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Essay

Correlation and Community Stability Analysis of Herbaceous Plants in Dashiwei Tiankeng Group, China

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Abstract: Studying the interspecific association and stability of herbaceous communities in different developmental stages of tiankeng is helpful to understand the relationship between tiankeng vegetation and the environment, and can provide an important theoretical basis for the protection and restoration of the karst tiankeng ecosystem. In this study, the herbaceous community of the Dashiwei Tiankeng Group in Guangxi was studied to analyze the interspecific relationships and community stability of herbaceous plants in four different habitats (the earlier stage, middle stage, late stage and the external forest of tiankeng), and to explore whether the herbaceous community structure gradually stabilized with the development of tiankeng. The variance ratio (*VR*), X^2 test, association coefficient (*JI*) and the Spearman rank correlation coefficient test were used to analyze the interspecific association of the main herbaceous plants in different developmental stages of tiankeng. The stability of the herbaceous community was analyzed by the stability measurement method of M. Godron. The results showed that: (1) the logarithm of the middle stage of tiankeng negatively correlated species was the highest (56.7%), and the logarithm of the later stage of tiankeng positively correlated species was the highest (57.2%). The positive and negative correlation ratio of main herbs decreased first and then increased, indicating that the middle stage of development was the period of high competition among herbs and the biggest difference in resource utilization. The ecological habits of herbaceous plants will be changed from sciophiles to hygrophytes to heliophiles and drought-enduring plants. (2) The earlier stage and middle stage of tiankeng overall relevance had a significant negative correlation, the later stage and external forest of tiankeng overall correlation were not significant positive correlation, and the X^2 test and the Spearman rank correlation coefficient of different developmental stages of tiankeng most major herbaceous species were not significant correlation, suggesting that the major herbs in tiankengs had weak association and strong independence. (3) The distance from the intersection point to the stable point (20, 80) was 19.799, 17.867, 18.922 and 17.706, respectively, of the four regression models of tiankengs herb community, which further indicated that the forest herb layers were in an unstable state. The forest outside is relatively more stable than the herbaceous community inside the tiankeng.

Keywords: interspecific association; community stability; community succession; underground forest; karst tiankeng

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1. Introduction

Species depend on each other and compete with each other in the process of plant community succession, and their abundance and composition can change drastically, showing certain interspecific associations, which in turn affect the stability of the whole community [1]. Interspecific associations refer to the interrelatedness of spatial distribution of different species under the influence of heterogeneous habitats [2], which is the result of species interactions, food chain synergy and gradual adaptation to the environment [3]. Currently, many scholars have used qualitative and quantitative methods to study interspecific relatedness in plant communities, i.e., using 2 × 2 linked lists to determine the presence or absence of species and quantitative analysis based on the number of species, and then the number of positively and negatively associated species pairs in the same habitat to determine the interspecific relationships of the community. It can interpret the composition structure and stability of plant communities at the present stage, determine the development dynamics of communities [4], reveal the ecological mechanisms during community succession, and help to understand the interactions and ecological relationships among species during community development [5], which is the basis for the formation and evolution of plant communities and one of the most important factors driving the stable development of communities [6].

Community stability is the basis for the continuous functioning of forest ecosystems and is a comprehensive characteristic of plant community structure and function [7]. Previous studies have generally used bioecological methods and M. Godron stability measures to describe community stability. The former was analyzed mainly by species composition and community age structure, while the latter was reflected by mathematical models. Interspecific associations are closely related to community stability, and studies combining the two have gradually increased in recent years, mostly focusing on elevation gradients [8], endangered species [9], grazing [10], and flooding disturbance [11], but there are few studies on interspecific associations and stability in different developmental stages of tiankeng. The relationship between plant individuals in different developmental stages is the result of long-term interaction between plant communities and the environment [12], and relevant studies can reflect the trend of plant community succession and development more reliably and deeply [13], judge the current status and stability of plant communities, and provide an important theoretical basis for population evolution, forest management, biodiversity conservation, and restoration and reconstruction of natural vegetation in the process of succession [14].

Karst landscapes are widely distributed in southwest China and are currently facing a series of problems such as biodiversity loss, soil erosion, rock desertification, and ecosystem degradation, making them an extremely fragile ecosystem [15,16]. The tiankeng is the most peculiar landform in the karst region, and the extraordinarily negative topography with deep sunken surface and high enclosed cliff walls make them possess relatively closed and independent karst tiankeng ecosystems compared with the surrounding karst areas [17]. Karst tiankeng ecosystems have unique karst habitats such as higher oxygen ion concentration, greater air humidity, lower temperature, and fertile soil, which provide favorable conditions for plant growth [18] and preserve the most intact tiankeng primitive or quasi-primitive forests due to the steep cliff walls and little interference from human activities, which are a refuge for modern karst forest plants [19]. At present, studies on the flora of tiankeng mainly focus on species diversity [20,21], plant functional traits [22–24], soil enzyme activity [25,26], and the relationship between tiankeng geomorphology and vegetation [27], etc. Few studies have been conducted on interspecific associations and do not link the development stages of the entire tiankeng, and few studies have been conducted on the interspecific associations and community stability of herbs in different developmental stages of tiankeng. There are few studies on the interspecific associations and community stability of herbaceous plants in different developmental stages and outside the forests of tiankeng.

Since tiankeng is formed, their geomorphology and environment have changed with the development of tiankeng; herbaceous plants are the pioneer species of tiankeng vegetation, while herbaceous communities will continue to evolve. In this study, we investigated the interspecific relationships and community stability of herbaceous plants in four habitats, namely, the early stage, middle stage, and later stage of tiankeng and the external forest of tiankeng. The following three scientific questions were explored: (1) Is the herbaceous community structure gradually stable as the tiankeng develops? (2) What are the interspecific relationships of the major herbs in different developmental stages of tiankeng? (3) Are the interspecific relationships and community stability different from those of the herbs in the karst forest around the tiankeng? The aim is to better understand the relationship between the tiankeng herbaceous community and the environment, reflect the composition structure, succession pattern and stability of the tiankeng herbaceous community, and reveal the mechanism of tiankeng herbaceous community construction, which is important for the protection and restoration of karst tiankeng ecosystem.

2. Materials and Methods

2.1. Study Area

The Dashiwei Tiankeng Group is located in Leye County, Guangxi Zhuang Autonomous Region, southwest China (106°21′49′′–106°49′37′′ E, 24°51′50′′–24°56′06′′ N), and is the largest tiankeng group in the world. There are 29 tiankengs in the group, all of which are formed and developed by the erosion of the Bailang underground river system and are collapsed tiankeng, concentrated on the midstream section of this underground river [28]. The area has a central subtropical monsoon climate with distinct dry and wet seasons, rain and heat in the same period, with an average annual rainfall of 1400 mm, rainfall in the rainy season (May–October) accounting for 85% of the average annual rainfall, annual relative humidity of 85%, and an average annual temperature of 16.4 °C. The soil is developed by the weathering of limestone and is dominated by limestone soil mixed with sandstone. The community is mainly a mixed evergreen and deciduous broad-leaved forest in the middle subtropical zone, and the main species of tree layer are *Acer tonkinense*, *Handeliodendron bodinieri* and *Choerospondias axillaris*, etc. The shrub layer is mainly composed of *Metapanax davidii* and *Machilus calcicola*, etc. The herb layer mainly includes *Strobilanthes cusia*, Elatostema, Pilea, etc. According to the projected area between the mouth and the bottom of the tiankeng, the tiankeng can be divided into three developmental stages: earlier stage, middle stage and later stage. The external forest of tiankeng is the stage after the tiankeng has completely degraded, and the habitats vary greatly in different developmental stages [29]. In the earlier early stage, the area of the mouth of the tiankeng is smaller than the projected area of the bottom, which is an inverted funnel type, with a dark environment, little light, humid air, and poor and shallow soil; in the middle stage, the area of the mouth of the tiankeng is about equal to the projected area of the bottom, which is a vertical well type, with stronger light and thicker soil; in the later stage, the area of the mouth of the tiankeng is larger than the projected area of the bottom, which is funnel type, with sufficient light, dry and flat bottom, and accumulation of rich soil and nutrients. The external forest is a typical karst rocky mountain forest outside the tiankeng, with sufficient light, shallow and discontinuous soil, an open environment, and high human interference [30].

2.2. Herpetological Survey

The plots for our plant community survey were established after a comprehensive understanding of the forest communities inside and outside the tiankeng based on several surveys of the vegetation of the Dashiwei Tiankeng Group and previous studies. For different developmental stages of tiankeng, the method of space instead of time was used, which is a common method for evaluating community successional changes [31]; herbaceous communities with good growth in each period were selected as experimental objects, namely, an earlier stage of tiankeng (Banyue Cave and Rose Hall), the middle stage of tiankeng (Shenmu and Sujia Tiankeng), and later stage of tiankeng (Dacao and Liuxing Tiankeng). We used the typical sample plot method to select the karst external forest that is close to the tiankeng, less disturbed and with continuous forest communities (Figure 1). Four 20 × 20 sample plots were set up in each of the different habitats, for a total of 16 sample plots, and 13 small 1 × 1 sample plots in each sample plot, for a total of 208 sample plots. All herbaceous plants (including ferns and herbaceous lianas) occurring in the sample plots were recorded, and herbaceous abundance, height and cover were measured. Habitat data such as latitude, longitude, elevation, depression, temperature and humidity, slope orientation, and disturbance level were also recorded at 11:00 a.m. (Table 1).

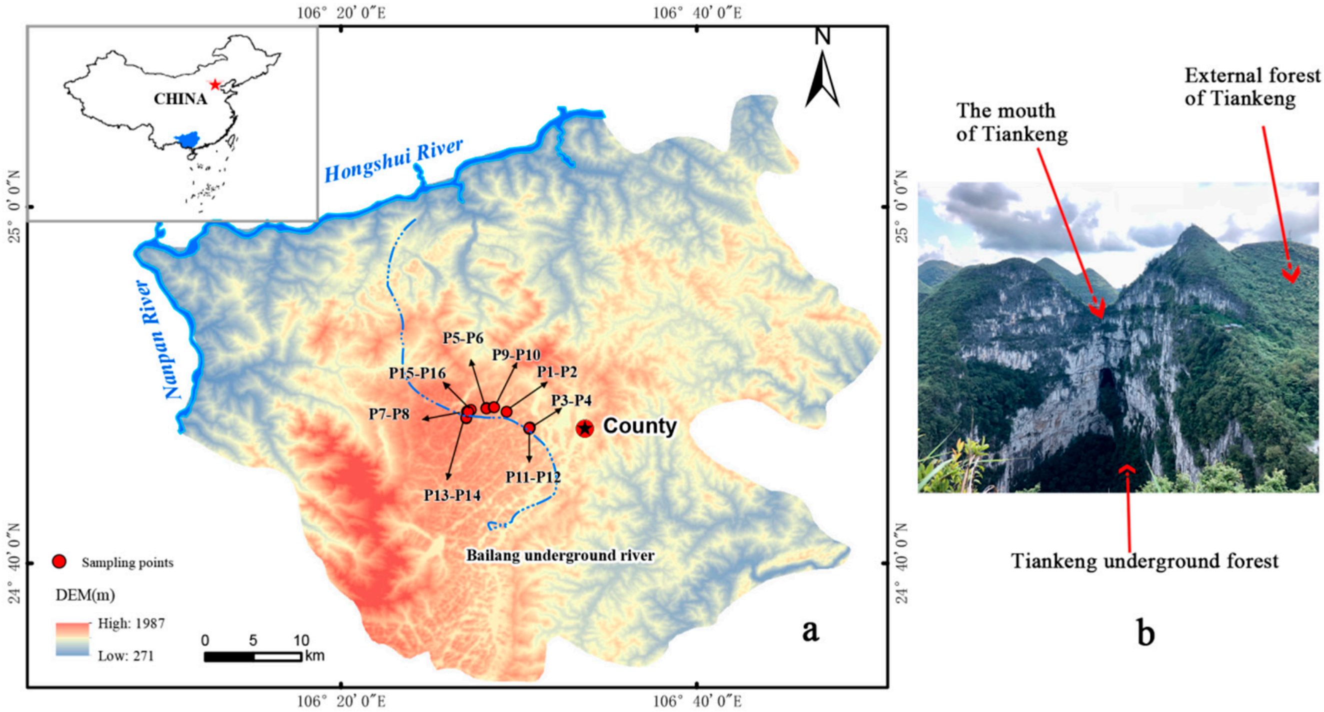

Figure 1. The Dashiwei Tiankeng Group in the study area is located in Leye County, Guangxi Zhuang Autonomous Region, China. The letter (**a**) represents the location of the study area and the sampling site; letter (**b**) is the location of the tiankeng forest and the external forest, and the mouth area and the bottom area are roughly the same, which belong to the middle stage of tiankeng.

Table 1. General situation of 16 sample plots of Dashiwei Tiankeng Group, China.

Habitat	Plot	Site	Longitude	Latitude	Altitude/m	Crown Density	Humidness/°C	Illumination Intensity (Lux)	Disturbance Degree
Earlier stage of tiankeng	P1	Banyue Cave	106°29′21″	24°48′26″	1142	0	86.1	306	Light
	P2	Banyue Cave	106°29′21″	24°48′26″	1092	0	84.8	341	Light
	P3	Rose Hall	106°30′37″	24°47′30″	980	0	85.4	357	Light
	P4	Rose Hall	106°30′37″	24°47′30″	1012	0	84.9	441	Light
Middle stage of tiankeng	P5	Shenmu	106°28′14″	24°48′39″	1205	82	88.5	393	Light
	P6	Shenmu	106°28′13″	24°48′38″	1242	86	88.4	538	Light
	P7	Sujia	106°27′09″	24°48′28″	1301	83	83.6	576	Light
	P8	Sujia	106°27′08″	24°48′27″	1260	80	88.2	754	Light
Later stage of tiankeng	P9	Liuxing	106°28′38″	24°48′41″	1139	68	78.3	612	Medium
	P10	Liuxing	106°28′39″	24°48′41″	1132	62	81.3	620	Medium
	P11	Dacao	106°30′40″	24°47′33″	1117	72	86.1	580	Light
	P12	Dacao	106°30′38″	24°47′31″	1061	78	84.9	643	Light
External forest of tiankeng	P13	Landianyao	106°27′05″	24°48′5″	1317	62	77.3	891	Medium
	P14	Landianyao	106°27′06″	24°48′6″	1323	75	78.6	786	Medium
	P15	Sujia outside	106°27′20″	24°48′32″	1310	65	72.1	1083	Medium
	P16	Sujia outside	106°27′12″	24°48′26″	1330	75	75.5	854	Medium

2.3. Data Analysis

2.3.1. Important Values

In this study, the importance values were used to characterize the status and role of each herb in the community and objectively reflect the dominance of herbs in the sample, and 16 major herbs were selected for interspecific association and correlation analysis. The following equations were used for the calculations.

$$IV = \frac{\frac{n_i}{\sum_{i=1}^{S} n_i} + \frac{ri}{\sum_{i=1}^{S} ri} + \frac{hi}{\sum_{i=1}^{S} hi} + \frac{fi}{\sum_{i=1}^{S} fi}}{4} \times 100$$

where n_i is the number of individuals containing herb i, r_i is the cover of herb i in the sample, h_i is the height of herb i, f_i is the number of samples in which herb i occurs, and S is the total number of herbs.

2.3.2. Overall Correlation Test

The binary data matrix of species presence or absence within the sample square was used as raw data to test the overall association among the major herbs of the plant community using the variance ratio (*VR*) proposed by Schluter [32], and the overall association was further tested for significance by the statistic *W*. The counting equation was as follows.

$$P_i = \frac{n_i}{N}$$
$$VR = \frac{S_T^2}{\delta_T^2} = \frac{\frac{1}{N}\sum_{i=1}^{N}\left(T_j - t\right)^2}{\sum_{i=n}^{S} P_i(1-P_i)}$$
$$W = VR \times N$$

where P_i is the frequency of occurrence of herb i, n_i is the number of sample squares containing herb i, N is the total number of herb samples, and S_T^2 is the variance of the number of species in all sample squares, the δ_T^2 is the overall sample variance, S is the total number of herbs, T_j is the number of species occurring in sample j, and t is the mean number of herbs in the sample.

Under the null hypothesis of independence, herbs within herbaceous communities are independent of each other and not significantly associated with each other, and the expected value of *VR* is 1. If *VR* = 1, the original hypothesis is accepted and herbs within herbaceous communities are not associated with each other in general; if *VR* > 1 or *VR* < 1, the original hypothesis is rejected and herbs are positively or negatively associated with each other in general. Since the positive and negative correlations among herbs can cancel each other out, the value of the variance ratio *VR* was further tested for significant deviation from 1 by the statistic *W*. If the value of W fell into the 90% confidence interval of the X^2 distribution $X^2{}_{(0.95,N)} < W < X^2{}_{(0.05,N)}$, the overall interspecific association of herbaceous communities was not significant, and if $W > X^2{}_{(0.05,N)}$ or $W < X^2{}_{(0.95,N)}$, the value of W fell outside the range, the overall interspecific association was significant.

2.3.3. X^2 Test

Based on the 2 × 2 column table, X^2 statistic was used to qualitatively study the association among the major herbs. Given the discontinuous samples in this study, the significance of interspecific association was determined by Yates' continuous corrected chi–square test, and the association among herbs was further determined by the positive and negative values of *V*. The equation of measurement was as follows [33]:

$$X^2 = \frac{N[|ad-bc|-0.5N]^2}{(a+b)(b+d)(c+d)(a+c)}$$
$$V = \frac{(a+d)-(b+c)}{(a+b+c+d)}$$

where N is the total number of samples, a is the number of samples in which both herbs appear, b is the number of samples in which herb B appears and herb A does not appear, c is the number of samples in which herb A appears and herb B does not appear, and d is the number of samples in which neither of the two herbs appears. If $X^2 < 3.841$, the association between herbs was not significant ($p > 0.05$); if $3.841 \leq X^2 \leq 6.635$, the association between herbs was significant ($0.01 \leq p \leq 0.05$); $X^2 > 6.635$, the association between herbs was considered highly significant ($p < 0.01$). The positive and negative association between herbs was then judged based on V value, so if $V > 0$, then interspecies was positively associated, if $V < 0$, then interspecies was negatively associated.

Due to the small sample and the high frequency of occurrence of major herbs, and the resulting in the frequency of occurrence of some herbs is 100%, b and d values are 0, then the denominator will also be 0. In order to avoid the formula is not computable, it is necessary to weigh the b and d values to 1, which objectively reflects the association of these two species and can obtain good results [34].

2.3.4. Linkage Factor JI Index

The Jaccard (JI) index can indicate the chance of species pairs occurring together and the degree of association, and the use of JI can better represent the degree of association among herbs [35]. The counting equation is as follows.

$$JI = \frac{a}{a + b + c}$$

In this case, the value range of JI is [0, 1], and the more the value of JI tends to 1, the highest probability of occurrence of inter-herb in the same square is indicated, while the more the value of JI tends to 0, the stronger the independence that inter-herb will not occur in the same square.

2.3.5. Spearman's Rank Correlation Coefficient Test

The X^2 test and JI index use binary data to calculate species associations, which inevitably ignore some information, such as multidegree data. In contrast, Spearman's rank correlation coefficient test is a nonparametric test to assess the degree of correlation between independent variables, which can be flexible and accurate to objectively reflect the degree of species pair correlation, and will further complement and improve the results of the X^2 test [36]. Therefore, Spearman's rank correlation coefficient test was performed using multi-degree data of 16 major herbs, and the counting formula was as follows.

$$r_S = 1 - \frac{6\sum_{k=1}^{N}\left(x_{ik} - x_{jk}\right)^2}{N^3 - N}$$

where $r_S(i,j)$ is the Spearman's rank correlation coefficient of herb i and herb j in sample k, respectively, with a value range of [−1, 1], and positive values indicate positive correlation for species pairs and negative correlation for negative values; N is the total number of samples; x_{ik} and x_{jk} are the ranks of herb i and herb j in sample k, respectively.

2.3.6. Community Stability Analysis

The M. Godron method is a more systematic and comprehensive mathematical ecological method for determining community stability, which has higher credibility in reflecting community development and change trends [37]. In this paper, we used the improved M. Godron stability determination method [38], i.e., the law of contribution method, to establish a regression model using the species of herbaceous communities and the frequency of that species to infer the major herbaceous changes during community succession. Firstly, all the herbs in the community were sorted in order of frequency, converted into relative frequency and accumulated in turn to obtain the cumulative relative frequency of each herb; secondly, the sum of all the herbs was taken as the reciprocal according to the above ranking and accumulated in turn, and finally multiplied by 100% to obtain the cumulative reciprocal percentage of each herb. Using the cumulative relative frequency as the x-axis and the cumulative inverse percentage as the y-axis, a binomial linear fit ($y = ax^2 + bx + c$) was used to establish a smooth curve model to intersect with the line $y = 100 - x$ to obtain the coordinates of the intersection point according to the trend of the scatter plot. The stability of the community was judged according to the Euclidean distance from the coordinates of the intersection point to the coordinates of the stability point (20, 80), and the closer the distance, the more stable the herbaceous community was.

2.3.7. Data Processing and Analysis

Excel 2010 (Microsoft Corporation, Redmond, WA, USA) was used to organize the data from the survey sample plots, calculate the importance values and community stability of herbs, and use the sp.assoc. and sp.pair functions in the "spaa" package of R 4.0.4 (R Core Team, Vienna, Austria) to calculate the X^2 test and *JI* index and Spearman rank correlation coefficient test for the major herbs of the four habitats. In this paper, all graphs were plotted using Origin 2021(OriginLab, Northampton, MA, USA), and herbaceous specimens were identified based on Guangxi Herbarium (IBK) and Chinese Virtual Herbarium (CVH) and January 2023 by consulting the Tropicos website (https://www.tropicos.org).

3. Results and Analysis

3.1. Species Composition

A total of 131 species of herbaceous plants in 49 families and 96 genera were recorded from all sample sites in the Dashiwei Tiankeng Group in China, including 59 species in 48 genera from 31 families in the earlier stage of tiankeng, 66 species in 52 genera from 29 families in the middle stage of tiankeng, 80 species in 62 genera from 38 families in the later stage of tiankeng, and 50 species in 45 genera from 27 families in the external forest of tiankeng (see Appendix A for detailed species). A total of 14 (10.6%) herbaceous species were recorded from inside and outside the tiankeng, and 62 (47.3%) species occurred only in one habitat, indicating that there were significant differences in the herbaceous community composition in different developmental stages and forest outside of tiankeng. In this study, we selected the top 16 species of herbaceous communities in 4 habitats and analyzed their interspecific associations (Table 2).

Table 2. Abbreviations, importance values and frequency of main herbs.

Species	Abbreviation	Earlier Stage of tiankeng		Middle Stage of tiankeng		Later Stage of tiankeng		External Forest of tiankeng	
		IV	*F*	*IV*	*F*	*IV*	*F*	*IV*	*F*
Strobilanthes cusia	Sc	14.98	10.91	6.37	4.15	3.58	4.08	—	—
Elatostema brachyodontum	Eb	7.52	5.01	—	—	—	—	—	—
Boehmeria macrophylla	Bm	7.19	6.19	—	—	2.70	2.81	—	—
Selaginella doederleinii	Sd	7.02	6.19	—	—	4.85	4.08	—	—
Pilea pumila	Pp	3.10	3.24	—	—	—	—	—	—
Tetrastigma obtectum	To	2.72	3.24	3.83	5.66	4.80	4.08	—	—
Pteris semipinnata	Ps	2.58	2.65	—	—	—	—	—	—
Trigonotis leyeensis	Tl	2.53	3.24	—	—	—	—	—	—
Urtica fissa	Uf	2.50	1.77	2.34	2.64	—	—	—	—
Elatostema ficJIdes	Ef	2.20	1.77	14.72	7.17	4.88	4.85	—	—
Ctenitis subglandulosa	Cs	2.17	2.06	2.91	2.26	—	—	—	—
Ophiorrhiza japonica	Oj	2.16	2.36	2.43	2.26	—	—	3.40	1.94
Dryopteris varia	Dv	2.13	3.24	—	—	—	—	—	—
Setaria viridis	Sv	2.12	2.36	—	—	—	—	—	—
Polystichum fimbriatum	Pf	2.05	2.36	—	—	—	—	—	—
Sambucus javanica	Sj	1.94	1.18	—	—	—	—	—	—
Pyrrosia calvata	Pc	—	—	5.22	6.04	—	—	5.16	5.54
Strobilanthes dimorphotricha	Sh	—	—	4.56	3.02	—	—	—	—
Pilea plataniflora	Pi	—	—	4.00	3.02	2.17	2.04	—	—
Hemiboea pseudomagnibracteata	Hp	—	—	3.38	2.64	—	—	—	—
Pilea angulata	Pa	—	—	3.31	2.64	3.37	2.55	—	—
Arthraxon hispidus	Ah	—	—	3.05	4.53	5.09	5.36	4.47	6.09
Leptochilus henryi	Lh	—	—	2.47	2.64	—	—	—	—
Elatostema oblongifolium	Eo	—	—	2.47	1.51	—	—	—	—
Gynostemma pentaphyllum	Gp	—	—	2.14	3.02	—	—	2.99	3.32

Table 2. *Cont.*

Species	Abbreviation	Earlier Stage of tiankeng		Middle Stage of tiankeng		Later Stage of tiankeng		External Forest of tiankeng	
		IV	*F*	*IV*	*F*	*IV*	*F*	*IV*	*F*
Goniophlebium amoenum	Ga	—	—	2.11	3.40	—	—	—	—
Phryma leptostachya subsp. *asiatica*	Pl	—	—	—	—	4.56	3.83	3.83	3.88
Strobilanthes atropurpurea	Sa	—	—	—	—	4.05	2.55	—	—
Nephrolepis cordifolia	Nc	—	—	—	—	3.35	2.55	—	—
Selaginella uncinata	Su	—	—	—	—	3.22	2.81	—	—
Pilea elliptilimba	Pe	—	—	—	—	3.12	3.32	—	—
Selaginella moellendorffii	Sm	—	—	—	—	2.48	1.53	—	—
Houttuynia cordata	Hc	—	—	—	—	2.36	2.30	—	—
Paraphlomis javanica	Pj	—	—	—	—	2.24	1.79	—	—
Disporum uniflorum	Du	—	—	—	—	—	—	7.80	7.48
Miscanthus floridulus	Mf	—	—	—	—	—	—	5.07	3.88
Lepisorus fortunei	Lf	—	—	—	—	—	—	6.84	5.54
Asparagus lycopodineus	Al	—	—	—	—	—	—	5.14	6.93
Liriope spicata	Ls	—	—	—	—	—	—	4.86	4.16
Aster trinervius	At	—	—	—	—	—	—	4.00	3.60
Dioscorea velutipes	Di	—	—	—	—	—	—	3.83	4.71
Pteridium revolutum	Pr	—	—	—	—	—	—	3.72	1.66
Pronephrium gymnopteridifrons	Pg	—	—	—	—	—	—	3.16	1.11
Lysionotus pauciflorus	Lp	—	—	—	—	—	—	2.89	3.05
Pteris multifida	Pm	—	—	—	—	—	—	2.91	4.16

IV: importance value; *F*: frequency.

3.2. Interspecific Relationships

3.2.1. Overall Interspecific Correlation

As can be seen from Table 3, the variance ratio *VR* values between the main herbs of the earlier and middle stage of tiankeng were less than 1, and the test statistic *W* values did not fall into the X^2 critical range, indicating that the overall interspecific herbaceous communities of the earlier and middle stage of tiankeng showed significant negative associations. The variance ratio *VR* values between the major herbs of the later stage and the external forest of tiankeng were greater than 1, and the test statistic *W* values fell into the X^2 critical range, indicating that the overall association between the herbaceous communities of the later stage and external forest of Tiankeng was not significantly positive.

Table 3. Overall association among main herbs.

Development Stages	Variance Ratio	Test Statistics	X^2 Threshold	Test Results
Earlier stage of tiankeng	0.282	1.128	(2.167, 14.067)	Significant negative association
Middle stage of tiankeng	0.174	0.696	(2.167, 14.067)	Significant negative association
Later stage of tiankeng	1.217	4.870	(2.167, 14.067)	Insignificant positive association
External forest of tiankeng	2.000	8.000	(2.167, 14.067)	Insignificant positive association

3.2.2. Interspecific Correlation

(1) X^2 test for major herbs

From Figure 2, the number of positively and negatively associated species pairs in the earlier stage of tiankeng were 58 and 24, respectively, accounting for 48.3% and 20% of the total number of pairs, and the ratio of positive to negative association was 2.42; the number of positively and negatively associated species pairs in the middle stage of tiankeng were 42 and 40, respectively, accounting for 35% and 33.3% of the total number of pairs, and the ratio of positive to negative association was 1.05. The number of positively and negatively associated species pairs in the later stage of tiankeng was 42 and 30, accounting for 35% and 25% of the total number of pairs, respectively, and the ratio of positive to negative associations was 1.4. The number of positively associated species pairs in the external forest of tiankeng was 111, accounting for 92.5% of the total number of pairs. It can be seen that the number of negatively associated species pairs was the highest in the middle stage of tiankeng (33.3%), with a positive-negative association ratio of 1.05; the number of positively associated species pairs was the highest in the external forest of tiankeng (92.5%); the positive-negative association ratio among the main herbaceous species pairs showed a decreasing and then increasing trend. However, in general, most herbaceous species pairs in the four habitats were not significantly associated.

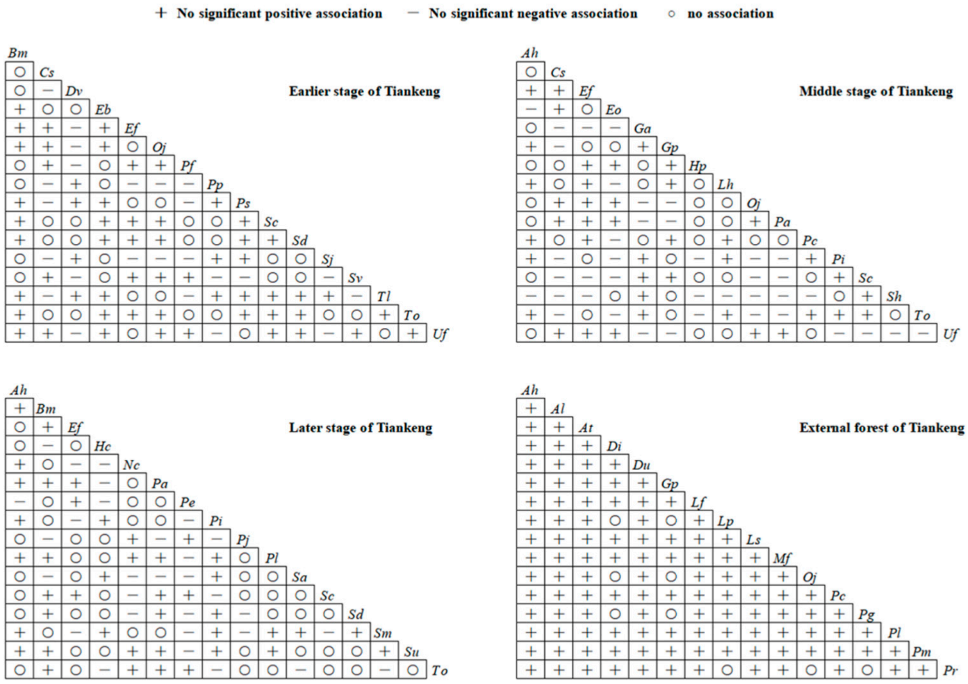

Figure 2. Half matrix graph of the interspecific association X^2 test among the main herbs. The species abbreviations in the figure need to be compared with Table 2.

(2) Linkage coefficient analysis

The Jaccard index (*JI*) results for the major herbs in different developmental stages of tiankeng further distinguished the strength of association among herbs. Since the X^2 test did not have significantly correlated species pairs, this study used percentage stacking plots to make the overall picture clearer (Figure 3). According to the *JI* results, there were 18 species pairs with $JI = 1$ in the earlier stage of tiankeng, 78 species pairs with $0.5 \leq JI < 1$, 80% of the total pairs with $JI \geq 0.5$, 15 species pairs with $0 < JI < 0.5$, 9 species pairs with $JI = 0$, 20% of the total pairs with $JI < 0.5$; 52 species pairs with $JI \geq 0.5$ in the middle stage of tiankeng, 43% of the total pairs with *JI* 43% of the total number of pairs and 68 pairs of species pairs with $JI < 0.5$, accounting for 57% of the total number of pairs; 53 pairs of species pairs with $JI \geq 0.5$ in the later stage of tiankeng, accounting for 44% of the total number of pairs and 68 pairs of species pairs with $JI < 0.5$, accounting for 56% of the total number of pairs. Overall, the highest number of species pairs had $JI \geq 0.5$ in the earlier stage of tiankeng, roughly the same *JI* index in the middle and later stage of tiankeng, but the lowest number of species pairs had $JI \geq 0.5$ in the middle stage of tiankeng, and all species pairs in the external forest of tiankeng had *JI* indices > 0.5. This shows that the Jaccard index and the X^2 test had roughly the same results, with the positively linked species pairs having $JI \geq 0.5$ in the X^2 test, and the negatively linked species pairs having $JI < 0.5$.

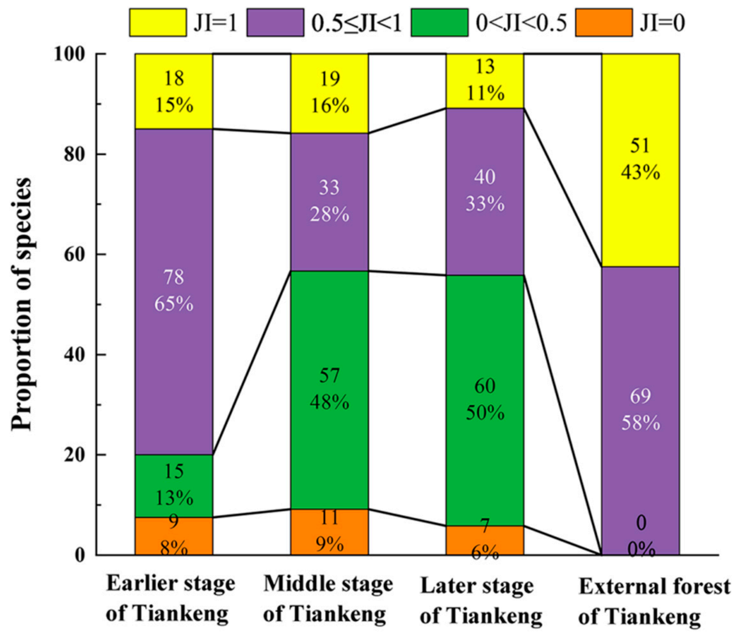

Figure 3. The Jaccard index of the main herbs.

(3) Spearman's rank correlation analysis

Figures 4 and 5 show the results of Spearman's rank correlation coefficient test for the major herbs in the Dashiwei Tiankeng Group. Among the 120 species pairs of major herbs, 55 species pairs were positively and 60 negatively correlated in the earlier stage of tiankeng, accounting for 45.8% and 50% of the total pairs, respectively, with a positive to negative correlation ratio of 0.92; among them, seven pairs were highly significantly correlated, such as *Dryopteris varia* and *Pilea pumila*, *Ctenitis subglandulosa* and *Setaria viridis*, *Elatostema brachyodontum* and *Trigonotis leyeensis* was a highly significant positive correlation ($p < 0.01$), and the correlation between *Polystichum fimbriatum* and *Elatostema brachyodontum*, *Dryopteris varia* and *Ophiorrhiza japonica*, *Ophiorrhiza japonica* and *Pilea pumila*, and *Polystichum fimbriatum* and *Trigonotis leyeensis* were highly significantly negatively correlated ($p < 0.01$). There were 50 pairs of positively correlated species pairs and 68 pairs of negatively correlated species pairs in the middle stage of tiankeng, accounting for 41.7% and 56.7% of the total pairs, respectively, with a positive to negative correlation ratio of 0.74; four pairs showed highly significant correlations ($p < 0.01$), such as *Ctenitis subglandulosa* with *Ophiorrhiza japonica*, *Ctenitis subglandulosa* showed highly significant positive correlation with *Pilea angulata*, *Ophiorrhiza japonica* with *Pilea angulata*, and *Elatostema ficJIdes* showed significant highly negative correlation with *Pyrrosia calvata*. In the later stage of tiankeng, 69 species pairs were positively correlated and 51 pairs were negatively correlated, accounting for 57.2% and 42.5% of the number of species pairs, respectively, with a positive to negative correlation ratio of 1.35; 8 pairs showed highly significant positive correlations, such as *Arthraxon hispidus* and *Phryma leptostachya* subsp. *asiatica*, *Arthraxon hispidus* and *Selaginella uncinata*, *Phryma leptostachya* subsp. *asiatica* and *Selaginella uncinata*, *Boehmeria macrophylla* and *Pilea plataniflora*, *Boehmeria macrophylla* and *Selaginella moellendorffii*, *Pilea plataniflora* with *Selaginella moellendorffii*, *Houttuynia cordata* with *Strobilanthes atropurpurea*, and *Pilea angulata* with *Selaginella doederleinii*. There were 50 positively correlated species pairs and 63 negatively correlated species pairs in the external forest of tiankeng, accounting for 41.7% and 52.5% of the species pairs, respectively, with a positive to negative correlation ratio of 0.79; among them, four pairs were highly significantly positively correlated, such as *Disporum uniflorum* with *Lepisorus fortunei*, *Disporum uniflorum* with *Ophiorrhiza japonica*, *Lepisorus fortunei* with *Ophiorrhiza japonica*, *Lysionotus pauciflorus* with *Pronephrium gymnopteridifrons*. This shows that the number of highly significant species pairs of Spearman's rank correlation coefficient test was significantly higher than the X^2 test for the major herbs in different developmental stages of tiankeng, and the number of positively correlated species pairs was also higher than the X^2 test. Overall, the highest number of positively correlated species pairs (57.2%) with a positive-to-negative correlation ratio of 1.35 was found in the later stage of tiankeng; the highest number of negatively correlated species pairs (56.7%) with a positive-to-negative correlation ratio of 0.74 were found in the middle stage of tiankeng, and the positive to negative correlation ratio among major herbaceous species pairs in the tiankeng showed a decreasing and then increasing trend. In addition, most of the major herbaceous species pairs in the tiankeng and the forest outside the tiankeng did not reach a significant correlation, which further indicated that the correlation of herbaceous species pairs was weak and the distribution of herbs existed independently.

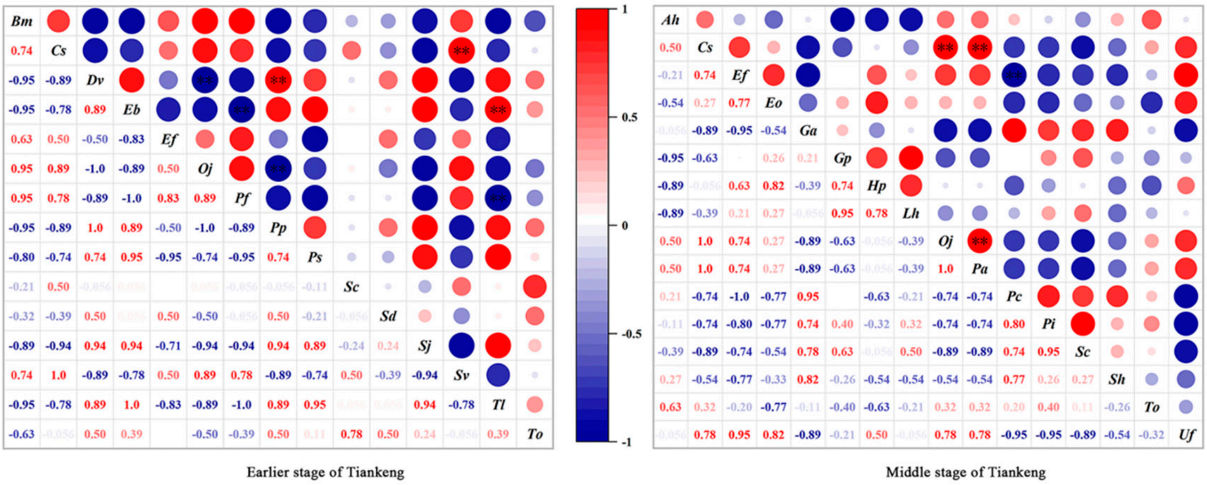

Figure 4. Semi-matrix of Spearman rank correlation coefficient test for major herbs in earlier stage and middle stage of tiankeng. **: indicates highly significant correlation ($p < 0.01$).

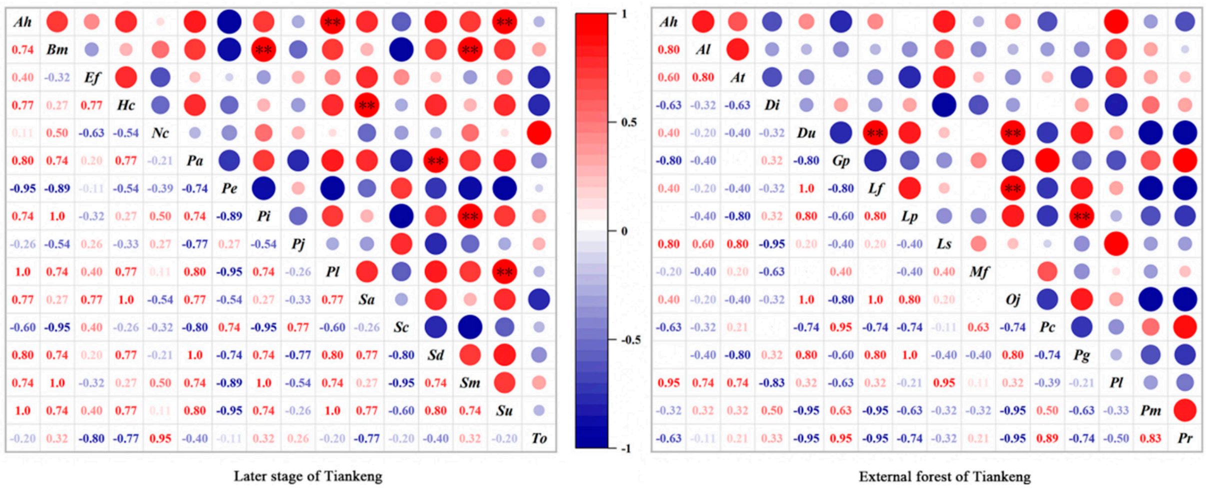

Figure 5. Semi-matrix of Spearman rank correlation coefficient test for major herbs in later stage and external forest of tiankeng. **: indicates highly significant correlation ($p < 0.01$).

3.3. Stability Analysis

The results and scatter plots of the M. Godron community are shown in Table 4 and Figure 6. The results show that the intersection points of the four regression models of the earlier stage of tiankeng, the middle stage of tiankeng, the later stage of tiankeng and the external forest of tiankeng herbaceous community are 19.799, 17.867, 18.922 and 17.706, respectively. According to the M. Godron stability judgment method, we can conclude that the herbaceous communities of different developmental stages and the forest outside of tiankeng are in an unstable state in the Dashiwei Tiankeng Group. The forest outside is relatively more stable than the herbaceous communities of the tiankeng.

Table 4. Stability analysis results of herbaceous community.

Development Stages	Curve Equation	R-Squared	Intersection Coordinate	Distance of Intersection Point and Stable Point	Results
Earlier stage of tiankeng	$y = -0.010x^2 + 1.768x + 17.034$	0.992 **	(34.00, 66.00)	19.799	Instability
Middle stage of tiankeng	$y = -0.013x^2 + 2.048x + 13.829$	0.984 **	(32.64, 67.36)	17.876	Instability
Later stage of tiankeng	$y = -0.012x^2 + 2.001x + 12.995$	0.988 **	(33.38, 66.62)	18.922	Instability
External forest of tiankeng	$y = -0.013x^2 + 2.140x + 11.722$	0.988 **	(32.52, 67.48)	17.706	Instability

** indicates highly significant correlation.

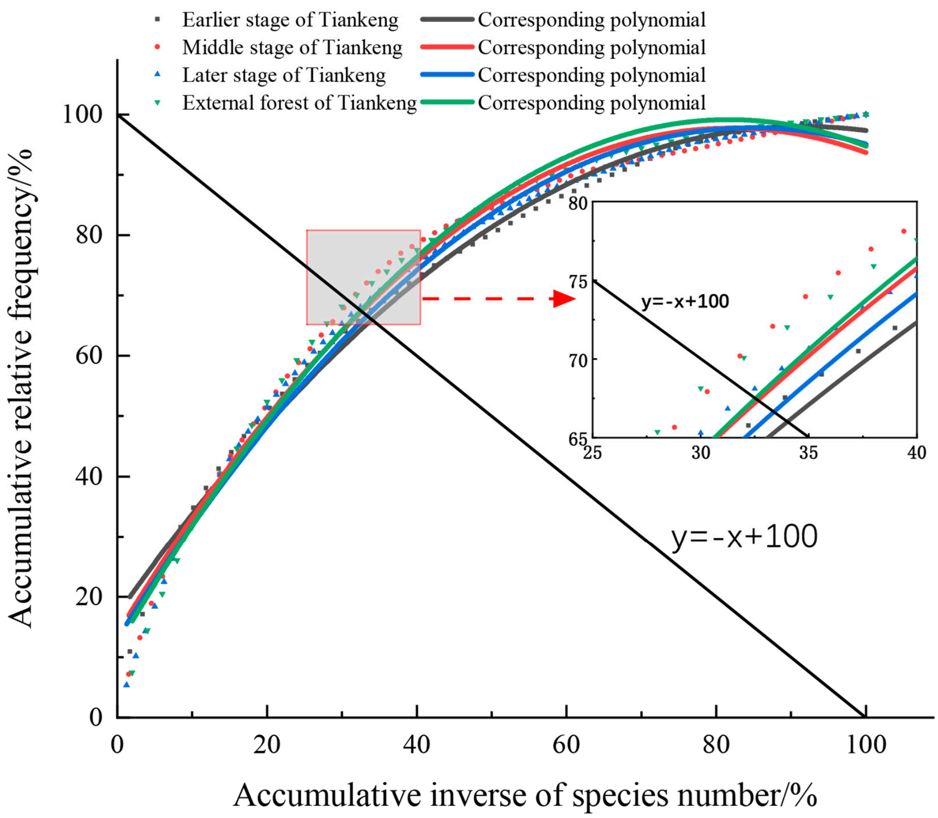

Figure 6. Stability analysis of herbaceous community.

4. Discussion

4.1. Interspecific Correlation Analysis and Correlation Analysis

This study was based on the significance values of species and the 2 × 2 association table, two analysis methods, the X^2 test and the Spearman rank correlation coefficient test, were used, and the results of the X^2 test were further validated using the Jaccard index. The interspecific association X^2 test analyzed the relationship between species qualitatively by the presence or absence of species within the sample, while the interspecific correlation Spearman rank correlation analysis was not limited to the presence or absence of species, but focused more on quantitative characteristics such as the multiplicity and importance values of species, which were quantitative relationships between species. Studies have shown that the Spearman rank correlation coefficient test is more sensitive than the X^2 test, and the number of pairs of highly significantly associated species increased significantly in this study, which is consistent with the previous results [11]. For example, in the X^2 test, none of the four habitat major herbs showed significantly related species pairs, while in the Spearman rank correlation coefficient test, several pairs of highly significantly related species pairs were found in each developmental tiankeng and the forest outside of tiankeng. However, due to the different principles of the two analysis methods, individual results differed, but the overall results were approximately the same. For example, the X^2 test showed the highest number of positively associated species pairs in the earlier stage of tiankeng (48.3%) and the Spearman rank correlation coefficient test showed the highest number of positively associated species pairs in the later stage of tiankeng (57.2%), but both indicated that the positive and negative correlation ratios among the major herbaceous species pairs tended to decrease and then increase with the developing tiankeng and most of the herbaceous species pairs did not reach significant association. Therefore, when studying the interspecific associations of plant communities, combining interspecific correlation analysis with interspecific correlation analysis can reflect the interrelationships between species and their adaptations to the environment in a more comprehensive and diverse way.

4.2. Correlation and Correlation Analysis among Major Herbaceous Species Pairs

The interspecific association is a good indication of the interconnectedness of species in different habitats, reflecting the interrelationship between species and their adaptability to the environment [39]. Plant interspecific relationships are complex, and in general, if species pairs exhibit positive associations, they are considered to be interdependent or mutually beneficial symbioses with similar ecological adaptations to habitats; if they exhibit negative associations, they are considered to be mutually exclusive or have differences in the use of resources and environments [40].

The interspecific relationships of major herbs by three methods (X^2 test, Jaccard index and the Spearman rank correlation coefficient test) showed that the highest number of negatively correlated species pairs and the smallest ratio of positive to negative correlations among major herbs in the middle stage of tiankeng. On the one hand, the middle stage is the transitional period of tiankeng development and the early stage of tiankeng forest formation, and herbaceous plants cannot completely compete with the fast-growing woody plants, and the shrinking ecological niche will lead to competition among herbs; on the other hand, compared with the earlier stage of tiankeng, the mouth of the middle stage of tiankeng is enlarged and light is enhanced, as well as heliophiles and semi-shade are increased [41], which differ from the original sciophiles and hygrophytes in terms of environmental resource requirements, resulting in a greater difference in the number of positively and negatively correlated species pairs. The differences are large. For example, *Elatostema ficJIdes* is negatively correlated with *Pyrrosia calvata*. *Elatostema ficJIdes* has high water content in its stems and leaves and likes moisture and shade, and its population usually grows in large areas under the forest or under the cliff wall with less light, while *Pyrrosia calvata* likes to grow on the rock surface, where the soil is shallow and vegetation is sparse, and the plants receive more care and are more resistant to drought. This study also showed that the number of positively correlated species pairs among major herbs in the later stage of tiankeng was the highest and the positive and negative correlation ratios were the largest, and the positive and negative correlation ratios of major herbs showed a trend of decreasing and then increasing. The reasons for this are that the later stage is well lit, the soils are rich in nutrients and the tiankeng is dry; the ecological habits of the main herbs are heliophiles and drought-enduring plants, the interspecific competition is weak, and they have the same ecological adaptation to the environment, so the positively correlated species pairs are higher than the negatively correlated species pairs. For example, the species pairs of *Arthraxon hispidus* and *Phryma leptostachya* subsp. *asiatica*, *Arthraxon hispidus* and *Selaginella uncinata*, and *Houttuynia cordata* with *Strobilanthes atropurpurea* were all highly significantly positively correlated, and there were no highly significantly negatively correlated species pairs. In addition, the number of positively associated species pairs of major herbs in the tiankeng was less than that in the forest outside the tiankeng, and the number of positively associated species pairs in the X^2 test reached 92.5% of the total number of pairs in the forest outside the tiankeng, and the *JI* index further verified that all species pairs in the forest outside the tiankeng were greater than 0.5. The karst forest outside the tiankeng was not shaded by the vertical rock wall and the habitat was open and the soil was arid. The ecological habits of most herbaceous plants are consistent, and they are all heliophiles and drought-enduring plants. It can be seen that the middle stage is the period of high interspecific competition and the greatest difference in resource utilization among herbs, and the ecological habit of herbs will change from sciophiles to hygrophytes to heliophiles and drought-enduring plants with the developing tiankeng.

4.3. Overall Interspecific Association Analysis

Overall, interspecific associations describe the static relationships among species in a community and reflect the stability of community structure and species composition [42]. The closer the community is to the apical stage, the greater the positive association of the community, and the species in the community usually achieve the maximum use of the resource environment and a perfectly symbiotic relationship between species [43]. In the present study, the overall negative interspecific associations between the earlier and middle stages of tiankeng herbaceous communities were significant, indicating that the earlier and middle stages of tiankeng herbaceous communities were in the early stage of succession, and the composition and structure of the communities were not yet stable, and the degree of interspecific associations was not high. The herbaceous communities in the later stage and external forest of tiankeng showed non-significant positive interspecific associations, indicating that the herbaceous communities in the later stage and external forest of tiankeng started to move towards the late successional stage, and the composition and results of the communities were gradually formed, and the ecological habits of the species were gradually similar to each other, but they did not reach significance and were still in an unstable state, and they were still some distance from the top communities. This is consistent with the results we see in reality.

We combined the variance ratio (*VR*), X^2 test and the Spearman rank correlation coefficient test to show that most of the major herbaceous species pairs in the Dashiwei Tiankeng Group did not reach significant association, which indicated that the linkage of major herb pairs in each developing tiankengs was weak and independent, not forming a close coupling relationship, and was in the stage of continuous improvement. As a closed negative terrain of large scale, the steep cliff walls of karst tiankeng block the communication between the bottom of the tiankeng and the outside world, and the habitats within the tiankeng are diversified, patchy, and complex, and the small-scale microhabitats nurture diverse endemic plants, which reduces the strength of interspecific associations [44] and increases the composition mode among herbs, resulting in obvious differences in the biological and ecological characteristics of herbs within the tiankeng, and the ability to use environmental resources. As a result, the interspecific relationships show many weak or unrelated species pairs, and the associations among species are more fragmented and independent.

4.4. Community Stability Analysis

The M. Godron method is an expression of interspecific relatedness [45], which is comprehensive and systematic in describing community stability and can further improve the analysis results of interspecific relatedness [46]. In this study, we further used the M. Godron method to find that the intersection points of the four regression models for the earlier stage of tiankeng, the middle stage of tiankeng, the later stage of tiankeng and the external forest of tiankeng in the Dashiwei Tiankeng Group were all far from the stability point, and the distance of the external forest is relatively closer to the stability point. It can be seen that each developing tiankeng and external forest herbaceous layer in the Dashiwei Tienkeng Group is in an unstable state, and the forest outside is relatively more stable than the herbaceous community inside the tiankeng.

The tiankeng is surrounded by a closed and steep cliff wall, which is like a special "land island" [47], and the growth and development of plants are greatly influenced by the environment inside the tiankeng itself. As the tiankeng develops, the influence of the tiankeng formed by the erosion of the underground river gradually decreases, and the water vapor in the tiankeng will gradually decrease. The erosion of the water causes the collapse of the rocks, so the tiankeng opening is expanding, with the temperature gradually increasing, and the direct light to the plant community at the bottom of the tiankeng increasing, which shows that light is an important limiting factor for the plant community in the tiankeng [48], and the vegetation at the bottom of the tiankeng will be damaged by the debris from the tiankeng opening at any time. Thus, it can be seen that the ecological environment of tiankeng is constantly undergoing subtle changes, and sensitive and small herbaceous plants are most vulnerable to subtle changes in the tiankeng habitat. The high heterogeneity of habitats and patchiness of microhabitats in the tiankeng, resulting in complex plant community composition, are also important reasons for the instability of herbaceous communities in tiankeng.

The later stage and external forest of tiankeng are more accessible and heavily disturbed by man. The unique habitat nurtures precious medicinal herbs. Tiankeng is located in a remote area and villagers have a single income and often go into the mountains to collect medicinal herbs. There is a lack of arable land in the Karst mountains, while the soil inside and outside the tiankeng is fertile, and villagers grow cash crops such as corn and prickly pear. Local villagers breed livestock, which also causes serious damage to the herbs inside and outside the tiankeng. Herbaceous plants are short in height and weak in resistance to disturbance and are vulnerable to various anthropogenic disturbances. However, disturbance can lead to habitat fragmentation, which can seriously affect the stability of herbaceous communities [49]. Huang [50] showed that the interspecific associations of woody plants in the tiankeng forest showed that the tree layer showed significant positive associations than when the shrub layer was stable.The herbaceous layer and shrub layer in the same community were unstable while the arboreal layer was in a stable state, which shows that the herbaceous layer is highly disturbed by the external environment, and human disturbance will destroy the stability of the herbaceous community in the tiankeng and surrounding forest. This is also consistent with the findings of Jian [51] on the stability of heavily degraded tiankeng grassland communities in Yunnan, which have been abandoned for a long time and are disturbed by grazing due to high accessibility, and the grassland communities are also in an unstable state.

From the interspecific relationships and stability of the herbaceous community of the tiankeng and the karst forest outside of tiankeng, the herbaceous community gradually tends to be stable from the earlier to later stage of tiankeng, and the interspecific relationships and stability of the later stage are close to those of the external forest of tiankeng. This indirectly supports the evolution theory of Prof. Zhu and Prof. Waltham [29] who inferred that tiankeng evolves with time and classified them into different developmental stages based on the ratio of the projected area of the tiankeng entrance to the tiankeng bottom for reliability. The exterior of the tiankeng will be more stable than the herbaceous community inside the tiankeng due to its own stable natural environment. As the tiankeng continues to develop, the species composition, community structure, and stability of the tiankeng forest will gradually converge to that of the forest community outside the tiankeng, but the community is also in an unstable state due to certain anthropogenic disturbances in its open habitat. The forest outside is the natural barrier of the tiankeng and the regional species pool of the tiankeng forest [30], which has an important role in maintaining soil and water and resisting human interference, etc. If it continues to be seriously damaged it will directly accelerate the degradation of the tiankeng ecosystem, and the precious scientific research value of the tiankeng will no longer exist, so we should pay attention to the protection of the ecological environment of the tiankeng and the surrounding forest, and with the increased protection of the tiankeng habitat. The herbaceous community outside of tiankeng will gradually tend to the top community stage, while the herbaceous community inside of tiankeng still has a long distance to go.

4.5. Tiankeng Vegetation Conservation Strategy and Outlook

In this study, the interspecific associations and community stability of the major herbs of each developing tiankeng and external forest in the Dashiwei Tiankeng Group in China were used to show that the herbaceous communities are still in an unstable stage. As a karst tiankeng kingdom in China, vegetation ecology has received widespread attention both at home and abroad [52]. The special geomorphology and habitats of tiankeng not only nurture unique plants, but are also modern refuges for primitive forest communities. It is of great scientific value to protect the ecological environment of tiankeng, reduce anthropogenic disturbance, maintain community stability, and promote the natural succession of tiankeng vegetation. Due to the poor understanding of the scientific value of tiankeng in early times, tiankeng and the surrounding karst areas suffered varying degrees of damage. Therefore, based on interspecific association studies, this paper, after understanding the ecological and biological characteristics of species in the process of community reconstruction and restoration, considers heterogeneous habitats and interspecific relationships among species and can select positively related species pairs with strong adaptability (e.g., *Disporum uniflorum* and *Lepisorus fortunei*) to prevent interspecific. It is important for the restoration of degraded karst habitats in and around tiankeng to promote the restoration and stability of forest communities. However, interspecific associations are often influenced by complex factors, and the specific reasons for their formation are still difficult to explain. Therefore, the overall forest community, soils, topography, and climate should be taken into account to obtain a more comprehensive analysis and propose more thorough and feasible solutions in future studies.

5. Conclusions

This paper investigates the interspecific associations and community stability of different developmental stages and external forests of tiankeng major herbs in the Dashiwei Tiankeng Group, China. The study showed that: (1) the middle stage was the period of high interspecific competition and the greatest difference in resource use among herbs, and the ecological habit of herbs would change from sciophiles to hygrophyte to heliophiles and drought-enduring plants as the tiankeng developed. (2) The main herb species pairs of each developing tiankeng are weakly connected and independent, have not formed a close coupling relationship, and are in the stage of continuous improvement. (3) With the development of tiankeng, the herbaceous community will gradually tend to be stable but still in an unstable state, and the forest outside the tiankeng is relatively more stable than the herbaceous community inside the tiankeng. However, the tiankeng and the surrounding karst ecosystem are suffering from different degrees of anthropogenic disturbance, and it is necessary to increase the protection of the tiankeng ecological environment, and the interspecific relationship can be used to restore the surrounding degraded karst forest and maintain the stability of the tiankeng ecosystem.

Author Contributions: All authors made significant contributions to the manuscript: Y.X., M.C. and F.M. conceived, designed, and performed the experiments; L.Z. and G.B. analyzed the data and results; Z.Z. and P.C. contributed materials/analysis tools; Y.X. and M.C. are the main authors who developed and revised 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 earlier stage of tiankeng herbaceous plants.

Number	Species	Family	Genus
1	*Strobilanthes cusia*	Acanthaceae	*Strobilanthes*
2	*Elatostema brachyodontum*	Urticaceae	*Elatostema*
3	*Boehmeria macrophylla*	Urticaceae	*Boehmeria*
4	*Selaginella doederleinii*	Selaginellaceae	*Selaginella*
5	*Pilea pumila*	Urticaceae	*Pilea*
6	*Tetrastigma obtectum*	Vitaceae	*Tetrastigma*
7	*Pteris semipinnata*	Pteridaceae	*Pteris*
8	*Trigonotis leyeensis*	Boraginaceae	*Trigonotis*
9	*Urtica fissa E*	Urticaceae	*Urtica*
10	*Elatostema ficoides*	Urticaceae	*Elatostema*
11	*Ctenitis subglandulosa*	Dryopteridaceae	*Ctenitis*
12	*Ophiorrhiza japonica*	Rubiaceae	*Ophiorrhiza*
13	*Dryopteris varia*	Dryopteridaceae	*Dryopteris*
14	*Setaria viridis*	Poaceae	*Setaria*
15	*Polystichum fimbriatum*	Dryopteridaceae	*Polystichum*
16	*Sambucus javanica*	Adoxaceae	*Sambucus*
17	*Asparagus lycopodineus*	Asparagaceae	*Asparagus*
18	*Liriope spicata*	Asparagaceae	*Liriope*
19	*Leptochilus henryi*	Polypodiaceae	*Leptochilus*
20	*Polygonatum cyrtonema*	Asparagaceae	*Polygonatum*
21	*Pilea elliptilimba*	Urticaceae	*Pilea*
22	*Pleuropterus multiflorus*	Polygonaceae	*Pleuropterus*
23	*Achyranthes aspera*	Amaranthaceae	*Achyranthes*
24	*Gynura procumbens*	Asteraceae	*Gynura*
25	*Arthraxon hispidus*	Poaceae	*Arthraxon*
26	*Carex hattoriana*	Cyperaceae	*Carex*
27	*Paraphlomis javanica*	Lamiaceae	*Paraphlomis*
28	*Pteris esquirolii*	Pteridaceae	*Pteris*
29	*Miscanthus floridulus*	Poaceae	*Miscanthus*
30	*Polystichum balansae*	Dryopteridaceae	*Polystichum*
31	*Pternopetalum trichomanifolium*	Apiaceae	*Pternopetalum*
32	*Nanocnide lobata*	Urticaceae	*Nanocnide*
33	*Cissampelopsis spelaeicola*	Asteraceae	*Cissampelopsis*
34	*Solanum americanum*	Solanaceae	*Solanum*
35	*Impatiens chlorosepala*	Balsaminaceae	*Impatiens*
36	*Tubocapsicum anomalum*	Solanaceae	*Tubocapsicum*
37	*Pteris arisanensis*	Pteridaceae	*Pteris*
38	*Cyrtomium caryotideum*	Dryopteridaceae	*Cyrtomium*
39	*Elatostema coriaceifolium*	Urticaceae	*Elatostema*
40	*Viola davidii*	Violaceae	*Viola*
41	*Asarum caudigerum*	Aristolochiaceae	*Asarum*
42	*Cyrtomium fortunei*	Dryopteridaceae	*Cyrtomium*
43	*Strobilanthes atropurpurea*	Acanthaceae	*Strobilanthes*
44	*Lepisorus ovatus*	Polypodiaceae	*Lepisorus*
45	*Gynostemma pentaphyllum*	Cucurbitaceae	*Gynostemma*

Table A1. *Cont.*

Number	Species	Family	Genus
46	*Adiantum capillus-veneris*	Pteridaceae	*Adiantum*
47	*Clematis smilacifolia*	Ranunculaceae	*Clematis*
48	*Chrysosplenium hydrocotylifolium*	Saxifragaceae	*Chrysosplenium*
49	*Pseudocyclosorus esquirolii*	Thelypteridaceae	*Pseudocyclosorus*
50	*Rubia edgeworthii*	Rubiaceae	*Rubia*
51	*Diplazium griffithii*	Athyriaceae	*Diplazium*
52	*Dryopteris fuscipes*	Dryopteridaceae	*Dryopteris*
53	*Pollia japonica*	Commelinaceae	*Pollia*
54	*Dioscorea collettii*	Dioscoreaceae	*Dioscorea*
55	*Hydrocotyle nepalensis*	Araliaceae	*Hydrocotyle*
56	*Lepisorus fortunei*	Polypodiaceae	*Lepisorus*
57	*Pteris deltodon*	Pteridaceae	*Pteris*
58	*Reineckea carnea*	Asparagaceae	*Reineckea*
59	*Corydalis saxicola*	Papaveraceae	*Corydalis*

Species catalogs are sorted by importance value; same below.

Table A2. The middle stage of tiankeng herbaceous plants.

Number	Species	Family	Genus
1	*Strobilanthes cusia*	Acanthaceae	*Strobilanthes*
2	*Boehmeria macrophylla*	Urticaceae	*Boehmeria*
3	*Selaginella doederleinii*	Selaginellaceae	*Selaginella*
4	*Pilea pumila*	Urticaceae	*Pilea*
5	*Tetrastigma obtectum*	Vitaceae	*Tetrastigma*
6	*Urtica fissa E*	Urticaceae	*Urtica*
7	*Elatostema ficoides*	Urticaceae	*Elatostema*
8	*Ctenitis subglandulosa*	Dryopteridaceae	*Ctenitis*
9	*Ophiorrhiza japonica*	Rubiaceae	*Ophiorrhiza*
10	*Setaria viridis*	Poaceae	*Setaria*
11	*Sambucus javanica*	Adoxaceae	*Sambucus*
12	*Asparagus lycopodineus*	Asparagaceae	*Asparagus*
13	*Liriope spicata*	Asparagaceae	*Liriope*
14	*Leptochilus henryi*	Polypodiaceae	*Leptochilus*
15	*Polygonatum cyrtonema*	Asparagaceae	*Polygonatum*
16	*Arthraxon hispidus*	Poaceae	*Arthraxon*
17	*Carex hattoriana*	Cyperaceae	*Carex*
18	*Pteris esquirolii*	Pteridaceae	*Pteris*
19	*Miscanthus floridulus*	Poaceae	*Miscanthus*
20	*Polystichum balansae*	Dryopteridaceae	*Polystichum*
21	*Pteris arisanensis*	Pteridaceae	*Pteris*
22	*Cyrtomium caryotideum*	Dryopteridaceae	*Cyrtomium*
23	*Elatostema coriaceifolium*	Urticaceae	*Elatostema*
24	*Viola davidii*	Violaceae	*Viola*
25	*Asarum caudigerum*	Aristolochiaceae	*Asarum*
26	*Lepisorus ovatus*	Polypodiaceae	*Lepisorus*
27	*Gynostemma pentaphyllum*	Cucurbitaceae	*Gynostemma*
28	*Clematis smilacifolia*	Ranunculaceae	*Clematis*
29	*Rubia edgeworthii*	Rubiaceae	*Rubia*
30	*Lepisorus fortunei*	Polypodiaceae	*Lepisorus*
31	*Reineckea carnea*	Asparagaceae	*Reineckea*
32	*Pyrrosia calvata*	Polypodiaceae	*Pyrrosia*
33	*Strobilanthes dimorphotricha*	Acanthaceae	*Strobilanthes*
34	*Pilea plataniflora*	Urticaceae	*Pilea*
35	*Hemiboea pseudomagnibracteata*	Gesneriaceae	*Hemiboea*
36	*Pilea angulata*	Urticaceae	*Pilea*
37	*Elatostema oblongifolium*	Urticaceae	*Elatostema*
38	*Goniophlebium amoenum*	Polypodiaceae	*Goniophlebium*
39	*Asplenium wrightii*	Aspleniaceae	*Asplenium*

Table A2. *Cont.*

Number	Species	Family	Genus
40	*Selaginella moellendorffii*	Selaginellaceae	*Selaginella*
41	*Lemmaphyllum drymoglossoides*	Polypodiaceae	*Lemmaphyllum*
42	*Arisaema decipiens*	Araceae	*Arisaema*
43	*Asplenium tenuifolium*	Aspleniaceae	*Asplenium*
44	*Ophiopogon bodinieri*	Asparagaceae	*Ophiopogon*
45	*Coptis chinensis*	Ranunculaceae	*Coptis*
46	*Chloranthus henryi*	Chloranthaceae	*Chloranthus*
47	*Stemona tuberosa*	Stemonaceae	*Stemona*
48	*Polystichum tsus-simens*	Dryopteridaceae	*Polystichum*
49	*Paris polyphylla*	Melanthiaceae	*Paris*
50	*Ophiorrhiza cantonensis*	Rubiaceae	*Ophiorrhiza*
51	*Rhapis excelsa*	Poaceae	*Rhapis*
52	*Athyrium filix-femina*	Athyriaceae	*Athyrium*
53	*Pteridium revolutum*	Dennstaedtiaceae	*Pteridium*
54	*Paris fargesii*	Melanthiaceae	*Paris*
55	*Phedimus odontophyllus*	Crassulaceae	*Phedimus*
56	*Cymbidium tracyanum*	Orchidaceae	*Cymbidium*
57	*Ranunculus cantoniensis*	Ranunculaceae	*Ranunculus*
58	*Alpinia brevis*	Zingiberaceae	*Alpinia*
59	*Chrysanthemum lavandulifolium*	Asteraceae	*Chrysanthemum*
60	*Pronephrium gymnopteridifrons*	Thelypteridaceae	*Pronephrium*
61	*Glabrella longipes*	Gesneriaceae	*Glabrella*
62	*Causonis japonica*	Vitaceae	*Causonis*
63	*Asplenium saxicola*	Aspleniaceae	*Asplenium*
64	*Rohdea delavayi*	Asparagaceae	*Rohdea*
65	*Cymbidium serratum*	Orchidaceae	*Cymbidium*
66	*Lysionotus pauciflorus*	Gesneriaceae	*Lysionotus*

Table A3. The later stage of tiankeng herbaceous plants.

Number	Species	Family	Genus
1	*Strobilanthes cusia*	Acanthaceae	*Strobilanthes*
2	*Boehmeria macrophylla*	Urticaceae	*Boehmeria*
3	*Selaginella doederleinii*	Selaginellaceae	*Selaginella*
4	*Pilea pumila*	Urticaceae	*Pilea*
5	*Tetrastigma obtectum*	Vitaceae	*Tetrastigma*
6	*Urtica fissa E*	Urticaceae	*Urtica*
7	*Elatostema ficoides*	Urticaceae	*Elatostema*
8	*Ctenitis subglandulosa*	Dryopteridaceae	*Ctenitis*
9	*Ophiorrhiza japonica*	Rubiaceae	*Ophiorrhiza*
10	*Setaria viridis*	Poaceae	*Setaria*
11	*Sambucus javanica*	Adoxaceae	*Sambucus*
12	*Asparagus lycopodineus*	Asparagaceae	*Asparagus*
13	*Liriope spicata*	Asparagaceae	*Liriope*
14	*Leptochilus henryi*	Polypodiaceae	*Leptochilus*
15	*Pilea elliptilimba*	Urticaceae	*Pilea*
16	*Achyranthes aspera*	Amaranthaceae	*Achyranthes*
17	*Arthraxon hispidus*	Poaceae	*Arthraxon*
18	*Carex hattoriana*	Cyperaceae	*Carex*
19	*Paraphlomis javanica*	Lamiaceae	*Paraphlomis*
20	*Pteris esquirolii*	Pteridaceae	*Pteris*
21	*Polystichum balansae*	Dryopteridaceae	*Polystichum*
22	*Solanum americanum*	Solanaceae	*Solanum*
23	*Cyrtomium caryotideum*	Dryopteridaceae	*Cyrtomium*
24	*Elatostema coriaceifolium*	Urticaceae	*Elatostema*
25	*Asarum caudigerum*	Aristolochiaceae	*Asarum*
26	*Strobilanthes atropurpurea*	Acanthaceae	*Strobilanthes*
27	*Gynostemma pentaphyllum*	Cucurbitaceae	*Gynostemma*

Table A3. *Cont.*

Number	Species	Family	Genus
28	*Clematis smilacifolia*	Ranunculaceae	*Clematis*
29	*Rubia edgeworthii*	Rubiaceae	*Rubia*
30	*Dioscorea collettii*	Dioscoreaceae	*Dioscorea*
31	*Lepisorus fortunei*	Polypodiaceae	*Lepisorus*
32	*Pyrrosia calvata*	Polypodiaceae	*Pyrrosia*
33	*Strobilanthes dimorphotricha*	Acanthaceae	*Strobilanthes*
34	*Pilea plataniflora*	Urticaceae	*Pilea*
35	*Hemiboea pseudomagnibracteata*	Gesneriaceae	*Hemiboea*
36	*Pilea angulata*	Urticaceae	*Pilea*
37	*Elatostema oblongifolium*	Urticaceae	*Elatostema*
38	*Goniophlebium amoenum*	Polypodiaceae	*Goniophlebium*
39	*Selaginella moellendorffii*	Selaginellaceae	*Selaginella*
40	*Lemmaphyllum drymoglossoides*	Polypodiaceae	*Lemmaphyllum*
41	*Ophiopogon bodinieri*	Asparagaceae	*Ophiopogon*
42	*Stemona tuberosa*	Stemonaceae	*Stemona*
43	*Polystichum tsus-simens*	Dryopteridaceae	*Polystichum*
44	*Pteridium revolutum*	Dennstaedtiaceae	*Pteridium*
45	*Alpinia brevis*	Zingiberaceae	*Alpinia*
46	*Chrysanthemum lavandulifolium*	Asteraceae	*Chrysanthemum*
47	*Pronephrium gymnopteridifrons*	Thelypteridaceae	*Pronephrium*
48	*Causonis japonica*	Vitaceae	*Causonis*
49	*Phryma leptostachya* subsp. *asiatica*	Phrymaceae	*Phryma*
50	*Nephrolepis cordifolia*	Nephrolepidaceae	*Nephrolepis*
51	*Selaginella uncinata*	Selaginellaceae	*Selaginella*
52	*Houttuynia cordata*	Saururaceae	*Houttuynia*
53	*Cyclosorus parasiticus*	Thelypteridaceae	*Cyclosorus*
54	*Ainsliaea latifolia*	Asteraceae	*Ainsliaea*
55	*Dioscorea velutipes*	Dioscoreaceae	*Dioscorea*
56	*Lepisorus thunbergianus*	Polypodiaceae	*Lepisorus*
57	*Tropidia nipponica*	Orchidaceae	*Tropidia*
58	*Pteris multifida*	Pteridaceae	*Pteris*
59	*Isodon excisus*	Lamiaceae	*Isodon*
60	*Asplenium antrophyoides*	Aspleniaceae	*Asplenium*
61	*Piper sarmentosum*	Piperaceae	*Piper*
62	*Sanicula rubriflora*	Apiaceae	*Sanicula*
63	*Arisaema franchetianum*	Araceae	*Arisaema*
64	*Asplenium prolongatum*	Aspleniaceae	*Asplenium*
65	*Begonia palmata*	Begoniaceae	*Begonia*
66	*Aster trinervius*	Asteraceae	*Aster*
67	*Anisomeles indica*	Lamiaceae	*Anisomeles*
68	*Disporum uniflorum*	Colchicaceae	*Disporum*
69	*Blumea axillaris*	Asteraceae	*Blumea*
70	*Parathelypteris glanduligera*	Thelypteridaceae	*Parathelypteris*
71	*Asplenium trichomanes*	Aspleniaceae	*Asplenium*
72	*Hemiboea cavaleriei*	Gesneriaceae	*Hemiboea*
73	*Pachysandra axillaris*	Buxaceae	*Pachysandra*
74	*Anemone hupehensis*	Ranunculaceae	*Anemone*
75	*Lepisorus macrosphaerus*	Polypodiaceae	*Lepisorus*
76	*Drynaria roosii*	Polypodiaceae	*Drynaria*
77	*Chrysosplenium delavayi*	Saxifragaceae	*Chrysosplenium*
78	*Amorphophallus variabilis*	Araceae	*Amorphophallus*
79	*Scutellaria pekinensis*	Lamiaceae	*Scutellaria*
80	*Arisaema yunnanense*	Araceae	*Arisaema*

Table A4. The external forest of tiankeng herbaceous plants.

Number	Species	Family	Genus
1	*Ophiorrhiza japonica*	Rubiaceae	*Ophiorrhiza*
2	*Setaria viridis*	Poaceae	*Setaria*
3	*Asparagus lycopodineus*	Asparagaceae	*Asparagus*
4	*Liriope spicata*	Asparagaceae	*Liriope*
5	*Polygonatum cyrtonema*	Asparagaceae	*Polygonatum*
6	*Arthraxon hispidus*	Poaceae	*Arthraxon*
7	*Pteris esquirolii*	Pteridaceae	*Pteris*
8	*Miscanthus floridulus*	Poaceae	*Miscanthus*
9	*Polystichum balansae*	Dryopteridaceae	*Polystichum*
10	*Cyrtomium caryotideum*	Dryopteridaceae	*Cyrtomium*
11	*Elatostema coriaceifolium*	Urticaceae	*Elatostema*
12	*Asarum caudigerum*	Aristolochiaceae	*Asarum*
13	*Lepisorus ovatus*	Polypodiaceae	*Lepisorus*
14	*Gynostemma pentaphyllum*	Cucurbitaceae	*Gynostemma*
15	*Clematis smilacifolia*	Ranunculaceae	*Clematis*
16	*Rubia edgeworthii*	Rubiaceae	*Rubia*
17	*Lepisorus fortunei*	Polypodiaceae	*Lepisorus*
18	*Pyrrosia calvata*	Polypodiaceae	*Pyrrosia*
19	Pilea *plataniflora*	Urticaceae	*Pilea*
20	*Hemiboea pseudomagnibracteata*	Gesneriaceae	*Hemiboea*
21	*Selaginella moellendorffii*	Selaginellaceae	*Selaginella*
22	*Lemmaphyllum drymoglossoides*	Polypodiaceae	*Lemmaphyllum*
23	*Ophiopogon bodinieri*	Asparagaceae	*Ophiopogon*
24	*Stemona tuberosa*	Stemonaceae	*Stemona*
25	*Polystichum tsus-simens*	Dryopteridaceae	*Polystichum*
26	*Paris polyphylla*	Melanthiaceae	*Paris*
27	*Pteridium revolutum*	Dennstaedtiaceae	*Pteridium*
28	*Paris fargesii*	Melanthiaceae	*Paris*
29	*Chrysanthemum lavandulifolium*	Asteraceae	*Chrysanthemum*
30	*Pronephrium gymnopteridifrons*	Thelypteridaceae	*Pronephrium*
31	*Causonis japonica*	Vitaceae	*Causonis*
32	*Lysionotus pauciflorus*	Gesneriaceae	*Lysionotus*
33	*Phryma leptostachya* subsp. *asiatica*	Phrymaceae	*Phryma*
34	*Ainsliaea latifolia*	Asteraceae	*Ainsliaea*
35	*Dioscorea velutipes*	Dioscoreaceae	*Dioscorea*
36	*Pteris multifida*	Pteridaceae	*Pteris*
37	*Sanicula rubriflora*	Apiaceae	*Sanicula*
38	*Aster trinervius*	Asteraceae	*Aster*
39	*Disporum uniflorum*	Colchicaceae	*Disporum*
40	*Blumea axillaris*	Asteraceae	*Blumea*
41	*Pachysandra axillaris*	Buxaceae	*Pachysandra*
42	*Anemone hupehensis*	Ranunculaceae	*Anemone*
43	*Lepisorus macrosphaerus*	Polypodiaceae	*Lepisorus*
44	*Amorphophallus variabilis*	Araceae	*Amorphophallus*
45	*Arisaema yunnanense*	Araceae	*Arisaema*
46	*Salvia cavaleriei*	Lamiaceae	*Salvia*
47	*Cypripedium henryi*	Orchidaceae	*Cypripedium*
48	*Pinellia ternata*	Araceae	*Pinellia*
49	*Begonia grandis*	Begoniaceae	*Begonia*
50	*Liparis gigantea*	Orchidaceae	*Liparis*

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