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Diversity and composition of spider assemblages in five vegetation types of the Terai Conservation Area, India

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Abstract. This study deals with the comparison of spider diversity and composition in a complex landscape of the Terai Conservation Area (TCA) characterized by alluvial floodplains of tall grassland interspersed with woodland, swamps, and riparian patches. High water table, annual flooding, and annual grassland fire maintain its dynamic complexity. A mosaic of five vegetation types was sampled for spiders from March 2005 to August 2006 by using pitfall traps and other semi-quantitative collection methods along transects. A total of 3666 adult spiders representing 22 families, 60 genera, and 160 species were found. Using the abundance-based estimator, Chao1, the predicted richness for the total area sampled is 173 ± 8.32 (SD) species. This indicates that the inventory was almost complete at the regional scale (92%). With similar proportions of captured species, rarefied richness value showed that species richness was highest in riparian swamp forest. Comparison of different sites revealed that species composition was much more similar within the same vegetation type than among different vegetation types. Assemblage composition differed the most between riparian swamp forest and plantation. Guild structure varied considerably in relation to the structural quality of vegetation.

Keywords: Terai ecosystem, species richness, species composition, guild structure

A central theme in community ecology is the understanding of what drives the variation in species diversity and composition (MacArthur 1972; Holyoak et al. 2005); the interest is not in knowing the exact number and identity of every species at a given site, but rather how the diversity and composition vary among sites. High diversity and complex interactions pose challenges to studies of ecological processes (Halaj et al. 2000). One approach to investigate multispecies systems is to focus on dominant taxa or a key assemblage, which is potentially critical for local community food-web dynamics (Polis & Strong 1996). Spiders are an excellent example of such a group because they are widespread intermediate-level predators and are among the most diverse groups on earth (Coddington & Levi 1991; Wise 1993). Moreover, spiders appear to be good subjects for studying biodiversity patterns (Platnick 1999) as their distribution and occurrence are strongly influenced by habitat structure and vegetation parameters (Greenstone 1984; Uetz 1991; Wise 1993; Buddle et al. 2000; de Souza & Martins 2004). The present study was carried out in the Terai Conservation Area (TCA), which represents the Terai landscape, one of the most diverse ecosystems of India (Kumar et al. 2002). This landscape is characterized by a complex of sal forest, tall grassland, and swamps maintained by periodic flooding. The knowledge of diversity and distribution of spiders in this area is sparse as compared to other Indian regions. In the present study we documented the richness and composition of ground and above ground spiders across five different vegetation types of TCA. Using this information, the community structure of spider assemblages in different vegetation types was compared, and the possible effect of habitat characteristics on species occurrence and observed pattern was explained.

METHODS

Study Area.—The study was conducted in the alluvial flood plains of TCA that cover an area of 7,896.6 km^2 between the Himalayan foothills and the Gangetic plains in the state of Uttar Pradesh, India (27°49′–28°43′N, 81°01′–81°18′E) from March 2005 to August 2006. TCA is made up of a spatially heterogeneous landscape of forest-grassland-wetland complex within a matrix of extensive agricultural land and with sparsely distributed habitations (Kumar et al. 2002). The terrain is on the flat flood plains of the Suheli, Mohana, and Sharda rivers. The climate of TCA is tropical monsoon type. The TCA experiences three distinct seasons: winter (November–March), summer (April–June), and monsoon (July–October).

We sampled spiders in localities across five vegetation types that contained contiguous and relatively homogeneous areas of each vegetation community. The vegetation types are as follows:

(a) Riparian Swamp Forest: This forest type was found in swampy depressions along streams and remains under water continuously for a long period during the rains or where deep black heavy waterlogged soils occur and is structurally characterized by extremely diverse overstorey and understorey structure relative to other vegetation types. This densely vegetated forest type is associated with rich humus soil. The most common tree species were *Syzygium cumini*, *Barringtonia acutangula* (patches occurred along rivers), *Trewia nudiflora*, *Terminalia alata*, *Lagerstromea parviflora*, and *Ficus racemosa*. *Clerodendrum viscosum*, *Glycosmis pentaphylla*, and *Murraya koenigii* are the prominent shrubs. *Ageratum conyzoides*, *Dioscorea belophylla*, and *Corchorus aestuans* were the important herbs in this type of forest. *Syzygium cumini* formed a dense crop with long clean boles. Structurally, these forests typically have a mixture of sparse and closed canopy, a diverse understorey, and a deep layer of leaf litter.

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(b) Grassland: Grasslands occurred in low-lying areas or depressions, which were waterlogged or marshy in nature. Such areas had alluvial soils, mostly sandy with clayey patches. These depressions mark old river channels. Structurally, these grasslands are characterized by an absence of trees and moderate to low herbaceous ground cover. Floristically, these grasslands were composed primarily of native and introduced grass species and a few scattered shrubs. These areas are annually burnt as part of the management practices in TCA. Prominent tree species were *Bombax ceiba*, *Ficus racemosa*, and *Syzygium cumini*. Prominent grasses were *Arundo donax*, *Phragmites karka*, *Themeda arundinacea*, *Sclerostachya fusca*, *Saccharum spontaneum*, and *Saccharum narenga*. The grasslands have interspersed swamps.

(c) Pure Sal Woodland: This vegetation type represents moist deciduous forest that occurs on higher alluvial terraces. *Shorea robusta* (Sal) occupied a major part of this woodland. This woodland was often associated with flat topography and loamy soil. Variation in overstorey structure is limited by the dominance of *Shorea* and the understorey structure is relatively diverse, composed of *Ardisia solanacea*, *Colebrookia oppositifolia*, *Clerodendrum viscosum*, and *Murraya koenigii*. Woody climber *Tiliacora acuminata* formed a dense carpet on the ground in several patches.

(d) Mixed Sal Woodland: This was the rarest vegetation type, which occurred only in five patches in the entire study area and was confined to the gentle slopes and old river terraces around grasslands. The overstorey was composed of old *Shorea robusta* with *Bridelia squamosai*, *Bauhinia racemosa*, *Mallotus philippensis*, *Syzygium cumini*, and *Terminalia alata*. Mixed Sal woodlands are structurally characterized by closed overstorey of *Shorea robusta* and *Terminalia alata*, while the dense understorey layer is composed of *Ardisia solanacea*, *Clerodendrum viscosum*, and *Glycosmis pentaphylla*.

(e) Plantation: Extensive plantations of *Acacia catechu*, *Ailanthus excelsa*, *Bombax ceiba*, *Dalbergia sissoo*, *Eucalyptus citriodora*, and *Tectona grandis* have been raised as gap planting as well as after clear felling. This vegetation type mostly represents large scale mechanized plantations of teak (*Tectona grandis*) and *Eucalyptus*. It was chosen to represent disturbed conditions since most of the patches were close to villages and on the periphery of the protected areas and continue to undergo grazing and other biomass extraction to varying extents. Structurally, plantations are characterized by moderate to low canopy cover and least herbaceous ground cover.

Sampling methods.—Spiders were collected along 50 m × 10 m transects, with 20 transects per vegetation type. These transects were treated as our basic sampling units, hereafter sites. Transects were placed randomly within stratified vegetation types. Sampling was carried out each month from March 2005 to August 2006. Spiders were sampled along the transects using pitfall traps and semi-quantitative sampling. Pitfall sampling was operated for 64 weeks and other semi-quantitative sampling performed on 64 occasions (once every week) at the same sampling sites. The principal purpose of this sampling design was to produce a relatively complete species list and associated abundance data for a representative example of each vegetation type in the region, and of the region as a whole.

Pitfall sampling: Pitfall traps consisted of cylindrical plastic bottles of 10 cm diameter and 11 cm depth (Churchill & Arthur 1999). Six pitfall traps were laid along each transect line at an interval of 10 m each. Traps were filled with preservative (69% water, 30% ethyl acetate, and 1% detergent). After seven days, specimens were removed from traps, which allowed us to maintain spider specimens in good condition before laboratory processing and identification. Since the limitations of this method are that the number of individuals trapped is affected by environmental, weather and species-specific factors (Mitchell 1963; Ahearn 1971; Parmenter et al. 1989; Krasnov & Shenbrot 1996), we have employed other time constrained semi-quantitative collection methods after Coddington et al. (1996) to maximize capture.

Semi-quantitative sampling: Aerial sampling (for upper layer spiders up to 1.5 m) involved searching leaves, branches, tree trunks, and spaces in between, from knee height up to a maximum overhead arm's reach. Ground collection (for ground layer spiders) involved searching on hands and knees, exploring the leaf litter, logs, rocks, and plants below low knee level. Beating (for middle layer spiders up to 1 m) consisted of striking vegetation with a 1 m long stick and catching the falling spiders on a tray held horizontally below the vegetation. Litter sampling was done by hand sorting spiders from leaf litter collected in a litter collection tray. Sweep netting (for middle layer spiders up to 1 m) was carried out in order to access foliage dwelling spiders. Each sampling method comprised 1 hour active sampling, measured with a stopwatch.

Spiders were identified to family and species using existing identification keys wherever possible (Pocock 1900; Tikader & Malhotra 1980; Tikader 1982, 1987; Koh 2000; Cushing 2001). Due to lack of available identification keys for many families and the time required for conventional taxonomic work, a morphospecies approach was used to classify spiders. This approach has been found to be effective for poorly known and species-rich taxa such as spiders and other invertebrates (Oliver & Beattie 1996; Krell 2004). Voucher specimens of each spider species collected are deposited at the Wildlife Institute of India, Dehradun and will ultimately be placed in the Arachnida Section, Zoological Survey of India, Kolkata.

Based on hunting methods and web building types from the literature (Uetz et al. 1999; Höfer & Brescovits 2001), combined with field observations, we grouped the spider families of Terai into the following five major guilds: 1) orb weavers: Araneidae, Tetragnathidae, and Uloboridae; 2) space weavers: Pholcidae and Theridiidae; 3) ground weavers: Hahniidae, Linyphiidae, Agelenidae, and Theraphosidae; 4) foliage runners: Clubionidae, Oxyopidae, Philodromidae,

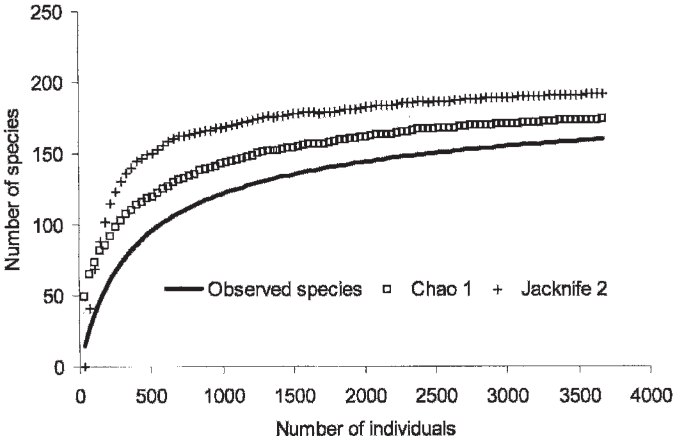

Figure 1.—Species-accumulation curve and estimation curves Chao1 and Jacknife2 for the regional (all samples pooled) dataset. Curves are generated from 100 randomizations.

Pisauridae, Scytodidae, Sparassidae, Salticidae, and Thomisidae; 5) ground runners: Lycosidae, Gnaphosidae, Oonopidae, Zodariidae, and Tetrablemmidae.

Data Analysis.—Spiders captured by pitfall traps and semiquantitative methods were pooled for each site. Species richness was estimated for each vegetation type, as well as for the regional data set using the nonparametric estimators Chao1 and Jacknife2. Accumulation curves were generated after 100 randomizations using EstimateS 8.0 © (Colwell 2006). Chao1 gives an estimate of the absolute number of species in an assemblage based on the number of rare species (singletons and doubletons) in a sample. Chao1 estimate of species richness is recommended for inventory completeness values, completeness being the ratio between observed and estimated richness (Sørensen et al. 2002; Scharff et al. 2003). Jacknife estimators in general, and Jacknife2 in particular, have been found to perform quite well in extrapolation of species richness with greater precision, less bias, and less dependence on sample size than other estimators (Palmer 1990, 1991; Baltanás 1992; Brose et al. 2003; Petersen et al. 2003; Chiarucci et al. 2003). To compare the species richness values of sites and to calculate expected species richness, individual-based rarefaction was used (Gotelli & Colwell 2001). These curves standardize different datasets on the basis of number of individuals and not on number of samples. The software program EcoSim7.0 (Gotelli & Entsminger 2001) was used for rarefaction analyses. Thereafter, the curves were rarefied to the lowest number of individuals recorded in a vegetation type (300) to ensure valid comparisons of species richness between different sites (Gotelli & Colwell 2001). Rarefaction was used as a diversity index because it considers the number of individuals collected and species richness (Magurran 2004), allows comparison of diversity between sites at similar sample size, and by showing the rate of new species accumulation, allows for verification that enough samples were collected to make proper comparisons of diversity (Gotelli & Colwell 2001; Magurran 2004; Buddle et al. 2005).

The similarity across sites was depicted as Bray-Curtis similarities (Krebs 1989), using both species and guild composition. Multidimensional scaling (MDS) plots were constructed based upon similarity values of species composition across vegetation types in program PRIMER (Clarke & Gorley 2001). Analysis of similarities (ANOSIM – Clarke 1993) was performed between each pair of vegetation types to determine whether there were significant differences between the spider assemblages in the five main vegetation types. The data were fourth-root transformed before analysis to reduce the weight of common species (Clarke & Warwick 1994). The ANOSIM procedure of PRIMER is a nonparametric permutation procedure applied to rank similarity matrices underlying sample ordinations (Clarke 1993). This method generates a global *R*-statistic, which is a measure of the distance between groups. An *R*-value that approaches one indicates strongly distinct assemblages, whereas an *R*-value close to zero indicates that the assemblages are barely separable (Clarke 1993). These *R*-values were used to compare spider assemblages between vegetation types. Where ANOSIM revealed significant differences between groups, SIMPER analyses (PRIMER) were used to identify those species that contributed most to the observed assemblage differences (Clarke & Gorley 2001). Similarity percentages (SIMPER) allowed identification of species and guilds important in discriminating between groups that differed significantly from each other. Cumulative contributions were cut arbitrarily at 50%. The species with the highest dissimilarity to standard deviation ratios were identified as good discriminators for each comparison (Clarke 1993).

RESULTS

Comparison of community structure between vegetation types.—We captured a total of 3666 adult spiders representing 22 families, 60 genera, and 160 species, which represent 11% of spider species recorded on the Indian mainland (Siliwal et al. 2005). The pooled species accumulation curve reached an asymptote for both Chao1 and Jacknife 2 (Fig. 1), indicating

Table 1.—Measures of species richness estimates and inventory completeness for each vegetation type and for the regional dataset. Richness estimator values (Chao1 & Jacknife2) represent the mean of 100 randomizations of sample order. Ratio of estimated and observed richness represents inventory completeness. All values rounded to the nearest integer.

	Pure Sal Woodland	Mixed Sal Woodland	Plantation	Grassland	Riparian Swamp Forest	Regional
No. of specimens	777	805	301	729	1054	3666
Observed richness	87	76	41	76	95	160
Number of singletons	19	18	8	13	28	35
Number of doubletons	11	7	5	3	10	13
Chao1	103	99	73	135	127	173
Jacknife2	108	98	60	99	136	191
% Completeness	84	77	56	56	75	92

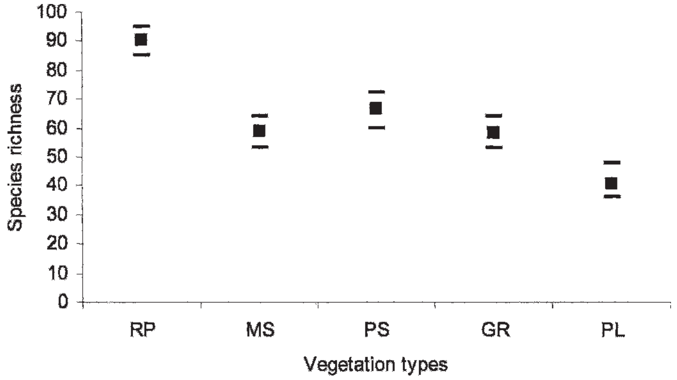

Figure 2.—Comparison of species richness values (± 95% confidence interval) at the lowest number of individuals (300) derived from individual-based species rarefaction curves of spider assemblages across the different vegetation types. RP, Riparian; MS, Mixed Sal; PS, Pure Sal; GR, Grassland; PL, Plantation.

that sampling was almost complete at the regional level. The estimated total species richness using Chao1 was 173 ± 8.32 (SD), and using Jacknife2 191 ± 1.82 (SD) for the complete sample. The ratio of observed to estimated (Chao1) number of species was 92% suggesting that at least 8% more species are to be expected in the area than were actually collected. However, at a local level, in plantation and grassland, we failed to collect such a high percentage of species (44% missing) compared with other vegetation types (Table 1). The most abundant families were Araneidae (41.78% of all captures), and Theridiidae (12.46%). Other dominant families comprised Lycosidae (295 individuals, 11 species), Tetragnathidae (253, 17), Linyphiidae (211, 19), Clubionidae (170, 4), Salticidae (133, 12), and Gnaphosidae (123, 7). All other families (14) were represented by less than 100 individuals each, and contributed only 29 species. From all species recorded, 35 were singletons (21% of all species) and 13 were doubletons (8% of all species). The most abundant species was *Chrysso picturata* Simon 1895 (Theridiidae) (112 individuals) and most of the individuals (70% of total catches) were found at plantation sites. The highest species richness was found in the riparian swamp forest (90 species), while the lowest species richness was in the plantation sites (41 species). The remaining three vegetation types did not differ statistically in richness considering the overlap of confidence intervals of richness values (Fig. 2).

Comparison of species composition between sites and vegetation types.—Comparing among different sites revealed that on average, species composition was much more similar within the same vegetation type than among different vegetation types. MDS plot generated from relative abundances of different spider species in each vegetation type showed that sampling sites from each vegetation type clustered together (Fig. 3a). Sampling sites of homogeneous grassland and plantation were well separated from heterogeneous forest habitats, which clustered together. Sampling sites in pure sal and mixed sal woodland grouped together and showed little overlap with other vegetation types. Pair wise ANOSIM test showed that most difference in species composition occurred between riparian swamp forest and plantation sites ($R = 0.79$, $P = 0.001$), while the least difference was seen between pure sal and mixed sal woodland ($R = 0.34$, $P = 0.011$). Further comparisons of dissimilarity in composition were made to identify the species contributing to the difference between groups of sites that differed most. Fifteen species contributed more than 50% to the difference between groups of sites. These species differed in mean abundance, which was reflected in the degree of group association. Eight species of family Araneidae, were almost absent from plantation sites and present in high abundance in riparian swamp forest, whereas *Chrysso picturata* and *Argyrodes* sp. 2 of family Theridiidae were found in greater abundance at plantation sites compared to riparian forest (Table 2a).

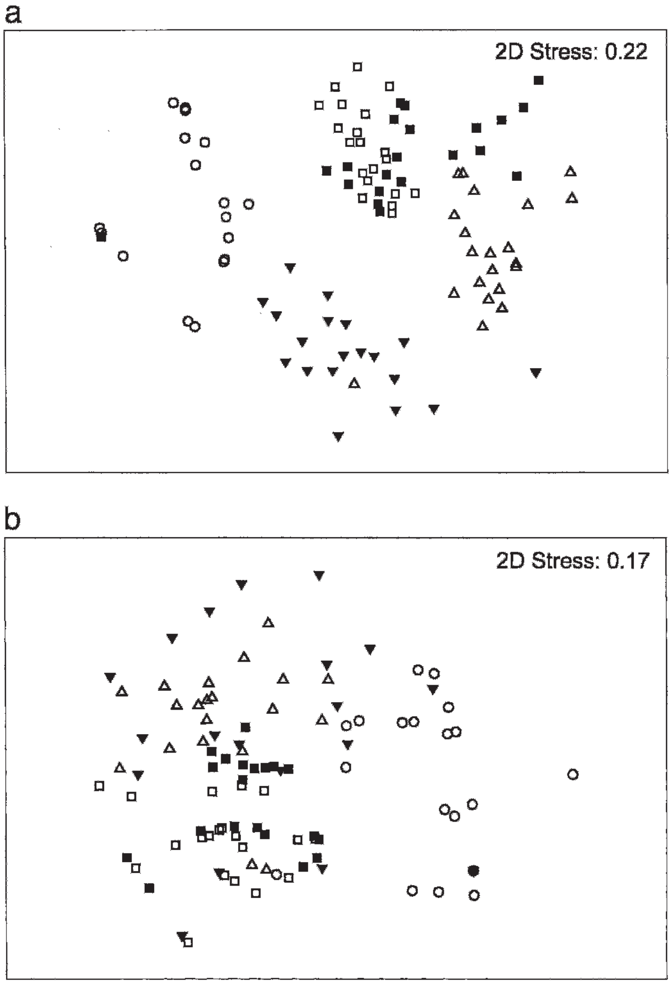

Figure 3.—MDS ordination plots of sampling plots in the Terai Conservation Area, generated by (a) species composition and (b) guild composition, sorted according to vegetation types (open triangle, Riparian sites; inverted closed triangle, Grassland sites; open square, Pure Sal sites; closed square, Mixed Sal sites; open circle, Plantation sites).

Comparison of guild between sites and vegetation types.—A MDS plot generated for relative abundances of different spider guilds showed distinct patterns with respect to the five vegetation types (Fig. 3b) and statistically significant differences ($R = 0.75–0.21$, $P < 0.001$) revealed by all pair-wise ANOSIM tests except pure sal vs. mixed sal ($R = 0.096$, $P = 0.19$). SIMPER analysis indicated that the orb weaver guild was the main contributor to dissimilarity between riparian

Table 2.—SIMPER analysis of differences in (a) species (average dissimilarity = 94.95%) and (b) guild (average dissimilarity = 50.00%) composition of spider assemblages between the two most dissimilar vegetation types studied.

		Vegetation type		
		Riparian	Plantation	
	Family	Mean abundance	Mean abundance	Cumulative contribution%
(a) Species				
Argiope pulchella (Thorell, 1881)	Araneidae	0.94	0.00	4.57
Chrysso picturata (Simon, 1895)	Theridiidae	0.06	0.82	8.80
Gasteracantha sp. 1	Araneidae	0.86	0.00	12.99
Gasteracantha dalyi (Pocock, 1900)	Araneidae	0.86	0.00	17.18
Hippasa sp. 3	Lycosidae	0.80	0.00	21.13
Eriovixia excelsa (Simon, 1889)	Gnaphosidae	0.39	0.67	24.54
Achaearanea sp. 2	Theridiidae	0.62	0.56	27.86
Neoscona mukerjei (Tikader, 1980)	Araneidae	0.66	0.00	31.14
Cyphalonotus sp. 1	Araneidae	0.64	0.00	34.17
Neoscona vigilans (Blackwell, 1865)	Araneidae	0.52	0.00	37.14
Myrmarachne sp. 1	Salticidae	0.62	0.00	40.00
Pardosa birmanica (Simon, 1884)	Lycosidae	0.57	0.00	42.79
Argyrodes sp. 2	Theridiidae	0.00	0.52	45.48
Neoscona biswasi (Bhandari & Gajbe, 2001)	Araneidae	0.58	0.00	48.03
Leucauge decorate (Blackwell, 1864)	Tetragnathidae	0.48	0.00	50.41
Araneus bilunifer (Pocock, 1900)	Araneidae	0.46	0.00	52.69
(b) Guilds				
Orb-weavers		5.10	1.57	48.49
Ground runners		3.09	0.69	82.29
Space weavers		1.79	2.62	100.00

swamp and plantation (Table 2b). Orb weaver was the dominant guild with the highest number of individuals (55% of total capture) and was abundant in all vegetation types except plantations (Fig. 4). Collectively in pure sal and mixed sal, 56% of total orb weavers were captured. Space weavers and foliage runners represented 13% and 12% respectively, while ground runners and ground weavers collectively contributed 12% of all collection.

DISCUSSION

The present study, an inventory of spiders, is the first of its kind in Terai and is one of the few studies on spider communities in India. As there is no species list available for TCA, it is difficult to know precisely what proportion of the actual local and regional species richness our study captured. However, based on estimated richness our inventory was almost complete at the regional scale (92%). In spite of the relative success of this study, it still cannot be described as comprehensive – undoubtedly species were missed at local scales. Sampling additional sites or using different methods would capture more species. Nevertheless, the inventory protocol utilized here provided a sufficiently thorough sample of local and regional spider species to permit an accurate comparison of species richness of different vegetation types. The community structure and spider diversity is not similar in different vegetation types. Comparatively, riparian swamp forests exhibit highly diverse assemblages, possibly due to higher structural complexity. The relatively open and diverse overstorey and understorey structure of riparian swamp forest supported the highest number of spider species while closed canopy woodland and plantation sites supported relatively few (Fig. 5). Additionally, these swamp forests are subjected to annual flooding, which may "reset" areas to earlier successional stages due to removal of existing substrate, organic matter, and organisms, and the deposition of sediments (Junk et al. 1989; Sparks et al. 1990; Richards et al. 2002). These processes may affect spider communities by alteration of microhabitats and their relative availability. The disturbances of successive floods are cumulative, and may lead to a highly heterogeneous patchy habitat condition. However, it is unclear whether such flooding may create higher species richness through removal of dominant species and creation of ecological space for other opportunist species, or through creation of diverse microhabitats, or a combination of these. Intriguingly, our results showed high species richness and diverse assemblage in grassland, considering the low structural diversity of this vegetation type. One of the possible reasons for this pattern may be the practice of annual, low intensity prescribed burning in the grassland. Burning is a management tool used to reduce fuel levels and facilitate regeneration of desired grass species for wild ungulate communities. This annual fire essentially increases structural complexity of grassland, where characteristic elements of both sparse and dense vegetation occur in close proximity, providing a rich mosaic of microclimatic conditions, capable of supporting a large number of spider species (Moretti et al. 2002). However, it would be interesting to observe what proportion of locally and regionally endemic or restricted species are affected negatively or positively by this practice. The spider composition in plantation showed the most dissimilar assemblage in comparison with those of other vegetation types. Possible reasons may be the scarcity of understorey vegetation, single tree species dominance, and isolation from nearest forest habitat, affecting the amount of different microhabitats

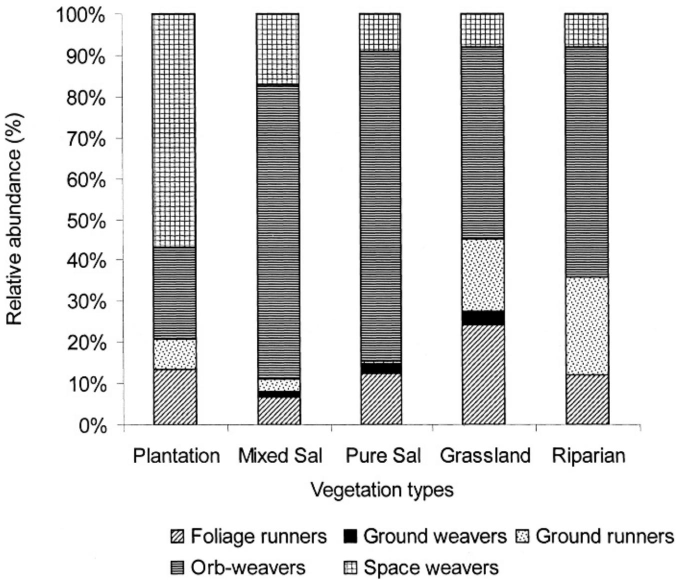

Figure 4.—Variation in guild structure of spider assemblages across different vegetation types in the Terai Conservation Area.

available to spiders. Patch isolation can act as a barrier to spider dispersal from other patches. Bonte et al. (2004) showed that the distribution of spider species depends on their aerial dispersal potential and on habitat connectivity. Plantations had higher abundance of space weavers and relatively few orb weavers. This pattern probably resulted from lack of suitable microhabitats for orb web construction (vegetation dominated by a few species of dense and short grasses, with low densities of herbaceous ground flora), as well as exposure to wind and rain due to relatively open canopy. Compared with orb weavers, space weavers can endure a higher level of disturbance, which may explain why they are more abundant (Tsai et al. 2006). In contrast, relative abundance of orb weavers was much higher in pure sal and mixed sal woodland, where dense canopy and stable microclimate prevails year round. These habitats have high vertical stratification (Robinson 1981; Scheidler 1990; Balfour & Rypstra 1998) and may offer more physical structures for web attachment, such as different kinds of branches. Such variation in species abundance of orb weavers can potentially be used to monitor changes of structural quality of vegetation parameters and habitat disturbances. However, serious lack of ecological and taxonomic understanding of Indian spiders hinders their use as indicators of habitat disturbance in India (Kapoor 2008). On a coarse scale, this study revealed the relative importance of habitat type on diversity and composition of spider assemblage in TCA. However, future studies need to quantify habitat characteristics, microclimate variability and disturbance factors in order to depict how these features affect community structure and composition and in what way they are correlated with species diversity at local as well as regional scales.

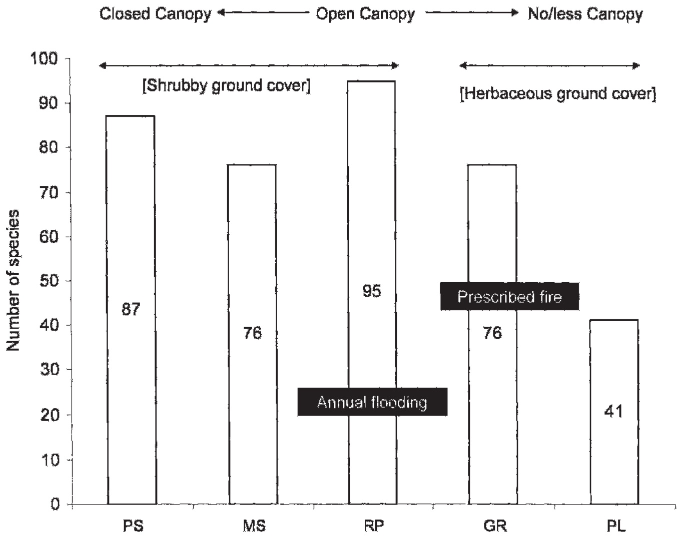

Figure 5.—Patterns of species richness of spider assemblages across vegetation types showing some gross ecological features shared among vegetation types in Terai. Arrows indicate gradient of ecological characteristics, brackets indicate features common to vegetation types. RP, Riparian; MS, Mixed Sal; PS, Pure Sal; GR, Grassland; PL, Plantation.

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