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ORIGINAL ARTICLE

Biogeography of the water flea *Daphnia* O. F. Müller (Crustacea: Branchiopoda: Anomopoda) on the Indian subcontinent

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ABSTRACT
Studies on Daphnia *distribution in Indian subcontinent have been few and regionally restricted despite* Daphnia *being by far the most studied cladoceran. We here present a first biogeographical assessment of the genus on the Indian subcontinent (Afghanistan, Pakistan, India, Nepal, Bhutan, Bangladesh and Sri Lanka). We collected all pertinent literature and considered nineteen bioclimatic variables along with latitude, longitude, and altitude for statistical analysis of factors governing distribution in space. Significant variables (determined by Kruskal Wallis test) were tested by nonparametric multivariate analysis of variance (PERMANOVA) to clarify whether* Daphnia *species had specific environmental requirements. Canonical correspondence analysis was used to understand how environmental variables affected distribution. Eight* Daphnia *(*Ctenodaphnia*) and 4* Daphnia *s.str. occurred at 100 different localities. The variables temperature, altitude and latitude differed among species and so did their bio-climatic requirements.* Daphnia *distribution responded positively to altitude and negatively to a decrease in latitude and temperature. We confirm the existence of three complexes of* Daphnia *in the Indian subcontinent: i) widely distributed species and species complexes; ii) high altitude endemics; and iii) low latitude* D. *(*Ctenodaphnia*) species.*

Key words: Ctenodaphnia*;* Daphnia magna*;* Daphnia pulex*; Himalayas; oriental zone; Western Ghats.*

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INTRODUCTION

The Cladocera (Crustacea: Branchiopoda) constitute an ancient group of primarily freshwater crustaceans whose major differentiation may have occurred before the Permian (Kotov and Taylor, 2011). Until the Late Cenozoic, the Cladocera (and other Branchiopoda) are believed to have been much species-richer than today (Kerfoot and Lynch, 1987; Korovchinsky, 2006). As a result of climatic changes in the Tertiary, maximum cladoceran species richness is now concentrated in the subtropical zone of both hemispheres and at higher elevations within the true tropics (Korovchinsky, 2006).

Daphnia (Anomopoda: Daphniidae) is among the best-studied freshwater organisms (Lampert, 2011). It has an origin estimated at more than 200 Myr (Taylor *et al.,* 1996; Kotov and Taylor 2010, 2011). Currently the genus is classified into three sub-genera (Adamowicz *et al.,* 2009) with 361 formally described species *in toto* of which c. 24% are considered valid (Kotov, 2015). Among them, only few inhabit the lowland equatorial zone (Fernando, 1980; Fernando and Kanduru,1984; Benzie. 2005), with species occurring only above particular altitudes (Dumont, 1980; Green, 1995).

The biogeographical patterns observed in many *Daphnia* species in the Neotropics, Neartic, Paleartic and Afrotropical regions have been assessed relatively adequately (Ishida and Taylor, 2007; Mergeay *et al.,* 2008; Adamowicz *et al.*, 2009) but little information is available on the Indian subcontinent. Yet, this region is interesting for biogeography because of i) a complex geological history; ii) a wide range of altitudes; and iii) a strong seasonality with a distinct rainfall season (Monsoon) (Mani, 1974; Briggs, 2003). This has allowed the formation of various biomes, ranging from tropical to Alpine forests and deserts (Mani, 1974) resulting in a combination of endemic, Oriental, Palaearctic as well as Gondwanan biota (Gower *et al.,* 2002; Whatley and Bajpai, 2006; Koehler and Glaubrecht, 2007; Kulkarni and Pai, 2016). Their presence has been explained by hypotheses like the 'Indian raft' and 'Out of Asia into India' (Chatterjee and Scotese, 1999; Karanth, 2003), but relevance of such scenarios for passively dispersed zooplankton is uncertain.

Here, our aim was to analyze *Daphnia* distribution on the Indian sub-continent, discuss associations between species and environmental variables, and evaluate the relative importance of selected climatic variables in elucidating the distributional patterns observed.

METHODS

Study area

Our study area (Fig. 1) extends from Afghanistan and Pakistan to the west, India in the centre, Nepal and Bhutan to the east and Sri Lanka to the south (between 38°N to 4°N latitudes and 60°E to 98° E longitudes). Geographically, this region includes the Hindukush in the northwest, Himalayas from north till north-east; Indo-Gangetic plains on the Himalayan slopes, a central plateau region (like Deccan plateau) flanked by the more continuous Western and more fragmented Eastern Ghats, and a peninsular region bordered by a narrow coastline (Mani, 1974).

An altitudinal gradient is seen as we move down along the latitude. The altitude of the Himalayas ranges from 6600 m asl in northern and northwestern part (Tibetan Himalayas) to 900-1200 m asl in the more southern Sivalik ranges. The Central Indian subcontinent (plateau region) has an altitudinal range of 350-900 m asl, the highest peak in peninsular region of the subcontinent reaches nearly 2600 m asl. The southernmost region of the subcontinent, viz. Sri Lanka, has an altitudinal range of 0-2500 m.

Most of the Indian subcontinent has a monsoon climate, with rains for 3-4 months, usually from June till September/October. Part of the southern region and the north-eastern zone also receive rains from the retreating monsoon in November and December.

Data collection and GIS analysis

Data were gathered through mining of the literature published on *Daphnia* faunistics, taxonomy and biology. We used a conservative approach in selecting literature

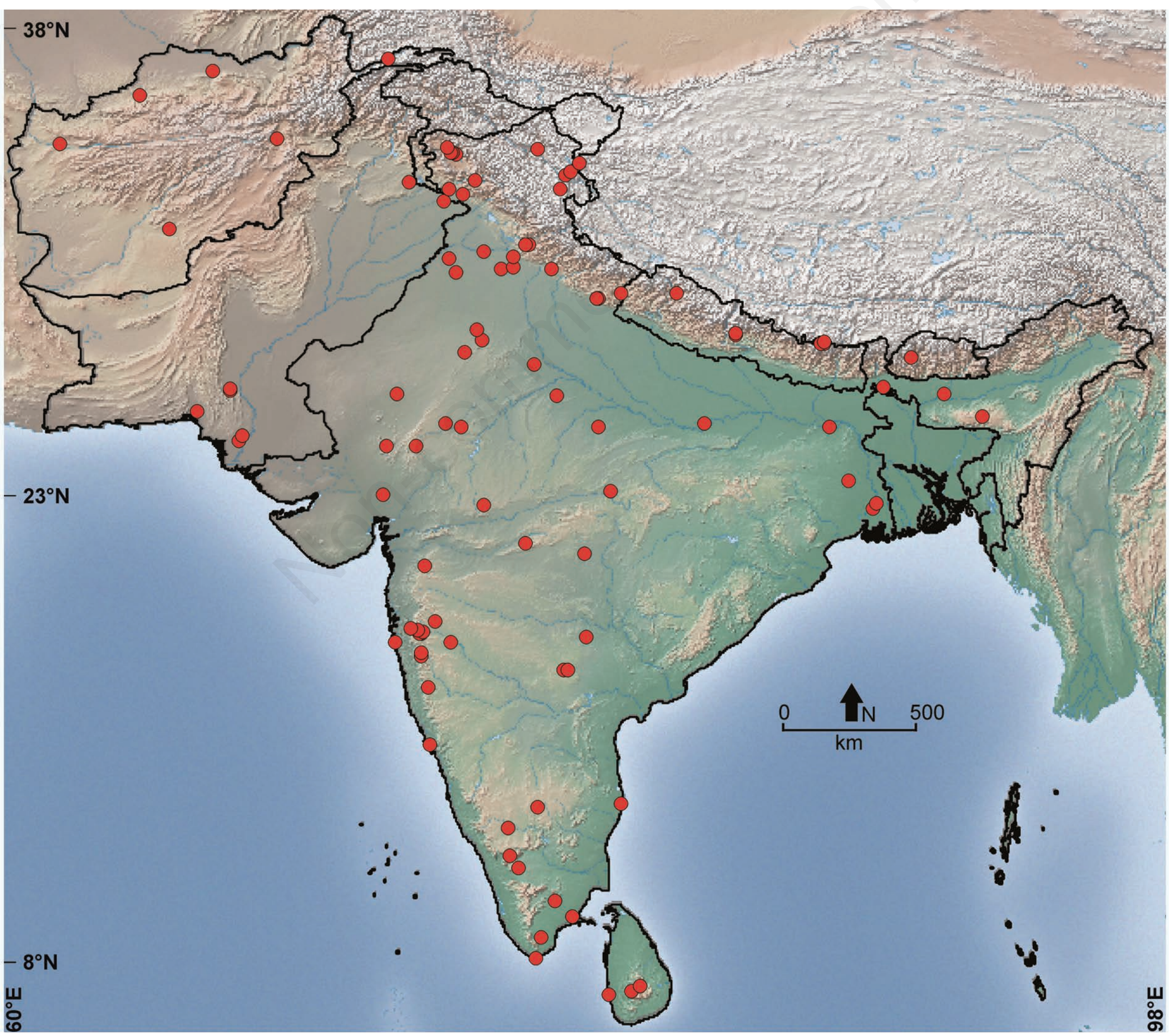

Fig. 1. Indian subcontinent considered for the study along with distribution of study sites (circles represent each locality).

on *Daphnia* occurrence because a large number of *Daphnia* records from the sub-continent are dubious (Chatterjee *et al.,* 2013). We only accepted records having at least some brief description of the animals with illustrations making possible a check of the identification of the cited species (for all records, see Supplementary Tab. 1). No reliable records of *Daphnia* could be obtained from Bangladesh and only a single report of *D. tibetana* was available from Bhutan (*H. Dumont, pers. obs.*).

Latitude and longitude data on each locality were obtained from Google Earth portal. A set of 19 bioclimatic variables and altitudes were extracted from the BIOCLIM dataset (http://www.worldclim.org; Hijmans *et al.*, 2005) at ten-minute spatial resolution (for names see Tab. 1). Broad scale resolution was used as many of the localities given were quite nonspecific (Ex. Kolkata as a locality).

Data analysis

Environmental variables including latitude, longitude, altitude and the 19 bioclimatic variables were considered for statistical analysis. Univariate normality of each variable was checked using Shapiro-Wilk test. Since all variables proved to be non-normal, variables that were significantly different among *Daphnia* species were identified using non-parametric Kruskal-Wallis one-way analysis of variance. As multiple tests were performed, the family-wise error rate was corrected using Bonferroni correction.

Significant variables were then used in analyzing *Daphnia* distribution. The null hypothesis that the data is multivariate normal was checked using an omnibus test (Doornik and Hansen, 2008). Since the data was not multivariate normal, nonparametric multivariate analysis of variance (PERMANOVA) was used to find out whether given *Daphnia* species had significantly different requirements for environmental variables (Anderson, 2001). Relationship of *Daphnia* species distribution to the bio-climatic variables was investigated using canonical correspondence analysis (CCA). This analysis was performed using the statistically significant variables identified by a Kruskal Wallis test (Tab. 2) and the *Daphnia* occurrence data for all the 100 localities. The significance of the analysis was tested using Monte Carlo permutations (n=999). Statistical analysis was performed in PAST (Hammer *et al.,* 2001).

RESULTS

Literature survey yielded a total of 134 records of *Daphnia* species from 100 different localities (Supplementary Tab. 2). The occurrence data were patchy in Northern and Central India, relatively well studied, while the Eastern, Northeastern region and North Western regions had a poorer coverage.

Diversity and taxonomy

Twelve species of *Daphnia* have been reported from the region (few comprising of presumable species groups) (Tab. 3), of which eight belong to the subgenus *D.* (*Cten-*

Tab. 1. Names of the BIOCLIM variables considered for the study.

BIOCLIM	Description
Bio1	Annual mean temperature
Bio2	Mean diurnal range (mean of monthly) (max temp - min temp)
Bio3	Isothermality - (Bio2/Bio7) (*100)
Bio4	Temperature seasonality (standard deviation *100)
Bio5	Max temperature of warmest month
Bio6	Min temperature of coldest month
Bio7	Temperature annual range (Bio5-Bio6)
Bio8	Mean temperature of wettest quarter
Bio9	Mean temperature of driest quarter
Bio10	Mean temperature of warmest quarter
Bio11	Mean temperature of coldest quarter
Bio12	Annual precipitation
Bio13	Precipitation of wettest month
Bio14	Precipitation of driest month
Bio15	Precipitation seasonality (coefficient of variation)
Bio16	Precipitation of wettest quarter
Bio17	Precipitation of driest quarter
Bio18	Precipitation of warmest quarter
Bio19	Precipitation of coldest quarter

Tab. 2. Kruskal-Wallis one-way analysis of variance test for the environmental variables across different species. Underlined P values are significant after Bonferroni correction.

Environmental variables	K	P
Latitude	57.6771	<0.0001
Longitude	18.0821	0.0797
Altitude	44.8522	<0.0001
Bio1	50.1070	<0.0001
Bio2	26.4818	0.0055
Bio3	48.3185	<0.0001
Bio4	50.2673	<0.0001
Bio5	45.4429	<0.0001
Bio6	62.5901	<0.0001
Bio7	37.2495	0.0001
Bio8	39.9302	<0.0001
Bio9	46.2505	<0.0001
Bio10	45.3273	<0.0001
Bio11	63.4260	<0.0001
Bio12	25.4819	0.0077
Bio13	21.8519	0.0255
Bio14	13.7414	0.2476
Bio15	21.0657	0.0327
Bio16	22.0630	0.0239
Bio17	14.5532	0.2039
Bio18	13.0524	0.2899
Bio19	28.8192	0.0024

odaphnia), and four to the subgenus *Daphnia* s.str. Among them, *Daphnia* (*C.*) *lumholtzi* and *D.* (*C.*) *carinata* s.l. are the most commonly reported species, while *D.* (*D.*) *dentifera* and *D.* (*D.*) *obtusa* s.l. have only two records each. *Daphnia* (*D.*) *pulex* was the most frequently reported *Daphnia* s.str. species followed by *D. (D.*) *longispina*. The highest number of species considering both sub-genera was observed at higher latitudes (>25°N) (9 species) and at low and mid altitudes (8 species) and decreased at high altitudes (>5000 m asl) (5 species) (Fig. 2 b,d) and lowlands.

Distribution patterns

The widely distributed *Daphnia* species (both *Daphnia* and *Ctenodaphnia*) showed similar ranges of annual mean temperature and seasonality (Tab. 3; Supplementary Tab. 2). *Daphnia* (*C.*) *carinata* s.l. was seen in localities having a wide range of temperatures and high seasonality while *D.* (*C.*) *cephalata* s.l. and *D.* (*C.*) *similis* s.l. had much narrower ranges of seasonality. *D.* (*C.*) *cephalata* s.l. and *D.* (*C.*) *similoides,* restricted to south India (Fig. 3b), showed similar temperature seasonality ranges. *Daphnia* (*D.*) *longispina* s.l. was observed at a wider range of average annual temperatures. Ranges of annual mean temperature broadly corresponded with the latitudinal and altitudinal distribution pattern seen in both *Daphnia* s.str. and *D.* (*Ctenodaphnia*) (Tab. 3; Fig. 2 a,c).

The highest species number has therefore been reported from higher latitudes and mid altitudes (median value of altitude for the study area is 2500 m) while the trans-Himalayas, the highest altitudinal and lowest temperature zones of the sub-continent seem to be the most impoverished zones, with only two species, *i.e. D.* (*C.*) *tibetana* and *D.* (*D.*) *dentifera* (Fig. 2 a and b, respectively). It was demonstrated earlier that these taxa prefer high altitudes (Manca *et al.,* 1994, 1998, 2006; Möst *et al*., 2013; Ma *et al*., 2015).

Based on temperature, latitudinal and altitudinal distribution patterns of *Daphnia*, three groups of species were observed:

a) Widely distributed taxa belonging to species complexes of both *Daphnia* and *Ctenodaphnia* subgenera*,* widely distributed in Eurasia (both in Palaearctic and Oriental zones): *D.* (*D.*) *pulex* s.l., *D.* (*D.*) *longispina* s.l.*, D.* (*C.*) *magna* s.l., *D.* (*C.*) *similis* s.l., *D.* (*C.*) *lumholtzi*;
b) Elements restricted to the high altitudinal Himalayan region: *D.* (*C.*) *fusca*, *D.* (*C.*) *tibetana* and *D.* (*D.*) *dentifera*;
c) Species restricted to lower latitudes with truly tropical climate (only *Ctenodaphnia*): *D.* (*C.*) *cephalata* and *D.* (*C.*) *similoides*, as also reported by Benzie (2005).

Environmental effects on distribution

Latitude, altitude and almost all bioclimatic variables pertaining to temperature were significant in determining *Daphnia* species distribution while none of the precipitation variables were significant, an unexpected conclusion (Tab. 2). The null hypothesis that all *Daphnia* species and species groups had similar requirements of environmental variables was rejected as per PERMANOVA (permutations=9999, F=8.423, P<0.001) (Supplementary Tab. 3).

The first two CCA axes explained 61.66% of variance (permutations=9999; trace=1.775; P<0.001) (Fig. 4). Altitude correlated positively on the first axis (r=0.72) while almost all the temperature climatic variables correlated negatively with Mean Temperature of Warmest Quarter (r=-0.69) and Annual mean temp (r=-0.67) being the highest. Latitude (r=-0.58) was negatively correlated with the second axis while Isothermality (r=0.54) correlated positively with the second axis.

Distribution of all the species and possible species groups of the sub-genus *Daphnia* positively correlated with latitude, altitude and negatively correlated with tem-

Tab. 3. List of species reported from the Indian subcontinent along with ranges of annual mean temperatures of their respective localities. See literature sources in Supplementary Tab. 1.

Species	Annual mean Temperature range (°C)
Daphnia (*Ctenodaphnia*) *carinata* King, 1853 s.l.	-6.8 to 29.1
Daphnia (*Ctenodaphnia*) *cephalata* King, 1853 s.l.	22.3 to 28.8
Daphnia (*Ctenodaphnia*) *fusca* Gurney, 1906	-1.1 to 26.7
Daphnia (*Ctenodaphnia*) *lumholtzi* Sars, 1885	15.3 to 27.3
Daphnia (*Ctenodaphnia*) *magna* Straus, 1820	11.7 to 28.6
Daphnia (*Ctenodaphnia*) *similis* Claus, 1876 s.lat.	24.1 to 25.8
Daphnia (*Ctenodaphnia*) *similoides* Hudec, 1991	15.8 to 27
Daphnia (*Ctenodaphnia*) *tibetana* (Sars, 1903)	-3.8 to 8.7
Daphnia (*Daphnia*) *dentifera* Forbes, 1893	-1.3
Daphnia (*Daphnia*) *longispina* (O.F. Müller, 1776) s.l.	4.9 to 28
Daphnia (*Daphnia*) *obtusa* Kurz, 1874 emend. Scourfield, 1942 s.l.	13.7 and 15.2
Daphnia (*Daphnia*) *pulex* Leydig, 1860 s. l.	-3.8 to 26.7

perature variables. For the subgenus *Ctenodaphnia*, three groups, based on the groups mentioned earlier, could be singled out, with distribution determined by latitude and altitude. *D.* (*C.*) *cephalata* s.l. and *D.* (*C.*) *similoides* were observed in localities where the variations in the temperatures were less. Conversely, *D.* (*C.*) *tibetana* and *D.* (*C.*) *fusca* were observed in localities having lower mean temperatures and a higher annual temperature variation.

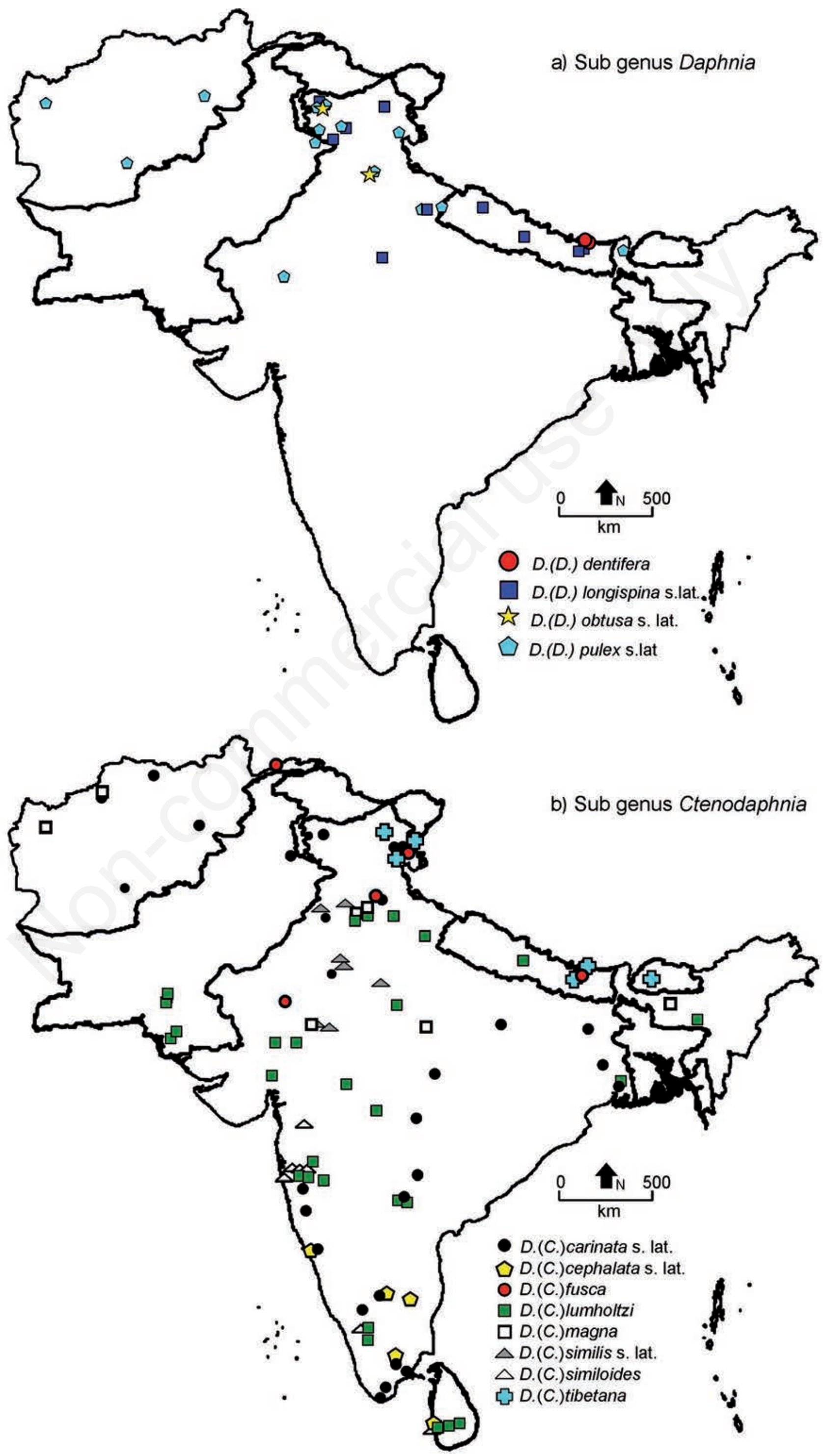

Fig. 2. Distribution of taxa from the a) subgenus *Daphnia* and b) subgenus *Ctenodaphnia.*

DISCUSSION

Confused taxonomy prevents final biogeographic conclusions

With the old concept of 'cosmopolitanism' in zooplankton being replaced by 'continental endemism' or 'regional endemism' (Gomez *et al.,* 2000; Fontaneto, 2011; Marrone *et al*., 2013), biogeographical studies of the components of this community have become more relevant. Cladoceran investigations currently provide many good examples of non-cosmopolitanism in the water fleas (Frey, 1987; Xu *et al.*, 2009).

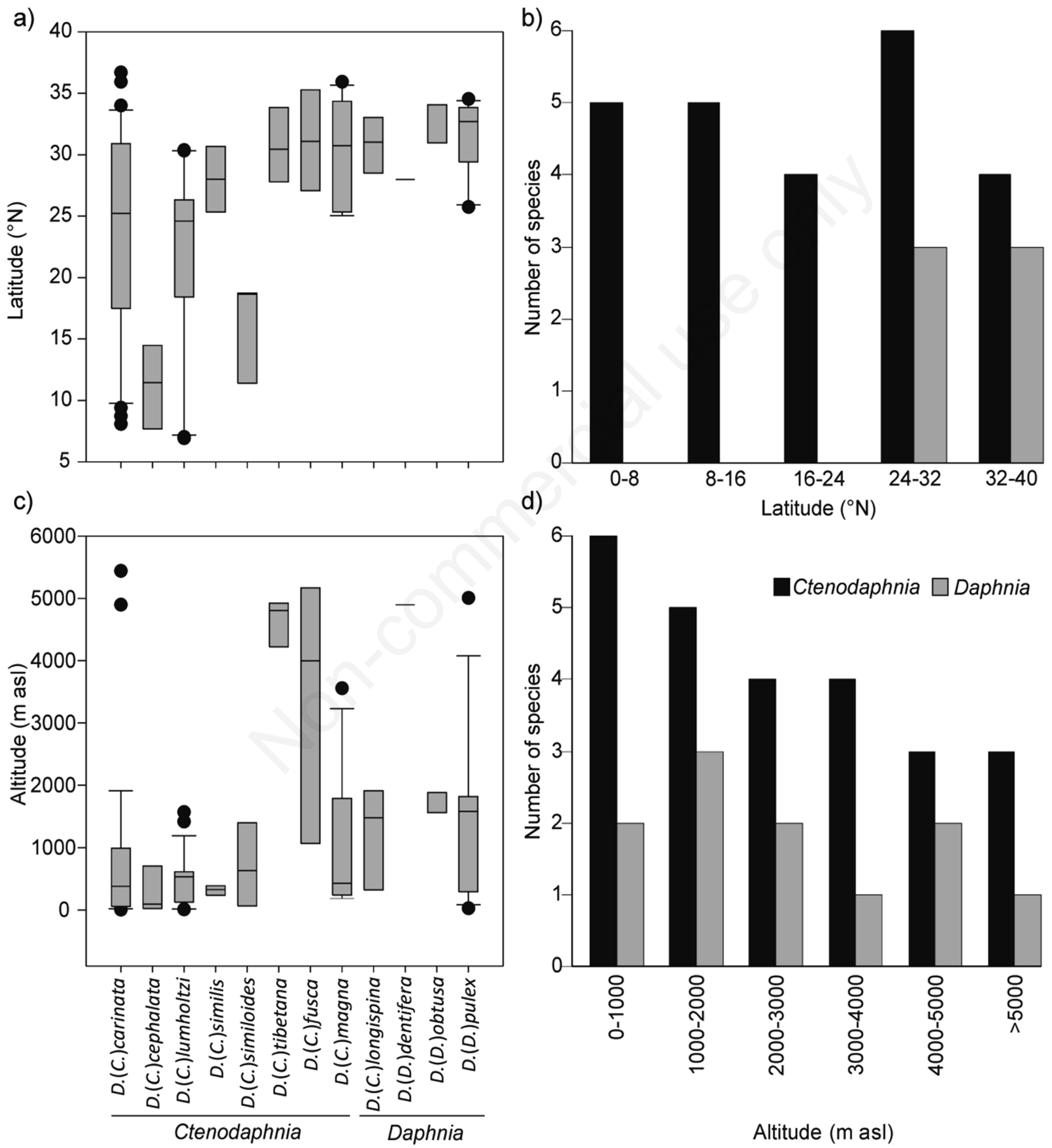

Fig. 3. a,c) Latitudinal and altitudinal ranges of all species. b,d) Total number of species of both sub genera observed across latitudinal and altitudinal classes.

The Indian sub-continent hosts only about 3.5% of the known *Daphnia* species (Popova and Kotov, 2013) with only few known regional endemics like *Daphnia* (*C.*) *fusca* Gurney, 1906 and *D.* (*C.*) *similoides* Hudec, 1991. This situation is most likely an artifact due to: i) a large area of the sub-continent remaining unexplored (Fig. 1), ii) nomenclatural inconsistencies in using of names in different geographical regions (Benzie, 2005; Petrusek *et al.,* 2008), namely a formal assignment of the Indian populations to European taxa without detailed morphological analysis (see Kotov and Taylor, 2010; Chatterjee *et al.*, 2013; Kotov, 2015); and iii) lack of DNA sequence data, which are becoming essential to *Daphnia* taxonomy in the light of the existence of complexes of cryptic or pseudo-cryptic species (Kotov, 2015).

Incomplete taxonomic and faunistic data of the Cladocera has long held up its zoogeographical study (Frey, 1987; Dumont and Negrea, 2002). True cosmopolitans are rare (Dumont, 1994; Crease *et al.*, 2012) while most species and phylogroups are limited in distribution (Havel and Shurin, 2004; Xu *et al.*, 2009). Detailed morphological and molecular studies across various regions have started resolving ranges in a more fine-grained way (Adamowicz *et al*., 2009). Highly prevalent *Daphnia* groups like *D.* (*C.*) *carinata* s.l., *D.* (*D.*) *longispina* s.l. and *D.* (*D.*) *pulex* s.l. are now understood to be species complexes having regionally restricted elements in different regions of the planet (Hebert and Wilson, 1994; Taylor *et al.,* 1996; Crease *et al.,* 2012).

There are undoubtedly more cryptic lineages of *Daphnia* yet to be discovered in Africa and Asia (Adamowicz *et al.,* 2009). A comparative analysis with other areas of the world at this stage can only be tentative. Based on the currently available data (*i.e*., Chatterjee *et al.,* 2013), the Indian species richness is lower than that of China, where 20 species are reported to occur (Xiang *et al.,* 2015) but it is higher than that of South-East Asia (3 species of *Ctenodaphnia*, Hudec, 1991; Korovchinsky, 2013). A thorough re-evaluation of the taxa listed above as 's.l.' could significantly increase the number of Indian species, though, 's.l.' taxa could themselves be also a subject of biogeographic studies (Fontaneto *et al.*, 2011).

Distribution of *Daphnia*

Distribution of *Daphnia* species in the region corresponds to their known preferences in terms of latitude and altitude. Indeed, *Daphnia* (*D.*) *longispina* s.l., *D.* (*D.*) *pulex* s.l. and *D.* (*C.*) *tibetana* are restricted to northern regions while species like *D.* (*C.*) *cephalata* s.l. and *D.* (*C.*) *similoides* occur only at lower latitudes (Benzie, 2005) (Fig. 3 a,b). This implies particular environmental requirements of temperature and restriction to specific altitudes and latitudes altitude and latitude (Fig. 4; Supple-

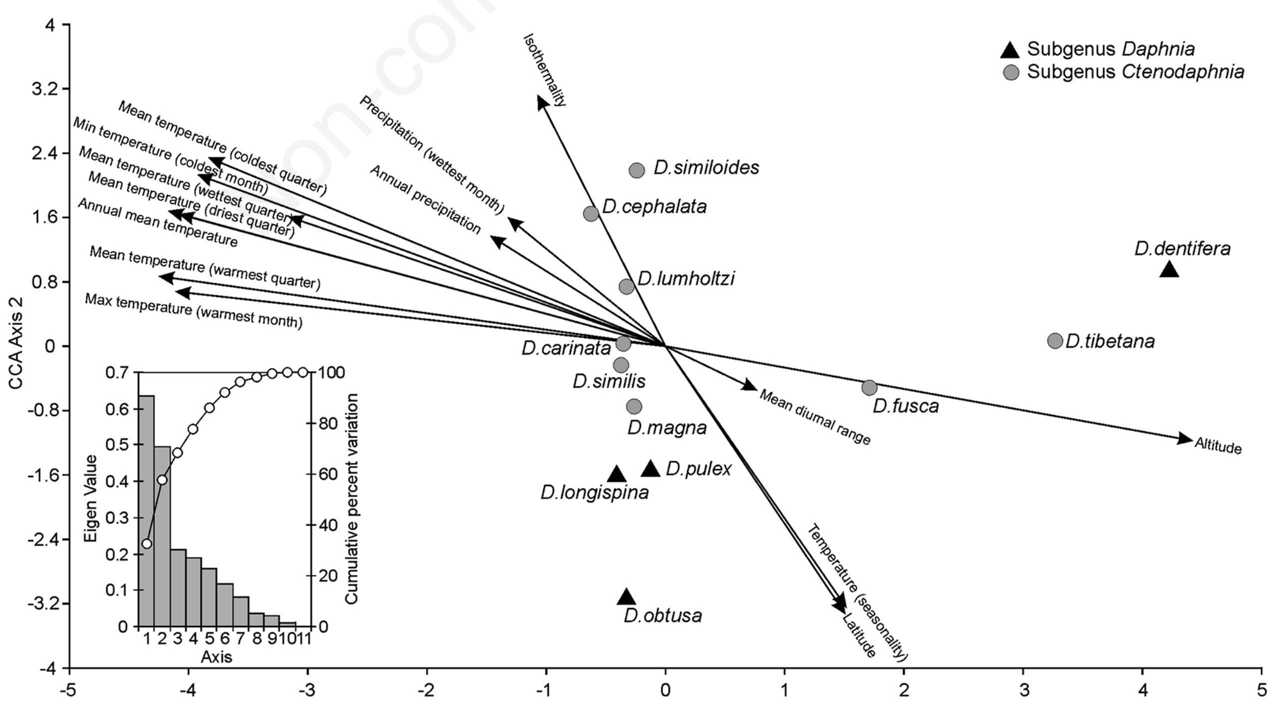

Fig. 4. Canonical correspondence analysis for *Daphnia* species and the environmental variables. Scree plot is provided in the inset.

mentary Tab. 3). Contrastingly, widespread species like *D.* (*C.*) *carinata* s.l. and *D.* (*C.*) *lumholtzi* occurring in a wide range of altitude and latitude were shown to be tolerant to a wide range of environmental (temperature) necessities (Fig. 4), as evident from the CCA analysis. Latitude (along with temperature and altitude) clearly separated the *Daphnia* s.str. species from the *D.* (*Ctenodaphnia*) species, and the high altitudinal endemics from the widely distributed species complexes (Fig. 4). The species richness patterning in subgenus *Daphnia* s.str. observed in the study area further confirmed the bipolar distribution observed in these cladocerans (Dumont, 1980; Popova and Kotov, 2013). Increasing diversity toward the tropics is a pattern shared across a broad range of animal taxa (Hillebrand, 2004; Mittelbach *et al*., 2007) but there are numerous exceptions in insect groups like Ephemeroptera, Plecoptera and crustaceans like Anostraca (Boyero *et al.,* 2011; Rogers, 2014). Observations by Fernando (1980) that all representatives of the subgenus *Daphnia* are restricted to >24° N in the Indian subcontinent can be supplemented by the difference in average temperature between the optimum zones for survival of *Daphnia* (25-50°N) and the true tropics (Korovchinsky, 2006) (for the study area, median annual temperature for 6-24°N zone=25.3°C and for 25-37°N zone=18.05°C). Irrespective of this difference, widely distributed *Daphnia* and *Ctenodaphnia* show overlapping ranges in many temperature and BIOCLIM variables, perhaps explaining why many of the species do not show significantly different temperature requirements (Tab. 3; Supplementary Tab. 2). *D.* (*C.*) *lumholtzi* and *D.* (*C.*) *carinata* s.l. are restricted to regions that are permanently warm or have hot summer (Fryer, 1991) which was not seen to be the case (Tab. 3; Fig. 3 a,c). Mid altitudes (1000-2000 m asl) harbored the maximum number of *Daphnia* species (n=9), while richness decreased with a further rise in altitude (Fig. 2d). The most common elevational pattern observed in species richness is a bell shaped distribution with highest numbers at the middle elevations (Lomolino, 2001). Very high altitudes (>3500 m asl) only sustained species like *D.* (*D.*) *dentifera* and *D.* (*C.*) *tibetana* (Fig. 3 a,b). Decline in productivity and resource diversity, unpredictable weather conditions and more UV radiation at high altitude are some of the possible reasons for lower species richness at high elevations (Cabrera *et al.,* 1997; Dvorkin and Steinberger, 1999).

Various studies, however, provide evidence that mountainous regions in the lower latitudes harbor a number of endemic cladoceran taxa allied to more northern forms (Kotov *et al.,* 2010) and that *Daphnia* species are often observed in the high altitudinal zones at lower latitudes of Africa and South America (Green, 1995; Kotov *et al.*, 2010; Kotov and Taylor ,2010). Such 'Löffler Islands' ('high altitude regions containing cold water habitats with extra-tropical freshwater faunas' (*sensu* Van Damme and Eggermont, 2011) harboring endemic strains of Palaearctic *Daphnia* in Africa (Green, 1995; Van Damme and Eggermont, 2011) are not known at lower latitudes of the Indian sub-continent. Even widely distributed species complexes like *D.* (*D.*) *pulex* s.l., *D.* (*D.*) *obtusa* s.l. and *D.* (*D.*) *longispina* s.l. are not found commonly at higher altitudes regions of lower latitudes. This is an indication that other factors co-influence the distribution of planktonic Cladocera, and hence one should not be too rigid in interpretations of altitudinal distributions (Green, 1995).

CONCLUSIONS

We confirm the existence of three complexes of *Daphnia* in the Indian subcontinent: i) widely distributed species and species complexes; ii) high altitude endemics; and iii) low latitude D. (*Ctenodaphnia*) species. Only few species are found in tropical lowlands, with *Daphnia* s. str. completely absent. Also, we demonstrated that just temperature variation (as a result of altitudinal and latitudinal gradients) influenced *Daphnia* distribution, explaining some of the species groups observed.

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