Biodiversity and Conservation **12:** 2173–2194, 2003.
© 2003 *Kluwer Academic Publishers. Printed in the Netherlands.*

Ground spider diversity in the Kenting uplifted coral reef forest, Taiwan: a comparison between habitats receiving various disturbances

YU-LUNG HSIEH[1], YAO-SUNG LIN[1] and I-MIN TSO[2,*]
[1]*Department of Zoology, National Taiwan University, 106 Taipei, Taiwan, ROC;* [2]*Department of Biology, Tunghai University, 407 Taichung, Taiwan, ROC;* [*]*Author for correspondence (e-mail: spider@mail.thu.edu.tw; fax: +886-4-2359-0296)*

Received 26 October 2001; accepted in revised form 27 November 2002

Key words: Biodiversity, Ground spider, Kenting National Park, Taiwan, Uplifted coral reef forest

Abstract. The effects of various disturbances on diversity and community structures of ground spiders in the Kenting National Park uplifted coral reef forest were investigated using pitfall traps. In each of the following five sampling sites, ten trap stations were established and were monitored once every month for a whole year: primary forest, primary forest with tourism activities, secondary forest, grassland with tourism activities and abandoned grassland. A total of 2237 adult spiders from 20 families and 110 species were collected, among which 86 (78.2%) were new or newly recorded species to Taiwan. Dominant species can be divided into two major groups according to temporal abundance variations: abundant in the dry season and abundant in the wet season. Habitat preference of 12 dominant species was assessed by comparing their relative abundance between sampling sites. Half of the species exhibited strong habitat preference and two species could only be found in habitats receiving no tourism disturbance. The Shannon–Weaver function, Simpson index and Evenness were not significantly different among the sites, suggesting that these sites had a similar community structure characterized by few dominant species and numerous rare species. However, the species composition differed considerably among the five sites. Results of a UPGMA analysis using pairwise Euclidean distance demonstrated that specimens from 50 trap stations can be divided into four major clusters: primary forest, secondary forest, grassland I and grassland II. Also, among 110 species obtained, 61 were distributed in one sampling site only, and each site had between 11 and 16 unique species. In addition to species composition, foraging guild composition also differed significantly among sampling sites. These results suggest that the diversity of ground spiders in the KTNP uplifted coral reef forest is quite heterogeneous, and any management activity should consider the uniqueness of each habitat type.

Introduction

Currently, how different ways of habitat management affect diversity and community structures of terrestrial animals in Taiwan is poorly understood. Most relevant studies focused on the effect of forestry on avian diversity and communities in middle and high elevation mountains (Ting 1993; Lee 1995; Shiu 1995; Chen 1996a; Fang 1996, 1997). Results of these studies showed that elevation, vegetation structure and physiognomy were the major factors determining avian community structures in mountainous areas of Taiwan. Few researchers focused on the diversity and community structure of terrestrial animals in tropical regions in southern

Taiwan, an area which potentially has much higher species diversity. Nevertheless, studies examining the diversity of terrestrial arthropods, whose abundance and diversity greatly exceed those of vertebrates (May 1992), are extremely rare.

Kenting National Park (KTNP), the first national park in Taiwan, was established in 1982 to protect the unique geological scenery and natural resources of tropical southern Taiwan. During the past 20 years the marine (Chang and Chen 1987, 1989; Chang and Dai 1987; Chang et al. 1988; Shen et al. 1990; Dai 1999), freshwater (Chang 1985b; Lin and Tseng 1985; Lue 1985), insect (Chu 1986; Chu et al. 1988; Yang et al. 1990) and vertebrate (Lue 1985; Wang 1986; Severinghaus 1991; Wang and In 1992) fauna have been well established. However, the diversity and community structure of other terrestrial arthropods are still poorly understood. The uplifted coral reef forest is situated in the southeastern part of KTNP. Being one of the few tropical forests in Taiwan, this area exhibits high conservation value. Although this area is currently managed by national park systems, most of the original vegetation has already been changed from primary to secondary forests and grasslands during hundreds of years of anthropocentric activities (Chang 1985a; Shiu et al. 1985). Even after the establishment of the national park, this area is still receiving increasing pressure from tourism activities. Therefore, an understanding of the effect of various disturbances on diversity and community structures of organisms inhabiting this area is urgently needed, to serve as an important reference for future habitat management conducts.

In this study we investigated the effect of various disturbances on ground spider diversity in the KTNP uplifted coral reef forest. Spiders are among the most speciose orders of animals (Coddington and Levi 1991), and globally around 106 families and 36 500 species are documented (Platnick 2000). They are the most abundant insectivorous predators of terrestrial ecosystems (Nyffeler and Benz 1987; Wise 1993; Nyffeler 2000). Spiders are high-rank predators of the food chain and their phenology and community structures are closely affected by disturbance and vegetation structures. Compared with species inhabiting undisturbed temperate areas, species in habitats subjected to a high level of disturbance tend to have more than one generation per year (Maelfait and DeKeer 1990; Draney and Crossley 1999). Habitats exhibiting a high level of spatial heterogeneity are associated with high abundance and species richness of spiders (Greenstone 1984; Döbel et al. 1990; Gunnarsson 1992; Hurd and Fagan 1992; Sundberg and Gunnarsson 1994; Rypstra and Carter 1995; Docherty and Leather 1997; Balfour and Rypstra 1998; Tóth and Kiss 1999). Lower spider abundance and species diversity are characteristic of areas subjected to a high level of disturbance such as grazing (Gibson et al. 1992; Zulka et al. 1997), agricultural practice (Topping and Lövei 1997; Feber et al. 1998; Downie et al. 1999; Pekár 1999), forestry (Pettersson 1996) and burning (York 1999). Because of the aforementioned characteristics, spiders are suggested to be a good indicator of the effect of environmental impact on biodiversity (Oliver and Beattie 1996; Churchill 1998; Griffin 1998; Maelfait and Hendrickx 1998; Marc et al. 1999; Riecken 1999).

The aim of this study is to document the community structure, diversity, guild composition and seasonal abundance of ground spiders in habitats in KTNP subjected to various degrees of disturbance. Although relevant studies are quite abundant in temperate regions, the studies on diversity of ground spiders in tropical areas are still rare. Nevertheless, the effects of disturbance on diversity and community structure of tropical Araneae fauna are poorly understood. In the KTNP uplifted coral reef forest five major types of habitats can be found: primary forest, primary forest with tourism activities, secondary forest, grassland with tourism activities and abandoned grassland. By comparing the diversity and community structure of ground spiders between these five types of habitats, we hope to understand the effect of various types of disturbance on terrestrial arthropods of this tropical area.

Materials and methods

Study area

The uplifted coral reef forest (20°58′ N, 120°48′ E) is situated in the Kenting National Park (KTNP), Pingtung County, in southern Taiwan. Consisting mostly of coral reef limestone, this area is estimated to have emerged about 9000 years ago due to tectonic dynamics and is still uplifting at a speed of 2.5 mm per year (Shih et al. 1989). The altitude of this monsoon tropical forest ranges from 200 to 300 m with a total area of 267 ha and annual rainfall averages 2200 mm per year (1961–1990) (Su 1994). Ninety percent of annual precipitation is received during the half-year long monsoon (from May to October), and the other half of the year can be considered as the dry season. The study sites are located on the highest area of the uplifted coral reef forest.

Sampling sites

Ground spiders were sampled from pitfall stations established at five types of habitats in the KTNP uplifted coral reef forest (Figure 1). The first site (site A) is in a primary forest dominated by the coast persimmon (*Diospyros maritime*) and the Philippine drypetes (*Drypetes littoralis*) (Yu 1999). This site is currently a nature reserve managed by the Taiwan Forestry Research Institute since 1994 and only research activities are allowed. The second site (site B) is also situated in a primary forest and its floral composition and structure are similar to those of site A. However, there are trails, recreational facilities and tourist activities because this area is a scenery spot operated by the Taiwan Forestry Bureau. The third site (site C) is in a secondary forest consisting mainly of the horsetail tree (*Casuairina equisetifolia*) and white popinac (*Leucaena glauca*). Although a small amount of gathering activities by local people does occur, recreational activity is nearly absent in site C. The fourth site (site D) is in a grassland with patchy forests consisting mainly of Taiwanese acacia (*Acacia confusa*). This site has received intensive agricultural activity for a long time and currently is one of the recreation areas of KTNP. There are recreation facilities such as pavilions and trails and tourist activity was the highest among the five sampling sites. Also, a small amount of grazing by water buffaloes occurs in this site. The last site (site E) is also situated in a grassland and was once a recreation area of KTNP. However, this site has been deserted for some years. Therefore, site E receives less tourist disturbance compared with site D.

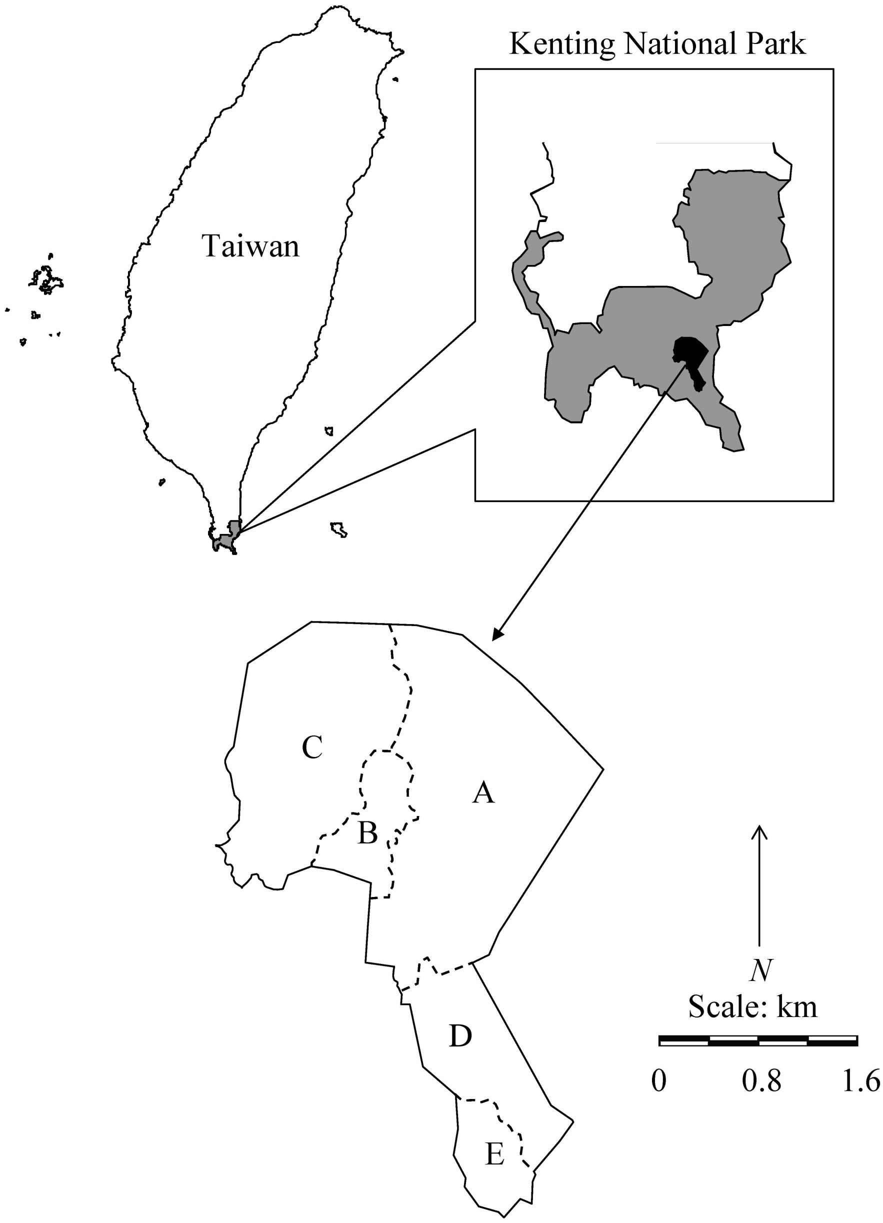

Figure 1. Map of the study sites in Kenting National Park uplifted coral reef forest area.

Sampling

Although having some disadvantages, pitfall traps have been extensively used to survey ground arthropods (Uetz and Unzicker 1976; Curtis 1980; Topping and Sunderland 1992; Topping and Luff 1995). Since the absolute density of spiders is not the goal of this study, we used pitfall traps to assess the community structure and diversity of ground spiders. In each site, 10 trap stations, each consisting of four collecting containers 11 cm in diameter and 14 cm in height, were established evenly along the trail. The average distance between two trap stations was about 100 m. The four containers were arranged in a ring with a diameter of 2.5 m. An inner cup was placed in each container for easy retrieval of specimens. Those containers were buried flush with the soil surface and filled with 0.5 l of 70% alcohol. A plastic plate was secured with sticks over each container to prevent rain or fallen leaves from entering the trap. Between February 2000 and January 2001, in each month the traps were opened for 7 days. Specimens obtained from four containers of each trap station were pooled together for analysis. Specimens collected were first sorted according to developmental stage and sex. Adult spiders were sorted into morphospecies and if possible identified to species by palpal organ or epigynum. Most immatures were identified to family and were not included in the analysis. Voucher specimens were deposited in the National Museum of Natural Science, Taichung, Taiwan.

Phenology

The abundance of 12 species of the ground spiders trapped was high enough to infer their reproductive activity patterns. The temporal abundance variation of trapped specimens can reflect both the density and activity level of a population (Uetz and Unzicker 1976). For many ground spiders, male spiders will increase their activity when searching for mate, and females will increase their activity while searching for food and suitable breeding sites (Draney 1997). Therefore, we used phenograms generated by temporal abundance variation of dominate species to infer dominant species' mating and breeding seasons.

Habitat preference

The distribution of a particular species of spiders among different sites can be used to assess its habitat preference pattern (Draney 1997). One way analysis of variance (ANOVA) tests were used to compare the relative abundance of 12 dominant species among five sampling sites. Fisher's least significant difference (LSD) tests were used to perform pairwise comparisons between sites. All the analyses were performed using SYSTAT 5.2 (Wilkinson et al. 1992).

Diversity and community structure analyses

The Shannon–Weaver function and Simpson index were used to compare the community structures of ground spiders among different sites. The Shannon–Weaver function (H) is expressed as

$$H = -\sum(P_i) \times (\ln P_i)$$

where P_i is the percentage of species i in the total community. Samples having high species richness and equal abundance between species will generate higher H values. The Simpson index (D) is expressed as:

$$D = \sum P_i^2$$

Samples represented by few dominant species and many rare species will generate large D values, therefore, the Simpson index can be used to assess the degree of dominance of the sample. The value of the Shannon–Weaver function is more sensitive to the presence of rare species in the sample. On the other hand, the value of the Simpson index is less affected by rare species. We also calculated the evenness index, which is expressed as

$$E = \frac{H}{\ln S}$$

where S is the species number of the community. The value of evenness ranges from 0 to 1, which measures the degree of homogeneity in abundance between species. For all three indices one-way ANOVA tests were used to compare the values derived from the five sampling sites.

Similarity between sampling sites

In addition to the often used indices such as H, D and E, we also used the similarity index to enable a closer examination of species composition in each sampling site. Although they differ in equations used, values of the aforementioned diversity indices are all derived from functions of the relative abundance of species obtained. Habitats having totally different species composition but similar species number and abundance pattern will have similar diversity index values. However, similarity indices can assess the similarity between habitats by considering both species composition and relative abundance. In this study, because a large sample was obtained, the quantitative Euclidean distance method (Krebs 1989) was used. Euclidean distance is expressed as

$$\Delta JK = \sqrt{\sum(X_{ij} - X_{ik})^2}$$

where ΔJK is the similarity between community J and K; X_{ij} the abundance of species i in community J and X_{ik} the abundance of species i in community K. A small ΔJK value means that the habitats are similar in terms of composition and relative abundance of species. The pairwise Euclidean distances were subjected to a UPGMA clustering analysis to visualize the association pattern of species collected in different trap stations.

Guild composition

Guild compositions of ground spiders in five different sites were compared to have another way of examining how community structure varies with habitat and disturbance. Many foraging modes are found in spiders, such as web-spinning, sit-and-wait ambush and active hunting. Each guild has a unique need for vegetation structure and microhabitat and each responds differently to disturbance. Therefore, a comparison of guild composition can provide insights about the effect of habitat alternation and disturbance on biodiversity. Spiders were assigned to the following guilds according to their mode of foraging (modified from Corey et al. 1998): (1) sit-and-wait ambusher: Lycosidae, Ctenidae, Heteropodidae, and Thomisidae; (2) active hunters: Clubionidae, Gnaphosidae, Oonopidae, and Salticidae; (3) aerial web spinners: Theridiidae, (4) ground level web builders: Agelenidae, Linyphiidae, Hahniidae; Hexathelidae, (5) the ant-eating Corinnidae and Zodariidae. For each site, the abundance of each guild was calculated and χ^2 tests of homogeneity were performed between each pair of sites.

Results

Ground spider fauna in the KTNP uplifted coral reef forest

A total of 4483 individuals were obtained from 50 trap stations operated for 12 months and 110 species from 20 families were found from adult specimens (n = 2247) (Figure 2, Table 1). Linyphiidae made up the largest portion of individual spiders collected (32.9%), followed by Lycosidae (30.6%), Clubionidae (9.9%), Zodariidae (9.5%), Theridiidae (8.2%), Ctenidae (3.1%), Gnaphosidae (1.8%) and Corinnidae (1.1%). Linyphiidae also has the greatest number of species (27), followed by Theridiidae (21), Lycosidae (12), Salticidae (10), Gnaphosidae (8) and Zodariidae (5). The most abundant species was Linyphiidae B; a total of 567 individuals (25.2%) were found. The second most abundant species was *Pardosa tschekiangensis* (n = 339, 15.1%), followed by *Phrurolithus lynx* (n = 221, 9.8%), *Lycosa boninensis* (n = 109, 4.9%), *Mallinella fulvipes* (n = 108, 4.8%), and *Mallinella shimojanai* (n = 100, 4.5%) (Table 2). Although only adult specimens were included in the analysis, the presence of numerous juvenile giant crab spiders (Sparrisidae) is worth mentioning. A total of 454 juvenile giant crab spiders were obtained. An ANOVA analysis examining their distribution across five sites showed that most of them inhabited the forest sites ($F = 16.08$, $P < 0.0001$).

Ten species of ground spiders were collected from all five sites, which included *Phrurolithus lynx*, *Ctenus yaeyamensis*, Linyphiidae B, Linyphiidae L, *Lycosa boninensis*, *Pardosa tschekiangensis*, *Pardosa* sp. J, Lycosidae L, *Mallinella shimojanai* and *Mallinella fulvipes*. Three species were found in four sites. Linyphiidae AB was found in all sites except C and *Venonia spirocysta* and *Dipoena mustelina* were only absent in site D. Sixty-one (55.5%) of the 110 species were collected at only one site (Table 1). Eighty-six (78.2%) species collected in this

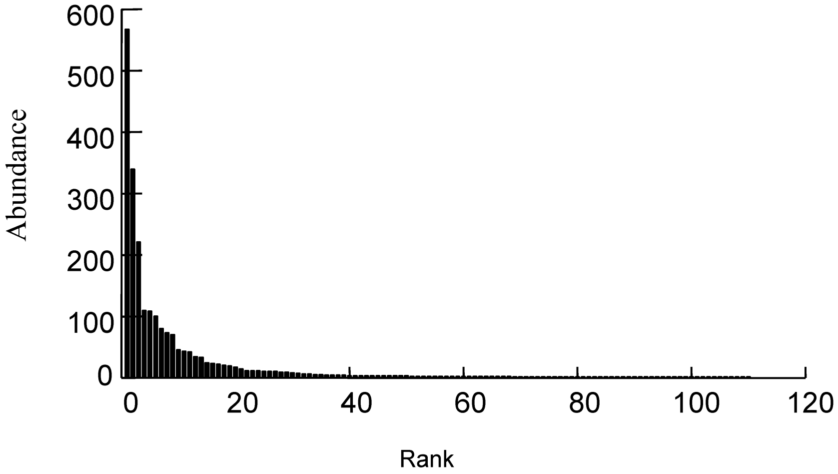

Figure 2. The abundance of each species ranked according to number of adult specimens collected.

study were new or newly recorded species to Taiwan. Among those novelties, species of the family Corinnidae and Mimetidae are found in Taiwan for the first time.

Phenology

Phenograms of the 12 most abundant species were generated according to their monthly abundance patterns (Figure 3). Among them three patterns can be distinguished: (1) abundant in the dry season (November–April of next year), including Linyphiidae B (Figure 3a), *Pardosa tschekiangensis* (Figure 3b), *Phrurolithus lynx* (Figure 3c), Theridiidae G (Figure 3h), *Ctenus yaeyamensis* (Figure 3i), Linyphiidae L (Figure 3j) and *Hippasa holmera* (Figure 3k). Most immature individuals of *P. tschekiangensis*, *P. lynx*, *C. yaeyamensis* and Linyphiidae L also appeared in this period. (2) Abundant in winter, including *Pardosa* sp. J. (Figure 3g) and Lycosidae L (Figure 3l). (3) Abundant in the wet season (May–October): most ground spider species strongly decreased in quantity during the monsoon, but the abundance of *Mallinella fulvipes* (Figure 3e), *M. shimojanai* (Figure 3f) and *Lycosa boninensis* (Figure 3d) peaked in that period.

Habitat preference

Results of ANOVA tests examining abundance of dominant spiders between five habitats indicate that *Pardosa tschekiangensis*, *Mallinella fulvipes*, *M. shimojanai*, Theridiidae G, *Ctenus yaeyamensis* and *Hippasa holmera* exhibited strong habitat preference (Table 2). *Mallinella fulvipes* and *M. shimojanai* tended to be more abundant in primary forest sites A and B. *C. yaeyamensis* was most abundant in the

Table 1. A list of ground spider species collected from KTNP uplifted coral reef forest.

Taxon	Sampling site (male/female)					Totals
	A	B	C	D	E	
Hexathelidae						
Macrothele gigas (Shimojana and Haupt 1998)			1/0			1
Macrothele holsti (Pocock 1901)	1/0	7/0		2/0		10
Totals						11
Agelenidae						
Paracoelotes taiwanensis (Wang and Ono 1998)		2/0	1/0			3
Totals						3
Clubionidae						
Phrurolithus lynx (Kamura 1994)	16/19	40/25	24/21	27/18	18/13	221
Clubionidae H		1/0				1
Clubionidae Q				1/0		1
Totals						223
Corinnidae						
Castianeira flavimaculata (Hu et al. 1985)	1/0			3/1	12/2	19
Corinnidae B				2/0	1/0	3
Corinnidae C					2/0	2
Corinnidae D				1/0		1
Totals						25
Ctenidae						
Ctenus yaeyamensis (Yoshida 1998)	15/25	6/9	0/8	2/1	3/1	70
Totals						70
Gnaphosidae						
Zelotes sp. A	1/0					1
Gnaphosidae B			1/0	2/0	7/1	11
Gnaphosidae BD				1/0		1
Gnaphosa sp. E			1/0	3/0	6/0	10
Gnaphosidae F		2/0	1/0		5/1	9
Gnaphosidae G				0/2	0/1	3
Zelotes iriomotensis (Hayashi 1994)		0/1			1/0	2
Gnaphosidae K	1/0		2/1			4
Totals						41
Linyphiidae						
Linyphiidae A	1/0		1/0			2
Linyphiidae B	101/24	99/34	47/26	69/10	144/13	567
Linyphiidae D	0/1		1/1	0/1		4
Linyphiidae L	0/6	0/6	0/22	2/2	0/7	45
Linyphiidae M			0/1	0/1		2
Linyphiidae N			1/0		1/0	2
Linyphiidae O			4/0			4
Linyphiidae P				2/0		2
Linyphiidae Q				0/3		3
Linyphiidae T	6/3	8/3	2/1			23
Linyphiidae W			1/0	3/2		6
Linyphiidae X				11/0	8/1	20
Linyphiidae AA					0/3	3
Linyphiidae AB	0/1	0/1		0/4	0/5	11
Linyphiidae AC					0/1	1
Linyphiidae AD					2/0	2
Linyphiidae AE					1/0	1
Linyphiidae AF					6/0	6
Linyphiidae AH					0/3	3
Linyphiidae AO		2/0				2
Linyphiidae AP	3/0	13/0	1/0			17

Table 1. (*continued*)

Taxon	Sampling site (male/female)					Totals
	A	B	C	D	E	
Linyphiidae AQ		1/0				1
Linyphiidae AR		1/0				1
Linyphiidae AT				2/0	6/1	9
Linyphiidae AU				1/0		1
Linyphiidae BF			1/0			1
Linyphiidae BH			1/0			1
Totals						740
Lycosidae						
Lycosidae A	2/0	0/1				3
Lycosa boninensis (Tanaka 1989)	15/16	13/20	6/2	8/5	16/8	109
Hippasa holmera (Thorell 1895)				10/2	23/8	43
Pardosa tschekiangensis (Schenkel 1963)	6/4	7/1	2/0	87/51	127/54	339
Pardosa procurva (Yu and Song 1988)		0/1		3/1	22/6	33
Pardosa sp. J	0/24	0/25	0/6	0/14	0/11	80
Lycosidae L	0/10	0/6	0/18	0/6	0/2	42
Lycosidae M	4/1	6/0	2/0			14
Venonia spirocysta (Cai 1993)	0/2	0/5	0/3		0/1	11
Arctosa meitanensis (Yin et al. 1993)		2/0	7/1			10
Lycosidae Q					3/0	3
Lycosidae X					1/0	1
Totals						688
Mimetidae						
Mimetus sp.	1/0					1
Totals						1
Nesticidae						
Nesticella taiwan (Tso and Yoshida 2000)	1/0					1
Totals						1
Oonopidae						
Oonopidae A	0/1					1
Oonopidae B				6/1	1/0	8
Oonopidae C	1/0					1
Oonopidae D				3/0		3
Totals						13
Oxyopidae						
Oxyopes sertatus (Koch 1877)				2/0	2/1	5
Totals						5
Pholcidae						
Pholcidae A	1/0					1
Totals						1
Salticidae						
Salticidae A		1/0				1
Plexippus setipes (Karsch 1879)				0/1	0/1	2
Salticidae C					3/0	3
Pancorius taiwanensis (Peng et al. 2002)		0/1	0/3		1/0	5
Sitticus wui (Peng et al. 2002)	0/1					1
Salticidae F		1/0				1
Salticidae G					1/0	1
Salticidae H			1/0			1

Table 1. (*continued*)

Taxon	Sampling site (male/female)					Totals
	A	B	C	D	E	
Phintella piatensis (Barrion and Litsinger 1995)		0/1				1
Plexippus paykulli (Audouin 1826)				1/0	1/0	2
Totals						17
Scytodidae						
Scytodidae A	1/0		0/1			2
Scytodes thoracica (Latreille 1804)				1/0		1
Totals						3
Sparrasidae						
Sparrasidae A			0/2			2
Sparrasidae B	1/0					1
Sparrasidae D		0/1				1
Totals						4
Tetragnathidae						
Leucauge sp.			0/1			1
Totals						1
Theridiidae						
Dipoena mustelina (Simon, 1888)	0/1	1/11	8/9		3/1	34
Theridiidae B		0/2				2
Theridiidae E	4/0	3/0		3/0	14/0	24
Theridiidae G	13/0	20/0	40/0			73
Dipoena sinica (Zhu 1992)		1/0				1
Theridiidae K		1/0				1
Theridiidae S	0/2					2
Theridiidae V				0/1		1
Theridiidae Z				1/0	3/0	4
Theridiidae AJ					1/0	1
Dipoena sp. AL	10/3	6/1	2/0			22
Dipoena sp. AM	4/0	3/0				7
Dipoena sp. AS	0/1		0/2			3
Theridiidae AV				0/1		1
Theridiidae CA			0/1			1
Theridiidae CB	1/0					1
Theridiidae CC			1/0			1
Theridiidae CD		1/0				1
Theridiidae CE	1/0					1
Theridiidae CF		2/0				2
Theridiidae CG		1/0				1
Totals						184
Thomisidae						
Thomisidae A				0/1		1
Thomisidae B				2/0		2
Totals						3
Zodariidae						
Zodariidae B		0/2				2
Mallinella shimojanai (Ono and Tanikawa 1990)	43/15	18/12	1/6	3/0	1/1	100
Mallinella fulvipes (Ono and Tanikawa 1990)	54/6	32/2	9/0	4/0	1/0	108
Australutica sp. E		0/2				2
Zodariidae F			0/1			1
Totals						213

Table 2. Results of ANOVA tests examining habitat preference of 12 abundant ground species from KTNP uplifted coral reef forest inferred from relative abundance between habitats.

Species	Abundance	Percentage (%)	Adults in each site					F ratio	LSD mean comparison	Significance levels
			A	B	C	D	E			
Linyphiidae B	567	25.2	125	133	73	79	157	0.43	A = B = C = D = E	NS
Pardosa tschekiangensis	339	15.1	10	8	2	138	181	11.98	D, E > A, B, C	***
Phrurolothus lynx	221	9.8	35	65	45	45	31	0.71	A = B = C = D = E	NS
Lycosa boninensis	109	4.9	31	33	8	13	24	1.07	A = B = C = D = E	NS
Mallinella fulvipes	108	4.8	60	34	9	4	1	2.71	A, B > C, D, E	*
Mallinella shimojanai	100	4.5	58	30	7	3	2	2.96	A, B > C, D, E	*
Pardosa sp. J	80	3.6	24	25	6	14	11	0.80	A = B = C = D = E	NS
Theridiidae G	73	3.2	13	20	40	0	0	1.01	B, C > A, D, E	***
Ctenus yaeyamensis	70	3.1	40	15	8	3	4	4.73	A > B, C, D, E	**
Linyphiidae L	45	2.0	6	6	22	4	7	0.83	A = B = C = D = E	NS
Hippasa holmera	43	1.9	0	0	0	12	31	4.66	E > A, B, C, D	**
Lycosidae L	42	1.9	10	6	18	6	2	1.11	A = B = C = D = E	NS

$^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. NS: Not significant at the $\alpha = 0.05$ level.

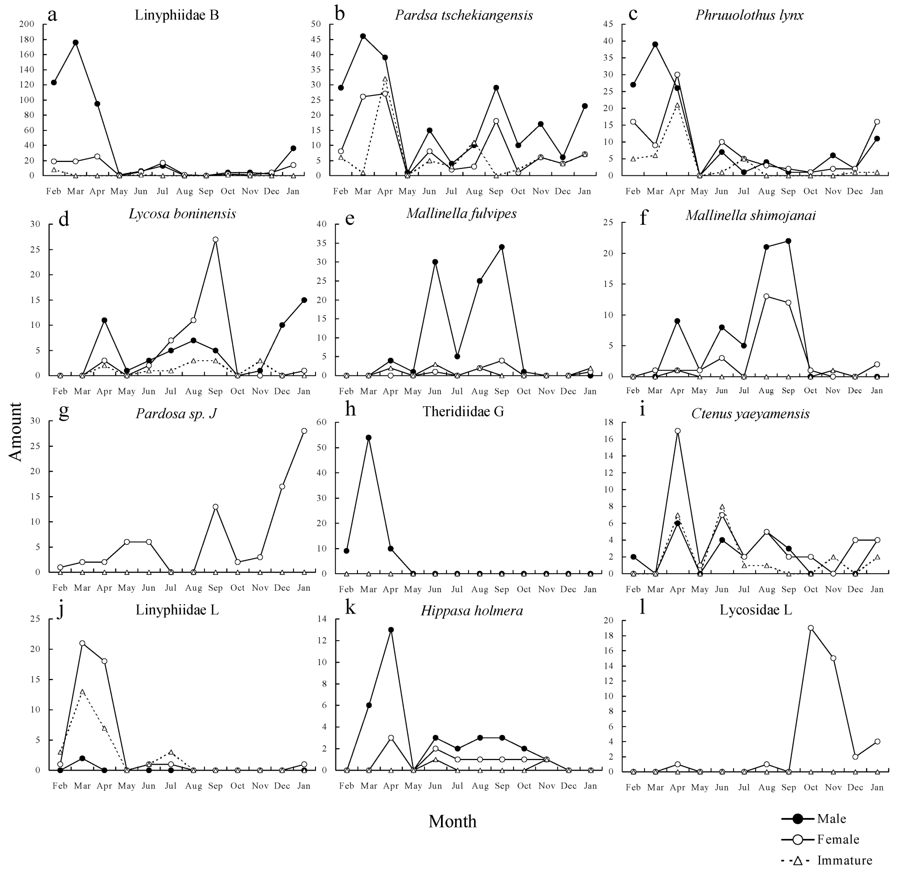

Figure 3. Phenograms of 12 most abundant ground spider species in KTNP uplifted coral reef forest.

primary forest site A. The aerial weaver Theridiidae G can only be found in forest sites A, B and C. On the other hand, *P. tschekiangensis* and *H. holmera* were more abundant in grassland sites D and E.

Community structure analyses

The number of species found in site E was the highest among the five sites (45 species; Table 3). The primary forest site A contained the lowest number of species sampled (39 species) but the highest number of families (16 families). The most abundant site is E; from 10 trap stations a total of 595 adult spiders were found. The least abundant site was C; only 307 adult spiders were sampled. Each site had a considerable number of unique species. There were 16 unique species in site B, but only 10 in site C. Although the five sites differed in abundance, species richness and number of unique species, they did not differ significantly in three diversity indices

Table 3. Richness, abundance, diversity indices and evenness of different sites.

Site	Species richness	Family richness	Abundance	Unique species	Shannon index	Simpson index	Evenness
A	39	16	475	11	2.57	0.88	0.70
B	44	11	474	16	2.72	0.88	0.72
C	41	13	307	10	2.73	0.89	0.73
D	42	14	397	12	2.42	0.82	0.65
E	45	11	595	12	2.43	0.83	0.64

examined (Shannon–Weaver function: $F = 0.40$, $P > 0.05$; Simpson index: $F = 0.56$, $P > 0.05$; Evenness: $F = 0.87$, $P > 0.05$).

Similarity between sampling sites

The result of a UPGMA analysis using Euclidean distance showed that specimens from the 50 trap stations could be clustered into four main groups (Figure 4). Most traps from sites A and B were grouped together (Primary forest, Figure 4) and most traps from site C were clustered together (Secondary forest, Figure 4). Trap stations from sites D and E were divided into two distinct groups. One cluster consisted of trap stations established near forest sites (Grassland II, Figure 4) and the other cluster represented trap stations situated in the interior areas of sites D and E (Grassland I, Figure 4). Most of the traps from sites A and B were grouped together, but some traps from site C were grouped with A and B. Some traps from site B were also grouped with site C.

Guild composition between sites

The guild composition of ground spiders in all five sites is shown in Figure 5. Pairwise comparisons between sites using χ^2 tests of homogeneity indicated that guild compositions in the five sites were all significantly different from each other (Table 4). The sit-and-wait ambushers tended to be more abundant in the grassland, and consisted mostly of Lycosidae. The aerial web spinner Theridiidae tended to be more abundant in the forest sites (A, B and C), and few individuals were found in the grassland. Ground level web builders, such as Linyphiidae, were equally

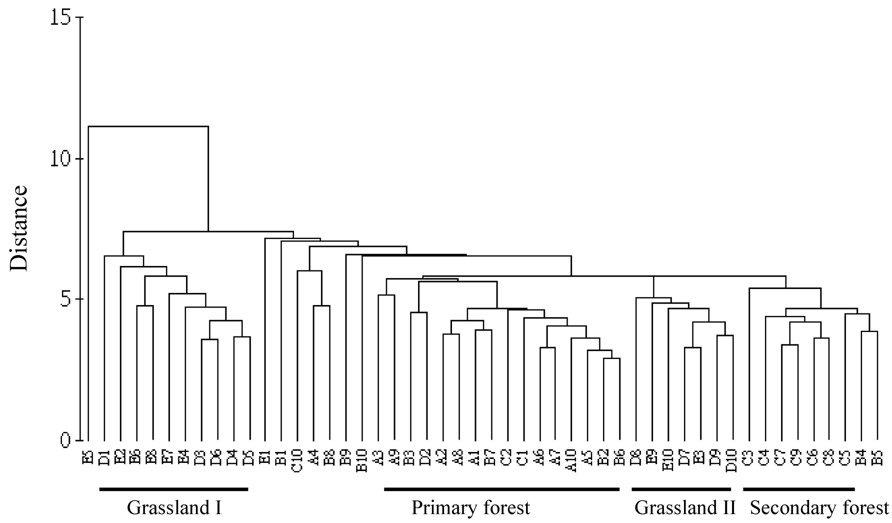

Figure 4. Results of a UPGMA analysis using Euclidean distance estimated from 50 trap stations established in five sites.

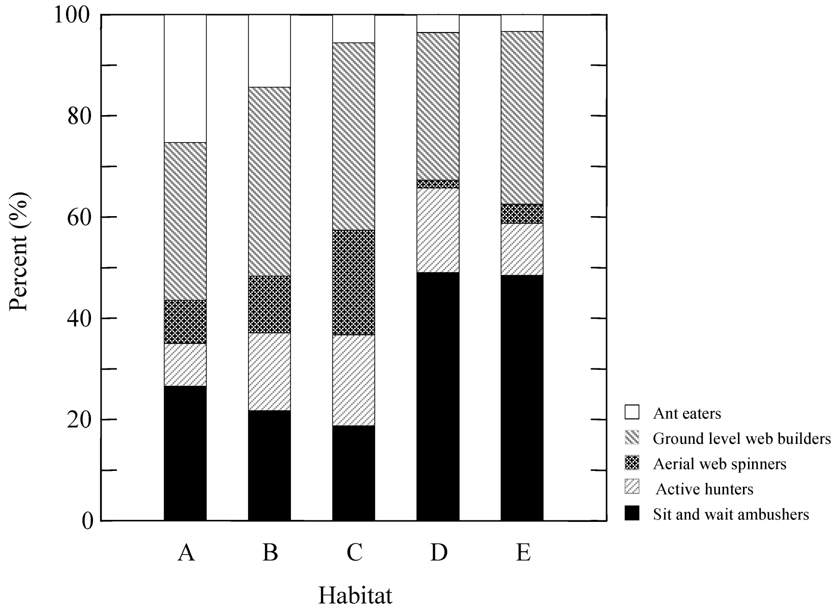

Figure 5. Ground spider guild composition of five sites in KTNP uplifted coral reef forest.

Table 4. Results of χ^2 tests of homogeneity examining ground spider guild composition between each pair of sites.

	A	B	C	D	E
A					
B	30.25***				
C	82.10***	25.90***			
D	126.46***	106.73***	112.28***		
E	140.51***	116.90***	119.68***	13.46**	

$^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

abundant in all five sites. Corinnidae and Zodariidae were most abundant in primary forest sites and were the major components of ground spider fauna there.

Discussion

This is the first study in Taiwan that aims to systematically examine the diversity and community structure of ground spiders. In addition to an understanding of how community structures vary with various types of habitat and disturbance, this study also yields many ground spider taxa new to the Taiwanese fauna. A total of 86 (78.2%) new or newly recorded species were found in this study. This finding greatly increases the number of documented Araneae species in Taiwan, for previously only less than 300 spider species were recorded (Chen 1996b). Among the 86 previously unrecorded species Linyphiidae is the most specious family (27 species) and it makes up the largest portion of individual spiders collected (32.9%). Currently, the diversity of Linyphiidae in Taiwan is poorly known, because most members of Linyphiidae are too small to collect and identify. Linyphiidae is also the most dominant ground spider taxon in most relevant studies conducted in temperate areas (Maelfait and DeKeer 1990; Gibson et al. 1992; Docherty and Leather 1997; Feber et al. 1998; Draney and Crossley 1999).

In the KTNP uplifted coral reef forest area, there are 60 (54.5%) species that can only be found in one sampling site. Among the five sampling sites, the number of unique species ranges from 11 to 16. The number of unique species in the primary forest (27) is higher than those in the secondary forest (10) and grassland (24); and the number of unique species in all the primary forest sites (37) is much higher than in all the grassland sites combined (D and E) (24). In terms of habitat structure, site A is similar to site B and site D is similar to site E. However, these sites each had a unique array of endemic species. Therefore, the distribution of species in the KTNP uplifted coral reef forest is not homogenous. Severe alteration of any habitat will result in loss of a number of unique species.

Based on the phenograms generated from the temporal abundance patterns of 12 dominant species, two major patterns can be concluded. The first pattern is represented by species whose abundance peaks in the dry season and dramatically decreases in the wet season. Most of the 12 dominant species follow this abundance pattern. The second pattern is characterized by species whose abundance peaks in the wet season. There were three species whose number peaked in the wet season, and they were all forest dwellers (*Lycosa boninensis*, *Mallinella fulvipes*, and *M. shimojanai*). This pattern suggests that species inhabiting forest habitats may gain more protection from heavy rainfall during the wet seasons. The temporal abundance patterns among sympatric ground spider species indicates that they might be active during different times of the year due to niche differentiation. For example, *Ctenus yaeyamensis*, *M. fulvipes*, and *M. shimojanai* are all abundant in site A. However, *C. yaeyamensis* is abundant in the spring (February–April) but *M. fulvipes* and *M. shimojanai* are abundant in the wet season (May–October). Species also abundant in site A but peaking in the winter, such as *Pardosa* sp. J and Lycosidae L, could be another case of niche differentiation. More research is needed to understand the ecological interactions between species exhibiting different types of temporal and spatial abundance patterns.

Among the five sampling sites, no difference is found in all three diversity indices examined, which indicates that their community structures are quite similar to each other. Low values of the Shannon–Weaver function and high values of the Simpson index suggest that the ground spider community in the KTNP uplifted coral reef forest is characterized by a few dominant species and numerous rare species (Figure 2). While there was no significant difference in diversity indices between sites, species composition differed considerably. Results of a UPGMA analysis showed that parts of sites D and E were clustered together and were separated from all other trap stations. This pattern indicates that the species composition differs considerably between the grassland and forest. The rest of the trap stations can be grouped into three major clusters. The first one is composed of trap stations in primary forest sites

A and B. This pattern suggests that although site B receives tourist disturbance, its species composition in general is not significantly different from that of the protected primary forest site A. The second cluster is composed of several trap stations from grassland sites D and E. The tree topology in Figure 4 shows that this cluster has a close relationship with forest sites. Trap stations in this cluster are those near patches of Taiwanese acacia (*Acacia confusa*), the dominant tree species in secondary forest. Other grassland trap stations in the open field are grouped in another cluster, which is distantly related to forest sites. Therefore, trap stations in the second grassland cluster seem to represent ecotone fauna between grassland and forest. The third cluster is composed of trap stations from secondary forest site C. Gibson et al. (1992) found that in some agricultural ecosystems the spider diversity in disturbed sites was an impoverished version of the undisturbed sites. In this study, however, the ground spider diversity in secondary forest site C was not an impoverished version of the primary forest sites A and B. Although some of the trap stations in site C were clustered with A and B, most were grouped by themselves into a coherent cluster. This result has important conservation implications, because in KTNP the ground spider diversity in secondary forests differs considerably from that of primary forests. Therefore, when a primary forest is replaced by secondary forest, although the community structure and species richness after recolonization may be similar, the preexisting unique fauna is lost.

When the spiders were assigned to different guilds according to their foraging mode and the guild composition of the five sites was compared, significant site-specific patterns emerged. For example, the abundance of sit-and-wait ambushers in habitats D and E is almost half of that obtained for all spiders. However, the percentage of this guild in the forest is only around 20%. *Pardosa tschekiangensis* is the dominant sit-and-wait ambusher in grassland site D. Theridiidae, the aerial web spinner, were abundant in sites A, B and C. This may result from Theridiidae's exclusive reliance on aerial webs, and forest sites provide more suitable microhabitats for web construction. Another major guild consisted of ant-eating Corinnidae and Zodariidae, which were abundant in primary forest sites A and B. More effort on these spiders' foraging behavior and ecology is needed to understand why these spiders prefer primary forest sites. While most guilds show a site-specific preference pattern, the ground level web spinners are distributed evenly among the five habitats. Most species of this guild are Linyphiidae, which exhibit strong dispersal abilities by ballooning (Decae 1987). Due to the small body size, members of the family Linyphiidae can even balloon at adult stages (Decae 1987). The strong dispersal ability exhibited by Linyphiidae may explain why they are the major foraging guilds in all five sites. Another guild showing more or less equal distribution across the five sites is active hunters. A higher mobility exhibited by members of this guild may be responsible for their homogeneous distribution pattern.

Disturbance generated by tourism activities seems to affect ground spider diversity not on the community but on the species level. The primary forest site B receives significantly more tourist disturbance than site A and the grassland site D also experiences heavier tourist activities than site E. However, no significant difference in community structure is found between A and B or between D and E. Moreover, results of UPGMA analysis showed that most pitfall stations from primary forest sites A and B were clustered together, and so were those from grassland sites D and E. However, at the species level, the presence of tourist disturbance does correlate with the abundance of certain species. For example, *Ctenus yaeyamensis* were significantly more abundant in site A than in site B and *Hippasa holmera* were significantly more abundant in site E than in site D. Distribution patterns of these species suggest that disturbance associated with tourism activities may affect biodiversity in KTNP, at least on the species level.

This study provides insights on both the conservation of biodiversity in KTNP and the methodology of diversity study. The three major habitat types in the KTNP uplifted coral reef forest (primary forest, secondary forest and grassland) each have a unique array of species, so all exhibit high conservation values. Even though the secondary forests were derived from the primary forests, their biodiversity is not merely a subset of that of primary forest but contains a considerable number of species not seen from other habitats. Although sites having similar habitat structure but receiving different levels of disturbance were similar in species composition and abundance pattern, certain species showed a significant preference for undisturbed areas. So, in both primary forest and grassland disturbance generated from tourism activities will affect biodiversity on the species level. Methodologically, the traditionally used diversity indices should not be solely relied upon in diversity studies because, as is shown in this study, habitats may have a quite different assemblage of species but have very similar index values. We should use different approaches and examine diversity at both community and species levels to be able to identify the effect of environmental factors on biodiversity.

Acknowledgements

We wish to thank the previous president W.S. Lee of Kenting National Park and C.D. Chien of the Taiwan Forestry Research Institute for many types of support. We are indebted to C.I. Tsai for accommodation, I.C. Chou for assistance in the field work, H.Y. Wu and M.W. Fang for providing detailed maps of study sites, and Dr D.L. Newquist for editing the manuscript. We also would like to thank many volunteers for assistance in field and laboratory work. This study is supported by a National Science Council (Taiwan, ROC) grant (NSC89-2311-B-002-031) to Y.S.L. and is partially supported by a NSC grant (NSC89-2621-Z-029-006) to I.M.T.

References

Balfour R.A. and Rypstra A.L. 1998. The influence of habitat structure on spider density in a no-till soybean agroecosystem. Journal of Arachnology 26: 221–226.

Chang H.M. 1985a. A study of plant communities in Sheng-Jiau Wan Coast Forest Ecological Reserve. Conservation Research Report Number 7. Kenting National Park, Taiwan, ROC (in Chinese).

Chang W.C. 1985b. A study of the ecology and distribution of terrestrial molluscs in Kenting National Park. Conservation Research Report Number 23. Kenting National Park, Taiwan, ROC (in Chinese).

Chang K.S. and Chen C.P. 1987. An ecological research on coral reef and marine fauna: an investigation on benthic invertebrates. Conservation Research Report Number 42-5. Kenting National Park, Taiwan, ROC (in Chinese).

Chang K.S. and Chen M.S. 1989. An ecological study of marine molluscs of Kenting National Park. Conservation Research Report Number 60. Kenting National Park, Taiwan, ROC (in Chinese).

Chang K.S. and Dai C.F. 1987. A study of coral reef and marine ecology in Kenting National Park: distribution and community ecology of corals. Conservation Research Report Number 42-4. Kenting National Park, Taiwan, ROC (in Chinese).

Chang K.S., Dai C.F. and Chen M.S. 1988. A study of the soft coral of Kenting National Park. Conservation Research Report Number 53. Kenting National Park, Taiwan, ROC (in Chinese).

Chen E.L. 1996a. The effects of edge on the bird community in Fushan, Master Thesis, National Taiwan University, Taipei, Taiwan, ROC (in Chinese).

Chen S.H. 1996b. A checklist of spiders in Taiwan. Annuals of Taiwan Museum 39: 123–156 (in Chinese).

Chu Y.I. 1986. A study of insect fauna in Kenting National Park. Conservation Research Report Number 36. Kenting National Park, Taiwan, ROC (in Chinese).

Chu Y.I., Lin M.J. and Liu L.D. 1988. The research of insects and spiders in Kenting National Park. Conservation Research Report Number 48. Kenting National Park, Taiwan, ROC (in Chinese).

Churchill T.B. 1998. Spiders as ecological indicators in the Australian tropics: family distribution patterns along rainfall and grazing gradients. Proceedings of the 17th European Colloquium of Arachnology, Edinburgh 1997. British Arachnological Society, Cambridge, UK, pp. 325–330.

Coddington J.A. and Levi H.W. 1991. Systematics and evolution of spiders. Annual Review of Ecology and Systematics 22: 565–592.

Corey D.T., Stout I.J. and Edwards G.B. 1998. Ground surface spider fauna in Florida sandhill communities. Journal of Arachnology 26: 303–316.

Curtis D.J. 1980. Pitfalls in spider community studies (Arachnid, Aaneae). Journal of Arachnology 8: 271–280.

Dai C.F. 1999. A study of the succession of coral communities in Kenting National Park. Conservation Research Report Number 105. Kenting National Park, Taiwan, ROC (in Chinese).

Decae A.E. 1987. Dispersal: ballooning and other mechanisms. In: Nentwig W. (ed.), Ecophysiology of Spider. Springer-Verlag, Berlin, Germany, pp. 348–356.

Döbel H.G., Denno R.F. and Coddington J.A. 1990. Spider (Araneae) community structure in an intertidal salt marsh: effects of vegetation structure and tidal flooding. Environmental Entomology 19: 1356–1370.

Docherty M. and Leather S.R. 1997. Structure and abundance of arachnid communities in Scots and lodgepole pine plantations. Forest Ecology and Management 95: 197–207.

Downie I.S., Wilson W.L., Abernethy V.J., McCracken D.I., Foster G.N., Ribera I. et al. 1999. The impact of different agricultural land-use on epigeal spider diversity in Scotland. Journal of Insect Conservation 3: 273–286.

Draney M.L. 1997. Ground-layer spiders (Araneae) of a Georgia piedmont floodplain agroecosystem: species list, phenology and habitat selection. Journal of Arachnology 25: 333–351.

Draney M.L. and Crossley D.A. Jr. 1999. Relationship of habitat age to phenology among ground-dwelling Linyphiidae (Araneae) in the southeastern United States. Journal of Arachnology 27: 211–216.

Fang Y.J. 1996. The relationship between forest structure and bird community: a case study on the influence of the timber stand improvement program in mid-elevation area, northern Taiwan, Master Thesis, National Taiwan University, Taipei, Taiwan, ROC (in Chinese).

Fang C.Y. 1997. The bird community in the Tatachia area pine forest three years after a forest fire, Master Thesis, National Taiwan University, Taipei, Taiwan, ROC (in Chinese).

Feber R.E., Bell J., Johnson P.J., Firbank L.G. and Macdonald D.W. 1998. The effect of organic farming on surface-active spider (Araneae) assemblages in wheat in southern England, UK. Journal of Arachnology 26: 190–202.

Gibson C.W.D., Hambler C. and Brown V.K. 1992. Changes in spider (Araneae) assemblages in relation to succession and grazing management. Journal of Applied Ecology 29: 132–142.

Greenstone M.H. 1984. Determinants of web spider species diversity: vegetation structural diversity vs. prey availability. Oecologia 62: 299–304.

Griffin R.E. 1998. Species richness and biogeography of non-acarine arachnids in Namibia. Biodiversity and Conservation 7: 467–481.

Gunnarsson B. 1992. Fractal dimension of plants and body size distribution in spiders. Functional Ecology 6: 636–641.

Krebs C.J. 1989. Ecological Methodology. Harper Collins Publishers, New York.

Hurd L.E. and Fagan W.F. 1992. Cursorial spiders and succession: age or habitat structure? Oecologia 92: 215–221.

Lee C.K. 1995. A comparison of bird communities between conifer plantation and natural broadleaf forest, Master Thesis, National Taiwan University, Taipei, Taiwan, ROC (in Chinese).

Lin Y.S. and Tseng C.S. 1985. Ecological study of aquatic fauna in Nanjenshan Ecological Reserve, Kenting National Park: a preliminary study of freshwater fish and invertebrates. Conservation Research Report Number 3-2. Kenting National Park, Taiwan, ROC (in Chinese).

Lue K.Y. 1985. A study of limnology and herpetological fauna in aquatic areas of Nanjenshan. Conservation Research Report Number 3-1. Kenting National Park, Taiwan, ROC (in Chinese).

Marc P., Canard A. and Ysnel F. 1999. Spiders (Araneae) useful for pest limitation and bioindication. Agriculture, Ecosystems and Environment 74: 229–273.

Maelfait J.P. and DeKeer R. 1990. The border zone of an intensively grazed pasture as a corridor for spiders Araneae. Biological Conservation 54: 223–238.

Maelfait J.P. and Hendrickx F. 1998. Spiders as bio-indicators of anthropogenic stress in natural and semi-natural habitats in Flanders (Belgium): some recent developments. Proceedings of the 17th European Colloquium of Arachnology, Edinburgh 1997. British Arachnological Society, Cambridge, UK.

May R.M. 1992. How many species inhabit the earth? Scientific American 267: 42–48.

Nyffeler M. 2000. Ecological impact of spider predation: a critical assessment of Bristowe's and Turnbull's estimates. Bulletin of British Arachnological Society 11: 367–373.

Nyffeler M. and Benz G. 1987. Spiders in natural pest control: a review. Journal of Applied Entomology 103: 321–339.

Oliver I. and Beattie A.J. 1996. Designing a cost-effective invertebrate survey: a test of methods for rapid assessment of biodiversity. Ecological Applications 6: 594–607.

Pekár S. 1999. Effects of IPM practices and conventional spraying on spider population dynamics in an apple orchard. Agriculture, Ecosystem and Environment 73: 155–166.

Pettersson R.B. 1996. Effect of forestry on the abundance and diversity of arboreal spiders in the boreal spruce forest. Ecography 19: 221–228.

Platnick N.I. 2000. Estimated species number. American Arachnology 61: 8–9.

Riecken U. 1999. Effects of short-term sampling on ecological characterization and evaluation of epigeic spider communities and their habitats for site assessment studies. Journal of Arachnology 27: 189–195.

Rypstra A.L. and Carter P.E. 1995. The web spider community of soybean agroecosystems in southeastern Ohio. Journal of Arachnology 23: 135–144.

Severinghaus L.L. 1991. A study on diurnal raptors of Kenting National Park. Conservation Research Report Number 64. Kenting National Park, Taiwan, ROC (in Chinese).

Shen S.J., Shao K.T., Chen L.S. and Chen C.P. 1990. A study of the marine fish fauna in Kenting National Park. Conservation Research Report Number 68. Kenting National Park, Taiwan, ROC (in Chinese).

Shih T.T., Tsai W.T., Shiu M.Y., Mezaki S. and Koba M. 1989. A study of the geology and dating of coral reef in Kenting National Park. Conservation Research Report Number 57. Kenting National Park, Taiwan, ROC (in Chinese).

Shiu H.J. 1995. The relationship between avian community structure and environmental factors in mature forests of mid-elevation mountain areas in Taiwan, Master Thesis, National Taiwan University, Taipei, Taiwan, ROC (in Chinese).

Shiu K.S., Chiu W.L., Chang H.C., Lue S.Y., Lin J.T., Chu C.B. and Fang F.H. 1985. A study of forest restoration techniques in tropical forests in Kenting National Park. Conservation Research Report Number 6. Kenting National Park, Taiwan, ROC (in Chinese).

Su H.J. 1994. The Ecology of Plants in Kenting National Park. Interpreter Handbook of Kenting National Park, Pingtung, Taiwan, ROC (in Chinese).

Sundberg I. and Gunnarsson B. 1994. Spider abundance in relation to needle density in spruce. Journal of Arachnology 22: 190–194.

Ting T.S. 1993. The community ecology of avian fauna in Yushan, Master Thesis, National Taiwan University, Taipei, Taiwan, ROC (in Chinese).

Topping C.J. and Lövei G.L. 1997. Spider density and diversity in relation to disturbance in agroecosystems in New Zealand, with a comparison to England. New Zealand Journal of Ecology 21: 121–128.

Topping C.J. and Luff M.L. 1995. Three factors affecting the pitfall trap catch of linyphiid spiders (Araneae; Linyphiidae). Bulletin of British Arachnological Society 10: 35–38.

Topping C.J. and Sunderland K.D. 1992. Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. Journal of Applied Ecology 29: 485–491.

Tóth F. and Kiss J. 1999. Comparative analyses of epigeic spider assemblages in northern Hungarian winter wheat fields and their adjacent margins. Journal of Arachnology 27: 241–248.

Uetz G.W. and Unzicker J.D. 1976. Pitfall trapping in ecological studies of wandering spider. Journal of Arachnology 3: 101–111.

Wang Y. 1986. An ecological study of avian fauna in aquatic areas of Nanjenshan Ecological Reserve, Kenting National Park. Conservation Research Report Number 24. Kenting National Park, Taiwan, ROC (in Chinese).

Wang Y. and In L.M. 1992. A study of diversity of ungulate and carnivorous mammals in Kenting National Park. Conservation Research Report Number 80. Kenting National Park, Taiwan, ROC (in Chinese).

Wilkinson L., Hill M. and Vang E. 1992. SYSTAT: statistics. Version 5.2. SYSTAT Inc., Evanston, Illinois.

Wise D.H. 1993. Spiders in Ecological Webs. Cambridge University Press, Cambridge, UK.

Yang P.S., Tseng C.S., Lee C.L., Chen M.L. and Yu S.W. 1990. A study of insects and their ecology in Nanjenshan. Conservation Research Report Number 83. Kenting National Park, Taiwan, ROC (in Chinese).

York A. 1999. Long-term effects of frequent low-intensity burning on the abundance of litter-dwelling invertebrates in coastal blackbutt forests of southeastern Australia. Journal of Insect Conservation 3: 191–199.

Yu M.S. 1999. Floristic composition and structure of the Kenting high coral reef forest, Master Thesis, Tunghai University, Taichung, Taiwan, ROC (in Chinese).

Zulka K.P., Milasowzky N. and Lethmayer C. 1997. Spider biodiversity potential of an ungrazed and a grazed inland salt meadow in the National Park 'Neusiedler See-Seewinkel' (Austria): implications for management (Arachnida: Araneae). Biodiversity and Conservation 6: 75–88.