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Habitat management by aboriginals promotes high spider diversity on an Asian tropical island

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Orchid Island, 92 km off the southeast coast of Taiwan, has the northernmost tropical forests in East Asia. We assessed effects of habitat management by Orchid Island inhabitants, the Yami people, on spider diversity by comparing assemblages collected from the ground to canopy among four habitats (natural forest, cultivated woodland, second growth forest and grasslands) that receive different degrees of disturbance. Species and guild composition did not differ among replicates of habitat but differed significantly among habitats. Variation in spider diversity was inversely correlated with vegetation density. Cultivated woodland subjected to an intermediate level of disturbances had a lower understory vegetation density than natural forest, but higher spider diversity. Neither insect abundance nor biomass varied significantly among habitats suggesting little room for effects of prey availability on spider diversity. It appears that the Yami people maintain high spider diversity on Orchid Island by generating novel habitat types with different vegetation structures and disturbance regimes.

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How aboriginal human activities impact tropical biodiversity is poorly understood outside of Australia and the tropical Amazon (Phillips et al. 1994, Bowman 1998). Zent and Zent (2002) suggested that disturbances caused by the Hoti people of the Venezuelan Amazon might have a considerable impact on the biodiversity of the Magigualida forest. The use of fire by Australian aboriginals and impact on plant and animal diversities has received some attention. Traditional habitat management by fire suppressed dominant herbaceous plants, reduced accumulation of fuel and risk of uncontrolled wild fire and thus increased habitat diversity (Lunt 1998, Yibarbuk et al. 2001). The habitat mosaic generated enhanced the survival of certain fauna and flora in the monsoon tropics of Australia (Bowman 1998). Nonetheless, understanding of how traditional management of aboriginals affects local biodiversity in the most densely populated and biologically diverse regions at tropical Asia is much more limited. With environmental conditions in tropical Asia rapidly deteriorating (Dudgeon 2003), information of how resource extraction behaviors of aboriginals affect tropical forest biodiversity may provide valuable insights for conservation of the region's rich biota. In this study, we provide empirical evidence that the traditional management methods of aboriginals in an Asian tropical island generate habitat diversity and maintain high spider diversity.

Orchid Island (Lanyu in Chinese) is a tropical island 92 km off the southeastern coast of Taiwan with the northernmost tropical forests in East Asia (Chen et al. 1982). Its aboriginal inhabitants, the Yami people, are of Malay-Polynesian origin and migrated from Batan Islands, Philippines, ca 700 yr ago (de Beauclair 1959). Yami culture and resource utilization patterns are closely

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associated with the sea (Wang 1984), but these people also affect the landscape by creating small yam plantings beside forests or taro plantings near streams (Huang 1995). In addition, the Yami obtain material to construct boats and huts through small scale logging.

Currently, >80% of Orchid Island is still covered by various types of forests (Wang et al. 2003). In contrast, on Green Island, only 76 km to the north of Orchid Island, the current vegetation pattern is significantly different. Green Island was originally also inhabited by Yami but the Han people from Taiwan immigrated into this island about two hundred years ago (Chen et al. 1982). Due to large-scale clear-cutting for agricultural practices and grazing, the original vegetation has virtually disappeared in Green Island (Chen et al. 1982), and these changes have significantly affected the biodiversity on Green Island. For example, the butterfly and bird diversities in Green Island are only one third those of Orchid Island (Chen et al. 1982). Although the way Yami people managing forests in Orchid Island has been well documented (Cheng and Lu 2000, Wang et al. 2000, 2003, Wang 2004), how such practices have affected biodiversity is still unclear. In this study, we use spiders as an indicator to investigate how habitat management by the Yami affects biodiversity on Orchid Island.

Spiders are among the most diverse and abundant invertebrate predators in terrestrial ecosystems (Wise 1993, Nyffeler 2000). They are easily sampled and spider assemblages are useful indicators for comparing the biodiversity of various environments and for assessing the effect of disturbances on diversity (Clauseu 1986, Topping and Lövei 1997, Churchill 1998, Maelfait and Hendrickx 1998, Riecken 1999, Marc et al. 1999). Spider guild composition responds to vegetation diversity and structural complexity (Hatley and Macmahon 1980, Greenstone 1984, Uetz 1991, Docherty and Leather 1997, Dennis et al. 1998, Rypstra et al. 1999, McNett and Rypstra 2000, Raizer and Amaral 2001) and local abundance of prey (mostly insects) is regarded as one of the major determinants of spider distribution (Moring and Stewart 1994).

Although the Yami people do not directly utilize spiders, disturbances generated by their habitat management may affect vegetation structure thus influence spider diversity. Chen and Tso (2004) performed a preliminary survey between habitats receiving different degrees of Yami management and suggested that traditional management can maintain a high spider diversity by introducing moderate disturbances into the system. However, Chen and Tso (2004) did not investigate the relationship between vegetation structure and spider diversity, and the sample size was small. In this study, we repeated the study by Chen and Tso (2004) but with a larger sample size. We also quantified the vegetation densities and prey availabilities in different habitats to determine possible factors responsible for the observed diversity pattern.

Methods

Study area

The study was conducted on Orchid Island (121.32°E, 22.03°N) located on the Luzon sill between Taiwan and the Philippines. It is of volcanic origin and ca 45.74 km^2 in total area (Cheng 2001). The island includes ten mountains with elevations over 400 m, two of which are higher than 500 m (Chen 1993). Thus, most areas on the island are steep and patches of alluvial plains are scattered along the coast.

The island's climate is characterized by high temperature (average 22.4°C) and rainfall (annual rainfall >2600 mm). Between May and September the daily mean temperature exceeds 25°C and typhoons are frequent (Wang 1984). Orchid Island is generally windy, especially during the winter months. The forests are classified as tropical mountain rain forests (Whitmore 1998) and are the northernmost tropical forests in East Asia (Chen et al. 1982).

We established study sites on the northern, eastern, and southern sides of the island, with each of these three study sites containing four habitat types (natural forest, cultivated woodland, second growth forest and grasslands) generated or maintained by the Yami people. The plant compositions in each habitat type and the management practices that generate them are as follows.

Natural forest

About 80% of Orchid Island is covered by primary forests (Chen et al. 1982) because the mountainous areas are steep and are difficult to access. However, the Yami avoid some alluvial forests for cultural reasons (Huang 1995) and these remain relatively undisturbed. Compared with other forest types, natural forests exhibit a higher woody plant diversity, basal area and density (Wang 2004). *Garcinia liniix*, *Bischofia javanica*, and *Ficus benjamina* are the dominant trees and *Freycinetia formosana* and *Cyathea fenicis* comprised most of the ground layer herbaceous plants (Wang 2004).

The natural forest is subjected to a low level of selective logging. Individual Yami use special slash marks on the trees to claim log ownership (Wang et al. 2003) and they re-slash the trees periodically. *Garcinia liniix* and *F. benjamina* are used as fishing gear or a part of boats (Wang et al. 2000). Yami eat the fruits of *B. javanica* and use *F. formosana* to decorate the cloth and rope (Wang et al. 2000).

Cultivated woodland

Cultivated woodlands are mixtures of primary and secondary growth, which are logged with primitive tools to obtain materials to construct houses and boats. This habitat is more severely disturbed than the natural forest, but is less altered than second growth and grassland areas. The forest undergrowth is frequently cleared to promote the growth of planted tree seedlings. Logging is a rare event; a planted tree is usually logged after 10–20 yr of growth (Wang 2004).

Ownership of trees in the cultivated woodland is divided among paternal groups of Yami and each usually maintains a forest patch for several generations (Wang 1984, Huang 1995). They remove weeds and seedlings of undesired tree species several times a year so that the ground layer vegetation of cultivated woodland is more disturbed than that of the natural forest (Wang 2004). *Pometia pinnata*, *Artocarpus incisus* and *Areca catechu* are the dominant tree species (Wang 2004) and are utilized by the Yami in ways ranging from food to material for huts or boats. The herbaceous ground layer is mostly composed of the herbaceous *Oplismenus hirtellus*, *Piper betle*, and *Alocasia odora* (Wang 2004), which are also used as ingredients of food (Wang et al. 2000). Tree diversity (92 species) is slightly decreased by the management of the Yami because they preferentially maintain certain tree species but diversity of herbaceous plants is enhanced. Wang (2004) reports 104 herbaceous plant species in natural forests as compared to 149 species in cultivated woodland.

Second growth forest

Second growth forests receive a high level of disturbance associated with cultivation of fast-growing tree species (mainly *Macaranga tanarius*, *Acalypha caturus* and *Ficus septica*) on land formerly used for yam or taro plantations (Wang 2004). At first, the Yami only harvest branches of the planted trees and leave the main trunk, creating a relatively open canopy in this habitat type (Wang 2004). After three to five years of firewood harvesting, the trees are clear-cut and burned to create lands for yam or taro plantations. The fruits of *M. tanarius* and *A. caturus* are used as food and *F. septica* is used as a repellent for evil spirits (Wang et al. 2000). *Cyclosorus acuminatus* var. *acuminatus*, *Piper betle* and *Oplismenus hirtellus* comprise most of the herbaceous ground layer (Wang 2004). The scale of habitat alteration achieved by the Yami people in forests is quite limited because cultivated woodlands and second growth forests are maintained by only a few male members of families during the non-fishing seasons (Huang 1995). Therefore, the size of these habitat types is rather small, and the total area of cultivated woodlands and second growth firewood plantations combined <10% of the total island area (Chen et al. 1982).

Grassland

Most grasslands are located near forest margins and are generated from clear-cutting of firewood plantations or from abandoned yam plantations (Chou 1998). About 6% of Orchid Island is grassland (Chen et al. 1982) and they receive the highest level of disturbance. The Yami periodically burn the grasslands to generated nutrient flushes and, therefore, grassland can be regarded as an intermediate stage of the Yami crop rotation (Chou 1998). The Yami usually allow the grass to grow in abandoned yam plantations for three to five years until the productivity of the land is recovered (Wang 1984). *Ipomoea pes-caprae* and *Miscanthus floridulu* are the two most abundant herbaceous plants. *Ipomoea pes-caprae* is used as firebrand in night time fishing activities and *M. floridulus* is used in many ways, ranging from repellent for evil spirits to roofing for Yami huts (Wang et al. 2000).

Spider sampling methods

Three field trips were made to Orchid Island, respectively, in January, April and July 2003. Five 5 × 5 m sampling plots separated from each other by >7 m were established in each habitat type in each of the three regions defined above to comprise a total of 60 sampling plots island-wide (Fig. 1). In each plot we collected spiders from canopy to ground level as follows. Two

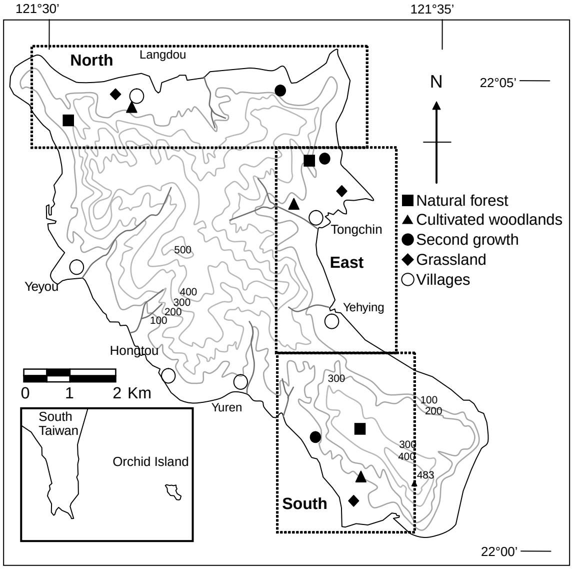


Fig. 1. Map of Orchid Island, Taiwan and the locations of study sites and sampling plots.

pitfall traps (a plastic cup 15 cm in height and 10 cm in diameter containing 70% alcohol) were established in each sampling plot to collect ground spiders. During each field trip the traps were opened for five days. Sweep-nets were used to collect spiders in the understory vegetation and we standardized the effort by sampling for 5 min. During which time one person sweep-netted back and forth all ground layer herbs and shrubs (up to 2 m in height) till all vegetation in the sampling plot had been swept thoroughly. Spiders in the canopy were collected by sweeping the canopy with nets mounted on eight-meter-long fishing poles. While sampling canopy spiders one person stood in the center of the plot then sweep-netted all the branches within the plot vigorously. Since it took more time to collect canopy spiders, we standardized the effort by sampling for 10 min. A complete set of reference specimens has been deposited in the National Museum of Natural Science, Taichung, Taiwan.

Spider and insect specimens were stored in 70% ethanol. Adult spiders were identified to species or morphospecies and juveniles to families. Both adults and juveniles were grouped into foraging guilds according to their web-building and prey-catching behaviors. We used the classification systems given in Uetz et al. (1999) and Höfer and Brescovits (2001) to group the spider families of Orchid Island into appropriate guilds. We calculated Jaccard similarity indicies (Kerbs 1989) between family pairs according to their shared foraging traits using SYSTAT 9 (SPSS, Chicago, IL, USA). Based upon the pairwise Jaccard similarities an unweighted pair-group arithmetic average clustering (UPGMA) was performed to visualize their grouping patterns using PRIMER 5 (Clarke and Warwick 2001).

In addition to spiders, insect specimens collected during the July 2003 field trip were also used in this study. Abundance and biomass of insects collected from the sampling plots were used as estimates of prey availability to determine whether they were significant determinants of spider diversity. Insects were weighed to the nearest 0.1 mg after being oven-dried at 50°C for two days to obtain biomass data.

Quantification of vegetation structure

Vegetation structure was measured during the July 2003 field trip. We measured percent canopy cover (PCC) and understory vegetation density (UVD) for each sampling plot. PCC was measured by a Nikon 4500 digital camera mounted with a fish-eye lens. The camera was mounted on a tripod placed in the center of the plot with the lend facing upward to take a hemispheric photograph for each plot. The photographs were transformed into black-and-white images to have a better distinction between the canopy and sky, and were analyzed by a Gap Light Analyzer, ver. 2.0 (Frazer et al. 1999). We used similar methods to quantify UVD but a pink cardboard (53 × 76 cm) was used as the background. The cardboard was held by one person standing at each of the four cardinal edges of the sampling plot. The photographer stood in the middle of the plot then took images of the cardboard and the vegetation in front of it with a Nikon 4500 digital camera. We used percent coverage of vegetation on the cardboard as an indication of vertical vegetation density in the plot. In each cardinal direction the cardboard was held at three different heights (low: ground to 60 cm; middle: 70–130 cm; high: 140–200 cm). Therefore, a total of 12 photographs were taken from each plot to have a better representation of the vertical stratification of the understory vegetation. The photographs were transformed into black-and-white images using Photoshop. For each height level the measurements from four cardinal directions were totaled and standardized to 100 cm^2. The PCC and low, middle and high level UVD values were then used in the subsequent analyses to assess if vegetation structures varied between habitats.

Statistical analyses

First we calculated spider density, Margalef Species Richness (D_{mg}), the Shannon-Wiener Function (H'), Simpson's index (D) and Evenness (J) (Magurran 1988, Krebs 1989) for each sampling plot. One-way ANOVA and LSD mean comparisons were used to compare the values of all indices among the four habitats. Lilliefor's tests were used to ensure that the data met the normality assumption. SYSTAT 9 was used to perform both tests. Although we sampled all study plots with equal intensity, a rarefaction analysis (Gotelli and Graves 1996) was also used to compare the number of species between the habitat types.

The similarity among sampling plots was depicted as Bray-Curtis similarities (Kerbs 1989), using both species and guild compositions. Multidimensional scaling plots (MDS) were constructed based upon the similarity values. Analysis of similarities (ANOSIM) was performed between each pair of habitats and between regions to determine the significance level. Similarity calculations, MDS construction and ANOSIM analyses were performed using PRIMER 5 (Clark and Warwick 2001). In addition to multivariate methods such as MDS and ANOSIM, we also used one-way ANOVA, as above, to examine whether the abundance of various spider guilds differed among habitats.

To examine relationships between environmental variables and spider diversity, we first used the BIO-ENV function of PRIMER 5 to determine the subset of variables that were most significantly correlated with spider guild composition. PCC, UVD from three height levels, abundance and biomass of insects were used as the potential environmental variables. In the BIO-ENV procedure, the Bray-Curtis similarities were first calculated between sampling sites using spider guild composition and ranked. Then, different combinations of environmental variables were used to calculate pairwise Euclidean distances between sampling sites and were also ranked. The BIO-ENV function then assessed the correlations between the two sets of rankings and determined which combination of environmental variables achieved the highest correlation with the similarity ranking derived from guild composition. Subsequently, a RELATE test was performed to determine whether such correlation was statistically significant.

In addition to examining the relationship between spider diversity and environmental variables, we also examined each variable respectively. Numerous studies demonstrated that understory vegetation was one of the most important factors determining spider diversity, therefore we used the multivariate method to assess whether UVD differed among sampling plots. UVD values of each of the three height levels were used to calculate Bray-Curtis similarities between each pair of sampling plots, then pairwise ANOSIM tests were performed to determine the level of significance. In addition to multivariate methods, we also used two-way ANOVA (region × habitat factors) and Fisher's LSD mean comparisons to test whether each of the environmental variables differed among habitats.

Results

Comparisons of community structures between habitats

A total of 3278 specimens were collected during our three field trips; among them 1178 were adults. From adult specimens 154 species from 22 families were identified. The three most abundant families were Theridiidae, Tetragnathidae, and Araneidae. The abundance of adults was the highest in cultivated woodland and the lowest in grassland (Table 1). Evenness and Simpson's index did not differ significantly among the four habitat types, however, Margalef Species Richness and the Shannon-Weiner function, were significantly higher for cultivated woodlands than for the remaining three habitats (Table 1). Rarefaction analysis also showed that cultivated woodland had more species than the other two forest habitat types at all specimen abundance levels (Fig. 2). However, rarefaction analysis also revealed that the lower spider diversity in grassland could depend strictly on the overall lower catch in grassalands.

Comparison of spider species composition between sites and habitats

The MDS plots generated from relative abundances of different spider species in sampling sites located in different regions of the island showed no obvious clustering pattern (Fig. 3a). Results of ANOSIM tests also showed no significant difference ($p > 0.05$) among sampling sites located in three regions (Table 2a). The MDS plot generated from relative abundances of different spider species in each habitat showed that sampling plots from each habitat type clustered together (Fig. 3b). Sampling plots in grasslands were well separated from the others and were also more heterogeneous, while those from human-disturbed forest habitats clustered more closely and were more homogenous. Sampling plots in natural forests grouped more distinctly by themselves and showed little overlap with other plots. Pair-wise ANOSIM tests showed significant differences in spider diversity between the four habitats (Table 2b).

Comparison of guild compositions between sites and habitats

Families of Araneae commonly seen in Orchid Island were grouped into the following five guilds: 1) orb weaver: Araneidae, Tetragnathidae, and Uloboridae; 2) space weaver: Dictynidae, Pholcidae, and Theridiidae;

Table 1. Number of spider species and mean (±SE) density, Richness (D_{mg}), Evenness (J), Shannon-Weiner function (H′) and Simpson index (D) of sampling plots in four habitats on Orchid Island, Taiwan and the results of ANOVA test and Fisher's LSD mean comparisons.

Habitat	Species	Density*	D_{mg}	J	H′	D
Natural forest (N)	78	21.20±2.10	3.96±0.24	0.93±0.01	2.36±0.07	0.93±0.01
Cultivated woodland (C)	88	24.33±2.32	4.42±0.25	0.94±0.01	2.50±0.06	0.94±0.01
Second growth (S)	62	19.73±1.78	3.57±0.20	0.94±0.01	2.27±0.07	0.93±0.01
Grassland (G)	70	13.60±1.59	3.00±0.19	0.91±0.02	1.92±0.10	0.89±0.02
F	–	5.24	7.34	0.84	10.79	2.31
p	–	0.00	0.00	0.48	0.00	0.09
LSD	–	C > N, S > G	C > N, S > G	–	C > N, S > G	–

*: per sampling plot (25 m^2)

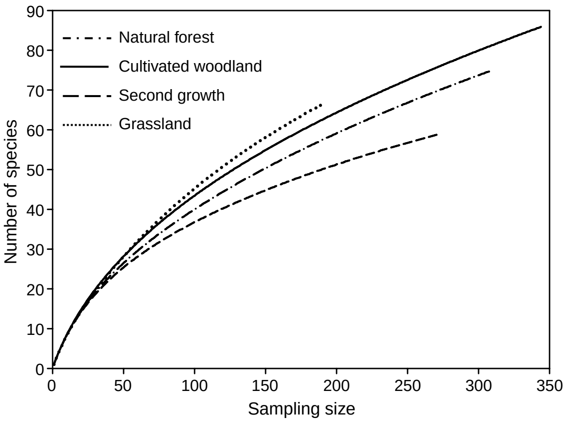


Fig. 2. Spider species diversity comparisons between four habitat types in Orchid Island, Taiwan using rarefaction.

3) ground weaver: Hahniidae, Linyphiidae, Agelenidae, and Amaurobiidae; 4) foliage runner: Clubionidae, Oxyopidae, Salticidae, and Thomisidae; 5) ground runner: Lycosidae, Gnaphosidae, Oonopidae, and Zodariidae. A MDS plot generated for relative abundances of different spider guilds showed no obvious patterns with respect to the three regions (Fig. 4a), nor were significant differences revealed by pair-wise ANOSIM tests (Table 3a).

Table 2. Results of pair-wise ANOSIM tests comparing spider species and guild compositions between different regions (a) and habitats (b).

Comparison	Species composition		Guilds composition	
	R	p	R	p
(a) Among study sites				
Global R	−0.104	0.902	−0.113	0.930
Northern vs eastern	−0.125	0.771	−0.125	0.771
Northern vs southern	−0.094	0.857	−0.167	0.971
Eastern vs southern	−0.104	0.800	−0.063	0.686
(b) Among habitats				
Global R	0.434	0.001	0.350	0.001
Natural forest vs cultivated woodland	0.373	0.001	0.240	0.001
Natural forest vs second growth	0.371	0.001	0.148	0.005
Natural forest vs grassland	0.487	0.001	0.536	0.001
Cultivated woodland vs second growth	0.203	0.003	0.002	0.461
Cultivated woodland vs grassland	0.698	0.001	0.674	0.001
Second growth vs grassland	0.593	0.001	0.637	0.001

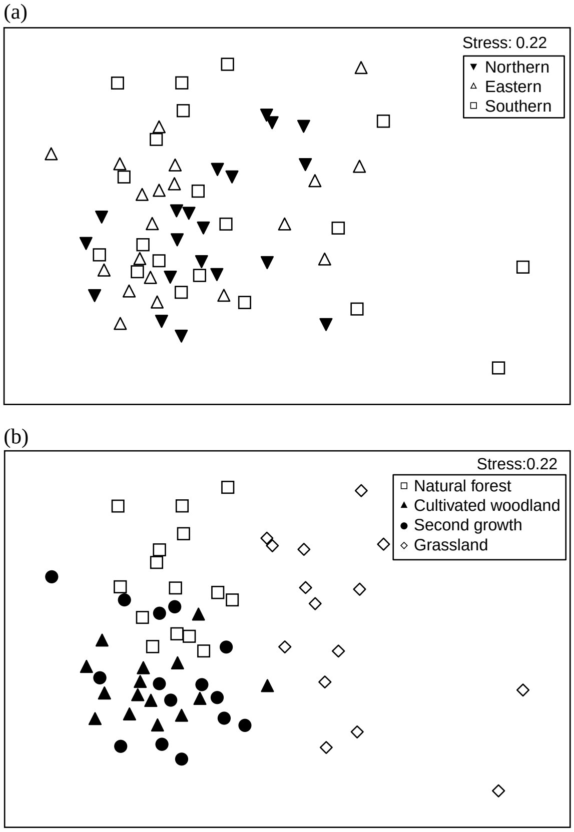


Fig. 3. MDS plots of sampling plots on Orchid Island, Taiwan generated by species composition sorted according to regions (a) and habitats (b).

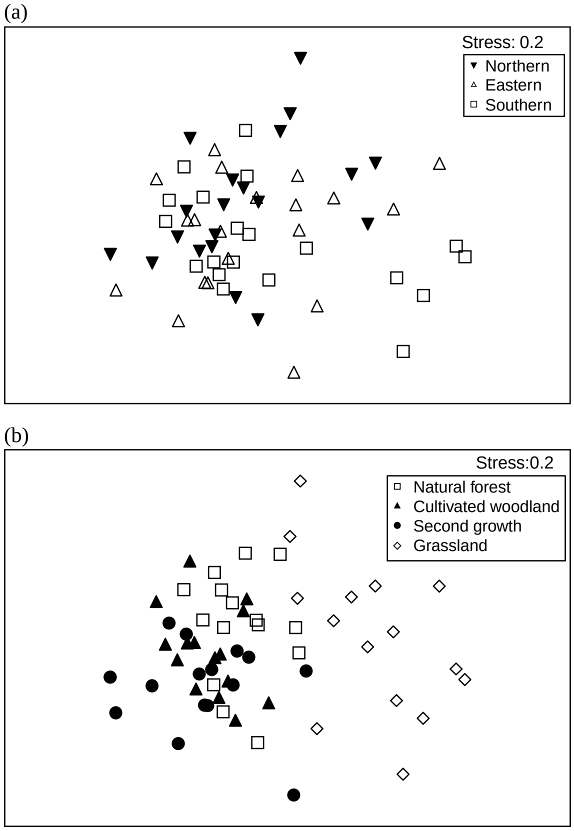


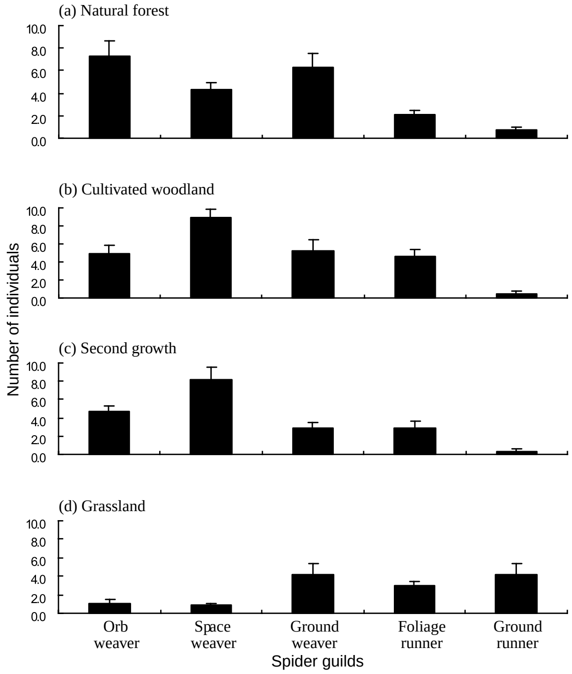
Fig. 4. MDS plots of sampling plots in Orchid Island, Taiwan generated by guild composition sorted according to regions (a) and habitats (b).

Table 3. Results of ANOVA (all except ground runner) and Kruskal-Wallis (ground runner) tests comparing the abundances of various spider guilds among different habitat types. (Nf: natural forest; Cw: cultivated woodland; Sg: second growth; G: grassland.)

Guild	F/K-W statistics	p	LSD
Orb weaver	9.100	0.000	Nf > Cw, Sg > G
Space weaver	15.820	0.000	Cw, Sg > Nf > G
Ground weaver	1.940	0.130	–
Foliage runner	2.750	0.040	Cw > Nf, Sg, G
Ground runner	24.010	0.000	–

The MDS plot generated from relative abundances of spider guilds was similar to that generated from spider species with respect to habitat associations. Grassland plots were well separated from forest plots and those in three forest habitats showed some overlap (Fig. 4b). Those in cultivated woodlands overlapped considerably with those of second growth. These patterns were consistent with the ANOSIM results as guild composition did not differ significantly between plots in cultivated woodland and second growth, although all the other pair-wise comparisons were statistically significant (Table 2b).

Data about spider guild abundance were square root transformed to meet the normality assumption for all but the ground runner guild. Non-parametric Kruskal-Wallis ANOVA was used to compare the abundance of this latter guild among habitats. Orb wearers were the most dominant guild in natural forest (Fig. 5a) but assemblages in cultivated woodland (Fig. 5b) and second growth (Fig. 5c) were both dominated by space weavers (Table 3), followed by orb weavers and others. Such a pattern might explain the non-significant ANOSIM results in spider guild composition between these latter two habitats (Table 2b). In grassland, ground weavers and non-weavers were the most abundant components of spider communities (Fig. 5d, Table 3).


(a) Natural forest

(b) Cultivated woodland

(c) Second growth

(d) Grassland

Fig. 5. Abundance (means ± SE) of various spider guilds in habitats receiving various degrees of Yami habitat management.

Comparison of environmental variables between habitats

The combination of PCC, middle and high level UVD were best correlated with spider guild composition according to the BIO-ENV analysis (RELATE test, Spearman rank coefficient Rho = 0.151, p = 0.019). These results indicate that vegetation structure was much more important than prey availability for determining spider diversity on Orchid Island.

Results of various multivariate and univariate tests on each environmental variable were congruent with the BIO-ENV results. Pair-wise ANOSIM tests comparing understory vegetation structures between habitats using UVD from three height levels showed significant differences between most habitat pairs (Table 4). The only insignificant ANOSIM test result was found between cultivated woodland and second growth. Results of PCC varied significantly among habitats (Table 5a), except between sampling plots of natural forest and cultivated woodland (Fig. 6a). UVD of three height levels were square root transformed to meet the normality assumption. Both high and middle level UVD varied significantly among habitats (Table 5b). In both height levels the density of cultivated woodland was significantly lower than that of the other habitats (Fig. 6b, c). Low level UVD also varied significantly among habitats (Table 5b), with three forest habitats exhibiting similar values but significantly larger value in grassland (Fig. 6d). The similarity in low level UVD among three forest habitats might explain why this variable was a non-

Table 4. Results of pair-wise ANOSIM tests comparing understory vegetation structures between different habitats in Orchid Island, Taiwan using UVD from three height levels.

Comparison	Understory vegetation complexity	
	R	p
Global R	0.305	0.001
natural forest vs cultivated woodland	0.213	0.004
natural forest vs secondary growth	0.098	0.031
natural forest vs grassland	0.709	0.001
cultivated woodland vs secondary growth	−0.044	0.860
cultivated woodland vs grassland	0.405	0.001
secondary growth vs grassland	0.456	0.001

Table 5. Results of two-way ANOVA tests comparing percent canopy cover (PCC) (a), understory vegetation density (UVD) (b) and insect availability (c) between different regions and habitats.

	Habitat		Region		Habitat × region	
	F	p	F	p	F	p
(a) PCC	496.513	0.000	5.2978	0.000	6.641	0.000
(b) UVD						
High level	4.157	0.011	6.631	0.003	3.859	0.003
Middle level	5.003	0.004	8.147	0.001	7.313	0.000
Low level	24.582	0.000	2.867	0.067	1.655	0.153
(c) Insect availability						
Insect abundance	2.451	0.075	2.364	0.105	3.295	0.009
Insect biomass	1.916	0.140	0.533	0.591	4.081	0.002

significant determinant of spider diversity in the BIO-ENV procedure.

Neither insect abundance (Fig. 7a) nor insect biomass (Fig. 7b) differed significantly between regions or habitats (Table 5c). Furthermore, the BIO-ENV procedure did not choose insect abundance or biomass as significant determinants of spider diversity. Our observations suggest that prey availability was generally quite homogenous among the four habitat types.

Discussion

Results of this study demonstrate that habitat management by the Yami affect spider communities of forests by altering vegetation structures. Overall species composition of spider assemblages and guild compositions varied among habitats, but insect abundance and biomass did not show a similar pattern. This result suggests that although insect prey availability can affect spider diversity through a bottom-up effect (Scheu and Schaefer 1998), it is not the major factor determining spider diversity on Orchid Island.

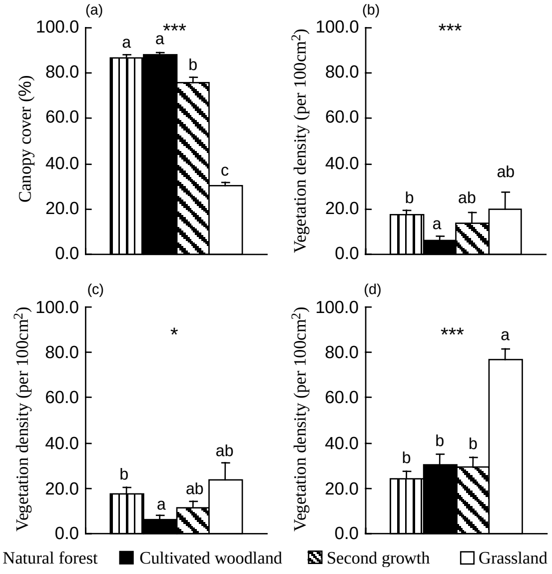


Fig. 6. Mean (±SE) canopy over (a) and high (b), middle (c), and low (d) level of understory vegetation complexities estimated from four types of habitats on Orchid Island, Taiwan. The labels above each graph are the result of one-way ANOVA test and Fisher's LSD mean comparisons. (*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$).

Comparison of PCC between natural forests and cultivated woodland indicates that long-term management by the Yami over several generations did not result in significant reduction of canopy cover. A significantly smaller canopy cover was seen in second growth, which received substantially more disturbances compared with those of the cultivated woodland. UVD in cultivated woodland and second growth were significantly lower, it seems as a result of Yami land management activity. In grassland, the open canopy cover permits development of a dense low level vegetation layer. The significant difference in spider composition between forest and grassland habitats may reflect also variation in microclimates and availabilities of web attachment sites. Grasslands have high abundance of ground runners but rather few orb and space weavers. This pattern probably resulted from lack of suitable microhabitats for web construction (vegetation too dense) and alternation in microclimates due to a much more open canopy (such as stronger wind).

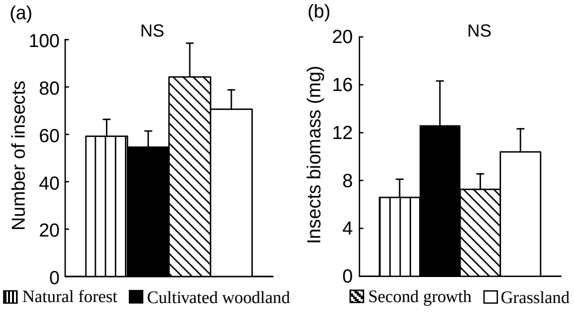


Fig. 7. Mean (±SE) insect abundance (a) and biomass (b) estimated from four types of habitats on Orchid Island, Taiwan. The labels above each graph are the results of one-way ANOVA test and Fisher's LSD mean comparisons. (NS: non significant at $\alpha = 0.05$ level.)

Although primary forests received a low level of disturbances and thus exhibited a high PCC and UVD, they did not have the highest spider diversity. Natural forest on Orchid Island was dominated by orb weavers, which construct more fragile webs than other groups and thus are more intolerant of frequent disturbances. Greenstone (1984) found a significant correlation between vegetation structural complexity and orb-weaver diversity in tropical forests in Costa Rica. Therefore, the dominance of orb weavers in sampling plots in natural forests might result from a high UVD and reflect the dominance of a few bush-dwelling orb-weaving species in relatively undisturbed rain forests as reported by Pfeiffer (1996).

Cultivated woodlands on Orchid Island exhibit the highest spider diversity. Clearing and logging conducted by the Yami at various scales may have reduced the abundance of the dominant species, thus increased the diversity of the spider communities. This hypothesis could be supported by a significantly higher Shannon-Weiner function in cultivated woodland. Compared with other diversity indices, the Shannon-Weiner function is more sensitive to the presence of rare species. Samples with higher species richness and more equal abundance between species will have higher values (Krebs 1989). A higher Shannon-Weiner function in cultivated woodlands indicates this habitat type has more species and a less skewed species abundance pattern. 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 understory vegetation layers. Compared with orb weavers, space weavers can endure a higher level of disturbance, which may explain why they are more abundant in cultivated woodland and second growth.

Chen and Tso (2004) also compared the spider diversity of habitats receiving different degrees of management, and found a higher spider diversity in cultivated woodland. Results of Chen and Tso (2004) and this study demonstrate that a moderate level of management seems to maintain high diversity in cultivated woodland. Such results are congruent with the intermediate disturbance hypothesis (IDH), which predicts the highest diversity or coexistence under intermediate level of disturbances (Connell 1978). Currently, studies investigating whether IDH plays significant role in generating high species diversity in tropical regions are few and almost all relevant studies examine tree diversity. The results show that intermediate level of disturbances generated by silvicultural operations, logging or hurricanes could enhance tree diversity (Cannon et al. 1998, Molino and Sabatier 2001, Sheil and Burslem 2003). So far, it is still not clear whether IDH also explains the high terrestrial animal diversity in tropical regions. Results of this study reveal an IDH pattern in spider diversities in a tropical island. While in previous relevant studies the gaps generated by disturbances are responsible for the changes in tree diversity in tropics, in our study the disturbances generated by Yami altered vegetation structure thus promote spider diversity. Currently, most relevant empirical studies (including ours) describe the IDH pattern rather than exploring the mechanisms (Shea et al. 2004). It will be worthwhile to conduct manipulative studies to assess the mechanisms generating the observed IDH pattern in Orchid Island.

Although the cultivated woodland and the second growth had similar spider guild composition and UVD, the later habitat exhibited lower species diversity and abundance. This might result from greater disturbance in the second growth forests. Second growth forests are all generated from clear-cuts and these forests are frequently harvested for twigs and branches to use as fuels (Wang 2004). In contrast, cultivated forests are rarely clear-cut. Moreover, significantly more open canopy cover in second growth is likely associated with a more variable range of microclimates. Although composition of various spider guilds was similar between these two habitats, dominant species differed among the various guilds. For example, the giant wood spider *Nephila pilipes* is one of the dominant orb weavers in cultivated woodland. But second growth was dominated by the smaller *Thelacantha brevispina*, *Tylorida striata* and *Leucauge decorata*. Spider guilds in second growth seem to be composed of small species with high dispersal abilities and tolerances to disturbances.

Currently, >80% of the island is covered by relatively stable primary forest, in which only 78 spider species were obtained. If the Yami did not inhabit Orchid Island and the whole island were covered by primary forest, the total spider diversity would be considerably lower than the current estimate of ca 160 species. However, the Yami introduce disturbance to the ecosystem through traditional practices and create habitat diversity, which are, in turn, inhabited by different assemblages of spiders.

Using simple tools and pure manpower, the Yami people have managed to convert <20% of primary forests into other habitats. However, these novel habitats enable the subsistence of spider species which are not able to subsist in primary forest, habitats which are dominated by orb weaving spiders. The Yami do not clear-cut primary forests on a large scale to create land for plantation but instead utilize existing habitats with a delicate rotation practice to maintain sustainable productivity of the land. In primary forests and cultivated woodlands, the Yami only conduct small-scale selective logging and seldom perform clear-cutting.

Second growth forests on Orchid Island are usually evolved from grassland or crop plantation. Large-scale disturbance is usually confined to fixed regions of the island, forests in the rest of the island only receive small-scale disturbance. So, in a small tropical island with an area of ca 46 km^2, the inhabiting aboriginals have efficiently extracted sufficient resources from the forests with delicate sustainable practices to support a population of ca 2000 people for 700 yr. By introducing small-scale disturbance to forests and confining large-scale disturbance to fixed regions, the diversity of the habitats are increased and the altered vegetation structure enhances a more diverse spider fauna.

Results of this study demonstrate that traditional habitat management by the Yami maintains and even promotes spider diversity in Orchid Island. However, the Yami are currently facing severe stresses from modernization and development (Severinghaus 1999). For example, although the Yami did not use currency 70 yr ago (Huang 1995), the use of money has greatly enhanced commercial activities of this island. Traditionally, natural resources were extracted only to fulfill the needs of individuals or the family groups (Cheng 2001). However, to meet various needs of modern society and tourists, some inhabitants are beginning to exploit natural resources to trade for money (Cheng 2001). Modernization step by step is changing the traditional values of the Yami (Huang 1995). Although the elderly people are still following traditional management practices, fewer and fewer younger Yami are involved in such practices (Cheng 2001). If this trend continues, the traditional management practices that have maintained the biodiversity of this island for hundreds of years may gradually disappear. Policies taking into account the roles of traditional habitat management in shaping the biodiversity, are urgently needed to conserve the cultural and biological diversities of Orchid Island.

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