abies* (e.g. *Abies georgei*) are often destroyed by the burden of the liverwort-cushions due to high humidity, and therefore the canopy is not longer closed, giving way to bamboo and rhododendrons, Hponkanrazi above 3200 m (photograph by Jürgen Kluge 2014).

Appendix F 2 Forests of rhododendrons (e.g. *Rhododendron arizelum*) in Hponkan Razi in 3400 m. Tree stems mostly covered by Hepaticae cushions due to high humidity.

Appendix F 3 Tree line ecotone at around 3600 m in Hponkan Razi. Steep slopes are exposed to slope gliding and cannot develop larger forests. Thickets of bamboo (bright green) and rhododendrons prevail together with shrubs of *Salix* (Salicaceae) and *Sorbus* (Rosaceae).

Appendix F 4 Thickets of bamboo on top of Hponkan Razi at around 3600 m (photograph by Georg Miehe 2014).

Appendix F 5 Epiphytes in the tree crown were collected by trained tree climbers. Climber is reaching for *Agapetes* spec. (Ericaceae) (left picture).

Appendix F 6 All species per plot were sampled, sorted, tagged with a specific number and entered into a vegetation record sheet (photographs by Jürgen Kluge 2014).

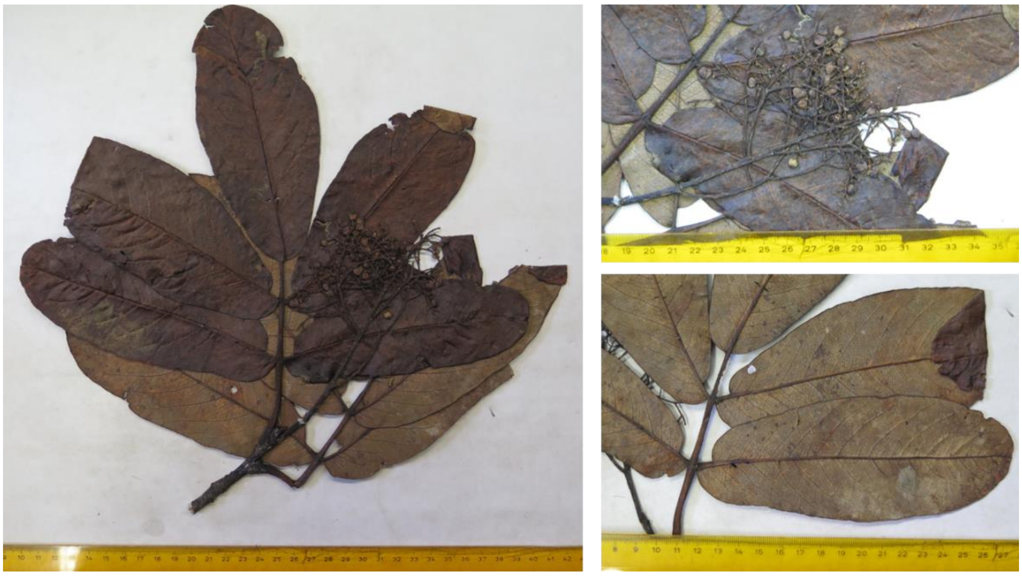
Appendix F 7 Example of a compound tree leaf (1) with dentate leaf margins (1) and remarkable tip (1) of size class b (1,500 – 180 cm²). Species not yet determined, probably Araliaceae. Found in 2839 m on an upper slope. Habitat: *Lithocarpus*- *Magnolia*- *Rhododendron* forest.

Appendix F 8 Example of a simple tree leaf (0) with smooth leaf margins (0) and without remarkable tip (0) of size class b (1,500 – 180 cm²). Species name: *Magnolia rostrata* (Magnoliaceae). Found in 2434 m. Habitat: *Magnolia*- Fagaceae- Bamboo forest.

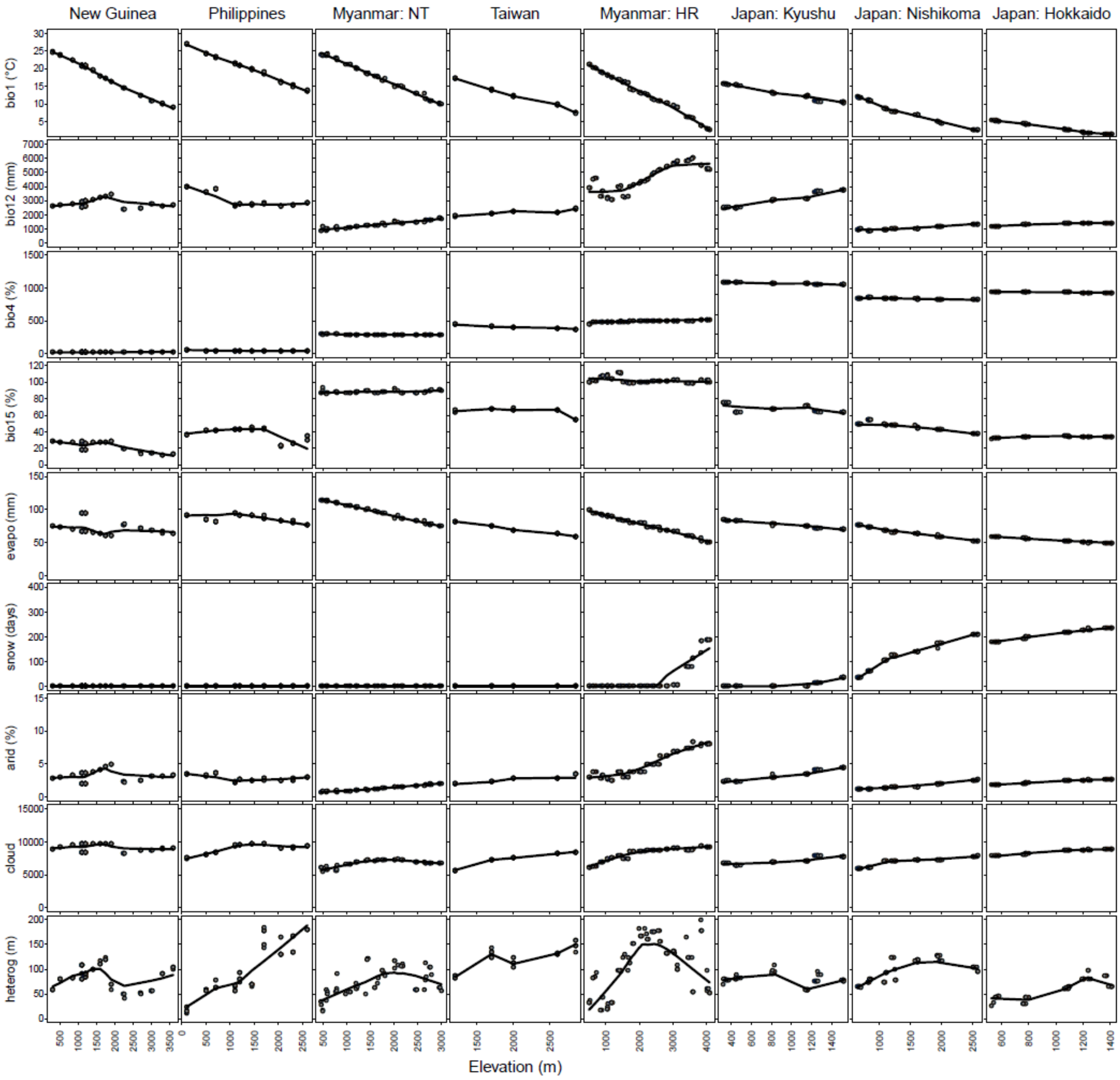
Appendix F 9 Example of a simple tree leaf (0) with dentate leaf margins (1) and with remarkable tip (1) of size class c (180 – 20 cm^2).Probably a species of the genus *Castanopsis* (Fagaceae). Found in 527 m. Habitat: Fagaceae- Dipterocarps forest.

Appendix F 10 Example of a simple tree leaf (0) with smooth leaf margins (0) and with remarkable tip (1) of size class b (1,500 – 180 cm^2). Species not yet determined, probably Moraceae. Found in 527 m. Habitat: Fagaceae- Dipterocarps forest.

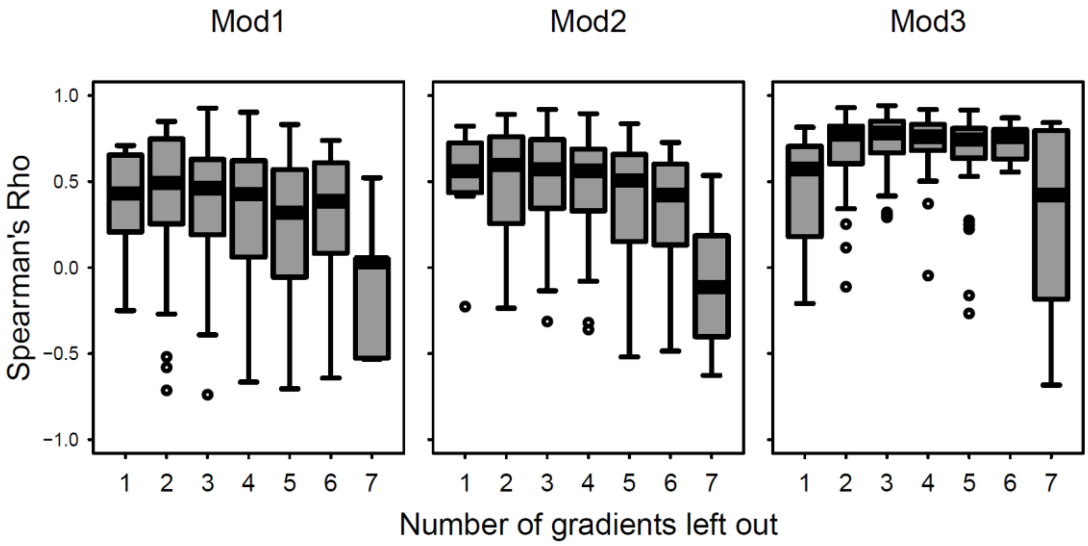
Appendix F 11 Example of a compound tree leaf (1) with dentate leaf margins (1) and without remarkable tip (0) of size class c (180 – 20 cm²). Species name: *Sorbus hypoglauca* (Rosaceae). Found in 3133 m on a upper slope. Habitat: Upper montane *Abies-Rhododendron* forest.



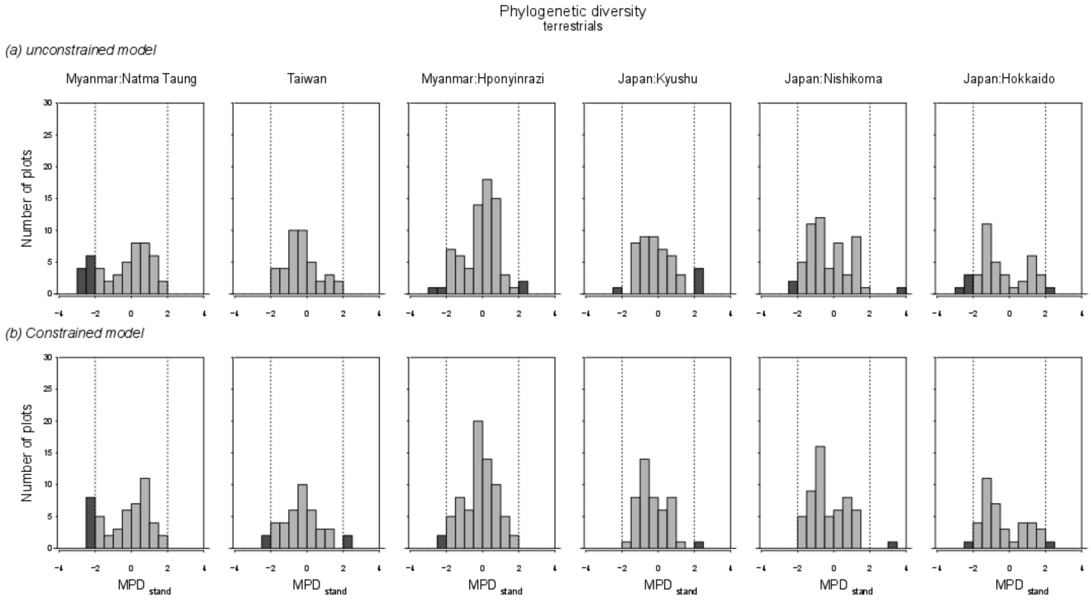
Appendix F 12 Example of a compound tree leaf (1) with dentate leaf margins (1) and without remarkable tip (0) of size class c (180 – 20 cm²). Species name: *Sorbus hypoglauca* (Rosaceae). Found in 3133 m on a upper slope. Habitat: Upper montane *Abies-Rhododendron* forest.



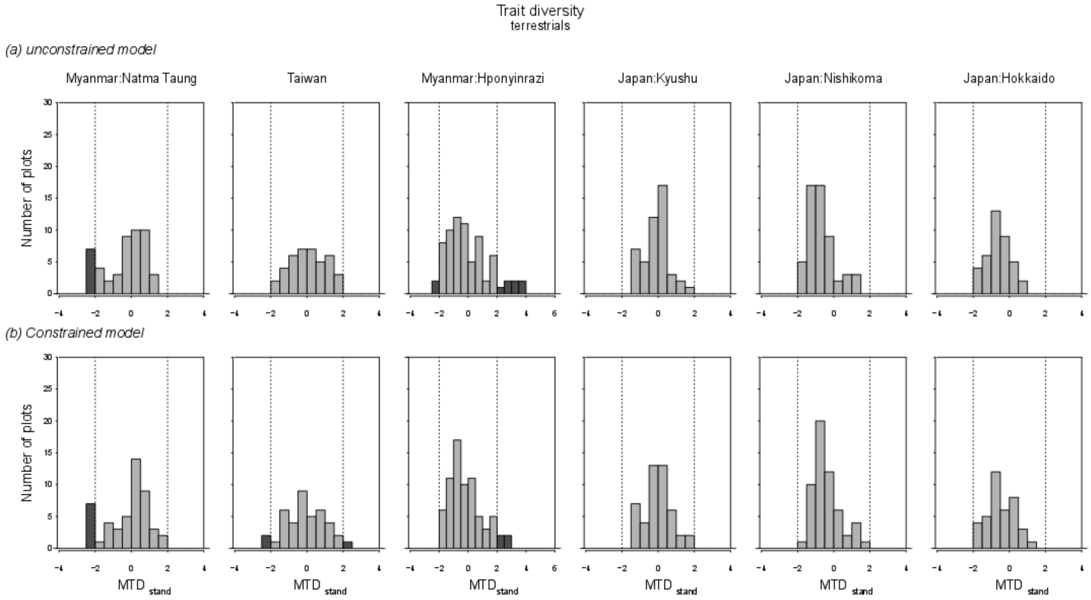
Appendix F 13 Elevational patterns of climate and spatial variables; mean annual temperature (bio1, °C), annual precipitation (bio12, mm), temperature seasonality (bio4, %), precipitation seasonality (bio15, %), evapotranspiration (evapo, %), snow cover (snow, days), aridity (arid, %), cloud cover (cloud) and heterogeneity (heterog, m; a proxy for habitat heterogeneity) for all East and Southeast Asia gradients. The data source for the environmental variables were CHELSA for bioclim (Karger et al., 2016), mean annual cloud cover (cloud) is from global 1-km cloud cover datasets (Wilson & Jetz 2016) and the global multi-resolution terrain elevation data 2010 for “heterog” (Danielson & Gesch, 2011). “heterog” was calculated as the standard deviation of elevations of all 25 surrounding cells (5 x 5 grid), based on the same area dataset, thus high standard deviations indicating a variable landscape relief.



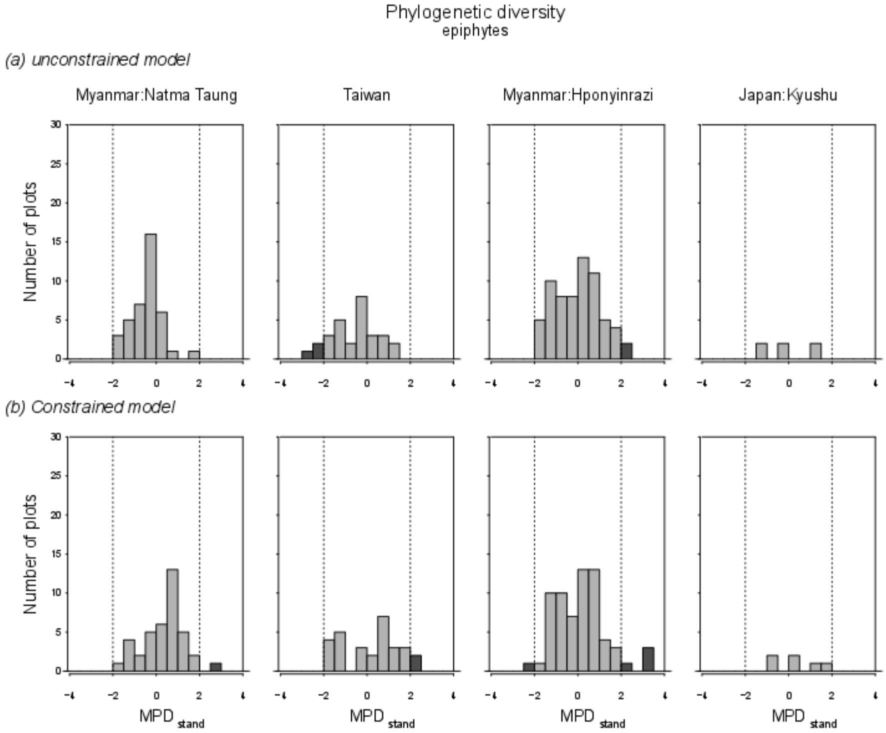
Appendix F 14 Spearman correlation between the predicted and observed species richness of full model with all variables (Mod1), variable reduction model (Mod2) and best predictive model (Mod3) is presented for each step of leave one out cross validation (LOOCV).



Appendix F 15 Histogram of standardized of mean phylogenetic diversity (MPD stand) of terrestrial species for both constraint and unconstraint model



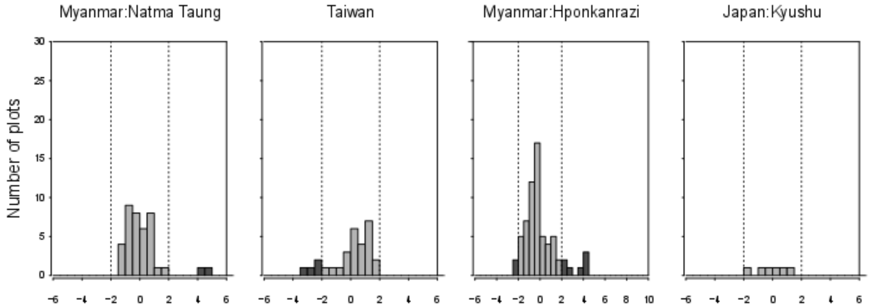
Appendix F 16 Histogram of standardized of mean trait diversity (MTD stand) of terrestrial species for both constraint and unconstraint model



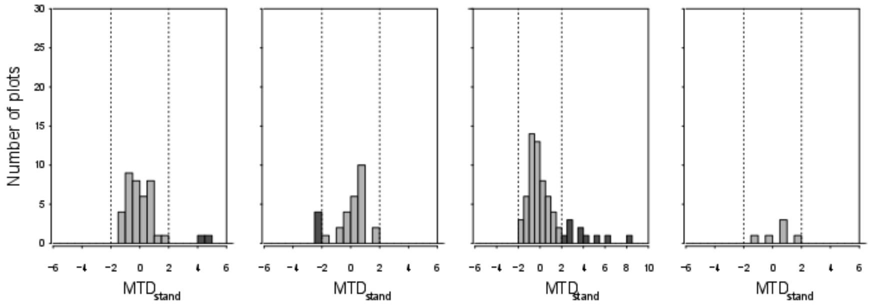
Appendix F 17 Histogram of standardized of phylogenetic diversity (MPD stand) of epiphytic species for both constraint and unconstraint model

Trait diversity
epiphytes

(a) unconstrained model



(b) Constrained model



Appendix F 18 Histogram of standardized of mean trait diversity (MTD stand) of terrestrial species for both constraint and unconstraint model

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Curriculum Vitae

Personal dates

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date of birth	27.06.1985 (Taungoo, Myanmar)

Education and Professional Experience

since March 2013	Ph D candidate Geography Faculty, Philipps University, Marburg, Germany
September – November 2014	3rd research expedition within DFG-project “Mountain Biodiversity Transect Studies in Myanmar: a stepping stone towards the Island Biogeography of Alpine Biota in the Southeast Himalayan Biodiversity Hotspot” of Prof. Dr. Georg Miehe, Prof. Dr. Thomas Nauss, Dr. Juergen Kluge and Dr. Lars Opgenoorth, Philipps University, Marburg, Germany
September – December 2013	2nd research expedition within DFG-project “Mountain Biodiversity Transect Studies in Myanmar: a stepping stone towards the Island Biogeography of Alpine Biota in the Southeast Himalayan Biodiversity Hotspot” of Prof. Dr. Georg Miehe, Prof. Dr. Thomas Nauss, Dr. Juergen Kluge and Dr. Lars Opgenoorth, Philipps University, Marburg, Germany
September - December 2012	1st research expedition within DFG-project “Mountain Biodiversity Transect Studies of Mt. Victoria (Natma Taung National Park, Chin State, Myanmar)” of Prof. Dr. Georg Miehe, Prof. Dr. Thomas Nauss and Dr. Juergen Kluge, Philipps University, Marburg, Germany
March 2010	Field studies in Vietnam, cooperation with Center for International Forestry Research (CIFOR); “Strengthening Rural Institutions to support Livelihood Security for Smallholders Involved in Industrial Tree-planting Programme in Vietnam and Indonesia”.
November 2009	Training in “Role of trees as anchor against landslide and soil erosion” Visayas State University, Philippines

2008 – 2010 Study of Master in Tropical and International Forestry
Georg- August University, Goettingen, Germany
Title of M.Sc. thesis:
"Stem volume and taper function for *Acacia hybrid*, *Acacia mangium* and *Eucalyptus urophylla* in Vietnam"

2001 – 2004 Study of Physics
University of Eastern Yangon, Yangon, Myanmar

List of presentations and poster in PhD study

(1) Biogeographical Transect Studies in the High Altitude Mountain Areas of Myanmar
Phyo Kay Khine
DAAD Stipendiatentreffen
19th to 21st April 2013 in Darmstadt, Germany

(2) Mountain Biodiversity in Myanmar
A stepping stone towards the
"Island Biogeography of Alpine Biota in the Southeast Himalayan Biodiversity Hotspot"
Georg Miehe - Phyo Kay Khine - Jürgen Kluge - Thomas Nauss - Lars Opgenoorth
5th international and interdisciplinary symposium of "Biodiversity and Natural Heritage of the Himalaya"
11th to 13th April 2014 in Erfurt, Germany

(3) Mountain Biodiversity in Myanmar
A stepping stone towards the
"Island Biogeography of Alpine Biota in the Southeast Himalayan Biodiversity Hotspot"
Georg Miehe - Phyo Kay Khine - Jürgen Kluge - Thomas Nauss - Lars Opgenoorth
Arbeitsgemeinschaft für Vergleichende Hochgebirgsforschung und Arbeitskreis Hochgebirge
Ressourcen der Gebirgsräume: Nutzung, Wandel, Bewertung
19th to 22nd June 2014 in Bern, Switzerland

(4) Biodiversity assessment in northern Myanmar
Expedition report and preliminary results
Phyo Kay Khine- Georg Miehe - Jürgen Kluge - Thomas Nauss - Lars Opgenoorth
Royal Botanic Garden Edinburgh, Scotland
07.07.2014

(5) Biodiversität am Fuß des Himalaya:
Expeditionsbericht und erste Ergebnisse
Phyo Kay Khine - Georg Miehe - Jürgen Kluge - Thomas Nauss - Lars Opgenoorth
Kultur und Wissenschaft: Schlüssel zur Zukunft - 60 Jahre diplomatische Beziehungen Deutschland - Myanmar
3rd September to 09th October 2014 in Berlin, Germany

(6) Mid- term report 21.11.2014
Mountain Biodiversity in Myanmar
Phyo Kay Khine – Georg Miehe
21.11.2014, Forest Department, Ministry of Environmental Conservation and Forestry, Nay Pyi Taw, Myanmar

(7) Mountain Biodiversity in Myanmar

A stepping stone towards the
"Island Biogeography of Alpine Biota in the Southeast Himalayan Biodiversity Hotspot"
Looking back and going ahead
Georg Miehe - Phyo Kay Khine - Jürgen Kluge - Thomas Nauss - Lars Opgenoorth
International Seminar on Cooperation on Biodiversity Conservation in Myanmar
A gathering to share information and experience among national and international institutions and NGOs working with MOECAF (to support the implementation of the National Biodiversity Strategy and Action Plan)
18th to 19th March 2015 in Yangon, Myanmar

(8) Elevational gradients in humid mountain forests of the Southeast Himalayan Biodiversity Hotspot
"First pteridophyte assessment in northern Myanmar"
Phyo Kay Khine - Georg Miehe - Jürgen Kluge - Win Naing Thaw
3rd conference on "Botanical Research in Tropical Asia"
6th to 11th December 2015 in Vientiane, Lao PDR

(9) "First plot based richness data of ferns and seed plants along elevational gradients in Myanmar"
Phyo Kay Khine - Georg Miehe - Jürgen Kluge
European Conference of Tropical Ecology and 29th Annual Meeting of the Society for Tropical Ecology
23rd to 26th February 2016 in Göttingen, Germany

(10) "First pteridophytes plot-based assessment along the elevational gradient in the Northern Mountain Forest Complex"
Phyo Kay Khine
Scientific research workshop on the Northern Mountain Forest Complex suggested as UNESCO World Heritage Site
June 7th 2016 in Yangon, Myanmar

(11) "Patterns of species distribution and diversity along elevational gradients in sparsely documented areas in Northern Myanmar"
Phyo Kay Khine- Georg Miehe - Jürgen Kluge - Thomas Nauss - Lars Opgenoorth
XIX International Botanical Congress
23rd to 29th July 2017 in Shenzhen, China

Publications

Khine PK, Lindsay S, Fraser-Jenkins C, Kluge J, Kyaw M, Hovenkamp P (2016) Selliguea kachinensis (Polypodiaceae), a new fern species of uncertain affinity from Northern Myanmar. *PhytoKeys* 25(62):73-81. doi: 10.3897/phytokeys.62.8101.

Khine PK, Fraser-Jenkins C, Lindsay S, Middleton D, Miehe G, Thomas P, Miehe G, Kluge J (2017) A contribution toward the knowledge of ferns and lycophytes from northern and northwestern Myanmar. *American Fern Journal* 107:219-256. doi: 10.1640/0002-8444-107.4.219

Nowak P, Khine PK, Homeier J, Miehe G, Leuschner C, Kluge J (2018) A first complete plot-based elevational assessment of richness, life forms and leaf traits of seed plants in the

Southeast Himalayan Biodiversity Hotspot, North Myanmar. *Plant Ecology and Diversity*, under revision.

Khine PK, Miehe G, Kessler M, Karger DN, Kluge J (2018) Elevational richness pattern of ferns and lycophytes within the context of the latitudinal diversity gradient in East and Southeast Asia: Climate tells just half the story. *Journal of Biogeography*, submitted manuscript.

Khine PK, Miehe G, Kluge J, Opgennoorth L (2018) Phylogenetic diversity along the southern Himalaya elevational gradient in North Myanmar. Basic and applied Ecology, manuscript in progress.

Erklärung

ich versichere, dass ich meine Dissertation

"Biogeographical transect studies in the high elevation mountain areas of Myanmar"

selbständig, ohne unerlaubte Hilfe angefertigt und mich dabei keiner anderen als der von mir ausdrücklich bezeichneten Quellen und Hilfen bedient habe.

Die Dissertation wurde in der jetzigen oder einer ähnlichen Form noch bei keiner anderen Hochschule eingereicht und hat noch keinen sonstigen Prüfungszwecken gedient.

Marburg (Lahn), den 27.04.2018 __________________________

Phyo Kay Kine