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Soil, Topography and Forest Structure Shape the Abundance, Richness and Composition of Fern Species in the Fragmented Tropical Landscape of Xishuangbanna, Yunnan, China

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Abstract: Understanding how forest fragment size, topography, forest structure, and soil properties affect plant diversity remains a crucial question in conservation biology, with ferns often being understudied. To address this knowledge gap, we surveyed the abundance, species richness, and composition of ferns in a tropical landscape in south China using 75 sites in 42 forest fragments. We then used a multi-model inference approach to assess whether fern abundance, richness, and composition were better explained by (a) fragment size, (b) topography (slope, aspect), (c) forest structure (tree basal area, light availability), or (d) soil properties (pH, Carbon, Nitrogen, Phosphorous, Calcium, Magnesium, water availability, and proportion of clay, silt, and sand). We also conducted a nestedness analysis to examine whether the composition of the fern communities in smaller fragments (0.4–1 km^2) differed or represented a subset of the communities found in larger fragments (e.g., >10 km^2). We found that (a) fern abundance was mostly influenced by soil properties, slope, and aspect, (b) fern species richness by soil properties and slope, and (c) fern species composition by forest structure, specifically, tree basal area. We also found that fern species composition was not nested in the landscape, suggesting that smaller forest fragments had different communities from larger fragments. Our results suggest also that soil properties play an important role in maintaining fern abundance and diversity and therefore protecting soil can help conserve ferns in fragmented landscapes.

Keywords: fragmentation; pteridophytes; soil; multi-model inference; nestedness

1. Introduction

The clearance of tropical forests is a major cause of the decline of their biodiversity. However, the impact of the associated fragmentation on the remaining forest is less clear, despite decades of research efforts. There has been a long unresolved debate about the relative importance of the total amount of forest remaining in the landscape and the sizes of the individual fragments [1]. The general view that has dominated the literature suggests that larger fragments are more important for conservation than smaller fragments [2]. On the other hand, plant species distributions are strongly influenced by edaphic and topographic factors [3–5]. Therefore, a key practical question is whether conservation efforts should focus mainly on fragment size or whether edaphic and topographic factors should also be considered.

In human-dominated landscapes, cultivated areas favor the best soils and the most accessible sites [6], leaving inaccessible sites, like those on steeper slopes, undisturbed, or with a low human impact [7]. At the same time, it has been shown that terrestrial fern species diversity tends to increase in areas with steep topography and higher air and soil humidity [8,9]. In general, terrestrial fern diversity in tropical regions have a hump

shape distribution with its pick around 2000 m a.s.l., with variations according to the local conditions [10]. Moreover, fern species diversity in tropical sites is influenced by forest structure and its level of disturbance. The reduction in canopy cover determines the changes in ground humidity, which influences fern species composition [11]. The local microclimate depends on differences in the forest structure, such as the number of trees, the total biomass in the above-ground forest, and light availability [12]. For example, studies have reported that plantations surrounding forest fragments can drain and reduce the forest's soil humidity [13]. This negative effect can be exacerbated in small fragments [14].

Terrestrial fern species diversity tends to be richer in soils with a high level of organic nutrients. In contrast, sites with high concentrations of sand and clay have fern species that can be specifically adapted to those conditions [15]. Macronutrients such as carbon, nitrogen, and phosphorous are significant drivers of plant distribution [16]. However, the micro-elements of magnesium and calcium also play an essential role in plant physiology and distribution since many terrestrial ferns avoid or are restricted by limestone substrates [17]. Moreover, soil texture, referring to the soil's percentage of clay, sand, and silt is related to soil drainage. Soil texture has been found to be among the major drivers of terrestrial fern distribution on both small and large scales [18]. Lastly, soil water availability is also intrinsically related to soil properties. Yet, together, these factors (i.e., micro- and macronutrients, soil texture, and water availability) have been poorly studied in terrestrial fern ecology.

In tropical fragmented landscapes, biotic impoverishment seems unavoidable due to the human pressure on the habitats. The forest fragments often differ significantly in size, spatial distribution, and degree of habitat transformation. These differences provide an opportunity to study whether the composition of the plant communities is nested within forest patches of increasing sizes in mosaic landscapes. Plant community nestedness was originally defined as the situation in which depauperate island faunas constitute a subset of the species of richer islands [19]. The plant species composition of islands of dissimilar sizes tend to suggest that smaller islands represent a subset of larger islands [20]. This pattern was also found for birds, small mammals, and butterflies, but not lizards [21,22]. For conservation purposes, it is crucial to understand whether the fern communities in smaller fragments represent a subset of the communities found in larger fragments or whether they are different [23].

Forested landscapes are often fragmented due to agricultural expansion, high rates of deforestation, and infrastructure development. This is particularly severe in tropical east Asia [24] due to the expansion of commercial plantations. Some of the plantations that have replaced forests in lowland tropical Asia are oil palm (*Elaeis guineensis*) and rubber (*Hevea brasiliensis*) plantations, leaving the landscape severely fragmented. In the tropical prefecture of Xishuangbanna, Yunnan, southwest China, more than 20% of the land is now covered by rubber plantations [25]. The expansion of rubber plantations in Xishuangbanna has spread from low to high elevations, peaking approximately at 1000 m a.s.l. [6]. It has even affected protected areas [26]. However, the collapse of the rubber price in 2012 curtailed the expansion of rubber and slowed deforestation. Nonetheless, other crops, such as tea (*Camellia sinensis*) and pineapple (*Ananas comosus*), are still expanding in the area, albeit at slower rates [25,27]. In this tropical landscape, the spatial distribution of the fragments has been found to be important for tree diversity, while topography and soil type have been found to be critical for bird and herpetofauna communities [7,28]. Moreover, tree species composition appears to be poorly explained by the size of the forest fragments [29]. Considering these findings, a comprehensive assessment of the potential effects of fragment size, topography, forest structure, and soil properties on the fern communities is important to improve our understanding of the drivers of herbaceous diversity in tropical fragmented landscapes. This understanding can have broad implications for conservation planning.

In this study, we investigated the factors influencing the abundance, species richness, and composition of ferns in the fragmented landscape of Xishuangbanna, China. Ferns and fern allies (hereafter called 'ferns') comprise the second richest vascular plant group after

angiosperms, totaling nearly 12,000 species, with most of them found in the tropics [29–31]. We chose to study ferns because they have been recognized as indicators of environmental change and they are often understudied [32].

We examined the following two questions:

(1) Is fern abundance, richness and composition explained better by forest fragment size, topography, forest structure, or soil properties?

(2) Is the composition of the fern communities in smaller forest fragments a subset of the communities found in larger fragments?

2. Methods

2.1. Study Area

The Xishuangbanna Prefecture (21°55′29″ N, 101°15′26″ E) is located in the southwest of Yunnan Province, China (Figure 1). It occupies an area of 19,690 km^2, and it has a mountainous topography with the highest peak at 2429 m a.s.l. and the lowest point at 480 m a.s.l. There is a cool, dry season from November to May and a hot, wet season from May to October, with >80% of the rainfall falling during the wet season. The total annual rainfall varies from 1193 mm at 740 m to 291 mm at 1979 m. The annual mean temperature ranges from 21.7 °C at 550 m to 15.1 °C at 1980 m. The hottest month is June with a mean temperature of 17.9 °C at 1980 m, and 25.3 °C at 550 m, while the coldest month is January with a mean temperature ranging from 8.8 °C to 15.6 °C. In March and April, temperatures can exceed 38 °C with relative humidity below 40% [33]. The vegetation is generally classified as tropical forest, with variations from lowland to mountain sites [34].

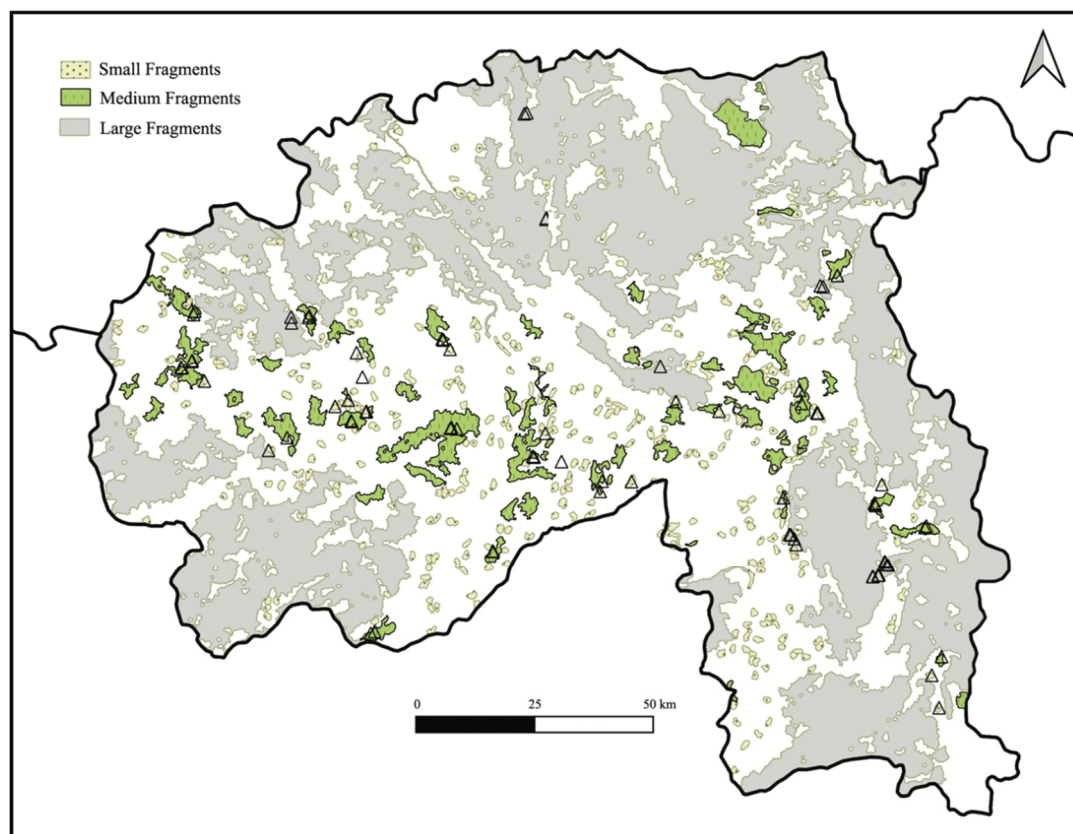**Figure 1.** Map showing the tropical fragmented forest landscape in the Xishuangbanna prefecture. Fragments were identified using the QGIS software and the Landsat-5 Thematic Mapper. Yellow colour indicates small forest fragments (0.4–1 km^2); green colour indicates medium forest fragments (1–10 km^2), and grey colour indicates large forest fragments (>10 km^2). The triangles represent the study sites.

2.2. Forest Map and Field Data Collection

First, we produced a forest map to identify the forest fragments within the Xishuangbanna landscape (Figure 1; Appendix A for more details). Then, we selected a total of 42 fragments, four of which were in protected areas, either entirely or partially. We ensured that the fragments were spread throughout the prefecture to obtain a representative sample. Within the 42 selected fragments, we established 75 sites. At each site we sampled three plots of 10 m × 10 m, separated by 30 m from each other, covering a total length of 90 m. This resulted in a total survey area of 22,500 m². When placing the sites, we avoided canopy gaps and areas with high levels of human disturbance. That said, most fragments outside National Parks showed minor levels of disturbance, due to local people being allowed to enter, but not to log trees. Moreover, only 4 sites out of the 42 were inside national parks and hence these minor differences are unlikely to have influenced the results. Furthermore, we also avoided edge effects by establishing the plots at least 50 m from the forest edge. When possible, we established pairs of sites on the north- and south-facing aspects at intervals of 500 m in elevation. Within each plot, we recorded all terrestrial fern species and estimated their abundance using the following classes: 0%–1%, 1%–5%, 5%–10%, 10%–20%, 20%–40%, 40%–60%, 60%–80%, and 80%–100% [35]. We collected fertile specimens to be identified and deposited at the Xishuangbanna Tropical Botanical Garden Herbarium (HITBC), Sichuan University (SZ) Chengdu, and Universiti Brunei Darussalam (UBDH).

2.3. Fragment Size, Topography, and Forest Structure

Using the above forest map, we classified fragments according to their size: small (0.4–1 km²), medium (1–10 km²), and large (>10 km²) (Figure 1) [36]. We then established 18, 22, and 35 sites across the small, medium, and large categories, respectively (Table A1; Appendix A).

At each plot, we measured (a) the elevation using a Garmin GPS, (b) the aspect using a compass, which we categorised as North (from 315 to 45 degrees) or South (from 46 to 314 degrees), and (c) the slope expressed in degrees using a clinometer. For the statistical analysis, we averaged these measurements at the site level. Within each plot, we also measured the tree diameter of all trees with a DBH > 10 cm. A higher frequency of older trees, with a higher value of total basal area (TBA), corresponded to a less disturbed forest [37] compared to a site with several small or medium trees. We recorded canopy cover using a camera with a fish-eye lens placed 1 m from the ground. A total of three photos were taken at each plot, between the hours of 9.00 am and 2.00 pm. The images were processed using the Gap Light Analyzer software (GLA 21, Cary Institute of Ecosystem Studies, Millbrook, NY, USA).

2.4. Soil Properties

We collected soil samples (100 g each) from each plot at a depth of 0–15 cm in the uppermost mineral soil layer after removing the superficial organic layer. The samples from each site were then mixed at the soil laboratory of the Xishuangbanna Tropical Botanical Garden (XTBG). The laboratory's researchers measured the soil's pH, total carbon (C), nitrogen (N), phosphorous (P), calcium (Ca), and magnesium (Mg), and the proportions of clay, silt, and sand. The proportions were obtained by implementing a standard soil survey method using a hydrometer and a sedimentation cylinder. This was in addition to the hydrometer reader used for each particle size measurement. Due to the sites' variation in forest structure and microclimatic conditions, which can significantly impact water availability, we also measured the soil's Availability of Water Content (AWC), expressed in percentage, and included it as a separate soil property in the statistical analyses. AWC is often used to estimate the water stored in the soil that is available to the plants [38]. To calculate AWC (Equation (1)), we estimated textural composition and the percentage of organic matter.

$$\text{AWC (mm H}_2\text{O/cm soil depth cm)} = 1.475 - 0.010\,(\%\ \text{coarse sand}) + 0.011\,(\%\ \text{silt}) + 0.138\,(\%\ \text{organic carbon}). \quad (1)$$

To visualize the soil property patterns among the sites, we performed a Principal Component Analysis (PCA) using the soil distance matrices of each soil factor per site separately [3]. As mentioned above, AWC was kept separate in the statistical models, and was not included in the ordination, due to its key role in fern ecology and species distribution. To test the effect of the soil properties on the fern abundance, species richness, and composition, we used the first and second PCA axes as explanatory variables in the regression models (described below in Section 4.5). In total, the first two axes of the ordination explained 93% of the soil properties (Figure A1; Appendix B). The first axis explained 75%, with total carbon and nitrogen as the main factors. The second axis explained 18%, with sand, silt, and clay, as the main factors (Figure A1; Appendix B).

2.5. Data Analysis

We considered the following three response variables in our regression models (a) fern abundance, (b) fern species richness, and (c) fern composition. Fern abundance was calculated as the sum of the cover for each species recorded across each site. Fern species richness represented the total number of species recorded at each site. Fern composition was measured using the first axes of a non-metric multidimensional scaling (NMDS), calculated from species abundance values [39], a standard approach used in the literature to assess species composition in regression models [28]. To assess the completeness of our sampling and to estimate the potential total number of forest fern species in Xishuangbanna, we used the Chao2 species richness estimator [40]. We conducted the calculation using the sample-based incidence (presence-absence) of fern species with the sites as the replicated sampling units.

As independent variables in each model we used the following factors Fragments: (1) fragment size; Topography: (2) elevation, (3) slope, (4) aspect; Forest structure: (5) DBH, (6) total basal area, (7) canopy cover; Soil properties (8) PCA1, (9) PCA2 and (10) AWC. For each of the three response variables, we developed a generalised linear mixed model (GLMM) with a Poisson distribution, using the R package 'lme4' package [41]. Fragment ID was used as a random effect.

We assessed collinearity by calculating the pairwise Pearson's correlation coefficient among all the independent variables. When the value was ≥ 0.70, the two variables were considered collinear [42] (Table A3; Appendix A). However, no variable showed collinearity and, therefore, all ten were retained in the models. As mentioned above, aspect was used as a categorical variable (i.e., North vs. South), and total basal area and fragment size were log-transformed.

We used a multi-model inference approach to assess the best models using the 'MuMIn' package in R (Barton, Wilson, NC, USA, 2020). This method tests all possible combinations of the explanatory variables and ranks the resulting models according to their corrected Akaike Information Criterion (AICc). We selected and averaged all models with an ΔAICc of <4 to measure the relationships between our three response variables and the corresponding explanatory factors [43]. We assessed the goodness-of-fit of the averaged models using the R^2 marginal and R^2 conditional values. This allowed us also to measure each time the variance explained by the fixed factors (R^2 marginal) and the whole model (R^2 conditional), i.e., including also the random effect [44].

2.6. Determining Nestedness

We applied a nestedness analysis to assess whether the fern communities in the smaller forest fragments were a subset of the communities found in larger fragments [45]. In the nested matrix, we ranked the sites in decreasing order of species richness. We then used null model 3 to randomly generate 1000 null communities and evaluated whether the fern communities were significantly nested [42]. In null model 3, the probability of each cell in the species-by-site matrix being occupied was the average of the row and column occupancy probabilities. We chose null model 3 because it has been shown to be associated with the smallest type I error. For all the other parameters, we used the recommended

default settings of the software BINMATNEST [46]. To examine the potential levels of nestedness, we ran a Spearman's rank correlation using the species ranks in the maximally packed matrix and the size of each forest fragment. The matrix was ordered by size in the columns and by species in the rows. A significant correlation coefficient suggests a nested pattern based on fragment size [21].

The sampling completeness and nestedness analyses were conducted using EstimateS [47] and BINMATNEST, respectively. All other analyses were conducted using the R programming language and the packages vegan, MuMIN, lme4, and Permute [47,48]

3. Results

3.1. Fern Species among the Transects

In total, we recorded 131 species belonging to 46 genera and 18 families. According to the Chao2 index, there were 168 ± 19 species in the entire study area, suggesting a sampling completeness of 78%. The number of species per site ranged from 1 to 13, averaging 5.7 (SE $\pm$ 0.33; median 6.0). The mean species richness was 5.2 in small forest fragments (SE $\pm$ 0.6; median 5.5), 5.9 in medium fragments (SE $\pm$ 0.67; median 6.0), and 5.8 in large fragments (SE $\pm$ 0.53; median 5.0). Five species contributed more than 50% of the total cover, whereas 77 species had a combined cover index of less than 5%. Those five species were, from higher to lower total cover values, *Woodwardia japonica* (L. f.) Sm., *Cibotium barometz* (L.) J. Sm., *Arachniodes cavaleriei* (Christ) Ohwi, *Athyrium dissitifolium* (Baker) C. Christensen, *Tectaria herpetocaulos* Holttum. All five species are native to China.

3.2. Fern Abundance Richness and Composition

Fern abundance was influenced by soil properties (PCA2), slope, and aspect. The concentration of sand silt and clay (PCA2) affected positively the abundance of ferns (Figure 2). Furthermore, sites exposed to the south and sites on steeper slopes had a higher fern abundance. The rest of the factors did appear to not have a significant effect, and the model had an $R^2_{marginal}$ value of 0.39 (Table A2 Appendix A).

Fern species richness was influenced mostly by soil properties and slope. Specifically, fern species richness was higher in areas with a lower concentration of soil carbon and nitrogen (PCA1) and areas with steeper topography (Figure 2). Forest structure and fragment size did not significantly influence species richness, and the model had an $R^2_{marginal}$ of 0.42.

Lastly, fern species composition was mainly influenced by the trees' total basal area. The other factors included in the model did not have a significant effect. The model's $R^2_{marginal}$ value was 0.11 (Table A2 Appendix A).
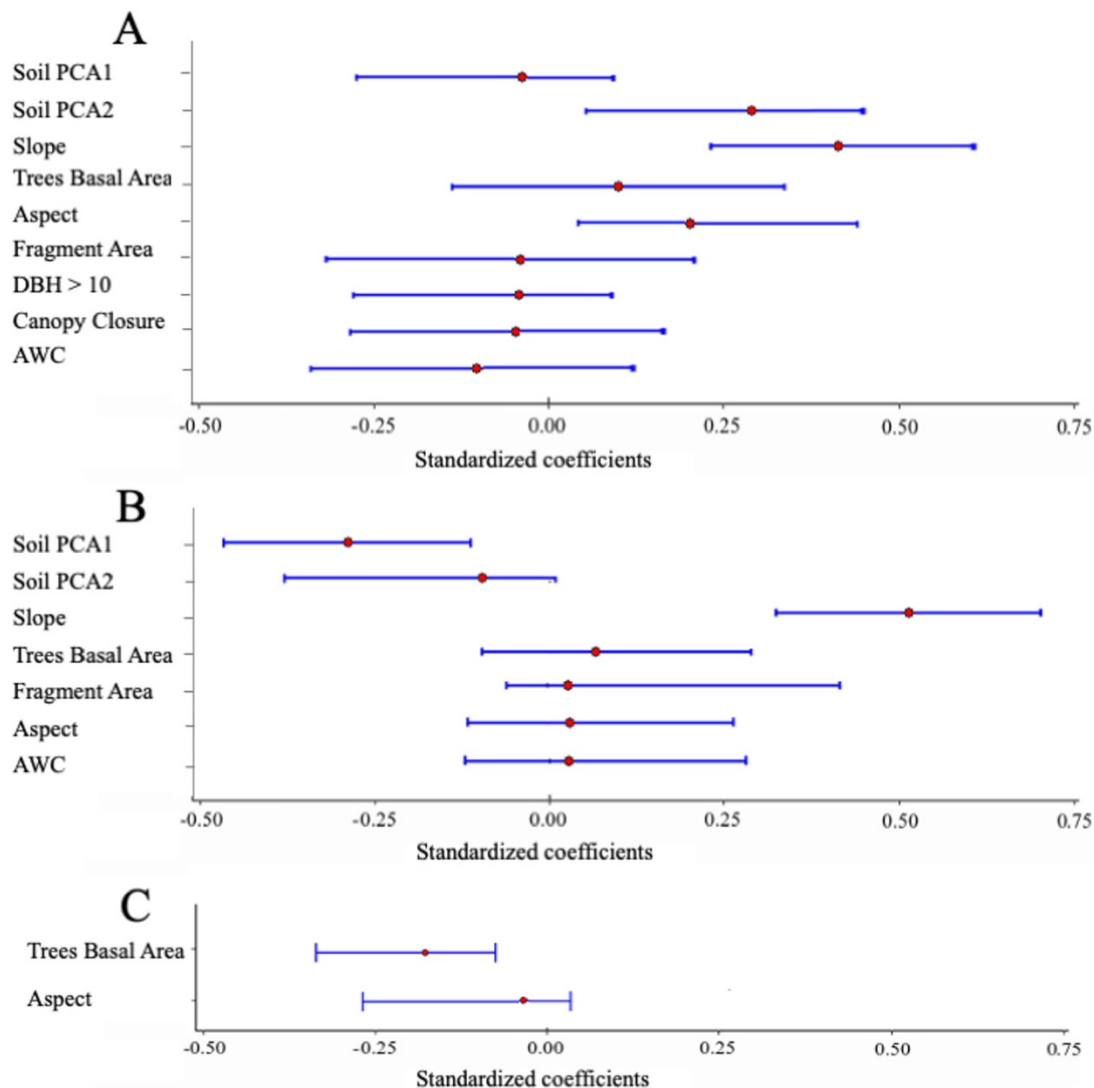
Figure 2. GLMM results showing the effect of forest structure, soil properties, topography, and forest fragment size on (**A**) fern abundance, (**B**) fern species richness, and (**C**) fern composition (full results given in Table A2 Appendix A). Red circles represent the coefficient estimates, blue lines represent the 95% confidence intervals. Figure showing only the variables that were selected during the model averaging process.

3.3. Species Nestedness

Our results show that the fern community was not significantly nested among the different forest fragments in Xishuangbanna (Spearman's rank correlation = −0.09, *p*-value = 0.3).

4. Discussion

We recorded a total of 131 fern species corresponding to 78% sampling completeness [29]. Among the 131 species, more than 50% have been recorded once or twice, demonstrating high levels of species richness with a low frequency of occurrence [49]. The spatial distribution of fern species abundance and richness appears to be primarily driven by soil properties, and topography. Whereas fern species composition is mainly influenced by the forest structure.

4.1. Fern Species Abundance

Topography and soil properties play an important role in determining tropical fern species abundance in our study area, supporting similar results based on other herbaceous

species and trees [3,50]. The high level of fern abundance was positively related to soil structure, such as the proportion of clay, sand, and silt. Conversely, the abundance of carbon and nitrogen (PCA1) has a detrimental effect. Overall ferns are more abundant in steeper drier sites, with humid soil. Among the 131 fern species, only five had an abundance value above 50%. Those five species, which are all native to China, were: *Woodwardia japonica*, *Cibotium barometz*, *Arachniodes cavaleriei*, *Athyrium dissitifolium*, and *Tectaria herpetocaules*. In some cases, *Woodwardia japonica* and *Cibotium barometz* were able to cover half or more of the site, especially in small forest patches. Their abundance can be explained by their vegetatively propagation, via rhizome, which facilitate the cover of large surfaces. Therefore, the abundance and biomass were driven by a subset of species and these common species have a broad altitudinal range, with source and sink populations (Cicuzza personal observation) [51] whereas some of them, like *Woodwardia japonica* and *Cibotium barometz*, tend to occur also in sites with higher light availability. The broad ecological adaptation of these species, their ability to propagate vegetatively, distribution from lowland to mountain sites, and with different degrees of light availability, could have determined their dominance across the range of a fragmented landscape.

4.2. Ferns Species Richness

Forest fragment size has been documented to be one of the major factors resulting in the impoverishment of plant communities [52], butterflies [45], mammals [53], as well as pollination networks [54]. In this study we found that fragment size and forest structure do not significantly influence species richness, supporting the importance of topography and soil properties over fragment size. In other words, if the right soil properties and topographic conditions are present in small forest fragments, we can deduce that they can potentially retain a level of fern richness similar to that of larger forest fragments. However, this can only be valid assuming other important conditions, such as the levels of human disturbance, remain similar among the forest fragments. Long term isolation of tropical forest fragments with continuous human disturbance, as in the Atlantic Forest, for example, has produced a homogenization of the tree species community [55]. The conversion of forests in Xishuangbanna is recent, but a similar phenomenon could be seen, with a negative impact on the fern species richness and the genetic pool of the community.

Furthermore, our species assessment has covered most of the ecological forest conditions in Xishuangbanna, however, our sample size was 300 m^2 per site whereas other studies have used a larger area [56,57]. Therefore, despite the overall 78% of sampling completeness, in some sites we may have underestimated the true richness.

It is worth noting that our results suggest that the abundance, richness, and composition of the fern species are not influenced by the same factors. When it comes to fern species richness, the slope was the most important variable due to the increase in the number of species in sites with a steeper slope (Table A1; Appendix A). A similar pattern has been also found for fern species in sites in Sulawesi [9]. This is likely because sites with steeper slopes tend to have emerging and fixed rocks that create niches for lithophytic fern species, increasing in this way the species richness [58–60]. On the other hand, species richness decreases in relation to soil macronutrients, such as carbon and nitrogen (PCA1). This finding partly contradicts other studies suggesting that soil properties such as micronutrients strongly influence the neotropical fern species [3,61,62]. Consequently, in many cases, the exact relationship depends on the local conditions and the stage of soil formation [18].

4.3. Fern Species Composition

Fern species composition differed in forest fragments with larger tree basal areas (Figure 2). This indicates that in mature forests, where the ecological conditions are stable, the species composition varied compared to disturbed sites where the community involves species with broader ecological traits. From a biogeographical point of view, the southern part of Yunnan represents the northern area of distribution of many species, with their main centre of distribution in Southeast Asia [34]. Many fern species with a distribution centre

in Malaysia tend to decrease in abundance and become rarer at the latitude of Xishuang-banna [63,64]. The high level of rarity and the distribution throughout the fragmented landscape [49], allows us to conclude that fern distribution is a result of a combination of ecological aspects as well as the species' evolutionary history and distribution. This emphasizes once more the importance of maintaining all forest patches distributed within the tropical fragmented landscape of the species' most northern distribution limit. However, it is important to note that the $R^2_{marginal}$ value of this model is 0.11 which is relatively low compared to the other two models suggesting that other factors not included in the analysis may be influencing fern species composition. [65]

4.4. Soil, Topography, and Conservation

In tropical regions, the reduction of vegetation cover and the cultivation of sites on steeper slopes using lower canopy cover crops has resulted in soil erosion and degradation [66], both of which can accentuate the impacts of land use and climate change [67,68] and reduce the condition of the local biodiversity [69]. Our study shows that soil properties and slope influence fern richness and abundance, particularly in the hilly lowland landscape of Xishuangbanna, where most of the native forest has been replaced with rubber plantations in recent decades. Ferns and other herbaceous species have, in general, a more superficial root system compared to trees and other woody species. The importance of soil and slope regarding fern species abundance and richness underlines the fact that the sites where most of the fern species richness is concentrated, are the sites where further disturbance (such as through the reduction in tree numbers and canopy cover), can change the soil properties with negative consequences for the entire habitat.

4.5. Determining Nestedness

Fern species composition was found to not be significantly nested within the forested landscape of Xishuangbanna. This result suggests that species composition in small fragments is not a subset of the communities found in larger fragments and that the fern community appears to be highly diverse within the different sizes of forest fragments. Our findings could be explained by several factors. The changes in species composition among the different sites are not determined by fragment size because a large proportion of species have low frequency and are distributed within fragments from large to small fragments. The hilly topography of the Xishuangbanna landscape, can preserve local ecological conditions that suit numerous fern species. We found an average of six species per site, while over 50% of the species are recorded once, suggesting that each site, from small to large fragments, harbor species with specific ecological requirements. The presence of these dissimilar species in the smaller fragments highlights the importance of preserving small forest patches for fern conservation. From a conservation perspective, this result suggests that small fragments are important for the preservation of ferns. However, more research is needed to understand how the community composition changes among the different forest patches.

5. Conclusions

Our study highlights that forest fragments of all sizes are important when it comes to preserving the diverse, non-nested, tropical fern community of Xishuangbanna, China. Additionally, our results suggest that soil protection is pivotal for the conservation of these herbaceous species, which respond rapidly to environmental change. Moreover, our study suggests that the distribution of the terrestrial ferns, with regards to their abundance, richness, and composition, is not explained by the same environmental factors. This finding is important because it shows that the different aspects of fern diversity are the result of the interaction with different environmental factors.

Author Contributions: D.C. conceived and designed the study. D.C. collected the data. D.C. and C.M. analysed the data. D.C. and C.M. wrote the manuscript. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. The table reports the variation of each abiotic factors in the study area. The factors are divided based on the three categories of forest fragments (Small, Medium Large), Number of plots and number of fragments for each category are provided. Each factor is summarized with Minimum and Maximum values, Mean Standard Error. The factor included are: Elevation, Area, Slope, Aspect, Canopy cover, Basal Area, DBH > 10 cm, Soil PCA1, Soil PCA2, AWC. In the GLMM model the Area (of forest fragments) and Basal Area was log transformed.

Large Fragments		Elevation m a.s.l.	Area (Km^2)	Slope (Degrees)	Aspect (Degrees)	Canopy Cover	Basal Area (m^2)	DBH > 10 cm	SoilPCA1	SoilPCA2	AWC
35 sites in 10 fragments	Min	710	14	14	25	53	0.46	7	−9.12	−3.011	1.21
	Mean ± SE	1234 ± 59	640 ± 139	27 ± 1	199 ± 15	74 ± 1	1.35 ± 0.10	22 ± 1	−0.16 ± 0.28	−0.11 ± 0.23	1.99 ± 0.10
	Max	2121	1824	39	357	100	2.74	41	1.04	5.96	3.70
Medium Fragments		Elevation m a.s.l.	Area (Km^2)	Slope (degrees)	Aspect (degrees)	Canopy Cover	Basal Area (m^2)	DBH > 10 cm	SoilPCA1	SoilPCA2	AWC
22 sites in 14 fragments	Min	611	1.1	0	22	53	0.45	17	−0.50	−1.45	1.33
	Mean ± SE	1225 ± 75	7.1 ± 0.7	26 ± 1.6	183 ± 19	76 ± 2	1.07 ± 0.10	24 ± 1	0.21 ± 0.05	0.02 ± 0.15	1.97 ± 0.09
	Max	1881	9.8	41	297	93	2.38	40	0.60	1.17	2.88
Small Fragments		Elevation m a.s.l.	Area (Km^2)	Slope (degrees)	Aspect (degrees)	Canopy Cover	Basal Area (m^2)	DBH > 10cm	SoilPCA1	SoilPCA2	AWC
18 sites in 18 fragments	Interval	603	0.45	0	20	53	0.39	14	−0.55	−1.04	1.41
	Mean ± SE	1149 ± 79	0.68 ± 0.03	24 ± 2	190 ± 24	70 ± 3	1.11 ± 0.11	24 ± 1	0.06 ± 0.07	0.23 ± 0.28	1.97 ± 0.11
	Max	1804	0.96	36	340	93	2.11	37	0.58	4.16	3.04

Table A2. Model averaged estimates (coefficients) of variables that explain the fern species abundance, richness, and composition among forest fragments. The factor included as dependent variables are DBH (number of trees > 10 cm), canopy closure, basal area, soil PCA1, soil PCA2, AWC, slope, elevation, aspect, fragment size. Model averaged estimates (unstandardized and standardized coefficients), confidence intervals (CIs), and relative importance (RI) values are shown for all variables. NA = Not applicable; variable not in the models with ΔAICc < 4.0.

	Factor	Unstandardized Coefficient	Standardized Coefficient	Confidence Interval 2.5%	Confidence Interval 97.5%	Relative Importance
			Fern abundance			
		R^2 marginal = 0.391; R^2 conditional = 0.646; ΔAICc 3.66				
Fragment size	Fragment size	−0.297	−0.033	−0.312	0.164	0.45
Topography	Slope	1.214	0.366	0.181	0.5522	1.00
	Aspect	14.168	0.244	0.066	0.421	1.00
Forest structure	DBH > 10	−0.110	−0.028	−0.275	0.073	0.280
	Canopy closure	−0.283	−0.033	−0.277	0.121	0.420
	Basal Area	5.223	0.098	−0.088	0.296	0.950
Soil properties	Soil PCA1	−0.761	−0.037	−0.225	0.105	0.610
	Soil PCA2	5.577	0.269	0.073	0.465	1.00
	AWC	−7.992	−0.176	−0.367	0.015	1.00
			Fern species richness			
		R^2 marginal = 0.416; R^2 conditional = 0.612, ΔAICc 3.97				
Fragment size	Fragment size	0.040	0.034	−0.061	0.497	0.180
Topography	Slope	0.223	0.512	0.141	0.306	1.00
	Aspect	0.225	0.030	−0.877	2.021	0.390
Forest structure	Basal area	0.292	0.042	−0.677	2.031	0.43
Soil properties	Soil PCA1	−0.754	−0.276	−1.234	−0.274	1.00
	Soil PCA2	−0.266	−0.098	−1.034	0.021	0.530
	AWC	0.159	0.027	−0.729	1.655	0.340
			Fern species composition			
		R^2 marginal = 0.111; R^2 conditional = 0.935; ΔAICc 3.99				
Forest structure	Basal area	−0.166	−0.191	−0.275	−0.073	0.84
Topography	Aspect	−0.011	−0.011	−0.217	0.024	0.120

Table A3. Results from the Pairwise Pearson correlation coefficient among all variables, none of them has a values superior to 0.70 therefore we confirm that there is not collinearity between the factors included in the models.

	GPS.Elev	Aspect	Slope	Canopy closure	DBH.10	AWC	SoilPC1	SoilPCA2	LogBasArea
GPS.Elev	1								
Aspect	0.184	1							
Slope	0.098	0.200	1						
Canopy closure	−0.363	−0.039	0.075	1					
DBH.10	0.086	0.119	0.032	0.011	1				
AWC	0.358	0.051	−0.126	−0.164	−0.102	1			
SoilPCA1	0.349	0.237	−0.042	−0.208	0.024	0.196	1		
SoilPCA2	−0.511	−0.156	−0.038	0.309	0.005	−0.113	0.000	1	
LogBasArea	−0.206	−0.083	0.055	0.256	0.083	−0.200	−0.106	−0.089	1

Appendix B. Development of the Forest Map

We used the freely available multispectral data from a Landsat-5 Thematic Mapper (TM) image (30-m spatial resolution). The image was acquired on 2013 and it represented the Xishuangbanna forest cover of February 2010, with the least cloud cover, and downloaded from the U.S. Geological Survey (USGS) Earth Resources Observation and Science (EROS) Centre. To determine the density of green on a patch of land, we used the Normalized Difference Vegetation Index (NDVI), widely used in land cover and vegetation classification [70], we calculated it using the Landsat image and GRASS GIS software 6.4.3 (GRASS Development Team, 2012). Rubber trees can be misclassified as deciduous, broad-leaf trees [71]. In Xishuangbanna, they have, within a year, two distinct seasons: with leaves and shed leaves. We measured the NDVI in February, at the pick of shed leaves seasonal, whit a low value of NDVI [72], important to distinguish the rubber plantation from the natural broad-leaf forest, and increase the accuracy, we used the threshold of NDVI = 0.55 [71,73]. To compare the forests and plantations, we selected large homogeneous areas of either forests or plantations using Google Earth. We used the same patches as training areas for and classified with a binomial division between natural forests and non-natural forests. These last included rubber plantations, other agricultural sites, and human settlements. For each land-cover class, we selected at least 10 training areas to reflect variation, due to topography and growing conditions [5]. Furthermore, we used a high-resolution Google Earth map to complete a final manual edit to remove and adjust the fragments with the margin that included part of roads, or other human construction (Figure A1).
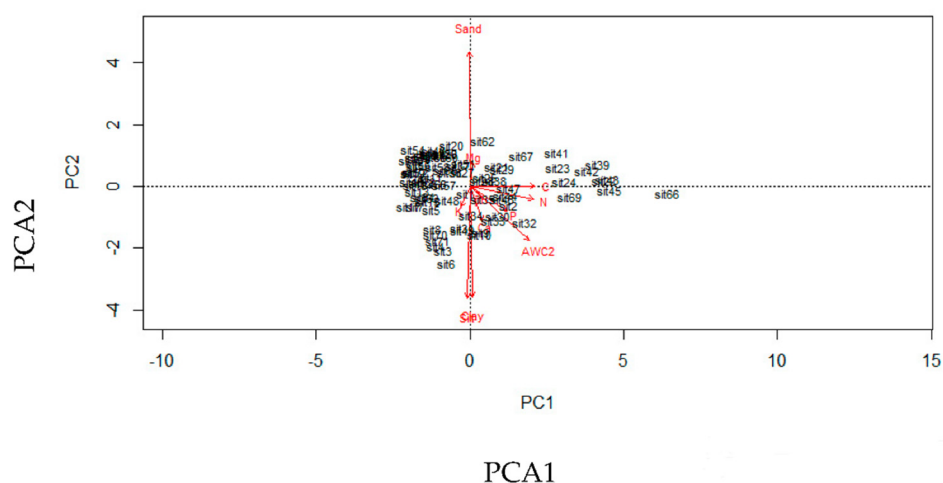

Figure A1. The Ordination analysis with all the factor related to the soil properties. First and second axes are used to summarize the soil property as organic matter (PCA1) and soil structure sand, clay and silt (PCA2). Stress: 0.1756, the first axis explained 75% of the total variance, with total carbon and nitrogen as the main factor, whereas the second axis explained soil structure as sand, silt, and clay, with 18% of total variance.

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