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Predicting the functional morphology of lotic and lentic populations of the invasive Mozambique tilapia *Oreochromis mossambicus* (Peters, 1852)

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ABSTRACT

A better understanding of the mechanism which connects the morphology of fishes and their ecological performance is a major goal in evolutionary studies. As accepted widely, intra-species polymorphism mostly arises from divergent selection pressures between different environments. The present study sought to understand the functional morphological variations exhibited by Mozambique tilapia *Oreochromis mossambicu*s (Peters, 1852) inhabiting heterogeneous habitats, using functional indices derived from the body. We found that *O. mossambicus* exhibited clear functional responses to divergent habitats indicating trait-habitat linkages. Fishes differed in three out of fifteen indices compared, which are mainly related to swimming performances. Fishes collected from the river possess more streamlined bodies and achieve higher values in indices related to swimming efficiencies. However, there were no significant intra-species differences in the indices related to feeding between habitats, indicating that functional divergences in *O. mossambicus* are mainly related to swimming and locomotion. The study confirmed that the morpho-functional variations observed in this species are primarily of selection pressure caused by habitat heterogeneities. The present findings further confirm our understanding of the predictive power of the trait-environment approach and indicate that fishes tend to change their traits related to swimming and foraging with changing ecological conditions of the habitat.

Keywords: Cichlids, Ecomorphology, Functional traits, Phenotypic variation, Trophic polymorphism

Introduction

Better understanding of an organism's response to environmental gradients is a central theme in evolutionary biology which builds on the theory that divergent selective regimes can lead to phenotypic divergences within species (Langerhans *et al*., 2003; Nonaka *et al*., 2015). Divergences become more intense when species living in extremely diverse ecological conditions lead to local adaptation and phenotypic modifications (Losos *et al*., 1998; Kocher, 2004). Selection pressures due to habitat modifications by both natural and anthropogenic influences are manifested in species in the form of phenotypic differences through either genetic variability, phenotypic plasticity, or a combination of both (Langerhans, 2003; Lisney *et al*., 2020). Phenotypic divergences also occur through evolutionary responses to selection pressures leading to significant changes in traits that are affected more, which can lead to speciation in many fishes (Langerhans *et al*., 2003; Burress and Wainwright, 2019). Cichlids are excellent models to study explosive speciation, adaptive radiation and phenotypic plasticity (Kocher, 2004; Maan *et al*., 2006).

A wide range of taxa showing this intra-species divergence related to environmental gradients, resource and habitat use is referred to as trophic polymorphism (Webster *et al*., 2011; Foster *et al*., 2015; Lisney *et al*., 2020). However, population mixing, mainly due to migration and gene flow, restricts the adaptive diversification in fishes (Collyer *et al*., 2015). Hence, adaptive divergence is considered as a tradeoff between selection and gene flow between different habitats (Webster *et al*., 2011). These selection pressures often lead to subtle variations in functional traits which are related to locomotion strategies, feeding and growth rate, called phenotypic plasticity (Webster *et al*., 2011; Capoccioni *et al*., 2013; Shuai *et al*., 2018) which gives a competitive advantage for their greater fitness (Webster *et al*., 2011; Capoccioni *et al*., 2013). So, functional divergences among species is a direct measure of phenotypic variation (Collyer *et al*., 2015). This allows us to predict the species responses to habitat alterations and to identify the species which are most susceptible and resilient to change (Ribeiro *et al*., 2016; Kelley *et al*., 2018).

Hydrodynamics is the major physical factor that significantly influences the ecological characteristics of aquatic habitats (Bracciali *et al*., 2016; Lisney *et al*., 2020). Higher flow velocity was found to increase the prey encounter rate which makes the feeding conditions energy-intensive, making food searching and manipulation more difficult (Stoll and Fischer, 2011). Functional traits related to physiological, life history, behavioural and stoichiometric traits are widely used to predict the performance or fitness of an individual in their habitat (Webster *et al*., 2011).

Mozambique tilapia *Oreochromis mossambicus* (Peters, 1852) is an omnivorous exotic fish, widely distributed in the region, that showed high phenotypic variations, both within and between populations (Firmat *et al*., 2012; Nanthini *et al*., 2019). The present study attempted to understand the functional variations in Mozambique tilapia inhabiting different aquatic habitats, using an eco-morphological approach (Kumar *et al*., 2017; Shuai *et al*., 2018). For this, functional indices derived from body measurements were used to understand the interaction between an organism and its ecology (Kumar *et al*., 2017; Rajeeshkumar *et al*., 2020). The hypothesis for the study was that these fishes exhibit variations in their functional indices in response to varying ecological conditions of the habitats, especially to flow velocity. The study addressed two questions: (1) How flow velocity affects intraspecific functional variations in *O. mossambicus* and (2) Which are the major functional indices responsible for the variation if any. Answers to these questions will enhance current understanding of trait-habitat linkages in fishes.

Materials and methods

Samples were collected from three different habitats in Kerala, India *viz*., Muvattupuzha River, Kumbalangi Lake (brackishwater lake) and a freshwater pond (used for composite fish culture, during 2019) (Fig. 1). Muvattupuzha River is a major perennial river system in Kerala that originates from the Western Ghats mountain chain which joins the Vembanad backwater, the largest Ramsar site in India (Padmalal, 1992). Kumbalangi Lake (second sampling location), is a part of this wetland system. The third sampling station, a freshwater pond, is a stagnant water body used for composite fish culture. All these habitats significantly differ in their biotic and abiotic characteristics (Padmalal, 1992; Menon *et al*., 2000).

A total of 86 healthy adult fishes were collected (N = 30, 27, 29 for the river, brackishwater and pond, respectively) in a snapshot sampling using a cast net. The fishes collected from the pond were in live condition, hence they were euthanised using clove oil @ 0.05 ml per 500 ml of water (Fernandes *et al*., 2017). All samples were preserved in ice and brought to the laboratory for further analysis. Eighteen morphological characteristics were measured from the fish using a digital vernier caliper (Mitutoyo, accuracy ±0.02 mm) (Albouy *et al*., 2011; Zhao *et al*., 2014; Villeger *et al*., 2017; Shuai *et al*., 2018) (Fig. 2). The weight of the fish was measured using a digital weighing balance (accuracy 0.01 g). Fifteen functional indices related to food acquisition, locomotion and maneuverability were calculated from these morphological measurements (Shuai *et al*., 2018) (Table 1). Functional trait data were standardised using the fish length (standard length, SL) by linear regression to remove the effect of fish size from the data (modified from Mouillot *et al*., 2005; Kumar *et al*., 2017). An allometric relationship of $X=aL^b$ was established between morphological data (X) and SL, where "b' is the coefficient of the relationship. The effect of fish size was removed by using the residuals of the common within-group slopes of linear regression for each component of body length (modified from Mouillot *et al*., 2005; Kumar *et al*., 2017).

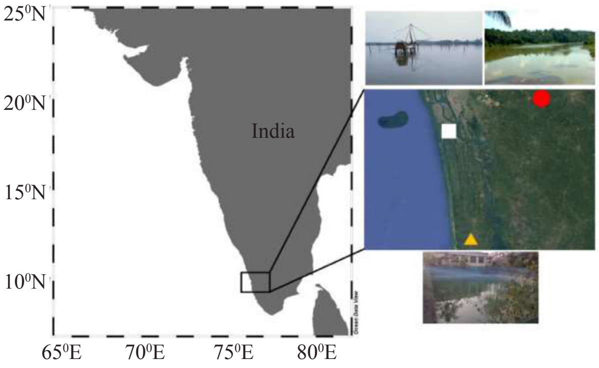

Fig. 1. Geographic locations of three different aquatic habitats for collecting *O. mossambicus* (White square : Brackishwater lake; Red circle: River; Yellow triangle: Freshwater pond)

Length-weight relationships using the allometric power equation ($Y= aX^b$; Huxley, 1924) were estimated, where Y is the weight (g) and X is the total length (cm). Length-weight data was transformed into logarithmic form and curvilinear plots were used for removing outlier values from the data (Froese, 2006; Froese *et al*., 2011). Regression parameters a and b were estimated by the least square regression method, where a and b are the intercept and slope, respectively (Froese, 2006). Analysis of covariance (ANCOVA) was done to compare the regression slope (b) between fishes from different habitats (Froese *et al*., 2006). Post-hoc analysis (Tukey-HSD) was used to test any significant variations in "b" among groups (habitats) if ANCOVA showed significant differences. Principal component analysis (PCA) was carried out on a variance-covariance matrix of functional indices to test the functional morphological differences among habitat

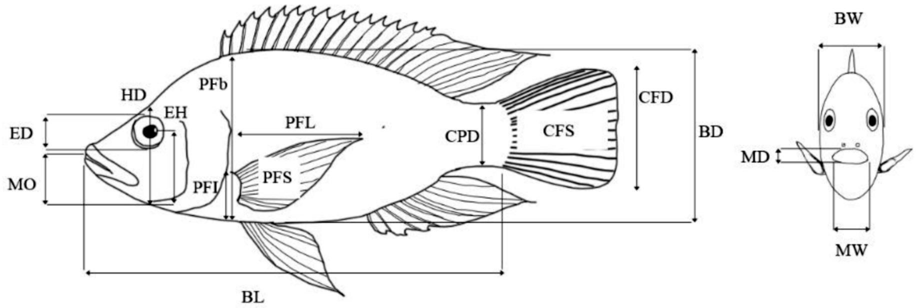

Fig. 2. Schematic representation of the morphological measurements of *O. mossambicus* measured for estimating the functional indices (BD: Body depth; BW: Body width; CPD: Caudal peduncle depth; CFD: Caudal fin depth; ED: Eye diameter; EH: Distance between the bottom of the head and the centre of eye; HD: Head depth along the vertical axis of the eye; MH: Mouth height; MO: Mouth opening; MW: Mouth width; PFB: Body depth at the pectoral fin insertion; PFi: Distance between the insertion of pectoral fin and the bottom of the body; PFL: Pectoral fin length; PFS: Pectoral fin surface; SL: Standard length.

Table 1. Abbreviations and formulae for estimating the functional indices from fish body (see Fig. 2). The letters given in parenthesis of functional traits indicate their use in feeding (F) or locomotion (L)

Functional trait	Abbrevation	Formula	Ecological meaning	References
Oral gape surface (F)	*Osf*	[*Mw* x *Md*]/[*Bw* x *Bd*]	Nature/size of the prey that can be captured	Karpouzi and Stergiou (2003)
Oral gape shape (F)	*Osh*	*Md*/*Mw*	Method to capture food items Shape varies from full circle to extended oval	Karpouzi and Stergiou (2003); Wainwright *et al.* (2007)
Oral gape position (F)	*Ops*	*Mo*/*Hd*	Feeding position in the water column. Position of the oral gape influences the retention of prey during ingestion	Kumar *et al*. (2017); Villeger *et al.* (2017).
Eye size (F)	*Edst*	*Ed*/*Hd*	Prey detection efficiency. It also influences the feeding rhythms (nocturnal *vs* diurnal), predator avoidance and also indicates the availability of light in the microhabitat	Boyle and Horn (2006); Bellwood *et al.* (2014)
Mass (F/L)	*M*	*log (W+1)*	Volume, Muscle mass	Zhao *et al.* (2014)
Eye position (L)	*Eps*	*Eh*/*Hd*	Vertical position in the water column	Watson and Balon (1984); Ribeiro *et al.* (2016)
Compression index (L)	*CI*	Bd^2/Bl x Bw	Body transversal or compressed shape	Shuai *et al.* (2018)
Body transverse shape (L)	*Bsh*	*Bd*/*Bw*	Vertical position of the fish in the water column as well as hydrodynamic efficiency	Villeger *et al.* (2017)
Pectoral fin position (L)	*PFps*	*PFi*/*PFb*	Maneuverability and position in the water column	Zhao *et al.* (2014)
Aspect ratio of the pectoral fin (L)	*ArPF*	PFl^2/PFs	Swimming ability, which helps in sustained swimming	Watson and Balon (1984); Casatti and Castro (2006)
Caudal peduncle throttling (L)	*CPt*	*CFd*/*CPd*	Caudal propulsion efficiency through the reduction of drag	Zhao *et al*. (2014)
Aspect ratio of the caudal fin (L)	*ArCF*	CFd^2/CFs	Caudal fin use for propulsion and /or direction	Bridge *et al.* (2016)
Body section area	*BSa*	$In\ ((\pi/4 \times Bw \times Bd)+1)/ln\ (M+1)$	Mass distribution along the body and hydrodynamism	Zhao *et al.* (2014)
Fins surface ratio (L)	*FSr*	(2 x *PFs*)/*CFs*	Swimming type (pectoral or caudal fin propulsion)	Zhao *et al.* (2014); Kumar *et al.* (2017)
Fins surface to body size ratio (L)	*FSb*	[(2 x *PFs*) + *CFs*] /(π/4 x *Bw* x *Bd*)	Endurance, acceleration, and/or maneuverability	Zhao *et al*. (2014); Kumar *et al*. (2018)

Mw: Mouth width; *Md*: Mouth depth; *Bw*: Body width; *Bd*: Body depth; *Hd*: Head depth; *Ed*: Eye diameter; *W*: Weight; *Eh*: Eye height; *Bl*: Body length; *PFi*: Pectoral fin insertion; *PFb*: Pectoral fin base; *PFl*: Pectoral fin length; *PFs*: Pectoral fin surface; *CFd*: Caudal fin depth; *CPd*: Caudal peduncle depth; *CFs*: Caudal fin surface; M: Mass groups (Shuai *et al*., 2018). Bonferroni's correction for post-hoc pairwise multiple comparisons using multivariate analysis of variance (MANOVA) on principal component scores was used to examine any significant functional difference among the habitat groups (Layman *et al*., 2005). A canonical variate analysis (CVA) was done on the PCA matrix to confirm whether the habitat groups are statistically different (Tuset *et al*., 2015). The classification success of different habitat groups was analysed using jack-knife cross-validation. All statistical analyses were performed in R (R Development Core Team, 2017) and PAST (PAlaeontologicalSTatistics, ver. V1.81). Results were considered statistically significant when $p<0.05$.

Results

Intra-species variations in the growth pattern

Length-weight relationship was significantly different in fishes collected from different habitats (ANCOVA, F=3.1425, df=2, $p<0.05$). The slope of the relationships (b) was higher in fishes that inhabited brackishwater (b=3.566) compared to those inhabiting rivers (b=2.769) indicating differences in growth pattern (Tukey-HSD, $p<0.05$). However, b value for the fishes from the pond (b=3.240) did not show any difference with the other two groups (brackishwater and river).

Intra-species functional morphological variation

The functional indices derived from fish body lengths for estimating intraspecies functional morphological variations, with their abbreviations and formulae are listed in Table 1. PCA successfully differentiated the fishes inhabiting different habitats. The first five PCA axes contributed 97.2% of the total variations and the first two axes together contributed 90% of the total variation (Fig. 3). PC1 axes (77.6%) differentiated the fishes based on functional indices related to swimming capacities such as ArPF (r= -0.647), ArCF (r= -0.662) and CPT (r= -0.232) (Table 2). The major differences in this axis were between brackishwater and riverine inhabitants. Fishes collected from the river showed higher values in indices related to swimming efficiencies. However, fishes from brackishwater showed higher body depth and fin surface. Fishes collected from the pond occupied an intermediate position in this axis. PC2 (12.47%) differentiated the fishes based on their swimming patterns (ArPF, r=0.663; ArCF, r= -0.351), body shape (CI, r= 0.362), vertical position in

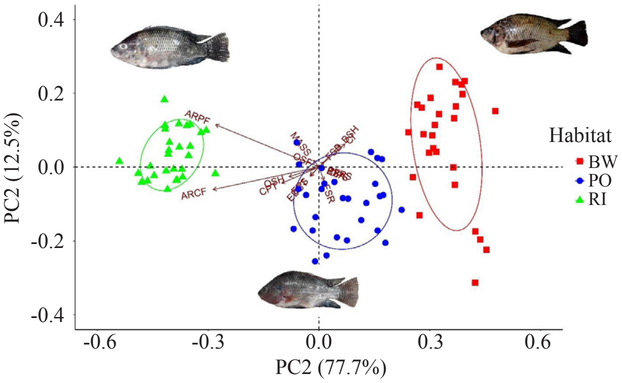

Fig. 3. Morpho-functional space from principal component analysis on functional indices estimated from morphological measurements of Mozambique tilapia, *O. mossambicus* collected from three different aquatic habitats (Brackishwater lake: Red square; River: Green triangle; Freshwater pond: Blue circle) (Codes of the morphological traits are described in Table 1)

Table 2. Correlation between principal components and functional indices (see Table 1 for acronyms) of *O. mossambicus* collected from three different habitats *viz.,* brackishwater lake, river and freshwater pond. Higher absolute correlation values (r>0.3) are represented in bold

	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
OSF	-0.018	0.02118	-0.0257	0.00792	-0.18618	0.0306396
OSH	-0.1869	-0.1511	**-0.9193**	0.16024	-0.00649	-0.187416
OPS	0.036	-0.0345	-0.0216	0.11419	0.036175	**0.5309542**
EDST	-0.0535	-0.1441	-0.0719	0.13174	-0.24733	**0.3259217**
EPS	-0.0558	-0.1377	-0.0461	0.09143	-0.00331	**0.5606848**
BSH	0.13032	**0.3438**	-0.202	-0.491	-0.23885	0.1425872
PFPS	0.01767	-0.0135	0.01396	0.01934	-0.07886	-0.077729
ARPF	**-0.6468**	**0.66273**	0.03967	**0.31286**	-0.03389	0.1120985
CPT	-0.2321	-0.252	0.22442	0.03087	**-0.66782**	-0.193093
ARCF	**-0.6617**	**-0.3513**	0.07042	**-0.5784**	0.157478	0.0435147
FSR	0.03099	-0.2055	-0.1342	-0.0828	-0.0823	**0.323863**
FSB	0.03154	0.08152	-0.0873	-0.0481	**-0.4274**	-0.178995
CI	0.16293	**0.36158**	-0.137	**-0.4616**	-0.17904	0.1486697
BSA	0.02326	-0.0214	0.06433	0.09145	-0.0827	0.032857
MASS	-0.033	0.10597	-0.0067	-0.1732	**0.373173**	-0.152334

the water column and hydrodynamic efficiency (Bsh, r= 0.344). Here, positive axes were represented by fishes from the river which exhibit pectoral fin mediated swimming patterns and a more streamlined body. Fishes from the pond, characterised by a caudal fin mediated swimming pattern and a higher fin area, occupied the negative axis.

MANOVA confirmed the hypothesis of significant functional differences in fishes inhabiting different habitats (Wilk's Lambda=0.0236, $F_{20,142}$=39.143, p<0.001). Pairwise comparison using sequential Bonferroni correction showed significant differences between habitat groups (p<0.001) (Table 3). Further, canonical variate analysis successfully separated three habitat groups. The first CV axis (97.36%) maximised the differences between the fishes collected from the river and brackishwater habitats (Fig. 4). Jackknife cross-validation indicated 98.8% classification success among different habitat types (96.4% for ponds and 100% for brackishwater and river, respectively).

Discussion

In the present study, *O. mossambicus* exhibited very clear functional responses to divergent habitats, which are in agreement with previous findings on trait-habitat linkages (Ribeiro *et al*., 2016; Kelley *et al*., 2018; Shuai *et al*., 2018). Intraspecific polymorphism mostly arises from divergent selection pressures between alternative environments (Shuai *et al*., 2018). Phenotypic differences can also result from either genetic differentiation or phenotypic plasticity, or both, as an adaptive response to divergent selection pressures (Foster *et al*., 2015).

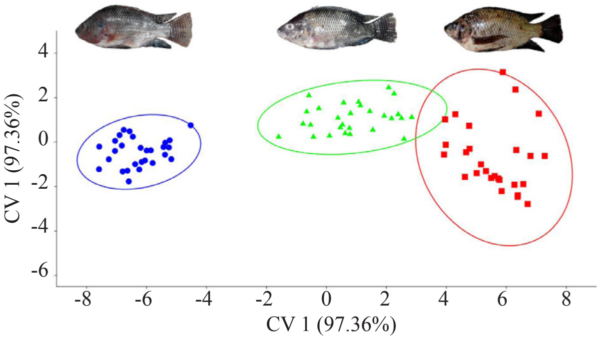

Fig. 4. Variations in functional indices of Mozambique tilapia *O. mossambicus* collected from three different aquatic habitats along first two CVA axes from negative (left) to positive (right) extreme values with the images of representative fishes (Brackishwater lake: Red square; River: Green triangle; Freshwater pond: Blue circle)

Table 3. Cross-validation indicating the predictive ability of *O. mossambicus* collected from three different habitats *viz.,* brackishwater lake, river and freshwater pond based on functional traits derived from fish body. Predicted group membership in each group are in bold letters and percentage of classification is in parenthesis

Habitat	Brackishwater	Pond	River	Total
Brackishwater	**27 (100)**	0	0	27
Pond	1	**27 (96.4)**	0	28
River	0	0	**28 (100)**	28

The results of the present study indicated that three indices *viz.,* ArPF, ArCF and CPt, which are mainly related to the swimming performances, were responsible for major variation, as reported in earlier studies of similar nature (Kelley *et al*., 2017). Fishes from the river (high flow velocity) presented a more streamlined body and higher values in indices related to swimming efficiencies (*viz*., ArPF, ArCF and CPt) (Zhao *et al*., 2015; Kumar *et al*., 2017). More fusiform shape and narrow caudal peduncle improve swimming efficiency by reducing the drag which helps to minimise energy expenditure for feeding, predator avoidance, and buoyancy maintenance (Langerhans, 2008; Kelley *et al*., 2017). Flow velocity was found to induce functional variations related to swimming and hydrodynamic efficiency in fishes (Langerhans and Reznick, 2010; Shuai *et al*., 2018). The fishes also exhibit distinct morphologies between lotic and lentic habitats (Bracciali *et al*., 2016; Kelley *et al*., 2017). Fishes living in brackishwater and pond habitats, where the flow velocity is less-to-moderate, possess a deeper body and high relative fin area, a characteristic feature of slow swimming fishes (Zhao *et al*., 2015; Villeger *et al*., 2017). The major differentiation between the fishes from freshwater pond and river were on the indices related to hydrodynamic efficiency and swimming patterns. As expected, fishes living in rivers possess more streamlined bodies with a pectoral fin facilitated swimming style. High relative fin area in pond fishes enhance faster turns, maneuverability, and endurance in swimming, a characteristic feature of fishes living in lentic ecosystems (Zhao *et al*., 2015; Villeger *et al*., 2017).

Fishes tend to possess defensive structures such as fin spines and armoured plates (Weber *et al*., 2012; Price *et al*., 2015) and an increase in body depth-to-length ratio (Johansson and Anderson, 2009; Frommen *et al*., 2011), as a plastic response to high predation pressures. The deeper bodies of fishes inhabiting brackishwater habitats also help to increase the handling time and escape from the gape-limited predators (Weber *et al*., 2012). Fishes from brackishwater habitats presented a high growth rate (higher *b* value) compared to those living in riverine conditions (Agboola and Anetekhai, 2008). Brackishwater habitats are mostly nutrient-rich, providing more fertile environments for fishes (Menon *et al*., 2000; Capoccioni *et al*., 2013) as compared to rivers, which are mostly oligotrophic especially in their upper stretches (Kiranya *et al*., 2018). The deeper bodies and higher growth rate in fishes living in ponds also could be the consequence of energy being allocated to a higher growth rate by decreased activity (Anderson *et al*., 2006). Fishes living in high flow velocity waters need to spend more energy for maintaining stability, maneuvering and feeding compared to those living in lentic habitats (Pang *et al*., 2020). In this condition, fish show a greater increase in length than height (Charo-Karisa *et al*., 2007; Olsson *et al*., 2007). The low prey availability and increased searching time leads to high energy expenditure for swimming and feeding, resulting in low *b* value in riverine fishes (Capoccioni *et al*., 2013), which is evident in the present study also. Stagnant water conditions and supplementary feeding in the freshwater pond may reduce the activity level of fishes for feeding, leading to more energy diversion towards better growth rates. The functional divergences in *O. mossambicus* are mostly related to swimming and locomotion. However, further studies on intraspecific variations in diet, feeding habits and predation pressure are necessary to elucidate these relationships more clearly.

The present study concludes that habitat structural variabilities would act as a major selection pressure that leads to functional variation in *O. mossambicus* (Kelley *et al*., 2018; Shui *et al*., 2018) which enable them to establish specific niches for specific morphotypes (Kelley *et al*., 2017). There is a chance of potential gene flow among the habitats (river and backwater) since both these habitats are interconnected at least in some regions. Hence, the influence of genetic variations on the functional differences needs to be checked to confirm this understanding (Langerhans *et al*., 2003). Gene flow should only constrain the magnitude of genetic differences, not plastic diversification (Scheiner 1993; Laurila *et al*., 2007). The present findings confirm our understanding of the predictive power of the trait-environment approach (Ribeiro *et al*., 2016; Kelley *et al*., 2018; Shuai *et al*., 2018). Understanding the intra-species polymorphism is useful for predicting the impact of ecosystem disturbances and modifications due to both, natural and anthropogenic causes (Langerhans and Reznick, 2010; Kelley *et al*., 2018). However, finding a general pattern of an organism's response to selection pressures is difficult as these relationships can be species specific.

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