

Spider Diversity on Orchid Island, Taiwan: A Comparison between Habitats Receiving Different Degrees of Human Disturbance

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Kuan-Chou Chen and I-Min Tso (2004) Spider diversity on Orchid Island, Taiwan: A comparison between habitats receiving different degrees of human disturbance. *Zoological Studies* 43(3): 598-611. Tropical forests exhibit very high spider diversity, but most related studies have examined a particular functional group or layer of the habitat and few have assessed the impacts of disturbance on tropical Araneae diversity. Orchid I. is 92 km off the southeastern coast of Taiwan, and its forests are the northernmost tropical forests in East Asia. In this study, the spider diversity was compared in 4 types of habitats with different degrees of human disturbances on this island. Habitat types examined in this study included primary forest, cultivated woodlands with a small degree of disturbance, firewood plantations with an intermediate level of disturbance, and grasslands generated from the clear-cutting of forests. We used 2 replicates for all habitat types, each containing four 5 x 5 m sample plots. Spiders from the ground, understory shrubs, and canopy were collected to obtain a comprehensive representation of diversity from all microhabitats in the sample plots. From the 1718 adult specimens obtained, 123 species from 19 families were identified. The abundance was the highest in the primary forest and lowest in the grassland plots. Plots in the 4 habitat types did not differ in Margalef species richness, Shannon-Weaver function, or Simpson index. However, plots in the primary forest had significantly lower evenness due to the high relative abundance of dominant orb weaver species. Results of a UPGMA analysis using pair-wise Euclidean distances showed that the sample plots could be clustered into 4 distinct groups, indicating that the composition of spiders among habitat types considerably differed. Plots in the primary forest, cultivated woodland, and firewood plantation habitats were dominated by space web builders and orb weavers, while those in the grasslands contained a much-higher proportion of wandering sheet weavers and ground runners. Results of this study suggest that various forest management activities conducted by the indigenous Yami people seemed to have increased the habitat heterogeneity of Orchid I., thus maintaining a high diversity of spiders. <http://www.sinica.edu.tw/zool/zoolstud/43.3/598.pdf>

Key words: Biodiversity, Araneae, Lanyu, Yami people.

Although spider diversity in temperate regions has been well studied, tropical areas have received relatively little investigation. Spiders are the most-diverse and abundant invertebrate predators in terrestrial ecosystems (Wise 1993, Nyffeler 2000), foraging primarily on insects. Because of their high abundance and insectivorous foraging, spiders are considered the major agent controlling insect communities in terrestrial ecosystems (Riechert and Lockley 1984, Nyffeler and Benz 1987, Marc et al. 1999, Nyffeler 2000). These characteristics make spiders a good indica-

tor for comparing the biodiversity of various environments and for assessing the effects of disturbances on biodiversity (Clauseu 1986, Churchill 1997 1998, Topping and Lövei 1997, Maelfait and Hendrickx 1998, Marc et al. 1999, Riecken 1999). However, most studies have focused on agricultural ecosystems in temperate areas such as the US and Europe (Young and Edward 1990, Carter and Rypstra 1995, Marc et al. 1999, Tóth and Kiss 1999, Uetz et al. 1999), while studies of spider diversity in tropical areas are rare. Moreover, although the effects of various disturbances on

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spider diversity are well known in temperate regions (Bultman and Uetz 1982, Maelfait and Keer 1990, Gibson et al. 1992, Pettersson 1996, Topping and Lövei 1997, Zulka et al. 1997, Feber et al. 1998, Downie et al. 1999), studies on the effects of environmental impacts on tropical fauna are extremely rare. Robinson and Robinson (1974) studied the abundance and composition of web spiders in a secondary forest in Wau, New Guinea and found that orb-weavers accounted for more than 80% of specimens sampled. Less-complex forest undergrowth and the concomitant lack of appropriate web sites for non-orb-weavers might have been responsible for such results. Lubin (1978) studied the web spider diversity in Barro Colorado I., Panama and found a lower spider abundance during dry seasons. Lubin (1978) suggested that the observed temporal abundance variation might result from seasonal changes in humidity and prey availability. Greenstone (1984) conducted a similar study in Costa Rica and found that vegetation structure but not prey availability significantly determined the diversity of web spiders. Pfeiffer examined the diversity of ground spiders (1996a) and arboreal spiders (1996b) in Puerto Rico. Compared with the ground spider abundance of temperate forests, that in the Puerto Rican rain forests was significantly lower due to a relatively thinner litter layer. In addition to population dynamics, the vertical distribution, and trophic interactions of arboreal web spiders, Pfeiffer (1996b) also studied the impacts of hurricanes on weaver diversity. Accumulation of foliage and branches shortly after Hurricane Hugo greatly increased the density of a dominant orb-weaving species but caused declines in other species. Using canopy fogging, Russel-Smith and Stork (1994) compared the abundance and diversity of canopy spiders at different elevations in Sulawesi and found that both were positively correlated with elevation. This short review demonstrates that most studies examined a particular functional group or layer of the habitat, and few of them focused on the impacts of disturbances on tropical Araneae diversity.

Orchid I. (Lanyu in Chinese) is a tropical island 92 km off the southeastern coast of Taiwan. The forests on Orchid I. are the northernmost tropical forests in East Asia (Chen et al. 1982). The aboriginals inhabiting this island are Yami people of Malay-Polynesian origin who migrated from the Batan I., Philippines about 800 years ago (de Beauclair 1959). Unlike other tribes in Taiwan, the

culture and resource utilization by the Yami people are closely associated with the sea (Wang 1984). However, they also carry out several forms of land utilization, primarily in the island's forests. Some forests near villages have been clear-cut to provide land for the planting of yam or taro. Small-scale logging also occurs in the forests to obtain materials for canoe and hut construction and for firewood. All of these activities generate various degrees of disturbance to the forest ecosystem. Recently, Tso and Tanikawa (2000) and Yoshida et al. (1998 2000) conducted preliminary taxonomic studies on web spider diversity on Orchid I. However, so far there has been no information about how the traditional activities of the Yami people affect the spider diversity of this island. In this study, the impacts of the Yami people's forest utilization practices on spider diversity were assessed by comparing spider diversities in habitats receiving various degrees of disturbance. Spiders from the ground litter up to 10 m in the canopy were systematically collected to obtain a comprehensive determination of spider diversity and the impact of various levels of disturbance.

MATERIALS AND METHODS

Orchid Island's tropical forests

Orchid I. is a tropical island 92 km off the southeast coast of Taiwan (121°32'E, 22°03'N) with a total area of about 45.74 km² (Chen et al. 1982). It was formed by volcanic activity and is located on the Luzon sill between Taiwan and the Philippines (Richard et al. 1986). On this small island there are 10 peaks with elevations over 400 m, two of which are higher than 500 m. Most areas on the island are steep mountainous regions, with patches of alluvial plains scattered along the coast. The features of its climate are high temperatures (average, 22.4°C) and plentiful rainfall (annual rainfall, > 2600 mm). Between May and Sept. the daily mean temperature exceeds 25°C, and during this time typhoons frequently occur (Wang 1984). Orchid I. receives strong winds year round, especially during the winter months. Due to the impact of the strong winds, forests on this island are somewhat different from a typical lowland tropical rain forest. They are classified as montane rain forests and are the northernmost tropical forests in East Asia (Chen et al. 1982).

Descriptions of the 4 types of habitats examined

In this study we selected 4 types of habitats which are typical of this island (Fig. 1). The 1st habitat type is primary forest. Most mountainous areas are steep, and access is difficult, so these areas are still covered by various types of primary forests. Currently, around 80% of Orchid I. is covered by primary forests (Chen et al. 1982). In addition, for certain cultural reasons, Yami people avoid some alluvial forests, and those areas also remain relatively undisturbed. The 2nd type is cultivated woodlands, which are mixtures of primary and secondary growth. Within this type of forest, the Yami people conduct small-scale logging with primitive tools to obtain materials for hut and

canoe construction. Furthermore, they frequently clear the undergrowth of forests to promote the growth of planted tree seedlings. Logging is a rare event in cultivated woodlands; a planted tree is usually logged after 10 to 20 years of growth. Compared with levels of disturbance received by the subsequent 2 habitat types, that of this habitat is relatively light. The 3rd type is the firewood plantation used for fuel collection. Yami people deliberately cultivate fast-growing tree species on land formerly used for yam or taro plantations and frequently harvest the wood before it is fully grown. Usually, Yami people only harvest the branches of the planted trees and leave the main trunk, creating a relatively open canopy in firewood plantations. After 3~5 yr of use as firewood plantations, these lands are clear-cut and burned to create

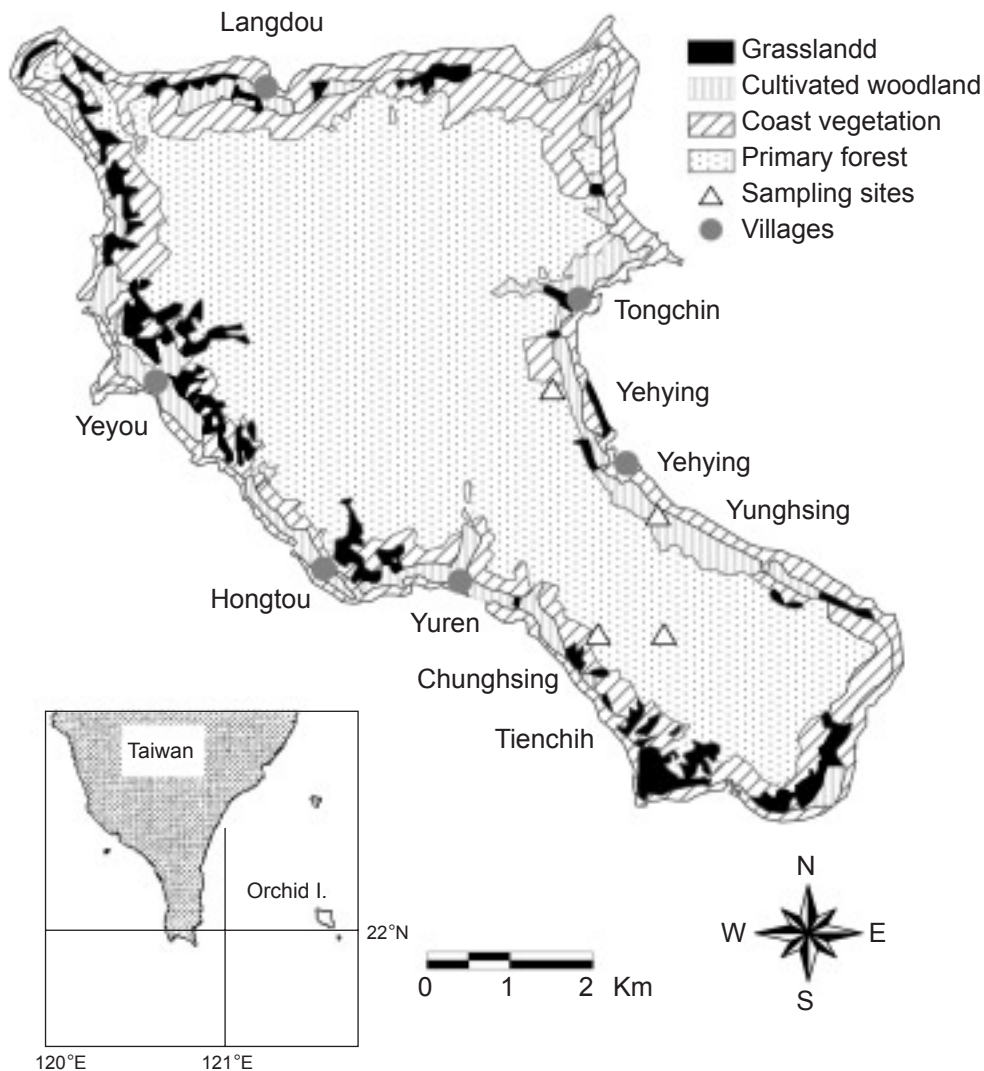


Fig. 1. Map of Orchid I. showing the locations of the study sites. (modified from Chen et al. 1982)

land for yam or taro plantations. Therefore, firewood plantations are purely secondary growth and receive an intermediate level of disturbance. The scale of habitat alteration achieved by the Yami people in forests is quite limited because cultivated woodlands and firewood plantations are maintained and operated by a few male members of families in the non-fishing season. Therefore, the size of these habitat types is rather small, and the total area of cultivated woodlands and firewood plantations combined is less than 10% of the total area (Chen et al. 1982). The 4th type is grassland, which is usually located near forest margins and is generated from clear-cutting of firewood plantations. About 6% of the land on Orchid I. is grassland (Chen et al. 1982). Grasslands are used for yam/taro plantations or for grazing and are burned every 2~3 yr. Therefore, among the habitats examined in this study, grasslands receive the highest level of disturbance. Each of these 4 habitats had 2 replicates located either at Yonsing Farm, Yeying Village, Chungshing Farm, or Tienchi (Fig. 1). In each replicate, four 5 x 5 m sample plots were established, and in the center of each plot, a pitfall trap was set up to collect ground-active spiders. The plant compositions of these 4 habitat types are given as follows.

(1) Primary forest

Both replicates are located at Tienchi. These 2 replicates are quite similar in plant composition and vegetation structure. *Bischofia javanica* and *Ficus benjamina* are the predominant trees in the 1st layer of the forest, and the canopy height is approximately 15~25 m. Growing in these trees are numerous epiphytes and vines. *Dysoxylum cumingianum* is the dominant tree in the 2nd layer of forest, and the canopy height is about 5~10 m. The primary forest sites are relatively undisturbed, and thus well-developed bushes composed of tree seedlings have formed. Because the closed canopy and numerous tree seedlings prevent most of the sunlight from penetrating through, the ground layer vegetation is poorly developed and is relatively sparse. The ground layer vegetation is composed mostly of *Elatostema edule* and *Cyathea fenicis*.

(2) Cultivated woodland

The 1st replicate is located on the western side of Yunghsing Farm. In this area, *Pometia pin-*

nata is the dominant tree species in the 1st layer of the forest, with a canopy height of approximately 15~20 m. The 2nd layer is composed of *Artocarpus incisus*, *Dendrocnide meyeniana*, and *Pometia pinnata* with a canopy height of about 6~8 m. The 3rd layer is composed mostly of *Melanolepis multiglandulosa* and *Nothapodytes mimoniana* with a height of 4~5 m. Because of the activities of the Yami people, the physical structure of the space between the canopy and ground layer vegetation is quite simple. Because the canopy of the cultivated woodland is more open than that of primary forest, ample sunlight generates a dense ground layer of vegetation composed mostly of *Donax cannaeformis* and *Piper philippinum*. The 2nd replicate is on the eastern side of Yunghsing Farm. *Acalypha grandis* and *Ficus ruficaulis* are the dominant trees here, with a canopy height of approximately 8~9 m. The ground layer vegetation is composed mostly of *Ipomoea pes-caprae*.

(3) Firewood plantation

The 1st replicate is at Chunghsing Farm. *Acalypha grandis* and *Macaranga tanarius* are the dominant tree species of this area. Canopy height is approximately 8~9 m, and the ground layer vegetation is composed mostly of *Alocasia macrorrhiza*, *Elatostema edule*, and *Xanthosoma nigrum*. The 2nd replicate is in Yehying Village. *Melanolepis multiglandulos* and *Ficus ruficaulis* are predominant trees there, and the canopy height is approximately 10 m. Due to the Yami people's frequent wood harvesting and undergrowth clearing, the ground layer vegetation is sparser than that of the cultivated woodland but it is denser than that of the primary forest. The ground layer vegetation is composed mostly of *Alocasia macrorrhiza* and *Schismatoglottis calyptata*.

(4) Grassland

The 1st replicate is located in Yehying Village. The sample plots are located near the edge of a yam plantation area composed of *Ipomoea batatas* and *Xanthosoma nigrum*. The 2nd replicate is located at Yunghsing Farm. The ground layer vegetation of the sample plots is composed mostly of *Ipomoea pes-caprae* with a few *Pipturus arborescens* and *Palaquium formosanum* bushes. The height of the ground layer vegetation is about 0.5 m in both replicates.

Sampling methods

Many previous studies on spider diversity have focused on fauna from a subset of the habitat, such as the ground (Uetz and Unzicker 1976, Curtis 1980, Topping and Sunderland 1992, Merwe et al. 1996, Oliver and Beattie 1996, Draney 1997, Corey et al. 1998), bushes (Johnson 1996, Kampichler et al. 2000), canopy, or foliage (Mason 1992, Russel-Smith and Stork 1994, Pettersson 1996). In this study, we collected spiders from the ground, bush, and canopy layers in order to have a comprehensive representation of diversity from all microhabitats in the plot. Three field trips were conducted in Aug. 2000 and Feb. and Apr. 2001 (due to bad weather, data from another field trip conducted in Oct. 2000 was incomplete and thus could not be used). To collect ground spiders, 1 pitfall trap (a plastic cup 15 cm in height and 10 cm in diameter containing 70% alcohol) was established in each sampling plot, and the traps were opened for 5 days during each field trip. Additionally, at the end of each field trip, we collected litter from a 0.25 m² area in each sampling plot. The litter was brought back to the laboratory in the Department of Biology, Tunghai University and was processed by Berlese funnels for 48 h. Specimens obtained from pitfall traps and litter samples were used to estimate spider diversity of the ground layer. The 3rd method was hand collection. Green (1999) demonstrated that identical sampling methods conducted diurnally or nocturnally might obtain quite-different results. Therefore, in each 5 x 5 m plot, we collected all spiders from the ground to 2 m in height by hand for 20 min during both daytime and nighttime. After hand collection, we sweep-netted the ground layer vegetation and bushes for 10 min. Specimens from hand collections and sweep net sampling were pooled to estimate spider diversity of the ground layer vegetation and bushes up to 2 m high (inclusively called the bush layer in this study). We used the canopy sweep net to collect spiders in the canopy up to 10 m above the ground. A sweep net was mounted on an 8-m-long retractable fishing pole. To sample the spiders in the canopy above the sample plots, 4 people, each with a sweep net, stood at the 4 corners of the sampling plot, and then shook the tree branches vigorously for 5 min. Specimens collected from all 4 sweep nets were pooled together to estimate the spider diversity of the canopy layer. A complete set of reference specimens was deposited in the National Museum of Natural Science,

Taichung, Taiwan.

Community structure and guild composition comparison

The traditionally used Margalef species richness, Shannon-Weaver function, Simpson index and evenness were used to describe the community structures of spiders among different habitats and different layers of the forests (Krebs 1989). One-way analysis of variance (ANOVA) tests and LSD mean comparisons were used to compare the values of all indices derived from all plots of the 4 habitats. Guild compositions of spiders in the 4 different habitats and in the 3 layers of the habitats were compared as another way of examining how community structure varied among habitats. A comparison of guild composition can provide insights into the effects of habitat alteration and disturbances on arthropod biodiversity (Stork 1987). Spiders collected from this study were divided into the following 8 guilds according to the classification system proposed by Uetz et al. (1999): (1) foliage runners: Scytodidae, Heteropodidae, and Clubionidae (except *Phrurolithus lynx*); (2) ground runners: Lycosidae, Tetrablemmidae, Oonopidae, Gnaphosidae, and Clubionidae (*Phrurolithus lynx*); (3) stalkers: Oxyopidae and Salticidae; (4) ambushers: Philodromidae and Thomisidae; (5) sheet web-builders: Hahniidae; (6) wandering sheet/tangle web weavers: Linyphiidae and Theraphosidae; (7) orb-weavers: Araneidae, Tetragnathidae and Uloboridae; and (8) space web builders: Pholcidae and Theridiidae. Chi-square tests of homogeneity were used to compare the abundance of each guild between each pair of habitats and between each pair of layers.

Similarities between sample plots

Habitats having totally different species compositions but similar abundance patterns might have identical diversity index values. Therefore, in addition to investigating the spider community structures with the popularly used indices, we also calculated the quantitative Euclidean distance (Krebs 1989) between each pair of sample plots, then used a UPGMA clustering analysis to visualize the association patterns of the sample plots. When the sample size is large enough, analysis using Euclidean distance can assess the similarity between sample plots by considering both species composition and relative abundance.

Habitat preference analyses

The distribution of a particular species of spider among different habitats can be used to assess the spiders' habitat preference pattern (Draney 1997). Judging from the abundance of specimens, 14 dominant species were identified in this study. We used one-way ANOVA tests to compare their relative abundances among the 4 types of habitats, and LSD mean comparisons were used to perform pair-wise comparisons between habitats. All analyses were performed using SYSTAT 5.2 (Wilkinson et al. 1992).

RESULTS

Comparison of community structures and guild compositions between habitats

In total, 1718 adult specimens were collected from 3 field trips, and 123 species from 19 families were identified (see Appendix). Considering the small area of this island (45.74 km²), the diversity is quite high. The 3 most-abundant families were the Theridiidae, Tetragnathidae, and Araneidae. Among them, the Theridiidae was the most-diverse family, with a total of 30 species found. The 4 types of habitat exhibited similar species richness values, but the density of adult specimens in sample plots significantly varied. The density of adults was the highest in primary forest and lowest in grassland plots (Table 1). The diversity (as assessed by Margalef species richness, the Shannon-Weaver function, and the Simpson index) did not significantly differ among the 4 habitat types (Table 1). However, the evenness of the

primary forest plots was significantly lower than that of the other habitat types. The high density and low evenness of the primary forest plots were probably caused by 2 dominant species, *Mesida gemma* and *Leucauge argentina*. They were so abundant that they accounted for almost 50% of the total number of spiders collected in the primary forest.

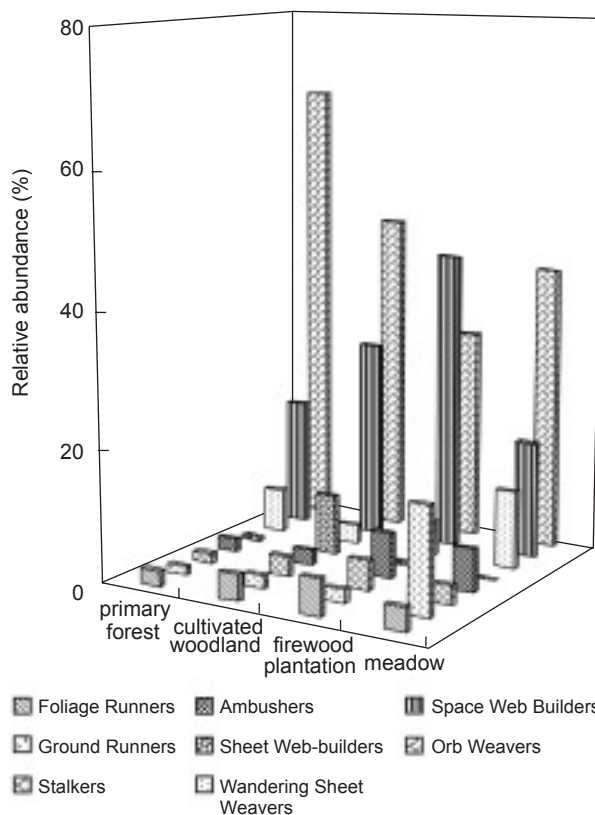


Fig. 2. Guild compositions of spiders collected from the 4 different habitats. Data from individual plots were combined.

Table 1. Results of ANOVA tests examining density, Margalef species richness, Shannon index, Simpson index, and evenness estimated from specimens collected from 4 habitat types: PF, primary forest; CW, cultivated woodland; FP, firewood plantation; and G, grassland

Habitat	No. of species	Adult abundance	Density (adults/100 m ²)	Richness	Shannon index	Simpson index	Evenness
Primary forest	60	557	278.50 ± 9.41	5.37 ± 0.14	2.54 ± 0.008	0.86 ± 0.008	0.80 ± 0.012
Cultivated woodland	64	404	202.0 ± 11.03	5.00 ± 0.25	2.72 ± 0.008	0.91 ± 0.008	0.89 ± 0.010
Firewood plantation	65	445	222.5 ± 18.94	4.85 ± 0.34	2.50 ± 0.013	0.88 ± 0.013	0.87 ± 0.014
Grassland	60	312	156.0 ± 23.11	4.26 ± 0.44	2.26 ± 0.027	0.85 ± 0.027	0.86 ± 0.028
Significance level	-	-	0.001	NS	NS	NS	0.01
LSD comparison	-	-	PF > CW, FP, G	-	-	-	PF < CW, FP, G
			FP > G				

Spider guild compositions of the 4 habitat types are shown in Fig. 2. Results of Chi-square tests between each pair of habitats showed that the compositions of guilds differed significantly among habitats (Chi-square values ranged from 156.64 to 308.61, all of them $p < 0.001$). All habitats were dominated by orb-weavers and space web builders (Fig. 2). In all habitat types except the grasslands, weavers comprised around 80% of the total catch. In the primary forest, orb-weavers comprised almost 70% of the specimens collected. However, more than 40% of the specimens found in the grassland belonged to other guilds: ground runners, stalkers, or wandering sheet weavers (Fig. 2). This result reflects that the grassland habitat had very little of a bush layer and no canopy cover, so the percentages of hunters and ground-level web builders increased. The compositions of guilds of different layers of the habitats are shown in Fig. 3. Guild composition also differed significantly among different layers (Chi-square values ranged from 252.98 to 1566.31, all of them $p < 0.001$). More than 80% of the fauna in

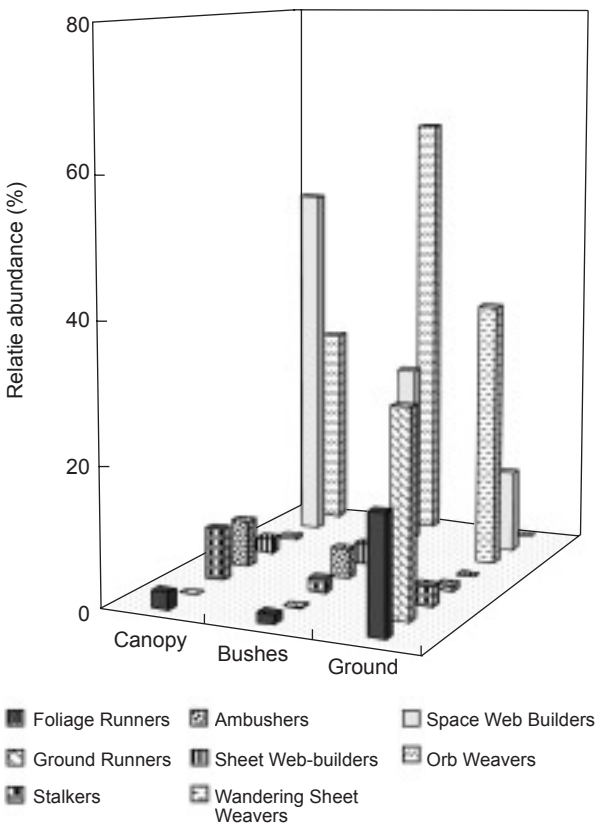


Fig. 3. Guild compositions of spiders collected from different layers of the wooded sample plots. Data from the primary forest, cultivated woodland, and firewood plantation plots were combined.

the canopy and bush layers were composed of orb-weavers and space web builders. However, the relative dominance pattern of these 2 guilds differed between canopy and bushes. The canopy was dominated by space web builders, while bushes were dominated by orb-weavers. The ground-

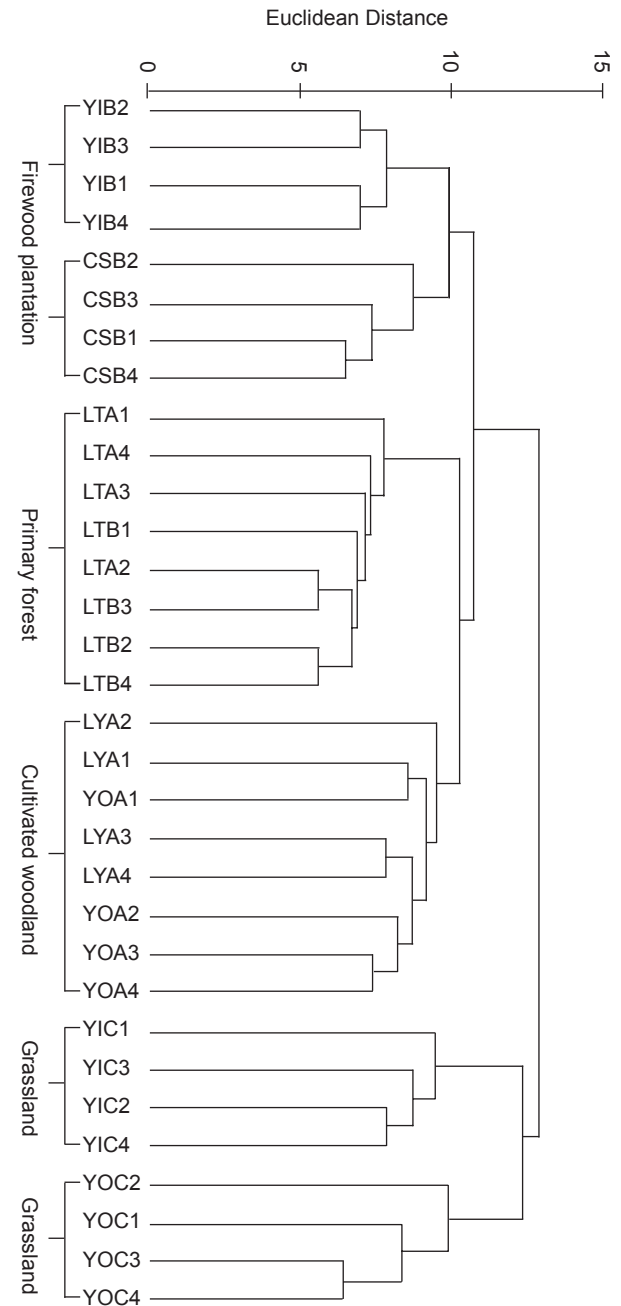


Fig. 4. Result of the UPGMA analysis using Euclidean distance estimated from 32 sample plots on Orchid I. (LTA and LTB, plots in the primary forest; LYA and YOA, plots in the cultivated woodland; YIB and CSB, plots in the firewood plantation; and YIC and YOC, plots in the grassland)

layer spider community was composed mostly of ground runners and wandering sheet weavers.

Similarities among sample plots

Results of the UPGMA analysis using Euclidean distances (Fig. 4) showed that similarities of plots located in the same habitat type were very high. Specimens from the sample plots could be divided into 4 groups. All plots could be further clustered into 2 major groups, forest (primary forest + cultivated woodland + firewood plantation) and grassland. This grouping pattern suggests that when the forests are cleared to provide land for crop plantation, the assemblages of spiders are dramatically altered. Although plots from all 3 forest habitats were grouped together, plots receiving the same disturbance level clustered together and were separated within this group. This clustering pattern indicates that habitat types receiving different levels of disturbances have characteristic spider assemblages. The habitats receiving higher levels of disturbance were not simply an impoverished version of the less-disturbed primary forest.

Habitat preferences of dominant species

The distributions of 10 of the 14 dominant species (Table 2) showed significant differences among the different habitat types. Species that specialized in only 1 habitat were: *Mesida gemma*

and *Leucauge argentina* in the primary forest; *Cyclosa confusa* and *Hahnia corticicola* in the cultivated woodland; *Chryso orchis* and *Anelosimus taiwanicus* in the firewood plantation; and *Pardosa tschekiagensis* in the grassland. Species that preferred 2 or 3 habitats but not all habitats were: *Gea zaragosa* in the primary forest and grassland; *Eriovixia sakiedaorum* in all except the grassland; and *Thelacantha brevispina* in the cultivated woodland and firewood plantation. Species that were distributed more or less evenly in all 4 habitats included *Achaearanea japonica*, *Argyrodes lanyuensis*, *Neoscona puntigera*, and *Phrurolithus lynx*.

DISCUSSION

Although the area of Orchid I. is quite small, the composition and structure of the spider communities there significantly differ among the different habitat types studied. Compared with those in other habitat types, plots in the primary forest habitat exhibited the highest density but the lowest evenness. Although the cultivated woodland and firewood plantation plots receive a certain level of disturbance, their evenness was significantly higher than that of the relatively undisturbed primary forest. In primary forests, 2 dominant species, *Mesida gemma* and *Leucauge argentina*, accounted for almost 50% of the spider community. In

Table 2. Results of ANOVA tests examining habitat preferences of 14 dominant species among different habitats: PF, primary forest; CW, cultivated woodland; FP, firewood plantation; and G, grassland. Significance levels: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; NS, not significant at the $\alpha = 0.05$ level)

Dominant species	No. of adults	Percentage (%)	Adults in each habitat				F ratio	LSD mean comparison	Significance level
			I	II	III	IV			
<i>Mesida gemma</i>	190	11.06	156	8	26	0	110.48	PF > CW, FP, G	***
<i>Leucauge argentina</i>	179	10.42	108	53	18	0	44.14	PF > CW > FP, G	***
<i>Chryso orchis</i>	115	6.69	2	19	89	5	37.88	FP > PF, CW, G	***
<i>Cyclosa confusa</i>	98	5.70	20	51	26	1	24.73	CW > PF, FP > G	***
<i>Argyrodes lanyuensis</i>	72	4.19	25	12	26	9	1.87	PF, CW, FP, G	NS
<i>Achaearanea japonica</i>	62	3.61	4	12	35	11	2.43	PF, CW, FP, G	NS
<i>Eriovixia sakiedaorum</i>	52	3.03	19	17	16	0	4.28	PF, CW, FP > G	*
<i>Pardosa tschekiagensis</i>	50	2.91	0	2	1	47	3.79	G > PF, CW, FP	*
<i>Gea zaragosa</i>	48	2.79	21	11	0	16	3.08	PF, G > CW, FP	*
<i>Thelacantha brevispina</i>	47	2.74	1	28	17	1	7.04	CW, FP > PF, G	**
<i>Neoscona puntigera</i>	42	2.44	12	7	8	15	1.51	PF, CW, FP, G	NS
<i>Phrurolithus lynx</i>	42	2.44	9	5	18	10	1.16	PF, CW, FP, G	NS
<i>Hahnia corticicola</i>	41	2.39	3	36	2	0	10.43	CW > PF, FP, G	***
<i>Anelosimus taiwanicus</i>	39	2.27	8	7	24	0	5.92	FP > PF, CW, G	**

contrast, the percentages of the top 2 dominant spider species in the other 3 types of habitat never exceeded 30% (21% in the cultivated woodland, 28.5% in the firewood plantation, and 20% in the grassland). The dominance of a few bush-dwelling orb-weaving species in relatively undisturbed rain forests was also reported by Pfeiffer (1996b). In that study, 1 orb-weaving species (*Leucauge regnyi*) accounted for 50% of the specimens sampled from El Verde, Puerto Rico. After Hurricane Hugo when the forest understory became structurally more complex due to the accumulation of fallen branches, *L. regnyi* even accounted for 86.4% of all spiders sampled.

Various scales of clearing and logging conducted by the Yami people may have reduced the abundance of the dominant species, thus increasing the evenness of the spider communities. Except for logging, most of the activities conducted by the Yami people are confined to the understory of the forest. These activities include the gathering of various forest products, the clearing of the undergrowth of selected trees, and the movement of people and domestic animals (pigs and goats). Almost all of these activities directly impact the ground layer vegetation and bushes. The most-abundant species in the primary forest, *Mesida gemma* and *Leucauge argentina*, primarily inhabited the ground layer vegetation and bushes. Compared with other habitats, bushes in the primary forest were well developed, but the ground layer vegetation was sparser. Since the abundance of orb-weavers are influenced by the physical structure of the vegetation and the availability of web sites (Greenstone 1984, Wise 1993), the undisturbed bushes and sparse ground-layer vegetation in primary forest might be able to support a larger population of orb-weaving spiders which require larger spaces for web construction. On the other hand, the traditional activities of the Yami people in the forest create a relatively open canopy, under-developed bushes, and dense ground-layer vegetation. Such physical features are not suitable for the space-demanding orb-weaving species, and thus *M. gemma* and *L. argentina* are prevented from monopolizing the habitats.

A comparison of spider diversity between different layers of the tropical forest on Orchid I. indicated that their guild compositions greatly differed. Although the architecture of the canopy was quite complex, its community structure and guild composition differed from those of the bush layer. The dominant guild in the canopy was comprised of

space web builders of the species *Chrysso orchis* and *Anelosimus taiwanicus* (both of the Theridiidae). However, the dominant guild in the bushes was comprised of orb-weavers of the species *Leucauge argentina* and *Mesida gemma* (both of the Tetragnathidae). Body sizes of bush-dwelling orb-weavers are larger than those of canopy-dwelling theridiids (Tso and Tanikawa 2000, Yoshida et al. 2000), and orb-weavers need larger open spaces for orb construction. Compared with the canopy, the bush layer might exhibit more-suitable microhabitats for orb web construction, and thus was inhabited by greater numbers of orb-weavers.

The UPGMA analysis results grouped all forest habitats together (Fig. 4). A close examination of spider communities of these 3 forest habitat types indicated that the differences in relative abundances of space web builders and orb-weavers might have been responsible for the observed clustering pattern. Spider communities in the 3 types of forest habitats were dominated by space web builders and orb-weavers (Fig. 2). The most-abundant species in the primary forest was *Mesida gemma*. It was present but not common in the cultivated woodland and firewood plantation plots (Table 2). Similarly, dominant species such as *Cyclosa confusa*, *Thelacantha brevispina*, and *Hahnina corticicola* in the cultivated woodlands (together comprising about 30% of the catch) were less-frequently found in the other 2 forest habitat types. In the firewood plantations, 89 *Chrysso orchis* individuals were collected, but only 16 were found in the other 2 habitats combined (Table 2). Since the Euclidean distance method used in this study considers both the species composition and relative abundance (Krebs 1989), the dramatic differences in abundances of dominant species between the 3 types of habitats were probably responsible for the separation of these plots in fig. 4. Therefore, in the Orchid I. tropical forest ecosystem, orb-weavers and space web builders seemed to be the groups distinguishing different habitats, while non-weaving spiders played a less-important role. A similar result was also found by Pfeiffer (1996b) in the Luquillo Experimental Forest in Puerto Rico. Large-scale disturbances by clear-cutting, plantation activities, and periodic burning caused a simple vegetation architecture of the grasslands. Species needing more-complex architecture on which to build their webs (Theridiidae or Araneidae) were not abundant in the grassland plots. The percentage of ground hunters and wandering sheet weavers was high, causing the grass-

land habitats to significantly differ from the other types (Fig. 2). Although the vegetation structure of grasslands is much simpler than that of primary forests, the evenness of the former was significantly higher than that of the latter. This might again have resulted from the high disturbance generated by the Yami people, which suppresses the abundance of dominant species.

One could argue that the observed clustering pattern of plots from the 4 habitat types may simply reflect spatial heterogeneity on Orchid I. The plots of the 4 habitat types were on various parts of this island (Fig. 1), and differences in diversity among habitats receiving different levels of disturbance may result from the fact that spider communities differ from place to place. However, the area of Orchid I. is small. Considering the excellent dispersal ability of spiders (Decae 1987), the observed differences in spider communities are more likely to have resulted from a variation in vegetation structure generated by different levels of disturbance rather than spatial variations. Furthermore, some plots receiving similar regimes of disturbances, such as those in grasslands and in firewood plantations, were located on different sides of the island. Despite the physical distance between those plots, they were tightly grouped together in the cluster analyses. Therefore, it is unlikely that spatial heterogeneity alone was responsible for the patterns detected.

Results of this study demonstrate how the traditional forest management patterns of a Malay-Polynesian tribe can affect the spider diversity of a tropical island in East Asia. Results of most spider diversity studies in temperate ecosystems have demonstrated that spider communities of disturbed areas usually exhibit a much-lower diversity, and some are merely an impoverished version of adjacent undisturbed areas (Gibson et al. 1992, Zulka et al. 1997, Feber et al. 1998, Downie et al. 1999). However, on Orchid I. the 4 habitat types receiving different degrees of aboriginal activities exhibited similar values for species richness and diversity, although with different species compositions. The traditional management conduct of the Yami people has not simply reduced the spider diversity, but another array of species has appeared that better tolerates the newly formed habitats. Therefore, the activities of the Yami people have not resulted in decreased spider diversity on Orchid I., but rather enhanced diversity by introducing habitat heterogeneity and moderate disturbance. Any resource management or conservation activities conducted on Orchid I. should take into considera-

tion that the Yami people's traditional activities are one of the major factors influencing the biodiversity of this tropical island.

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Appendix: (Cont.)

Species name	Habitats										Total										
	PF					CW						FP					G				
	F	M	F	M	F	F	M	F	M	F		F	M	F	M	F					
Linyphiidae S	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	2	5
Total	14	21	5	6	2	20	5	30	103												
Lycosidae																					
<i>Arctosa meitanensis</i> Yin et al., 1993	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	7
<i>Pardosa tschekiagensis</i> Schenkel, 1963	0	0	0	2	1	0	23	24	50												
<i>Trochosa ruricoloides</i> Schenkel, 1963	0	0	0	0	0	1	0	0	1												
Lycosidae A	0	0	0	0	1	0	0	0	1												
Total	0	3	0	2	2	1	23	24	55												
Oonopidae																					
<i>Gamasomorpha</i> sp.A	1	1	1	0	0	1	0	0	4												
<i>Ischnothyrens</i> sp.A	0	0	0	0	0	1	0	1	2												
Oonopidae A	0	0	0	0	0	1	0	0	1												
Oonopidae B	0	0	0	0	0	1	0	0	1												
Oonopidae C	0	0	2	0	2	0	0	0	4												
Total	1	1	3	0	2	4	0	1	12												
Oxyopidae																					
<i>Oxyopes sertatus</i> L. Koch, 1877	0	0	1	0	1	0	3	0	5												
Total	0	0	1	0	1	0	3	0	5												
Philodromidae																					
<i>Philodromus subaureolus</i> Bösenberg and Strand, 1906	0	0	0	0	1	1	0	0	2												
Total	0	0	0	0	1	1	0	0	2												
Pholcidae																					
Pholcidae A	1	1	5	0	0	0	0	0	7												
Total	1	1	5	0	0	0	0	0	7												
Salticidae																					
<i>Marpissa</i> sp.A	1	0	3	2	3	4	1	0	14												
<i>Myrmarachne</i> sp.A	0	0	1	0	0	0	0	0	1												
<i>Myrmarachne</i> sp.B	0	0	0	0	0	1	0	0	1												
<i>Myrmarachne</i> sp.C	0	0	1	0	0	0	0	0	1												
<i>Myrmarachne</i> sp.D	0	0	1	0	0	0	0	0	1												
<i>Phintella</i> sp.A	0	2	0	0	0	0	0	0	2												
Salticidae A																					
<i>Salticidae</i> A	0	0	0	0	0	3	0	0	3												
<i>Salticidae</i> B	1	0	0	1	5	2	1	0	10												
<i>Salticidae</i> C	0	0	0	0	0	0	1	0	1												
<i>Salticidae</i> D	1	3	2	0	0	0	0	0	7												
<i>Salticidae</i> E	0	0	0	0	0	0	0	0	1												
Total	3	5	8	3	11	8	3	3	44												
Scytodidae																					
Scytodidae A	3	0	0	0	1	1	0	0	5												
Total	3	0	0	0	1	1	0	0	5												
Tetrablemmidae																					
<i>Tetrablemma</i> sp.A	0	2	1	1	0	0	0	0	4												
Total	0	2	1	1	0	0	0	0	4												
Tetragnathidae																					
<i>Leucauge argentina</i> (Hasselt, 1882)	80	28	42	11	12	6	0	0	179												
<i>Leucauge decorata</i> (Blackwall, 1864)	0	0	0	2	1	0	9	8	20												
<i>Mesida gemma</i> (Hasselt, 1882)	80	76	5	3	16	10	0	0	190												
<i>Nephila pilipes</i> (Fabricius, 1793)	8	2	1	1	6	2	1	0	21												
<i>Tetragnatha praedonia</i> L. Koch, 1878	1	0	0	1	2	4	1	0	9												
<i>Tylorida striata</i> (Thorell, 1877)	0	0	0	0	2	3	17	2	24												
Total	169	106	48	18	39	25	28	10	443												
Theraphosidae																					
<i>Yamia watasei</i> Kishida, 1920	0	1	0	0	0	1	0	1	3												
Total	0	1	0	0	0	1	0	1	3												
Theridiidae																					
<i>Achaearanea japonica</i> (Bösenberg and Strand, 1906)	2	2	4	8	28	7	11	0	62												
<i>Achaearanea lanyuensis</i> Yoshida, Tso and Severinghaus, 2000	1	9	3	0	0	0	0	0	13												
<i>Achaearanea quadrimaculata</i> Yoshida, Tso and Severinghaus, 2000	0	0	0	0	2	1	0	1	4												
<i>Achaearanea tepidariorum</i> (C. L. Koch, 1841)	4	0	15	0	0	0	0	0	19												
<i>Anelosimus taiwanicus</i> Yoshida, 1986	4	4	5	2	10	14	0	0	39												

Appendix: (Cont.)

Species name	Habitats										Total									
	PF					CW						FP	G							
	F	M	F	M	F	F	M	F	M	F				F	M					
<i>Argyroides cylindrogaster</i> (Simon, 1889)	0	0	0	1	1	0	0	1	0	0	1	0	0	0	0	0	2			
<i>Argyroides fissifrons</i> O. P. Cambridge, 1869	4	2	5	1	0	0	0	0	0	0	12	0	0	0	0	0	0	1	0	1
<i>Argyroides labiatus</i> Zhu and Song, 1991	0	0	0	0	2	0	1	0	0	0	3	0	0	2	0	0	0	0	0	2
<i>Argyroides lanyuensis</i> Yoshida, Tso and Severinghaus, 1998	14	11	10	2	14	12	6	3	72	54	49	66	48	106	91	28	26	468		
<i>Argyroides nigroris</i> Yoshida, Tso and Severinghaus, 2000	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	4
<i>Argyroides sinicus</i> Zhu and Song, 1991	0	1	0	0	0	0	1	0	2	0	0	0	0	3	0	2	0	0	5	
<i>Chrosiothes fulvus</i> Yoshida, Tso and Severinghaus, 2000	0	0	1	4	0	1	0	0	6	0	0	1	1	0	1	0	3	0	6	
<i>Chryso argyrodiformis</i> (Yaginuma, 1952)	0	0	0	0	1	1	1	3	6	0	0	1	0	4	0	0	0	0	5	
<i>Chryso orchis</i> Yoshida, Tso and Severinghaus, 2000	1	1	8	11	42	47	0	5	115	4	1	3	1	9	4	1	1	24		
<i>Chryso spiriventris</i> (O. P.-Cambridge, 1869)	0	0	0	0	3	3	1	0	7	0	0	0	0	0	0	0	0	0	2	
<i>Coleosoma floridanum</i> Banks, 1900	0	1	1	0	1	3	2	11	19	0	0	0	0	4	2	0	0	6		
<i>Dipoena mustelina</i> (Simon, 1888)	4	4	0	0	0	0	0	0	8	3	2	0	0	0	0	0	0	5		
<i>Moneta mirabilis</i> (Bösenberg and Strand, 1906)	4	3	0	0	1	0	0	0	8	0	0	1	0	0	0	0	0	1		
<i>Theridion xianfengensis</i> Zhu and Song, 1992	0	6	0	2	0	0	0	0	8	0	0	0	0	0	0	1	0	1		
<i>Dipoena</i> sp.A	0	1	0	4	0	0	0	0	5	7	4	7	2	20	8	10	10	68		
Theridiidae A	2	0	3	0	1	0	0	0	6	0	0	5	3	0	0	0	0	1	9	
Theridiidae B	1	0	0	0	0	0	0	0	1	3	0	2	0	1	0	0	0	6		
Theridiidae C	6	0	3	0	0	0	0	1	10	4	2	0	0	0	0	0	0	6		
Theridiidae D	0	0	0	9	0	0	0	0	9	7	2	7	3	1	0	0	1	21		
Theridiidae E	3	1	1	1	0	0	0	0	6	312	245	268	136	226	219	166	146	1718		
Theridiidae F	0	1	0	0	0	0	0	0	1	Total										
Total	312	245	268	136	226	219	166	146	1718											