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Tree Cover Improved the Species Diversity of Understory Spontaneous Herbs in a Small City

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Abstract: A large number of trees have been planted in built-up areas to improve the urban environment, but the effects of tree cover on spontaneous understory herbs are not yet well understood. This study surveyed spontaneous herbs in two kinds of habitats (habitats with and without tree cover) in the built-up area of the small city *Junlian* in Sichuan Province, China. A total of 222 species of spontaneous herbaceous plants in 180 genera of 71 families were recorded, including a vulnerable species and six species endemic to China. Although the overall species richness values were similar in the two kinds of habitat, the average species richness per quadrat of all plants, perennials, plants with the dwarf growth form, and animal-dispersed plants was significantly higher in the habitats with tree cover than in those without tree cover. The overall species association was significantly positive in the habitats with tree cover (VR = 1.51, $p < 0.05$) and neural (VR = 0.86) in the habitats without tree cover. Among the top 25 frequently recorded species in each kind of habitat, the species association of plants with the same trait combination type differed greatly in the two kinds of habitats. For the species association between annuals, only 13.33% of species pairs were significantly associated in the habitats with tree cover, while 22.22% of the species pairs were significantly negatively associated in the habitats without tree cover. For the species association between plants with tall growth forms, the proportion of significant positive associations in the habitats with tree cover was approximately twice than in the habitats without tree cover. For the species association between plants with the dwarf growth form, the proportion of negative associations in the habitats without tree cover was approximately twice that in the habitats with tree cover. Species with the same dispersal mode generally had a very low proportion of negative interspecific associations or a high proportion of positive interspecific associations in habitats unfavorable to their establishment. Our findings suggest that tree cover can improve the species richness of the spontaneous herbaceous species beneath them and profoundly influence interspecific coexistence relationships in a built-up area.

Keywords: species richness; species association; life form; growth form; dispersal mode

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1. Introduction

Tree cover profoundly alters the availability of understory resources, such as light, nutrients, and water [1–3], thus exerting strong environmental filtering effects on the composition of understory plants [2,4,5]. For example, Woods et al. observed a decrease in the understory diversity in an old growth, cool-temperate forest [6]. Tinya and Ódor reported that canopy light conditions are closely related to understory plant composition and diversity in a temperate, mixed forest [7]. However, Germany et al. observed no significant effects of tree layer richness on herbaceous layer richness [8]. Brudvig et al. reported that seed dispersal modes, rather than competition for light in the understory, limited the recovery of understory herbs [9].

Most studies on the effects of tree cover on understory herbs have focused on natural woodlands, and these issues are not yet well understood in urban environments. As a critical component of urban biodiversity, spontaneous plants have received increasing attention in recent years [10,11]. Spontaneous plants are widely distributed in various urban habitats [10,12], although most urban vegetation is artificially cultivated and managed. The light, soil and human activities in the understory space may differ greatly from those in open grasslands, thus profoundly affecting the composition of spontaneous plants.

Some researchers have noted the effect of tree cover on the composition of urban spontaneous plants. For example, Omar et al. found that spontaneous plants varied greatly within urban tree bases according to tree trunk diameter, solar radiation, urban tree species, and other environmental factors [13]. At the same time, Li et al. reported that the species richness of spontaneous plants under trees did not significantly differ from that on the lawn in Beijing Olympic Forest Park [14].

The effect of tree cover on the interspecific association of herbaceous layers is also worth studying. If environmental filtering dominates community construction, then species with similar functional traits will have a high co-occurrence probability [15,16]. Conversely, if competition dominates community construction, competitive exclusion will result in a low co-occurrence probability of species with similar functional traits [17]. Studying the effects of tree cover on the interspecific associations of spontaneous plants can help understand the community assemblage mechanisms of spontaneous plants in human-dominated landscapes.

Compared to large cities, small cities or towns have fewer studies on spontaneous plants. Although small cities cannot be understood in terms of population alone [18], it is generally accepted that small cities are urban agglomerations with a population of no more than 500,000 [19]. Small cities are limited in size, but they are numerous and widely distributed all around the world [20]. Most small cities have low population densities and close connections with the surrounding nature [21,22]. In addition, due to the lack of public revenues, most small cities have limited funds for public green space maintenance, which may leave more space for wildlife [23].

To explore the effects of tree cover on the species diversity and interspecific associations of spontaneous understory herbs, we investigated spontaneous herbs in habitats with and without tree cover in the small city *Junlian* in Sichuan Province, China. The study focused on the following questions: (1) Compared with habitats without tree cover, could habitats with tree cover have a significantly higher species richness of spontaneous herbs? (2) How do spontaneous herbs in habitats with tree cover differ from those without tree cover in terms of life form, dispersal mode, and growth form? (3) Does tree cover increase the co-occurrence probability of spontaneous understory herbs? This study could contribute to the understanding of the adaptive mechanisms of spontaneous herbs in built-up environments.

2. Study Site and Methods

2.1. Study Site

Junlian is a small city located at the southern edge of Sichuan Province, China (27°20′ N–28°14′ N, 104°17′ E–104°47′ N). With a subtropical humid monsoon climate zone, emphJunlian has an annual temperature of 17.6 °C and annual precipitation of 1111.7 mm. The built-up area of the city is approximately 30 km^2, with a population of 151,300 people (http://www.scjlx.gov.cn/) accessed on 21 March 2022. The natural vegetation type is evergreen broad-leaved forest (http://www.scjlx.gov.cn/) accessed on 21 March 2022.

In the urban green space, the woody layer is rich in plant species, mainly including *Cinnamomum camphora*, *Koelreuteria paniculata*, *Ailanthus altissima*,*Bauhinia purpurea*, *Photinia serrulata*, according to our investigation on urban green space. Except for street trees, trees are often accompanied by other vegetation, such as shrubs, hedges, or grasses beneath. Most of the ground under street trees is hard pavement. As a small and economically underdeveloped city, grassland mowing is infrequent. The location and overview of *Junlian* city is shown in Figure 1.

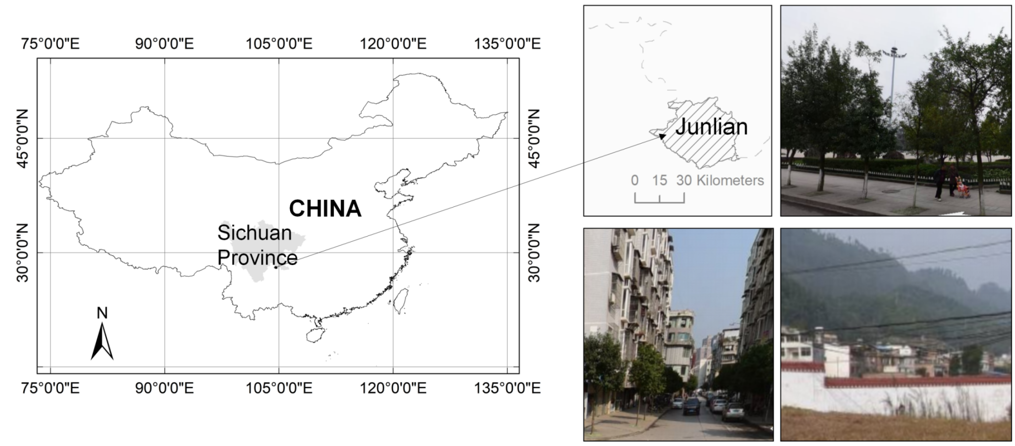

Figure 1. The location and overview of *Junlian* city, Sichuan Province, China.

2.2. Plant Survey and Identification

Spontaneous plants grow widely in soil, brick joints, and wall surfaces in *Junlian* city. To avoid the influence of the substrate, we selected habitats with soil as substrates, including urban forests, lawns, grassland, and vacant lands. We surveyed the species composition of spontaneous herbs in habitats with and without tree cover in the built-up area of *Junlian* during April–October 2020. Quadrats with tree cover were located underneath tree canopies, while the quadrats without tree cover were set in open fields at least 5 m away from tree canopies. All the quadrats were randomly positioned around the buildup area of *Junlian* city. We established 416 standard quadrats (1 m × 1 m) for each kind of habitat.

The study identified plants based on the online version of 'Flora of China' (http://www.cn-flora.ac.cn/) accessed on 28 March 2022. Chinese endemic or vulnerable plants were determined based on the book 'Diversity of Endemic Seed Plants of China and their Geographical Distribution' [24] and other literature [25,26].

All spontaneous herbs were classified into two life forms, perennial and annual (with a few biennials), according to their life span. Information about their life spans was acquired from the book 'Flora of China' (http://www.cn-flora.ac.cn/) accessed on 28 March 2022.

Based on the morphological characteristics and growth form of aboveground parts, spontaneous plants were classified into three major types: dwarf, tall, and liana. The dwarf growth form included the rosette form, procumbent form, branched form, and tussock form. The tall growth form included the erect form, partial rosette form, and pseudo-rosette form. The information about growth form was mainly acquired from the book 'Chinese Colored Weed Illustrated Book' [27] and 'Flora of China' (http://www.cn-flora.ac.cn/) accessed on 28 March 2022.

According to Kew (http://www.kew.org) accessed on 2 April 2022, TRY Plant Trait Database (http://www.try-db.org) accessed on 3 March 2022, and 'Flora of China' (http://www.cn-flora.ac.cn/) accessed on 28 March 2022, all spontaneous plants were classified into four dispersal modes: (i) unassisted-dispersed (e.g., gravitropic or ballistic); (ii) wind-dispersed (anemochorous) plants; (iii) animal-dispersed (zoochory, dispersed by birds, rats, insects, etc.); and (iv) other dispersed, including water-dispersed and dispersal—mode unknown.

A table of the trait data for all species identified in this study is presented in Supplementary Material Table S1.

2.3. Data Analysis

(1) Average species richness of each trait type

Average species richness of each trait type was estimated as follows:

$$R_m = \sum_{j=1}^{N} (richness_j^m)/N$$

$$PR_m = \sum_{j=1}^{N} (richness_j^m/richness_j)/N$$

where R_m is the average species richness of plants with trait type m. PR_m is the average species richness proportion of plants with trait type m. N is the total number of quadrats in habitats with/without tree cover (N = 416), $richness_j^m$ denotes the richness of species with trait type m in $quadrat_{j,}$ $richness_j$ donates the species richness in $quadrat_j$

The differences between R_m in the habitat with and without tree cover were tested (independent sample t tests). If a species had two (or more) dispersal modes, then the species were counted separately in the species richness of the corresponding dispersal mode.

(2) Frequency

Frequency of species i was estimated as follows:

$$Freq_i = \frac{n_i}{N}$$

where n_i represents the number of quadrats in which species i occurred, N is the total number of quadrats (N = 416).

(3) Species association

We used the variance ratio (VR) test to examine the overall association [28]. For the top 25 frequently recorded species, the association coefficient (AC) index was used to measure the pairwise species association. The significance of the AC index was examined using a *Chi-square* test. Overall species association and species pairwise species association were calculated using *spaa* package of R language 4.0.3 version [29]. The details about these indices are described in the help file of the package.

According to the life form, growth form, or dispersal mode of each species, a pair of species was marked as '$pair_{annual*annual}$', '$pair_{tall*dwarf}$', and '$pair_{animal*animal}$'. Then, we calculated the proportion of significantly positive, negative, and neutral associations of each trait combination type.

3. Results

3.1. Species Composition

3.1.1. Species Richness

A total of 222 species in 180 genera of 71 families of spontaneous herbaceous plants were recorded, mainly perennials, totaling 135 species (60.81%) (Table 1). Asteraceae plants were the most abundant, with 39 species, followed by Graminaceae (19 species), Lamiaceae (11 species), Polygonaceae (11 species). *Oxalis corniculata* was the most frequently recorded species, with a frequency of 32.21%, followed by *Alternanthera sessilis* (28.13%) and *Plantago asiatica* (20.19%).

In the habitats with and without tree cover, we recorded 177 species in 150 genera of 64 families and 172 species in 144 genera of 60 families, respectively. The average species richness per quadrat in the habitats with tree cover (6.37 ± 0.14) was significantly higher than that in the habitats without tree cover (5.08 ± 0.10) (Figure 2a).

Table 1. Species richness of each functional trait type in the two kinds of habitats.

Trait Type	Overall			Top 25 Species	
	Habitat 1	Habitat 2	Habitat 1 and 2	Habitat 1	Habitat 2
Total	177	172	222	25	25
Life-form					
Perennial	105 (59.32%)	104 (60.47%)	135 (60.81%)	15 (60.00%)	16 (64.00%)
Annual	72 (40.68%)	68 (39.53%)	87 (39.19%)	10 (40.00%)	9 (36.00%)
Growth-form					
Dwarf	73 (41.24%)	66 (38.37%)	86 (38.84%)	11 (44.00%)	12 (48.00%)
Tall	86 (48.59%)	95 (55.23%)	117 (52.70%)	13 (52.00%)	13 (52.00%)
Liana	18 (10.17%)	11 (6.40%)	19 (8.56%)	1 (4.00%)	0 (0.00%)
Dispersal mode					
Animal	60 (33.90%)	61 (35.47%)	76 (34.23%)	11 (44.00%)	8 (32.00%)
Wind	55 (31.07%)	50 (29.07%)	67 (30.18%)	6 (24.00%)	12 (48.00%)
Unassisted	62 (35.03%)	56 (32.56%)	78 (35.14%)	8 (24.00%)	5 (20.00%)
Other	3 (1.69%)	5 (2.91%)	5 (2.25%)		

Habitat 1—habitat with tree cover; Habitat 2—habitat without tree cover.

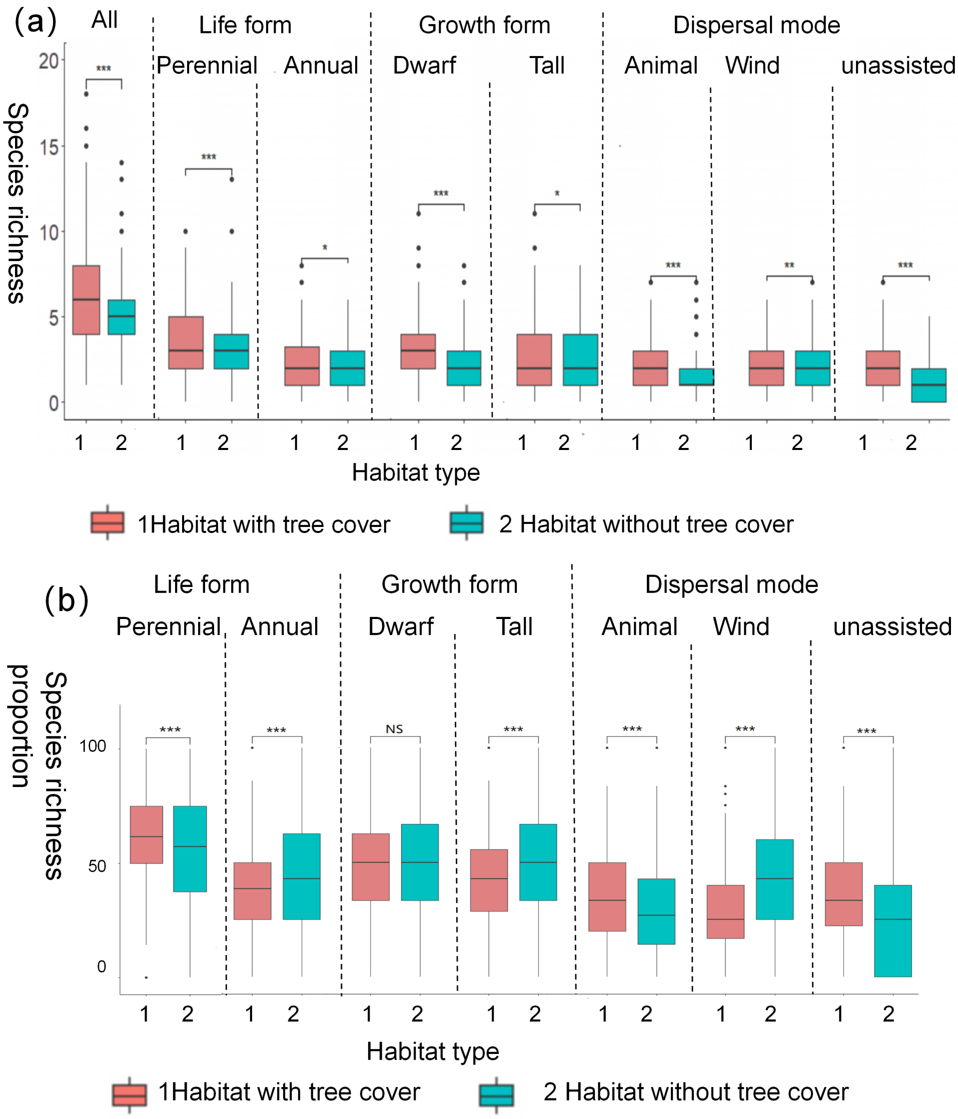

Figure 2. Difference in the species richness (proportion) between habitats with and without tree cover (**a**) species richness. (**b**) species richness proportion.(Characters (NS) indicate no significant difference. Asterisks (*) indicate significance at $p < 0.05$, asterisks (**) indicate significance at $p < 0.01$, asterisks (***) indicate significance at $p < 0.001$.

3.1.2. Vulnerable and Endemic Species

A vulnerable species (*Asarum sieboldii*) was recorded in both kinds of habitats, with a total frequency of three. Four species endemic to China (*Polygonum runcinatum var. Sinense*, *Selaginella uncinat*, *Aristolochia tubiflora*, *Carex schneideri*) were recorded with a total frequency of 34 in the habitats with tree cover. There were also four species endemic to China (*P. runcinatum var.* Sinense, *S. uncinata*, *Impatiens davidi*, and *Cyrtomium caryotideum*) in the habitat without tree cover, but the total frequency was only nine.

3.2. Species Richness of Each Functional Trait Type

3.2.1. Perennial/Annual

Perennial species were dominant in the habitats with and without tree cover, with similar species richness values of 105 species and 104 species, respectively, (Table 1).

However, the $R_{perennial}$ in the habitats with tree cover was significantly higher than that without tree cover, at 3.88 ± 0.10 species for the former and 2.85 ± 0.08 species for the latter (Figure 2a). The $PR_{perennial}$ in the habitats with tree cover reached 62.46 ± 0.98%, which was also significantly higher than that without tree cover (55.16 ± 1.26%) (Figure 2b).

For annual species, R_{annual} was also significantly higher in the habitats with tree cover than in those without tree cover(Figure 2a), but the PR_{annual} in habitats with tree cover (37.54 ± 0.98%) was significantly less than that in habitats without tree cover (44.84 ± 1.26%) (Figure 2b).

3.2.2. Tall/Dwarf Growth Forms

More species with the dwarf growth form were recorded in the habitats with tree cover than in the habitats without tree cover, at 73 species for the former and 66 species for the latter. The R_{dwarf} in the habitats with tree cover (3.17 ± 0.09 species) was also significantly higher than that in the habitats without tree cover (2.47 ± 0.07 species) (Figure 2a).

Fewer species with tall growth forms were recorded in habitats with tree cover than in habitats without tree cover, with species richness values of 86 and 95, respectively. However, the R_{tall} (2.74 ± 0.09 species) in the habitats with tree cover was significantly higher than that in the habitats without tree cover (2.50 ± 0.07 species) (Figure 2a), while the PR_{tall} in the habitats with tree cover (42.18 ± 8.88%) was significantly less than that in those without tree cover (48.44 ± 7.39%) (Figure 2b).

3.2.3. Dispersal Mode

The species richness of animal-dispersed species in the habitats with tree cover was 60, which was quite close to that without tree cover (61 species). However, the $R_{animal\text{-}dispersed}$ in the habitats with tree cover (2.25 ± 0.07 species) was significantly higher than that in those without tree cover (1.50 ± 0.06 species) (Figure 2a), as was the $PR_{animal\text{-}dispersed}$ (Figure 2b).

The species richness of the wind-dispersed species in the habitats with tree cover was 55 species, which was more than that in those without tree cover (50 species). However, $R_{wind\text{-}dispersed}$ in the habitats with tree cover (1.85 ± 0.07 species) was significantly less than that in those without tree cover (2.16 ± 0.07 species) (Figure 2a), as was the $PR_{wind\text{-}dispersed}$ (Figure 2b).

The species richness of the unassisted dispersed species in the habitats with tree cover was 62, which was more than that in those without tree cover (56 species). The $R_{unassisted\text{-}dispersed}$ in the habitats with tree cover (2.15 ± 0.07 species) was also significantly higher than that in those without tree cover (1.34 ± 0.05 species) (Figure 2a), as was the $PR_{unassisted\text{-}dispersed}$ (Figure 2b).

3.3. Species Association in Habitats with/without Tree Cover

3.3.1. Overview of Species Associations

The overall species association of all spontaneous herbs was significantly positive in the habitats with tree cover (VR = 1.51, $p < 0.05$) and neutral (VR = 0.86) in the habitats without tree cover. Among the 300 species pairs composed of the top 25 species in the habitats with and without tree cover, 27% and 25% of the pairs were significantly positively or negatively associated, respectively.

3.3.2. Paired Species Associations of Each Life-Form Combination

The life-form compositions of the top 25 species in the two kinds of habitats were quite similar. More specifically, there were 15 and 16 species of perennials and ten and nine species of annuals in the habitats with and without tree cover, respectively, (Table 1).

In the habitats with tree cover, only 13.33% of the $\text{pair}_{\text{annual*annual}}$ was significantly associated, and most associations were positive. In the habitats without tree cover, 30.55% of the $\text{pair}_{\text{annual*annual}}$ were significantly associated, and the majority of them were negative (22.22%) (Figure 3).

In the habitats with and without tree cover, 35.24% and 22.50% of the $\text{pair}_{\text{perennial*perennial}}$ were significantly associated, respectively. The proportion of significant positive associations was greater than the proportion of negative associations in both kinds of habitats (Figure 3).

For the $\text{pair}_{\text{perennial*annual,}}$ the proportion of significant association was close in the two kinds of habitats, and both of them were majorly positive (Figure 3).

Figure 3. Proportions of neutrally and significantly positively or negatively associated species pairs with each functional trait combination type. The area of a block represents the proportion of species pairs that were neutrally and significantly positively or negatively associated. There was only one liana species in the top 25 species, so the species pairs involving liana species were omitted.

3.3.3. Paired Species Association of Each Growth-Form Combination

The species richness of plants with tall growth forms was 13 for the top 25 species in both kinds of habitats. The species richness values of the dwarf growth-form plant species among the top 25 species were similar, at 11 for the habitats with tree cover and 12 for the habitats without tree cover (Table 1).

For the $\text{pair}_{\text{dwarf*dwarf}}$ in the habitats with and without tree cover, significant associations accounted for 23.64% and 31.82%, respectively. However, the proportion of negative associations among $\text{pair}_{\text{dwarf*dwarf}}$ in the habitats without tree cover was approximately twice than those with tree cover (Figure 3).

For the $\text{pair}_{\text{tall*tall}}$ in the habitats with and without tree cover, significant associations accounted for 33.33% and 19.23%, respectively, and the proportion of significant positive associations among $\text{pair}_{\text{tall*tall}}$ in the habitats with tree cover was approximately twice that of those without tree cover (Figure 3).

For the $pair_{dwarf*dwarf}$ in the habitats with and without tree cover, the proportions of significant associations were similar, and each was mostly positive (Figure 3).

3.3.4. Paired Species Association of Each Dispersal Mode Combination

Among the top 25 species in each kind of habitat, the species richness of the animal-dispersed plants in the habitats with tree cover was much greater than those without tree cover, at 11 for the former and 7 for the latter (Table 1). For the $pair_{animal*animal}$, the proportions of significant associations were similar between the two kinds of habitats. However, the proportion of significantly negative and positive associations was approximately equal in the habitats with tree cover, while the proportion of significantly positive associations was much greater than that of the significantly negative associations in the habitats without tree cover (23.81% and 4.76%, respectively) (Figure 3).

Among the top 25 species in each kind of habitat, wind-dispersed species in the habitats with tree cover were much fewer than those in the habitats without tree cover, at 6 for the former and 12 for the latter (Table 1). In the habitats with tree cover, only 20% of the $pair_{wind*wind}$ were significantly associated, and all of them were positive. In the habitats without tree cover, 40.91% of the $pair_{wind*wind}$ were significantly associated, and the proportion of significantly negative and positive associations did not differ substantially (Figure 3).

Among the top 25 species in each kind of habitat, the species richness values of the unassisted-dispersed plants were similar, at eight for the former and six for the latter (Table 1). In the habitats with tree cover, only 14.29% of the $pair_{unassisted*unassisted}$ were significantly associated. In the habitats without tree cover, 33.33% of the $pair_{unassisted*unassisted}$ were significantly associated. Among the significant associations of $_{unassisted*unassisted}$, positive associations were dominant in both kinds of habitats (Figure 3).

For $pair_{animal*unassisted}$ or $pair_{wind*animal}$, the proportion of neutral, positive, or negative associations did not differ substantially in the two kinds of habitats. $Pair_{wind*unassisted}$ had a much higher proportion of positive associations in the habitats with tree cover than in those without tree cover, at 20.83% for the former and 1.39% for the latter (Figure 3).

4. Discussion

Most urban spontaneous plants are widespread species that can survive in a variety of urban habitats [12,30]. Spontaneous plants often have high composition similarity across cities, such as the convergence of the structure, environment, and human activity of urban ecosystems [31–33]. For example, Wheelerd et al. reported that spontaneous vegetation from residential lawns was highly similar in different regions of the United States [34]. As a result, urban spontaneous plants are often regarded as weeds and have low biodiversity conservation value. However, urban habitats are highly fragmented and heterogeneous and may thus provide space for sensitive species with special environmental requirements [35–37]. In a floristic survey in northwestern Munich, Germany, it was found that urban environments may provide unique ecological niches for threatened species that are not adapted to calcareous traditional grasslands [38]. *Junlian* is located in the mountainous region of southwestern China, with an undeveloped economy, low population density, and well-preserved natural vegetation in the surrounding area, which provides a rich seed pool for spontaneous plants. We found that the small *Junlian* city had a rich diversity of spontaneous plants in its built-up area, including one vulnerable species and six endemic species to China. In the natural environment, tree cover might reduce understory diversity by competing for resources [7]. In our study, the habitats with tree cover had higher species richness per quadrat than those without tree cover. Moreover, the frequency of species endemic to China in the habitats with tree cover was much greater than that in the habitats without tree cover. The findings suggested that tree cover can be conducive to spontaneous plants in built-up areas. The following reasons might explain the findings.

First, habitats with tree cover are more stable and less disturbed, and disturbance levels significantly influence plant diversity in urban grasslands [39]. Generally, in comparison to annual plants, perennials require more stability [40]. In our study, the species richness and species proportions of perennials were significantly higher in the habitats with tree cover than in the habitats without tree cover, indicating that former habitats are more stable. In *Junlian* city, most trees are accompanied by various plants, such as shrubs, hedges, or grasses, beneath them. These plants could limit various outdoor activities under tree canopy, thus decreasing the trampling and other kinds of anthropogenic disturbance and provide stable habitats for the diverse spontaneous plants.

Second, the tree canopy may have attracted animals [41], increasing the species richness of the animal-dispersed plants beneath. In built-up areas, habitats for animals are very scarce. Tree crowns can attract birds, insects, and other animals to settle or forage [42,43], thus facilitating the colonization of animal-dispersed plants. In our study, the species richness and proportion of animal-dispersed plants were significantly higher in the habitats with tree cover than in those without tree cover.

Although urban open grasslands can also provide foraging sites for birds or insects [44,45], they might be more susceptible to anthropogenic disturbance than understory habitats. Compared with the habitats with tree cover, those without tree cover contained fewer animal-dispersed species.

Third, microhabitat heterogeneity in habitats with tree cover may be higher, which can provide various opportunities for different plants. In urban greening, tree species composition, spatial configuration, and community structure often vary greatly from site to site [41], resulting in diverse microhabitats for spontaneous plants beneath [13,46]. For example, Omar et al. reported that spontaneous plants varied greatly within urban tree bases according to tree trunk diameter, solar radiation, urban tree species, and other environmental factors [13].

One exception was that, in this study, the species richness of wind-dispersed plants per quadrat in understory habitats was lower than that in the habitats without tree cover, and only six species of wind-dispersed plants were found in the top 25 frequently recorded species. Tree cover reduces wind speed in the surrounding microhabitats [47,48], thus discouraging colonization by wind-dispersed plants. In open grasslands or lawns, higher wind speeds could be beneficial for the colonization of wind-dispersed plants.

The interspecific association also differed greatly in two kinds of habitats. The overall species association of spontaneous herbs was significantly positive in the habitats with tree cover and neural in the habitats without tree cover. This result suggests that the overall probability of plant coexistence was higher in the habitats with tree cover than in those without tree cover. Moreover, the paired species association patterns differed greatly between the two habitats.

In the habitats with tree cover, $pair_{annual*annual}$ was predominantly neutral, suggesting that stochastic processes might dominate the coexistence of perennial plants. In contrast, 22.22% of $pair_{annual*annual}$ were negatively associated in the habitats without tree cover, indicating that there might be intense competition among annual plants in the habitats without tree cover. For $pair_{perennial*perennial}$, both positive and negative associations were common in two kinds of habitats with tree cover, suggesting complex interspecific interactions between perennials. Plant growth form is a simple but important trait correlated with many life functions, such as competitive ability, reproduction allocation, and environmental adaptation strategies [49,50]. Herbs with high growth forms often require a well-lit environment [51]. The canopy layer reduces the understory light intensity and spectral quality [52,53], which might give species with dwarf growth forms an advantage over species with tall growth forms. Although species with the dwarf growth form were dominant in the habitats with tree cover, negative associations among the top 25 species were rare, indicating that resource deficiency might not necessarily lead to intensive competition between species with the dwarf growth form. At the same time, the higher proportion of negative associations among the species with the dwarf growth form suggested increased interspecific competition in the habitats without tree cover.

For tall-growing plants, species associations among them were predominantly neutral in the habitats without tree cover where the light was adequate. In the habitats with tree cover, the increase in positive associations indicating canopy cover might promote the concentration of plants with tall growth forms in well-lit understory habitats, such as gaps in canopy shading.

Species with the same dispersal mode generally had a very low proportion of negative interspecific associations or a high proportion of positive interspecific associations in habitats unfavorable for establishment. For example, in the habitats without tree cover where there were only seven animal-dispersed species among the top 25 species, the negatively associated $pair_{animal*animal}$ was as low as 4.76%. Similarly, in the habitats with tree cover where there were only six wind-dispersed species among the top 25 species, no negative association was detected for $pair_{wind*wind}$. There were only 6 species of unassisted-dispersed plants among the top 25 species in the habitats without tree cover, but the 26.67% $pair_{unassisted*unassisted}$ was positively associated. This finding may indicate that the competition between species with the same dispersal modes was limited in adverse habitats.

Species pairs composed of different trait types generally had a lower proportion of negative associations and a higher proportion of positive associations in the habitats with tree cover than in those without tree cover, except for $pair_{animal*unassisted}$ and $pair_{wind*animal}$. This result indicates that habitats with tree cover might be more favorable for the coexistence of species with different dispersal modes than habitats without tree cover.

It has been suggested that, if environmental filtering dominates community construction, then species with similar functional traits will have a high co-occurrence probability [15,16]. Conversely, if competition dominates community construction, competitive exclusion will result in a low co-occurrence probability of species with similar functional traits [17]. Our study indicated that the functional trait type might mediate the effects of environmental filtering and interspecific competition on the co-occurrence of species with similar functional traits. The microenvironment could not only affect species colonization but also interspecific relationships. Our study suggested that cultivated trees in urban environments could directly or indirectly influence the composition and interspecific relationships of spontaneous plants. The interactions between cultivated and spontaneous plants should not be neglected in shaping urban biodiversity patterns. In *Junlian* city, the tree cover may help to create relatively stable microhabitats under the canopy, thus contributing to spontaneous plant diversity, interspecific coexistence and the succession of spontaneous plant communities from annuals to perennials. For small cities with limited funds for green space management, increasing tree cover and reducing grass mowing will not only help save public funds, but also contribute to urban biodiversity conservation.

5. Conclusions

As a small city, *Junlian* has a rich diversity of spontaneous plants in its built-up area with one vulnerable species and eight species endemic to China. Although the overall species richness was similar in the habitats with and without tree cover, the average species richness per quadrat was significantly higher in the habitats with tree cover than that without tree cover. Compared to the habitats without tree cover, the habitats with tree cover were more favorable for perennial, dwarf-growing, and animal-dispersed spontaneous plants. Although tree cover increased the overall co-occurrence probability of understory spontaneous herbs, the paired species associations with different functional trait combinations differed a lot between the two kinds of habitats. Our findings suggested that tree cover increased the diversity of spontaneous understory herbs, but whether it could increase the probability of coexistence among paired-species depended on the functional trait type of the species.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f13081310/s1 Table S1: The spontaneous herbaceous plants recorded in *Julian* city.

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Data Availability Statement: The following is available online at http://map.baidu.com/ (accessed on 21 October 2021). Figure 1. The location and overview of *Junlian* city, Sichuan Provience, China.

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