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Ants as bioindicators of ecosystem health in Shivalik Mountains of Himalayas: assessment of species diversity and invasive species

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ABSTRACT. The Northern-Indian Shivalik mountain range has recently come under strong anthropogenic pressure. Ants were used as bioindicators to assess ecosystem health of the area. We measured diversity, community patterns, species composition and the influence of invasive species of Formicidae by collecting at 75 sites from 44 locations in three habitats: primary forest (PF), secondary forest (SF) and non-forest areas (NF) using six collection techniques. We obtained the most comprehensive dataset compiled for Indian ants to date (sample coverage 94 % to 97 %) and sampled 31,487 ant specimens, representing 181 species from 59 genera and 9 ant families. Thirty of the 59 genera were represented by a single species, 12 genera by more than five species and 26 species were new to science. Species richness differed significantly between habitats, with 151 in SF, 120 in PF and 110 in NF. Species richness rose with altitude and was influenced by precipitation, northern latitude and eastern longitude. As demonstrated by redundancy analysis and beta diversity, habitats also differed in species composition. Nineteen invasive/tramp species, comprising ca. 13% of total abundance, were distributed among the three habitats (including PF). Our findings point towards a disrupted, degraded ecosystem with high anthropogenic impact and reduced ecosystem health, even in the primary and protected forest areas. Invasive species pose a serious threat to the native species of Himalaya. At present the ant invasions are limited to lower mountain ranges, but with increases in global temperatures invasive species will soon spread to Himalayan highlands.

Keywords: alien fauna, biodiversity, ecosystem distress syndrome, Formicidae, habitat degradation, India, species inventory, tramp species

This article is accompanied by Electronic Supplementary Material, available at www.asian-myrmecology.org

INTRODUCTION

Ants are widely used to assess landscape disturbance, ecological functioning and species diversity of habitats (e.g. Andersen & Majer 2004, Paknia & Pfeiffer 2011). These insects constitute an important fraction of the animal biomass in terrestrial ecosystems and respond to stress on a much finer scale compared to vertebrates (Andersen & Majer 2004). Ants perform major ecological functions such as predation, scavenging, soil turnover, nutrient cycling and pollination, and are also responsible for dispersal of numerous plant species (Folgarait 1998, Lach et al. 2010). Moreover, ants are present at almost all the trophic levels of the food web (Pfeiffer et al. 2013), making them indispensable for the proper functioning of most terrestrial ecosystems and the resulting ecosystem services (Del Toro et al. 2012).

Habitat disturbances and transformation affect ant communities in many ways, either by changing habitat structure, microclimate and resource availability or by altering the balance of competitive interactions (Philpott et al. 2010). Previous research suggests that ant communities respond predictably to stress and disturbance and this knowledge has been used to assess the ecological status of habitats by monitoring the change in composition and diversity of their ant communities (Bernal & Espadaler 2013, Gibb et al. 2015, Mezger & Pfeiffer 2011, Ribas et al. 2012). These studies demonstrate that habitat disturbance or fragmentation facilitates the introduction of exotic/invasive ants which strategically dominate over native species by means of their anthropophilic nature and successful life history patterns, including having multiple queens, polydomous colonies etc. (Wittman 2014). Invasive ants are usually habitat generalists, which have the ability to invade and establish themselves in undisturbed habitats (Passera 1994).

The Shivalik landscape (29° 57' to 31° 20'N and 77° 35' to 79° 20'E, Fig. 1) is the youngest mountain range of the Himalayas and is aligned parallel to the Lesser Himalayas. The area has been categorised as Indo-Gangetic plains and is biogeographically significant due to the presence of both Indo-Malayan and Palaearctic elements (Mani 1968; Wadia 1975). It is characterised by fragile land formation, sub-tropical climate, varied topography and rich alluvial soils. The entire Shivalik belt covers an area of approximately 40,000 km^2, of which only 3000 km^2 is listed as wildlife protected area network. The study site, the North-west Shivaliks, spans six Indian states namely, Jammu and Kashmir, Himachal Pradesh, Punjab, Haryana, Uttrakhand and Uttar Pradesh. The forest ecosystem of the abovementioned States is at present in a highly degraded form, with only little remaining of the primary forest that once covered large areas. A total of 21 protected areas have been designated in the abovementioned States, but due to poor management the conditions within such protected areas seem not to be appreciably different from outside. The Shivalik hills are considered to be one of India's eight most degraded agro-ecosystem (Sivakumar et al. 2010), although few efforts have been made to monitor their condition in more detail. While the vegetation of the area has been subject to different studies that have documented the high impact of alien or invasive plant species (Jaryan et al. 2013, Khuroo et al. 2011, Khuroo et al. 2010), little is known about the insect life of the Himalaya foothills, especially Shivalik. However, a recent altitudinal gradient study of ants in Jammu-Kashmir Himalaya revealed a high impact of invasive species and pointed towards the disturbance of this ecosystem, especially at lower altitudes (Bharti et al. 2013).

The health of an ecosystem can be assessed using measures of resilience, productivity and organization, the latter including functional and species diversity (Rapport et al. 1998). "Unhealthy" ecosystems are dysfunctional and less able to provide ecosystem services. Stressed ecosystems show an ecosystem distress syndrome, including reduction in biodiversity and an increase in dominance by exotic species (Rapport 1995).

During the present study, we used ants, a proven group of ecological indicators, to assess the ecological status of the Shivalik hills. We took two measures of ecosystem health into consideration: species diversity and the impact of invasive species. Specifically, we studied composition and abundance of the ant communities and the invasion of tramp species in different habitats of Shivalik range of Himalayas. For the purpose of this study, sites were divided into primary, secondary and non-forest habitats, the latter being the most degraded for which we expected the lowest species diversity and number of endemic species and the highest impact of invasive species.

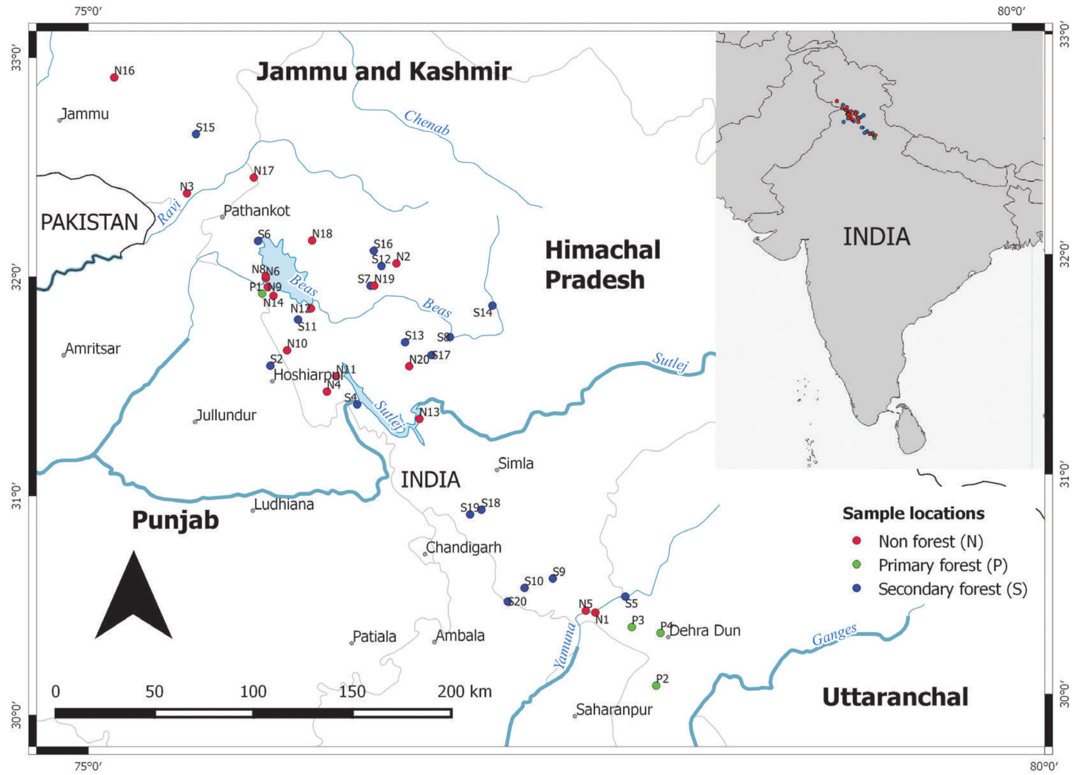

Fig. 1. Location of our study plots in the Shivalik Mountains in northern India at the Pakistani border. Sample plots of different habitats are indicated with different colours. The names of some of the Indian States are given in bold letters.

MATERIALS AND METHODS

Study sites

The landscape of Himalayas' youngest mountain system Shivalik consists of low rolling hills, bisected by innumerable gullies and seasonal streams. At present, very little area of primary forest is left and the majority of land mass is now under the effect of anthropogenic activities, including agriculture, land clearing, industrial activities, human settlements and urban construction. Ants were collected at altitudes between 237 m and 1500 m a.s.l. from 44 locations in different habitats: primary forest (PF); secondary forest (SF), and non-forest area (NF; see Table 1, Fig.1).

(a) Primary forests in the sub-Himalayan tracts are restricted to four areas: Sansarpur Terrace (Himachal Pradesh); regions under the administration of the Forest Research Institute, Dehradun; Rajaji National Park forest area and Selaqui (Uttarakhand). Primary forests mainly consisted of tropical and subtropical moist broadleaf forests.

(b) Secondary forest: Most of the forest cover in Shivalik is of secondary type due to regular forest fires and deforestation. In the present study, wildlife protected areas such as sanctuaries and national parks are considered to be secondary forests. A total of 20 areas containing a total of 25 sites were marked under this sub-heading, covering the six states in the Shivalik region of Himalayas (Table 1). Secondary forest sites of Shivalik are covered with northern tropical dry deciduous forests and Himalayan subtropical pine forests.

(c) Non-forest area: The non-forest sites in the present study consist of agriculture fields, dam sites, playing fields, community parks and college and University campuses.

Table 1. Sample locations of our study, given are forest type, name, GPS coordinates and altitude of our plots in Shivalik, Himalayas. Locations with more than one research plot are marked with asteriks.

Forest type	Location	North	East	Altitude
PF*	Terrace	31.92	75.93	367m
PF*	Rajaji Forest	30.1	77.98	445m
PF*	Selaqui	30.37	77.86	528m
PF*	FRI	30.34	78.01	679m
SF	Kotla	31.35	75.62	237m
SF	Chohal	31.59	75.97	362m
SF	Kandwal	32.28	75.78	405m
SF	Bakhra	31.41	76.43	466m
SF	Dakpathar	30.51	77.83	476m
SF	Rehan	32.16	75.91	526m
SF	Samba	31.95	76.51	774m
SF	Mandi	31.71	76.93	802m
SF	Renuka	30.6	77.45	860m
SF	Nahan	30.56	77.3	911m
SF	Bharwain	31.8	76.12	953m
SF	Andretta	32.04	76.57	988m
SF	Ropar	31.69	76.69	1056m
SF	Bajaura	31.85	77.16	1100m
SF	Sukrala	32.65	75.58	1100m
SF	Palampur	32.11	76.53	1243m
SF	Rewalsar	31.63	76.83	1336m
SF	Ghatti	30.92	77.08	1338m
SF	Dharampur	30.9	77.02	1425m
SF	Kala Amb	30.5	77.21	1500m
NF	Assan Barrage	30.44	77.67	401m
NF	Baijnath	32.05	76.65	1025m
NF	Kathua	32.38	75.53	350m
NF	Una	31.47	76.27	390m
NF	Poanta Sahib	30.45	77.62	399m
NF	Khatiyar	31.99	75.95	441m
NF	Jassur	32.28	75.85	443m
NF	Siholi	32	75.95	449m
NF	Ghamroor	31.95	75.96	450m
NF	Gagret	31.66	76.06	467m
NF	JogiPanga	31.54	76.32	480m
NF	Dhaliara	31.85	76.19	552m
NF	Bilaspur	31.34	76.76	569m
NF	Bari	31.91	75.99	637m
NF	Ranger's College	30.32	78.05	679m
NF	Udhampur	32.91	75.14	689m
NF	Dunera	32.45	75.89	720m
NF	Yol	32.16	76.2	726m
NF	Guga	31.95	76.53	770m
NF	Dehra	31.58	76.71	767m

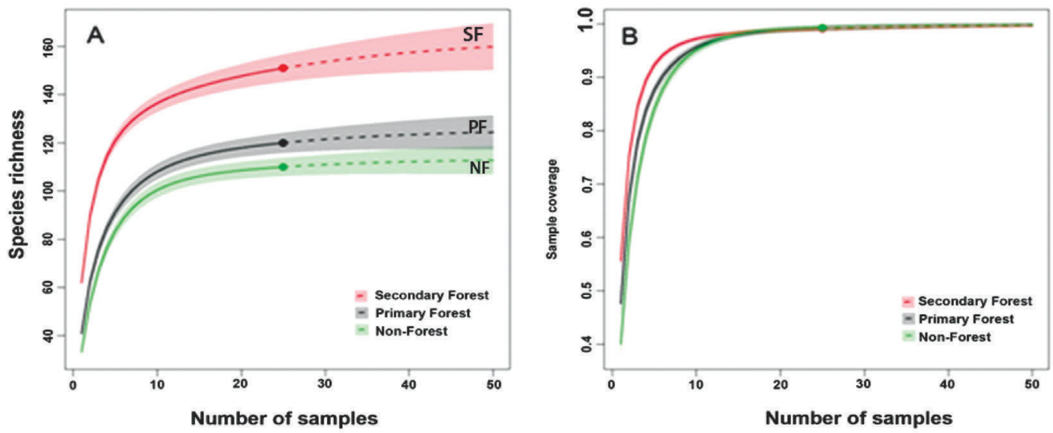

Fig. 2. Rarefied and extrapolated sample data from of Himalayan ants. Solid lines mark actual sample numbers, while dashed lines show extrapolated samples. The dot marks the highest sample number or sample coverage achieved in reality. All figures were calculated with software by Hsieh & al. (2013). a) Species richness estimates for the rarefied and extrapolated samples with sample size up to double the reference sample size. All three sites reached species saturation. b) Sample completeness (as measured by sample coverage) with respect to sample size. This curve provides a bridge between sample-size- and coverage-based rarefaction and extrapolation. All three sites reached extremely high sample completeness within a few samples, thus leading to overlaying curves.

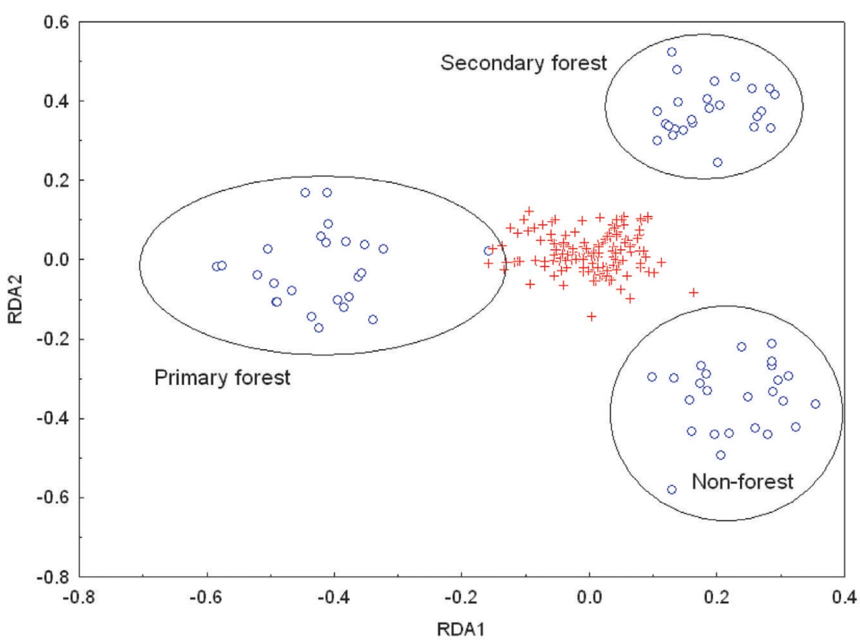

Fig. 3. Redundancy analysis of ant communities in the Himalaya. Blue circles mark plots that are clustered according to habitat. Red crosses mark ant species, most of them contributed to several communities in different habitats. All three habitats differed significantly from each other. RDA1 axis explained 57.1% and RDA2 axis 42.9% of the accumulated constrained eigenvalues.

Table 2. Measures of ant diversity in three Himalayan habitats. Given are Hill numbers (N0, N1, N2), Shannon entropy (H), and sample coverage, as well as estimations for species richness (Est N0), Shannon entropy (Est H), and Shannon Diversity (Est N1). Also, estimated sample coverage (C25) for our data (n = 25) and a prediction of species richness (S50) is calculated for doubled samples sizes (n= 50).

	Observed species richness	Shannon entropy	Shannon diversity^	Simpson diversity^	Estimated species richness Chao 2 +	Sample coverage	Chao entropy*	Chao-Estimated Diversity*	Estimated sample coverage*	Estimated species richness at double sample size#
	N0	H	N1	N2	Est N0	N0/Est N0	Est H	Est N1	C25	S50
Primary forest	120	4.56	95.21	82.22	124.3	0.97	4.60	99.58	0.99	124.4
Secondary forest	151	4.80	121.21	108.01	162.2	0.93	4.83	125.587	0.99	159.9
Non-forest	110	4.51	91.05	78.50	112.4	0.98	4.56	95.871	0.99	112.8
All	181	4.87	130.71	110.26	192.8	0.94	4.89	132.49	1.00	190.5

^ according to Jost 2006
+ calculated with Chao 1987
* according to Chao et al. 2013
# see Chao et al. 2014

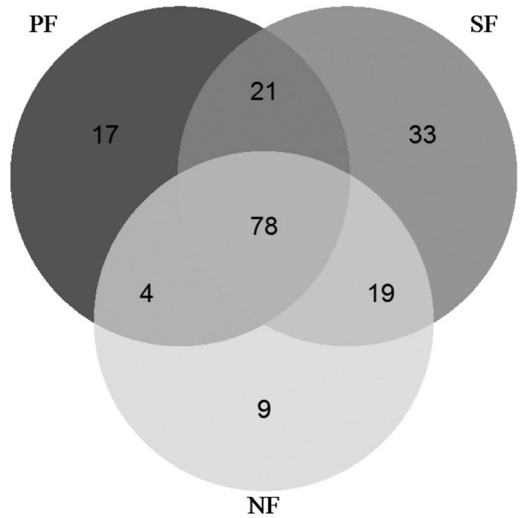

Fig. 4. Venn diagram of species overlap in the three investigated habitats (PF = Primary forest, SF = Secondary forest, NF = Non forest area).

Sampling of ants

A broad range of techniques including Winkler's leaf litter extractors, pitfall traps, soil core sampling, beating vegetation, honey baits and hand collection formed the mainstay of the survey. These procedures were carried out within the research period that lasted from August, 2008 to July, 2012. Research plots were carefully selected to avoid edge effects. At each plot one 50 m transect was established, along which the samples were collected with the six different methods.

From each site we collected about 100 m^2 of leaf litter along the transect (resulting in 24 mini Winkler sacs) that were extracted with six Winkler apparatus to collect ants. Sacs had a wire sieve with square holes of 1cm × 1cm. Litter was collected mainly from primary and secondary forests, while most of the non-forested habitat was devoid of leaf litter. Ants were extracted from sifted litter after a 48 hour period.

Test tubes (1.5 cm in diameter), partly filled with 5% ethylene glycol solution, buried with the rim at soil surface, constituted the pitfall traps. At each site, six pitfall traps were installed in a more or less straight transect line with 10 m spacing between traps. Pitfall traps were cleared after 48 hours.

Six soil cores, each 20 × 20 × 15 cm, were taken at equal intervals (10 m) along the transect. These soil cores were sifted through a hand sieve pan to collect ants.

Ants foraging on the vegetation were sampled by beating the vegetation (to dislodge ants from plants on to sheets) and collecting ants with a beating tray for two person hours per site within an area of 100 m left and right of the transect.

Ants attracted to honey applied to six plastic sheets (A4 size) spaced equally (15 m) along transect were collected after 48 hours.

Hand collection was carried out with two persons per hour per site within an area of 100 m either side of the transect, by searching for ants on rotten logs, stumps, dead and live branches, twigs, low vegetation, termite mounds and under stones.

Data collection from the Internet

For the collection of environmental data we used monthly global gridded high resolution (30 arc sec) station (land) data for air temperature and precipitation collected from 1979-2013 and provided at http://chelsa-climate.org (Karger et al. 2016).

Statistical analysis

For statistical analysis, samples from the six methods were combined and all collections of

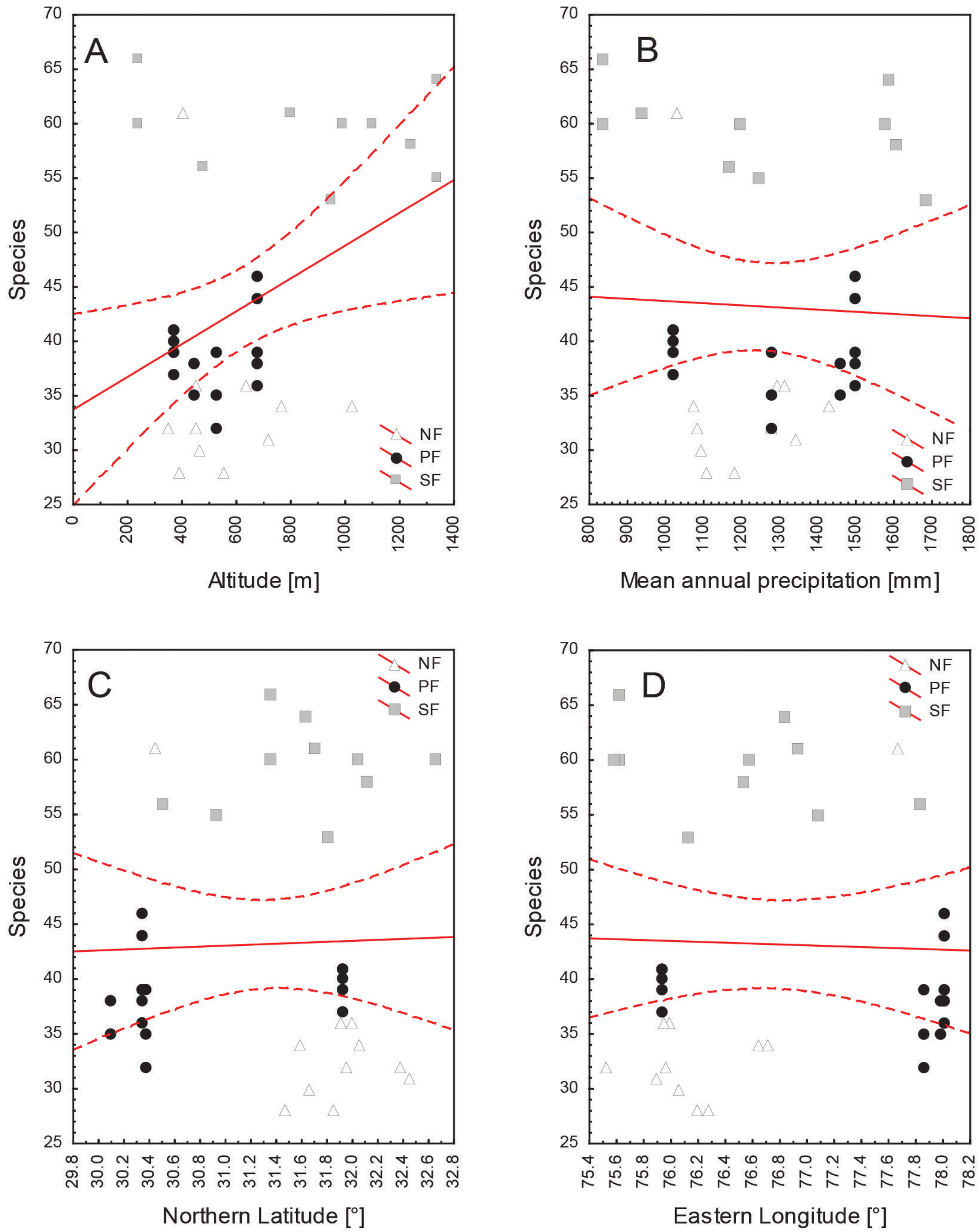

Fig. 5. Univariate relationships between ant species number with (A) altitude of sites (Pearson correlation r = 0.38, p = 0.21), (B) long term precipitation data (Pearson correlation r = -0.04, p = 0.82, n.s.), (C) northern latitude (Pearson correlation r = 0.03, p = 0.87, n.s.) and (D) eastern longitude (Pearson correlation r = -0.31, p = 0.86, n.s.). A regression line over all samples is given to visualize the relationship. Some of the non significant relationships became significant in Multiple regression or after exclusion of NF plots (see text).

one plot were considered as one sample. All 25 such samples from each habitat were used for statistical analysis (n = 75). These traversed 20 regions each in case of secondary and non-forest area, and four regions in case of primary forest.

As ants are social insects, nesting patterns of ants can dramatically influence the abundance of sampled specimens in a single trap, but this does not necessarily reflect the true abundance of a species in the sample area which may be better described by presence-absence data of species in a higher number of samples. Therefore we pooled all samples from the six different methods and only counted the occurrence of a species at one of the 75 sampling points. Species incidences at the 25 sites in each of the three habitats (PF, SF, NF) were then used to create a species sample data sheet (Chao et al. 2014). We used the R package *vegan* (Oksanen et al. 2013) to calculate diversity measures following the framework of Jost (2006) and using scripts of Bochard et al. (2011). Two recent publications of Chao and co-workers (Chao et al. 2014; Chao et al. 2013) present novel estimators for entropy and species richness, while Colwell et al. al. (2012) established the extrapolation of rarefaction curves. We used the online tool *ChaoEntropyOnline* (Lee et al. 2014) to calculate the unbiased *ChaoEntropy* estimator for Shannon entropy and the *iNext* online tool (Hsieh et al. 2013) for the estimation of sample coverage and the prediction of species richness at doubled sample size (1000 Bootstrap replications each). We followed Mezger and Pfeiffer (2011) and used Redundancy analysis (RDA) on a Hellinger transformed species matrix to assess the differences of the three habitat types with R package *vegan* and a permutation test with 500 runs. Calculation of *Chao 2* species richness estimator as well as Beta diversity and its estimators was performed with Estimate S software version 9.1.0 (Colwell 2013). STATISTICA software was used for calculation of ANOVA and Multiple regression. Invasive species were classified according to McGlynn (1999).

RESULTS

A total of 31,487 ant specimens representing 181 species (with 3412 species incidences) spanning across 59 genera were recorded from the Shivalik range of Himalayas (Electronic Supplementary Material Appendix S1). Of the 10 known subfamilies from India (Bharti 2011), representatives of nine subfamilies were found. Only subfamily Ectatomminae, represented in India by the genus *Gnamtogenys*, was absent.

Thirty of the 59 genera were represented by single species, whereas 12 genera were represented by more than five species. The 12 most speciose genera which accounted for 57.46% of the total species collected were [(sub-)species numbers in brackets] in Formicinae: *Camponotus* (13), *Lepisiota* (11), *Polyrhachis* (8) and *Nylanderia* (6); in Myrmicinae: *Tetramorium* (15), *Monomorium* (11), *Pheidole* (10), *Crematogaster* (7) and *Carebara* (8); in Ponerinae: *Anochetus* (6) and *Leptogenys* (6); and in Dorylinae: *Aenictus* (8).

Species richness was highest in SF, where we observed 151 species, while PF had 120 species and NF had 110 species of ants. Species richness in these plots differed significantly (ANOVA $F_{(2,35)} = 29.791$, $p < 0.001$). Mean species richness per transect was 62 (SF), 41 (PF) and 33 (NF). Similarly, Shannon and Simpson diversity were highest in SF compared to PF and NF (Table 2).

Of the 35 endemic species (19.33% of all species) recorded from the Shivalik range, 28

Table 3. Number of singletons and doubletons per habitat.

	Primary forest	Secondary forest	Non-forest	ALL
Number of singletons	9	15	6	16
Number of doubletons	7	8	5	9

Table 4. Beta diversity of the three habitats as calculated with Estimate S software. Given are the observed numbers of shared species, the estimated shared species, the Jaccard and Soerensen indices and the incidence based Chao-Soerensen-Estimator of beta diversity.

First Sample	Second Sample	Shared Species Observed	Chao Shared Species Estimated*	Jaccard Classic	Sorensen Classic	Chao-Sorensen-Estimator Incidence-based^
PF	SF	99	99.956	0.576	0.731	0.831
PF	NF	81	81.728	0.544	0.704	0.776
SF	NF	95	96.215	0.572	0.728	0.861

*According to Chen et al. 1995
^Chao et al. 2005

Table 5. Incidences of invasive ant species collected in the three different habitats. PF = Primary forest, SF = Secondary forest, NF = Non-forest area.

Species name	PF	SF	NF	Total
Cardiocondyla nuda (Mayr, 1866)	14	14	5	33
Cardiocondyla wroughtonii (Forel, 1890)	6	5	7	18
Cerapachys biroi (Forel, 1907)	14	15	4	33
Hypoponera confinis (Roger, 1860)	37	33	12	82
Hypoponera ragusai (Emery, 1894)	3	13	8	24
Monomorium destructor (Jerdon, 1851)	10	9	10	29
Monomorium floricola (Jerdon, 1851)	0	6	0	6
Monomorium pharaonis (Linnaeus, 1758)	0	5	5	10
Ochetellus glaber (Mayr, 1862)	0	7	0	7
Paratrechina longicornis (Latreille, 1802)	14	21	20	55
Solenopsis geminata (Fabricius, 1804)	0	1	0	1
Tapinoma melanocephalum (Fabricius, 1793)	15	17	8	40
Technomyrmex albipes (Smith, 1861)	11	10	3	24
Tetramorium bicarinatum (Nylander, 1846)	5	2	0	7
Tetramorium caespitum (Linnaeus, 1758)	0	2	0	2
Tetramorium caldarium (Roger, 1857)	0	0	6	6
Tetramorium lanuginosum (Mayr, 1870)	7	10	5	22
Tetramorium simillimum (Smith, F. 1851)	0	16	0	16
Tetramorium tonganum (Mayr, 1870)	1	11	4	16
Total number of species incidences	137	197	97	431
Percentage of total incidences	13.4	12.7	11.6	12.6
Total number of species	12	18	13	19

species were found in SF, 14 in PF and only 10 in NF. Out of the above-mentioned endemic species, eight species were collected as singletons or doubletons and seven species were collected with less than or equal to 10 specimens. Thus, a total of 15 endemic species were observed to be rare.

As proven by rarefaction curves and extremely high sample coverage (Fig. 2), the sampling of ant communities was almost complete. Due to the high sampling effort for each plot and the sample size of 25 plots in each of the habitats, sample coverage ranged between 93% and 98%, with estimated sample coverage C25 ranging between 99.4% and 100 % (Table 2). For the combined samples with 181 observed species, the *Chao 2* species estimator produced an estimate of 192.8 species (sample coverage 94%) and predicted a species richness (at double sample size (n = 150) following Chao et al. (2013)) of 190.5 species. Accordingly, estimated values for species richness in each of the single habitats were only slightly higher than observed species richness (Fig. 2b). Estimated values differed more strongly from the observed values in SF, presumably because of the large number of singleton and doubletons found there (Table 3).

A Redundancy analysis of ant communities with two constrained axes (eigenvalues of axes: RDA1 0.085, RDA2 0.064; total inertia: 0.59; proportion of explained inertia: 14.87%) showed a good separation of the ant communities from the three habitats (RDA, adjusted $R^2 = 0.13$, ANOVA $F_{(2, 72)} = 6.3$, $P = 0.005$), with RDA1, separating PF from both the other habitats and RDA2 separating all three habitats (Fig. 3).

The separation of ant communities in the three habitats was corroborated by the analysis of Beta diversity that comprised values of 0.54 to 0.57 for the Jaccard index and values between 0.77 and 0.84 for the estimated Chao-Sorensen index (Table 4). A Venn diagram (Fig. 4) of the collected species in three habitats shows that 78 out of 181 species collected were recorded from all three habitats, whereas 33 species were exclusively found in SF (18.23%), 17 in the PF (9.39%) and only nine (4.97%) in NF. PF and SF were observed to share the maximum numbers of species.

As demonstrated by Multiple regression (Adjusted $R^2 = 0.27$, $F_{(3,31)} = 4.381$, $p < 0.01$), species richness of plots was positively impacted by altitude ($\beta = 0.91$, $p < 0.001$) and negatively by the monthly long-term mean of precipitation ($\beta = -0.44$, $p < 0.05$) and northern latitude ($\beta = -0.98$, $p < 0.05$), while eastern longitude was a not significant factor ($\beta = -0.82$, $p = 0.102$; see Fig. 5 for the single effect plots). When we excluded the NF plots from the calculation, precipitation and northern latitude became non-significant and were excluded from the equation, while eastern longitude gained influence and beta of the altitudinal factor decreased (Multiple regression, Adjusted $R^2 = 0.42$, $F_{(2,22)} = 9.82$, $p < 0.001$, altitude $\beta = 0.51$, $p < 0.01$, eastern longitude $\beta = -0.50$, $p < 0.01$).

We recorded a total of nineteen tramp/ invasive species from the Shivalik range of Himalayas (Table 5). Surprisingly, the tramp/ invasive species were found to inhabit all three habitats almost equally. Twelve tramp species were recorded from PF, eighteen from SF and thirteen from NF areas. As evident from the data, the maximum number of tramp species (with highest numbers of incidences) was recorded from SF, but the percentage representation of invasive species was highest in PF: 137 of 1024 species incidences (13.4%) were invasives.

DISCUSSION

In the present study we used community composition and local diversity patterns of ants to provide a detailed indication of the environmental conditions in the lower Himalayas. Ants are a dominant faunal group in most terrestrial ecosystems and thus sensitive to range threatening processes such as logging, fire, mining and agriculture (Andersen et al. 2006, Silva et al. 2009, Vasconcelos et al. 2000). For that reason, they have been frequently used as indicators for ecosystem health (Nash et al. 1998, Philpott et al. 2010, Ribas et al. 2012, Whitford et al. 1999).

The data we present here make this one of the most comprehensive studies of Indian ant communities to date. As demonstrated by rarefaction curves and sample coverage, our sample efforts were comprehensive for all of the three habitats. As far as we know, we sampled the highest number of species obtained up to now in any ant study from India, thus providing an excellent overview of the ant fauna in the lower Himalayas and making the Shivalik ant communities some of the best studied worldwide. Given the high effort of our study and the poor knowledge we still have on the Indian ant fauna, it is not surprising that many of the species recorded are new to science. Twenty-six new species have been described from the sampled material, including new species of *Leptogenys* (Bharti & Wachkoo 2013b), *Cryptopone* (Bharti & Wachkoo 2013a) *and Dilobocondyla* (Bharti & Kumar 2013). They add to the knowledge of the Himalayan ant fauna for which only little information has until now been available (Bharti 2008, Bharti et al. 2013).

The protection status of the Shivalik area is incomplete and does not represent all important ecological habitats (Sivakumar et al. 2010). For example the PF in our investigation area have not been protected up to now. All wildlife-protected areas surveyed in our study were situated in SF that, in our area, provided the maximum of habitat heterogeneity in terms of vegetation structures. Accordingly, SF harbored the highest species richness, species diversity and the highest number of endemics and rare species of the three habitats under study. At the same time PF and NF were similar in diversity. But as we had hypothesized, diversity and number of endemic species was lowest in NF areas. The low relative abundance (only 4.43% of the total) of the rare and endemic species clearly indicates the vulnerability of these species to extinction processes.

Species richness of plots was higher in higher altitudes: an unusual pattern in tropical ecosystems (Araujo & Fernandes, 2003; Malsch et al. 2008) that again points towards the damaged ecological status of the Shivalik Mountains, where more people live at lower elevations. Primary forests at lower elevation are unprotected and less diverse than secondary forests with lesser human impact at higher elevations. Also most NF sites in our study were situated at lower elevation. A similar pattern was found in the Chinese Gaoligongshan Mountains, where forest destruction and habitat loss decreased ant diversity at the lower altitudes (Xu et al. 2001). As a result, altitude was the major impact on ant species richness in Shivalik Hills, while the impact of precipitation was significant, but it was negligible.

Although RDA indicated that species composition of the habitats differed strongly, only 59 species (= 33%) were actually restricted to one of the habitats. Between 81 and 99 species were shared among habitats, a high proportion of these non-native species. Interestingly the number of observed species differed little from those estimated by species estimators, which points towards the comprehensive sample coverage of our study (see above). Especially, the estimations of beta-diversity demonstrate a high similarity of the different ant communities between habitats. The *Chao-Sorensen*-Estimator demonstrated the highest similarity between NF and SF, and a high overlap of PF and NF.

The highest number and highest abundance of invasive species was found in SF, the habitat that included the protected areas. However, the highest percentage of invasives was recorded in PF. This is in contrast to our prediction that the highest occurrence of invasive species would be in the non-forest areas. Like in the Indian Western Ghats, invasive species are mainly encouraged by the impacts of humans (Narendra 2011).

The secondary forests may act as corridors for the spread of a number of species from disturbed habitats to primary forest and vice-versa. The invasive species in general possess higher rates of dispersal and therefore can increase their spread, population densities, and ecological impacts into connected patches (Resasco et al. 2014). The 19 invasive species in our study were present in high abundance. These species represented 12.6% (431) of the total species incidences, more than the 11.4% of the 35 endemic species recorded.

Taken together, these results point towards a disrupted, degraded ecosystem with high anthropogenic impact and reduced ecosystem health, even in the primary and protected forest areas. Differences in composition of species communities and functional diversity among habitats have been eroded; the distribution of invasive species even in PF indicates a threat to the natural habitats in the Shivalik area. While our hypotheses are based on the assumption that mainly non-forest habitats would be impacted by human activities, the current distribution of invasive species of ants show clearly that the ecological status of the Shivalik Mountains as a whole is highly degraded, with many areas already showing clear symptoms of ecosystem distress syndrome. Climate change and increasing population density will doubtlessly further increase the threats to the unique Shivalik landscape. For these reasons, enhanced protection and habitat rehabilitation of the Shivalik Mountains is urgently needed to conserve the fragile ecosystem, prevent further loss of biodiversity and curb the encroachment of invasive species.

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REFERENCES

Andersen AN, Hertog T and Woinarski JCZ, 2006. Long-term fire exclusion and ant community structure in an Australian tropical savanna: congruence with vegetation succession. *Journal of Biogeography* 33: 823 – 832.

Andersen AN and Majer JD, 2004. Ants show the way Down Under: invertebrates as bioindicators in land management. *Frontiers in Ecology and the Environment* 2: 291 – 298.

Araujo LM and Fernandes GW, 2003. Altitudinal patterns in a tropical ant assemblage and variation in species richness between habitats. *Lundiana* 4(2): 103 – 109.

Bernal V and Espadaler X, 2013. Invasive and socially parasitic ants are good bioindicators of habitat quality in Mediterranean forest remnants in northeast Spain. *Ecological Research* 28: 1011 – 1017.

Bharti H and Kumar R, 2013. Five new species of *Dilobocondyla* (Hymenoptera: Formicidae) with a revised key to the known species. *Asian Myrmecology* 5: 29 – 44.

Bharti H, Paul SY, Bharti M and Pfeiffer M, 2013. Ant species richness, endemicity and functional groups, along an elevational gradient in the Himalayas *Asian Myrmecology* 5: 79 – 101.

Bharti H and Wachkoo AA, 2013a. *Cryptopone subterranea* sp. nov. a rare new cryptobiotic ant species (Hymenoptera: Formicidae) from India. *Asian Myrmecology* 5: 1 – 4.

Bharti H and Wachkoo AA, 2013b. Two new species of the ant genus *Leptogenys* (Hymenoptera: Formicidae) from India, with description of a plesiomorphic ergatogyne. *Asian Myrmecology* 5: 11 – 19.

Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK and Ellison AM, 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs* 84: 45 – 67.

Chao A, Wang YT and Jost L, 2013. Entropy and the species accumulation curve: a novel entropy estimator via discovery rates of new species. *Methods in Ecology and Evolution* 4: 1091 – 1100.

Colwell RK, 2013. EstimateS: Statistical Estimation of species richness and shared species from samples, 9.1.0 edn. University of Connecticut.

Colwell RK, Chao A, Gotelli NJ, Lin S-Y, Mao CX, Chazdon RL and Longino JT, 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *Journal of Plant Ecology* 5: 3 – 21.

Del Toro I, Ribbons RR and Pelini SL, 2012. The little things that run the world revisited: a review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). *Myrmecological News* 17: 133 – 146.

Folgarait PJ, 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity and Conservation* 7: 1221 – 1244.

Gibb H, Sanders NJ, Dunn RR, Watson S, Photakis M, Abril S, Andersen AN, Angulo E, Armbrecht I, Arnan X, Baccaro FB, Bishop TR, Boulay R, Castracani C, Del Toro I, Delsinne T, Diaz M, Donoso DA, Enríquez ML, Fayle TM, Feener DH, Fitzpatrick MC, Gómez C, Grasso DA, Groc S, Heterick B, Hoffmann BD, Lach L, Lattke J, Leponce M, Lessard J-P, Longino J, Lucky A, Majer J, Menke SB, Mezger D, Mori A, Munyai TC, Paknia O, Pearce-Duvet J, Pfeiffer M, Philpott SM, de Souza JLP, Tista M, Vasconcelos HL, Vonshak M and Parr CL, 2015. Climate mediates the effects of disturbance on ant assemblage structure. *Procedings of the Royal Scociety B* 282: 20150418;.

Hsieh TC, Ma KH and Chao A, 2013. iNEXT online: interpolation and extrapolation. (Version 1.3.0) Available from http://chao.stat.nthu.edu.tw/blog/software-download/.

Jaryan V, Uniyal S, Gupta RC and Singh RD, 2013. Alien Flora of Indian Himalayan State of Himachal Pradesh. *Environmental Monitoring and Assessment* 185: 6129 – 6153.

Khuroo AA, Reshi ZA, Rashid I and Dar GH, 2011. Towards an integrated research framework and policy agenda on biological invasions in the developing world: A case-study of India. *Environmental Research* 111: 999 – 1006.

Khuroo AA, Weber E, Malik AH, Dar GH and Reshi ZA, 2010. Taxonomic and biogeographic patterns in the native and alien woody flora of Kashmir Himalaya, India. *Nordic Journal of Botany* 28: 685 – 696.

Lach L, Parr CL and Abbott KL, (eds.), 2010. *Ant Ecology*, 1 edn, pp 402. Oxford University Press, Oxford.

Lee Y-H, Tseng K-S and Chao A, 2014. ChaoEntropy online. Assessed at 29. 6. 2015 from http://spark.rstudio.com/mikelee/ChaoEntropy/

Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann N, Linder HP. and Kessler M, 2016. Climatologies at high resolution for the Earth land surface areas. *arXiv*:1607.00217 [physics].

Malsch AKF, Fiala B, Maschwitz U, Mohamed M, Nais J and Linsenmair KE, 2008. An analysis of declining ant species richness with increasing elevation at Mount Kinabalu, Sabah, Borneo. *Asian Myrmecology* 2: 33 – 49.

Mani MS, 1968. *Ecology and Biogeography of High Altitude Insects*. The Hague: Dr. W. Junk N.V. Publisher.

Mezger D and Pfeiffer M, 2011. Influence of the arrival of *Anoplolepis gracilipes* (Hymenoptera, Formicidae) on the temporal development of an ant community on a clearing in Gunung Mulu National Park, Sarawak, Malaysia. *Asian Myrmecology* 4: 98 – 98.

Narendra A, Gibb H and Ali, TM, 2011. Structure of ant assemblages in Western Ghats, India: role of habitat, disturbance and introduced species. *Insect Conservation and Diversity*, 4: 132 – 141.

Nash M, Whitford W, Van Zee J and Havstad K, 1998. Monitoring changes in stressed ecosystems using spatial patterns of ant communities. *Environmental Monitoring and Assessment* 51: 201 – 210.

Oksanen J, Blanchet GF, Kindt R, Legendre P, Minchin PR, O'Hara BR, Simpson GL, Solymos P, Stevens MHH and Wagner H, 2013. *VEGAN*: Community Ecology Package. R package version 2.0 – 10.

Paknia O and Pfeiffer M, 2011. Steppe versus desert: multi-scale spatial patterns in diversity of ant communities in Iran. *Insect Conservation and Diversity* 4: 297 – 306.

Passera L, 1994. Characteristics of tramp species. In: *Exotic ants* (Williams D, ed), Westview Press, Boulder, 22 – 43.

Pfeiffer M, Mezger D and Dyckmans J, 2013. Trophic ecology of tropical leaf litter ants (Hymenoptera Formicidae) - a stable isotope study in four types of Bornean rain forest. *Myrmecological News* 19: 31 – 41.

Philpott S, Perfecto I, Armbrecht I and Parr CL, 2010. Ant diversity and function in disturbed and changing habitats. In: *Ant Ecology* (Lach L, Parr CL, Abbott KL, eds), 1 edn, Oxford University Press, Oxford, 137 – 156.

Rapport DJ, Costanza R and McMichael AJ, 1998. Assessing ecosystem health. *Trends in Ecology and Evoution* 13: 397 – 402.

Resasco J, Haddad NM, Orrock JL, Shoemaker D, Brudvig LA, Damschen EI, Tewksbury JJ and Levey DJ, 2014. Landscape corridors can increase invasion by an exotic species and reduce diversity of native species. *Ecology* 95: 2033 – 2039.

Ribas CR, Campos RBF, Schmidt FA and Solar RRC, 2012. Ants as indicators in Brazil: A review with suggestions to improve the use of ants in environmental monitoring programs. *Psyche* 2012, Article number 636749.

Silva PSD, Bieber AGD, Leal IR, Wirth R and Tabarelli M, 2009. Decreasing abundance of leaf-cutting ants across a chronosequence of advancing Atlantic forest regeneration. *Journal of Tropical Ecology* 25: 223 – 227.

Sivakumar K, Satyakumar S and Rawat GS, 2010. A preliminary review on the conservation status of Shivalik landscape in North-west India. *Indian Forester*: 1376 – 1382.

Vasconcelos HL, Vilhena JMS and Caliri GJA, 2000. Responses of ants to selective logging of a central Amazonian forest. *Journal of Applied Ecology* 37: 508 – 514.

Wadia DN, 1975. *Geology of India.* 4th edn. Tata-McGraw Hill Publishing Company, New Delhi, 508 pp.

Whitford W, Van Zee J, Nash M, Smith W and Herrick J, 1999. Ants as indicators of exposure to environmental stressors in North American desert grasslands. *Environmental Monitoring and Assessment* 54: 143 – 171.

Wittman SE, 2014. Impacts of invasive ants on native ant communities (Hymenoptera: Formicidae). *Myrmecological News* 19: 111 – 123.

Xu Z-H, Li J-G, Fu L and Long Q-Z, 2001. A study on the ant communities on west slope at different elevation of the Gaoligongshan Mountain Nature Reserve in Yunnan, China. *Zoological Research* 22: 58 – 63.

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