

RESEARCH ARTICLE

Effect of environment on functional traits of co-occurring water beetles

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Abstract – We investigated trait-environment relationships of co-occurring aquatic Coleoptera specifically true water beetles in anthropogenic ponds from the Western Ghats, India for the first time. Our objectives were to: (1) identify species assemblages; (2) study species traits; (3) study trait-environment relationships of co-occurring species. We analysed 132 samples collected using standardised quantitative method during the years 2016 and 2017. We found 16 significant assemblages using Fager's index, where most of the pairs have body size ratio of 1.3 or more. For example, *Laccophilus parvulus* and *Hydaticus satoi* pair has body size ratio of 3.98, and both are predators, indicating that body size is a function of food size. Moreover, factor analysis revealed three major swimming categories of studied beetles, namely fast swimmers, maneuverers and poor swimmers. Further, the RLQ analysis, and combined approach of RLQ and fourth-corner analysis showed that environmental variables affected species traits. For instance, odonate nymphs and submerged vegetation were positively associated with fast swimmers like *Laccophilus inefficiens* and *Hydaticus satoi*. The assemblage of congeners *Hydroglyphus inconstans* and *H. flammulatus* can be predator-mediated as these beetles showed negative association with odonate nymphs as well as competitive to obtain resource by showing positive association with chironomid larvae. Therefore, the traits studied were important for ecological performances of species in ponds. This study has also highlighted the importance of anthropogenic ponds in the Western Ghats as biodiversity refuges of ecologically unique and evolutionary old major extant lineages of water beetles.

Keywords: Coleoptera assemblages / species traits / body size / functional morphology / RLQ analysis

1 Introduction

Organismal traits are functional characteristics ranging from morphology to behaviour of organisms that affect their ecological performance or fitness and are important for species assemblages (McGill *et al.*, 2006; Violle *et al.*, 2007; Yates *et al.*, 2014; Nock *et al.*, 2016). An assemblage is the smallest functional community of co-occurring species, in space and time, controlled by dispersion and environmental filtering (Trivellone *et al.*, 2017). There is growing evidence from research on extant plants and animals that species traits are crucial for community assembly (*e.g.* Stevens *et al.*, 2003; Heino, 2005; Heino *et al.*, 2005; Barnett *et al.*, 2007; Kraft *et al.*, 2008; Farias and Jaksic, 2009; Ruhí *et al.*, 2009; Stuart-Smith *et al.*, 2013; Vogt *et al.*, 2013; Maglianesi *et al.*, 2014; Hébert *et al.*, 2016; Ochoa-Hueso *et al.*, 2018; Padhye, 2020;

Scotti *et al.*, 2020). These characteristics of organisms decide species response to surrounding environment (response traits) as well as effect of species on ecosystem-effect traits (Nock *et al.*, 2016). Further, species traits can be soft traits that are easily measurable for example, body size, or hard traits that are comparatively difficult to measure for instance, feeding habits or metabolic rates (Nock *et al.*, 2016).

The aquatic Coleoptera have been classified in six ecological groups based on their associations with water (Jäch, 1998; Jäch and Balke, 2008), which had developed as consequences of independent macroecological shifts with 300 Mya of evolutionary history (Short, 2018). One of such coleopteran groups is true water beetles of which adults are submerged or partly submerged (Jäch, 1998; Jäch and Balke, 2008). These beetles occupy various microhabitats (Richoux, 1994; Fairchild *et al.*, 2000), and show a range of behavioural and morphological adaptations to environmental constraints under water (Jäch, 1998; Jäch and Balke, 2008). For instance, body size and shape of these aquatic organisms are adapted for

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swimming compared to their terrestrial counterparts (Ribera and Nilsson, 1995). The swimming abilities of these organisms defined by morphological adaptations affect their performances in aquatic ecosystems such as capturing prey (growth), escaping predators (survival) and finding their mates (reproduction) (Violle *et al.*, 2007; Lancaster and Downes, 2013; Nock *et al.*, 2016). Further, water beetles belong to various functional feeding groups such as predators, algivores, detritivores and herbivores (Fairchild *et al.*, 2000). Moreover, significance of such species traits, namely functional feeding groups and swimming strategies have been studied with respect to community structures of freshwater invertebrates from temperate as well as tropical regions (for example, Heino, 2000; Cummins *et al.*, 2005; Tomanova *et al.*, 2006; Heino, 2008; Masele *et al.*, 2014; Rizo *et al.*, 2017; Padhye, 2020). Additionally, functional feeding groups of lotic macroinvertebrates in Finland (Heino *et al.*, 2005), Italy (Scotti *et al.*, 2020) and neotropical savanna (Ferreira *et al.*, 2017) were shown to have structured their assemblages along environmental gradient in streams. Similar work on lentic macroinvertebrates in Italian ponds revealed associations between habitat structure and functional groups (Bazzanti and Bella, 2004). However, such studies on water beetles are totally lacking from India.

Pond ecosystems are known to hold high freshwater biodiversity with unique species and, are in fact 'migration corridors' for dispersing species (Bratton, 1990; Briers and Biggs, 2003; De Meester *et al.*, 2005; Céréghino *et al.*, 2008; Chester and Robson, 2013; Williams *et al.*, 2004). Further, anthropogenic ponds are small landscape elements, created as a result of quarrying and mining activities (Chester and Robson, 2013; Williams, 2006). Several studies on anthropogenic water bodies across Europe and North America, revealed their potential as biodiversity refuges, however, such ecosystems are less studied from tropics and south Asia (Chester and Robson, 2013; Kulkarni *et al.*, 2015).

Hortal *et al.* (2015) defined seven biodiversity shortfalls based on information gaps. Of these, the Eltonian shortfall relates to limited or lack of knowledge on interspecies interactions or among groups of species (Hortal *et al.*, 2015). These interactions are parts of food chain and food web, in turn ecological networks. Further, the Raunkiaeran shortfall occurs when there is a shortage of information on functional traits (Hortal *et al.*, 2015). The species traits of interacting species determine species performance (Nock *et al.*, 2016). Therefore, both the aforementioned shortfalls are interdependent. In our case lack of information is due to these two shortfalls, namely Eltonian and Raunkiaeran.

Our objectives were therefore: (1) To identify species assemblages in the ponds (to rectify Eltonian shortfall), (2) to study functional morphology of co-occurring species with respect to swimming strategies related to their performance in aquatic ecosystem (to rectify Raunkiaeran shortfall), and (3) to study the relationship between environment and species traits of the co-occurring beetles.

2 Methods

2.1 Study area

Anthropogenic ponds studied for the present work are abandoned stone quarries that are known to have existed for

more than 40 years (personal observation by Ghate). The ponds namely, University pond (18°33'16.92"N, 73°49'26.86"E), ARAI pond (18°31'49.80"N, 73°49'4.82"E) and Dighi pond (18°38'17.16"N, 73°52'39.87"E) face various levels of anthropogenic pressure as they are located in and near Pune city. These ponds vary considerably in area (approximate maximum dimensions measured using Google Earth: University pond 33 m × 27 m; ARAI pond 398 m × 162 m; Dighi pond 374 m × 187 m), and are inundated by rainfall which starts late in June and dry out by April in summer. The substrate of University pond and ARAI pond consists of mud plus rock while the Dighi pond has muddy substrate. The four types of aquatic vegetation were recognised namely, floating (*Nymphoides* sp., *Lemna* sp., *Potamogeton* sp.), submerged (*Hydrilla* sp., *Ceratophyllum* sp., *Chara* sp.), emergent (*Typha* sp.) and semiaquatic (*Ipomoea* sp) in the ponds (Appendix 1).

2.2 Sampling

The minimum number of sweeps to collect maximum number of species were determined using a growth model, the non-linear Michaelis-Menten equation (saturation curve; Appendix 2) as most of the biological models are nonlinear (Motulsky and Christopoulos, 2003, Jukić *et al.*, 2007). The species saturation for sweeps numbers was tested in PAST 3.15 (Hammer *et al.*, 2001).

To identify species assemblages, the ponds were sampled for water beetles using a pond net (1 mm mesh size, EFEGB nets, United Kingdom) during 2016 and 2017. A total of 172 samples were collected using standardised method. Every sample was composed of standardised 15 sweeps in 1 m area along the vegetation bed of sampling point. The time required for net sweeping was 30 seconds. The depth of sampling area varied from 20 cm to 40 cm in the marginal zone. The adults of water beetles were preserved in absolute alcohol. The beetle larvae were excluded because of inadequate literature on Indian aquatic beetle larvae. All ponds were visited twice per month for sampling, however, the beetles were preserved only on the first visit per month to avoid oversampling. On every second visit per month, the beetles were identified using magnifying glass on field and released back to the pond after noting the abundance per species. Out of these 172 samples, beetles were found in 132 samples which were analysed further.

Environmental variables were noted on the day of sampling at each sampling point. The presence/absence data of selected biological variables such as tadpoles, odonate nymphs, chironomid larvae and fish were noted at group level. The reason behind choosing these biological variables is as follows: the adults of predatory beetles are mainly dytiscids of which smaller species actively feed on dipteran larvae (Campos *et al.*, 2004) including chironomids (Aditya and Saha, 2006), while larger species feed on tadpoles and fish (Balke *et al.*, 2004). Another biotic component crucial for niche partitioning in aquatic habitats is odonate predation where odonates dominate open waters while aquatic beetles prefer dense vegetation (Larson, 1990). Additionally, fish predation is known to influence beetle communities (Bendell and McNicol, 1987). Every time, the categorical data of aquatic vegetation was noted before disturbing the pond by

sweeping. The abiotic variables, namely pH, temperature, conductivity, salinity, total dissolved solids were noted on the day of sampling. Phosphate (HANNA HI96717), Ammonia (HANNA HI96733), and calcium hardness (HANNA HI3812) were measured in laboratory using aforementioned photometers and kits (ranges of physicochemical parameters are provided in Appendix 3).

2.3 Species identification

The water beetles were sorted in the laboratory, identified at species level and their abundances were noted. The literature used for identification of beetles is provided in the supplementary section of Sheth *et al.* (2019).

2.4 Functional morphology and functional feeding groups

Morphological variables related to adaptations to swimming were measured as per Ribera and Nilsson (1995). A total of sixteen individuals per species were measured in horizontal position under Lawrence and Mayo stereo-zoom microscope with ocular micrometre. Details of variables are provided in Appendix 4.

The functional feeding group of every genus studied for the current work is based on literature only and appropriate references are presented in Appendix 5. The data on genera *Sternolophus* (Hydrophilidae) and *Canthydrus* (Noteridae) were presented up to family level due to lack of information. (For more information please refer to Merritt and Cummins, 1996; Balke *et al.*, 2004; Ribera *et al.*, 2008; Klecka and Boukal, 2012).

2.5 Data analyses

Fager's index of affinity was calculated as a measure of co-occurrence for the aquatic beetles observed in a species assemblage (Southwood, 1966; Maeda-Martínez *et al.*, 1997). The abundance data were converted to presence/absence. The index was calculated by the formula:

$$IF = \frac{2n_{(1+2)}}{n_1 + n_2}$$

where $n_{(1+2)}$ is the number of joint occurrences of species 1 and 2, n_1 is the total number of occurrences of species 1 and n_2 is the total number of occurrences of species 2.

Factor analysis of morphometry data was performed in SPSS 20 to identify morphometric swimming groups. The data were size-adjusted, and all measurements were used as a percent of total length to avoid the bias that could occur due to its variation. Factor analysis is a model of underlying or latent variables that are responsible for observed variables (DeCoster, 1998). The benefit of this analysis is that it allows testing data suitability and possible number of factors using parallel analysis, before actual analysis. Data suitability was tested using the Kaiser-Meyer-Olkin test which examines sampling adequacy for each observed variable in the model (Norusis, 1986). The sphericity of the correlation matrix was tested using Bartlett's test (Dziuban and Shirkey, 1974).

Parallel analysis was run using SPSS syntax <https://people.ok.ubc.ca/briocconn/factors/nfactors.html> to decide the number of factors to be retained in the factor analysis. The factors were extracted using principal components analysis method (Ribera and Nilsson, 1995). The average score of each species with its standard deviation was plotted in PAST 3.15 (Hammer *et al.*, 2001).

RLQ analysis was performed in RStudio 4.0 (<https://rstudio.com/products/rstudio/download/>) to test the relationship between environmental variables and species traits of water beetles. It is a multivariate analysis that provides a structure out of three tables, namely environmental variables, species abundances and species traits. Data were further analysed by the combined approach of RLQ and fourth-corner analysis. The fourth-corner analysis tests bivariate associations and is complementary to RLQ analysis. Each method has its own drawback when used individually, therefore to nullify those effects the combined approach was used (Dray *et al.*, 2014).

3 Results

A total of 22 species of water beetles belonging to four families namely, Dytiscidae, Hydrophilidae, Noteridae and Halplidae were found in the studied ponds (Tab. 1). The significant assemblages of water beetles were identified (0.4 or more, Maeda-Martínez *et al.*, 1997; Tabs. 2-4). Dytiscids were the most frequent species in the significant assemblages.

The Kaiser-Meyer-Olkin test (0.7) and Bartlett's test ($p < 0.001$) showed that the data are adequate for factor analysis (Dziuban and Shirkey, 1974; Norusis, 1986). The three factors in factor analysis explained 37% (36.64), 19% (19.43) and 12% (11.98) of the total variance with 5.13, 2.72 and 1.68 eigenvalues, respectively (Appendix 6). The analysis revealed five morphometric swimming groups belonging to three main categories viz fast swimmers, maneuverers and poor swimmers that are explained below (Fig. 1), the variable loadings and species scores are provided as Appendices 7 and 8, respectively Appendices 6 to 9 are available as supplementary material.

Group 1: Fast swimmers. These species have flat, narrow body, short transverse head and pronotum, short hind femora and tibiae. The species belong to two subfamilies viz *Laccophilinae* and *Dytiscinae*. The group members are: *Laccophilus flexuosus*, *L. inefficiens*, *L. obtusus*, *L. parvulus*, *Hydaticus incertus*, *H. satoi*, *H. vittatus* and *H. luczonicus*.

Group 2: Globular maneuverers. These species have spherical shape of body, long and wide head, long and wide pronotum, long hind femora and tibiae. The species belong to two tribes viz Hyphyrini and Hygrotini. The group members are: *Hyphyrus renardi*, *H. intermixtus* and *Hygrotus musicus*.

Group 3: Poor swimmers. Body outline discontinuous, long hind tarsi, maximum width and height in more posterior position. The group includes predators and scavengers belonging to family Dytiscidae and Hydrophilidae. The members are *Peschetius toxophorus*, *P. quadricostatus*, *Berosus indicus* and *B. pulchellus*.

Group 4: Convex maneuverers. Short hind tarsi, maximum width and height in more anterior position. These are Noteridae members viz *Canthydrus luctuosus* and *C. laetabilis*.

Table 1. The list of species with their presence/absence per locality and abbreviations.

Species	Abbreviation	University	ARAI	Dighi
Family: Dytiscidae				
<i>Hydroglyphus flammulatus</i> (Sharp, 1882)	Hgfl	1	1	1
<i>Hydroglyphus inconstans</i> (Régimbart, 1892)	Hgin	1	1	1
<i>Hygrotus musicus</i> (Klug 1834)	Hrmu	0	1	1
<i>Hyphydrus renardi</i> Severin, 1890	Hyre	1	0	1
<i>Hyphydrus intermixtus</i> (Walker, 1858)	Hyin	1	1	1
<i>Peschetius toxophorus</i> Guignot, 1942	Peto	0	0	1
<i>Peschetius quadricostatus</i> (Aubé, 1838)	Pequ	0	0	1
<i>Yola indica</i> Biström, 1983	Yind	0	0	1
<i>Laccophilus flexuosus</i> Aubé, 1838	Lfle	1	1	1
<i>Laccophilus inefficiens</i> (Walker, 1859)	Line	1	1	1
<i>Laccophilus parvulus parvulus</i> Aubé, 1838	Lpar	0	1	1
<i>Laccophilus parvulus obtusus</i> Sharp, 1882	Lobt	1	1	1
<i>Hydaticus satoi satoi</i> Wewalka, 1975	Hsat	0	1	0
<i>Hydaticus incertus</i> Régimbart, 1888	Hinc	0	1	0
<i>Hydaticus vittatus</i> (Fabricius, 1775)	Hvit	0	1	0
<i>Rhantus taprobanicus</i> Sharp, 1890	Rtap	0	1	1
Family: Hydrophilidae				
<i>Berosus pulchellus</i> MacLeay, 1825	Bepu	0	1	1
<i>Berosus indicus</i> (Motschulsky, 1861)	Bein	0	1	1
<i>Sternolophus rufipes</i> (Fabricius, 1792)	Stru	0	1	1
Family: Noteridae				
<i>Canthydrus luctuosus</i> (Aubé, 1838)	Calu	1	1	1
<i>Canthydrus laetabilis</i> (Walker, 1858)	Cale	1	1	1
Family: Haliplidae				
<i>Haliplus arrowi</i> Guignot, 1936	Haar	1	0	1

Table 2. The matrix representing species co-occurrences at University pond. Lower part demonstrates the number of times the two species co-occurred (joint occurrences). Upper part demonstrates the Fager's affinity index ($\times 100$). For full names of species, please refer to Table 1.

	Hgfl	Hgin	Lfle	Line	Bepu	Calu	Haar
Hgfl		33.3	40.0	60.0	28.6	57.1	–
Hgin	3		64.3	44.4	26.7	26.6	13.3
Lfle	4	9		40.0	23.5	23.5	11.8
Line	3	4	4		28.6	57.1	–
Bepu	1	2	2	1		50.0	–
Calu	2	2	2	2	1		–
Haar	0	1	1	0	0	0	

Group 5: *Hydroglyphus inconstans*, *H. flammulatus* and *Haliplus arrowi* have low scores for all the extracted factors and hence have not extreme characteristics.

Group 6: *Sternolophus rufipes*, *Rhantus taprobanicus* and *Yola indica* showed complex morphology based on species scores and did not belong to any of the previous groups. Therefore, this group contains miscellaneous species.

The first RLQ axis explained 77.6% of total inertia (Fig. 2A–C; Appendix 9). The descriptors, namely calcium hardness, salinity and presence of chironomid larvae showed significant positive association with the axis. The species positively associated with this axis belong to swimming group 5,

namely *Hydroglyphus flammulatus* and *H. inconstans*. The presence of odonate nymphs and submerged vegetation showed significant negative association with the axis. The species with significant negative association belong to swimming group 1, namely *Laccophilus inefficiens*, *L. flexuosus*, *L. obtusus*, *L. parvulus*, *Hydaticus satoi*, *Hydaticus vittatus* and *Hydaticus incertus*.

The combined approach of RLQ and fourth-corner analysis also showed that calcium hardness, salinity and chironomid larvae have significant positive association with first axis and, odonate nymphs and submerged vegetation have significant negative association with the first axis (Fig. 3A, B, C; Appendix 9).

Table 3. The matrix representing species co-occurrences at ARAI pond. Lower part demonstrates the number of times the two species co-occurred (joint occurrences). Upper part demonstrates the Fager's affinity index ($\times 100$). For full names of species, please refer to Table 1.

	Hgfl	Hgin	Hyin	Lfle	Line	Lpar	Lobt	Hsat	Hinc	Bepu	Bein	Calu	Cale
Hgfl		42.4	9.1	59.1	41.0	8.0	37.0	8.3	8.3	3.3	15.4	6.5	7.4
Hgin	7		–	42.4	21.4	–	50.0	–	–	16.0	26.7	10.0	12.5
Hyin	2	0		–	21.1	–	–	–	50.0	25.0	–	–	–
Lfle	13	7	0		55.2	16.0	22.2	8.3	–	33.3	15.4	19.4	14.8
Line	8	3	2	8		9.0	27.3	–	21.1	38.7	19.0	38.5	18.2
Lpar	1	0	0	2	1		–	40.0	–	11.8	–	–	–
Lobt	5	4	0	3	3	0		–	–	21.7	22.2	14.3	20.0
Hsat	1	0	0	1	0	1	0		–	25.0	–	–	–
Hinc	1	0	1	0	2	0	0	0		25.0	–	18.2	–
Bepu	6	2	2	6	6	1	2	2	2		12.5	26.1	–
Bein	2	2	0	2	2	0	0	0	0	1		–	22.2
Calu	1	1	0	3	5	0	1	0	1	3	0		40.0
Cale	1	1	0	2	2	0	1	0	0	0	1	3	

Table 4. The matrix representing species co-occurrences at Dighi pond. Lower part demonstrates the number of times the two species co-occurred (joint occurrences). Upper part demonstrates the Fager's affinity index ($\times 100$). For full names of species, please refer to Table 1.

	Hgfl	Hgin	Hrmu	Hyin	Peto	Lfle	Line	Lobt	Bepu	Bein	Calu
Hgfl		71.6	24.0	4.8	17.8	41.9	25.5	13.0	59.7	9.3	16.7
Hgin	24		43.2	6.9	25.0	36.7	23.5	6.0	51.9	13.1	17.1
Hrmu	6	8		–	–	31.3	11.8	25.0	48.6	15.4	11.1
Hyin	1	1	0		28.4	–	–	–	–	40.0	–
Peto	4	4	0	1		29.6	–	18.2	6.0	–	–
Lfle	13	9	5	0	4		6.0	14.3	28.6	8.0	6.7
Line	6	4	1	0	0	1		15.4	23.5	–	40.0
Lobt	3	1	2	0	1	2	1		30.3	–	–
Bepu	20	14	9	0	1	7	4	5		–	17.1
Bein	2	2	1	1	0	1	0	0	0		–
Calu	4	3	1	0	0	1	3	0	3	0	

4 Discussion

The present work contributes to rectify the Eltonian and Raunkiaeran shortfalls by studying (1) species assemblages and (2) functional traits of these co-occurring species from Western India using true water beetles as a model system. Here we discuss trait-environment relationship regarding co-occurring beetles in studied ponds. The importance of studied traits of water beetles to perform ecological functions (species performance) in ponds are discussed as follows.

Body size is a soft trait that contains huge information on interspecies interactions which affect structure and dynamics of food webs in ecological networks, and governs a wide array of hard traits that are vital for ecological processes at all levels of biological organization (Woodward *et al.*, 2005; Nock *et al.*, 2016). In this study, when two predatory beetles co-occurred in the ponds, they differed in body size by a ratio of 1.3 or more, except some congeners (Tab. 5). For example, the co-occurring species *Laccophilus parvulus* and *Hydaticus satoi* differ by a size ratio of 3.98. As the body size is a function of food size, these different-sized predators must be preferring different-sized food to minimize competition, and therefore co-exist in the ponds (Woodward *et al.*, 2005; Basset and Angelis, 2007;

Scheffer *et al.*, 2015). The predatory beetles actively capture their prey. These beetles generally have streamlined body to attain fast swimming by minimizing drag forces under water (Ribera and Nilsson, 1995). Both the species are fast swimmers in the aforementioned assemblage, and were found to be associated with submerged vegetation and odonate nymphs (Figs. 2 and 3). Heino (2008) suggested that more prey base can be found by predatory freshwater invertebrates in vegetated areas. Law *et al.* (2019) highlighted the importance of aquatic vegetation for assessing diversity of aquatic beetles, odonates and molluscs in British ponds, as the number of microhabitats increases with the complexity of vegetation (McAbendroth *et al.*, 2005). Therefore, aquatic vegetation is one of the important factors for species niche partitioning and selection of species traits (Larson, 1990; Cooper *et al.*, 2005; McAbendroth *et al.*, 2005). Similar pattern was observed in case of co-occurring hydroporine beetles in Australian aquifers which showed size ratio of 1.6 (Scheffer *et al.*, 2015). These different-sized species may perceive the same habitat differently and hence use it in different ways for predation, shelter and egg laying (Morse *et al.*, 1985; Raffaelli *et al.*, 2000; Law *et al.*, 2019). Additionally, body size is directly related to hard traits like metabolic rates, growth and giving-up

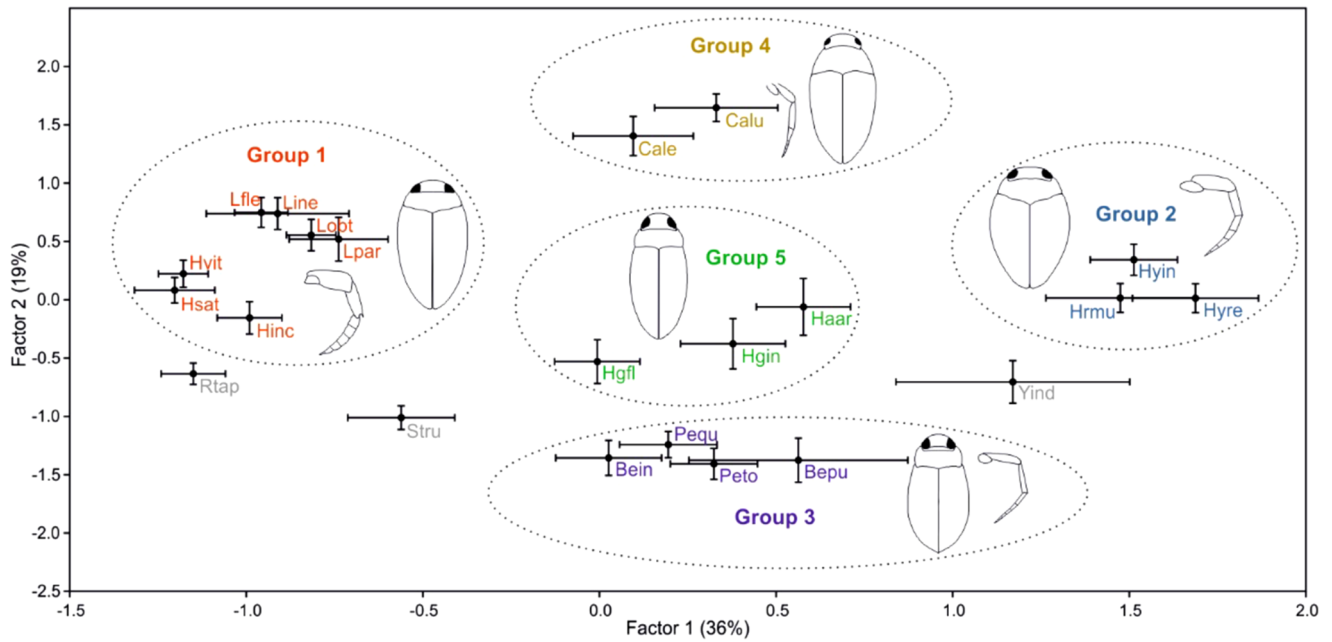


Fig. 1. The factor analysis of morphometry representing average species scores for factor 1 and 2. Morphometric swimming groups of species are shown.

Table 5. The table shows information on functional traits of significant species pairs (co-occurring species based on Fager’s index of affinity). For swimming groups please refer to Fig. 1. For feeding strategies please refer to Appendix 5; P = predator, S = scavenger. Body size ratio = Body size of larger species/ Body size of smaller species in each pair.

Species	Abbreviation	Swimming group	Feeding group	Body size ratio
<i>H. flammulatus</i> - <i>L. flexuosus</i>	Hgfl-Lfle	5 and 1	P and P	1.90
<i>H. flammulatus</i> - <i>L. inefficiens</i>	Hgfl-Line	5 and 1	P and P	1.66
<i>H. flammulatus</i> - <i>C. luctuosus</i>	Hgfl-Calul	5 and 4	P and P	1.33
<i>H. inconstans</i> - <i>L. flexuosus</i>	Hgin-Lfle	5 and 1	P and P	2.50
<i>H. inconstans</i> - <i>L. inefficiens</i>	Hgin-Line	5 and 1	P and P	2.20
<i>L. inefficiens</i> - <i>L. flexuosus</i>	Line-Lfle	1 and 1	P and P	1.14
<i>L. inefficiens</i> - <i>C. luctuosus</i>	Line-Calul	1 and 4	P and P	1.25
<i>B. pulchellus</i> - <i>C. luctuosus</i>	Bepu-Calul	3 and 4	S and P	1.02
<i>H. flammulatus</i> - <i>H. inconstans</i>	Hgfl-Hgin	5 and 5	P and P	1.32
<i>H. inconstans</i> - <i>L. obtusus</i>	Hgin-Lobt	5 and 1	P and P	1.97
<i>L. parvulus</i> - <i>H. satoi</i>	Lpar-Hsat	1 and 1	P and P	3.98
<i>C. luctuosus</i> - <i>C. laetabilis</i>	Calul-Cale	4 and 4	P and P	1.14
<i>H. inconstans</i> - <i>H. musicus</i>	Hgin-Hrmu	5 and 2	P and P	1.54
<i>H. flammulatus</i> - <i>B. pulchellus</i>	Hgfl-Bepu	5 and 3	P and S	1.31
<i>H. inconstans</i> - <i>B. pulchellus</i>	Hgin-Bepu	5 and 3	P and S	1.74
<i>H. musicus</i> - <i>B. pulchellus</i>	Hrmu-Bepu	2 and 3	P and S	1.12

behaviour between large and small consumer species (Basset and Angelis, 2007).

Furthermore, body size is known phenotypic trait to shape communities not only of freshwater and European marine invertebrates (Warwick and Clark, 1996; Woodward *et al.*, 2005; Basset and Angelis, 2007; De Bie *et al.*, 2012) but also vertebrates like birds and mammals (Hutchinson, 1959). This indicates that resource is a main limitation that influences community assembly (Vogt *et al.*, 2013). Thus, body size is one of the important traits for the co-existence of species which is

influenced by environment, and there is a limit to the species similarity to avoid competition (Hutchinson, 1959; Juliano and Lawton, 1990a; Scheffer *et al.*, 2015).

The predation on water beetles caused by odonate nymphs is known to influence niche partitioning of these beetles (Bendell and McNicol, 1987; Larson, 1990). For example, the co-occurring congeners *Hydroglyphus flammulatus* and *H. inconstans* were negatively associated with odonate nymphs in the ponds (Figs. 2 and 3), possibly escaping these odonate predators. Therefore, the coexistence

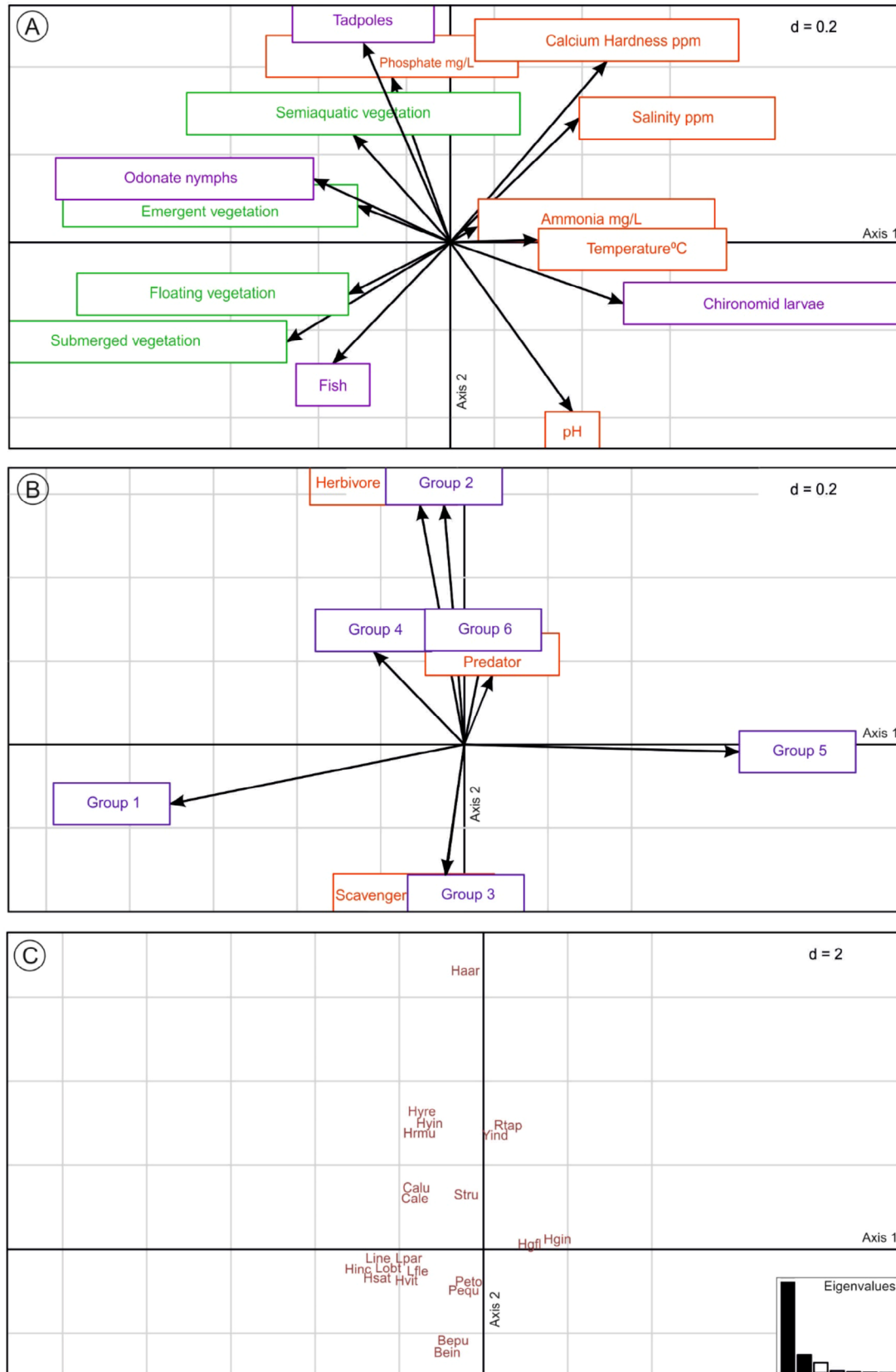


Fig. 2. The plots show first two axes of RLQ analysis ($d = \text{grid size}$). The coefficients presented here were obtained in RLQ analysis (RLQ analysis first performs separate analysis on tables of species, traits and environmental variables, and then obtains coefficients to get linear combinations of traits (species scores) and site scores (environmental variables)).: (A) coefficients for environmental variables, (B) coefficients for traits, and (C) eigenvalues and scores of species (the inset represents eigenvalues). For full forms of species names, please refer to [Table 1](#).

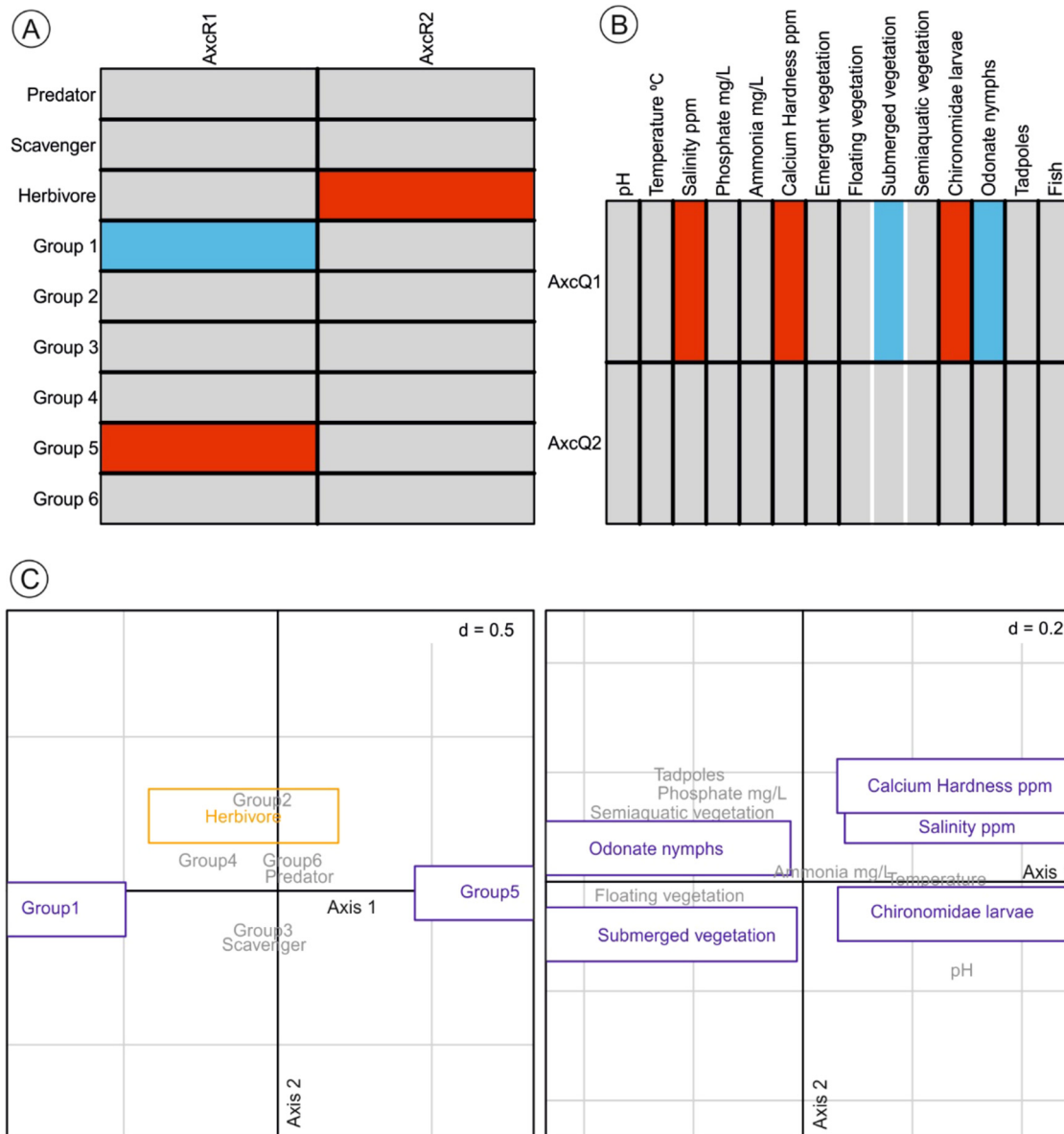


Fig. 3. Combined approach of RLQ and fourth corner analysis. The fourth-corner analysis tests significance of bivariate associations between RLQ axes and traits/environmental variables. The significance level was $\alpha = 0.05$.: (A) Representation of tests between the first two RLQ axes for environmental gradients (AxR1/AxR2) and species traits. (B) Representation of tests between the first two RLQ axes for trait conditions (AxQ1 and AxQ2) and environmental variables. The black lines separate environmental variables and white line separates modalities for categorical variables. Significant positive associations are represented in red, significant negative associations are represented in blue and, non-significant associations are represented in grey. (C) The significant associations with first axis are represented in blue, with second axis in orange and non-significant associations are represented in grey.

of these congeners in the ponds can be justified as a consequence of predator-mediated co-occurrence of the beetles (Caswell, 1978). Additionally, these congeners have body size ratio of 1.32, and were positively associated with chironomid larvae (explained below), suggesting competitive assemblage of congeners for the resource (Kehl and Dettner, 2003).

Furthermore, in this study, a predator (*Hygrotus musicus*) co-occurred with scavenger (*Berosus pulchellus*), where former is a maneuverer and the latter is a poor swimmer (Fig. 1). The species have body size ratio of 1.12. This type of co-existence of similar-sized species belonging to different

swimming and functional feeding groups can be justified as niche-oriented association (MacArthur, 1970; Vandermeer and Pascual, 2006). In such assemblages, the species have different food habits and therefore species can co-exist by reducing resource competition (MacArthur, 1970; Vandermeer and Pascual, 2006). These two beetles perform different ecological functions with respect to their feeding mode and swimming behaviour in ponds.

For motile aquatic organisms, swimming is a behavioural trait to perform fundamental activities (or functions) such as capturing prey, escaping predators and finding their mates (Lancaster and Downes, 2013). These activities of organisms

influence ecosystem functioning (Woodward *et al.*, 2005). For example, in an assemblage of *Laccophilus inefficiens* and *Canthyrus luctuosus*, the first is a flat fast-swimmer while the latter is a convex-maneuverer (Tab. 5). These swimming abilities (traits) will decide how these two species respond to surrounding environment and affect the pond ecological networks (Woodward *et al.*, 2005). Further, the body shape of aquatic animals is an adaptation that controls their swimming abilities, and regulates their velocity and manoeuvrability under water (Daniel, 1984; Cooper *et al.*, 2005; Ribera and Nilsson, 1995). According to Nachtigall (1974) the flat streamlined species are fast swimmers, with high velocity but with decreased ability to turn whilst spherical species are adapted to manoeuvre because body shape and size define the way of swimming (Schmidt-Nielsen, 1972). For instance, body shape is known to influence swimming abilities of freshwater fishes in north America (Seiler and Keeley, 2007). Likewise, in freshwater drift-feeding minnows, deep and short bodied fishes had more success rate in capturing food than fusiform fishes. Therefore, more streamlined species may have higher ability to capture prey *i.e.* performance (Rincón *et al.*, 2007). Further, fin size of the zebrafish, *Danio rerio* affected swimming abilities in laboratory observations (Plaut, 2000). Thus, morphological adaptations help to understand swimming abilities (traits) of aquatic organisms which are important for their performance or fitness (Nock *et al.*, 2016).

The observed swimming traits in this work are similar to the beetles from north-western Spain (Ribera and Nilsson, 1995; Ribera and Foster, 1997). Further, some hydrophilids (detritivores) and haliplids (herbivores) are poor swimmers as these species are not active predators (Balke *et al.*, 2004), therefore lacking abilities for high velocity and manoeuvrability (Ribera and Foster, 1997). Species like *Rhantus taprobanicus* and *Sternolophus rufipes* probably perform complex functions (facultative predators or scavengers). Thus, these two species did not fall into any particular morphometric swimming group in the factor analysis (Fig. 1).

The association between *Hydroglyphus* species and chironomid larvae can be supported by the laboratory study on aquatic beetles from sandpit ponds in Germany, which showed that *Hydroglyphus geminus* feed on chironomid larvae (Kehl and Dettner, 2003). Further, salinity and calcium hardness affected distribution of water beetles in this study. These two factors are known physiological constraints to shape aquatic communities (Hooper *et al.*, 2008; Millán *et al.*, 2011; Arribas *et al.*, 2014; Villastrigo *et al.*, 2018). For example, some Hygrotini (dytiscids) members, hydrophilids and hydraenids have developed physiological tolerance during the evolution as an adaptation to saline habitats (Millán *et al.*, 2011; Arribas *et al.*, 2014; Villastrigo *et al.*, 2018). Additionally, calcium hardness is one of the important factors for the ecological niche of *Daphnia magna* (Hooper *et al.*, 2008).

The anthropogenic ponds in this study harbour locally rare species, namely *Hygrotus musicus* and *Haliplus arrowi* (Sheth *et al.*, 2019). This is in support of earlier work on the freshwater ponds in temperate region (Bratton, 1990; Collinson *et al.*, 1995; Briers and Biggs, 2003; Williams *et al.*, 2004). For example, a comparative study on types of freshwater bodies in Southern England showed that unique species of wetland plants and invertebrates inhabit the ponds

with high numbers (Williams *et al.*, 2004). Thus, anthropogenic water bodies are potential refuges. As mentioned earlier, the species studied here are adapted for aquatic mode of life and these associations of beetles have developed over 300 Mya of evolutionary period (Bilton *et al.*, 2019). Therefore, the ponds we studied hold ecologically unique and evolutionary old major extant lineages, and are subjects of conservation.

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Supplementary Material

Appendix 6: The table depicting total variance explained by extracted components in factor analysis.

Appendix 7: The component matrix showing loadings of variables on three extracted factors.

Appendix 8: The average species scores on Factor 1 and Factor 2.

Appendix 9: The summary of RLQ and, Combined RLQ and Fourth-corner analysis.

The Supplementary Material is available at <https://doi.org/10.1051/limn/2020030>.

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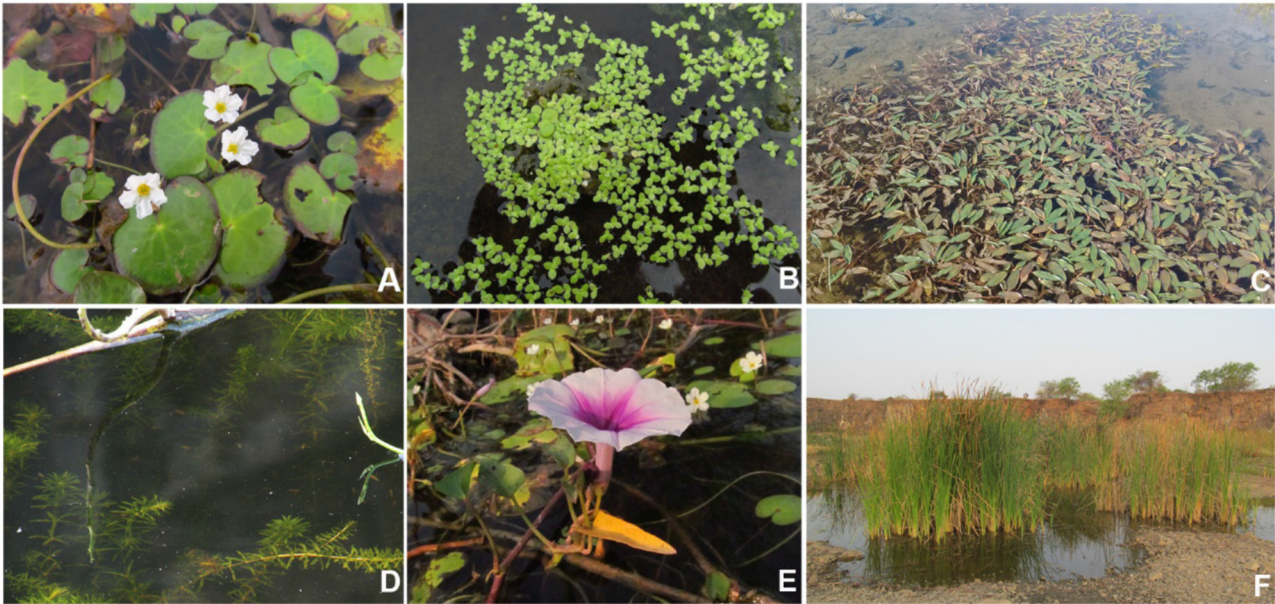
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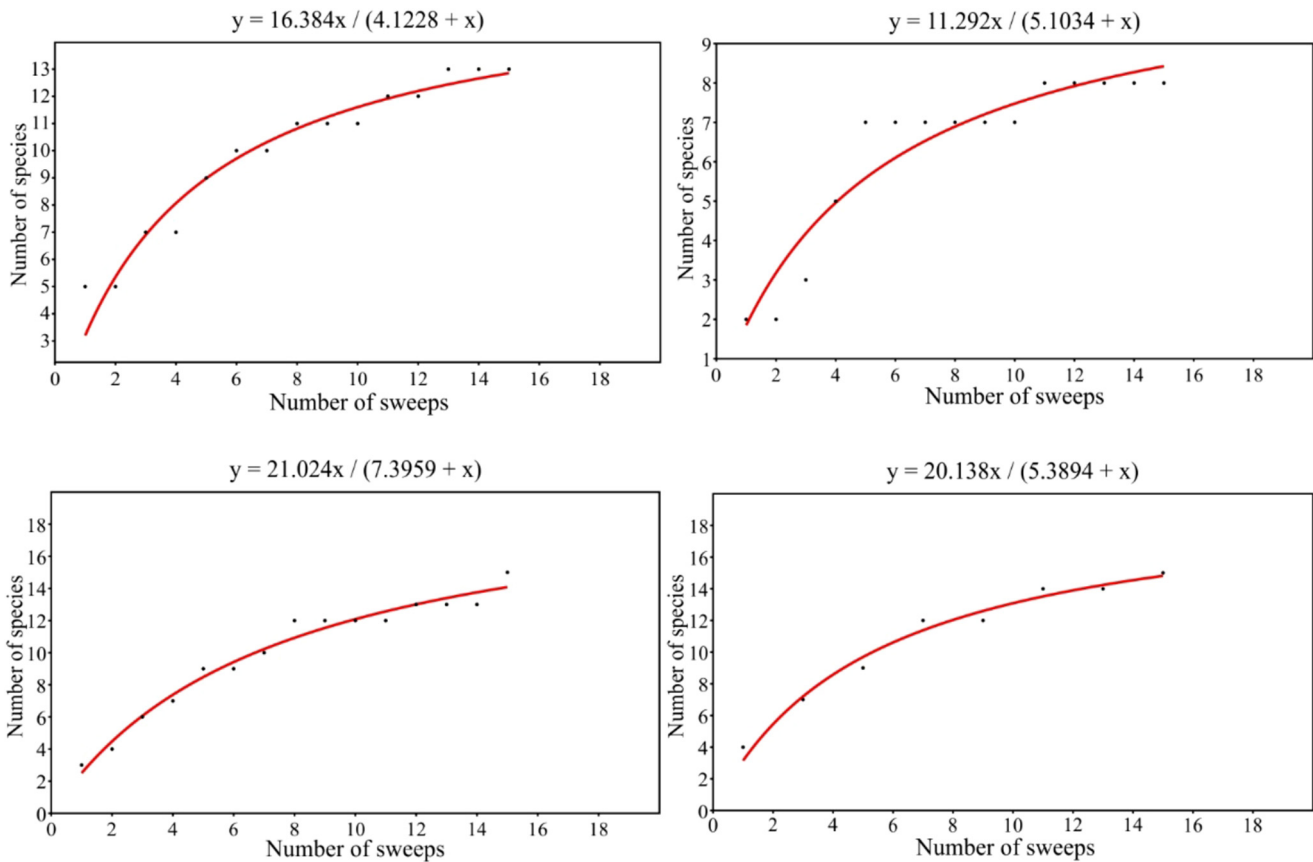
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Appendix 1: Types of aquatic vegetation found in studied ponds (A, B and C) floating; (D) Submerged; (E) Semiaquatic; (F) Emergent vegetation



Appendix 2: Standardisation of number sweeps using Michaelis-Menten equation for quantitative sampling



Appendix 3: The ranges of physicochemical parameters of water per locality during sampling period

	pH	Temperature °C	Salinity (mg/L)	Phosphate (mg/L)	Ammonia (mg/L)	Calcium hardness (mg/L)
University	7.2–8.4	16.6–28.6	163–1390	0–2.4	0.5–27.9	120–231
ARAI	7.8–9.6	15.5–29.2	75.1–538	0–4.5	0–3.8	42–170
Dighi	7.8–10	22.5–34.0	195–337	0–1.7	0–3.9	0–285

Appendix 4: Morphological variables used to identify morphometric swimming groups

Variable	Description
TL	Length of anterior border of pronotum to tip of elytra
HL	Length of clypeal border to posterior side between eyes
HW	Maximum width across eyes
PL	Median length of pronotum
PW	Maximum width of pronotum
MW	Maximum width of body
DW	Distance between level of maximum width to tip of elytra
DM	Distance between end of metacoxae to tip of elytra
FL	Length of metafemur
FW	Width of metafemur
BL	Length of metatibia
RL	Length of metatarsus
EH	Maximum length of elytra (lateral)
MH	Maximum height of body (lateral)
DH	Distance between level of maximum height to tip of elytra

Appendix 5: The feeding strategies of the beetles under this study with appropriate references. *The family level information is provided for the genera *Canthydrus* and *Sternolophus* due to lack of data

Family	Genus	Functional feeding group	References
Dytiscidae	<i>Hydroglyphus</i>	Predator	Kehl and Dettner 2003
Dytiscidae	<i>Hydaticus</i>	Predator	Klecka and Boukal 2012
Dytiscidae	<i>Hyphydrus</i>	Predator	Juliano and Lawton 1990b
Dytiscidae	<i>Hygrotus</i>	Predator	Kehl and Dettner 2003; Heino 2008
Dytiscidae	<i>Peschetius</i>	Predator	Ribera <i>et al.</i> , 2008
Dytiscidae	<i>Laccophilus</i>	Predator	Roberts <i>et al.</i> , 1967
Dytiscidae	<i>Rhantus</i>	Predator	Aditya and Saha 2006; Yee 2010
Dytiscidae	<i>Yola</i>	Predator	Ribera <i>et al.</i> , 2008
Noteridae	<i>Canthydrus</i> *	Predator	Campos <i>et al.</i> , 2004
Haliplidae	<i>Haliplus</i>	Herbivore	Wiggins <i>et al.</i> , 1980; Heino 2008
Hydrophilidae	<i>Berosus</i>	Scavenger	Archangelsky 1999
Hydrophilidae	<i>Sternolophus</i> *	Scavenger	Levesque and Levesque 1995