SPIDER DIVERSITY ALONG ALTITUDINAL GRADIENT AND ASSOCIATED CHANGES IN MICROCLIMATE ATTRIBUTES IN NANDA DEVI BIOSPHERE RESERVE, UTTARAKHAND, INDIA

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INTRODUCTION

Global species diversity patterns are likely to change across spatial gradients in response to changes in climate, area, latitude, altitude, productivity, available resources and habitat complexity (MacArthur, 1972; Rosenzweig, 1995; Trevelyan and Pagel, 1995). As altitudinal gradients are usually characterized by rapid environmental changes over short horizontal distances, they are thus known to be ideal for investigating diversity patterns (Hodkinson, 2005). The patterns of species diversity of invertebrates along the elevation gradient have long been a contentious topic. The two general patterns that emerge are a monotonic decrease in species richness with increasing elevation (MacArthur, 1972; Stevens, 1992) and a hump-shaped relationship, with a peak at intermediate elevations (Rahbek, 1995). Studies have been conducted on several taxa along elevation gradients that reveal that there is a large variation in diversity patterns. Both patterns have been documented in a variety of habitats and taxa (Terborgh, 1977; Stevens, 1992; Brown, 1995; Rahbek, 1995; Rosenzweig, 1995). However, the two most commonly observed patterns of species richness along altitudinal gradients are a steady decline in diversity with increasing elevation and a unimodal pattern (Nogués-Bravo *et al*., 2008). It is observed that diversity generally decreases at higher elevations in plants (Hamilton and Perrott, 1981; Kessler, 2001; Hemp, 2002) and animals (Rahbeck, 1995).

The negative effect of altitude (Stevens, 1992; Brown *et al.*, 1996) is explained as a consequence of the wider ecological forebearance of organisms at higher elevations. It is a crucial characteristic that has to be possessed in order to withstand the wider climatic fluctuations to which they are exposed. The effect of elevation on species richness can be attributed to the following reasons: (i) reduction in productivity with elevation; (ii) reduction in total area; (iii) reduction in resource diversity; and (iv) harshness and unpredictability of the conditions prevailing at higher elevations (Lawton *et al.*, 1987). Colwell and Lees (2000) have suggested the mid domain effect, i.e. the peak in species richness at mid elevations, due to the increasing overlap of species ranges towards the centre of a domain or minor peaks at transitions between elevational communities, to be very robust among different taxa. Another phenomenon associated with negative effect of altitude is the 'rescue effect' i.e. the reduced likelihood of a population at higher elevations to be rescued by individuals dispersing from other zones, compared with populations at lower elevations (Brown and Kodric-Brown, 1977). Thus, it could be that the species richness is overblown in lower altitudes by the emigration of high-altitude species at the margins of their ranges due to wider tolerance, while taxa from lower elevations cannot expand their upper limit of elevation range as immigration rates also decrease with elevation (Stevens, 1992).

For insects, the empirical evidence for both peaks in species richness at low elevations (Wolda, 1987; Fernandes and Price, 1988; McCoy, 1990; Kearns, 1992; Stevens, 1992; Olson, 1994; Sparrow 1994) and peaks in species richness at intermediate elevations has been established through several studies (Janzen, 1973; McCoy, 1990; Olson, 1994; Sanchez-Rodriguez and Baz, 1995; Fleishman *et al.,* 1998; Sanders, 2002). Most studies have revealed a hump-shaped distribution (Holloway *et al.*, 1990; McCoy, 1990; Olson, 1994; Holloway, 1997; Pyrcz and Wojtusiak, 2002), whereas Wolda (1987) found a general

decrease with increasing elevation. Although several invertebrate groups have been studied across altitudinal gradients, for example, butterflies, moths, ants, dragonflies and beetles, only few studies have been conducted so far on spiders in the Indian subcontinent. *Waide et al.* (1999) considered spiders as model taxa for investigating the effects of spatial gradients on species assemblages on a scale of 200-4000 km. As they are ubiquitous, abundant, easily collectible and sensitive towards fine-scale environmental changes, they can be used to reflect ecological change. Thus, they easily respond to changes in habitat heterogeneity *(Downie et al.,* 1995), temperature and humidity (*DeVito et al*., 2004), as a result of which species assemblage patterns may be assessed at a regional scale. Chatzaki *et al.* (2005) found that the species richness of ground-dwelling spiders (Gnaphosidae) followed a hump-shaped pattern in Crete, Greece. Maurer and Hänggi (1991), who studied the altitudinal variation of spider species in Switzerland, reported a more or less linear decline and an abrupt decrease in the number of species above the timberline. An ecological survey of ground spiders along altitudinal gradients in Norway (Otto and Svensson, 1982) found the same pattern of species decline with altitude from 0 to 800 m.

This study intended to describe the species diversity patterns along the three altitudinal gradients (sites) of the Nanda Devi Biosphere Reserve (NDBR). The objectives of the study were (1) to describe the regional species diversity and composition, (2) to inspect if the species composition changes along the altitudinal gradient and (3) to examine the altitudinal patterns of species diversity. With these objectives, the following research questions were raised: (i) Is there a general trend of altitudinal species diversity, or does it vary between sites? (ii) What is the most parsimonious yet robust species diversity pattern? (iii) Are these altitudinal trends of diversity similar between guilds? The three alternative hypotheses that were tested were the following: (a) the altitudinal species diversity pattern follows a general trend at the regional scale; (b) the altitudinal species diversity pattern follows similar trends in the region but with random site effects; and (c) the altitudinal species diversity pattern differs between sites. Further, (d) whether this altitudinal diversity is linearly declining or unimodal was tested. As spiders are also adapted to a rather narrow set of abiotic factors such as temperature, humidity and pH, (e) whether these factors influence local diversity was also tested.

METHODS

SPIDER SAMPLING

Selected sites with substantial altitudinal ranges were sampled in the NDBR. As spiders are diverse in their ways of life, in order to collect them from all habitats, the sampling needed a combination of methods. So we used six different collection techniques, *viz.*, pitfall trapping, vegetation beating, litter sampling, ground hand collection, aerial hand collection and sweep netting (*Coddington et al.*, 1996). Nine pitfall traps (cylindrical plastic bottles of diameter 9 cm and depth 11 cm, mainly for collecting ground-dwelling spiders) were arranged within the quadrates in three horizontal rows and three vertical rows, each at a distance of 5 m from the nearest neighbour, thus forming four smaller grids of 5 m × 5 m within the sampling plot (Figure

Figure 1.
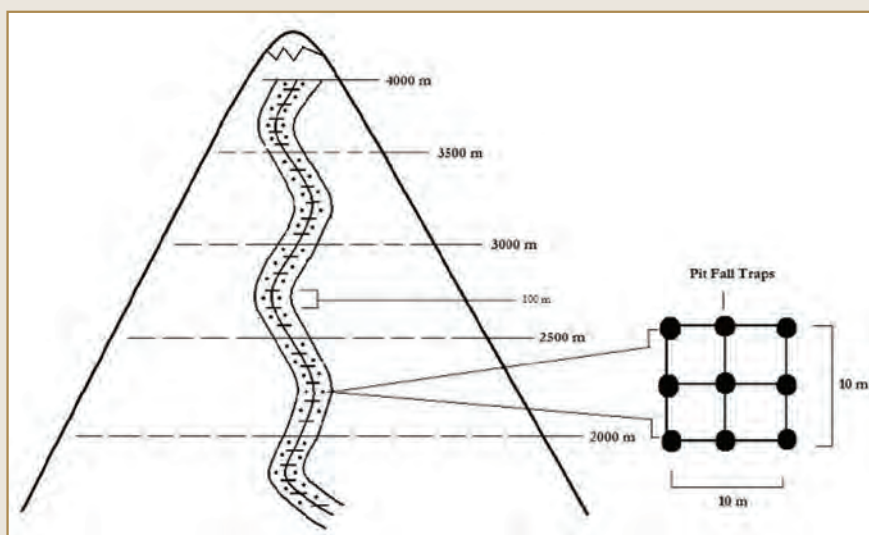
Sampling design

1). The traps were filled with liquid preservative (69% water, 30% ethyl acetate and 1% detergent). Other methods were used to collect web builders, ambushers, and ground-running spiders. Specimens were identified up to the family, genus and species levels when possible. Sampling was carried along the gradient in three sites: Lata Kharak (Site 1, 2000-4000 m); Bhyundar Valley (Site 2, 1800-4100 m) and Malari (Site 3, 3000-4000 m). At all these sites, 106 quadrate plots (10 m × 10 m) were laid randomly along the altitudinal gradient (40 plots at Lata Kharak, 40 at Malari and 46 at Bhyundar Valley).

DATA ANALYSIS

Spider samples captured in pitfall traps and using other semi-quantitative methods were used to estimate community parameters in a hierarchal fashion (plot to site to region). First, the sampling adequacy was examined from species accumulation curves. For this data were pooled across plots for each site and rarefaction (by numbers) curves were generated from 100 randomizations using Estimates 8.0 (Colwell, 2006). The nonparametric estimators Chao1 and Jacknife2 were used to estimate the species richness of a site. Chao1 gives an estimate of the absolute number of species in an assemblage based on the number of rare species (singletons) in a sample. An estimate of Chao1 is recommended to obtain the inventory completeness value, completeness being the ratio between the observed and estimated richness. Jacknife2 has been found to perform well in extrapolation of species richness, with greater precision, less bias and less dependence on sample size compared with other estimators (Palmer, 1990, 1991). So, we derived Chao 1 and Jacknife2 estimates on 100% and 50% of the sample plots and selected the best species richness estimator between the two values on the basis of the consistency of estimates across sub samples.

Second, the spider community composition was examined in the three sampling sites along the altitudinal gradient. For this non-metric multidimensional scaling (NMS) (Kruskal, 1964) in PC-ORD version 4.17 (McCune and Mefford, 1999) was used. This technique calculated the Bray-Curtis (Sørensen index) similarity matrix between sites on the basis of species assemblages. Thereafter, it generated synthetic axes, reconstructed the distance matrix and calculated the stress as the difference between the original and synthetic similarity matrices. It reiterated the process until the best possible solution was reached in terms of minimizing the stress through the minimum number of axes. Finally, scatter plots were used to inspect the distribution of sampling plots in the reduced species space (NMS axes), grouping plots into eco-climatic classes.

Third, the patterns of species diversity were examined along eco-geographical gradients (primarily altitude; secondarily pH, humidity, ground cover, *etc*). For this, the species diversity of each plot was estimated using the Shannon-Wiener index. This index is sensitive to changes in abundance of rare species in a community and is based on the number of species in a taxon and the total number of species in a sample (Magurran, 1988). Then alternative ecological hypotheses were formulated regarding species diversity patterns corresponding to the research questions. For this,the species diversity at the plots was modelled alternately with altitude (linear and quadratic functions) and sites as random or fixed (additive and interactive) effects, along with pH and humidity. Linear and linear mixed models in SPSS version 16 release 2.0 (SPSS Inc., Chicago, IL, USA) were used and candidate models compared using the Bayesian information criterion (BIC). This exercise described the most robust and parsimonious species diversity pattern in this region.

Lastly, the effect of altitudinal gradient on the species diversity across guilds was examined. For this, the species were grouped into functional groups or guilds. These guilds were grouped based on the available information on their habitat preferences and predatory methods. Thus, they were classified into three major guilds (PW, plant wanderers; GW, ground wanderers; WB, web builders). Similarly, as in the foregoing, the values of the species diversity at plots were estimated using the Shannon-Wiener index and regressed with altitude at the different sites. The altitudinal patterns of shrub and herb diversity were examined simultaneously. However, the tree diversity was not quantified as the canopy spider diversity was beyond the scope of this study.

RESULTS

SPIDER DIVERSITY AND COMPOSITION

A total of 244 species belonging to 108 genera and 33 families were collected during the entire sampling period. It was observed that the family with the highest number of total species was the family Araneidae, with 18% (44 species), followed by the families Salticidae and Thomisidae, with 11.5% (28 species) each, Linyphiidae, with 7.4% (14 species), Uloboridae and Tetragnathidae, with 4.5% (11 species) each, Theridiidae, with 8.6% (21 species), and Gnaphosidae, Oxyopidae, Sparassidae and Lycosidae, 4.1% (10 species) each (Fig. 2). The species accumulation curve (pooled for each site) reached an asymptote for both the Chao1 and Jackknife2 estimators, indicating that the sampling efforts were adequate at the regional level for all the three sites and caught most of the species that occur there (Fig. 3). The total species richness estimated using the abundance-based Chao1 predicted the richness at the three sites as 153.43 ± 0.9 (Lata Kharak), 162.75 ± 1.24 (Malari) and 206.43 ± 0.9 (Bhyundar Valley). This indicated that the inventory was complete at the regional scale (91%).

Figure 2 .
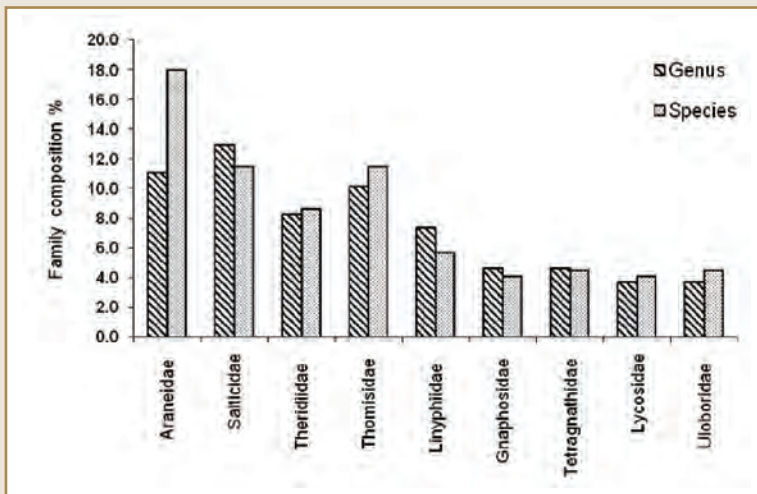
The contributions of families of spiders (>4.0%) in the NDBR in terms of total number of genera and species recorded during the entire sampling period, expressed as percentages
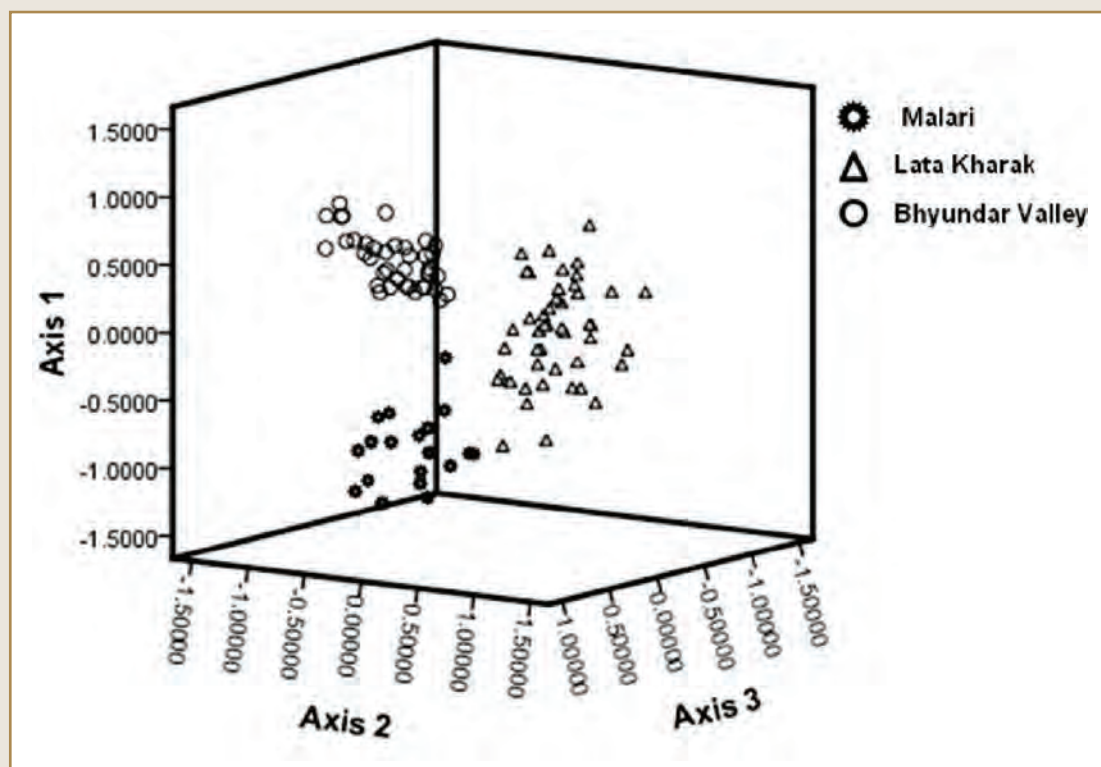
Figure 3.
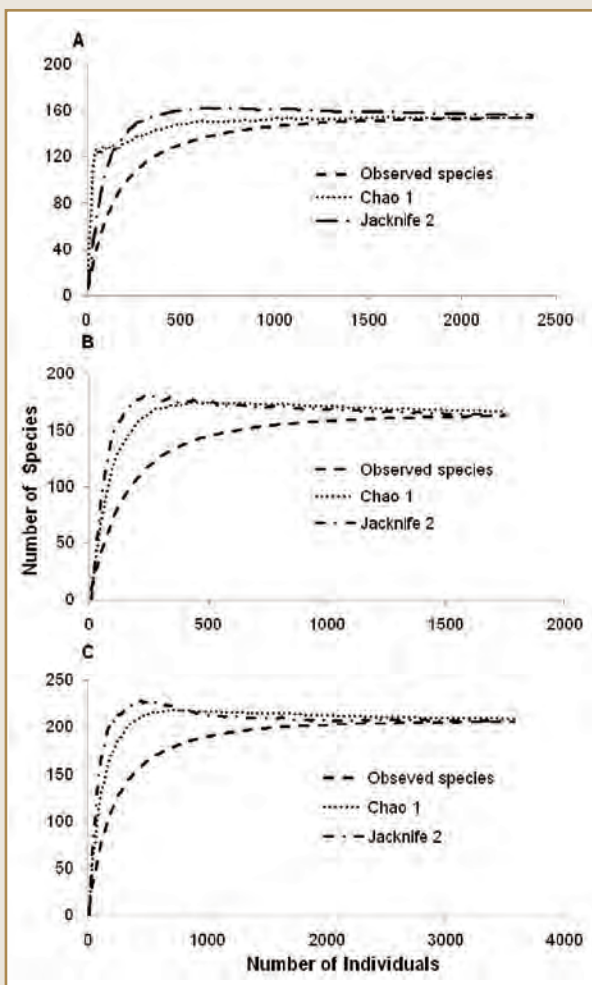
Species accumulation curve and estimation curves of Chao1 and Jacknife 1 for (A) Lata Kharak, (B) Malari and (C) Bhyundar Valley (all samples pooled for each site)

COMMUNITY COMPOSITION

Figure 4.

NMDS graph showing spider species composition across the three sampling sites (stress, 17.32; number of iterations, 400)

The mean altitudes of the three sampling sites, viz. Lata Kharak (2.78 ± 0.57 km), Bhyundar Valley (3.13 ± 0.62 km) and Malari (3.53 ± 0.32 km), differ significantly from each other ($F_{2, 103} = 12.78$ and $p < 0.001$; Fig. 4). The plots sampled at the three sites were plotted in a three-dimensional space from the NMS in PC-ORD. The plotting was done mainly to interpret the dissimilarities between the plots of the three sites on the basis of the spider species composition recorded from each plot. The NMS graph shows distinct clusters of the sampled plots for the three sites, which reveals that the three sites are different from each other in terms of species composition. The three sites, having different altitudinal ranges, acted as three distinct habitats with different species composition. Thus, different altitudinal ranges influence spider species composition as a whole in the NDBR landscape.

PATTERNS OF SPIDER DIVERSITY ACROSS ALTITUDINAL GRADIENT
Species diversity declined linearly across the three sampling sites (Fig. 5).

Figure 5.
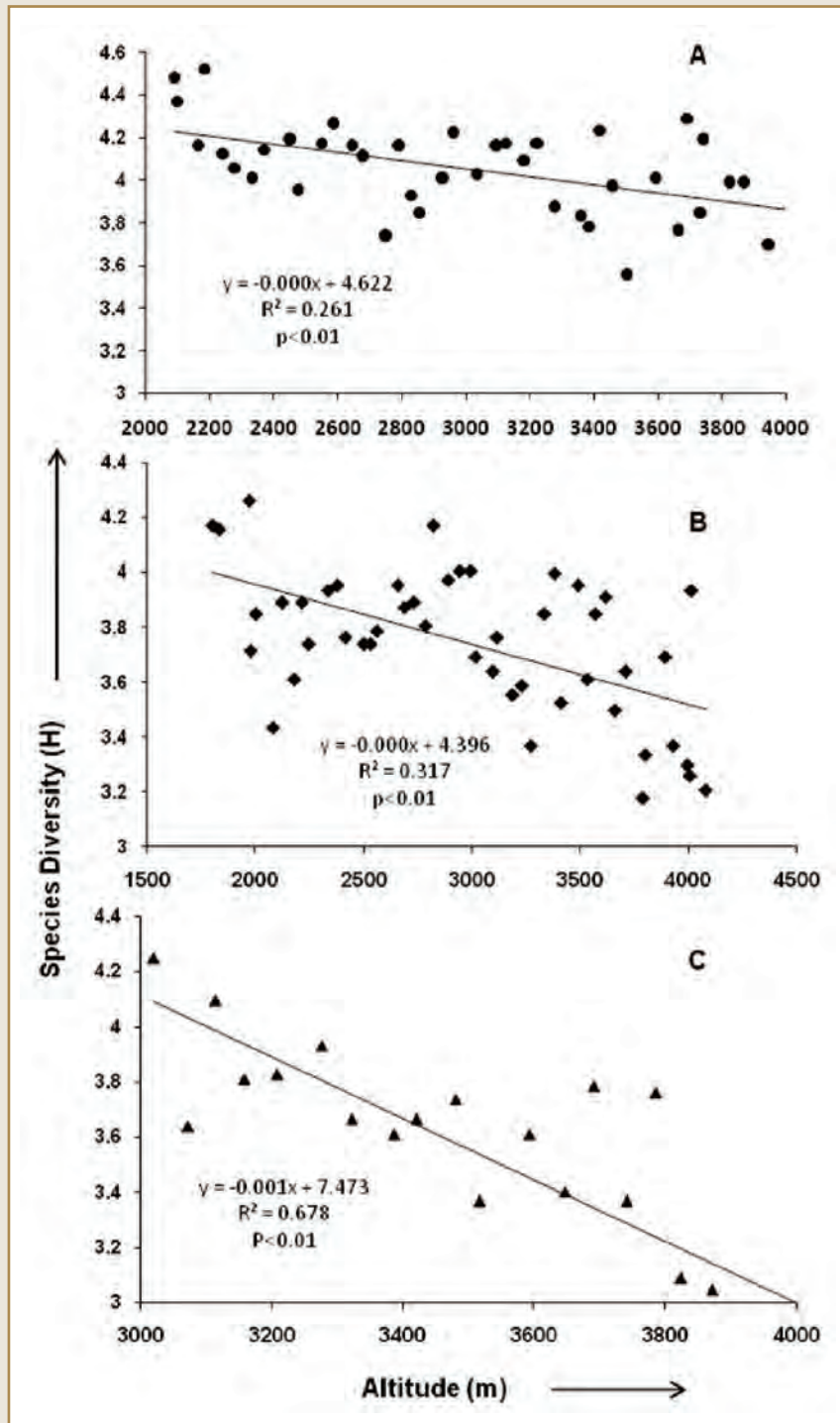
Patterns of species diversity along the altitudinal gradient in the three sampling sites: (A) Lata Kharak, (B) Bhyundar Valley and (C) Malari

The Pearson's correlation matrix at the regional scale indicated that the species diversity was negatively related to altitude. However, the explanatory variables were not correlated (Table 1).

Table 1.

Pearson's correlation matrix for the habitat covariates with regional species diversity (sites combined) as the dependent variable

Variable	Diversity	Altitude (km)	Temperature (°C)	Ground cover (%)	Humidity	Litter depth (mm)	pH
Diversity	1	-0.476	-0.04	0.056	-0.113	-0.029	-0.244
Altitude (km)	-0.476*	1	-0.011	-0.171	0	0	0
Temperature (°C)	-0.04	-0.011	1	-0.193	0.033	-0.031	0.152
Ground cover (%)	0.056	-0.171	-0.193	1	-0.11	0.069	-0.014
Humidity	-0.113	0	0.033	-0.11	1	-0.223	0.074
Litter depth (mm)	-0.029	0	-0.031	0.069	-0.223	1	0.097
pH	-0.244**	0	0.152	-0.014	0.074	0.097	1

* Correlation is significant at the 0.001 level.

** Correlation is significant at the 0.05 level.

Table 2.

The regional species diversity patterns could be explained most parsimoniously and robustly as an interactive effect of site and altitude (Table 2).

Model	Parameters (number)	-2 Log L	AIC	BIC	ΔBIC
D ~1	2	75.6	79.6	84.9	43.6
D ~1+alt	3	48.4	54.4	62.4	21.1
D ~1+alt+alt²	4	48.3	56.3	66.9	25.6
D ~(1/site)+alt	4	35.3	43.3	54	12.7
D ~(1/site)+alt+alt²	5	35.3	45.3	58.6	17.3
D ~1+site+alt	5	25.2	35.2	48.6	7.3
D ~1+site+alt+alt²	6	25.2	37.2	53.2	11.9
D ~1+site*alt	7	8.6	22.6	41.3	0
D ~1+site*alt²	8	5.9	21.9	43.2	1.9
D ~1+site*alt+pH	8	6.3	22.3	43.6	2.3
D ~1+site*alt+humidity	8	8.4	24.4	45.7	4.4

Comparison of alternate candidate models to describe species diversity (D) using information theoretic approach; model parameters,-2 loglikelihood value, Akaike's Information Criterion (AIC), and Bayesian Information Criterion (BIC)and ΔBIC have been reported. The best-fit model predicted the spider species diversity to be an interactive function of region and altitude.

Table 3. Parameter estimates for the best-fit model

Parameter	ß	Standard error	T	Sig.
Intercept	6.70	0.63	10.60	0.01
Lata Kharak	-2.20	0.66	-3.31	0.00
Bhyundar Valley	-2.68	0.66	-4.05	0.00
Altitude_km	-0.89	0.18	-4.97	0.00
Lata Kharak * Alt(km)	0.73	0.19	3.80	0.00
Bhyundar Valley * Alt(km)	0.80	0.19	4.24	0.00

The best fit model indicated that the species diversity declined linearly, by 0.89 units with unit increase in altitude (km). Compared with Malari, the species diversity values of Lata Kharak and Bhyundar Valley were less by >2 units. However, the rate of altitudinal decrease of species diversity was less in Lata Kharak and Bhyundar Valley, compared with Malari (Table 3).

GUILD DIVERSITY PATTERN ALONG ALTITUDINAL GRADIENT

Guild-wise analysis across the elevations showed that among the three guilds (GW, PW, WB), the ground-dwelling spiders had a hump-shaped decline in all the three sampling sites. The responses of the other two guilds, PW and WB, to the altitudinal gradient differed in all the three sampling sites. In Malari and Lata Kharak, the distribution first gradually increased with altitudinal gradient and was maximum at a moderate elevation, after which it decreased gradually with a further increase in the altitude. However, in the third site (Bhyundar Valley), both the guilds did not show any distinguishable trend (Fig. 6). The patterns of herb and shrub diversity were also tested. It was observed that in Lata Kharak and Bhyundar Valley the herb diversity increased with increasing elevation, whereas the pattern of shrub diversity was not very clear (Figs. 7 & 8). In Malari both the herb diversity and shrub diversity showed a declining pattern with increasing altitude (Fig. 9).
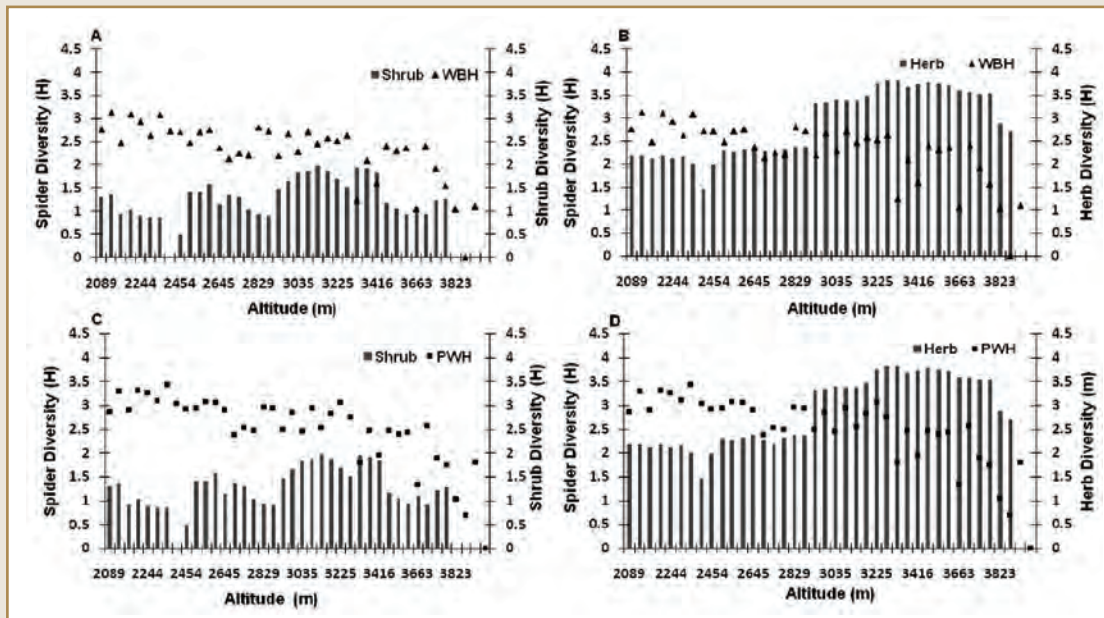
Figure 6.
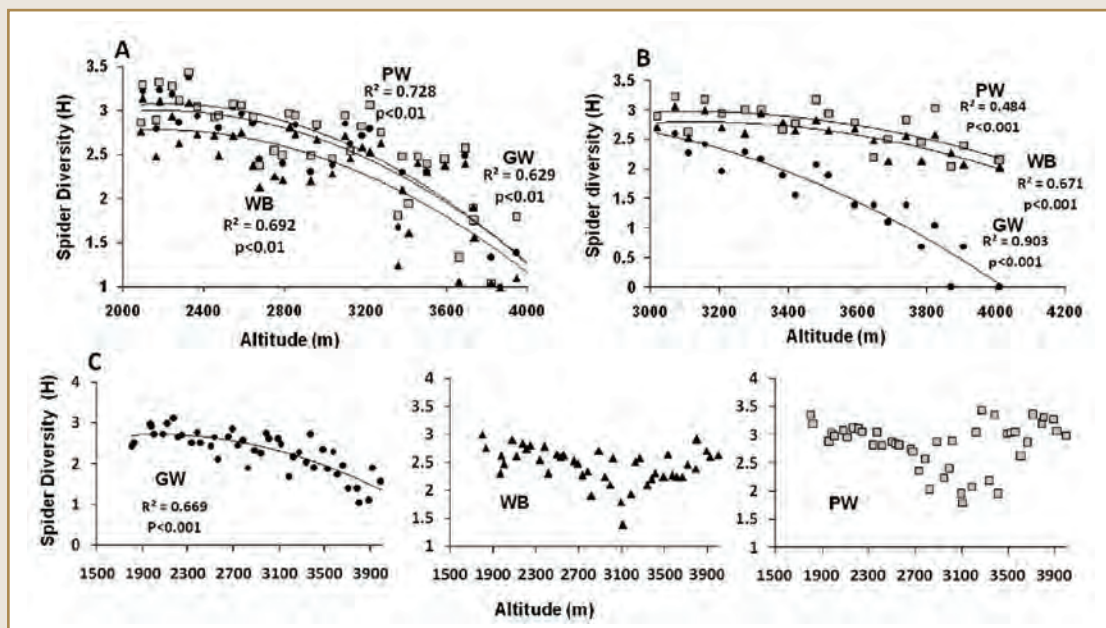
Guild diversity patterns in the three sites: (A) Lata Kharak, (B) Malari and (C) Bhyundar Valley
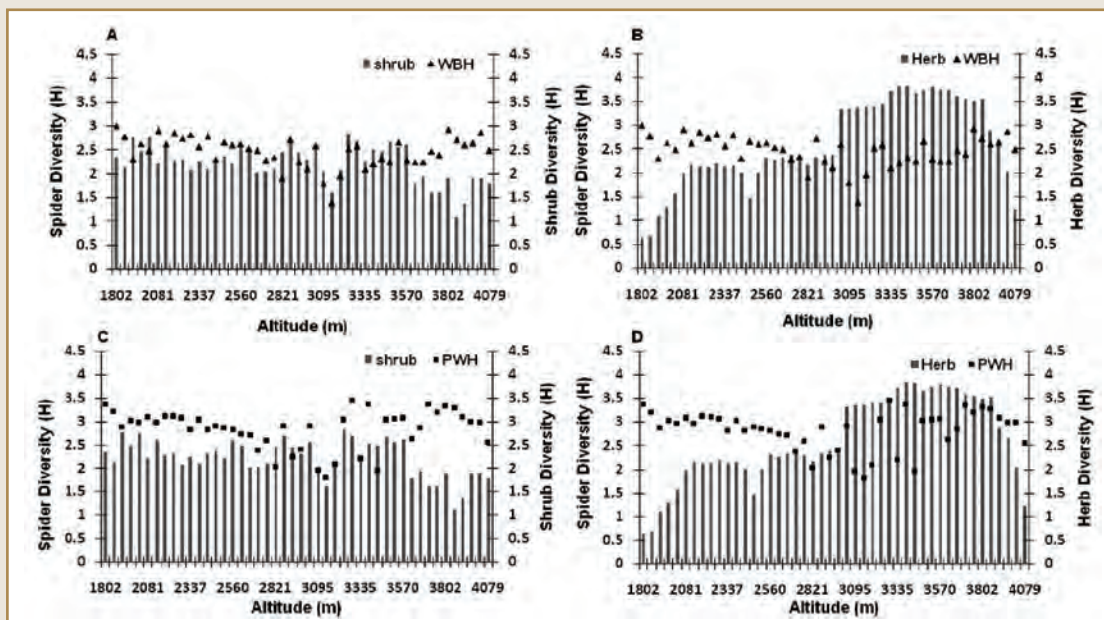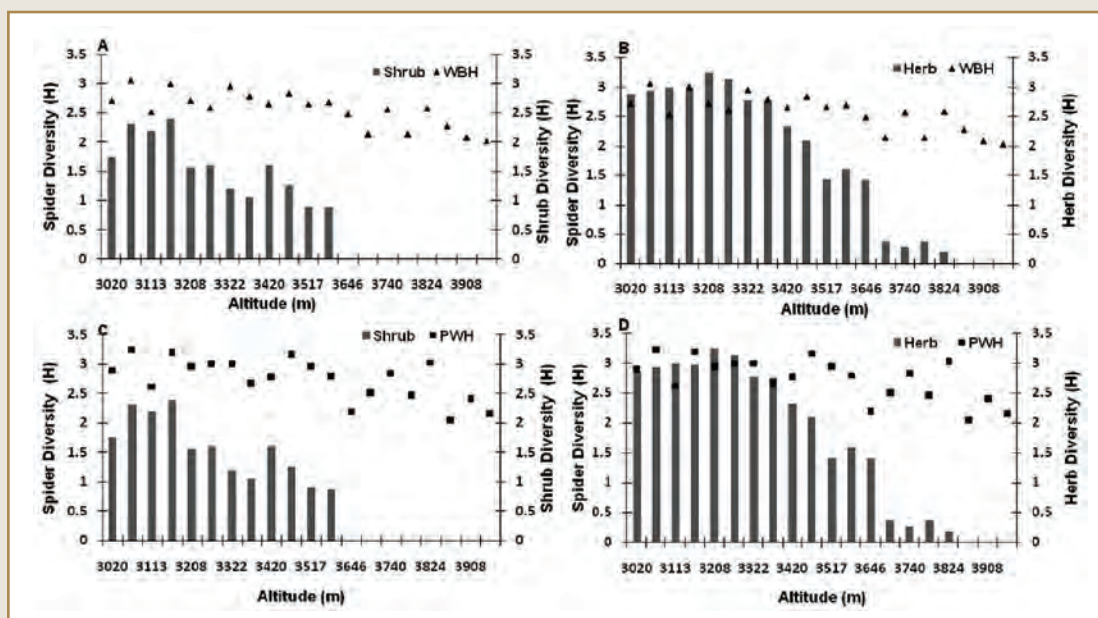
Figure 7.

Patterns of guild diversity of spiders (A-B, WB (web-building spiders); C-D, PW (plant–wandering spiders) along with herb and shrub diversity at Site 1 (Lata Kharak)

Figure 8.

Patterns of guild diversity of spiders (A-B, WB (web-building spiders; C-D, PW (plant–wandering spiders) along with herb and shrub diversity at Site 2 (Bhyundar Valley)

Patterns of guild diversity of spiders (A-B, WB (web-building spiders); C-D, PW (plant–wandering spiders) along with herb and shrub diversity at Site 3 (Malari)

DISCUSSION

It is increasingly important to understand patterns of species diversity in the high-altitude regions of the Indian Himalaya and obtain baseline data with which to compare future changes resulting from spatial shifts in climate and habitat. This study quantifies spider assemblages and shows that spiders partition space and habitat according to the niche they occupy along elevational gradients. A total of 244 species belonging to 108 genera and 34 families were documented during the entire sampling period. This represents 16.1% of the species diversity, 28.6% of the generic diversity and 56.7% of the family diversity reported from India (Sebastian and Peter, 2009). Some of these families and species were observed to have limited distributions, but this may be because they are cryptic or have patchy distributions and thus may not have been adequately sampled.

The results showed that the species diversity decreased with increasing altitude in all the three sampling sites. As spiders are sensitive to small changes in the environment, especially changes in the vegetation, topography and climate, the patterns of linear decline are probably related to the more severe climatic conditions, terrain and landscape of the NDBR, leading to species declines and absences of less tolerant species. Similar findings of spider abundance declining linearly with elevation were observed in the studies of Otto and Svensson (1982) and McCoy (1990). Along the altitudinal gradient of NDBR, two main patterns are evident: first, a steady decline in family diversity, and then, a hump-shaped decline of species. Species are gradually filtered out depending on their tolerance and appropriate habitats, and in most cases they are not replaced by others. From the guild-wise variations with elevation, it was observed that the ground-dwelling spiders showed a hump-shaped decline in all the three sampling sites. Chatzaki *et al*. (2005) also found similar results in Crete: along a broad elevational gradient, the richness of ground-dwelling spiders showed a hump-shaped response to changes in elevation. However, similar hump-shaped responses of plant wanderers and web builders were found in Lata Kharak and Malari, but there was no effect of elevation on these guilds in Bhyundar Valley. The hump shape could be the result of a greater habitat diversity and stability of environmental factors as compared with the higher-altitude zones.

For ground-dwelling spiders, the timberline does not play any major role (Chatzaki *et al.*, 2005). Because they live on the ground, the changing vegetation above the timberline does not affect them directly but only through a decline in food availability, which results from the reduction of habitat diversity and complexity. However, with other spider families that are probably dependent on the vegetation type of their habitat due to their way of life and foraging, the vegetation plays a significant role in shaping these communities. In particular, the formation of ground vegetation and the resulting microclimate

are most likely to affect the diversity and distribution of ground-dwelling spider species, and this is probably a major reason for the formation of specific species assemblages in a habitat (Bultman and Uetz, 1982; Hurd and Fagan, 1992; Gibson *et al.*, 1992). The patterns of species diversity and species composition are probably related to harsh climatic conditions (such as extremes of temperature, humidity, precipitation, wind intensity) and to the landscape, leading to a species decline and an absence of less tolerant species. Species richness is supposed to peak at mid elevations via primary productivity, which is considered to peak at mid elevations. However, Jiménez-Valverde and Lobo (2007) found that spider richness was more strongly correlated with habitat complexity and maximum temperature than with elevation at a regional scale of investigation. Earlier works suggest that species diversity is correlated with the structural complexity of a habitat (Uetz, 1979; MacArthur, 1964; Pickett *et al*., 1991; Androw, 1991; Hawksworth and Kali-Aroyo, 1995; Rosenzweig, 1995). As the habitat structure and complexity change with increasing altitude, shifts in the composition of potential prey species are also expected to occur; supporting a dual process that is probably determining spider assemblages in the area. However, some families, such as the Lycosidae, which are more tolerant and overcome harsh conditions, were also collected from higher elevations.

Changes along spatial gradients associated with changes in habitat can have significant effects on the structures of spider assemblages, but responses vary among sites at different altitudes. Studies conducted by Samu *et al*. (1999) in agricultural ecosystems found that spider abundance/diversity and environmental (including microclimate, habitat and disturbance) diversity were, in general, positively and variably correlated at different scales. Hore and Uniyal (2010) found that habitat heterogeneity in the Terai Conservation Area is mediated largely by the structural diversity of the vegetation rather than microclimatic variations. Structural changes in the vegetation tend to override imminence much before any microclimatic change takes effect in space. Studies have confirmed that residence time is related to disturbance or web destruction (Enders, 1974; Hodge, 1987), microhabitat features such as temperature and humidity (Biere and Uetz, 1981), growth of the spider and an appropriate change in the structural requirements of web construction (Lubin *et al.*, 1993) and prey capture success (Bradley, 1993; McNett and Ryptra, 1997).

From the ordination analysis performed using NMS, it was found that the species composition differed in different mountain systems. It is possible that with increasing altitude, resources get limited and only the tolerant species are able to cope. NMS has been used as a tool for descriptive multivariate data analysis, and the principles and mechanics have been documented well (McCune and Grace, 2002). NMS is well suited to community data, particularly when the β diversity is high (i.e., the data matrix contains many zeroes) (Faith *et al.*, 1987), and permits robust analysis of many data types. In analyses of simulated data with known gradients, NMS has shown a superior ability to recover the underlying data structure compared wtih principal components analysis, principal co-ordinates analysis and reciprocal averaging (Fasham, 1977; Minchin, 1987).

There are several other environmental factors that may also affect the spider species diversity apart from altitude and seasonality, *viz.,* spatial heterogeneity, competition, predation, habitat type, environmental stability and productivity (Rosenzweig, 1995). Other factors are important in influencing spider diversity and species richness in the Himalayan ecosystem, *viz.*, intra- and inter-specific competition, surrounding habitats and climatic factors. However, the role of biotic factors cannot be ruled out as the availability of food and processes such as dispersal may also significantly influence the dynamics and structuring of spider assemblages. Shifts in vegetation structure are also expected to assist changes in diversity, and as the abundance of arthropods such as spiders depends heavily on arthropod prey, dynamic shifts in the prey base are likely to limit the spider assemblage.

The NDBR has an interestingly diverse spider fauna. Similar research in other parts of the biosphere reserve will surely supplement the available information. It is also important to note that the spider fauna is ubiquitous in nature and that its diversity cannot be explained by quantifying any one aspect of the environment. It does depend on many other factors or a combination of factors, apart from altitudinal variations and habitat structure. Looking into these factors will surely bring in more interesting results of relevance to the maintenance and management of this diversity.

ACKNOWLEDGEMENTS

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