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Taxonomic, Phylogenetic, and Functional Diversity of Ferns at Three Differently Disturbed Sites in Longnan County, China

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Abstract: Human disturbances are greatly threatening to the biodiversity of vascular plants. Compared to seed plants, the diversity patterns of ferns have been poorly studied along disturbance gradients, including aspects of their taxonomic, phylogenetic, and functional diversity. Longnan County, a biodiversity hotspot in the subtropical zone in South China, was selected to obtain a more thorough picture of the fern–disturbance relationship, in particular, the taxonomic, phylogenetic, and functional diversity of ferns at different levels of disturbance. In 90 sample plots of 5×5 m^2 along roadsides at three sites, we recorded a total of 20 families, 50 genera, and 99 species of ferns, as well as 9759 individual ferns. The sample coverage curve indicated that the sampling effort was sufficient for biodiversity analysis. In general, the taxonomic, phylogenetic, and functional diversity measured by Hill numbers of order q = 0–3 indicated that the fern diversity in Longnan County was largely influenced by the level of human disturbance, which supports the 'increasing disturbance hypothesis'. Many functional traits of ferns at the most disturbed site were adaptive to the disturbance. There were also some indicators of fern species responding to the different disturbance levels. Hence, ferns may be considered as a good indicator group for environmental stress.

Keywords: phylogenetic diversity; functional diversity; Hill numbers; increasing disturbance hypothesis; indicator species analysis

1. Introduction

Ferns are the second most diverse group among vascular plants with approximately 11,000 species [1–3]. Ferns are distributed globally, but they have the highest density in the tropical mountains [4]. Ferns are sensitive to the indicators of environmental conditions [5–10], with various adaptative strategies to variations in climatic and edaphic parameters [11,12]. Hence, fern diversity shows clear patterns along environmental gradients at different spatial scales [8,13,14].

In contrast to many other groups of plants and animals, the taxonomic diversity of fern gradients generally follows a hump-shaped unimodal pattern along the elevational gradient [4,9,10,15–30]. The main drivers for such unimodal patterns are the combined effects of different climatic factors, including the temperature, precipitation, and cloud cover [4,8–10,21,27–35]. Generally, fern diversity tends to be high in temperate and humid habitats but low in cold, hot, and arid habitats [10,36]. The elevational range in a region and the macroevolutional history of specific fern groups are essential to the development of the latitudinal diversity pattern of ferns [25,32,37]. Human activities, environmental heterogeneity, soil, and topography also affect fern diversity at different elevations [8,23,34,38,39]. Researchers have argued that geometrical constraints, such as the mid-domain and area effects, might help to explain the hump-shaped patterns [9,22,26,36,40]. Another cause of diversity patterns is that different fern groups show different latitudinal and elevational diversity patterns [24,35,39,41]. For example, the richness of terrestrial xerophytic ferns often decreases with elevation; whereas, the richness of epiphytic ferns and terrestrial hygrophytic ferns generally increase with elevation [24,41].

At the local (habitat) scale, fern diversity is often controlled by light, moisture, soil, and topographic conditions [42–48]. For instance, high canopy openness may increase light but reduce moisture and thus decrease the ground fern diversity [49]. In a study in Uganda, both the soil fertility and distance to the nearest Pleistocene forest refugium could explain most of the variance in fern diversity [14]. Fern diversity also depends on the topography, and is typically higher on the slopes than on ridges [50]. In South China, fern diversity is higher on the east- and north-facing slopes than it is on the west- and south-facing slopes [51]. In contrast, slopes affect species composition but not the species richness of ferns and lycophytes in tropical Brazil [52]. Finally, interspecific interactions, and especially competition, also contribute to the local diversity of ferns [4,42]. Strong correlations have also been found between epiphyte fern diversity and body size, plant height, height below twigs, and species composition of their phorophytes [53].

In the age of Anthropocene, human impacts have significantly changed the whole biosphere and are threatening ecosystems and biodiversity worldwide [54]. The distribution, diversity, and dynamics of fern assemblages are profoundly affected by human disturbances [8,12,15,55–65]. Disturbances might modify the external conditions and interspecific interactions to lead to changes in the fern assemblages [15,66]. However, compared to seed plants, the diversity patterns of ferns along a disturbance gradient are much less studied [61–63], let alone the mechanisms behind the patterns [38,46,62]. There are several possible patterns of the fern diversity–disturbance relationship: (1) the "intermediate disturbance hypothesis" proposes that the highest diversity occurs at moderate disturbance levels [67]; (2) the "increasing disturbance hypothesis" (i.e., increased disturbance hypothesis or environmental stress hypothesis) states that diversity decreases when disturbances increase [68]; (3) the "habitat specialist hypothesis" assumes that the highest diversity of habitat specialists occurs at less disturbed sites [69]; (4) whereas the "opportunistic species hypothesis" claims that the dominance of the generalist (opportunistic) group increases in disturbed areas [68].

Biodiversity can be described using indicators at different levels, often focusing on composition (taxonomic diversity), but also taking into account the functional relationships in the ecosystem (functional diversity) and even the regional evolutionary history (phylogenetic diversity) [33,70]. There is no single method that can reflect the overall pattern of biodiversity, and each diversity metric reveals different aspects of the overall diversity [33]. Accordingly, different diversity measurements do not always show consistent patterns with each other [12,33,70,71]. The reinterpretation of diversity around the Hill numbers [72] is a powerful tool for unifying the comparisons between habitats and scales [73–78]. Therefore, it is better to select multiple diversity elements together to evaluate overall fern biodiversity [12,71,79,80].

Compared to angiosperms, studies on the phylogenetic and functional diversity of ferns along the environmental and disturbance gradients are much fewer [12,33,70,71,79–83]. For example, the phylogenetic diversity of Neotropical ferns increases significantly with decreasing soil fertility [82]. The phylogenetic diversity of ferns has no noticeable elevational trend in either Central Japan [70] or Central America [71]. The functional diversity of ferns in Central Japan is overdispersed at lower elevations but clustered at higher elevations, suggesting competitive interactions at low elevations and environmental filtering at high elevations [70]. The functional diversity of epiphytes in Central America [71] and of ferns and lycophytes in Mexico [12] is the highest at intermediate elevations, which has been interpreted as environmental filtering at low and high elevations. However, the functional diversity of ferns and lycophytes shows no general relationship with habitat disturbances [12].

In summary, the overall diversity of ferns along the disturbance gradient is still poorly known and requires further study. In our study, we set out to address the following issues: (1) to contribute to a more thorough picture of the fern–disturbance relationship and (2) assess the Hill number-based taxonomic, phylogenetic, and functional diversity of ferns at different levels of disturbance.

2. Materials and Methods

2.1. Study Sites

Longnan County (24.91° N, 114.79° E) is located in South China, with a subtropical monsoon climate and with an elevational range of 190–1430 m a.s.l. We selected three study sites (Figure 1; Table 1) to carry out fern investigations. The distance between the three sites is approximately 65 km (Jiulianshan National Nature Reserve (JLS) to Leigongshan Family Farm (LGS)), 37 km (JLS to Anjishan Provincial Forest Park (AJS)), and 33 km (AJS to LGS). The annual rainfalls of the three sites fall in the isohyet of 1500–1600 mm, while their mean temperatures in January and July fall in the isotherm of 8 °C and 28 °C, respectively [84]. According to the maps of the U.S. Geological Survey, the generalized geologic ages of all three sites are Paleozoic/Precambrian (PzpCm) [85]. Detailed descriptions of Longnan County and the three sites were provided in our previous studies [86–89].

Figure 1. The locations of three study sites in Longnan County, China. The imagery data of Longnan County were obtained from Map World (http://www.tianditu.gov.cn) and produced with QGIS 3.8 [90].

Table 1. The information of three study sites in Longnan County, China.

Study Sites	Specific Sample Routes	Distance to County Town (km)	Main Vegetation	Disturbance Level	Elevational Range of Samples (m)
Jiulianshan National Nature Reserve (JLS)	Daqiutian-Hengkengshui-Xiagongtang	80	Primary evergreen broad-leaved forests	low	approximately 490 ± 80
Anjishan Provincial Forest Park (AJS)	Qingchahu- Anjishan-Zhongping	30	Secondary evergreen broad-leaved forests and economic forests	intermediate	approximately 410 ± 50
Leigongshan Family Farm (LGS)	Around Leigongshan orchards	10	Chinese fir forests and navel-orange orchards	high	approximately 310 ± 30

2.2. Sampling Techniques

We chose typical roads/trails across the dominant vegetation type of each site for fern investigation. At each study site, we placed 30 sampling plots in suitable habitats at the roadsides. There were a total of 90 plots in our study. Each plot was 5 m × 5 m, as in some previous local-scale practices [48,51,52,91,92], which is suitable for roadside sampling, especially for the managed forests and orchards at LGS. The distances between every two plots were all above 600 m. We covered large areas and thus encountered more fern species at each site. For the analyses, we treated all 30 plots at each site as one assemblage.

We identified and counted all the ferns in each plot. The undetermined fern species were marked and taken back to the laboratory for further identification using keys. As lycophytes are not ferns [93], we excluded them from our analyses. Fern species names were verified with the R package 'plantlist' [94].

2.3. Data Analyses

We used the number of individuals for every fern species in an assemblage to calculate the following diversity indices:

(1) Based on the assemblage datasets (Table S1), taxon richness were computed with Microsoft Excel 2016.

(2) At present, we do not have the molecular sequences of all fern species and could not build a species-resolution phylogenetic tree. Therefore, we generated a genus-resolution phylogenetic tree (Figure S1, File S1) with the R package 'V.PhyloMaker' using the 74,533-species mega-tree GBOTB.extended.tre, which covers all families in extant vascular plants [95]. The mega-tree is updated from two recent mega-trees [96,97], with the function to bind the undetermined species to their close relatives in the phylogenetic tree [95]. Phylogenetic diversity indices were calculated with the R package 'picante' [98].

(3) We extracted the fern traits (Table S2) from publications and websites. We took into account 17 traits, including the maximum lamina length, maximum lamina width, petiole length, frond heterophylly, lamina texture, leaf arrangement, rhizome type, rhizome position, lamina dissection, lamina shape, sori shape, sori position, indusia, reproduction type, phenology, habit and scales/hair density [12,70,71], to calculate the functional distances between species and hence the functional diversity of the three assemblages. For the quantitative traits, we used the measured values directly; for the presence/absence traits, we assigned 1–0 values; and we quantified qualitative traits with biological/ecological ranks(Table S2). The summary statistics, including the mean, median, minimum, maximum, and standard deviation of each trait value, are listed in Table S2. The functional diversity indices were obtained with the R package 'FD' [99].

(4) Taxonomic, phylogenetic, and functional diversity through Hill numbers (q) are unified standardization methods to quantify the diversity of different communities [73–78]. The equivalent diversity indices linked to Hill numbers of order q = 0, 1, 2 are listed in Table 2. In every case, we performed these analyses with the R package 'hillR' [100].

Table 2. The equivalent diversity indices linked to Hill numbers of order q = 0, 1, 2.

Diversity Component	Hill Number Series	All Species (q = 0)	Common Species (q = 1)	Dominant Species (q = 2)	References
taxonomic diversity @	the effective number of species $^qTD = \left(\sum_{i=1}^{S} p_i^q\right)^{1/(1-q)}$	S	e^H	$1/\lambda$	[73,74,101,102]
phylogenetic diversity #	the effective total phylogenetic distance between species $^qPD = \frac{1}{T}\left[\sum_{i \in B_T} L_i\left(\frac{a_i}{T}\right)^q\right]^{1/(1-q)}$	FPD/T	$e^{A/T}$	$1/(1-Q/T)$	[73,103]
functional diversity $	the effective total functional distance between species $^qFD = \left[\sum_{i=1}^{S}\sum_{j=1}^{S} d_{ij}\left(\frac{p_i p_j}{Q}\right)^q\right]^{1/(1-q)}$	FAD	-	$\frac{Q^2}{Q-GS}$	[101,104–106]

@ p_i = the relative abundance of the ith species; S = the number of species (i.e., species richness); H = Shannon's entropy; λ = Simpson's dominance index [73,74,101,102]. # T = the age of the root node of the ultrametric phylogenetic tree; B_T = the set of all branches in the time interval $[-T, 0]$; L_i = the length of the ith branch; a_i = the total abundance descended from the ith branch; FPD = Faith's phylogenetic diversity; A = Allen's phylogenetic entropy; Q = Rao's quadratic entropy; the corresponding equations and the equivalent diversity indices for taxonomic classification and nonultrametric phylogenetic tree can refer to [73,103]. $ d_{ij} = the functional distance between the species pair (i, j); $p_i p_j$ = join probability for the species pair (i, j); S = the number of species; Q = Rao's quadratic entropy; FAD = Functional attribute diversity; GS = the weighted Gini-Simpson's index [101,104–106].

We performed indicator species analysis based on the number of individuals for all fern species in the 90 sample plots. Indicator species for different disturbance levels were obtained using the R package 'indicspecies' [107].

All the R codes (Codes S1 and S2) with datasets (Files S2–S4) were run with R 3.6.3 [108] in Rstudio 1.2.5033 [109].

3. Results and Discussion

3.1. Sample Coverage

Overall, we recorded a total of 4 subclasses, 9 orders, 20 families, 50 genera, and 99 species of ferns, as well as 9759 individual ferns (Table S1; Figure S1). The sample coverage curves of the ferns at three sites indicated that all sampling efforts were sufficient as they began to level off at the 26th, 19th, and 15th plot (i.e., 650 m^2, 475 m^2, and 375 m^2) for JLS, AJS, and LGS, respectively (Figure 2).

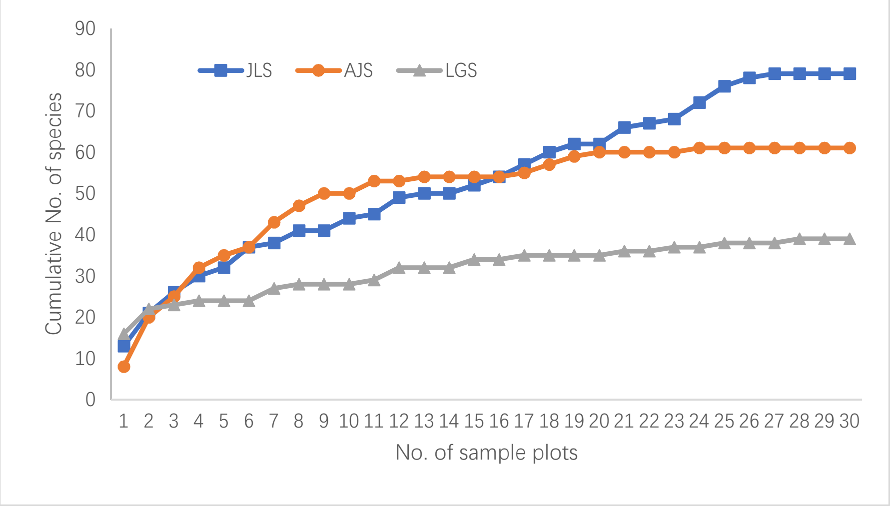

Figure 2. The sample coverage curves for ferns at three sites in Longnan County, China.

A sampling area of 600 m^2 is enough for human-made forests, while 900 m^2 is suggested for natural forests in the tropical regions of Malaysia and Singapore [110]. Our study sites were located in the subtropical regions, so the minimum sampling areas were smaller than those in the tropical regions. Our results also agreed that the minimum sampling areas should increase from economic to natural forests [110]. The total sampling area of 750 m^2 (i.e., 30 plots) should be enough to show the relative biodiversity values at different disturbance levels.

3.2. Taxonomic, Phylogenetic, and Functional Diversity

On average, in each plot, we recorded 9.2 fern species, with an average of 11.0 species (range 6–19) at JLS, 7.8 (3–16) at AJS, and 8.6 (3–18) at LGS. The phylogenetic tree of all the ferns (Figure S1) showed that we recorded all four subclasses of PPG I and nine orders (Equisetales, Ophioglossales, Marattiales, Osmundales, Hymenophyllales, Gleicheniales, Schizaeales, Cyatheales, and Polypodiales, 9 of 11 from PPG I). Among the nine orders, 50% of the families and 86% of the species were from the Polypodiales, the most diverse group among the ferns.

The taxonomic diversity indicators all showed the same arrangement from higher to lower values at the three study sites: JLS > AJS > LGS, except in the abundance of individuals, which was greater at LGS (Table 3). This trend was consistent along with the increasing q values of Hill numbers for all species (${}^{0}TD$ or species richness S), common species (${}^{1}TD$ or e^{H}), and dominant species (${}^{2}TD$ or $1/\lambda$) (Figure 3a). The same pattern was found for phylogenetic diversity, including Faith's phylogenetic diversity (linked to ${}^{0}PD$) and Rao's quadratic entropy (linked to ${}^{1}PD$) (Figure 3b) and for functional diversity, including functional attribute diversity (*FAD* or ${}^{0}FD$) and the weighted Gini-Simpson index (linked to ${}^{2}FD$) (Figure 3c).

Table 3. The taxonomic diversity of ferns at three sites in Longnan County, China.

Taxonomic Diversity Index	JLS [1]	AJS	LGS
Species richness ($S = {}^{0}TD$)	**79**	61	39
Exponential of Shannon's entropy ($e^{H} = {}^{1}TD$)	**54**	39	21
Inverse of Simpson's index ($1/\lambda = {}^{2}TD$)	**22**	15	9
Genus richness	**47**	38	23
Family richness	**20**	17	11
Order richness	**9**	7	4
Subclass richness	**4**	**4**	1
Individual number	3250	2905	**3604**

[1] Number in bold indicating the maximum value at the three sites.

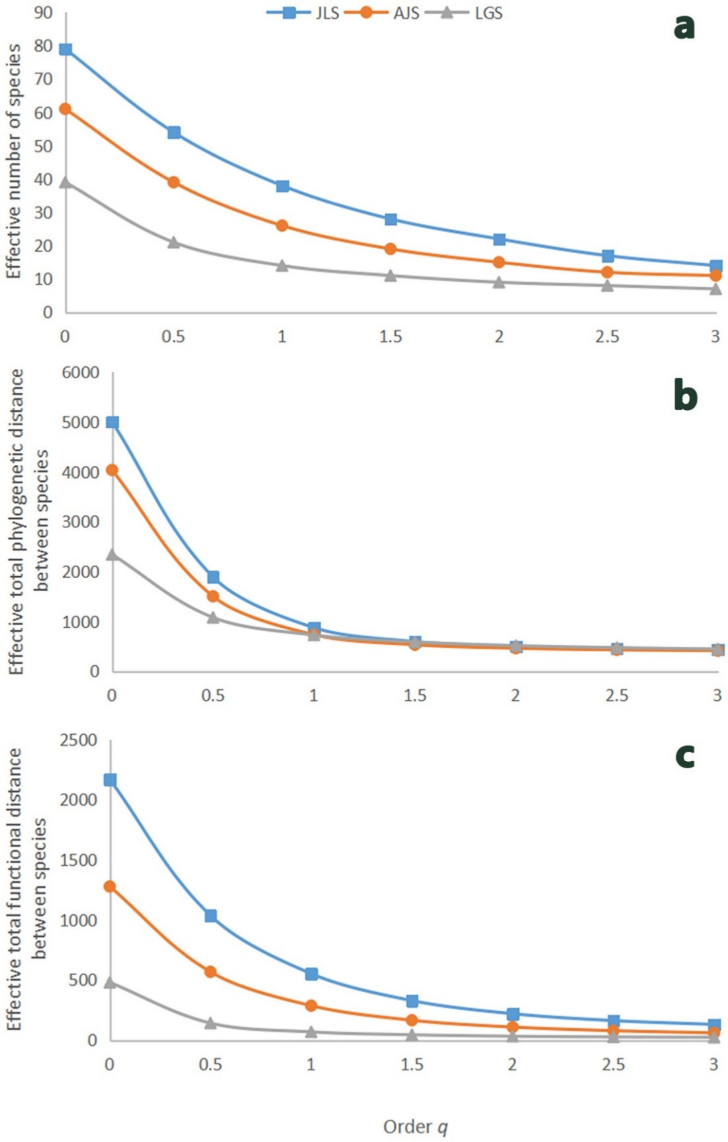

Figure 3. The Hill number-based diversity profiles of ferns at three sites in Longnan County for increasing order q values (0 to 3): (**a**) taxonomic diversity; (**b**) phylogenetic diversity; and (**c**) functional diversity.

The trends of the Hill number-based taxonomic, phylogenetic, and functional diversity all leveled off, and the differences between three sites became smaller (Figure 3) when the weighting of the relative abundance of each species (p_i) increased with the increase of order q (Table 2). The phylogenetic diversity among the three sites became similar when $q > 1$, one possible reason might be that our phylogenetic tree was at the genus resolution rather than species resolution (Figure S1).

Hence, all three diversity components (taxonomic, phylogenetic, and functional) of fern assemblages studied here showed the same pattern of decreasing diversity with the increase of disturbance degrees, which is in accordance with the 'increasing disturbance hypothesis' [8,55,57,65,111]. Our sampling was conducted along roadsides, which are disturbed habitats in themselves. Thus, we are careful to interpret them in direct relation to disturbances as such, as they likely combine the effects of different degrees of disturbances at the regional level (study sites) and at the local scale (individual roadsides). A previous study in Mexico found that the functional diversity of ferns and lycophytes decreased with disturbance in species-rich habitats, but not so in species-poor habitats [12]. As our study sites were located close to each other and have similar ecological conditions, we may assume that they originally shared a similar fern flora; thus, we cannot assess the effect observed in Mexico. Clearly, the relationship of fern diversity to habitat disturbance is complex and requires further case studies.

Previous studies have found inconsistent trends among the taxonomic, phylogenetic, and functional diversity along disturbance gradients [112–115]. However, in our study, all three diversity elements consistently indicated that the biodiversity was the highest along the roadsides within the natural forests at JLS but at the lowest in the severely disturbed LGS.

Many functional traits of ferns showed differences from the species of the less altered site to those of the most disturbed site (Table 4). We found that ferns in the more strongly disturbed sites tended to have longer, narrower, and thinner laminae, and more commonly had monomorphic fronds, with sori in one row on either side of the veins, and false indusia. They also had less vegetative reproduction. At the most disturbed site of LGS, the petioles were longest, the rhizomes were all below ground, long creeping rhizomes were less common, the fronds were more strongly divided, and the scales or hairs became denser. It is tempting to interpret these trends as adaptive directly; however, it should be borne in mind that many of them show strong phylogenetic patterns, being present in some clades and not in others. Accordingly, certain traits may be overrepresented in some habitats, not because they themselves are adaptive, but rather because some other trait of a group of ferns is adaptive. Bearing these limitations in mind, some patterns deserve closer consideration. Disturbed sites have higher solar radiation and lower air humidity, which is suitable for drought-tolerant ferns but not for humidity-dependent ones [12].

Table 4. The community-level weighted means of fern trait values at the three sites in Longnan County.

Functional Traits	JLS [1]	AJS	LGS
Lamina length	66.048	68.277	**88.670**
Lamina width	**21.373**	17.624	17.748
Petiole length	36.720	33.146	**43.481**
Frond heterophylly	**1.096**	1.080	1.084
Lamina texture	**2.178**	2.149	2.087
Frond arrangement	2.066	**2.386**	2.119
Rhizome type	2.228	**2.444**	2.148
Rhizome position	1.069	**1.094**	1.000
Lamina dissection	2.617	2.351	**3.131**
Lamina shape	linear-lanceolate	linear-lanceolate	linear-lanceolate
Sori shape	orbicular	linear	orbicular
Sori position	medial_on_veins	1_row_on_either_side_of_veins	1_line_on_each_side_of_costule
Indusia	0.677	0.682	**0.878**
Reproduction type	1.021	**1.023**	1.002
Phenology	1.014	1.030	**1.031**
Habit	**1.109**	1.068	1.000
Scales or hair density	1.186	1.155	**1.259**

[1] Numbers in bold indicate the maximum value at three sites.

Several of the functional traits recovered as being overrepresented in the disturbed site in our study were previously suggested to be adaptations to disturbance. Thus, in dry and hot environments, plants have narrower and pinnate leaves to allow for heat dissipation [116], and ferns show more coriaceous leaves, succulent rhizomes, denser leaf scales, and higher cell wall elasticity [15]. Rhizome type is related to space/light competition [117], frond heterophylly to spore dispersal facilitation, high lamina thickness to frost/drought adaptations, high scale and hair density to heat/water/herbivory protection, hydathodes to water transport facilitation, indusia to spore protection from water washing, and buds to wet environments [71].

3.3. Indicator Fern Species for Different Disturbance Levels

There were seven indicator fern species for the roadside in the strongly disturbed study sites, four for the site with an intermediate disturbance level, seven for the site with a low disturbance level, and one for the latter two sites combined (Table 5).

Table 5. Indicator fern species for different disturbance levels in Longnan County, China.

Disturbance Level	Indicator Species	Indicator Value	*P*-Value	Significance Code [1]
High	*Dicranopteris pedata*	0.692	0.0001	***
	Blechnum orientale	0.612	0.0001	***
	Odontosoria chinensis	0.579	0.0001	***
	Lygodium microphyllum	0.376	0.0004	***
	Cyclosorus parasiticus	0.366	0.0015	**
	Christella dentata	0.274	0.016	*
	Pteris semipinnata	0.264	0.0165	*
Intermediate	*Leptochilus hemitomus*	0.429	0.0001	***
	Diplazium virescens	0.331	0.0034	**
	Arachniodes chinensis	0.330	0.0005	***
	Coniogramme japonica	0.248	0.0001	***
Low	*Ctenitis subglandulosa*	0.536	0.0001	***
	Angiopteris fokiensis	0.434	0.0002	***
	Cyathea hancockii	0.378	0.0001	***
	Cornopteris opaca	0.333	0.0001	***
	Dictyocline wilfordii	0.314	0.0039	**
	Arachniodes amabilis	0.300	0.0057	**
	Plagiogyria adnata	0.261	0.0007	***
Intermediate + low	*Osmunda vachellii*	0.243	0.047	*

[1] Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

Many fern groups, such as Gleicheniaceae, Dennstaedtiaceae, Pteridaceae, and Schizeaceae, include species that are clearly adapted to open, sunny habitats with poorly developed soils and that quickly colonize disturbed sites. Many tropical landslides are quickly colonized by Gleicheniaceae [118]. Among the seven high-disturbance indicators, previous studies found that *Dicranopteris pedata* and *Blechnum orientale* dominate the early successional stage on landslide trails [119]; *Odontosoria chinensis* frequently colonizes disturbed places [120]; *Lygodium microphyllum* has the ability to invade hurricane-disturbed areas [121]; *Cyclosorus parasiticus* adapts to disturbed habitats [122]; *Christella dentata* is common along roadsides but can also dominate in undisturbed, lightly disturbed, and moderately disturbed forests [123], which makes it a poor disturbance indicator; *Pteris semipinnata* is a dominant understory species in the economic needle-leaf forest of *Pinus massoniana* [124]. Our results are thus in accordance with the previous observations and point to a certain generality of the results obtained by us.

Among the seven low-disturbance indicators and one intermediate + low disturbance indicator: *Ctenitis subglandulosa* is a dominant species in the herbaceous layer in a natural evergreen forest [125]; the tree fern *Cyathea hancockii* is a nationally protected plant in China; and *Angiopteris fokiensis* and *Osmunda vachellii* are provincially protected plants in Jiangxi. Clearly, much less is known about these species than about the species of the highly disturbed sites, which may partly reflect that the disturbance-adapted species typically have large ranges and are common.

4. Conclusions

In general, the taxonomic, phylogenetic, and functional diversity of ferns in Longnan County has been greatly influenced by human disturbances, which supports the 'increasing disturbance hypothesis'. Many functional traits of ferns have adapted accordingly to the increasing disturbance degree. We also identified some indicator fern species corresponding to different disturbance levels. Hence, ferns are an effective indicator group for environmental stress. Compared to the traditional diversity indices, Hill number-based diversity profiles provided a continuous and thorough picture of fern diversity patterns among different disturbance levels. However, the relationship of fern diversity to habitat disturbance is complex and requires further case studies. In the future, more sites should be included, and the disturbance levels should be quantified. Standard sampling protocols, molecular-based species phylogeny, and unified functional traits should also be adopted to obtain meaningful comparisons with previous publications and to obtain global-scale patterns of fern diversity.

Supplementary Materials: The following are available online at http://www.mdpi.com/1424-2818/12/4/135/s1, Code S1: Hill number-based diversity analysis.R, Code S2: Indicator species analysis.R, Figure S1: Phylogenetic tree of all fern species.tif, File S1: Phylogenetic tree of all fern species (in Newick format).txt, File S2: Fern community data ferncomm2020.txt, File S3: Fern traits data ferntraits2020.txt, File S4: Indicator species data indicatorspecies.txt, Table S1: Individual numbers of all fern species.xlsx, Table S2: Functional traits of all fern species.xlsx.

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