

## **Benthic community resilience in two differently impacted tropical estuaries: taxonomic vs functional approaches**

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### **Abstract**

Estuaries experience incessant modifications due to various stressors causing shifts in the benthic species community structure and ecosystem functioning. Two tropical estuaries along Northwest India, exposed to varied intensities of anthropogenic perturbations, were sampled seasonally for two consecutive years. Specific aims were to assess, compare and link the macroinvertebrate taxonomic and functional structures, to evaluate the resilience of estuarine benthic ecosystems by employing the multiple-trait approach and to identify major influencing environmental drivers for patterns discerned. Taxonomic and functional compositions in both the estuaries produced varied segregations along the estuarine zones, driven primarily by natural estuarine gradients like salinity and sediment grain size, despite extant anthropogenic stressors. Multiple traits contributed to the variance in benthic functioning. The Biological Trait Analysis (BTA) revealed that both the estuaries had similar trait compositions in the lower zones, while the middle and upper zones of each estuary presented different permutations of traits. The functional complexity at different estuarine sections was influenced by the variability in taxonomic composition and species dominance. However, relationships between Functional Diversity (FD) and species diversity were equivocal, signifying that taxonomic diversity may not be an efficient proxy for benthic functioning. As the zones had differential stressors and disturbance acts as a filter, discrete functional trait profiles of opportunistic traits were visualized along the potentially impacted zones. Thus, the less impacted lower zones had multiple traits, while the mid-upper zones that were subject to both anthropogenic and natural stressors had fewer traits. A more consistent functional structure, higher functional redundancy and substantial proportion of recolonisation traits (small-sized, short-lived, motile forms) suggested better resilience in one study estuary than the other one. Our study advocates that the inclusion of both taxonomical and functional metrics can provide in-depth inferences related to the macrobenthic community resilience and this coupled approach is imperative for effective future management programs.

**Keywords:** Macroinvertebrates; functional traits; taxonomic structure; functional redundancy; estuarine zones; resilience .

## 1. Introduction

Estuarine ecosystems are under the constant threat of multifarious stressors, both natural and anthropogenic, that has led to the degradation of biodiversity, habitat loss and shifts within species communities (Garaffo et al., 2018). This can potentially cause these systems to lose their capacity to maintain its original structure and functions (Walker et al., 2004; Egres et al., 2019). Ecosystems are now being monitored periodically to understand the functioning and the modifications occurring as a consequence of multiple pollutants. In the burgeoning field of biomonitoring, conventional measures to assess changes in the environment have often been based on taxonomical approaches such as species composition, relative abundance of various taxa (Aarnio et al., 2011; Veríssimo et al., 2012) and diversity indices (Pilo et al., 2015). However, studies based solely on species diversity provide rather limited information about ecosystem functioning i.e. it portrays only the identity of species present in the system and thus may be inadequate to monitor the changes in biotic communities (Alves et al., 2014; Bolam et al., 2017). Alternatively, other methods such as linking the faunal changes to environmental parameters often give few clues about the ecosystem functioning (Oug et al., 2012). As such, research focus has recently moved towards including the faunal functional attributes while evaluating the effect of stressors (Veríssimo et al., 2012). Analogous to taxonomic-based approaches, insights regarding what these organisms do within the habitat (i.e. their functional ‘traits’) potentially can improve our understanding of the benthic ecosystem functioning (Bremner, 2008). Ecosystem functioning is an amalgamation of processes, services rendered thereof and resilience to various stressors (van der Linden et al., 2012). Nevertheless, to understand the ecosystem functioning in estuaries, acquaintance of both the taxonomical and functional facets is essential (Elliott and Quintino, 2007; van Hoey et al., 2010). In natural systems such as the estuaries, the benthic structure and function may respond in tandem (Díaz and Cabido, 2001) or independently and thus, linking the two still remains a key challenge (Culhane et al., 2014). The convenience of using macrobenthos in biomonitoring studies have been highly acknowledged in many studies worldwide (Egres et al., 2019). These organisms are also considered as suitable candidates for the assessment of benthic functioning studies since they play vital roles in nutrient cycling, sediment reworking, organic matter decomposition, oxygen and dissolved matter transport (Bremner et al., 2006; Olsgard et al., 2008; Oug et al., 2012).

Earlier studies have mainly focussed on the functional characteristics based on a single trait, for example the feeding behaviour for trophic group analysis (Dolbeth et al., 2003). Although it provides valuable information, it gives a reductionist view of functioning (Veríssimo et al., 2012)

since individual measures (feeding trait) does not account for the functional difference among species within certain groups (Petchey and Gaston, 2002; Xu et al., 2018). Single trait studies also present the disadvantage of missing out on relevant ecological functions performed by organisms (Mancinelli et al., 1998). An alternative approach, which is based on habitat template theory that species' characteristics evolve in response to habitat constraints (Southwood, 1977), is the Biological Traits Analysis (BTA; Statzner et al., 1994), a method proposed for describing ecological functioning (Dolédec and Statzner, 1994; Verberk et al., 2013). BTA is a multivariate approach that combines the structural data of taxa with the information of their functional traits (Tonroos and Bonsdorff, 2012). The multiple trait concept was initiated by Bremner et al. (2003) by taking into account a series of life-history, morphological and behavioural traits (mobility, feeding type, size, life span, reproductive technique etc) of the species present in assemblages as a proxy of their ecological functioning. BTA can be further used to assess the functional diversity, i.e. the breadth of functions performed by species in an assemblage (Petchey and Gaston, 2006). When the species in an assemblage differ greatly in their functional traits, higher values of functional diversity are expected (Garaffo et al., 2018). Hence, this is an advanced step to highlight patterns within ecosystems that are not apparent with traditional taxonomic based methods (van der Linden et al., 2017). Furthermore, trait-based analysis when coupled with functional redundancy can evaluate the stability of ecosystem functioning (Breine et al., 2018). Functional redundancy (FR) was put forth by van der Linden et al. (2012) which is defined as the portion of functional traits shared by the species of a community. FR proposes that the substitution of some taxa that perform similar functions in ecosystems may result in little repercussion on the functional processes (Schmera et al., 2016). Therefore, it is generally considered to be a proxy for the resilience of an ecosystem versus environmental changes (Darr et al., 2014). It is also now understood that ecosystems with high species and functional diversity are stable and can withstand environmental upheavals (Bellwood et al, 2003).

BTA, with its genesis in freshwater and terrestrial waters, is now increasingly being applied in marine waters (Bremner et al., 2003; Veríssimo et al., 2012). Use of trait-based descriptors is flourishing in monitoring studies since it is a suitable measure to describe functional changes in response to anthropogenic disturbance (Bolam et al., 2016). Importantly, it portrays the species ability to cope with stressors which to some extent is governed by its traits (Mouchet et al., 2010) and hence provides a link between taxa, environment and ecosystem processes (Oug et al., 2012). The application of BTA has been undertaken mostly in European estuaries (Veríssimo et al., 2012; van der Linden et al., 2012; 2015; Pilo et al., 2016; Taupp and Wetzel, 2019), whereas studies

applying the BTA approach on macrobenthic communities in tropical estuaries are extremely scarce or restricted to certain areas (van der Linden et al., 2017; Egres et al., 2019; de Souza et al., 2021, all Brazilian estuaries). So far, the functional studies that have been conducted in the Indian marine waters, have concentrated mostly on a single or fewer traits i.e. one (Manokaran et al., 2013; Ingole et al., 2014; Sukumaran et al., 2016; Rehitha et al., 2017; 2019), two (Srinivas et al., 2019), three (Sivadas et al., 2013) and five (Vijapure et al., 2019; Srinivas et al., 2020; Bhowmik and Mandal, 2021) traits. Thus far, only one study has employed nine traits (Sivadas et al., 2020). However, focussing on a solo trait or a handful of traits, may be unrepresentative of overall functioning (Gamfeldt et al., 2008) and ignoring the other functions of the organisms may cause important trends to be missed (Culhane et al., 2014). Therefore, as the estuarine ecosystem functioning is governed by multiple functions; the use of numerous traits could be useful to get a snapshot of the functions governing the estuarine processes.

The estuaries along the Northwest coast of India are subjected to unbridled industrialisation and urbanisation which has imposed deleterious effects on the macrobenthic community structure (Dias et al., 2018; Mulik et al., 2020a). However, little is known on the impact of natural and anthropogenic stressors on the benthic functioning in these estuaries and the resilience of the estuarine benthic ecosystems. In the present study, two tropical estuaries were chosen: Kundalika and Vashishti, both located along the North west coast of India and subjected to anthropogenic perturbations (e.g. dredging, agricultural practices, industrial and domestic wastes etc). This study was intended to gain insights into the macrobenthic communities using the template of taxonomical and multi-trait approach and compare the inferences of both the estuaries, with the assumption that it will pinpoint the key drivers of ecosystem functioning. The main aims were: i) to assess, compare and link the distributional patterns of macrobenthic communities in terms of their taxonomic diversity vis-a-vis functional trait compositions ii) to discern the major environmental factors that structure the macrobenthic diversity and functionality patterns and iii) to evaluate the resilience of the benthic ecosystem of the two estuaries.

In tropical estuaries, the seasonal fluctuations also result in shifts in macrobenthic communities causing defaunation during monsoon followed by recruitment and resettlement of species during the non-monsoon periods (Gaonkar et al., 2013; Dias et al., 2018). These seasonal patterns also depend on the life history, behavioural characteristics and biological traits of organisms (Beche et al., 2006). In addition, the estuarine salinity gradient plays a major role in structuring the macrobenthic communities, where the low saline areas naturally support less diverse species

compared to the higher saline areas of the estuary (de Paz et al., 2008). In turn, the natural estuarine gradients may consequently be expected to result in modifications of the ecosystem functioning (Oug et al., 2012 and references therein). Hence, a salinity preference trait was recently added to the list to overcome the inadequacy of the BTA in estuaries (van der Linden et al., 2017). Therefore, we hypothesise that i) the variability in taxonomic composition of species will be mirrored in their biological traits at different estuarine sections ii) discrete functional trait profiles along the estuarine zones of stress (naturally or anthropogenic-mediated) would be visualized iii) salinity is the major influencing factor for both the taxonomic and functional trait compositions.

## **2. Materials and methods**

### **2.1 Study area**

The study was undertaken in two tropical estuaries located along the Northwest coast of India: the Kundalika (18°31'21.72" N 72°56'01.40" E) and the Vashishti (17°34'06.95" N 73°13'40.11" E) estuaries (Fig. 1). Both estuaries have mudflats and mangroves on their banks. Tides are semi-diurnal in nature and water level varies considerably depending on the tidal state and the distance from the mouth. The seasons in this biogeographical zone are the premonsoon (February to May), monsoon (June to September) and postmonsoon (October to January). The comparative salient features of both estuaries are presented in Table 1.

Both the estuaries are exposed to diverse anthropogenic pressures of varying intensities. At the Kundalika mouth, there is a port and a fish landing centre at Revdanda and another fishing jetty at Agrav. The mid-estuary is subject to dredging activities and acts as an ideal sink for suspended sediment matter. A chemical industrial cluster releases their effluents ( $14000 \text{ m}^3 \text{ d}^{-1}$ ) directly into the estuary in the upper zone. The estuary also receives around  $1400 \text{ m}^3 \text{ d}^{-1}$  of domestic wastes (NIO, 2018). Similarly, Vashishti mouth has the Dabhol port and fishing jetties. The upper estuary receives around  $7000 \text{ m}^3 \text{ d}^{-1}$  of industrial wastewater through a point subsurface outfall near the confluence with the Jagbudi river. This estuary is subjected to sand mining and also receives agricultural wastes (Dandekar, 2010; Nasnodkar and Nayak, 2018). In addition to the industrial waste, the estuary also receives domestic waste of about  $7700 \text{ m}^3 \text{ d}^{-1}$  (NIO, 2018). Although, it is difficult to disentangle the effects of stressors and intensities in estuaries, Kundalika was subjected to higher level of perturbation as compared to Vashishti due to more effluent load and other anthropogenic activities (Table 1).

## 2.2 Sampling strategy and processing

The estuarine segments of Kundalika and Vashishti under investigation were divided into three zones (lower, middle and upper) based on the distance from the sea (Fig. 1). The lower zone (LZ) which has free connections with open sea comprised of 4 stations (1-4) located in and around the estuary mouth. The middle zone (MZ) that is subjected to strong salt and freshwater mixing consisted of 3 stations (5-7). The upper zone (UZ) that receives copious freshwater inputs but subjected to tidal action was comprised of 3 stations (8-10). Totally for both estuaries, eight sampling surveys were conducted spanning a total of 20 stations. Sampling was conducted for two consecutive years from 2014 to 2016, during the premonsoon and postmonsoon seasons. Sample collections were conducted at all stations of Kundalika (K1-K10) and Vashishti (V1-V10) during the ebb tides. During each sampling survey, bottom water samples were collected in duplicates using Niskin bottles. The samples stored in ice post collection were analysed for salinity, dissolved oxygen (DO), suspended solids (SS), phosphate-phosphorus ( $\text{PO}_4^{3-}\text{-P}$ ), nitrite-nitrogen ( $\text{NO}_2^-\text{-N}$ ), nitrate-nitrogen ( $\text{NO}_3^-\text{-N}$ ) and ammonia-nitrogen ( $\text{NH}_4^+\text{-N}$ ) using standard procedures (Grasshoff et al., 1999). Additionally, sediment samples were taken using van Veen grab ( $0.04\text{m}^2$ ) to determine total organic carbon (TOC) and sediment grain size. For TOC, the sediment sub-samples were oven-dried at  $85^\circ\text{C}$  to a constant weight, homogenised in an agate mortar and pestle and analysed using a TOC analyzer (SHIMADZU SSM-5000A series) and expressed as percentage of sediment dry weight. Analysis of grain size was performed using the wet-sieving pipette method (Buchanan, 1984). At each station, four sediment samples (replicates) were taken with a van Veen grab ( $0.04\text{ m}^2$ ) for macrofaunal analyses. Macrobenthic samples were sieved through a 0.5mm mesh and the material retained was preserved in 5% buffered formalin solution containing Rose Bengal stain. In the laboratory, the specimens were sorted, counted and identified to the lowest possible taxonomic level, usually up to species with the help of available identification keys and literature.

## 2.3 Data analyses

### 2.3.1 Biological Trait Analysis (BTA)

To evaluate the functioning of Kundalika and Vashishti estuaries, traits were chosen to encompass the range of important functional attributes of the macrofaunal assemblages. A suite of 11 biological traits sub-divided into 45 modalities were considered informative (Table 2) with respect to life-history ('life span' and 'mode of reproduction'), morphological ('body size' and 'morphology') and behavioural characteristics ('motility', 'feeding mode', 'living habitat', 'bioturbation', 'position in sediments'). Besides, traits such as 'salinity preference' and 'ecological sensitivity' were also

included as the former is important for environmental filtering (McLusky, 1971) and are known to influence the species distribution as well as functional composition (van der Linden et al., 2012) and the latter gives the species sensitivity in response to anthropogenic disturbance (Pilo et al., 2016). The information of these traits for each taxon was extracted through a combination of sources such as laboratory observation (e.g. 'Body size'), a variety of published sources, mostly papers (Macdonald et al., 2010, Queiros et al., 2013; Darr et al., 2014; Jumars et al., 2015), online databases such as Biological Traits Information Catalogue - BIOTIC (MarLIN, 2006), Polytraits (Faulwetter et al., 2014), Encyclopaedia of life (EOL, <http://eol.org>) and AZTI Marine Biotic Index (AMBI) species list of v. June 2017 (presented in the AMBI software program v.5.0, <http://www.azti.es>). For species lacking previously published functional information, we applied the common set of functional attributes of the same genus or other species in the same family, depending on the extent of missing information across the traits.

The BTA procedure as described by Bremner et al. (2003, 2006) was adopted where in, each taxon was assigned to the trait categories depending on their affinity using the fuzzy coding approach (Chevenet et al., 1994). This approach was used to account for multiple trait categories of an individual taxon and seems to be more accurate as it allows the capture of the oscillations in the affinity of a given taxon to the different modalities of a particular trait (Statzner and Bêche, 2010). Each modality was allocated a score range between 0 and 3, where 0 conveys no affinity, 1 or 2 indicates partial affinity and 3 expresses high affinity. Also, a species can exhibit different scores for more than one modality traits. For instance, if a species exhibits all trait modalities equally and there were three categories, then each modality will be assigned a value of 1 so that the total value for that specific trait is 3. If a species showed affinity towards one modality most of the time than the other modalities showing less affinity, then this modality would be assigned a higher score than the others. When information on a certain trait was not found, score 0 was given for all categories. These scores were then standardised to proportions totalling to 1 (or 100%) for each trait in order to give the same weight to each taxon and each trait in further analysis. To carry out the BTA, three different matrices were compiled: i) taxa by station matrix: taxa abundance in each station ii) taxa by trait matrix: traits of all the taxa and iii) trait by station matrix: traits of taxa in each station. The third matrix was constructed by combining the data from the first two matrices, where fuzzy coded scores of each taxon were multiplied by its abundance at each station and the trait categories were summed over all taxa (weighted abundance).

### 2.3.2 Taxonomic and functional diversity metrics

The macrofaunal species abundance data per station were subjected to univariate analysis to estimate the total density ( $N$ ); number of species ( $S$ ); Margalef richness index ( $d$ ); Pielou's evenness index ( $J'$ ) and Shannon-Weiner Index ( $H' \log_2$ ). A shade plot (a.k.a. heat map) was used to represent the relative abundance of most dominant species in each of the three zones of both the estuaries. Prior to analysis, the species frequency was standardised to square-root transformation and only species contributing to >5% of the abundance in both estuaries combined were considered.

Functional diversity (FD, (Petchey and Gaston, 2002) was measured as the expression of functional traits exhibited by the macrobenthic species at each station. The advantage of using FD is that the index is not influenced by species richness (Petchey and Gaston, 2002). Boxplots were created to represent the taxonomic and functional diversity indices. To assess the resilience of the estuarine benthic ecosystem, functional redundancy (FR) was estimated (Kokarev et al., 2017). FR was calculated by the ratio between FD and  $H'$  ( $FD/H'$ ) following van der Linden et al. (2012). One advantage of FR is that it is unaffected by dominant or rare species since it measures trait similarity between species and not individuals (van der Linden et al., 2016). A linear regression of FD on  $H'$  was also tested to examine the relationships between species and functional diversity for both the estuaries separately. The strong relationship with slope close to 1 indicates low redundancy (each species plays a unique functional role), whereas slope close to zero indicates high redundancy (multiple species have similar functional traits) (Kokarev et al., 2017).

### 2.4 Statistical tests

Firstly, analyses of variance (one-way ANOVA) were performed to test for the differences in the environmental variables among estuaries using Statistica 7. Prior to ANOVA, data were first examined for normality using Shapiro-Wilk's  $W$  test followed by log transformation when the assumptions of variance were significantly different. In those cases where the assumptions of parametric analyses (normal distribution of variance) were not met even after log transformation, non-parametric analysis (Kruskal-Wallis test) was applied (Zar 2010). Further, we used a principal component analysis (PCA) to account for the variability between stations in terms of the environmental variables. Ordination of environmental variables was carried via PCA for each of the two estuaries after normalization of log transformed variables. Non-metric multidimensional scaling (nMDS) based on the Bray-Curtis similarity matrix was performed on the fourth-root transformed macrobenthic species abundance matrix to detect the differences in the macrobenthic species composition between the two estuaries. Additionally, nMDS was also performed for individual



estuary to discern spatial and seasonal trends in macrobenthic species diversity. Furthermore, Permutational Multivariate Analysis Of Variance (PERMANOVA; Anderson 2001) was applied to elucidate spatio-temporal variations between estuaries, seasons and zones. Differences in taxonomic diversity were evaluated by performing PERMANOVA on the macrobenthic species abundance matrix and the variation patterns in functional diversity were discerned by using the 'traits by station' matrix. Three factors were considered: 'estuary' (2 fixed levels; Kundalika and Vashishti); 'season' (2 fixed levels; premonsoon and postmonsoon) and 'zone' (3 fixed levels; lower, middle and upper).

Functional patterns of macrobenthos were deciphered by the application of Fuzzy Correspondence Analysis (FCA, Chevenet et al., 1994). In FCA, the trait by stations matrix was ordinated on a multi-dimensional plane using Euclidean distances. Two-dimensional plots were produced for both the estuaries separately. For FCA analysis and estimation of FD, R ver. 3.5.1 open-source software (R Development Core Team, 2018), with 'ade4' (version 1.7-13, Dray and Dufour, 2007) and 'vegan' (version 2.5-6, Oksanen et al., 2011) were used. To identify the predictor environmental variables which significantly explained the variation in macrobenthic assemblages based on taxonomic structure and functional traits across the estuarine zones, multivariate regression analyses based on Distance-based Linear Modelling (DistLM) using the Best selection procedure and Akaike's Information Criterion corrected (AICc) selection criterion were carried out. A distance-based redundancy analysis (db-RDA) plot was produced for the two estuaries separately to provide a visual representation of the significant environmental variables (Anderson et al., 2008) along the estuarine zones. PERMANOVA, DistLM and dbRDA were performed using the software package PRIMER v.7 with PERMANOVA+ add on. All the univariate and multivariate analyses were performed using the software package PRIMER v.7 (Clarke and Gorley, 2015).

### **3 Results**

#### **3.1 Environmental characteristics**

In both the estuaries, salinity and DO gradients were more distinct spatially than seasonally with higher values in the LZ and a decreasing trend towards the UZ (Table 3). Concentrations of nutrients ( $\text{NH}_4^+$ -N,  $\text{NO}_3^-$ -N and  $\text{PO}_4^{3-}$ -P) released from the industries were much higher in Kundalika than Vashishti, signifying the higher level of anthropogenic stress in the former. Elevated concentrations of inorganic forms of nitrogen were present at the MZ and UZ of both estuaries (Table 2). Higher concentrations of SS were observed in the Kundalika as compared to Vashishti, the values being particularly high in the MZ and UZ. The granulometric composition indicated that at both the estuaries, silt was the dominant component at LZ whereas UZ had higher representation of

sand. The  $C_{org}$  content ranged from 1.7-2.6% in Kundalika and 1.2-2.8% in Vashishti and was generally higher during the postmonsoon. The Mann-Whitney  $U$  test indicated that  $PO_4^{3-P}$ ,  $NH_4^{+}-N$  and SS were significantly higher in all the zones of Kundalika than in Vashishti ( $p < 0.01$ ). DO and  $NO_3^{-}-N$  showed high significance in the LZ, while  $C_{org}$  and sediment grain size (sand, silt and clay) were highly significant ( $p < 0.001$ ) in the MZ of Kundalika. In the UZ of Kundalika, only clay was significant ( $p < 0.05$ ). No significant differences were found for the other variables between both estuaries.

PCA ordination plots revealed that the physico-chemical parameters showed clear spatial differences than seasonal between the three estuarine zones for both the estuaries (Fig. 2). The first two axes of the PCA plot accounted for 52.3% of the total variance with 28.3% for PC1 and 24.0% for PC2. The common patterns that emerged from both the estuaries were: (i) the UZ was characterised by lower salinity, DO and higher nutrient concentrations and sand content; (ii) the MZ was clearly a transitional zone influenced by the high salinity of LZ and high nutrients from the UZ; (iii) the LZ was marked by higher salinity, DO, silt content and lower nutrients.

### 3.2 Macrobenthic taxonomic diversity, structure and distribution

Polychaetes, amphipods and oligochaetes together constituted 91-93% of abundance in both the estuaries. The remaining represented the minor phyla (<2%) and were not taken into account in further analyses due to less numbers and missing trait information which could produce a bias in our results. The macrobenthic community (considering only polychaetes, amphipods and oligochaetes) was composed of totally 145538 individuals belonging to 126 species and 73 genera. From Kundalika, 104 species (25988 individuals) were identified and from Vashishti, 85 species (119550 individuals) were accounted for. 32 most abundant species (>5%) in both the estuaries are represented zone-wise in the shade plot matrix (Fig. 3). It was observed that the number of species in both the estuaries decreased towards the UZ. Evidently, more species were present in the LZ of both estuaries which decreased towards UZ. In Kundalika, *Paraprionospio patiens* (32.8%) and *Cossura coasta* (17.9%) were most abundant in LZ; *Nephtys paradoxa* (15.2%) and *Prionospio sexoculata* (10.0%) in MZ; and *Namalycastis senegalensis* (36.5%) and *Pristina* sp. (15.3%) in the UZ. Similarly, *P. patiens* (28.9%) and *Prionospio* sp. (12.7%) dominated the LZ of Vashishti, while the other two zones had high occurrence of the amphipod *Corophium volutator* (MZ - 75.3%, UZ - 58.7%) followed by *Eriopisella sechellensis* (MZ - 8.1%, UZ - 10.2%).

The species number ( $S$ ) and richness ( $d$ ) decreased steadily from LZ to UZ of Kundalika (Figs. 5a and 5b), evenness ( $J'$ ) was lowest at UZ and steady at the other two zones (Fig. 5c). The

Shannon-Weiner diversity index ( $H'$ ) had the highest average values in the LZ ( $2.2\pm 1.1$ ) of Kundalika and lowest at UZ ( $0.7\pm 0.7$ ) (Fig. 5d). In Vashishti, species numbers and richness were higher and comparable at LZ and MZ, whereas UZ demonstrated lower values (Figs. 5a and 5b).  $J'$  indicated a steady decline from LZ to UZ (Fig. 5c). Higher values of  $H'$  were presented in the LZ ( $2.1\pm 0.7$ ) and MZ ( $2.0\pm 0.8$ ) whereas lower values were observed at UZ ( $1.4\pm 0.8$ ) (Fig. 5d) of Vashishti.

The composite MDS plot indicated intra-estuarine segregation of macrobenthic communities of both estuaries though some overlap existed between stations of Kundalika and Vashishti (Fig. 4). The significant difference between macrobenthic taxonomic structure of the estuaries was substantiated by PERMANOVA ( $F=3.55$ ,  $p=0.0001$ ). Around 33 macrobenthic species were restricted to Kundalika, 26 species were present only in Vashishti, whereas 58 species were common between both estuaries. The macrobenthic species distribution appeared to have followed the estuarine gradient in both Kundalika and Vashishti which was supported by PERMANOVA. The factor 'zone' was significantly different for Kundalika ( $F=3.92$ ,  $p=0.0001$ ) and Vashishti ( $F=3.35$ ,  $p=0.0001$ ) estuaries whereas the factor 'season' was insignificant. The zonal clusters for Kundalika estuary in the nMDS plot were well segregated, whereas in the Vashishti estuary, though the LZ stations were well separated, there was considerable overlap between the stations of UZ and MZ.

### **3.3 Macrobenthic functional diversity, structure and redundancy**

The relative compositions of 44 (Vashishti) to 45 (Kundalika) trait modalities belonging to 11 functional traits occurring at the three estuarine zones of both estuaries are represented in Figs. A.1 and A.2. At zonal level, composition of dominant trait modalities of each functional trait varied widely representing the diverse functions of the macrobenthic community. The traits observed in the LZ of Kundalika and Vashishti were similar and the zone was mostly characterized by species that were sedentary, deposit feeders, tube-dwellers, infaunal, large sized, upward conveyors (translocation of sediments towards the surface), soft-bodied, gonochoristic type (separate sexes throughout life), second order opportunists with medium lifespan and affinity for high salinity. Conversely, in the other zones there was only little similarity in the trait categories between the estuaries. The MZ of both the estuaries had few traits in common such as crawlers, deposit feeders and small-sized individuals. Most traits indicated varied trends for instance, the MZ of Kundalika was predominantly free living, tube dwelling, indifferent (species indifferent to enrichment showing slightly unbalanced condition), first and second order opportunistic, large sized infauna, whereas the UZ were populated majorly by burrowers, omnivores, diffusive mixers (vertical and/or horizontal

movement of sediment), large sized, second order opportunistic, free-living infauna. While in Vashishti, the MZ and UZ had similar combinations of trait modalities and were dominated by burrowers, swimmers, and suspension feeders, short lived, surface depositors (deposition of particles at the sediment surface) with exoskeleton, gonochoristic, tolerant epifauna preferring low to high salinities (Fig. A.2).

PERMANOVA based on the trait-by-station matrix data, indicated significant differences between estuaries ( $F=6.35$ ,  $p=0.0001$ ). Significant differences were registered for the factor 'zone' for Kundalika ( $F=5.62$ ,  $p=0.0001$ ) and Vashishti ( $F=5.42$ ,  $p=0.002$ ). However, the factor 'season' was not significant for both the estuaries.

The average FD showed an incremental trend from LZ (Kundalika:  $1.6\pm 0.8$ ; Vashishti:  $1.5\pm 0.4$ ) to MZ (Kundalika:  $1.9\pm 0.7$ ; Vashishti:  $1.9\pm 0.7$ ) (Fig. 5e). However, in the UZ, FD decreased in Kundalika (av  $0.8\pm 0.6$ ) and increased in Vashishti (av  $2.0\pm 0.5$ ).

The ratios between FD and Shannon-Weiner diversity ( $H'$ ) increased along the estuarine gradient from LZ to UZ at both the estuaries (Fig. 5f). The average functional ratios (FD/ $H'$ ) were comparatively lower in the LZ ( $0.6\pm 0.3$ ) and MZ ( $0.8\pm 0.3$ ) of Kundalika and LZ ( $0.8\pm 0.5$ ) and MZ ( $1.1\pm 0.8$ ) of Vashishti. Conversely, the ratio was appreciably higher in the UZ of Kundalika (av  $2.1\pm 4.3$ ) and Vashishti (av  $4.6\pm 9.5$ ). At Kundalika, linear relationship between FD and  $H'$  was visualized (Fig. 6a), whereas there was no relationship between FD and  $H'$  at Vashishti (Fig. 6b).

### 3.4 Biological trait analysis (BTA)

In order to analyse the composite functional composition of macrobenthic communities, FCA ordinations were performed for individual estuaries based on trait-by-station matrix data (Fig. 7). Both the estuaries varied greatly in terms of functional traits and contribution of each trait to the total variability was reflected in the correlation ratios (Table 4).

Kundalika: The first two axes of the FCA accounted for 47% of the total variability of which 30% was explained by F1 and 17% by F2. AMBI EG, morphology, body size and motility were strongly correlated with both the axes. Bioturbation, feeding mode, living habitat were well separated on F1 axis, whereas mode of reproduction was discriminated on F2 axis. In the FCA plane, deposit and suspension feeders, upward conveyers and surface depositors, large sized, second-order opportunistic, tube-dwellers, sedentary soft-bodied organisms were prevalent in the LZ stations (K1, K2, K3, K4) and one MZ station (K5) located on the left side of axis F1 (Figs. A3 and 7a). Omnivores, deposit feeders, diffusive mixers, burrowers, soft-bodied and free-living forms, large-

sized and second-order opportunistic individuals were observed to have affinities to the UZ stations (K8, K9, K10) which were separated on the right side of F1 axis. Deposit feeders, crawlers, free-living, diffusive mixers organisms with medium lifespan prevailed in the MZ stations (K6, K7) placed on the F2 axis.

Vashishti: The first two axes accounted for 46% of the total variability, of which 29% and 17% was explained by F1 and F2 axes respectively. The main traits contributing to the variability of axis F1 were feeding mode, body size, morphology, bioturbation and motility, whereas axis F2 was influenced by life span and AMBI EG. The FCA plane (Fig. 7b) showed that most of the LZ stations (V1, V2, V4) and one mid-estuarine station (V5) were clustered together. Deposit and suspension feeders, large-sized individuals, soft-bodied, upward conveyors, second-order opportunistic fauna with medium lifespan populated this zone (Fig. A4). Species with exoskeleton, surface depositors, suspension feeders, tolerant, small-sized and short-lived forms mostly corresponded with the cluster comprising of UZ (V8, V9, V10), MZ (V6, V7) and LZ (V3) stations.

### 3.5 Taxonomical and functional responses to environmental variables

The marginal tests of DistLM analyses based on taxonomic structure indicated that salinity was the most significant predictor variable that accounted for variability in macrobenthic community structure of Kundalika and Vashishti respectively. The significant predictor variables in Kundalika were salinity, clay and SS, whereas in Vashishti, salinity and  $\text{NO}_3^-$ -N revealed significant variation (Table 5). In the accompanying dbRDA plots, the first two axes explained 100% of the fitted variation for Kundalika and Vashishti (Figs. 8a and 8b). Salinity separated the LZ and MZ from the UZ in both the estuaries indicating its influence on the macrobenthic community. However, in the upper zone, grain size (clay) in Kundalika and  $\text{NO}_3^-$ -N in Vashishti were influential factors for the variation in species abundances.

A considerable portion of the variation in macrobenthic functional structure of Kundalika and Vashishti were explained by the predictor variables of the DistLM analyses based on the functional trait matrix. The overall best model solution was provided by the predictor variables such as salinity, DO and clay in Kundalika and  $\text{NO}_3^-$ -N, salinity, clay and  $\text{C}_{\text{org}}$  in Vashishti respectively (Table 5). The accompanying dbRDA plots showed that the first two axes accounted for 100% of fitted variation of both the estuaries (Figs. 8c and 8d). The distributional patterns in the functional traits in the LZ and MZ of both the estuaries were largely driven by the salinity gradient which was also the case for variation in taxonomic structure. The other fitted variables that explained the functional structure of both estuaries were sediment type, DO and  $\text{NO}_3^-$ -N.

## Discussion

### 4.1 Environmental background

The variations in environmental factors along the spatial gradient i.e. LZ versus UZ were largely evident in Kundalika and Vashishti estuaries. The variability was more pronounced spatially than seasonally especially in terms of salinity, as mostly observed in other tropical estuaries (Dias et al., 2018; Mulik et al., 2020b). The PCA analyses emphasized the zonal differences in both the estuaries with the UZ having elevated levels of nutrients than the other zones. These can be attributed to the anthropogenic inputs in both the estuaries, as there are several industrial complexes located in the hinterland and domestic wastes were also being released (Dias et al., 2018; Nasnodkar and Nayak, 2018; NIO, 2018). Additionally, the Vashishti receives wastes from agricultural practices (Dandekar, 2010) that might have led to the perceptible increase in nitrate concentrations. Both the estuaries showed differences in SS owing to various controlling factors such as freshwater discharge, tidal fluctuations and sediment sources (Rao et al. 2011). However, there are other factors responsible for the high suspended load in the upper Kundalika such as shallow depth, stronger tidal currents and may be partly due to anthropogenic wastes (effluents) (NIO, 2018).

The trend of LZ having higher salinity, DO and low nutrients versus the UZ having low salinity and high nutrients observed in Kundalika and Vashishti has been reported from other tropical estuaries as well (Mulik et al., 2020a, van der Linden, 2017). The effect of seasonality in the study region on the environmental parameters was less defined except for the sediment grain size composition in the UZ of Vashishti, where sand during premonsoon was replaced by silt during postmonsoon. The high hydrodynamic conditions must have favoured the deposition of coarser sediments in this area during premonsoon and with transition from high to low energy during postmonsoon, it might have led to the silt deposition (Volvoikar and Nayak, 2013). The MZ of Vashishti was coarser as it was subjected to the high energy runoff associated with the Tambdi and Jagbudi tributaries that join this estuary at this zone (Nasnodkar and Nayak, 2018). The organic carbon content increased during postmonsoon due to the prevailing silty sediments that have larger surface area to support the accumulation of  $C_{org}$  (Zhou et al., 2007). Although the other zones had other ongoing anthropogenic actions such as fishing port activities, barge movements, dredging, etc. in both the estuaries, pollutants were in minimal concentrations indicating less stress as compared to the UZ. Dias et al. (2018) confirmed that the LZ of Kundalika was only moderately polluted despite the local anthropogenic activities due to the excellent flushing time. The LZ of Vashishti has very good assimilative capacity for pollutants thus, making it less impacted (NIO, 2018).

## 4.2 Selection of functional traits

The major challenges faced while describing the functional trait profiles are the considerable man hours required for preparing the various data matrices and the contradictory information given by different sources, which has also been reported by several authors (Marchini et al., 2008; van der Linden et al., 2012). Another important concern that arises in trait-based studies is the choice of type and number of traits from the large array of existing traits as different selections can portray contradictory perceptions on the ecosystem functioning (Veríssimo et al., 2012). In the absence of an accepted protocol for selection of suitable traits, there is a general tendency to choose traits for which information on majority of benthic taxa are available (Bremner, 2008; Bolam and Eggleton, 2014). There is an unending debate on which and/or how many traits to include in BTA studies, eg. Maire et al. (2015) suggested using >5 traits depending on taxa and focus of the study, Costello et al. (2015) recommended using 10 traits and several other authors (Marchini et al., 2008; Paganelli et al., 2012) suggested the usage of more number of traits to get complete and informative analysis. Bremner et al. (2006) and Pilo et al. (2016) suggested inclusion of all possible traits after careful scrutiny for a comprehensive understanding of ecological functions. However, Jimenez et al. (2016) restricted the traits to 10 numbers which according to them allowed the inclusion of maximum species for assessment. In this study, we collated information on 11 functional traits sub-divided into 45 modalities related to life-history, morphology and behaviour that were widely used in numerous benthic studies, had sufficient information for majority of taxa and which could be easily coded (Liu et al., 2019). The selection of the 11 traits were justified as except for two traits ('salinity preference' and 'position in sediments'), the rest were observed to have contributed significantly to the variation of the first two axes of the estuaries (Table 4).

## 4.3 Macrobenthic taxonomical structure and functional trait profile

Although considerable numbers of common species were encountered in both the estuaries (58 out of 126 spp), differential trends in MZ and UZ were observed in terms of species dominance for instance, the opportunistic polychaetes dominated in Kundalika (72%) as against the predominance of tolerant amphipods (92%) in Vashishti. Major presence of Polychaeta is a common occurrence in Indian estuaries (Mulik et al., 2020a) whereas the preponderance of amphipods in Vashishti was a unique observation for the estuaries of this region. The amphipod *Corophium volutator* contributed largely to the macrobenthic community of Vashishti resulting in higher number of individuals than Kundalika. The LZ of both estuaries displayed similarity in trait modalities of macrobenthos despite having dissimilar species assemblages. Comparatively, lower fluctuations of

salinity in this zone must have resulted in stable conditions mandating similar biological characteristics to survive. Clear intra-estuarine differences in the functional trait profiles were visualized in the MZ and UZ. Similar differential functional patterns at different estuarine zones were reported from a temperate estuary by van der Linden (2012). In general, it was observed that the dominance of trait modalities was generally related to the abundant species occurring in the respective zones. For instance, the similarity in macrobenthic taxo-functionality between the LZ of both estuaries could be attributed to the equal dominance of the opportunistic *Paraprionospio patiens* in this zone, resulting in similar functional attributes. The functional trait groups were very distinct at the MZ and UZ of Kundalika due to the presence of different combination of species in the respective zones; more sensitive types being prevalent at MZ and only opportunistics dominating the UZ. The MZ (69.4%) and UZ (80.2%) of Vashishti indicated similar trait matrix because of the analogous dominance of the amphipod, *Corophium volutator* in both zones. Thus, the spatial effects on the functional trait structure may be explained by the distributions of individual species and their consequent trait differences (Heino, 2005; Zhang et al., 2018). Decrease in functional diversity due to the dominance of a taxon was reported by Llanos et al. (2020). Also, the removal or addition of a species may result in the reduction or addition in the number of traits of the community (van der Linden et al., 2016). The functional ratios were significantly negatively correlated with evenness ( $J'$ ) values in both estuaries which further strengthened the argument that species dominance was detrimental to functional redundancy. Thus, our first hypothesis was proved that the variability in taxonomic composition and species dominance could potentially influence the functional composition at different estuarine sections as well.

#### **4.4 Linkages between taxonomical and functional diversity: implications on benthic community resilience**

The resilience of an ecosystem is dependent heavily on more species of differing sensitivities undertaking similar functions, which enables it to withstand various perturbations even after the loss of some taxa. Taxonomic analyses revealed that the macrobenthic communities appeared to follow a continuum of higher species diversity at LZ to lower diversity at the UZ (Chainho et al., 2007; Dias et al., 2018). However, in terms of functional diversity, both estuaries displayed contradictory trends wherein, Kundalika followed a decreasing pattern from LZ to UZ mirroring the taxonomical trend whereas stable FD with slight enhancement at UZ was observed at Vashishti. The important functional attribute is that as the ratio of FD to species diversity increases, the functional redundancy (FR) decreases and vice versa (van der Linden et al., 2012). Lower FR implies diminished ecological



redundancy, resulting in loss of unique traits and impaired functioning (Calapez et al., 2018). Distinct trends of FR were revealed in both the estuaries. Low FR indicating that the constituent species had unique functional roles was observed at the UZ of Kundalika and Vashishti. The low degree of redundancy implies that there may be loss of functions when species diversity declines (Micheli and Halpern, 2005) as few species occupy the available functional niche having fewer traits in common (van der Linden et al., 2012; Kokarev et al., 2017). Conversely, high FR was signalled at the LZ and MZ of both estuaries which indicated that several species performed similar roles, enabling ecosystem functions to be maintained despite loss of species.

Overall, the Kundalika displayed an incremental linear relationship between FD and species diversity exhibiting low redundancy unlike the Vashishti. Low FR makes the ecosystem less buffered and thus more susceptible to species losses or structural shifts caused by environmental changes (Liu et al., 2019). This is in line with other similar observations carried out by several authors in various ecosystems (Kokarev et al., 2017; Liu et al., 2019). The Vashishti showed no relationship between FD and species diversity regardless of the differential structural and functional trends in the zones. This signalled that increasing species turnover did not result in increased functional diversity, in all probability due to trait convergence. High FR ensures the relative independence of community functions from species turnover over space and/or time (Liu et al., 2019). As such, FR is of significance in the assessment of various stressors in an ecosystem, as it can confirm the systems' stability (resilience and resistance) against the loss of functions following the decline in species diversity (Mouillot et al., 2014). Our results showed that although the LZ and MZ indicated low ratios, Vashishti demonstrated stability between FD and species diversity when considered as a whole. This potentially means that Vashishti had higher resilience against perturbations than Kundalika. This result has the caveat that higher FR alone does not signify better functioning. Overt FR can result in functional weakness in the sense that when many species excessively subscribe to small number of functions, the ecosystem will face a loss of several other critical functions (Mouillot et al., 2014). Therefore, FR and FD are both equally important for the sustenance of ecological processes of the estuary. In this case, Vashishti had slightly higher FD ( $1.8\pm 0.5$ ) than Kundalika ( $1.4\pm 0.6$ ). Resilience is often higher in communities composed of relatively small-sized and short-lived fauna as these types recolonise degraded sites fastest (Breine et al., 2018). The Vashishti had a higher proportion of small-sized short-lived forms (r-strategists) relative to Kundalika which could contribute to its improved resilience. Recovery processes are dependent on the available number of motile organisms that can potentially recolonise zones facing species loss (Gogina et al., 2014). Vashishti had lower proportion of sedentary types and higher representation of crawlers and

swimmers at MZ and UZ than Kundalika that is expected to promote recovery of assemblages in these areas, in case of species loss. Proportional representation of various trait modalities was more consistent at the MZ and UZ of Vashishti signalling stable functional structure (Figs. A.1 and A.2). Previous studies have found taxonomic diversity to be correlated with FD, thus proving to be an effective surrogate for the latter (Culhane et al., 2014; van der Linden et al., 2016). However, in this study only Kundalika followed this pattern whereas in Vashishti, the functionality was unrelated with diversity indicating disparate linkages between species diversity and FD. This implies that species diversity index may not serve as a dependable proxy for FD universally and thus incorporation of FD is very much essential to have a holistic overview of the mechanisms governing ecosystem functioning.

#### **4.5 Biological Trait Analysis (BTA)**

The FCA analyses affirmed that several traits contributed to the variance in benthic ecosystem functioning displaying considerable functional heterogeneity. The infaunal species dominated in all the zones of Kundalika and the LZ of Vashishti. Epifauna dominated in the MZ and UZ of Vashishti, dictated by the high dominance of amphipod *C. volutator*. Although the traits that governed the functional distribution varied widely between the two estuaries, the most common traits that contributed to the variability along the first (the major) axis were 'feeding mode', 'bioturbation', 'body size', 'morphology' and 'motility'. The importance of these traits has been highlighted in other regions worldwide (eg. Papageorgiou et al., 2009; Otegui et al., 2016; Wouters et al., 2018; Vijapure et al., 2019). All 45 modalities included in the study were displayed at least in one zone of both estuaries which indicated considerable resource partitioning. Better resource partitioning encourages species co-existence and averts competition (Alexandridis et al., 2017).

Higher feeding diversity in the LZ of Vashishti and MZ of Kundalika signified the availability of miscellaneous food sources in the area thus supporting different trophic pathways (Sigala et al., 2012; Rehitha et al., 2017). It is possible that the higher species diversity at these zones resulted in more individuals that subscribed to multiple feeding methods indicating myriad carbon sources. The good mangrove cover at the LZ and MZ of the estuaries also probably added to potential sources of food (Kathiresan, 2012; Abrantes et al., 2015). The LZ were also characterised by the even distribution ( $J' \geq 0.7$ ) of species which favoured different traits indicating functional heterogeneity. Similarly, the occurrence of a greater number of trait modalities in the LZ of both estuaries, including sensitive traits (large sized, sedentary) was ascribed to the stable environment preferred by the diverse species despite the zone being subjected to various perturbations. In the MZ

of Kundalika, the species partial to varied modalities co-existed. In this zone, more sensitive species (EG I, II, III) were present as compared to other zones which implied that the area was only moderately affected. Gonochorism was the prevalent mode of reproduction in all zones of both estuaries. The gonochoristic species are generally characterized by the higher population growth rate as they have the advantage of attaining sexual maturity early, allowing them to carry out only one function and produce one type of gametes (Prevedelli et al., 2006). In Kundalika, organisms indicated a shift in body size from medium to large size in the UZ despite the zone being more impacted than the other zones. The unforeseen prevalence of large sized traits in the UZ of Kundalika could be attributed to the dominance of the opportunistic polychaete, *N. senegalensis* ( $\geq 92\%$ ). Besides being tolerant to various stressors, *N. senegalensis* are known to have affinity for low salinity, thus restricting their presence only to certain salinity zones (Mulik et al., 2020b). The overall dominance of the nereid (*N. senegalensis* in this study) can trigger a swing in the proportion of certain trait modalities (larger species, omnivores, diffusive mixers and second order opportunistic free-living forms), possibly masking other important modalities (Breine et al., 2018). The MZ and UZ of Vashishti had a similar set of functions due to the overall dominance of the amphipod *Corophium volutator* ( $\geq 77.5\%$ ) which were characterised by small size, short lifespan, surface depositors, burrow-dwellers, low-high salinity affinity and tolerant to stress. A study conducted by Bolam et al. (2016) reported high dominance of surface depositors and diffusive mixers in dredged material disposal sites and suggested that these traits can make alterations in the sediment bed to regenerate nutrients via enhanced biotic activity (Biles et al., 2002). It has been reported that the high representation by species with short lifespans was an indication of disturbance and unstable conditions (Veríssimo et al., 2012). Comparatively, in this study Vashishti MZ and UZ had high presence of short-lived fauna than Kundalika which was more impacted. However, the short-lived modality that was predominant at Vashishti was due to the preponderance of the amphipod, *Corophium* spp at these areas. However, this is a known tolerant (EGIII) organism whereas *N. senegalensis*, a second-order opportunistic (EGIV) polychaete contributed to medium-lived modality at the stressed zones of Kundalika. The amphipod *C. volutator* was present only in the MZ and UZ of Vashishti where it flourished despite the presence of high nutrients in the water column. This could be attributed to its high tolerance to pollutants and preference of variable salinities (De-Bastos and Hill, 2016). Also, their burrowing nature which facilitates avoidance of the polluted sediment by choosing more desirable sediment (Okladen et al., 1984) probably helped them thrive in the area. A study conducted by de-la-Ossa-Carretero et al. (2012) in sewage areas off the Castellon coast, Spain

reported that amphipod species including *C. volutator* with feeding behaviour such as deposit and suspension feeders were less sensitive to sewage disposal and are even able to increase in abundance.

Habitat specific environmental filtration was indicated in both estuaries in the form of traits that are more frequently expressed as a result of better adaptability to the local environment and its stressors (Zhu et al., 2020). Overall, r-strategist traits (deposit feeding, small sized, burrowers, short-medium lifespans, diffusive mixers, surface depositors) were majorly visualized with some representation of sensitive characteristics (suspension feeding, large sized, long lived, upward and downward conveyors) in all zones of both estuaries. The prevalence of opportunistic traits is expected in an estuarine environment as an adaptive measure to the constant state of flux. The intra-zonal differences in functional trait assemblages may be attributed to the complexity of environmental factors that were quintessentially estuarine. The mosaic of functional attributes was resultant of a combination of factors, i.e. the LZ were away from polluting sources in the UZ but were influenced by local perturbations. Additionally, the functional composition was probably heavily influenced by the sediment texture (Paganelli et al., 2012; Breine et al., 2018) i.e. predominantly coarser texture in upstream areas supporting opportunistic characteristics. In most of the tropical estuaries, the upstream is composed of coarser sediments due to river runoff and tidal action which transports the finer sediments towards downstream (Rao et al., 2019) which was observed in our study as well.

The functional trait matrices of MZ and UZ of the two estuaries were clearly dictated by the extant distinct species assemblages. Thus, these zones in Kundalika where opportunistic polychaetes and oligochaetes proliferated, the major functional characters established (omnivores, deposit feeders, free living, small-large sized, medium lifespans, diffusive mixers, EGIV and V) were characteristic of these two groups. In contrast, similar zones in Vashishti demonstrated a set of functional attributes of amphipods (deposit and suspension feeders, burrowers, small-sized, short-lived, surface depositors and EGIII). Several authors (Villnäs et al., 2011; van der Linden et al., 2012; Veríssimo et al., 2012) have confirmed that small size and short longevity are typical traits that occur in stressed habitats which also coincide with the Pearson and Rosenberg, (1978) model. Similarly, other traits that indicate disturbance in an area include surface depositors and diffusive mixers (Bolam et al., 2016), deposit feeders, medium lifespan, crawlers (Pilo et al., 2016), burrowers (Papageorgiou et al., 2009), omnivores (Wolff, 1973), burrow and tube-dwellers (Okladen et al., 1984; Hu et al., 2019), tolerant, first and second-order opportunistics (Borja et al., 2000; Vinagre et al., 2017). Results of our study were contrary to these expected trends and generalizations as the

above characteristics were observed more frequently in the less impacted Vashishti than the more polluted Kundalika. This occurred due to the dominant presence of amphipods, an EGIII group. Conversely, the 'large size', 'long-lifespan' and 'free living' traits of nereids does not fall under the anticipated opportunistic trait category, despite their prominent presence in the impacted UZ of Kundalika. Hu et al. (2019) reported the unexpected presence of 'large size' traits in disturbed zones and attributed it to the surplus food available in the form of organic carbon. Bolam et al. (2016) observed higher bioturbatory faculties and long-lived organisms in stressed zones relative to reference stations contrary to expectations. Breine et al. (2018) emphasised that large species generally tend to belong to long living modality and coarser sediments harbour more free-living forms, thereby causing diffusive mixing. As large sized, long-lived opportunistic nereids were more representative of stress than small sized short-lived amphipods, it was concluded that the ecological sensitivity may be the important functional trait to consider while evaluating stress. The AMBI ecological groups merge many traits into one ecological trait according to the sensitivities of the species (Marchini et al., 2008; Paganelli et al., 2012), thus serving as a key discriminatory trait to recognise any sort of disturbance. In this case, the amphipods being more sensitive were indicative of a moderately affected area. In Kundalika, apart from 'body size', 'living habitat', other traits displayed by the polychaetes were opportunistic in nature. Although, more of opportunistic traits were expected in the impacted Kundalika estuary, it might be possible that the functional assemblages were determined by intra-estuarine gradients than by inter-estuarine (van der Linden et al., 2017).

The UZ of the estuaries had both natural (low salinity) and anthropogenic (effluent) sources of stress which was observed to extend to the MZ (Table 3). In these two zones, the functionality of species displayed a combination of opportunistic trait modalities (e.g. 'deposit feeders', 'omnivores' 'small size', 'short or medium' lifespan, 'surface depositors', 'burrow dwellers', 'crawlers', 'diffusive mixers', 'tolerant', 'second-order and first-order opportunistics) that differed from the LZ (Figs 6b and 7b). Thus, the BTA allowed the distinct segregation of station clusters based on functional trait matrices along the estuarine stress gradient, thus addressing our second hypothesis.

#### **4.6 Effect of environmental variables on taxonomic and functional structure**

Taxonomical and functional patterns mirrored each other in the dbRDA plots with sites discriminating as per the salinity gradient. Many studies have also indicated salinity as the crucial factor influencing the functioning of macrobenthic communities (Dauvin, 2008; Nunes et al., 2008; van der Linden et al., 2012). Sediment composition was the other factor that mostly influenced the taxonomy and functioning of macrobenthos of both estuaries. It is already established that sediment

granulometry plays an important role in structuring macrobenthic community taxonomy and functioning (Lin et al., 2016). The role of sediment type is important for the species distribution which directly can have implications on their functions and therefore, the ecosystem functioning (Tillin et al., 2006; Otegui et al., 2016; Breine et al., 2018). The sand component at Vashishti was appreciably higher than Kundalika which probably promoted the significant abundance of suspension feeders in the estuary. SS was higher in Kundalika which had a higher proportion of fine sediments and may have influenced the taxonomical patterns particularly in the MZ and UZ due to the smothering and clogging effects on organisms in this estuary (Rehitha et al., 2017; Al Usmani, 2019). Finer sediments can result in higher re-suspension due to estuarine hydrodynamics affecting the feeding modes of resident benthos (Snelgrove, 1999). This could be another reason that suspension feeders were less represented in Kundalika than Vashishti.

Besides the common factors of salinity and sediment texture, the other significant factors indicated for functioning in Kundalika was DO whereas for Vashishti they were  $\text{NO}_3^-$ -N and  $\text{C}_{\text{org}}$ . It is possible that  $\text{C}_{\text{org}}$  had influenced the functional attributes in tandem with sediment types as its distribution is primarily determined by the grain size (Rao et al., 2019). Sedimentary character and  $\text{C}_{\text{org}}$  as major influential factors of functional trait composition of macrobenthic communities have been reported previously (Nasi et al., 2018; Hu et al., 2019). The lower salinity zones (MZ, UZ) of Vashishti also were sites of higher  $\text{NO}_3^-$ -N; in Kundalika the oligohaline UZ was a low oxic zone. Consequently,  $\text{NO}_3^-$ -N indicated a significant inverse relationship with salinity in Vashishti whereas DO was positively correlated with salinity in Kundalika. Hence, it is possible that DistLM indicated  $\text{NO}_3^-$ -N and DO as major variables due to its co-existence with low salinity making it difficult to discern the confounding effects of these variables influencing the benthic patterns in both estuaries. Such scenario is common in tropical estuaries wherein the 'Estuarine Quality Paradox' comes into play which makes it difficult to discriminate between natural and anthropogenic stressors (Dauvin, 2007; Mulik et al., 2020b).

The abiotic variables explained higher percent of variance in functional than taxonomic structure due to the result of environmental conditions that sort species to coexist in particular communities via specific set of traits but not species identity per se, giving credence to the habitat templet theory (Townsend and Hildrew, 1994; Li et al., 2019). These traits are those that can help organisms exist under that particular set of conditions. Most of the trait modalities were observed mostly in the high saline LZ as also observed elsewhere (Gaston et al., 1998). It is difficult to determine whether the functional trait patterns were solely structured by environmental variables

(Clarke, 1993) as there may be other intrinsic factors masking the patterns or factors which were not measured in this study. As benthic taxonomic and functional patterns are known to be heavily influenced by natural gradients viz. salinity and grain size, it is challenging to trace the responses to co-existent anthropogenic stressors due to synergistic effects of multiple stressors (Egres et al., 2019, De Juan et al., 2007). Adding to the complexity, traits that are categorised as 'opportunistic' may be observed in relatively less impacted zones (Townsend et al., 1997) as observed in this study. Thus, our third hypothesis that salinity was the major environmental filter for both the taxonomic and functional trait compositions was proven.

#### **4.7 Implications on ecosystem functioning: taxonomic vs functional**

Ecosystem functioning is a combination of processes and resources shaping the energy flow through biotic and abiotic components of ecosystems (Díaz and Cabido, 2001), where species are adapted to their biotic and abiotic environment. In our study, both the estuaries were different in nature depending on their peculiar characteristics and existing scenarios in each zone. Thus, the disparate trends obtained for the taxonomic assemblages corroborated with the different functional facets obtained in the various estuarine zones. Different assemblages may reflect dissimilar levels of ecosystem functioning (Otegui et al., 2016). Ecosystem functioning can be maintained when there are higher number of functionally similar species in a system as there is a high probability that some of these species will survive to environmental changes (Díaz and Cabido, 2001; van der Linden et al., 2012). It was observed that all the functional traits showed fluctuations across the zones except for 'position in sediments', 'morphology' (Kundalika) and 'mode of reproduction' (both estuaries) which were somewhat constant throughout the estuary. The species assemblages varied zonally with little overlap of traits which implied that functioning cannot be maintained in the same way in case of species loss (Pacheco et al., 2010). Comparatively, Vashishti had slightly lower species diversity but had higher representation of EGI, II and III and superior FR. Hence, it is the species composition rather than the species diversity that played a pivotal role in the sustenance of benthic ecological functioning.

Though the relationship between FD and species diversity were equivocal, species diversity index may not serve as a dependable proxy for FD. However, the species identity may matter most to functioning as the current study indicated that the abundance-driven variations in the functional traits. Thus, both taxonomic and functional facets should be considered for ecosystem management and not rely entirely on species diversity or particular traits alone. Additionally, species diversity

along with functional diversity served as an important link to gain insights into the functioning of benthic systems and its resilience.

## **Conclusion**

Many Indian estuaries remain poorly investigated and even the baseline species data are unavailable for many transitional waters. This multi-species trait study provides novel insights into the tropical benthic functioning based on both taxonomic and functional facets of macrobenthos and their resilience against estuarine stress gradient in the backdrop of multifarious anthropic stressors. The taxonomic and functional structural patterns in the Kundalika and Vashishti estuaries differed largely across the estuarine zones and were independent of seasonality. The variability in species composition was reflected in their biological traits zonally due to the dominance of certain species and subsequent trait modalities. Natural estuarine gradients like salinity and sediment were major determinants of the taxonomic and functional structure. The low FR revealed that the Kundalika was more vulnerable than Vashishti to stress related impacts. This meant that the estuary was susceptible to loss of functions upon future species loss and regime shifts resulting in low buffering of the ecosystem. Vashishti showed higher resilience to perturbations as it had more species sharing similar functional traits. The two estuaries suffered from different perturbations which were reflected in BTA wherein, the less impacted LZ of both estuaries had diverse but identical functional traits, while the impacted MZ and UZ had a combination of opportunistic traits that were dependant on the species-trait matrix and distinctive of each estuary. Therefore, the coupling of taxonomic and functional approaches together rendered as a promising approach in understanding the ecosystem functioning of Kundalika and Vashishti estuaries. Indeed, understanding the processes that affect the ecosystem functioning is not straight-forward and the combination of different set of traits may give divergent results depending on the environment conditions. To combat this, a crucial step is to choose suitable traits or to include a greater number of traits in order to avoid away inferences more so, in perturbed environments. Therefore, more studies should be undertaken taking into account numerous traits and many environmental descriptors in different geographical regions particularly, the estuaries in tropics.

Contradictory trends to expected generalizations in functional traits were observed in the study. This was resultant of sensitive organisms also sharing traits that are termed opportunistic such as 'small size', 'short-life' span etc. The study indicated more opportunistic traits in the less stressed estuary dictated by the major constituent fauna. Thus, to evaluate the ecological status of an environment that is naturally supporting of opportunistic traits, such as in estuaries, it will do well to



apply ample caution during trait assignation and to choose the indicative traits based on its effectiveness and sensitivity to draw reliable conclusions. More quantum of similar studies are required to ascertain the limitations and uncertainties of the BTA approach. Future projections of impact of species loss on the functioning in the marine realm are scanty mostly due to paucity of information on benthic functioning (Bremner, 2008). The detailed functional database compiled in this investigation can be a pre-cursor for similar future estuarine studies in tropical latitudes that can aid predictive assessment studies.

### **Credit authorship contribution statement**

**Heidy Q. Dias:** Investigation, Conceptualization, Writing - original draft, Writing - review & editing, Visualization.

**Soniya Sukumaran:** Investigation, Conceptualization, Writing - original draft, Writing - review & editing, Visualization, Supervision, Project administration.

**Neetu S.:** Investigation, Software, Formal analysis, Writing - review & editing, Visualization.

**Hurmine Ridha:** Methodology, Formal analysis, Writing - review & editing, Visualization.

### **Declaration of competing interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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# Figures

## Fig. 1

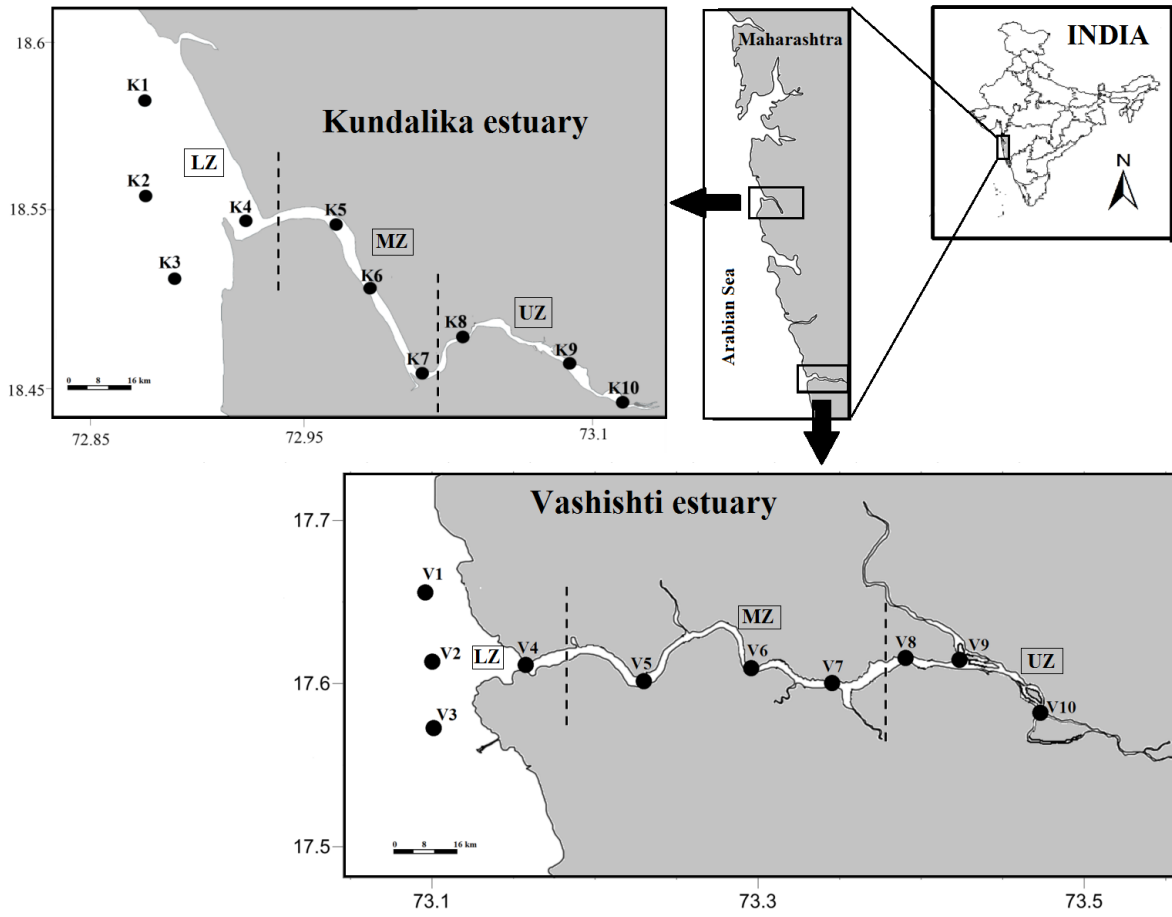


Fig. 2

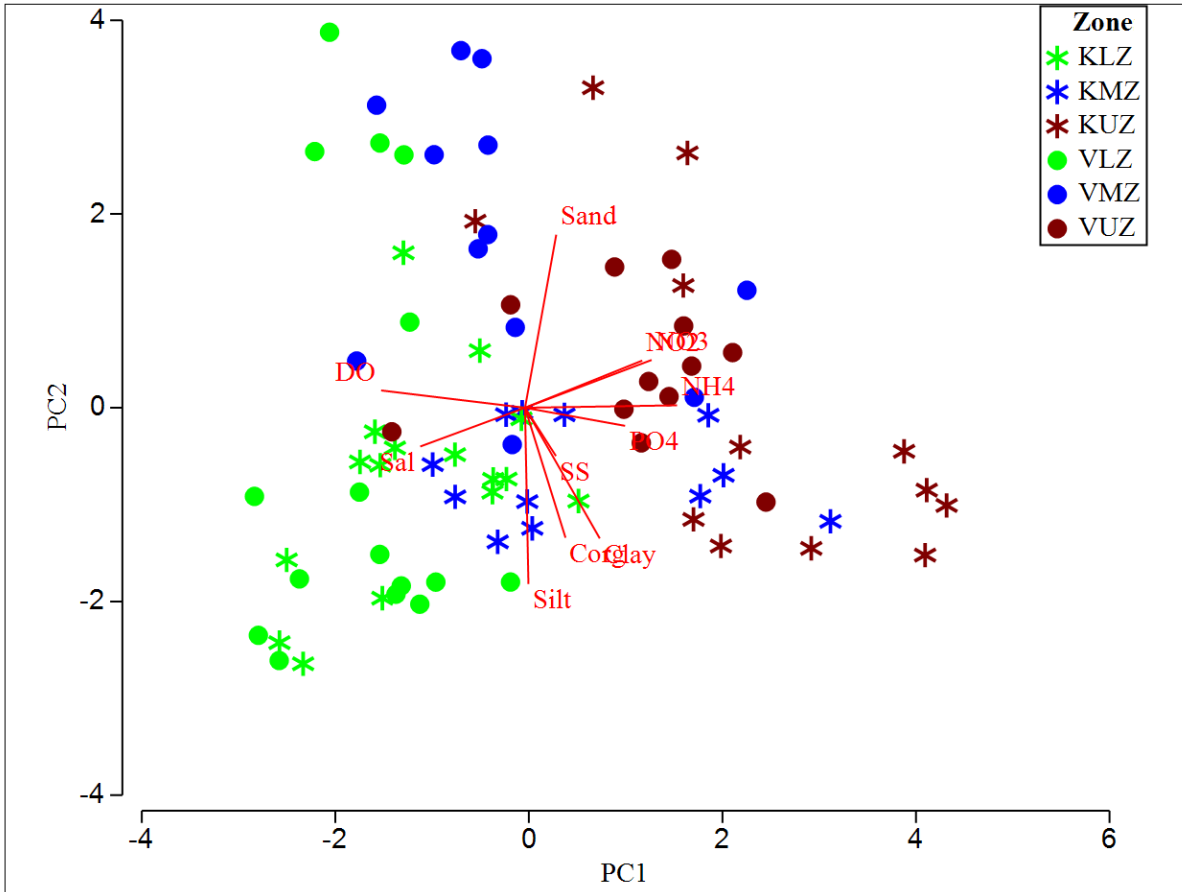


Fig. 3

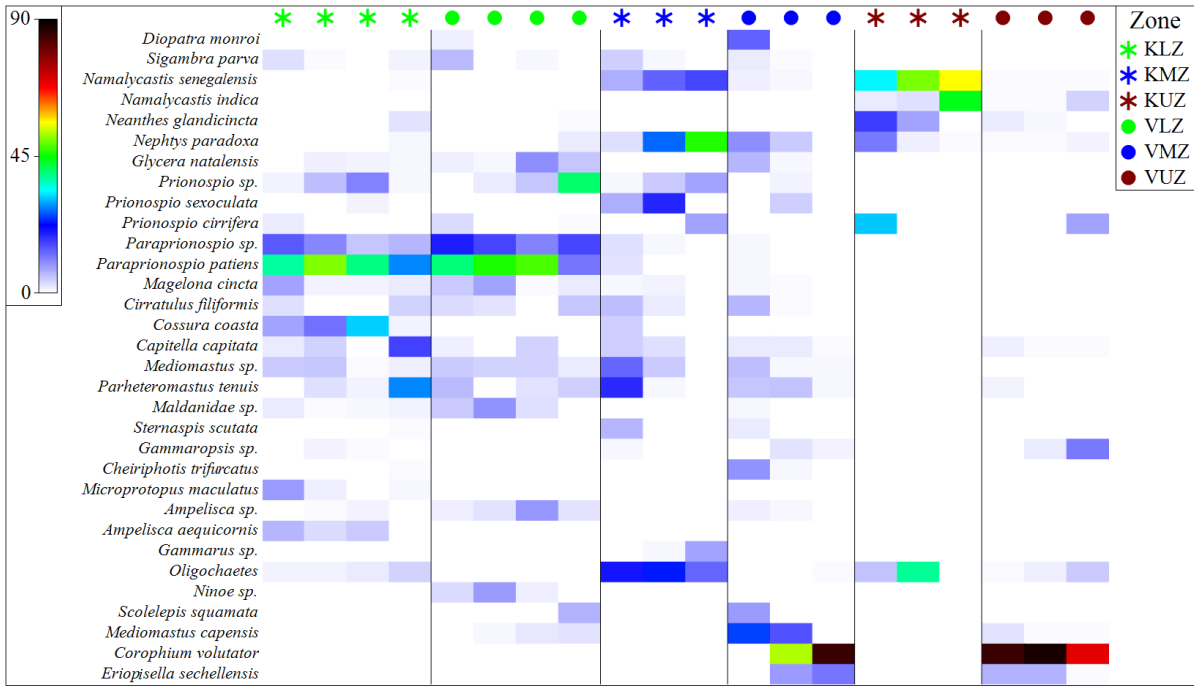


Fig. 4

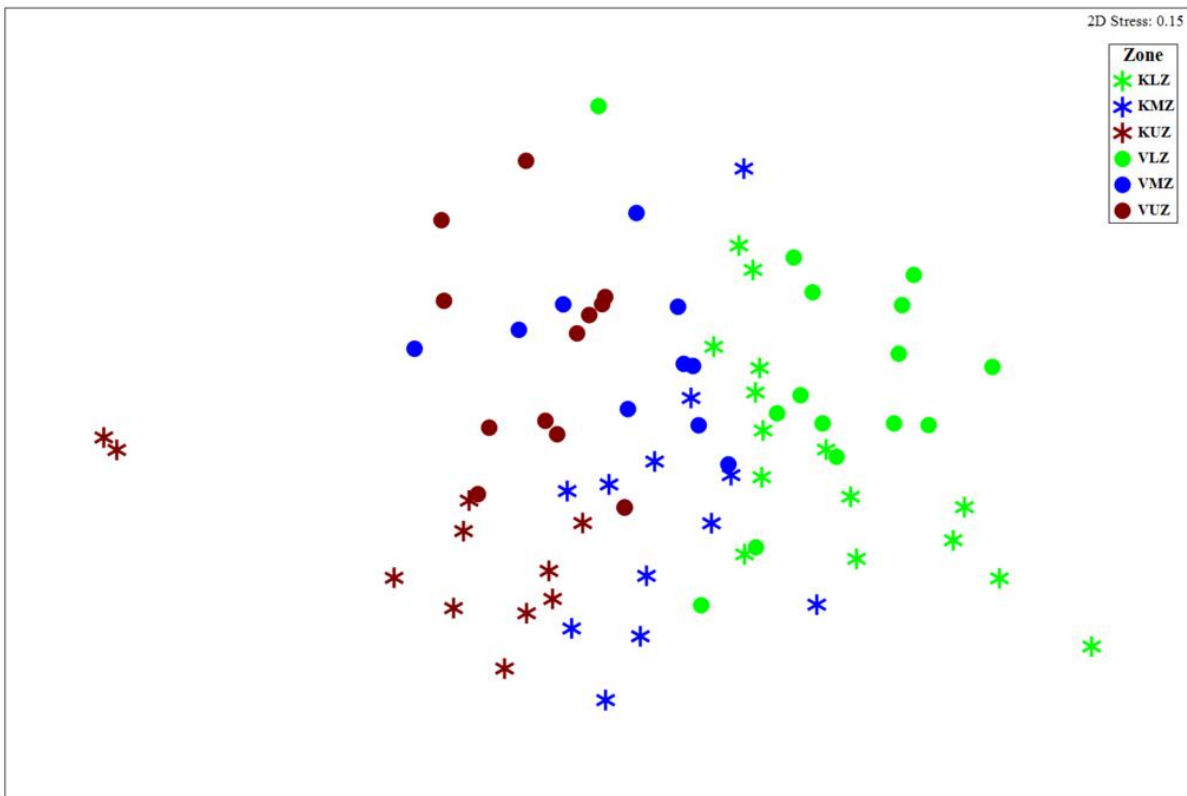




Fig. 5

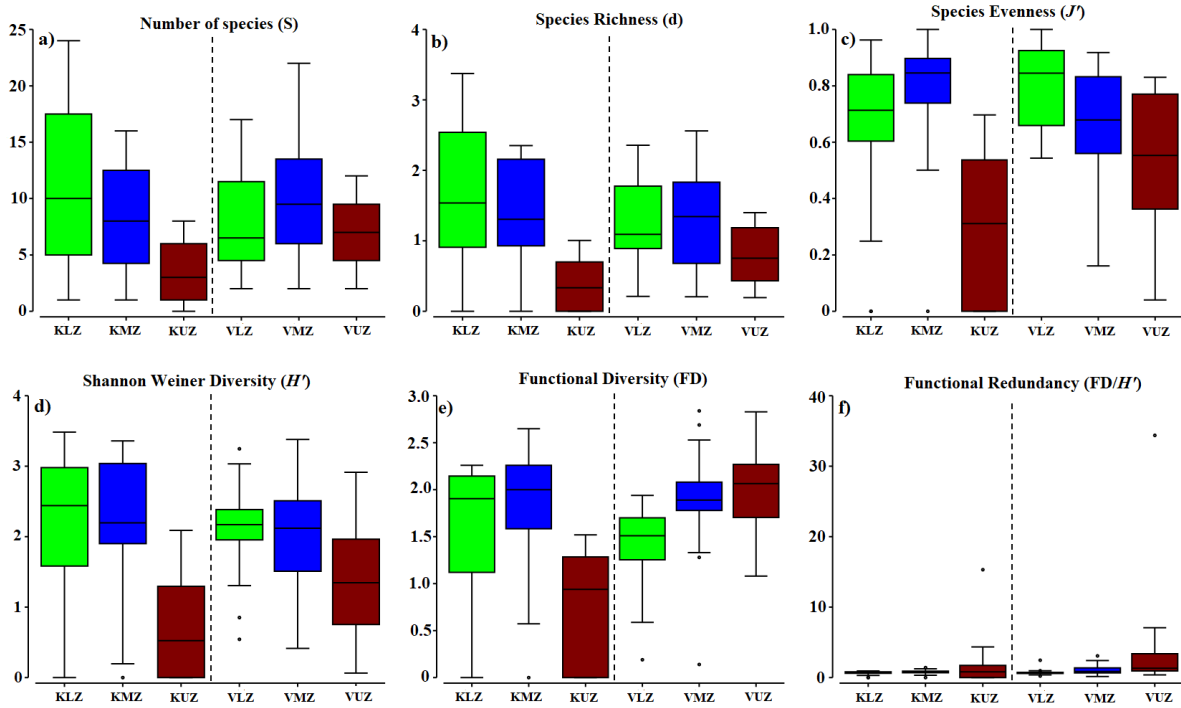


Fig. 6

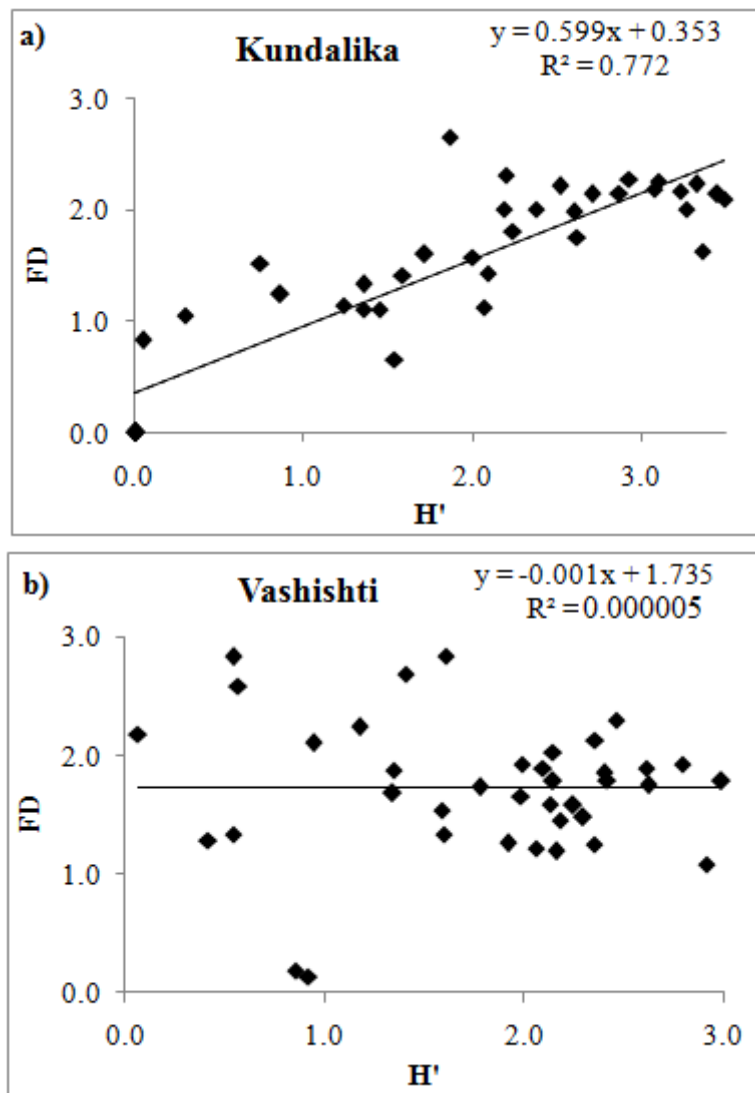


Fig. 7

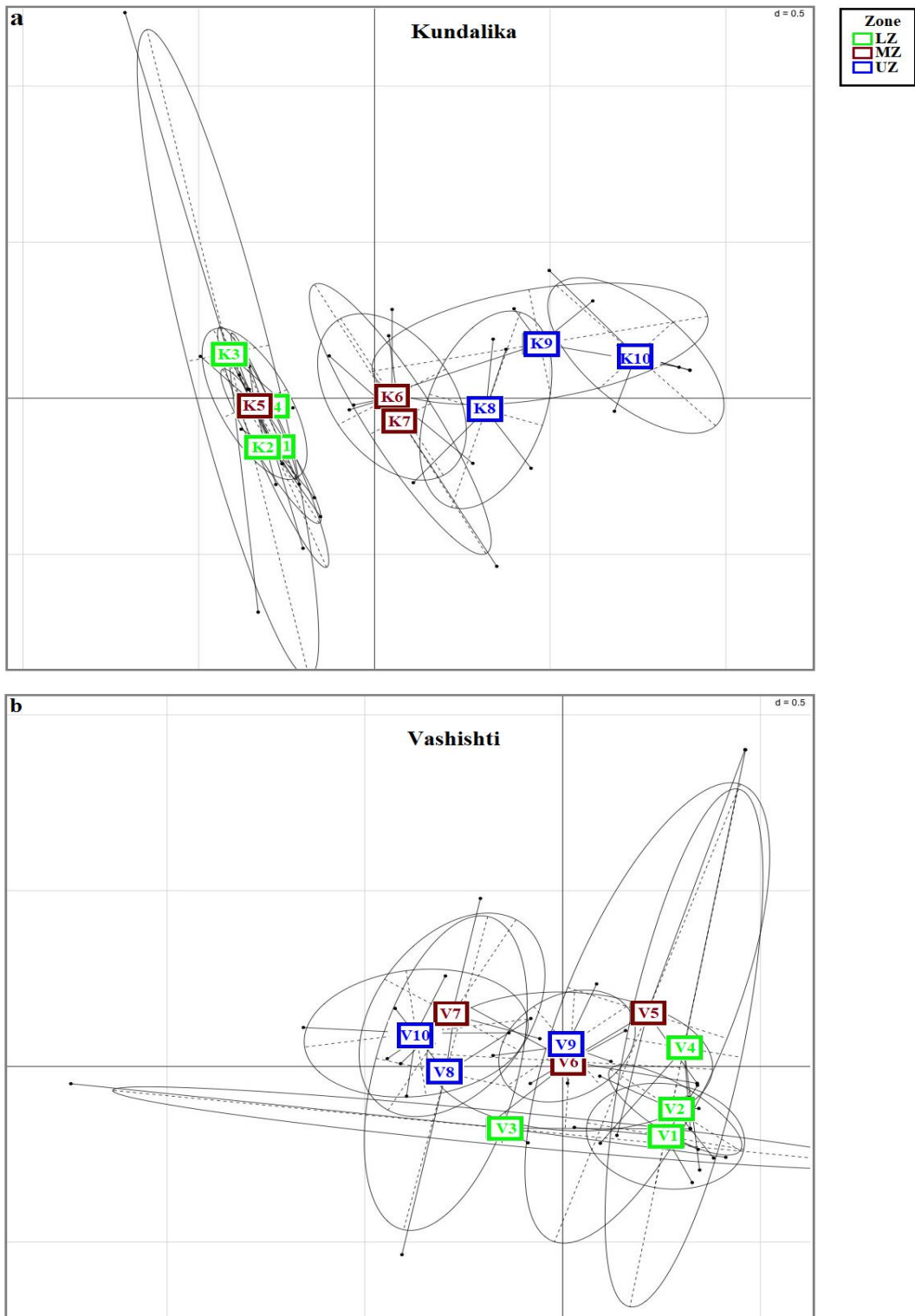
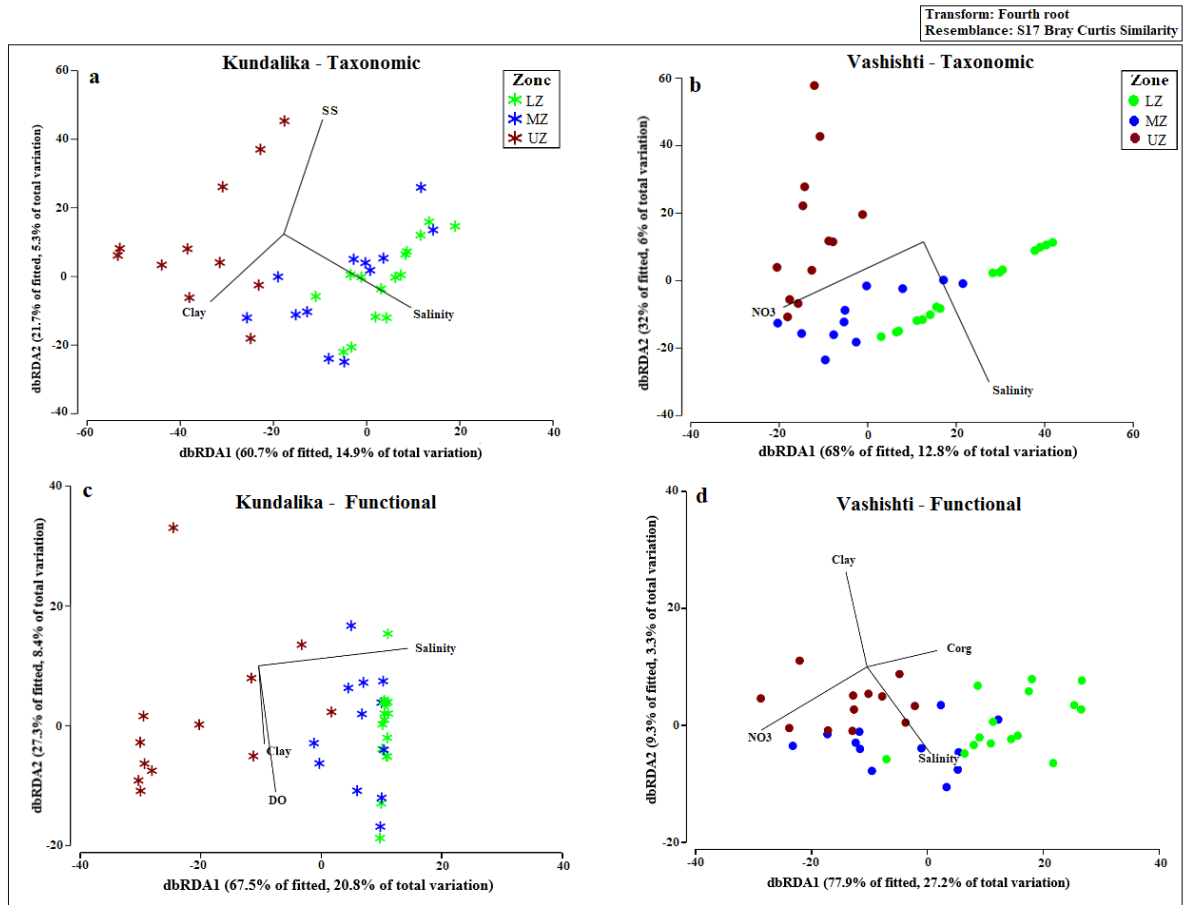


Fig. 8



# Graphical abstract

