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ORIGINAL PAPER

Distinctive patterns in habitat association and distribution of tiger beetles in the Shivalik landscape of North Western India

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Abstract The purpose of the paper is (a) to describe the distribution pattern of tiger beetles in *Shorea robusta* dominated forest ecosystems at landscape level of north western Shivalik Himalaya in environmental space and (b) to evaluate the nature of microhabitat association amongst recorded species of tiger beetles. Twenty-five species of tiger beetles belonging to ten genera were recorded from six protected areas in the tropical dry deciduous Shivalik region with an altitudinal gradient of 350–1,400 m above mean sea level in north western India. Sampling for tiger beetles was carried out using strategically designed sample plot in ten distinct habitat types with five collection methods employed. Species composition of tiger beetles varied significantly between microhabitat types of the protected areas (Shannon $H' = 0.436–1.069$) and habitat specialists were found in only few of habitats. Bray–Curtis cluster analysis clustered the ten habitats into five cluster groups based upon the species composition with *Shorea robusta* most distinct from agricultural habitats. Riverine area was found to be the most diverse (with 18 or 72% of total species) as well as abundant (457 ± 33.61 SE individuals recorded per sample plot). Khair, Syzygium and pine forests were least rich and had only three species each. Two species *J. crassipalpis* and *M. melancholica* were found only in riverine habitat. Though late summer to mid-monsoon was found most favorable for tiger beetles, only one species, *C. chloris* was persistently found even during modest winter months. Bulla's diversity index showed that habitat breadth of species ranged from 0.00 to 6.66, an indicative of their habitat restrictiveness. Indicator species analysis revealed as many as 14 species indicative of particular habitat conditions. Descriptions of some important ecological and behavioral aspects are included for these species. The observed C-score (299.43330) showed that there is less co-occurrence among species pairs alongwith lower niche overlap (Pianka's index $= 0.14191$) thereby illustrating ample resource partitioning at microhabitat level. Further, co-occurrence index among guilds (C-score $=$ 213.16250 with variance 1,949.76300) was found to be smaller than expected, revealing that feeding guilds are differing significantly from one another in their levels of co-occurrence. Canonical correspondence analysis identified canopy cover, litter and average tree density as the most important habitat variable defining the distribution of tiger beetles in environmental space. Such assemblage patterns among species of tiger beetle would thus provide a solid basis to interpret changes in microclimatic conditions, caused by humans directly or through long term climate change and would thus help establishing a baseline in long term monitoring of these forest ecosystems.

Keywords Shivalik · Protected areas · Tiger beetles · Sample plot · Habitat types · Wildlife sanctuary · Sampling · Diversity · Specificity · Habitat attributes and associations

Introduction

The tiger beetles (Coleoptera: Cicindelidae) constitute an insect group of considerable interest to many entomologists (considered by some as a subfamily or tribe within the Carabidae). Adult tiger beetles are colorful, elegant, fast-flying and fast-running insect predators that occupy diverse habitats in temperate and tropical areas. They are relatively easy to observe and generalizations of their biodiversity are reflected in other taxa (Pearson and Cassola 1992). The

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taxonomy of this family is unusually well known worldwide (Wiesner 1992). Moreover, the family's size (around 2,600 species) is small enough to be studied by single specialist authors but large enough to reveal useful and illuminating patterns of biogeography and biology (Pearson and Vogler 2001).

Although some species of the family are arboreal, occupying tree trunks, low bushes, hedges, and under story growth (Naviaux 1994, 2002), the majority are terrestrial (adults are active on soil and vegetation substrates while the larvae hunt for prey from vertical burrows, primarily at the soil surface). India (including the Andaman and Nicobar islands) with 208 species of tiger beetles has the second highest number in the world (only Indonesia, with 237 species, has more). Of these, 52% (108 species) are endemic to India (Acciavatti and Pearson 1989; Cassola and Pearson 2000). The goal of the present study is to examine the diversity patterns (spatial and temporal) of tiger beetles in six protected areas across the Shivalik landscape of the north western India.

Methods

Study areas

Shivaliks: The low mountains that make up the Shivalik landscape were formed by a deposition of detritus and sediment as a skirt at the southern base of the rising Himalayas. This narrow strip is 2,000 kilometers long and forms a continuous chain with an average elevation of 900–1,200 m above mean sea level and in places, a width of only 16 km. Following study areas were selected in Shivaliks for the purpose of present study (Fig. 1).

Pong Dam Wetland sanctuary (PWLS)

This sanctuary (31°50′–32°07′N and 75°58′–76°25′E) lies in the Kangra district, Himachal Pradesh over an area of 307 sq. km. There is a little submerged aquatic vegetation and shoreline does not support much emergent vegetation due to the pronounced seasonal changes in water level. There is an extensive swamp with river beds and grasslands in the seepage area below the dam (Gaston 1985, 1986). The surrounding hillsides support mixed deciduous and chir pine forest. The dominant trees being chir pine (*Pinus roxburghii*), khair (*Acacia catechu*), *Mallotus philipennsis*, *Cassia fistula*, *Bombax ceiba*, and *Ehretia laevis.* The undergrowth consisted of shrubs *Murraya koenigii*, *Adathoda vasica* and *Lantana camara*.

Naina Devi wildlife sanctuary (NWLS)

The sanctuary (31°16′–31°24′N and 76°25′–76°35′E), lies in Bilaspur district, Himachal Pradesh over an area of 123 sq. km with an altitude gradient of 500–1,000 m. The vegetation is mostly mixed deciduous forests with *Mallotus philipennsis*, *Ehretia laevis*, *Syzygium cumini* and some *Ficus* sp.

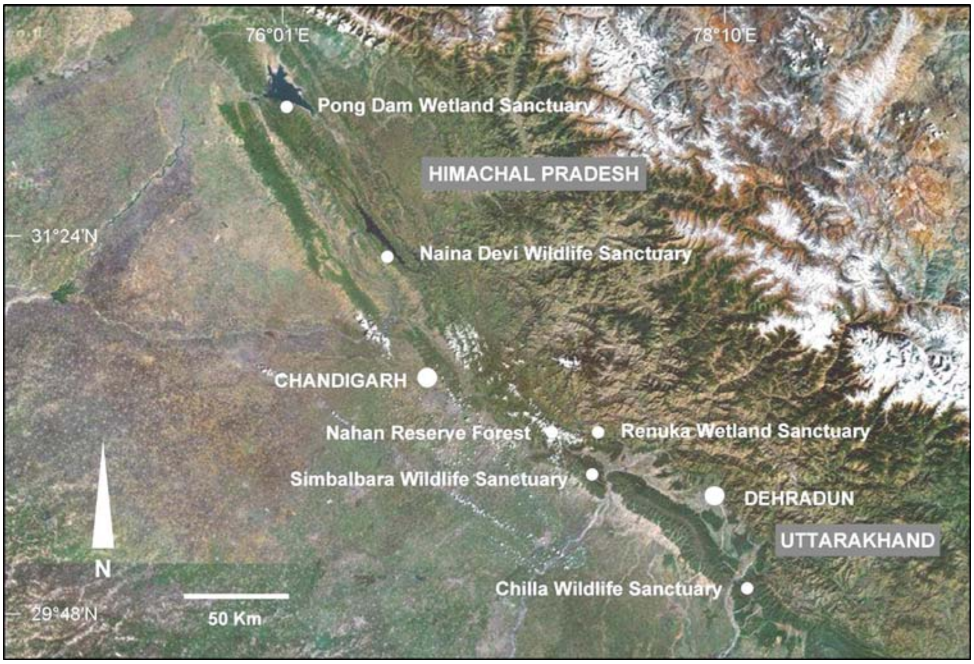


Fig. 1 The study area along the Shivalik Himalaya in north western India showing location of different protected areas (small white dots)

Nahan reserve forest (NRF)

These reserve forests (30°37′43″N and 77°17′10″E) consist of pine (*Pinus roxburghii*) forests interspersed with *Pyrus* sp. at an altitude between 1,200 and 1,400 m. The undergrowth mainly has shrubs such as *Murraya koenigii*, *Carissa carandus*, *Lantana camara*, *Rubus* sp., *Berberis* sp., and seedlings of *Mallotus philipennsis* and pine.

Renuka Wetland wildlife sanctuary (RWLS)

It is a small sanctuary (30°35′58″–30°37′08″N–77°26′34″–78°28′21″FE) occupying an area of 4 sq. km. in Sirmaur district, Himachal Pradesh with a mean altitude of 220–880 m above mean sea level. The vegetation is mainly dry mixed deciduous forest and submerged aquatic vegetation.

Simbalbara wildlife sanctuary (SWLS)

This sanctuary (30°24′21″–30°28′13″N and 77°27′18″–77°31′26″E) is a representative of lower Shivalik region. It lies in confluence of peninsular plains and main Shivalik system and thus flora, fauna and physical features show affinities to western Himalaya, Punjab plains and upper Gangetic plains (Biogeographic zones 2B, 4A and 7A, respectively, Rodgers et al. 2002). The altitudinal range is 350–700 m above mean sea level. The hills are composed of unconsolidated sandstone and conglomerate that are extremely prone to erosion. The soil here is extremely porous and thereby highly drained. However, in many low-lying areas springs emerge and create perennially moist microhabitats for tiger beetles. Moist forests dominated by dipterocarp tree species called Sal (*Shorea robusta*) and northern dry mixed deciduous forests characterize much of the sanctuary.

Chilla wildlife sanctuary (CWLS)

This sanctuary (148 sq. km) is a part of Rajaji National Park (820 sq. km) (29°52′–30°15′N and 77°55′–79°80′E) and situated at Shivalik foothills of Uttarakhand near river Ganges. The altitudinal ranges from 300 to 1,350 m above mean sea level. The area is hilly that is bisected by monsoon sandy river beds (*raus*), a prime habitat for tiger beetles. CWLS is thickly foliated predominantly by the sal (*Shorea robusta*) mixed forest and a number of other forest types which includes the western Gangetic moist and northern dry deciduous and khair-sissoo forests, and interspersed *Terai* grasslands. Major tree species are *Shorea robusta*, *Mallotus philipennsis*, *Ehretia laevis*, *Tectona grandis*, and *Haplophragma adenophyllum*.

Sampling

Vegetation sampling

Vegetation for each transect was quantified using stratified random sampling. Square plot of 10 m × 10 m was laid on either side of transect at 100 m interval to quantify trees. Square plot 5 m × 5 m were laid on either side of transect at 100 m interval to quantify shrubs. In each of these plots, two plots of 1 m × 1 m were laid for estimating herb abundance and grass cover including the grass height. The following variables were measured in each vegetation plot viz. average density of trees, shrubs, and herbs, grass cover, snag, termite mound, tree height, average girth at breast height (av. GBH), grass height, and canopy cover (using canopy densitometer). IVI was calculated for each dominant tree species in each transect (Curtis 1959).

In addition to major forest types found in these protected areas, there are also small areas of mixed woodlands and plantation forests. We observed and sampled tiger beetles in ten distinctive habitats across the landscape based on importance value index (IVI) (Curtis 1959) of dominant tree species of each habitat types. Thus following habitats were delineated based on IVI and sampled for tiger beetles viz. Sal (*Shorea robusta*) forest (SF), *Eucalyptus* plantation mixed forests (EP), Teak (*Tectona grandis*) mixed forests (TP), Khair (*Acacia catechu*) mixed forest (KF), Riverine forests (RP), Mixed forest (MF), *Syzygium cumini* mixed forest (SY), *Bamboo bambusae* mixed forest (BF), Agricultural land (AL), and Pine (*Pinus roxburghii*) forest (PM). We conducted the study from September 2004 to August 2007 to obtain reliable data from different years and seasons.

Habitat variables

Abiotic habitat variables such as temperature and relative humidity (RH) were recorded using digital thermometer and digital hygrometer (from Forestry suppliers, USA), respectively. Other soil variables like percentage organic content (% OC) (using Walkley and Black 1934), pH (using digital soil pH meter), soil texture (using Bouyoucos 1962), and litter depth (using Faith et al. 1998) were also recorded and/or calculated for each transect in field and in the laboratory.

Tiger beetle sampling

Because of their agility and speed, we spent several days learning to find and identify tiger beetles in the various habitats. We sampled diurnal tiger beetles from 08:30 to 11:00 h, the period of maximum activity on most days. Because many species of tiger beetles are attracted to night lights (Pearson and Vogler 2001), we used light traps to measure their activity from 19:30 to 21:00 h in summer and monsoon. During winter dormancy, we sampled adults by looking for aggregations in different hibernation sites, such as under stones, crevices, and below decaying logs. For diurnal sampling during active seasons, we used several methods to sample populations of tiger beetles within each habitat type. These methods included beating trays (BT) using a 1.8 × 1.2 m white insect collection sheet, sweep net capture (SN) using standard sweeping net, hand sorting (HS) by visual observation, and conventional pitfall traps (PT) in each sample plot.

Sample plot

It was the most basic and smallest sampling unit grid with 50 m × 50 m dimensions i.e., an area of one-fourth of a hectare (Fig. 2). Five such sample plots were marked on each linear transect measuring 300 m in length in each habitat along open forest paths. Thus we had one transect containing five sample plots. Thus, over entire Shivalik landscape in north western Himalaya we had a total of 46 transects containing 230 sample plots in ten different habitats in six different protected areas (Table 1). The spatial distance between two transects in each protected area was maintained at minimum 500 m. The contiguous sample plots in each habitat were separated from each other by a distance of 10 m that stood as no-sampling zone to maintain adequate sampling distance between any two contiguous sample plots. These sample plots were monitored for tiger beetles during winter, summer, and monsoon months for three seasons to obtain consistent data.

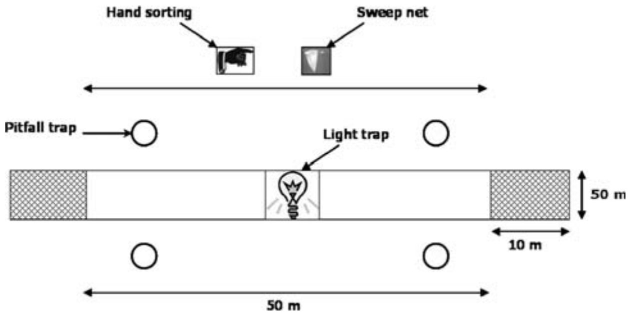


Fig. 2 Sample plot showing different collections methods employed for sampling of tiger beetles (Figure not to scale)

Table 1 Representation of transects in different protected areas in the Shivalik landscape

Study area	No of transects	No of sample plots	Transect pseudo replicates of each habitat[a] type
PWLS	11	55	2, 2, 0, 0, 5, 2, 0, 0, 0, 0
NWLS	3	15	1, 0, 0, 0, 0, 2, 0, 0, 0, 0
NRF	3	15	0, 0, 0, 0, 0, 0, 0, 0, 0, 3
RWLS	2	10	0, 0, 0, 0, 0, 2, 0, 0, 0, 0
SWLS	17	85	5, 2, 1, 1, 2, 2, 1, 1, 1, 1
CWLS	10	50	3, 0, 0, 0, 3, 2, 0, 0, 2, 0
Total	46	230	–

[a] Read as SF, EP, TP, KF, RP, MF, SY, BF, AL, PM

In each sample plot BT, SN, and HS were employed throughout the median axis of each sample plot. But pitfall traps (four in number) were strategically placed in each sample plot about 10 m from the start point and 5 m away from the median axis of the transect. Plastic jars measuring 10 cm × 6 cm filled with 50 ml of 10% ethyl acetate–saline solution were used as pitfall traps. The pitfall traps were left open and specimens were collected every tenth day and traps were restored with fresh solution. We used an incandescent light (18 W × 2) for setting up light trap and held it over a white sheet (1.8 × 1.2 m) acting as its background. The light trap was placed at the center of each sample plot on median axis to sample tiger beetles in each habitat. This nocturnal light trap helped us determine the presence of primarily nocturnal species as well as nocturnal activity of otherwise diurnal species (Pearson and Vogler 2001). Combining these different methods thus maximized the likelihood of our adequate sampling for habitat associations, spatial patterns, and community structure of the tiger beetles.

Statistical analyses

Diversity, abundance and seasonal patterns of tiger beetles and their activity

We used program BioDiversity Pro (McAleece et al. 1997) to calculate Shannon index (H') to measure diversity and evenness (Pielou 1969) of tiger beetles across the six protected areas in altitudinal gradient of 350–1,400 m above mean sea level in Shivalik landscape of western Himalaya (Shannon and Weaver 1949). We studied the spatial distribution and abundance pattern of tiger beetles across the landscape in ten different habitats using ordination of relative abundance (scaled to 100%) in relation to habitats. Comparison of patterns of seasonal abundance for each species was studied using error graphs (SPSS 2007 ver.16.0). Bray–Curtis cluster analysis (single link) was performed to find out the clustering of habitats into distinct groups based on the species composition using PC-Ord ver.4.26 (McCune and Mefford 1999).

Habitat specificity and indicator species

Although there are disagreements as to which evenness index is most appropriate and how serious are the assumptions associated with each (Camargo 1995), we applied Bulla's index (Bulla 1994) as a relatively simple quantification of habitat specialization for each species, as a measure of habitat breadth (H) in different habitat types. We used the data on relative frequency of each species in each habitat type to calculate H. Thus, species restricted to one habitat type have minimum habitat breadth, and have a value of H equal to zero. While if a species is evenly distributed across all habitat types, H would be equal to total number of habitats. Indicator species analysis (Dufrene and Legendre 1997) was performed using PC-Ord ver.4.26 (McCune and Mefford 1999) to determine tiger beetle species characteristic of particular microhabitat conditions. Monte-Carlo randomization test was used to determine if the value is greater than expected by chance; thus species with only one or a very few individuals are unlikely to be considered indicators, even if they appear in only one habitat type.

Habitat attributes and effect of habitat variables

For understanding co-occurrence amongst species, we calculated the C-score value (Stone and Roberts 1990) using Ecosim (Gotelli and Entsminger 2001) and maintained row and column totals in the simulation, so that the numbers of occurrences of each species in the null communities were the same as in the original data set. Niche overlap between species was calculated from Pianka's index (Pianka 1973) using Ecosim and we followed randomization algorithm (RA) 3 as it retains the niche breadth of each species, and randomizes "*which*" particular resource states are utilized. It also retains the amount of specialization for each species, but allow it to potentially use other resource states. Pianka's niche overlap index measures the relative amount of habitat overlap between each pair of species and ranges from a minimum of 0.0 (no shared habitats) to a maximum of 1.0 (identical habitat use). Since tiger beetles are generalist carnivores, their grouping into different feeding guilds was delineated using the habitat use of each species in different season and habitats. Further, an overall value integrating all feeding guilds (including the testing of favored state hypothesis) was calculated from C-score using Ecosim (Gotelli and Entsminger 2001) as it tests whether the mean and the variance co-occurrence index among guilds are larger or smaller than expected by chance. Thus an unusually large variance would mean that the guilds differ significantly from one another in their levels of co-occurrence, while an unusually small variance would mean that guilds are strikingly similar to one another in the level of co-occurrence observed. Canonical correspondence analysis (CCA) (ter Braak 1986) was performed using PC-Ord (McCune and Mefford 1999) to find out the effect of habitat variables and their importance in predicting distribution of tiger beetles community composition in relation to environmental variation.

Results

We surveyed a total of 46 transects with 230 permanently marked sample plots across the Shivalik landscape of north western India and recorded 25 species of tiger beetles belonging to ten genera from six different protected areas (Table 2).

Diversity, abundance and seasonal patterns of tiger beetles and their activity

SWLS was found to be the richest as 18 (or 72%) of tiger beetle species were recorded from there, followed by CWLS with 12 (or 48%) species. RWLS was poorest with three (or 12%) species followed by NRF with four (or 16%) species (Table 2). Though it appears that with the increase in altitude from 350–750 m (in SWLS) to 300 to 1,350 m (in CWLS) to 500–1,000 m (in NWLS) and to 1,200–1,400 m (in NRF), there is significant decline in species richness (one way ANOVA, F value $= 10.116$, P value $= 0.00518$, $F_{\mathrm{crit}} = 4.413$) but it is inferred that tiger beetles preferred open habitats like riverine tracts and/or forests with open canopy cover found in some protected areas than the upper hilly reaches. Further, the change in vegetation composition is commendable with difference in dominant tree species and this was reflected in the tiger beetle species diversity. As it could be established that Shannon H' and $H_{\max}$ varied significantly between different habitats (Fig. 3; Table 3). It was maximum in RP (1.069), followed by MF (1.039) and least in PM (0.436) and KF (0.465). Though this landscape is dominated by sal (*Shorea robusta*) forests, the diversity of tiger beetles in sal dominated habitats (0.944) was low as compared to other habitats like RP and MF suggesting preference of open and diverse habitat conditions by these species.

Shannon evenness (J') varied from 0.853 to 0.999 illustrating that proportional abundances are the same. But the pattern of spatial distribution of abundance differed considerably among the habitats in relation to species. All ten habitats were occupied by tiger beetles, but not all were relatively equally abundant (Fig. 4). Two habitats RP and MF were dominated by maximum 18 and 12 species, respectively. These were followed by SF (10 species), TP (9 species), AL (8 species), BF (5 species), and EP (4 species). While three habitats were least dominated by three species like KF by *C. intermedia*, *C. plumigera*, and *C. venosa*; SY by *C. grammophora*, *C. intermedia*, and *C. plumigera*; and PM by *C. intermedia*, *H. pulchella*,

Table 2 Presence–absence matrix of tiger beetles in protected areas across Shivalik landscape

S. no.	Species	PWLS	NWLS	NRF	RWS	SWLS	CWLS
1	*Calochroa bicolor*	–	–	–	–	*	*
2	*Calochroa flavomaculata*	*	–	–	–	–	–
3	*Calomera angulata*	*	–	–	–	*	*
4	*Calomera chloris*	*	–	–	–	*	*
5	*Calomera plumigera*	*	–	–	–	*	*
6	*Cicindela erudita*	–	–	–	–	*	–
7	*Cicindela fastidiosa*	–	–	–	–	–	*
8	*Cicindela multiguttata*	–	–	–	–	–	*
9	*Cicindela parvomaculata*	–	–	–	–	–	*
10	*Cicindela vigintiguttata*	–	–	–	–	–	*
11	*Cosmodela intermedia*	*	*	*	*	*	*
12	*Cylindera bigemina*	*	–	–	–	*	–
13	*Cylindera grammophora*	*	–	–	–	*	–
14	*Cylindera spinolae*	–	–	–	–	*	–
15	*Cylindera subtilesignata*	*	*	*	*	*	–
16	*Cylindera venosa*	–	–	–	–	*	*
17	*Cylindera viduata*	–	–	–	–	*	–
18	*Heptodonta pulchella*	–	*	*	–	–	–
19	*Jansenia chloropleura*	–	*	*	–	–	*
20	*Jansenia crassipalpis*	*	–	–	–	*	–
21	*Lophyra striolata*	–	–	–	–	*	–
22	*Myriochila melancholica*	*	–	–	–	*	–
23	*Myriochila undulata*	–	–	–	–	*	*
24	*Neocollyris bonellii*	–	*	–	–	*	–
25	*Neocollyris saphyrina*	–	*	–	*	*	–
	Grand total	**10**	**6**	**4**	**3**	**18**	**12**

*, Present, –, absent

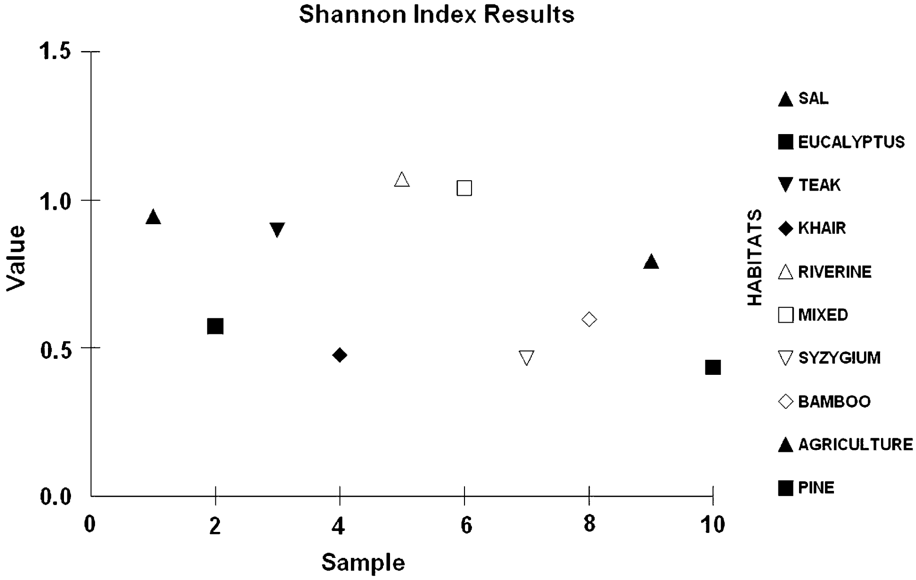


Fig. 3 Shannon diversity (H') measure in different habitat types across study area

and *L. striolata*. Two species of tiger beetles were restricted to a single habitat i.e., *J. crassipalpis* and *M. melancholica* both recorded in RP.

Further, the mean abundance of tiger beetle species per transect also showed distinct patterns of assemblage in different habitats (Fig. 5). It was found that RP supported

Table 3 Comparison of species richness of tiger beetle assemblages in habitat types across Shivalik landscape

Index\habitats	SF	EP	TP	KF	RP	MF	SY	BF	AL	PM
Shannon H' log base 10	0.944	0.574	0.898	0.477	1.069	1.039	0.465	0.596	0.794	0.436
Shannon H_{max} log base 10	1	0.602	0.954	0.477	1.23	1.079	0.477	0.699	0.845	0.477
Shannon J'	0.944	0.953	0.941	0.999	0.869	0.963	0.974	0.853	0.939	0.914
Simpsons diversity (1/D)	8.861	4	7.403	3.182	10.106	10.462	3.122	3.49	6.883	2.565

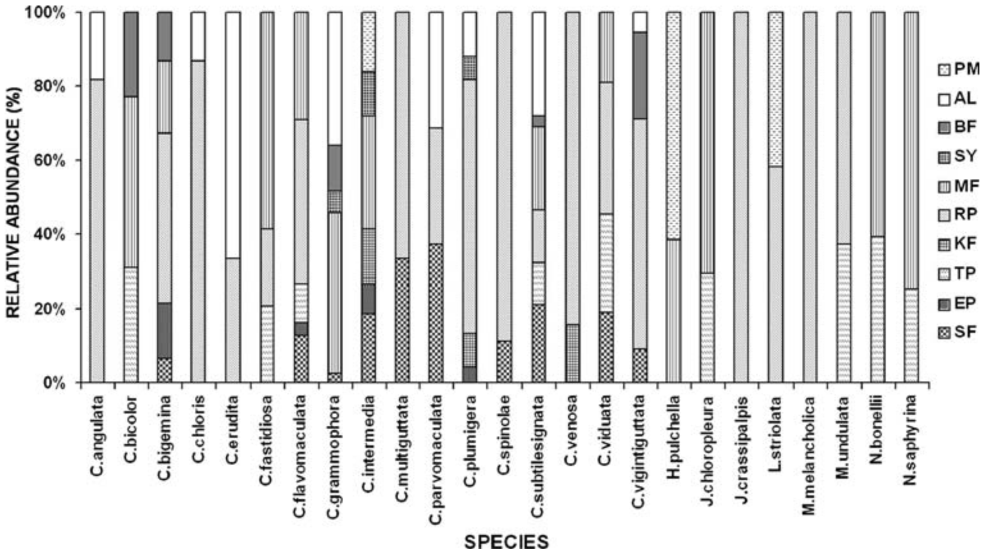


Fig. 4 Habitats in the study area showing the relative composition of tiger beetle species (mean abundance scaled to 100% of relative proportion)

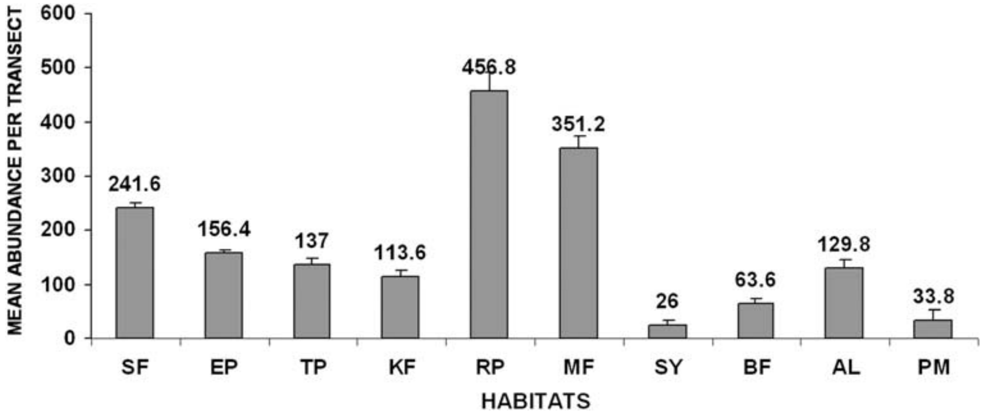


Fig. 5 Mean abundance of tiger beetles per transect (error bars are SE of mean)

more than 26% (457 ± 33.61 SE specimens) while the SY had less than 3% (only 26 ± 7.33 SE specimens) tiger beetles recorded in the study. MF (351.2 ± 23.58 SE specimens) supported more than the SF (241.6 ± 9 SE specimens) dominant landscape. An interesting pattern of assemblage, communal roosting, was also recorded amongst tiger beetles in the riverine area. This behavior on undergrowth plants occurred most commonly amongst *C. plumigera*, *C. angulata*, and *C. chloris* in some of the riverine area (Uniyal and Bhargav 2007). These large roosts often included more than 5,000 individuals at its peak activity, though fluctuating anywhere from 300 to 3,500. Usually, such tiger beetle communal roosts have social function, for food information exchange, and population regulation (Pearson and Anderson 1985). But in our study, communal roosting was persistently associated with overcast conditions, decreased temperature, and precipitation for the purpose of protection from predation, and ensuring thermoregulation advantages.

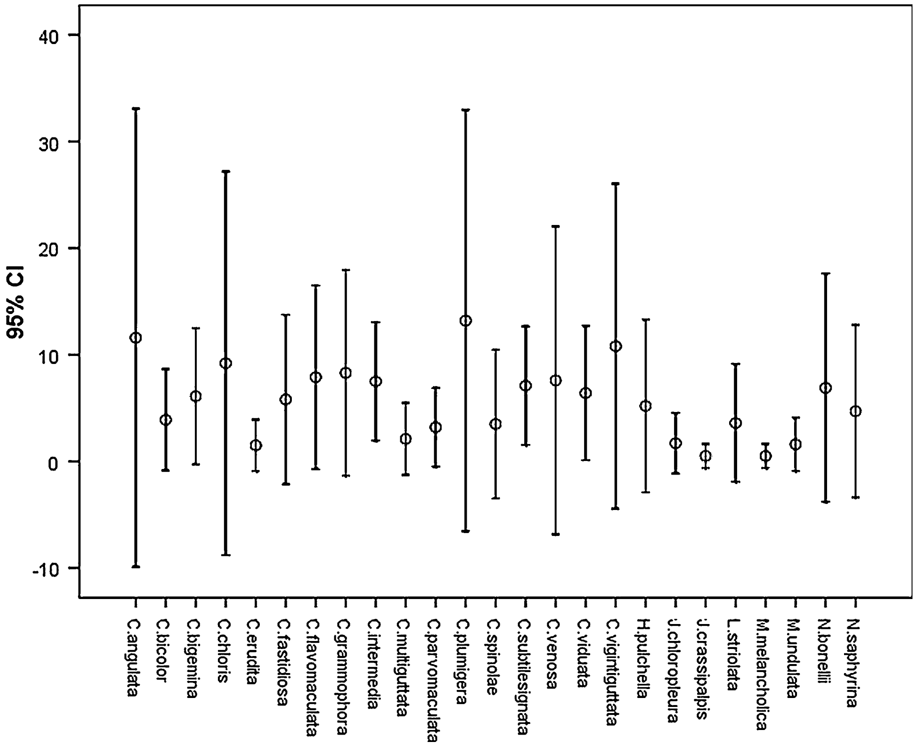
In total, *C. angulata* was the most abundant species with 264 specimens followed by *C. plumigera* 232 specimens recorded in all habitats especially in RP. These were followed by *C. vigintiguttata* (206 specimens) and *C. chloris* (184 specimens). Three species *M. melancholica* (26 specimens), *M. undulata* (32 specimens) and *J. crassipalpis* (37 specimens) were the least abundant.

C. grammophora (164 specimens) was the most abundant in MF and AL, *H. pulchella* (104 specimens) in PM, and *N. bonellii* (138 specimens) and *N. saphyrina* (94 specimens) were most abundant in MF.

In general all the tiger beetle species showed a spike in activity with the onset of the monsoon as evident from the mean abundance per transect at 95% CI pooled over three seasons i.e., winter, summer, and monsoon. This spike was large for some species, such as *C. angulata*, *C. plumigera*, *C. chloris*, and *C. vigintiguttata* and smaller for other species, such as *M. melancholica* and *J. crassipalpis* (Fig. 6). During winter, the adult population size of tiger beetle species fell to none or only a few, as most of the species underwent hibernation. Although adults of some species, such as *C. angulata* and *C. chloris*, were active together on the riverine area throughout year, *C. chloris* was particularly more abundant during the dry part of the year, and in winter while *C. angulata* was predominant during the monsoon season.

Sorensen (Bray–Curtis) similarity measure with flexible β group linkage (distance, $\beta = -0.25$) was used for cluster analysis based upon the species composition of tiger beetles in ten different habitats to generate hierarchy of clusters (Fig. 7). Five such cluster groups were obtained

Fig. 6 Mean abundance of tiger beetles per transect (pooled season wise data for each species) at 95% confidence interval



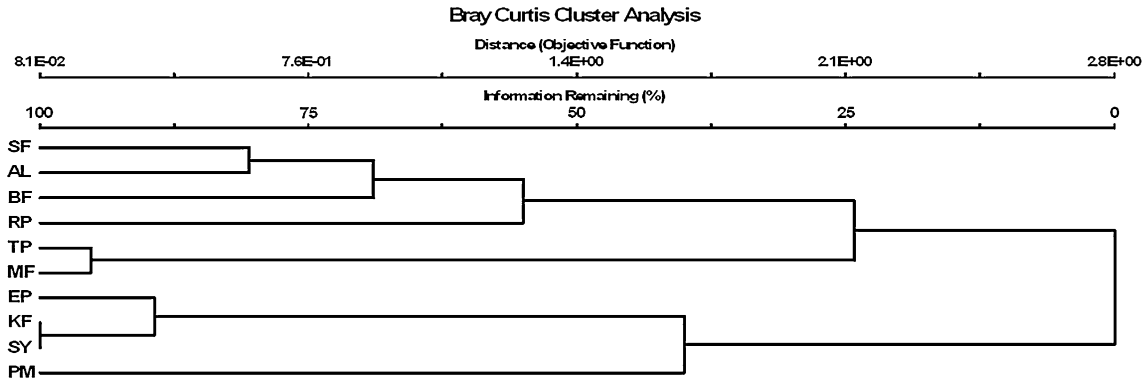


Fig. 7 Bray–Curtis cluster analysis dendrogram showing the distance relationship between habitats according to species assemblage composition

viz. cluster 1 includes SF, AL, and BF; cluster 2 includes only RP as separate and distinct group; cluster 3 includes TP and MF; cluster 4 includes EP, KF, and SY indicating different patterns of species composition; and cluster 5 includes only PM as separate and distinct group.

Habitat specificity and indicator species

Based on combined capture data, we used Bullas's diversity index (Bulla 1994; Rodriguez et al. 1998) to calculate the proportion of available habitat spectrum used by each of the tiger beetle species as well as overlap among species (Table 4). Two species *J. crassipalpis* and *M. melancholica* were the most habitat specific/restricted (Habitat breadth, $H = 0$). The remaining species used several habitats, but none was present in all the habitat types, hence no species could be found with $H = 10$. The most widely occurring species was *C. intermedia* ($H = 6.66$), followed by *C. subtilesignata* ($H = 6.60$) and *C. plumigera* ($H = 5.88$). H for 17 species (or 68%) ranged between 1 and 5 showing greater degree of habitat restriction in at least five habitats; while H for four species ranged between 5 and 6 depicting lesser habitat specialization. Thus, habitat breadth ranged from 0.00 to 6.66 for all the species recorded and the different altitudes did not have any bearing on habitat specialization unlike richness (one way ANOVA, F value = 1.219, P value = 0.284, $F_{\text{crit}} = 4.413$). H could thus be dependent on pertinent factors like floral diversity, foliage density, shading, and microhabitat conditions and/or indirectly on the diversity and abundance of potential prey items for the tiger beetles, specific for each protected area. Therefore, variations in species richness across the landscape were attributed to the differences in the range of habitat types present in each of these protected areas. SWLS being a biogeographically significant protected area (Bhargav and Uniyal 2008) and CWLS offered different microhabitat conditions conducive for many tiger beetle species to occur together, sharing similar habitat but occupying different niches. NRF largely being pine forest supported only three species like *H. pulchella*, *C. intermedia* and *L. striolata*.

Table 4 Habitat breadth (using Bulla's diversity index) of tiger beetles in habitat types across Shivalik landscape

S. no	Species	*N*	Habitat breadth (*H*)
1	*Calochroa bicolor*	78	3.33
2	*Calochroa flavomaculata*	148	5.67
3	*Calomera angulata*	264	2.51
4	*Calomera chloris*	184	2.22
5	*Calomera plumigera*	232	5.88
6	*Cicindela erudita*	53	1.31
7	*Cicindela fastidiosa*	116	3.60
8	*Cicindela multiguttata*	55	1.20
9	*Cicindela parvomaculata*	72	3.11
10	*Cicindela vigintiguttata*	206	4.91
11	*Cosmodela intermedia*	136	6.66
12	*Cylindera bigemina*	118	5.50
13	*Cylindera grammophora*	164	5.71
14	*Cylindera spinolae*	66	1.77
15	*Cylindera subtilesignata*	127	6.60
16	*Cylindera venosa*	152	1.90
17	*Cylindera viduata*	116	4.78
18	*Heptodonta pulchella*	104	2.06
19	*Jansenia chloropleura*	44	1.13
20	*Jansenia crassipalpis*	37	0.00
21	*Lophyra striolata*	72	1.54
22	*Myriochila melancholica*	26	0.00
23	*Myriochila undulata*	32	1.11
24	*Neocollyris bonellii*	138	1.67
25	*Neocollyris saphyrina*	94	1.43
	Total	2,834	–

N number of specimens recorded per habitat

Thus indicator species analysis was performed to find out the "genuine" species indicative of particular habitats (Table 5). 14 (or 56%) out of total 25 species of tiger beetles were found to be adequately representing particular habitat conditions. One of the most important amongst them was *C. bicolor* an indicator species for high canopy cover, as this species was particularly found in mixed forests with more than 32% closed canopy (one way ANOVA, F value = 14.512, P value = 0.016, $F_{\text{crit}} = 10.116$). Some species like *C. bigemina*, *C. erudita*, *C. venosa*, and *C. vigintiguttata* were particularly indicative of ecotones and were found predominantly at interfaces of forest-agriculture land, riverine-grassland, and riverine-agriculture areas.

Habitat attributes and effect of habitat variables

Abiotic variables did not differ significantly in their values across different habitat types in the sampling seasons. This was reflected in Pearson correlation (SPSS 2007 ver.16.0) of mean species richness of tiger beetles with mean temperature and relative humidity across habitats. It was found that these abiotic factors temperature ($r = 0.22$, $P < 0.05$) and relative humidity($r = 0.17$, $P < 0.05$) did not contribute significantly to the differences in species composition across the habitats. Nevertheless, these variables did have a dramatic effect on the seasonal abundance of tiger beetles. Soil variables were found frequently associated with differences in species composition as reflected from Pearson correlation with pH ($r = 0.67$, $P < 0.05$), organic content ($r = 0.78$, $P < 0.05$) and litter depth ($r = 0.88$, $P < 0.05$) except for the soil texture (plays an important factor during oviposition and

Table 5 Indicator species analysis (after Dufrene and Legendre, 1997) computing indicator value (IV) coefficient of tiger beetles across Shivalik landscape

Indicator values							
S. no	Column	Maxgrp	Observed indicator value (IV)	IV from randomized groups		*P**	Indicator habitat
				Mean	SD		
1	*C. angulata*	9	57	10.1	5.63	**0.001***	Riverine
2	*C. bicolor*	3	40.7	9.4	5.99	**0.002***	High canopy cover
3	*C. bigemina*	8	40.9	10.7	5.33	**0.001***	Riverine–agriculture interface
4	*C. chloris*	9	47.4	10	5.82	**0.001***	Riverine
5	*C. erudita*	9	55.4	9.1	5.67	**0.001***	Forest–agriculture interface
6	*C. fastidiosa*	3	50.9	10.2	5.53	**0.001***	Riverine
7	*C. flavomaculata*	3	31.5	11.4	6.1	0.014	–
8	*C. grammophora*	9	59.4	11	5.47	**0.001***	Agriculture
9	*C. intermedia*	7	28.5	11.8	4.8	0.006	–
10	*C. multiguttata*	5	22.2	9.4	6.03	0.036	–
11	*C. parvomaculata*	9	73.2	9.9	6.01	**0.001***	Mixed forest
12	*C. plumigera*	9	29.6	11.5	6.05	0.02	–
13	*C. spinolae*	5	32.5	10.5	6.6	0.014	–
14	*C. subtilesignata*	9	54.9	11.8	5.71	**0.001***	Mixed forest
15	*C. venosa*	4	42.4	10.3	6.22	**0.002***	Riverine–grassland interface
16	*C. viduata*	3	55.4	12	5.58	**0.001***	Mixed forest
17	*C. vigintiguttata*	8	57	10.8	6.19	**0.001***	Riverine–grassland interface
18	*H. pulchella*	10	55.3	10.8	5.69	**0.001***	Pine
19	*J. chloropleura*	3	29.8	9.2	6.24	0.014	–
20	*J. crassipalpis*	5	16.7	8.6	5.16	0.035	–
21	*L. striolata*	10	28.4	10.4	5.92	0.024	–
22	*M. melancholica*	5	13.3	8.9	5.74	0.1331	–
23	*M. undulata*	3	31.3	9.1	5.75	0.008	–
24	*N. bonelli*	3	81.8	10.4	5.67	**0.001***	High shrub density
25	*N. saphyrina*	3	28.2	9.4	6	0.015	–

* Monte Carlo test of significance of observed maximum indicator value for species

999 permutations

Random number seed: 1,000

construction of larval burrows, Hadley et al. 1990) in case of adult tiger beetles. These soil variables correlations were particularly accurate for major species of tiger beetles inhabiting riverine area. Majority of the species like *C. angulata*, *C. plumigera*, and *C. chloris* preferred open, large riverine tracts without any forest cover. But the other cardinal variables that were quintessentially associated with tiger beetle species richness and habitat specificity was vegetative cover i.e., average tree density ($r = 0.95$, $P < 0.05$), average shrub density ($r = 0.85$, $P < 0.05$), and canopy cover ($r = 0.80$, $P < 0.05$). This was particularly true for forest dwelling species like *C. bicolor*, *N. saphyrina*, and *N. bonellii* that particularly inhabited mixed forest stands, latter two being arboreal. Further, habitat types differed greatly in terms of composition of flora mainly trees, under story growth, herbs and grasses and foliage profile/density across the landscape. In some cases, the overlap of species ($H > 3.00$) was most like due, at least in part, to the spatial proximity of several sample plots and/or the similarity in floristics.

As far as co-occurrence amongst tiger beetles is concerned, the observed C-score for co-occurrence for the tiger beetles assemblage was 299.43330 (Table 6). In contrast, the average of the 5,000 simulated matrices was 285.75390, and none of the simulated matrices had a C-score larger than the observed. So, compared to the simulated universe of random matrices with identical row and column sums, there is much less co-occurrence in the tiger beetles matrix than expected by chance ($P = 0.0002$). But the observed niche overlap between each individual pair of species was 0.14191 (Pianka's index). The species pairs in the matrix most similar in resource utilization (highest

Table 6 Habitat attributes of tiger beetles across Shivalik landscape

Co occurrence	
Index	C-score
Observed index	299.43330
Mean of simulated indices	285.75390
Variance of simulated indices	1.18389
Niche overlap	
Index	Pianka index
Observed mean	0.14191
Mean of simulated indices	0.09836
Variance of simulated indices	0.00002
Guild structure	
Index	C-score
Observed index	213.16250
Mean of simulated indices	299.04710
Variance of simulated indices	1,949.76300
Favored state analysis	
Index	C-score
Observed index	75.0000
Mean of simulated indices	82.03200
Variance of simulated indices	10.66564

overlap) were 0.5333 between *C. subtilesignata* and *C. grammophora*; and the pair with most dissimilar resource utilization (lowest overlap) was 0.0054 between *C. flavomaculata* and *L. striolata*. The third attribute analyzed was ecological guilds that represent groups of species within a community that share common resources. Hence, the species within a guild may be more likely to interact or compete for resources than are species in different guilds and larger the C-score, the more segregation between species. The observed C-score ranged from 99.33 for the *Cicindela* guild to 457.66 for the *Heptodonta* guild. For the 1,000 simulated assemblages, the average C-score was approximately 213.16 for all the eight guilds. Further, the random result for the variance was quite high at 1,949.76300 meaning that the level of co-occurrence among guilds is still less as would be expected if the species were assigned randomly to different guilds. Lastly, favored states analysis (Fox 1987, 1999; Fox and Brown 1993), that measures the distribution of species among guilds, whether it is unusually uniform or even among communities. Because if communities are formed by sequentially adding species in different guilds or functional groups, there should be an unusually large number of favored states compared to the null model. The observed index score was found to be 75.000 that illustrate an unfavored state amongst tiger beetle guilds, because the guilds were not filled as evenly as possible.

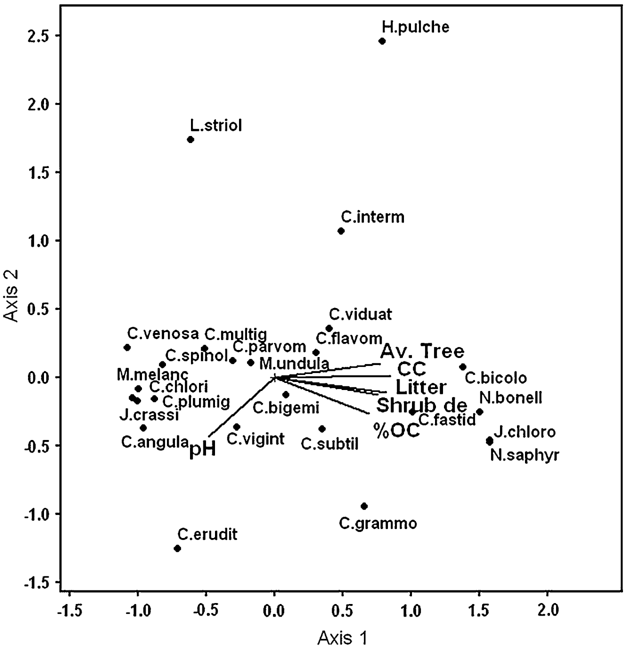


Fig. 8 Biplot from canonical correspondence analysis showing the distribution of 25 species of tiger beetles in relation to habitat variables. The length of the arrow signifies the relative contribution of that variable to the species composition, while the direction signifies its contribution to the differences between assemblages

Broad assemblages of tiger beetle species in responses to habitat variables are displayed in the form of a biplot (biplot r^2 cutoff = 0.25) derived from the canonical correspondence analysis (CCA) (Fig. 8). The axis summary statistics results of the CCA are presented in Table 7. The arrows depict the relative influence of the habitat variables on the composition of the tiger beetles assemblage, with the line length relative to the other variables, rather than an absolute degree of influence (ter Braak and Verdonschot 1995). Mixed forest habitats were characterized by high tree and shrub density while riverine area was characterized by large open tracts with grass cover at the interfaces with forest and agriculture land. Interset correlations between habitat variables identified canopy cover (CC) and litter as statistically significant variables and were found to have significant influence on the species composition across habitats (Table 7). Other habitat variables like average tree and shrub density made only a minor significant contribution to the observed differences in species composition. The first axis of the CCA explained the most variance in the data, while axes 2 explained relatively little at the Monte-Carlo test at the 0.05 level (Table 8).

Discussion

The distribution range of tiger beetles is from about 3,500 m above mean sea level to −220 m below sea level (Pearson and Cassola 1992) and tend to absent from habitats at extremely high altitudes because their fossorial larvae cannot survive in soil that is too cold (Hadley et al. 1990). This is the first study for quantitative establishment of these narrow habitat use patterns among tiger beetle species of the Shivalik region in north western Himalaya. The area is largely a sal dominated forest ecosystem and forms an important transition point from the plains and high mountainous regions. Further, the climatic conditions and vegetation largely represents tropical dry deciduous region, that favor increased insect diversity. Tiger beetles are well known worldwide (Wiesner 1992) and generalizations of their biodiversity are reflected in other taxa (Pearson and Ghorpade 1989; Pearson and Cassola 1992; Pearson and Carroll 1998, 2001), hence they are one of the most studied taxa for conservation research. Pearson and Cassola (1992) and Pearson (1994) have thus elaborated on the usefulness of tiger beetles (Cicindelidae) as an indicator taxon for monitoring and inventory studies.

The major finding of this research work is on understanding the habitat association of tiger beetles in relation to key habitat variables that define their assemblage pattern. It was observed that species diversity of tiger beetles to be quite high in the riverine area irrespective of the protected area sampled whether it was in SWLS, CWLS, or PWLS though separated by more than hundred kilometers. Present study of tiger beetles also provides a background for identifying centers of species richness and abundance within the protected areas of the Shivalik landscape. Such studies can provide a more scientific basis by which to plan and manage a system of protected areas around these centers in accordance with the convention on biological diversity (Glowka et al. 1994). Nevertheless, two habitats stood out amongst others pertaining to the cumulative abundance of tiger beetles viz. riverine area and mixed forest area, as these two habitats were found to be the repository of tiger beetles. The seasonality pattern shown by tiger beetles was of a generalist nature, as may e found

Table 7 Results from canonical correspondence analysis (CCA) of tiger beetle assemblage across Shivalik landscape

Axis summary statistics			
Number of canonical axes	3		
Total variance ("inertia") in the species data	5.8125		
	Axis 1	Axis 2	Axis 3
Eigenvalue	0.540*	0.259	0.190
Variance in species data			
Variance explained (%)	9.3	4.5	3.3
Cumulative explained (%)	9.3	13.8	17.0
Pearson correlation, Spp-Envt*	0.915*	0.707*	0.730
Kendall (rank) Corr., Spp-Envt	0.599*	0.457	0.417

Inter-set correlations for 9 habitat variables

Variable	Correlations		
	Axis 1	Axis 2	Axis 3
1. Temperature	−0.429	0.154	−0.156
2. Relative Humidity	0.593*	−0.163	−0.064
3. pH	−0.515	−0.429	−0.187
4. Org. content (%)	0.739*	−0.259	0.266
5. Litter	0.868*	−0.112	−0.066
6. Canopy cover	0.901*	0.016	−0.008
7. Av. GBH	0.585*	0.129	0.017
8. Average tree density	0.824*	0.101	0.056
9. Average shrub density	0.806*	−0.125	0.044

Monte Carlo randomisation test, 998 runs

*$P < 0.001$

Table 8 Results from canonical correspondence analysis (CCA) of tiger beetle assemblage showing correlations and biplot scores across Shivalik landscape

Correlations and biplot scores for 9 variables

Variable	Correlations*			Biplot scores		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
1. Temperature	−0.469	0.218	−0.214	−0.402	0.156	−0.141
2. Relative humidity	0.648*	−0.231	−0.088	0.556*	−0.165	−0.058
3. pH	−0.563	−0.607	−0.257	−0.483	−0.433	−0.17
4. Org. content (%)	0.807*	−0.366	0.365	0.692*	−0.262	0.241
5. Litter	0.949*	−0.158	−0.09	0.813*	−0.113	−0.06
6. Canopy cover	0.985*	0.023	−0.011	0.844*	0.017	−0.007
7. Av. GBH	0.639*	0.182	0.024	0.548*	0.13	0.016
8. Average tree density	0.901*	0.142	0.077	0.772*	0.102	0.051
9. Average shrub density	0.881*	−0.176	0.06	0.756*	−0.126	0.039

Correlations are "intraset correlations" of ter Braak (1986)

*$P < 0.001$

for other insect group would do so, but the most important thing was presence of some species like *C. chloris* even in the winter season utilizing different habitat conditions. Further, the species quickly emerged during summer season and gained peak in abundance concomitant to onset of monsoon season. In spite of sal dominant forest ecosystems, it was apparent that these were not the obvious preference of tiger beetles. Analysis showed distinct patterns of grouping amongst habitat types, and surprisingly sal habitats were found most similar to agricultural habitats. This has a severe conservation implication because this is a direct instance of increased anthropogenic influence on forest ecosystems in these areas as species composition was quite similar in these two habitats. Future studies would thus give an insight into the degree of landscape modification using tiger beetles as indicator species. Another interesting aspect of distribution of tiger beetles was their subdued presence in *Eucalyptus*, *Khair* and *Syzygium* plantation mixed forest habitats. Again this has some implication for the management of protected areas for the park managers. It appears as if the habitat conditions in these plantation mixed forests were not appropriate for tiger beetles directly and indirectly for its diverse prey species. Thus, for better conservation and management of forests, it is thus indispensable to look for the effects of plantations on local species. Though not presented here, the authors have also observed a similar pattern of decreased species diversity for other beetle families like carabidae (ground beetles), scarabaeidae (dung beetles), and stapylinidae (rove beetles) in managed forests unlike natural stands. Further, though one would expect tiger beetles more in open forest areas, but in our study we found many species to be particularly fond of forested habitats, so much so that one particular species *C. bicolor* was found only in the forested habitats with varying degree of canopy openness. Other belonging to the genera *Neocollyris* preferred forested habitats with reasonably good shrub cover to forage upon prey like chrysomelids.

The study shows strong correlations of tiger beetle richness with vegetation variables like floral diversity, foliage density, shading and microhabitat temperature (Fanelli et al. 2006) and thus indirectly on the diversity and abundance of potential prey items for the tiger beetles. There is considerable evidence from studies of tiger beetles that prey abundance strongly influences the occurrence of tiger beetle species (Pearson and Mury 1979; Pearson 1988; Pearson and Vogler 2001; Sinu et al. 2006). Interesting aspect documented was the unique habitat utilization by tiger beetles. Though all habitats had one or other kind of species, their richness as well as abundance were quite dissimilar. Increased habitat specificity, one of the cardinal requirements of bioindicator species (Noss 1990; Pearson and Cassola 1992; Pearson 1994), could be observed for many species. Further, indicator species could be observed for many habitat conditions, like canopy cover and ecotones. Although habitat loss is often a major cause of biodiversity loss (Desender 1989), often by this time many management options are no longer available. Using sensitive bioindicators to detect more subtle and earlier perturbations may be significant for habitat management by making remedial action less costly and timelier. Such habitat use patterns are thus critical both in justifying the use of these tiger beetles as surrogates and in establishing a baseline in long term monitoring.

In spite of good pragmatic abundance of tiger beetles, they showed a low degree of co-occurrence and niche overlap suggesting increased resource partitioning and judicious microhabitat utilization by adult tiger beetles along the lines of the Gause's law of competitive displacement (DeBach 1966). This was also reflected in the feeding guilds, as many of the species though belonging to same guild showed circadian and temporal variation and occupying different microhabitats with respect to feeding and reproduction. Also, many species were separated seasonally and had different times of emergence and peak populations. Present study also provide a firm basis to interpret changes in microclimatic conditions, caused by humans directly or though long term climate change by monitoring these species. For example, if future fires, over grazing, tourism pressure or other human perturbations are imposed intentionally or unintentionally on forest ecosystems of Shivalik Himalaya, we now have a barometer to quickly and readily measure the cause and effect of impacts. Presence-absence data as well as population trends of the tiger beetle species in respective habitats can warn us of impending changes to the entire habitat long before they become evident in other inhabitants of these habitats, such as the more long-lived and less sensitive vertebrates and plants. In addition, results from studies at this relatively small spatial scale may have ramifications for other areas and at larger scales. Several of the tiger beetle species observed in this study are widely distributed across Asia. Their sensitivities and usefulness as bioindicators of habitat perturbation might well extend over their entire ranges (Carroll and Pearson 1998). So, tiger beetles as bioindicators should be the excellent candidates for long term monitoring of forest ecosystems, ecosystem health and its measurement over a variety of landscapes.

Conservation implications

Future studies of tiger beetles as bioindicators also need to focus on their response to specific prey and other less defined biotic or abiotic factors, within the context of dynamic successional stages of each habitat, whether naturally caused or from the influence of humans. Several claims have been made that the larval forms of tiger beetles are even more specialized in habitat than the adults. The larvae in their tunnels are more difficult to observe, but they are also easier to use in laboratory experiments about the influence of feeding regimes, temperature, predation and competition on survival and fecundity (Pearson and Vogler 2001). An advantage of such biomonitoring is its comparatively low cost and the integrative recording character of ecosystems on the other (Fränzle 2006). Such ecological risk assessment and environmental monitoring are potentially complimentary activities (Suter 2001). Monitoring a few indicator species therefore is a widely used method to measure the ecological sustainability and ecosystem health since it is often so difficult to measure and monitor the natural or anthropogenic induced landscape modification and their effects on all species or environmental conditions (Landres et al. 1988; Kuliopulos 1990; Hilden and Rapport 1993; Kremen et al. 1993). The high degree of habitat specificity among the tiger beetle species in these protected areas are similar to that found in tiger beetle species around the world (Pearson and Vogler 2001). Since specialization is usually associated with sensitivity to habitat alteration (Pyle et al. 1981; Rosenberg et al. 1986; Pearson 1994), identifying the costs and benefits of a monitoring program will assist in the prioritization process more frequently, as the true costs of monitoring are not recognized and are, therefore, underestimated. Benefits from such monitoring studies are rarely evaluated, because they are difficult to quantify (Caughlan and Oakley 2001). An ecosystem health approach is thus needed as it also allows for a more explicit connection between the state of the environment and human well being (Rapport et al. 1998; Rapport and Singh 2006). Even though the current study has focused mainly on protected areas in the Shivalik landscape with its diverse habitat types, extrapolating the present study to different forest habitat types in different parts of the landscape and to even different geographical regions with different land use patterns would definitely strengthen our knowledge of response of bioindicators to various disturbance variables. Environmental monitoring should thus determine the status and trends to determine whether the environment is improving or not (Montreal Process 2000). Continuous efforts are a prerequisite to make gathering of future data and continued monitoring as simple as possible. With this quality added to the biological characters that make tiger beetles so ideal, park guards, local volunteers, and residents can become involved with minimal training and maximum input into management plans and execution.

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