

Ant species richness, endemism and functional groups, along an elevational gradient in the Himalayas

HIMENDER BHARTI¹, YASH PAUL SHARMA¹, MEENAKSHI BHARTI¹ AND
MARTIN PFEIFFER²

¹Department of Zoology and Environmental Sciences, Punjabi University, Patiala, Punjab, India. ²Department of Ecology, National University of Mongolia, Ulaanbaatar, Mongolia

Corresponding author: Dr Himender Bharti, Department of Zoology and Environmental Sciences, Punjabi University, Patiala, Punjab, India-147002
Corresponding author's email: himenderbharti@gmail.com

ABSTRACT. In this study we investigate variation in species density, species richness, abundance and functional-groups composition along an elevational gradient in Jammu-Kashmir Himalaya. We tested the hypotheses that (1) species richness and abundance decrease with increase in elevation with respect to temperature change, and (2) assemblage composition changes with an increase in elevation with respect to functional-group composition. We employed different sampling methods like pitfall traps, leaf-litter sifting, stick beating, soil cores, honey baits and hand picking to sample ants. Among the 144 species collected, the first two elevations (500 and 1000 m) were dominated by Indo-Malayan elements, while above 2000 m assemblages were dominated by Palaearctic elements. We observed that ant species richness increased with an initial increase in elevation, peaked at mid-elevation and thereafter decreased, thus forming a mid-elevation peak. The pattern observed could be attributed to the optimal climatic conditions present at mid-altitude. While seven functional groups of ants were collected at the lowest altitude, only three functional groups were detected at the highest altitude, namely “General Myrmicinae”, “Opportunists” and “Cold-climate Specialists”. Twenty-three percent of the recorded species are endemic to the study region, with *Myrmica* species dominating this group. The presence of invasive species at lower elevations indicates a high degree of disturbance in the Himalayan ecosystem.

Keywords: ants; abundance; biological conservation, endemism; functional groups; Himalaya; mid elevation peak; species richness; zoogeographical affinities; India

INTRODUCTION

Elevation-gradient studies with different model organisms date back to the early days of biogeography. As examples of a strong ecological pattern, elevation gradients provide an insight into the historical and contemporary forces that shape life on earth (Lomolino 2001; Rahbek 2005; McCain 2009; Colwell & Rangel 2010). Moreover, these studies

help to measure the health of ecosystems, as the organisms which constitute an ecosystem generally encapsulate all aspects of their environment, and therefore are genuine indicators of perturbations and anthropogenic disturbances. Ants, well known for their significance in ecology, are being used for monitoring ecosystem health, being diverse, abundant and hypersensitive to environmental changes (Lach *et al.* 2010 and references therein).

The Himalayas or ‘Himalaya’, the youngest mountain system in the World (Mani 1995), has been colonised at different times by Malayan, Afrotropical, Mediterranean, Central Asian and temperate faunal elements. The stressful environment has acted upon this mix of geographical forms, leading to the extinction of species, the breaking up of distributional ranges and the induction of genetic variation, with or without speciation. Thus the flora and fauna, which have passed through various transitional stages during the geomorphological evolution of this region, show a high degree of endemism (Bharti 2008). But growing anthropogenic activities have made this important ecosystem vulnerable and fragile. There is hence an urgent need to understand the ant species richness and distribution along an elevational gradient in the Himalayas. This will assist in developing a framework for the long-term management and conservation of this region.

To better understand the impact of stress and disturbance on community composition of ants at different elevations, the species collected were broadly categorised on the basis of functional groups provided by Andersen (2000). The categorising of ants into functional groups or groups of ecologically-similar species not only helps analysis across taxonomic and biogeographic boundaries, but also provides an insight into the community composition of an area in response to stress (factors affecting productivity) and disturbance (factors removing biomass). In our study eight functional groups of ants were identified and used as benchmark for monitoring the effects of environmental stress and disturbance on ant community composition. These are: “Generalised Myrmecines”, “Tropical-climate Specialists”, “Opportunists”, “Cold-climate Specialists”, “Subordinate Camponotini”, “Cryptic Species”, “Specialist Predators” and “Hot-climate Specialists”. The “Dominant Dolichoderinae” category, in some ways at the heart of the Australian classification, is not represented in our study region.

In this study we aim to describe the variation in species density, species richness, abundance, and composition of functional groups, along an elevation gradient in the Jammu-Kashmir region of Himalaya; and to identify environmental correlates of this pattern. In the

past, two diversity trends along an elevation gradient have been observed: (1) a decline of species richness with increase in altitude (Brühl *et al.* 1999; Araujo & Fernandes 2003; Malsch *et al.* 2008) and (2) a mid-elevation peak or humped-shaped curve. The latter pattern may be explained by various factors including climatic optima at mid-elevations, by the ecotone effect, which predicts higher diversity in transition areas, and /or by the mid-domain effect (MDE), which is due to geometric constraints (Fisher 1999; Colwell & Less 2000; Sanders *et al.* 2003; Grytnes & MacCain 2007; Rahbek 1995, 2005; Longino & Colwell 2011). During this study, the following hypotheses were tested: (1) species richness and abundance decrease with an increase in elevation as a consequence of differences in the temperature regime; and (2) assemblage composition with respect to functional groups changes with an increase in elevation.

METHODS

STUDY SITES. The study was conducted in the Jammu-&-Kashmir part of the western Himalayas. The sampling sites were selected at an altitude of 500 m, 1000 m, 2000 m, 3000 m and 4000 m a.s.l. and represent the typical pattern of climate and vegetation along an altitudinal gradient in the region (Mani 1962, 1968). The study sites at different altitudes were as follows (Fig. 1, Table 1; plant species nomenclature according to www.theplantlist.org):

500 m: Barwal (Kathua District, southwest Jammu-&-Kashmir), 32° 28'27" N, 75° 28'55" E; a sub-montane zone, which includes part of the lower Shivalik hills in the Outer Himalayas. The vegetation generally consisted of a subtropical dry deciduous type. Trees at the study site included *Acacia catechu* (L.f.) Willd., *Dalbergia sissoo* Roxb., *Tectona grandis* L.f. and common subdominant genera like *Cedrela*, *Albizia*, *Terminalia*, *Melia* etc.

1000 m: Sukarala (Kathua District), 32° 37'43" N, 75° 36'55" E; a sub-tropical mixed pine-and-deciduous forest in the upper Shivalik hills, dominated mainly by trees of *Pinus roxburghii* Sarg., *Dalbergia sissoo*, *Olea europaea* subsp. *cuspidata* (Wall. & G. Don) Cif. and *Albizia amara* (Roxb.) B. Boivin.



Fig. 1. Map showing the five study sites in Himalaya. Given is the area of Kashmir, with India's northernmost state *Jammu and Kashmir* in colour. The blue dots represent our study sites: 1 Barwal 500 m; 2 Sukarala 1000 m; 3 Sarthal 2000 m; 4 Sandar 3000 m; 5 Affarwatt 4000 m. Different colours represent differing political subdivisions, some of which are pooled.

2000 m: Sarthal (Kathua District), 32° 48'46" N, 75°45'45" E; a plot in the Lesser Himalayas dominated mainly by trees like *Pinus*, *Quercus*, *Rhododendron*, *Populus*, *Juglans* and *Larix* spp., and a sub-tropical-temperate transitional zone in the Himalayas.

3000 m: Sandar (Kishatwar District), 32°29'10" N, 75°50'29" E; a moist temperate forest in the Lesser Himalayas, consisting mainly of trees of *Cedrus*, *Pinus*, *Picea*, *Abies*, *Taxodium*, and *Betula*.

4000 m: Affarwatt (Gulmarg, Baramulla District, northwest Jammu-&-Kashmir), 33°54'28" N, 74°24'22"E; an alpine zone in the Upper Himalayas that included shrubs like *Rhododendron* spp., mosses, lichens, and wild flowers such as *Meconopsis* spp. and *Leontopodium alpinum* Colm. ex Cass.

ANT SAMPLING. The sampling was carried out using standard protocols designed for elevation-gradient studies by Fisher (2004). At each elevation a 250 m transect along the contour was set with 25 plots. Each plot was 5m² in size and they were placed 5 m apart along the transect. At each plot we used six different sampling techniques (pitfall traps, Winkler sacks, stick beating, soil core, honey bait and hand picking) to

collect ants. Ants from all the collection methods were pooled to provide one measure for each plot. At 4000 m only hand-picking (two visits) was used. Each site was sampled on three occasions (two at 4000 m), spanning the summer months (Table 1), from 2007 to 2010. During a sampling month each site was visited on one day, and again two to three days later to collect the pitfall-trap contents. On the second visit each month (from 06:00 h to 18:00 h) the other sampling methods were applied, and abiotic factors were measured.

Pitfall traps were made up of test tubes with an internal diameter of 18 mm and a length of 150 mm, which were partly filled to a depth of about 50 mm with soapy water and 5% ethylene glycol solution, inserted into PVC sleeves, and buried with the rim flush with the soil surface. Traps were set for 48 to 72 hours each time. After emptying the traps on the second visit each month, leaf litter inside each quadrat/plot was collected and sifted through a wire sieve with square holes of 1 × 1 cm; before sifting, the material was chopped with a machete to disturb ant nests in small twigs and decayed logs. Ants and other invertebrates were extracted from the sifted litter during a 48-hour period in Winkler sacks. To sample ants on trees, bushes etc. the stick beating

Table 1: Data regarding abiotic and biotic factors pertaining to different elevations. Given are altitude of sample site; range of collecting months; mean daytime air temperature during sampling months, with standard deviation and range during the collection period; range of annual rainfall as obtained from local meteorological stations; local relative humidity at time of sampling; thickness of the leaf-litter as measured during sampling; and remarks on the species composition of vegetation at sampling sites.

Altitude (m)	Range of collecting months	Average temperature (°C)	Annual rainfall (mm)	Relative humidity (%)	Leaf-litter thickness (cm)	Vegetation
500	April-October	35 SD ± 3.65 27.0 - 40.1	1,100-1,300 mm	65%	0.5 cm	Subtropical dry deciduous forest (<i>Acacia catechu</i> , <i>Dalbergia sissoo</i> , <i>Acacia modesta</i> , <i>Bombax ceiba</i> , <i>Eucalyptus robusta</i> , <i>Dendrocalamus strictus</i> , scattered small trees, shrubs and coarse grasses)
1000	April-October	30.8 SD ± 4.67 25.0 - 38.9	1,115 -1,136 mm	36%	1.5 cm	Subtropical mixed pine-deciduous forest (<i>Pinus roxburghii</i> , <i>Dalbergia sissoo</i> , <i>Olea europaea cuspidata</i> , <i>Albizia amara</i> and other broad leaved species)
2000	May-September	23.5 SD ± 2.89 18.0 - 27.1	1,100-1,476 mm	37%	2.7 cm	Subtropical-temperate transitional zone (<i>Cedrus deodara</i> , <i>Pinus wallichiana</i> , <i>Picea smithiana</i> , <i>Juglans regia</i> , <i>Acer laevigatum</i> , <i>Prunus persica</i> , <i>Aesculus indica</i> and <i>Fraxinus excelsior</i>)
3000	May-September	15.4 SD ± 2.08 12.9 - 19.1	600-900 mm	26%	2.3 cm	Himalayan moist temperate forest (<i>Cedrus deodara</i> , <i>Pinus wallichiana</i> , <i>Picea smithiana</i> , <i>Pinus gerardiana</i> , <i>Abies pindrow</i> , <i>Juglans regia</i> , <i>Kalopanax septemlobus</i> , <i>Parud avium</i> var. <i>avium</i> , <i>Aesculus indica</i> , <i>Fraxinus floribunda</i> and <i>Quercus pubescens pubescens</i>)
4000	July-September	8.4 SD ± 2.06 5.4 - 11.4	200-500 mm	16%	-	Mountain shrub (above tree line) (<i>Rhododendron</i> shrub, <i>Doronicum</i> , <i>Delphinium</i> , <i>Gentiana</i> , <i>Polygonum</i> , <i>Caragana</i> , <i>Saxifraga</i> , <i>Draba</i> and <i>Gypsophila</i>)

method was used. Soil core extraction was used to target hypogaean ants, where soil cores 20 x 20 x 15 cm deep were taken at equal intervals along the transect. These soil cores were sifted using a hand sieve pan to collect ants. Finally, ants were collected by honey baits (set for 30 to 40 minutes) and hand picking methods (one person working for five hours) as well.

To maximise ecosystem representativeness of the study we preferentially sampled sites far

inside typical habitats, to minimise edge effects. Habitat/abiotic parameters, such as temperature (recorded hourly from 06:00 h to 18:00 h on sampling days), humidity, and leaf-litter layer thickness, were recorded at each site during the time of sampling, and precipitation data was procured from local meteorological stations.

DATA ANALYSIS. To analyse the species abundance and species diversity at each elevation and the differences in community composition

between different elevations, data was analysed on the basis of true/actual abundances using software 'EstimateSWin 8.0.0.' (Colwell 2006) and several beta-diversity indices. Samples were also analysed for worker density, species density, species-specific worker density and occupancy rate for each elevation.

Assemblage species richness was calculated using non-parametric methods, Chao incidence-based coverage estimator (ICE) and Chao 2. Sample heterogeneity was given according to Jost's (2006) three different orders of diversity, with 0D = species richness, 1D = Shannon diversity (exponential of Shannon entropy) and 2D = inverse Simpson concentration. The different orders of diversity can be calculated according to the general formula,

$${}^qD \equiv \left(\sum_{i=1}^S p_i^q \right)^{1/(1-q)}$$

with the order of diversity q being the exponent and superscript of the formula (Jost 2006).

Faunal turnover between two sites was the inverse of the proportion of species present at the first site that were also present at the second site. If an ant species was absent from one altitude but present at an altitude above and below, it was assumed that the species was missed during sampling rather than absent from that altitude. The species was therefore recorded as potentially present and the faunal turnover was calculated using present plus potentially-present species.

Faunal similarity was calculated using the Sorensen quantitative index and Jaccard similarity index. Community dissimilarity (β -diversity) was measured with the help of Whittaker's index.

To comprehend the impact of stress and disturbance on community composition of ants at different elevations in the region of study, the species collected were broadly categorised on the basis of functional groups distinguished by Andersen (2000) and field observations by the first author spanning a period of 15 years. Eight functional groups (FGs) were identified and used to categorise the Himalayan ant community based on habitat use, feeding

ecology, competitive interactions and phylogeny of species. The "Dominant Dolichoderinae" group was not observed in this study; although Dolichoderinae were present, they did not exert such a dominant impact. Nevertheless all Camponotini (*Camponotus* and *Polyrhachis* spp.) were assigned to the "Subordinate Camponotini" category, due to their similar behaviour and low trophic position, i.e. herbivory (Pfeiffer, unpublished observations). "Generalised Myrmicinae" included abundant species of that subfamily, e.g. all species of *Pheidole*, *Crematogaster* and *Messor*; "Cryptic Species" comprised typical inconspicuous leaf litter genera, e.g. *Mayriella*; "Hot-climate Specialists" included taxa of hot dry climates, for example *Cataglyphis*, while "Specialised Predators" were ants with morphological adaptations to hunting, e.g. *Anochetus* and other Ponerinae. "Tropical-climate Specialists" incorporated species with moist-tropical origin and centre of distribution, e.g. *Oecophylla* and *Tetraponera*. While "Cold-climate Specialists" comprised mainly *Formica* and *Lasius* species and climate specialists from other genera, the "Opportunists" included unspecialised, poorly-competitive ants which predominate where stress or disturbance limit other ants, and we put most species of *Myrmica*, *Aphaenogaster* and *Tetramorium* there, as well as invasives like *Nylanderia bourbonica*.

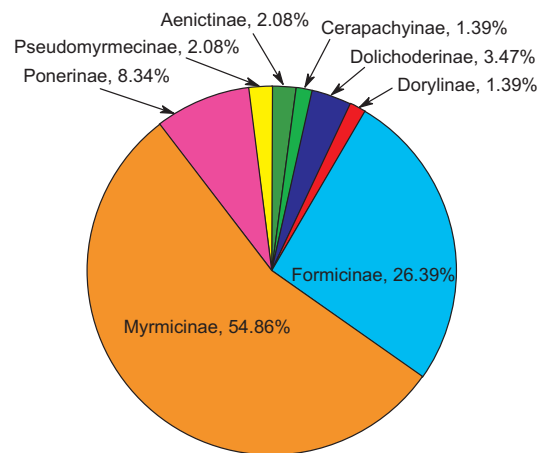


Fig. 2. Species-richness pattern of subfamilies in Jammu-Kashmir Himalaya. Given are the members of subfamilies as percentages of a total of 274 species occurrences.

Appendix 1. List of species recorded at different elevations along with their representation as per functional group scheme. Given is subfamily and species of ants; functional group (FG) identity coded as CCS = Cold-climate Specialist, CRY = Cryptic Species, GM = Generalised Myrmicinae, SC = Subordinate Camponotini, HCS = Hot-climate Specialist, OPP = Opportunist, SP = Specialist Predator, TCS = Tropical-climate Specialist; and presence at different altitudes. Invasive species are marked with *, while endemic species are marked with #.

Subfamily	Species	FG	500 m	1000m	2000m	3000m	4000m
Aenictinae	<i>Aenictus aitkenii</i> Forel, 1901	TCS	7	9	0	0	0
	# <i>Aenictus doryloides</i> Wilson, 1964	TCS	0	4	0	0	0
	<i>Aenictus pachyverus</i> (Smith, F., 1858)	TCS	6	6	0	0	0
Cerapachyinae	<i>Cerapachys biroi</i> Forel, 1907	SP	15	3	0	0	0
	<i>Cerapachys longitarsus</i> (Mayr, 1879)	SP	6	1	0	0	0
Dolichoderinae	<i>Chronoxenus myops</i> (Forel, 1895)	TCS	11	18	0	0	0
	<i>Dolichoderus taprobanae</i> (Smith, F., 1858)	TCS	0	10	0	0	0
	<i>Dolichoderus thoracicus</i> (Smith, F., 1860)	OPP	0	0	11	0	0
	* <i>Tapinoma melanocephalum</i> (Fabricius, 1793)	OPP	10	5	6	9	0
	* <i>Technomyrmex albipes</i> (Smith, F., 1861)	OPP	5	14	0	0	0
Dorylinae	<i>Dorylus labiatus</i> Shuckard, 1840	TCS	7	0	0	0	0
	<i>Dorylus orientalis</i> Westwood, 1835	TCS	14	9	11	0	0
Formicinae	<i>Camponotus compressus</i> (Fabricius, 1787)	SC	2	11	10	0	0
	# <i>Camponotus himalayanus</i> Forel, 1893	SC	0	0	18	7	0
	<i>Camponotus oblongus binominatus</i> Forel, 1916	SC	2	0	0	0	0
	<i>Camponotus parvus</i> Emery, 1889	SC	3	10	0	0	0
	<i>Camponotus rufoglaucus</i> (Jerdon, 1851)	SC	0	2	0	0	0
	<i>Camponotus sericeus</i> (Fabricius, 1798)	SC	8	2	0	0	0
	<i>Camponotus wasmanni</i> Emery, 1893	SC	9	4	0	0	0
	# <i>Cataglyphis cugiai</i> Menozzi, 1939	HCS	0	0	12	9	0
	<i>Cataglyphis longipedem</i> (Eichwald, 1841)	HCS	7	0	0	0	0
	<i>Formica clara</i> Forel, 1886	CCS	0	0	11	7	0

<i>Formica cunicularia</i> Latreille, 1798	CCS	0	0	0	10	13	0
<i>Formica fusca</i> Linnaeus, 1758	OPP	0	0	11	11	0	3
<i>Formica gagates</i> Latreille, 1798	CCS	0	0	0	0	0	5
<i>Formica gagatoides</i> Ruzsky, 1904	CCS	0	0	3	3	8	0
<i>Formica sanguinea</i> Latreille, 1798	CCS	0	0	5	5	8	0
<i>Formica truncorum</i> Fabricius, 1804	CCS	0	0	10	10	7	0
<i>Lasius alienoflavus</i> Bingham, 1903	CCS	0	0	7	7	7	0
<i>Lasius alienus</i> (Foerster, 1850)	CCS	0	0	7	7	8	0
<i>Lasius brunneus</i> (Latreille, 1798)	CCS	0	0	10	10	13	0
<i>Lasius niger</i> (Linnaeus, 1758)	CCS	0	0	5	5	9	0
<i>Lasius talpa</i> Wilson, 1955	CCS	0	0	11	11	12	0
<i>Lepisiota capensis</i> (Mayr, 1862)	CRY	5	4	11	11	11	0
* <i>Lepisiota frauenfeldi integra</i> (Forel, 1894)	OPP	3	5	0	0	0	0
* <i>Lepisiota opaca</i> (Forel, 1892)	OPP	0	7	0	0	0	0
<i>Lepisiota opaca pulchella</i> (Forel, 1892)	CRY	6	0	0	0	0	0
<i>Nyländeria aseta</i> (Forel, 1902)	OPP	12	0	0	0	0	0
<i>Nyländeria bourbonica</i> (Forel, 1886)	OPP	13	0	0	0	0	0
<i>Nyländeria taylori</i> (Forel, 1894)	OPP	0	11	4	4	0	0
<i>Oecophylla smaragdina</i> (Fabricius, 1775)	TCS	10	12	0	0	0	0
* <i>Paratrechina longicornis</i> (Latreille, 1802)	OPP	10	0	0	0	0	0
<i>Plagiolepis dichroa</i> Forel, 1902	CRY	9	11	0	0	0	0
<i>Plagiolepis jerdonii</i> Forel, 1894	CRY	0	10	10	10	0	0
<i>Polyrhachis exercita</i> (Walker, 1859)	SC	11	0	0	0	0	0
<i>Polyrhachis illaudata</i> Walker, 1859	SC	1	6	10	10	0	0
<i>Polyrhachis lacteipennis</i> Smith, F., 1858	SC	9	5	16	16	0	0
<i>Polyrhachis punctillata smythiesii</i> Forel, 1895	SC	10	0	0	0	0	0

<i>Prenolepis naoroji</i> Forel, 1902	CCS	0	4	0	0	0	0	0	0
<i>Pseudolasius familiaris</i> (Smith, F., 1860)	TCS	0	0	9	9	9	9	0	0
<i>#Aphaenogaster cristata</i> (Forel, 1902)	OPP	0	0	9	13	0	0	0	0
<i>Aphaenogaster feae</i> Emery, 1899	OPP	0	3	12	10	0	0	0	0
<i>Aphaenogaster rothmeyei</i> (Forel, 1902)	OPP	0	0	8	11	0	0	0	0
<i>#Aphaenogaster sagei</i> (Forel, 1902)	OPP	0	0	6	9	0	0	0	0
<i>Aphaenogaster sagei pachei</i> (Forel, 1906)	CCS	0	0	0	0	6	0	0	6
<i>#Aphaenogaster smythiesii</i> (Forel, 1902)	OPP	0	0	8	7	0	0	0	0
<i>#Aphaenogaster smythiesii prudens</i> (Forel, 1902)	OPP	0	0	3	9	0	0	0	0
<i>*Cardiocondyla nuda</i> (Mayr, 1866)	OPP	9	16	0	0	0	0	0	0
<i>*Cardiocondyla wroughtonii</i> (Forel, 1890)	OPP	0	11	0	0	0	0	0	0
<i>Cataulacus taprobanae</i> Smith, F., 1853	TCS	0	0	5	0	0	0	0	0
<i>Crematogaster anthracina</i> Smith, F., 1857	GM	0	10	0	0	0	0	0	0
<i>Crematogaster biroii</i> Mayr, 1897	GM	10	8	0	0	0	0	0	0
<i>Crematogaster flava</i> Forel, 1886	GM	5	10	4	0	0	0	0	0
<i>Crematogaster politula</i> Forel, 1902	GM	0	5	16	12	0	0	0	0
<i>Crematogaster rogenhoferi</i> Mayr, 1879	GM	0	9	0	0	0	0	0	0
<i>#Crematogaster sagei</i> Forel, 1902	GM	0	2	14	8	0	0	0	0
<i>Crematogaster subnuda</i> Mayr, 1879	GM	7	7	10	0	0	0	0	0
<i>#Lophomyrmex ambiguus</i> Rigato, 1994	TCS	0	17	0	0	0	0	0	0
<i>Lophomyrmex bedoti</i> Emery, 1893	TCS	10	9	0	0	0	0	0	0
<i>Lophomyrmex quadrispinosus</i> (Jerdon, 1851)	TCS	9	9	0	0	0	0	0	0
<i>Mayriella transfuga</i> Baroni Urbani, 1977	CRY	7	7	0	0	0	0	0	0
<i>Meranoplus bicolor</i> (Guerin-Meneville, 1844)	HCS	12	8	0	0	0	0	0	0
<i>Messor himalayanus</i> (Forel, 1902)	GM	5	9	8	8	0	0	0	0
<i>Messor instabilis</i> (Smith, F., 1858)	GM	8	9	7	13	0	0	0	0

<i>Monomorium aberrans</i> Forel, 1902	GM	6	8	0	0	0	0
* <i>Monomorium destructor</i> (Jerdon, 1851)	OPP	11	11	7	0	0	0
* <i>Monomorium floricola</i> (Jerdon, 1851)	OPP	5	4	0	0	0	0
* <i>Monomorium glabrum</i> (Andre, 1883)	OPP	0	6	7	0	0	0
* <i>Monomorium indicum</i> Forel, 1902	OPP	9	9	13	0	0	0
* <i>Monomorium orientale</i> Mayr, 1879	OPP	0	9	12	0	0	0
* <i>Monomorium pharaonis</i> (Linnaeus, 1758)	OPP	8	1	4	13	0	0
* <i>Monomorium sagei</i> Forel, 1902	GM	0	17	0	0	0	0
<i>Monomorium scabriceps</i> (Mayr, 1879)	GM	6	9	0	0	0	0
<i>Myrmica aimonissabaudiae</i> Menozzi, 1939	OPP	0	0	12	10	0	0
* <i>Myrmica cachmiriensis</i> Forel, 1904	OPP	0	0	12	1	0	0
* <i>Myrmica elmesi</i> sp. nov.	OPP	0	0	4	0	0	0
* <i>Myrmica foreliana</i> Radchenko & Elmes, 2001	OPP	0	0	12	0	0	0
* <i>Myrmica fortior</i> Forel, 1904	OPP	0	0	7	10	0	0
* <i>Myrmica longisculpta</i> sp.nov.	OPP	0	0	7	10	0	0
* <i>Myrmica nitida</i> Radchenko & Elmes, 1999	OPP	0	0	6	7	2	0
* <i>Myrmica ordinaria</i> Radchenko & Elmes, 1999	OPP	0	0	9	11	0	0
* <i>Myrmica pachei</i> Forel, 1906	OPP	0	0	16	0	0	0
* <i>Myrmica radchenkoi</i> Bharti & Sharma, 2011	OPP	0	0	7	0	0	0
* <i>Myrmica rhytida</i> Radchenko & Elmes, 1999	OPP	0	0	13	9	3	0
* <i>Myrmica rugosa</i> Mayr, 1865	OPP	0	0	14	10	0	0
* <i>Myrmica rupestris</i> Forel, 1902	OPP	0	0	5	12	3	0
* <i>Myrmica smythiesii</i> Forel, 1902	OPP	0	0	7	8	4	0
<i>Myrmica varisculpta</i> Radchenko & Rigato, 2009	OPP	0	0	5	7	0	0
* <i>Myrmica wardi</i> Radchenko & Elmes, 1999	OPP	0	0	7	5	0	0
* <i>Myrmica wittmeri</i> Radchenko & Elmes, 1999	CCS	0	0	0	0	3	0

<i>Myrmecaria brumea</i> Saunders, 1842	GM	9	5	0	0	0	0
<i>Pheidole binghamii</i> Forel, 1902	GM	0	10	0	0	0	0
<i>Pheidole fervens</i> Smith, F., 1858	GM	0	5	13	0	0	0
<i>Pheidole indica</i> Mayr, 1879	GM	15	7	13	0	0	0
<i>#Pheidole jucunda</i> Forel, 1885	GM	0	0	0	9	3	0
<i>Pheidole jucunda fossulata</i> Forel, 1902	GM	8	7	6	0	0	0
<i>Pheidole latinoda angustior</i> Forel, 1902	GM	6	0	0	0	0	0
<i>Pheidole latinoda major</i> Forel, 1885	GM	0	17	0	0	0	0
<i>Pheidole longipes</i> (Latreille, 1802)	GM	0	7	0	0	0	0
<i>#Pheidole sagei</i> Forel, 1902	GM	0	0	8	8	4	0
<i>Pheidole sharpi</i> Forel, 1902	GM	9	0	0	0	0	0
<i>Pheidole smythiesii</i> Forel, 1902	GM	0	11	10	0	0	0
<i>Pheidole spathifera aspatha</i> Forel, 1902	GM	4	7	0	0	0	0
<i>Pheidole spathifera</i> Forel, 1902	GM	8	0	0	0	0	0
<i>Pheidole watsoni</i> Forel, 1902	GM	3	0	0	0	0	0
<i>Pheidole woodmasoni</i> Forel, 1885	GM	2	5	0	0	0	0
<i>Pheidologeton affinis</i> (Jerdon, 1851)	GM	0	2	0	0	0	0
<i>Recurvidris recurvispinosa</i> (Forel, 1890)	CRY	0	3	0	0	0	0
<i>*Solenopsis geminata</i> (Fabricius, 1804)	OPP	0	0	6	0	0	0
<i>#Stenamma</i> sp.	CCS	0	0	9	0	0	0
<i>#Temnothorax desioi</i> (Menozzi, 1939)	CCS	0	0	0	11	0	0
<i>#Temnothorax desioi melanicus</i> (Menozzi, 1939)	CCS	0	0	0	6	0	0
<i>#Temnothorax fultonii</i> (Forel, 1902)	CCS	0	0	10	13	0	0
<i>Temnothorax rothneyi</i> (Forel, 1902)	CCS	0	0	6	12	0	0
<i>**Tetramorium caespitum</i> (Linnaeus, 1758)	OPP	2	0	7	8	0	0
<i>**Tetramorium lanuginosum</i> Mayr, 1870	OPP	5	2	1	0	0	0

	<i>*Tetramorium similinum</i> (Smith, F., 1851)	OPP	0	0	0	12	0	0	0
	<i>*Tetramorium smithi</i> Mayr, 1879	OPP	0	7	0	0	0	0	0
	<i>Tetramorium walshi</i> (Forel, 1890)	OPP	8	3	0	0	0	0	0
Ponerinae	<i>Anochetus graeffei</i> Mayr, 1870	SP	0	6	0	0	0	0	0
	<i>Harpegnathos venator</i> (Smith, F., 1858)	SP	9	3	0	0	0	0	0
	<i>Hypoponera confinis</i> (Roger, 1860)	CRY	0	12	9	0	0	0	0
	<i>Leptogenys diminuta</i> (Smith, F., 1857)	SP	8	3	11	0	0	0	0
	<i>Leptogenys sp.</i>	SP	0	0	12	0	0	0	0
	<i>Odontomachus monticola</i> Emery, 1892	SP	6	0	0	0	0	0	0
	<i>Odontomachus rixosus</i> Smith, F., 1857	SP	0	12	0	0	0	0	0
	<i>*Odontoponera transversa</i> (Smith, F., 1857)	SP	17	6	0	0	0	0	0
	<i>Pachycondyla bispinosa</i> Smith, F., 1858	SP	13	13	0	0	0	0	0
	<i>Pachycondyla luteipes</i> (Mayr, 1862)	SP	4	7	11	0	0	0	0
	<i>Pachycondyla rufipes</i> (Jerdon, 1851)	SP	12	6	7	0	0	0	0
	<i>Pachycondyla sulcata</i> (Mayr, 1867)	SP	5	0	0	0	0	0	0
Pseudomyrmecinae	<i>Tetraponera allaborans</i> (Walker, 1859)	TCS	4	4	6	0	0	0	0
	<i>Tetraponera nigra</i> (Jerdon, 1851)	TCS	4	2	0	0	0	0	0
	<i>Tetraponera rufonigra</i> (Jerdon, 1851)	TCS	5	2	0	0	0	0	0

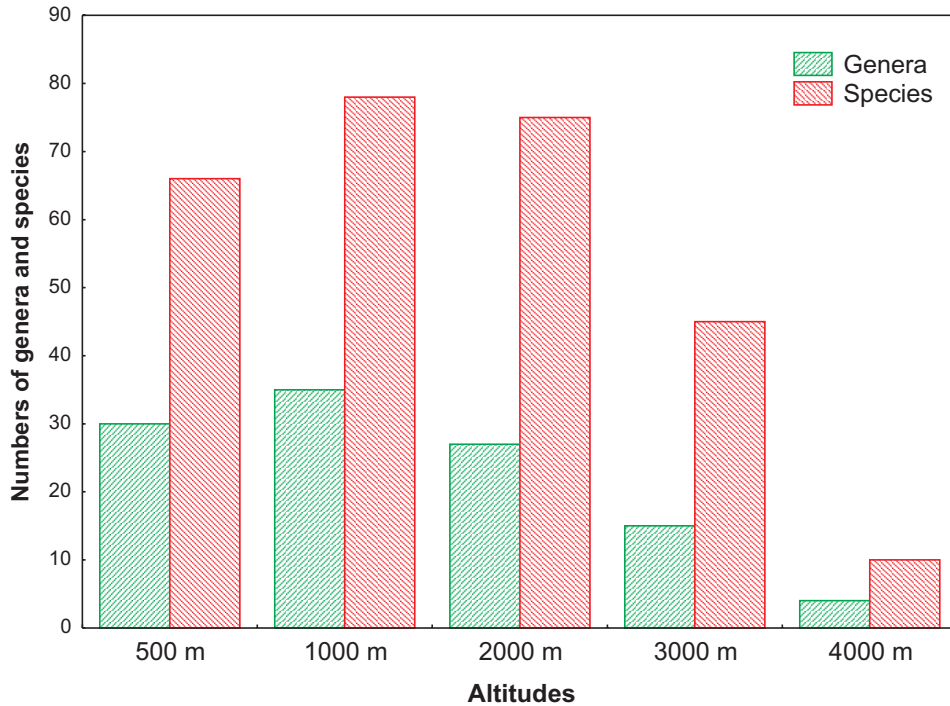


Fig. 3. Numbers of ant genera and species at different altitudes along our altitudinal transect.

Table 2: Important ecological parameters of the ant communities at different altitudes. Given are the following parameters: **occupancy rate**, the proportion of samples with ants; **worker density**, the mean number of workers per sample, log-transformed; **species density**, the mean number of species per sample; **maximum species number** per sample; **proportion of the single most abundant species at each site**, a species-specific measure of relative worker density; and **mean population density per species**, the ratio of mean (log transformed) ant worker density to species richness.

	Altitude (m)				
Parameters	500	1000	2000	3000	4000
Occupancy rate	1.00	1.00	1.00	1.00	0.88
Worker density (log n+1)	2.84	2.92	2.94	2.85	1.65
Species density	18.6	23.7	27.0	16.6	1.44
Maximum species number	47	60	55	24	4
Proportion of single most abundant species at each site	0.64	0.64	0.64	0.6	0.24
Mean population density	0.04	0.03	0.03	0.06	0.16

RESULTS

A total of 8022 ant individuals were recorded, and identified to 144 species from 45 genera representing eight subfamilies (Fig. 2, Appendix

1). Species richness and number of genera was highest at 1000 m, with 78 species from 35 genera, and decreased with the further increase in elevation to only ten species, from four genera, at 4000 m (Fig. 3). *Pheidole* was the only genus

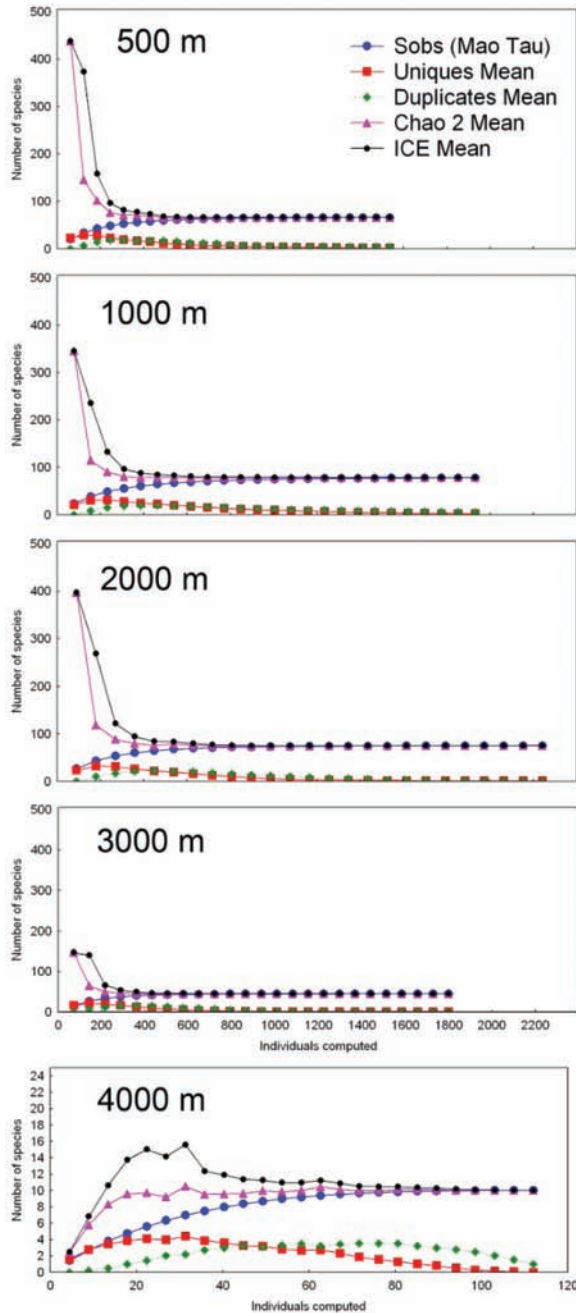


Fig. 4. Comparison of observed species richness with richness estimators, Chao 2 and ICE. The unit of the abscissa was taken as number of individuals (Longino *et al.* 2002) and all estimator curves were plotted with number of individuals on the abscissa. As richness estimates are highly influenced by rare species, the uniques and duplicates were also plotted along with the estimators for each elevation. Note the different scaling of Y- and X-axes for the 4000 m graph.

observed to be present along the whole transect.

Samples were analysed for occupancy rate, worker density, species density, species-specific worker density of the most abundant species, and mean population density (all results in Table 2). The occupancy rate (proportion of samples containing ants) was 100% up to 3000 m and then dropped to 88% at 4000 m. Mean worker density (mean number of workers per sample) showed a rise up to 2000 m, slightly declined at 3000 m and then abruptly fell at 4000 m. Species density remained high up to 2000 m and then declined at 3000 m and attained a very low value at 4000 m. Occupancy by the single most abundant species, a measure of numerical dominance, was constant at the first three elevations, then decreased at 3000 m and abruptly dropped at 4000 m. From the above stated values it was observed that the decrease in occupancy rates and worker density with increase in elevation was occurred at higher elevation than that of species density. Mean population density per species was constant up to 2000 m, almost doubled at 3000 m and was greatest at 4000 m.

Non-parametric species-richness estimators ICE and Chao 2 were plotted along with the observed species richness to estimate the species richness at different elevations (Fig. 4). Estimators were quite high at lower sample numbers, but quickly consolidated and aligned with observed species richness, thus demonstrating the high coverage of our samples. Similarly, rare species (ratio of number of species that occur in one sample to the number of species that occur in two) declined with higher sample number. Only at 4000 m altitude did 'uniques' and duplicates rise for half of the samples pooled, which could be attributed to low worker density at this altitude.

True Shannon diversity 1D was 54.7 at 1000 m and 63.7 at 2000 m (Table 3). These high values reflected the huge number of species per sample recorded at these altitudes. On the other hand high Simpson diversity 2D stressed the dominance of certain species, especially at lower elevations.

Table 3: Alpha diversity measurements for different elevations. Given is altitude, species richness 0D , Shannon Index H, Shannon Diversity 1D and Simpson Diversity 2D , as calculated from the inverse of the Simpson concentration and Simpson Evenness.

Altitude (m)	Species richness 0D	Shannon Index H	Shannon Diversity 1D	Inverse* of the Simpson concentration 2D	Simpson Evenness ($E_{1/D}^2$)
500	66	3.98	53.8	48.6	0.74
1000	78	4.00	54.7	44.4	0.57
2000	75	4.15	63.7	55.2	0.74
3000	45	3.76	42.9	42.8	0.95
4000	10	2.24	9.38	9.45	0.95

*Calculated as ${}^2D = 1 / \left(\sum_{i=1}^S p_i^2 \right)$

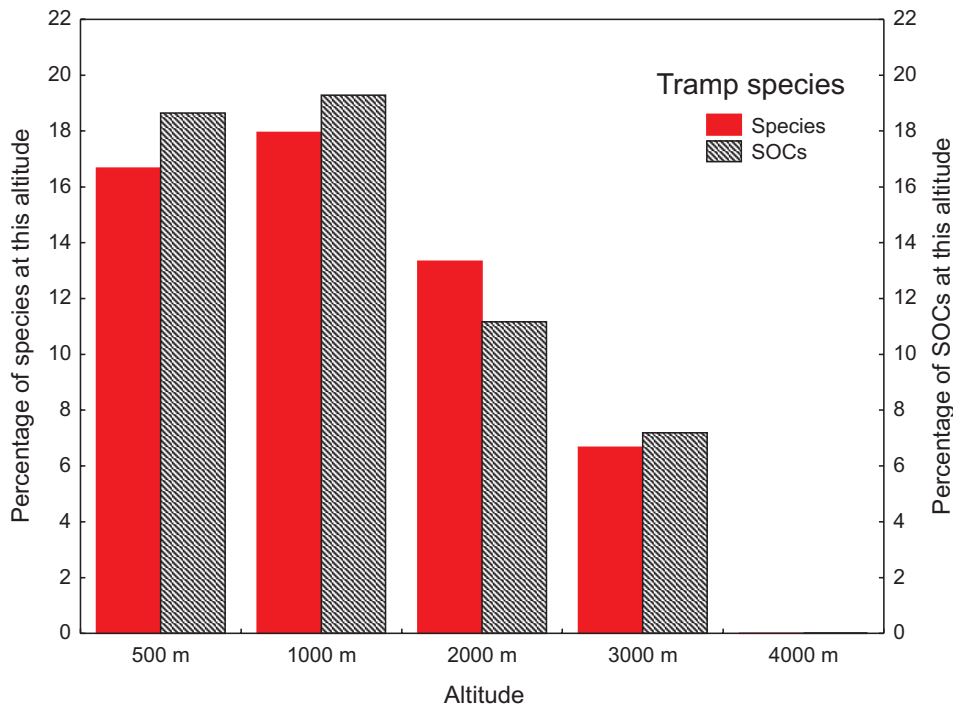


Fig. 5. Distribution pattern of tramp (invasive) species of ants at different elevations in Jammu-Kashmir Himalaya. Given are the percentage of all species which are tramp species, and the percentage of all species occurrences (SOCs) which are tramps, at each altitude.

Disturbance at lower elevations can also be judged by the high presence of invasive/tramp and opportunistic species at these altitudes (Fig. 5, Appendix 1). Study of the inventory of ants at different altitudes revealed that at 500 m, 11 (17%) of 66 species were invasive and 21% were “Opportunists” (Fig. 6). Similarly at 1000 m, 14

(18%) of 78 species were invasive and 22% were “Opportunists”. At 2000 m, the percentage of “Opportunists” rose to 45% (i.e. 34 species out of 75 represented this altitude) and 10 invasives. The number of invasive species decreased to two at 3000 m, and none were reported from 4000 m. The ant assemblages at 3000 m and

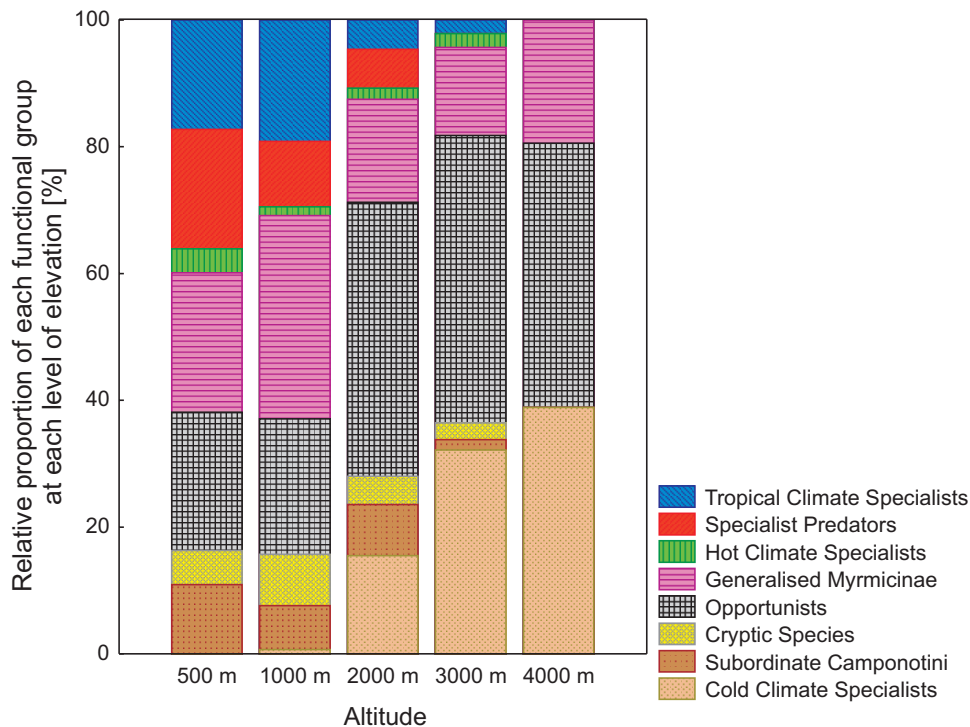


Fig. 6. Functional-group composition of ants in Jammu-Kashmir Himalaya. Given is the percentage of total species occurrences in each functional group. Invasive species are included in the “Opportunist” group.

4000 m were mainly composed of stress-tolerant high-altitude species.

The relationship of community composition to elevation was calculated using present plus potentially-present species (Table 4). All 146 ant species were included in the analysis. The highest faunal turnover between adjacent

altitudes was between 3000 m and 4000 m, where 84.8 % of the species changed (Table 5).

The similarity indices Sorensen quantitative and Jaccard similarity index (Table 6), based on abundance data and incidence data, indicated that the most similar pairs of communities were at 500 m and 1000 m, and at 2000 m and 3000 m. The dissimilarity in the ant fauna between two elevations was calculated by Whittaker’s measure and the results revealed that assemblages at 500 m and 1000 m were completely dissimilar to that at 4000 m (Table 7) and did not share even a single species, thereby indicating very high beta diversity.

Table 4: Number of ant species recorded at each elevation in Jammu-Kashmir Himalaya with potentially present species, which were recorded at the elevations below and above.

Altitude (metres)	Number of species	
	Present	Present + Potentially present
500	66	66
1000	78	79
2000	75	75
3000	45	46
4000	10	11

DISCUSSION

Species richness and ant density

Species richness is usually enhanced on mountain slopes (Lomolino 2001), and the Himalayan altitudinal gradient we studied corroborates this. Using a set of different methods, we collected

Table 5: Faunal turnover between different altitudes (%), computed as the proportion of species at a given elevation that is not present at another elevation. Table is read by row to column, so that only 6.5% of the species in the 3000 m community were absent at 2000 m, whereas 42.7% of the species at 2000 m were absent at 3000 m. Faunal turnover was highest (100%) in both directions between 500 m and 4000 m, and between 1000 m and 4000 m.

Altitude (m)	Altitude (m)				
	500	1000	2000	3000	4000
500	-	22.7	68.2	90.9	100
1000	35.4	-	60.8	88.6	100
2000	72.0	58.7	-	42.7	92.0
3000	87.0	80.4	6.5	-	84.8
4000	100	100	40.0	30.0	-

Table 6. Sorensen quantitative index (below diagonal) and Jaccard similarity index (above diagonal) as measures of beta diversity among different altitudes.

Altitude (m)	Altitude (m)				
	500	1000	2000	3000	4000
500		0.543	0.175	0.057	0.000
1000	0.626	-	0.252	0.078	0.000
2000	0.247	0.309	-	0.551	0.076
3000	0.111	0.131	0.675	-	0.150
4000	0.000	0.000	0.051	0.066	-

Table 7. Whittaker's index of beta diversity.

Altitude (m)	Altitude (m)			
	500	1000	2000	3000
1000	0.305	-	-	-
2000	0.702	0.608	-	-
3000	0.892	0.870	0.300	-
4000	1.000	1.000	0.858	0.745

144 species and subspecies, from 45 genera and eight subfamilies, of Formicidae, including several species previously unknown to science. We recorded ants along the whole gradient from 500 m to 4000 m. The occupancy rates and worker density decreased slowly with increase in elevation as compared with species density which decreased sharply. High-altitude genera like *Formica* and *Myrmica* showed higher densities than their counterparts in dominance (like *Myrmecaria*, *Aenictus*, *Oecophylla* etc.) at lower elevations. As a result the mean population density per species increased exponentially with increase in elevation, so at higher altitudes the decrease in diversity was compensated by an increase in worker density for each species, a pattern named by Longino & Colwell (2011) as “density compensation”.

Zoogeographical affinities and endemism in the Himalayas

‘Himalaya’ is biogeographically most complex and diverse. Any attempt to understand the altitudinal patterns of diversity in the region must be based on a biogeographical assessment. Our study in North-western Himalaya is the first effort to depict the elevational gradient in the ant fauna of the region, and gives a very interesting picture. The elevations of 500 m and 1000 m fall within the Shivalik or Sub-Himalayan range. The Shivalik range is quite young in origin (25 mya) and low-lying, harbouring a subtropical type of vegetation (Table 1). Temperature is high and the ant fauna is dominated by tropical genera of the Oriental, like *Pheidole*, *Polyrhachis* and *Crematogaster*, and wet tropical species like *Harpegnathos venator*, *Lophomyrmex bedoti* and *Meranoplus bicolor*.

On the other hand, land at an elevation of 2000 m falls under the temperate zone and geologically represents the Lesser Himalayas (the ranges of Nagtiba, Dholadhar, Pir-Panjaj, North-Kashmir, Mahabharat, Mussoorie and Ratanpir). The ant community at this elevation is dominated by Palaearctic elements, followed by Indo-Malayan elements and others, contributed by modern tramp species (Afrotropical, Australian, Malagasy, Neotropical and Nearctic elements) (Bharti 2008). The dominance of

Palaearctic species, which are well adapted to low-temperature stress, is clearly attributed to the lower temperature; mean daytime temperature in the collection months (24°C) was 7°C lower than at 1000 m. This effect can be noticed on the vegetation as well, as cold-tolerant *Cedrus* forest starts dominating at 1,800 m a.s.l. Moreover, this altitude represents a transition boundary between the Indo-Malayan and Palaearctic regions in terms of the ant fauna in Himalaya. Faunal turnover values indicate community replacement of about 60% between 1000 m and 2000 m.

Elevations of 3000 m and 4000 m geologically represent the Greater Himalayas. The lower temperature at these elevations has a marked impact on ecology. The zone at 3000 m is dominated by gymnosperms, but above this limit closed forests disappear. These ecological factors favour the proliferation of Palaearctic elements, and the highest turnover between successive ascending altitudes was found here (Table 5). The ant assemblage at these elevations is mainly dominated by the cold-resistant genera *Formica*, *Aphaenogaster*, *Myrmica* and *Temnothorax*.

As stated by Mani (1995) the customary phyto-geographical division of the Himalayan forests separates a Western Himalayan forest province, as distinct from the Eastern Himalayan forest province. The flora of the former region has its affinities with Indo-Malayan elements and at high altitudes most of it is Palaearctic, with some Afrotropical and Mediterranean elements. Almost the same pattern was observed during the present study in the case of the ants, the ecological conditions up to 2000 m favour Indo-Malayan elements and above 2000 m the region is purely dominated by Palaearctic elements, while elements of other faunas are restricted to tramp species, e.g. *M. pharaonis*, *T. lanuginosum* and *T. simillimum*.

Twenty-three percent of the species have been found to be endemic to this region (Fig. 7). Almost half of these are contributed by *Myrmica* (45%). As elucidated by Radchenko & Elmes (2010), *Myrmica* species from Himalaya have plesiomorphic features, and many of the species and species-groups of this region possess morphological characters that are unique and are rarely found in the *Myrmica* species reported from adjacent regions. It has been suggested

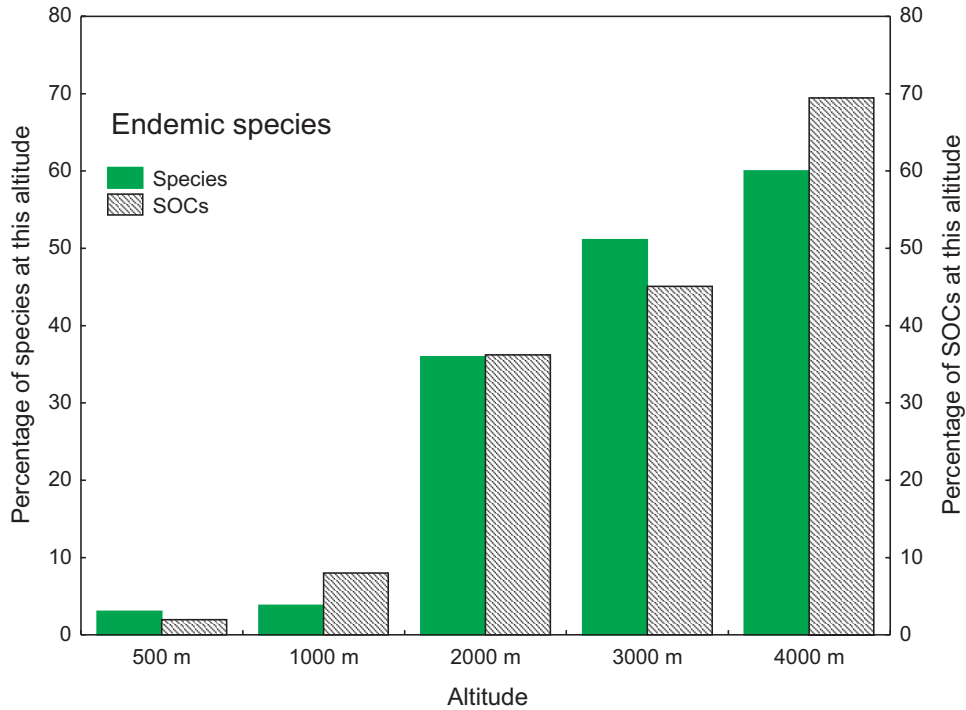


Fig. 7. Occurrence of endemic ant species at different elevations in Jammu-Kashmir Himalaya. Given are the percentages of all species which are endemic to the Himalayas, and the percentages of all species occurrences (SOCs) which are Himalaya-endemic, at each altitude.

that the *Myrmica* fauna of the Himalayas has remained fairly isolated from adjoining regions (Bharti 2008; Radchenko & Elmes 2010; Bharti & Sharma 2011a, b, c), since the Himalayan ranges to the North and East might have formed an almost-insuperable geographical barrier for *Myrmica*, while further south, tropical and subtropical conditions limited the opportunity for interchange with other faunas. Long-term isolation of the genus *Myrmica* from adjoining regions may have led to high degrees of endemism in this group. The present study found that endemism (the proportion of species endemic to the Himalayas) increased with elevation and peaked in high-altitude sites (Fig. 7). This can be attributed to species radiation operating in the region and points towards environmental filtering at higher altitudes: the harsh environmental conditions allow only a subset of ant genera to persist, and these may undergo a radiation into empty ecological niches.

Analysis in terms of functional groups

The elevations under study fall under three climatic zones: sub-tropical (500 m and 1000 m), sub-temperate (2000 m) and temperate (3000 m and 4000 m). Elevations of 500 m and 1000 m are warm and open habitats with an average daytime temperature of 35°C and 30°C, respectively (April to October). The impact of low-temperature stress is negligible at these two altitudes and therefore the community composition at these levels should mainly be regulated by competition (Andersen 2000). These elevations were observed to be behaviourally dominated by “Generalised Myrmicines” > “Opportunists” > “Tropical-climate Specialists” (Fig. 6). But the presence of disturbance specialised “Opportunist” species of *Paratrechina*, *Tapinoma*, *Tetramorium* and *Monomorium* indicates severe disturbance at these elevations, as was observed by Narendra *et al.* (2011) who found similar genera as indicators of disturbed habitat in the lowlands of the Indian Western Ghats. Similarly, Greenslade & Greenslade (1977) reported from the Solomon

Islands that tree-clearing favoured opportunist species of the above-mentioned genera. Habitats at an elevation of 2000 m were cool and open (average daytime temperature 24°C) and experienced moderate levels of low-temperature stress. This elevation was dominated by “Opportunists” (43%), “Generalised Myrmicines” (16%) and “Cold-climate Specialists” (15%). This proliferation of “Opportunists”, which made up 35 out of 75 species, is especially interesting as the group comprises both tropical and Palaearctic elements, the former characterised by mostly pantropical tramp species that signify fragmented/disturbed habitats (20 species in genera like *Monomorium*, *Tapinoma* and *Technomyrmex*), the latter stress-specialists (*Formica*, *Myrmica*) whose presence indicates low-temperature stress. This corroborates the finding that “Opportunists”, apart from being indicators of disturbance, are also more ecologically important in cool-temperate regions (Andersen 2000).

A marked decrease in “Cryptic Species” was also observed at 2000 m. The areas at 2000 m and 3000 m remain snow-clad for three to four months in a year, and frost and ice reduce the ability for “Cryptic Species” to make nests or forage on/in the ground. The elevations of 3000 m and 4000 m (average daytime temperature during collection times: 15°C and 8.4°C respectively) are subject to extreme low-temperature stress (a primary stressor). These elevations were observed to be behaviourally dominated by “Opportunists” (45% at 3000 m and 42% at 4000 m) and “Cold-climate Specialists” (32% at 3000 m and 39% at 4000 m). While the allocation of species between these categories is debateable, the behavioural dominance of stress-tolerant formicines (*Formica*, *Lasius*) could be related to thermoregulation properties of their nests, as some species have nest mounts, which produce heat with decaying materials, or rely on metabolic heat production (Holldobler & Wilson 1990). Other species of *Formica* and *Myrmica* use a combination of nest architecture and biochemical mechanisms for cold-resistance. While their nests maintain a temperature about 10° C higher than necessary for survival, ants can overwinter in a supercooled state, which allows them to survive very low temperatures, e.g. *F. gogatoides* Ruszk can resist -27°C to -31°C (Berman *et al.*

2010). In Siberia this species exists in extreme habitats and is known as *polyarny muravey* (the polar ant); we have found it only up to 3000 m, but as its physiological abilities would allow it to reach much higher altitudes, it could also be found higher up. Interestingly we also found two species of *Pheidole* which were able to inhabit the highest zone.

The adverse climatic conditions prevalent at higher altitudes reduced the number of functional groups from a maximum of eight to three. But the loss of functional groups due to environmental filtering was compensated by an increase in the number of species per functional group (S/F ratio). Similarly density compensation at higher altitudes maintains the local biomass of an area, and also ecosystem reliability to a certain extent (Colwell & Lees 2000).

The functional-group (FG) classification (Andersen 2000 and papers cited within) is based on ants from Australia, and its application to non-Australian ant faunas is problematic (e.g. Pfeiffer *et al.* 2003; Narendra *et al.* 2011). Its value has repeatedly been questioned, and it has not been helpful in predicting species interactions in Western Ghats’ ant communities in India; however, it proved to be useful in predicting habitat use of species (Narendra *et al.* 2011). An uncritical use of this classification should be avoided (Andersen 2010), and although the species classifications we have applied in the present study are based on years of careful investigation in local conditions (Bharti, unpublished) some, e.g. the almost blanket-grouping of *Myrmica* as “Opportunists”, merit further discussion, as some members of this genus exhibit extraordinary cold-hardiness (Bermann *et al.* 2010) and might equally be counted as “Cold-climate Specialists”, so borders between these groups are flexible. Hence other authors may place certain species in different FGs, depending on local situation (e.g. Nur-Zati *et al.* 2011). For the present study, however, we regard the adapted FG classification as helpful, although we recognise the need for further studies which may refine the crude genus-based FG classification with more species-based categories or the use of refined functional groupings, e.g. according to nest type (Ryder Wilkie *et al.* 2010).

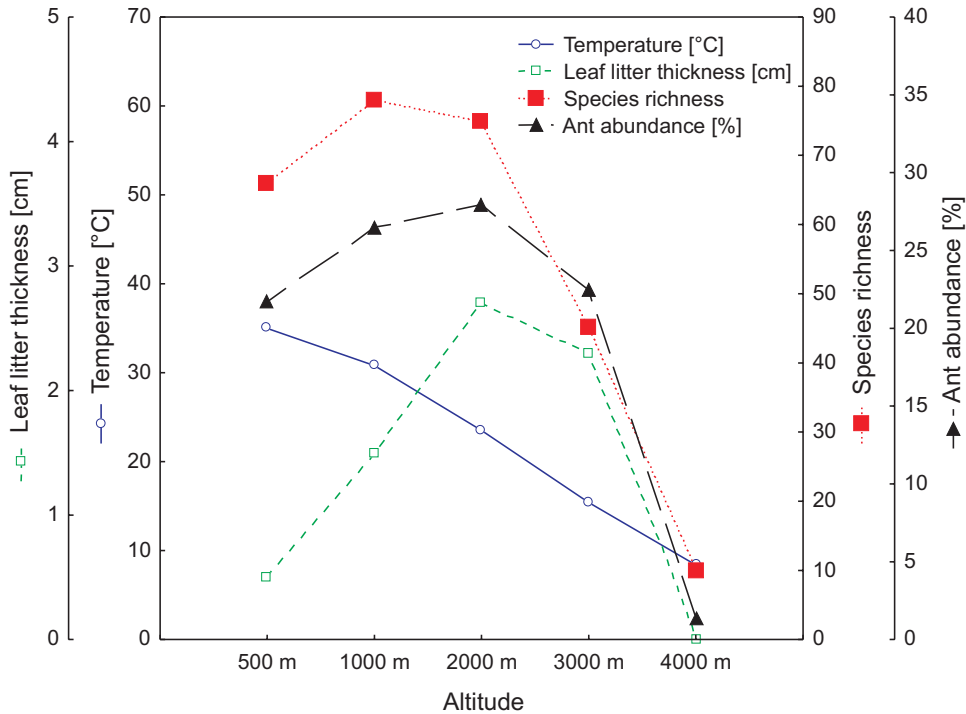


Fig. 8. Species richness and abundance compared to temperature and leaf litter thickness along the altitudinal transect. A pronounced mid- elevation peak in terms of species richness and abundance coincides with a peak in leaf litter thickness, while temperature declines linearly. Note the four Y axes, each with differing units and scales: Y left [temperature in °C], Y'left [leaf litter thickness in cm], Y right [number of species], Y' right [abundance as a percentage of total ant abundance at all altitudes].

Altitudinal pattern of diversity

As expected diversity was lowest at highest elevations. The lowest diversity and species density were found at 4000 m, and although these data might be influenced by lower sampling-effort, they mainly reflect the adverse climate conditions at the highest sampling point.

Although species richness was highest at 1000 m altitude, with 78 species recorded, Shannon and Simpson diversity both peaked at 2000 m, thus indicating an increasing overlap of species ranges towards the centre of the domain, which could well be explained by the mid-domain effect (MDE). The elevational range of a species is bounded by the highest and lowest elevation possible in the region. A peak in species richness at mid-elevations may be due to the limits imposed by geographic boundaries of species with different altitudinal ranges: species with larger ranges will automatically overlap in the centre (Sanders 2002). Furthermore worker density, species density and

occupancy rates were highest at an elevation of 2000 m, pointing towards a mid-elevation peak in terms of both species richness and abundance, and above this elevation a gradual decrease (Fig. 8). Underlying this pattern is the overlap of biogeographical realms at 2000 m, with species of the Oriental dominating below and those of the Palearctic above.

Similar patterns have been recorded by Fisher (1996, 1997, 1998, 1999, 2004) in Madagascar and by Samson *et al.* (1997) for arboreal and ground-dwelling ant species in the Philippines. In a widespread survey of leaf-litter ant diversity, Ward (2000) found that species richness peaked at mid-elevations in the tropics, but decreased continuously with elevation in temperate regions. In contrast, Brühl *et al.* (1999) observed a decrease in species diversity with increase in altitude, at Mount Kinabalu in tropical Borneo, where no mid-domain effect was recorded. Recently, Longino & Colwell (2011) also recorded a mid-domain effect in their study

on Barva Transect in Costa Rica. A decrease in species diversity at elevations above 2000 m during the present study could be due to adverse environmental conditions like the decrease in temperature, food stress, other altitude-related stress, lack of trees, scarcity of litter, or nesting stress coupled with foraging difficulty.

Invasive species and habitat disturbance

On the other hand, our study also points towards habitat disturbance in the Himalayan ecosystem. Although the sampling was conducted in the interior of the forest to avoid ecological edge effects, of the 144 species recorded, 19 were tramp/invasive. Most invasive species occurred at the lower sites at 500 m and 1000 m, their number and occurrence decreasing dramatically at 3000 m and none being reported from 4000 m (Fig. 5). Moreover opportunistic species – after exclusion of cold-stress specialists – comprised more than 20% of the ant assemblage at the first two elevations and 25% at 2000 m. At the same time the number and proportion of endemic species rose strongly with altitude (Fig. 7). While the lower abundance of invasive species at the higher altitudes may be due to their lower cold-tolerance as well as the lower habitat disturbance in higher areas, the high numbers of opportunistic and invasive species at the lower altitudes demonstrates the anthropogenic disturbance of these sites.

According to Connell (1978), the occurrence of low evenness values may indicate a fragmented/disturbed habitat, and disturbance can cause an increase in both richness of the ant assemblage and variation in species abundance (i.e. lower evenness). While diversity was highest at 2000 m and species richness at 1000 m, the lowest evenness was at 1000 m, followed by 500 m and 2000 m. Although natural stochasticity cannot be ruled out, an influence of human impact is supported by the high richness of invasive and opportunistic species.

Thus our finding of the mid-domain peak in diversity could stem from human disturbance of habitats at the foot of the mountains. As Wolda (1987) pointed out, sampling over long time periods generally reveals greatest richness at lower elevations, and the presence of mid-

elevation peaks in richness could be due to anthropogenic or other sorts of disturbance at lower elevations which affect natural diversity (see also Dunn *et al.* 2010). In fact, in most of the tropical and subtropical regions, the lower domain is heavily impacted by long-term human disturbance, e.g. forest lost and habitat degradation and fragmentation (Sodhi *et al.* 2007 and references cited therein). This was also the case in the Himalayas, where the naturally high richness of tropical species may be impacted by the presence of opportunist species, pointing to a habitat undergoing transformation because of perturbations caused by human activities.

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