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Alien attack: trophic interactions of flowerhorn cichlids with endemics of ancient Lake Matano (Sulawesi, Indonesia)

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ABSTRACT

Background: The ancient Malili Lakes (Sulawesi, Indonesia) harbour an exceptional diversity of freshwater animals, including several endemic species flocks. Lake Matano, the hydrological head of the lake system, has seen the successful invasion of a man-made hybrid fish, the flowerhorn cichlid. In less than one decade, flowerhorns colonized the entire shoreline of Lake Matano. However, little is known about the flowerhorn's ecology in the wild, its potential impact on the ecosystems it invades, or the reasons for its invasive success.

Question: Do flowerhorn cichlids prey on endemic species and do they compete for dietary resources with endemic fish radiations?

Methods: We studied stomach contents of 136 flowerhorns from six locations around Lake Matano, investigated ontogenetic dietary niche shifts, and compared diets to available stomach-content data from two endemic fish radiations (*Telmatherina*).

Results: Flowerhorns undergo a pronounced ontogenetic dietary niche shift. While juveniles mostly prey on aquatic insects, adults have a generalized diet and prey on species of all major endemic radiations. Although flowerhorns consume most of the resources that dominate the diets of the *Telmatherina* radiations, dietary overlap between single endemic species and flowerhorns is limited. Minimal dietary overlap of juvenile flowerhorns with both adult conspecifics and endemic *Telmatherina* combined with omnivory and territoriality of adults potentially facilitated their invasive success.

Keywords: competition, flowerhorn cichlid, invasion, ontogenetic niche shift, predation, *Telmatherina*.

INTRODUCTION

Non-indigenous freshwater fishes can influence native biota in various ways, including the introduction of parasites (Strecker, 2006), hybridization (Ludwig *et al.*, 2008), habitat alteration (Starling *et al.*, 2002), competition for trophic resources (McHugh *et al.*, 2006; Meeuwig *et al.*, 2011), and

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predation pressure (Witte *et al.*, 1992), potentially leading to the extinction of prey species or competitive exclusion of trophic analogues (for a review, see Cucherousset and Olden, 2011). Flowerhorns, also referred to as Lohan or Kirin cichlids, are members of a man-made hybrid complex, and were generated for the ornamental fish trade from parental species of the Neotropical cichlid genera '*Cichlasoma*', *Amphilophus*, and *Paraneetroplus* (*Vieja*) (Nico *et al.*, 2007; Ng and Tan, 2010). They are reportedly aggressive, predatory fishes with parental brood care (Knight, 2010) and famous among fish keepers, especially in Asia. Accordingly, introductions to the wild have been reported from several countries in South East Asia (Nico *et al.*, 2007; Ng and Tan, 2010), from the Indian subcontinent (Knight, 2010), and also Florida, USA (http://nas.er.usgs.gov, 26 November 2017).

Although flowerhorn cichlids are widespread invaders (Nico *et al.*, 2007), data are lacking on their general ecology and their ecological impact in the regions of concern. This is also true for the Malili Lakes system in the highlands of central Sulawesi (Indonesia), which has seen the successful invasion of flowerhorn cichlids (Herder *et al.*, 2012). With an estimated age between 1 and 4 million years, the Malili Lakes are the only hydrologically interconnected ancient lake system in the world, and famous for their high rate of endemism (Abendanon, 1915; Brooks, 1950; Vaillant *et al.*, 2011). Members of endemic species flocks of diverse aquatic taxa, including gastropods, shrimps, crabs, and fishes (especially Telmatherinidae), have served as model systems for evolutionary biology. Studies have addressed, for example, the mechanisms driving lacustrine adaptive radiations (von Rintelen *et al.*, 2004, 2010; Gray *et al.*, 2008a; Pfaender *et al.*, 2010), gene flow among evolving species (Herder *et al.*, 2008; Schwarzer *et al.*, 2008; Walter *et al.*, 2009), ecological speciation in sympatry (Herder *et al.*, 2008; Pfaender *et al.*, 2011, 2016), the genetic underpinnings of evolutionary innovations (Hilgers *et al.*, 2018), and the evolution of male colour polymorphisms (e.g. Gray *et al.*, 2008a; reviewed in Vaillant *et al.*, 2011 and von Rintelen *et al.*, 2012). Lake Matano, a deep (590 m), ultra-oligotrophic lake, forms the hydrological head of the system (Fig. 1). Endemic sailfin silversides (Atherinomorpha: Telmatherinidae) form the most diverse fish species flock in the Malili Lakes, with two radiating lineages restricted to Lake Matano (Herder *et al.*, 2006a, 2006b). In the course of adaptive radiations, 'roundfins' (*Telmatherina antoniae* 'large', *T. antoniae* 'small', and *T. prognatha*) and 'sharpfins' (*T. sarasinorum*, *T. opudi*, *Telmatherina* sp. 'elongated', *T. wahjui*, and *Telmatherina* sp. 'thicklip') adapted to different habitats and diets, including trophic specialization on copepods, shrimps (Herder *et al.*, 2008; Pfaender *et al.*, 2010, 2011), and eggs (Gray *et al.*, 2008b; Cerwenka *et al.*, 2012). Trophic specialization most likely resulted from diversifying selection, generated by competition for limited trophic resources in this ultra-oligotrophic lake (Herder *et al.*, 2008; Pfaender *et al.*, 2010, 2011).

Besides intensive surface nickel mining, pollution, urbanization, and commercial fisheries (e.g. Bramburger *et al.*, 2017), the endemic species flocks of Lake Matano are exposed to at least 14 introduced fish species (Herder *et al.*, 2012). Based on limited investigations to date of alien species in Lake Matano, the recently introduced 'flowerhorn' cichlid stands out among invaders owing to its rapid establishment, very high abundance, and rapid range expansion following its first observation (Herder *et al.*, 2012). Notably, flowerhorns were only observed at the southern shore of Lake Matano during an intensive survey of 160 locations in 2010, but were highly abundant along the entire shoreline in 2012, which illustrates the dispersal potential of this alien species (Herder *et al.*, 2012). Based on these facts, it is estimated that flowerhorns were introduced into Lake Matano no earlier than 2005, most likely in the Soroako area (Fig. 1) (Herder *et al.*, 2012). Since the isolated Malili Lakes are of outstanding economic, ecological, and scientific value (Vaillant *et al.*, 2011), it is important to assess the potential impact of flowerhorn cichlids on this unique ecosystem.

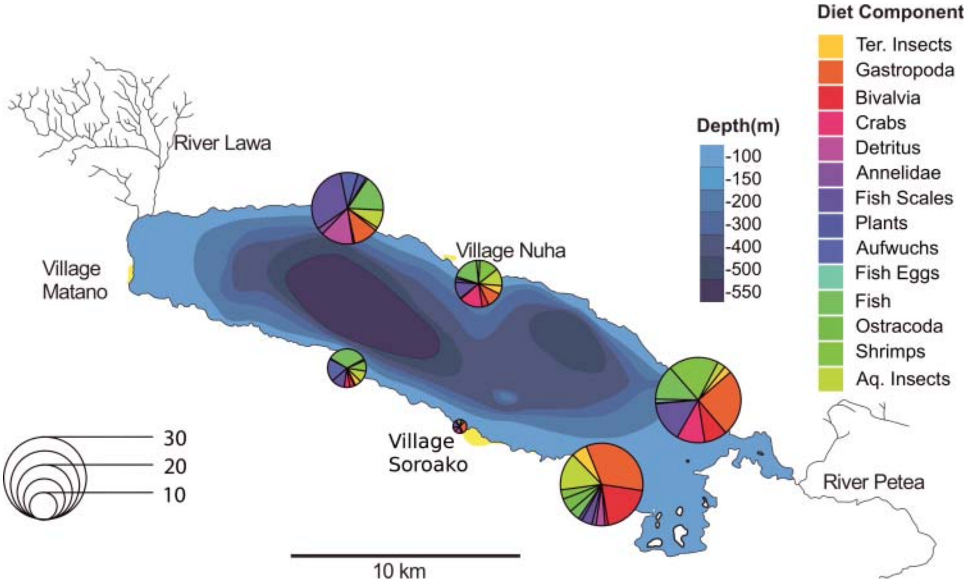


Fig. 1. Diet composition of flowerhorn cichlids (>40 mm) at the six sampling sites around Lake Matano, central Sulawesi, Indonesia. Sample sizes at the six sites are indicated by pie chart area. The map of Lake Matano was modified with the permission of T. von Rintelen.

All radiations endemic to the Malili Lakes studied to date share trophic specialization as a key component driving adaptive divergence (for comparative reviews, see Vaillant *et al.*, 2011 and von Rintelen *et al.*, 2012), and it is plausible that trophic resources are a limiting factor in these ultra-oligotrophic lakes (Haffner *et al.*, 2001). The effects of invading species are hence expected to be related to both competition for trophic resources and predation. In turn, competition can influence the chance of successful invasions because resource availability is crucial for the establishment of alien species (Shea and Chesson, 2002). Hence, a generalist diet and ontogenetic dietary shifts of invaders can increase invasion success by reducing competition for limited trophic resources (Claessen and Dieckmann, 2002; Shea and Chesson, 2002; Tilman, 2004; Vazques, 2006; Hill *et al.*, 2015).

Here we investigate the trophic interactions of flowerhorn cichlids with all species of the two endemic sailfin silversides radiations. We hypothesize that flowerhorns (1) exhibit trophic profiles promoting invasion success such as a generalist diet or ontogenetic niche shifts, (2) compete for trophic resources with the endemic *Telmatherina*, (3) prey on endemic species of the major radiations, and thus (4) pose a serious threat to the unique ecosystem of ancient Lake Matano.

MATERIALS AND METHODS

Specimen collection

Flowerhorns ($n = 136$) were caught at depths of 1–3 m at six sampling locations around the shoreline of Lake Matano (Fig. 1), covering the full range of macrohabitats and substrate structures, including different types of sediment (rock, gravel or sand), submerged structures (rocks or trees), and canopy-covered littoral zones (for a habitat distribution map, see von Rintelen *et al.*, 2010). Sampling was carried out during the dry season in November 2013, using snorkelling-aided gillnetting, with flowerhorns being guided into the nets by a snorkeler. Specimens were preserved in 4% formalin and subsequently stored in 70% ethanol. To assess potential dietary overlap between flowerhorns and the endemic sailfin silversides radiations, stomach content data from previous studies which characterized feeding ecology in Lake Matano's *Telmatherina* (Pfaender *et al.*, 2011, 2016) were incorporated into the analyses. Thus, analyses included data from the 'roundfin' species flock [*T. antoniae* 'large', *n* = 17; *T. antoniae* 'small', *n* = 20; and *T. prognatha*, *n* = 20 (Pfaender *et al.*, 2011)] and from the 'sharpfin' radiation [*T. sarasinorum*, *n* = 229; *T. opudi*, *n* = 426; *Telmatherina* sp. 'elongated', *n* = 192; *T. wahjui, n* = 56; and *Telmatherina* sp. 'thicklip', *n* = 28 (Pfaender *et al.*, 2016)].

Stomach content analysis

Standardized photographs and high-resolution X-ray images of each specimen were taken in the laboratory prior to dissection. All X-ray images included a size standard, and were taken with a digital X-ray device (Faxitron X-Ray LX 60). The whole of the gastrointestinal tract was removed and the gutted body, gonads, liver, stomach contents, and gut were weighed to the nearest 0.001 g (Satorius E2000D). To calculate the standard length (distance between the most anterior point of the upper jaw and the hypural plate), two landmarks were placed on digital X-ray images using the software tpsDig v. 2.17 (Rohlf, 2013). The distance between the two landmarks was extracted with an in-house script and the R package geomorph (Adams and Otárola-Castillo, 2013; R Development Core Team, 2013).

Stomach contents were extracted and food items were either embedded in Gelvatol (Polyvenylalcohol) or stored in 70% ethanol. In the absence of a clear delimitation of the stomach and the remaining digestive tract, only the contents of the first third of the intestinal tract was analysed, since easily digestible prey are absent in hindguts, affecting the accuracy of dietary analyses (Sutela and Huusko, 2000). Prey items were determined to the lowest feasible taxonomic level and assigned to diet components (Annelidae, Bivalvia, Copepoda, Gastropoda, Ostracoda, shrimps, aquatic insects, terrestrial insects, fish, fish scales, fish eggs, crabs, aufwuchs, detritus, plants, unidentifiable). A reference sampling of fish scales, incorporating Lake Matano's major species flocks (Hemiramphidae, Gobiidae, and Telmatherinidae) was photographed and compared with the fish scales ingested by the flowerhorns. As fish scales were often found without any additional fish parts, fish scales were not necessarily considered an indicator of true piscivory. This is because fish scales are not only ingested by consuming prey species, or in a failed attempt to do so – they may serve as a significant food resource in their own right (Sazima, 1984). Accordingly, if stomachs contained fish scales, but neither bones nor tissue that could be assigned to fish, they were labelled a separate food category, i.e. fish scales. The relative volumetric proportions (as percentages) of food components were estimated for each individual using a photo binocular (Olympus SZX12) (for further details, see Herder and Freyhof, 2006). Fish with no or unidentifiable stomach contents (4 of 136 individuals) were classified as empty and excluded from further analyses. The already available data for sailfin silverside stomach contents (Pfaender *et al.*, 2011, 2016) was generated in a similar fashion to that of the flowerhorns described above.

Ontogenetic niche shift and dietary overlap

Our flowerhorns ranged from small juveniles (16 mm standard length, SL) to mature specimens (120 mm SL), allowing us to investigate potential ontogenetic niche shifts. To reduce the dimensionality of the stomach content data and to remove autocorrelations between diet components, we performed a principal components analysis (PCA) using the dudi.pca function implemented in the R package ade4 (Chessel *et al.*, 2004). As eigenvalues of the diet principal components (PCs) reached a plateau at PC7, and declined more rapidly after PC9 (Fig. 2a), the first nine PCs (75.2% cumulative variance explained) were included in further analyses. To investigate ontogenetic changes in diet composition, linear regression models [lm, stats (R Development Core Team, 2013)] were fitted using the first nine PCs as dependent variables and log-transformed standard length (log(SL)) as the predictor variable including sampling site as a fixed effect.

To determine the standard length at which a potential trophic niche shift from juvenile to adult foraging occurs, fish were pooled into two-centimetre size classes (<40 mm, $n = 9$; 40–59.99 mm, $n = 43$; 60–79.99 mm, $n = 55$; 80–99.99 mm, $n = 21$; 100–120 mm, $n = 4$). The first two size classes (0–19.99 mm and 20–39.99 mm) were combined since the first group (<20 mm) only contained two individuals. One-way analyses of variance [anova, stats (R Development Core Team, 2013)] were applied to estimate diet differences between size classes for all diet PCs that were significantly correlated with log-transformed SL. A Levene test [levene.test, lawstat (Hui *et al.*, 2008)] was used to check for unequal variances. In the case of unequal variances, a Kruskal-Wallis rank sum test [kruskal.test, stats (R Development Core Team, 2013)] was used instead of a one-way ANOVA. If one-way ANOVAs/Kruskal-Wallis rank sum tests were significant, a Bonferroni-corrected LSD test [LSD.test, agricolae (De Mendiburu, 2010)] was used to determine pairwise differences between size classes. Niche width was calculated using the Shannon index (SI) of niche width [niche.width, spaa (Zhang *et al.*, 2013)].

Since the composition of diets differed significantly between flowerhorns < 40 mm and individuals ≥ 40 mm, size classes were merged into two groups (<40 mm and ≥40 mm) to calculate pairwise dietary overlap with endemic sailfin silversides using the Schoener index (Schoener, 1971) [niche.overlap, spaa (Zhang *et al.*, 2013)]. This index ranges between 0 (no overlap) and 1 (complete overlap) and is considered significant at a value > 0.6 (Schoener, 1971). Finally, EcoSimR (Gotelli and Ellison, 2013) was used to determine whether observed niche overlaps (Metric: Pianka) deviated significantly from what might be expected by chance based on a simulated null distribution (10,000 replications) of resource usage taking into account the observed niche width (setting 're3') of each species. This method was employed for both the community of endemic species in our analysis as well as all pairwise comparisons of flowerhorns with endemics.

RESULTS

Diet and ontogenetic niche shift

The wide range of food items present in the flowerhorn stomach contents (Figs. 1, 2) confirms that these cichlids are predatory generalists. Diet varied between the different sites, e.g. snails were much more abundant in samples from the two westernmost sites that are characterized by relatively gentle slopes (Fig. 1). Linear models that included sampling site as a fixed effect revealed significant correlations of log-transformed standard length with the first ($P < 0.001$; $R^2_{\mathrm{adj}} = 0.18$; slope = −1.55; SE = 0.34) and the second ($P < 0.001$; $R^2_{\mathrm{adj}} = 0.35$; slope = 1.82; SE = 0.29) principal components of the diet dataset. The first principal component (PC1) summarized variation (11.3%) between hard-shelled prey, such as gastropods and bivalves, and softer prey dominated by ostracods and aquatic insects (Fig. 2a). Variation between a predatory diet including fish, crabs and shrimps, and smaller less well armed or less agile prey such as ostracods and aquatic insects was summarized by PC2 (10.3%) (Fig. 2a). Significant differences between size classes (< 40 mm, $n = 9$; 40–59.99 mm, $n = 43$; 60–79.99 mm, $n = 55$; 80–99.99 mm, $n = 21$; 100–120 mm, $n = 4$) were apparent in both PC1 (ANOVA: $P = 0.005$) and PC2 (Kruskal-Wallis rank sum test: $P < 0.001$). In both axes, the first size class (<40 mm) differed significantly from all remaining size classes (≥40 mm) based on a Bonferroni-corrected LSD test ($\alpha = 0.05$) (Fig. 2b, c). Consequently, individuals smaller than 40 mm were labelled immature feeders while larger specimens were assumed to exhibit an adult feeding strategy and were thus labelled adults, even though sexual maturity is reached later in life [60–70 mm SL in the field and aquarium (Jobst Pfaender and Leon Hilgers, personal observations)]. While immature foragers, which were collected at four of the six sample sites, occupied a narrow trophic niche (Shannon index = 0.86) and fed mainly on aquatic insects (75.6%) and ostracods (15.0%), adult feeders exhibited a more omnivorous diet (Shannon index = 2.34) that included gastropods (19.7%), fish (14.6%), fish scales (14.4%), aquatic insects (9.3%), shrimps (*Caridina*) and bivalves (both 8.5%) (Fig. 2d).

Predation pressure

Determination of prey items revealed that flowerhorns consumed species of all major lake radiations (see Table 1). Most prey items could not be determined to species level owing to partial ingestion, destruction or digestion. Prey species that were identified to species level included the crab species *Nautilotelphusa zimmeri* and the shrimp species *Caridina lanceolata*. Flowerhorns consumed multiple shrimp species of the genus *Caridina* as well as gastropods of the families Tadeidae, Pachychilidae (*Tylomelania*), and likely Planorbidae*,* the latter of which has not been recorded from Lake Matano to date. The diet of flowerhorns also included water mites (Hydrachnidae), Hymenoptera, Nepomorpha, and the larvae of Trichoptera and Diptera, together with one individual of Odonata. Additionally, flowerhorns preyed on conspecifics, small gobies (*Mugilogobius*), and sailfin silversides (*Telmatherina*). Ingested bivalves mainly belonged to the family Corbiculidae, but Sphaeriidae were also observed.

Niche width and dietary overlap

Adult flowerhorn cichlids occupied a wider trophic niche than the sympatric sailfin silversides (see Table 2). The highly specialized zooplankton feeder *T. antoniae* 'small' and juvenile flowerhorns had the smallest trophic niche width, while the two remaining roundfins, *T. antoniae* 'large' and *T. prognatha*, also occupied very distinct trophic niches. Compared with the other sharpfins, the specialized shrimp feeder *Telmatherina* sp. 'thicklip' had the narrowest trophic niche, followed by the copepod- and gastropod-feeding *T. wahjui* and the egg-feeding *T. sarasinorum. Telmatherina opudi* and *Telmatherina* sp. 'elongated' exhibited the largest trophic niche breadths of the endemic species examined (Table 2).

Flowerhorns utilized most of the trophic resources that dominated the diet of sailfin silversides with the exception of copepods (0%), which were most abundant in the diet of

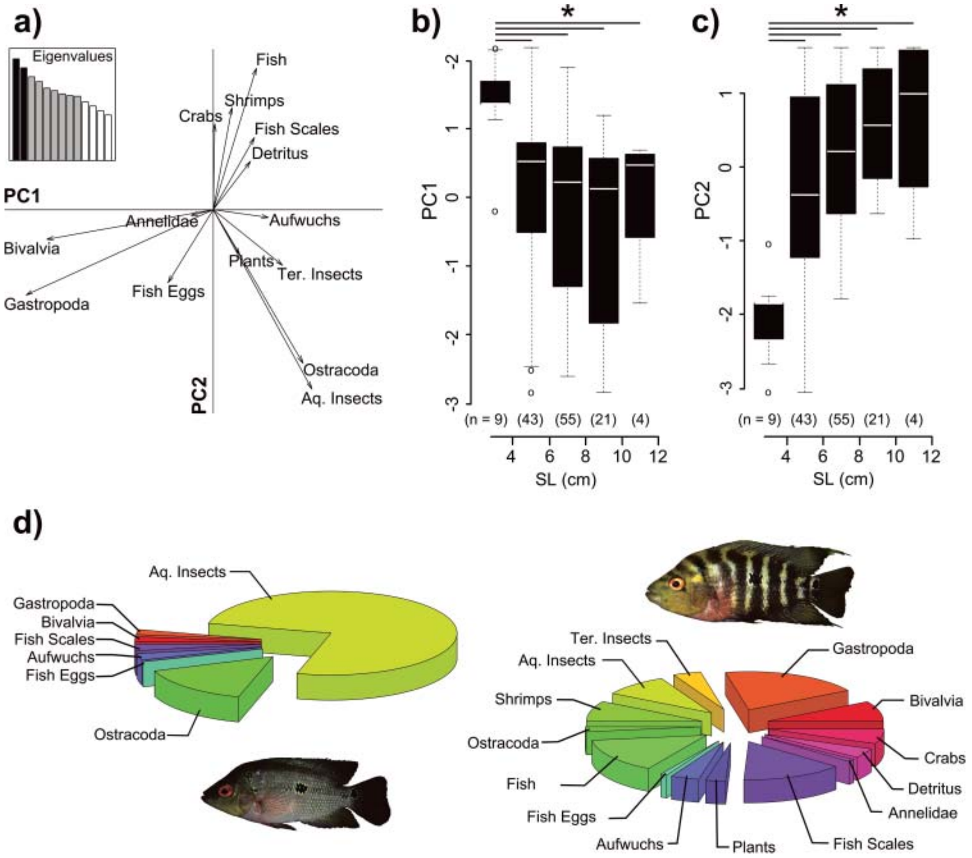
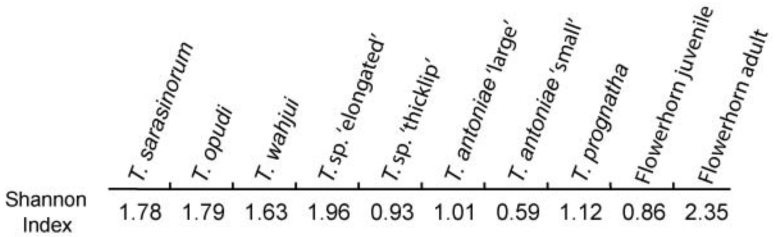


Fig. 2. Ontogenetic niche shift in flowerhorn cichlids. (a) Biplot of the two principal components (PCs) of the flowerhorn diet, which exhibited a linear correlation with standard length and the corresponding eigenvalues (black bars). Eigenvalues of further PCs that were included in the analysis are shown in grey. Angles between variable trajectories indicate similarity and length represents the influence of the respective variables. PC1 divides hard-shelled molluscs and softer prey, including ostracods, terrestrial insects, and aquatic insects. PC2 differentiates between small crustaceans and aquatic insects on the one hand, and a predatory diet including fish, crabs, and shrimps on the other. Boxplots of diet principal components PC1 (b) and PC2 (c) indicate a trophic niche shift between size classes 1 (>4 cm) and 2 (4–5.99 cm). Asterisks indicate significant ($P > 0.05$) differences between the first and all other size classes in both diet PCs. Pie charts show volumetric proportions of diet composition in juvenile and adult foragers. The diet of juveniles (SL < 4 cm) is dominated by aquatic insects and ostracods (d – left), whereas individuals ≥ 4 cm SL exhibit an omnivorous predatory diet (d – right).

T. antoniae ‘small’ (82%), and fish eggs (0.9%), which were primarily ingested by *T. sarasinorum* (39%) (see Fig. S1, evolutionary-ecology.com/data/3112Appendix.pdf). Additionally, the stomachs of adult flowerhorns contained considerable amounts of fish scales (14.4%), bivalves (8.5%), and crabs (6.3%), which were almost entirely absent from the diet of *Telmatherina*.

Table 1. Diet composition of flowerhorn cichlids in Lake Matano and identified prey taxa

Prey category	Consumed by *n* individuals	% of population	Mean volume (%) of diet	Identified taxa
Bivalvia	38	28.79	8.11	Corbiculidae Sphaeriidae
Gastropoda	63	47.73	18.66	Planorbidae Tadeidae *Tylomelania* sp.
Shrimps	21	15.91	8.00	*Caradina* sp. *Caradina lanceolata*
Ostracoda	15	11.36	2.88	NA
Crabs	17	12.88	5.87	*Nautilotelphusa zimmeri*
Aquatic insects	53	40.15	13.31	Hydrachnidae Diptera Nepomorpha Trichoptera Odonata
Terrestrial insects	20	15.15	3.67	Hymenoptera
Fish eggs	10	7.58	0.89	NA
Fish	28	21.21	13.71	*Telmatherina* sp. *Mugilogobius* sp. Flowerhorn cichlid
Fish scales	39	29.55	13.64	*Telmatherina* sp. *Mugilogobius* sp. *Glossogobius* sp. Flowerhorn cichlid



	T. sarasinorum	*T. opudi*	*T. wahjui*	*T. sp. 'elongated'*	*T. sp. 'thicklip'*	*T. antoniae 'large'*	*T. antoniae 'small'*	*T. prognatha*	Flowerhorn juvenile	Flowerhorn adult
Shannon Index	1.78	1.79	1.63	1.96	0.93	1.01	0.59	1.12	0.86	2.35

Table. 2. Shannon index indicating trophic niche width for *Telmatherina*, as well as juvenile and adult flowerhorns

Dietary overlap was generally highest among sharpfin sailfin silversides with the exception of *Telmatherina* sp. 'thicklip' (Fig. 3). *Telmatherina wahjui* and *T. opudi* (Schoener index, SI = 0.89) displayed the most prominent dietary overlap, followed by the combinations *Telmatherina* sp. 'elongated'/*T. sarasinorum* (SI = 0.7), *Telmatherina* sp. 'elongated'/*T. opudi* (SI = 0.69), *T. sarasinorum*/*T. opudi* (SI = 0.66), and *Telmatherina* sp.

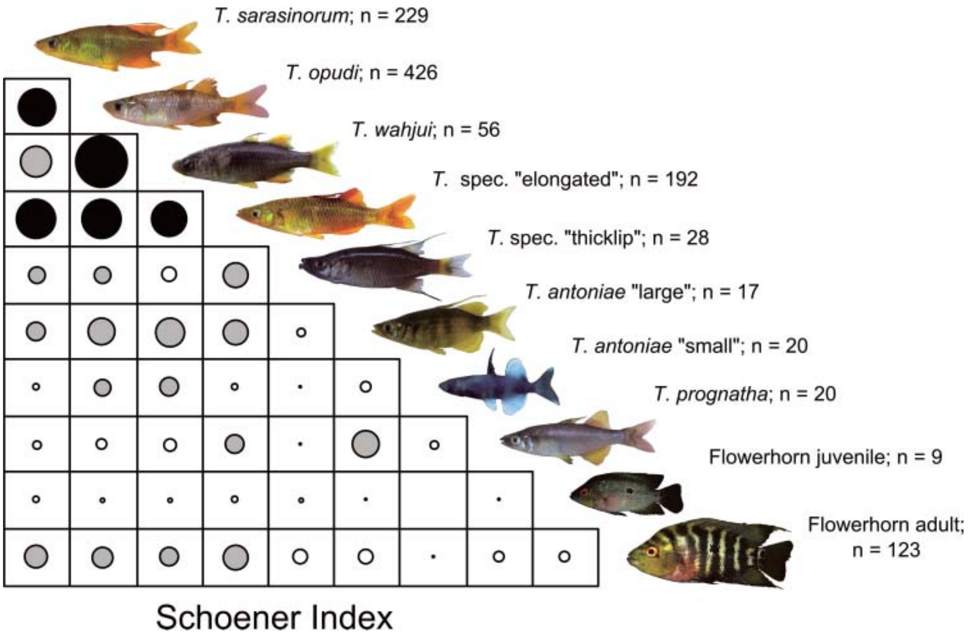


Fig. 3. Dietary overlap (Schoener index) between endemic sailfin silversides and invasive flowerhorn cichlids. The extent of dietary overlap between species pairs is indicated by different sized circles. Solid black circles indicate significant dietary overlap (Schoener index > 0.6), while grey circles indicate dietary overlap > 0.3.

'elongated'/*T. wahjui* (SI = 0.63). The highest dietary overlap despite sharpfin/sharpfin interactions was observed between *T. antoniae* 'large' and *T. wahjui* (SI = 0.51). In line with these observations, null distributions of niche overlap simulated with EcoSimR (Gotelli and Ellison, 2013) revealed that niche overlap among endemic *Telmatherina* was significantly higher ($P = 0.0002$; observed = 0.44; mean simulated = 0.22; standardized effect size = 5.73) than expected by chance given their niche width (Appendix Fig. S2a).

Adult flowerhorns had low to medium dietary overlap with endemic species of the genus *Telmatherina* and pairwise niche overlap between endemics and the invader was never significantly above that expected based on EcoSimR (Gotelli and Ellison, 2013). The greatest dietary overlap with adult flowerhorn cichlids was observed for *Telmatherina* sp. 'elongated' (SI = 0.44), followed by *T. sarasinorum* (SI = 0.43), *T. opudi* (SI = 0.39), and *T. wahjui* (SI = 0.35). *Telmatherina antoniae* 'small' was the only species for which niche overlap with adult flowerhorns was significantly lower than expected based on the simulated null distribution ($P = 0.012$; observed = 0.02; mean simulated = 0.233; standardized effect size = −1.31) (Appendix Fig. S2b). Juvenile flowerhorns showed minimal dietary overlap with the endemic species investigated (SI ranged from no overlap in the case of *T. antoniae* 'small' to 0.15 for *Telmatherina* sp. 'elongated'). The highest though still limited dietary overlap of immature flowerhorns was found with mature conspecifics (SI = 0.21). Niche overlap of endemics with juvenile flowerhorns never deviated significantly from that expected based on the simulated null distribution.

DISCUSSION

The global aquarium trade is a major source of aquatic invasions and thus poses a significant threat to global biodiversity (Magalhães and Vitule, 2013). Lake Matano is the hydrological head of the Malili Lakes system and is faced with the invasion of a hybrid fish generated for the ornamental fish trade, the flowerhorn cichlid. The Malili Lakes system harbours an outstanding diversity of endemic species flocks and has even been referred to as the 'submerged Galapagos' (von Rintelen *et al.*, 2007). Here we investigate trophic interactions between flowerhorn cichlids and endemic species flocks of Lake Matano.

Predation pressure

Flowerhorn cichlids preyed on members of all major endemic radiations, including aquatic snails (*Tylomelania*), shrimps (*Caridina*), fishes (*Telmatherina*, *Mugilogobius*), and crabs (Parathelphusidae). Furthermore, its diet frequently included Ramshorn snails (Planorbidae) that to date have not been described from Lake Matano. These could represent either an as yet undetected endemic or another introduced species, which indicates both the potential for undetected consequences of additional alien invasions and the need for further research on this ecosystem. Since the introduction of non-native predators can be fatal to the biota of island habitats (Davis, 2003; O'Dowd *et al.*, 2003), the recent introduction of flowerhorn cichlids has to be considered highly threatening for the endemic species of ancient Lake Matano. The impact of food web alterations and energy flows is beyond the scope of this study, but far-reaching effects via these pathways have been reported for other invasions (O'Dowd *et al.*, 2003; Baxter *et al.*, 2004; Simberloff, 2011). Accordingly, flowerhorn cichlids prey on various endemic species, some of which – such as crabs – are completely absent from the diet of roundfins and sharpfins. Even though such species may originally have been preyed upon by other endemics such as gobies, which were not included in our analysis, additional predation pressure by a predator, with which the endemic species shares no adaptive history, may significantly reduce the abundance of prey species, and may even lead to species extinctions (Witte *et al.*, 1992; O'Dowd *et al.*, 2003). If an introduced predator has no functional correlate in the invaded ecosystem, prey species are often not adapted to that predator and are thus often unequipped to withstand the resulting predation pressure (Case and Bolger, 1991; O'Dowd *et al.*, 2003). Prey species may lack the physiological capabilities to avoid excessive predation (O'Dowd *et al.*, 2003), or, as hypothesized for many freshwater invasions, show inappropriate behaviour in the face of the newly introduced predator (Cox and Lima, 2006). This appears to be the case in the guarding behaviour of endemic *Glossogobius* gobies, where flowerhorns were observed to feed on a clutch of eggs, with no reaction on the part of the guarding male (Herder *et al.*, 2012).

Generally, the food items analysed in this study allowed identification to species level in a minority of cases only. Further investigations are needed to help predict how flowerhorn predation will affect individual members of the diverse species flocks of Lake Matano.

Competition for trophic resources

Despite the debate about how frequently competition for resources leads to species extinctions (Davis, 2003), it is generally accepted that competition can result in competitive exclusion of native species in resource-limited environments (Mooney and Cleland, 2001; Bøhn *et al.*, 2008). Thus, increased competition for trophic resources following the introduction of flowerhorns has the potential to considerably affect resource availability for endemics.

Although flowerhorns utilized most trophic resources that dominated the diet of sailfin silversides, our data revealed no major dietary overlap between flowerhorns and any single endemic species (Fig. 3). Accordingly, pairwise dietary overlap between endemics and the invader was never significantly higher than expected by chance, given their niche width. Instead, dietary overlap among endemic *Telmatherina* was significantly higher than expected by chance (Appendix Fig. S2), which is in line with previously described ongoing trophic specialization in a resource-limited environment (Herder *et al.*, 2006a; Gray *et al.*, 2008; Pfaender *et al.*, 2010, 2016). However, *Telmatherina* species with almost identical diets differ significantly in their habitat use (see Herder *et al.*, 2008; Pfaender *et al.*, 2010, 2016), reducing competition for similar prey. *Telmatherina* sp. 'elongated', *T. sarasinorum, T. wahjui*, and *T. opudi* – the species showing the greatest dietary overlap with flowerhorn cichlids (Fig. 3) – all have at least one substantial trophic resource (>20% of their diet) that is rarely consumed (<5%) by flowerhorns. Such resources may serve as trophic refuge and buffer effects of increased competition. Nonetheless, the omnivorous feeding habits of flowerhorns are contrasted by the trophic specialization of endemics. The effects of increased competition are likely to have a greater impact on specialists, because resources that are competed for account for a larger proportion of specialists' diets, which is not reflected by the symmetric Schoener index. Furthermore, changing resource usage based on availability throughout the year and thus seasonal changes in competition requires further study, because the flowerhorns analysed in this study were sampled during the dry season only. Nonetheless, the available data suggests that competition for trophic resources likely poses a less significant threat to the investigated native fauna than predation pressure. Analysis of the population sizes of endemics, before and after the invasion, as well as their diets and habitat use of flowerhorn cichlids is needed to make detailed predictions on species-wise invasion effects.

Invasion success

The successful and very recent invasion of Lake Matano by flowerhorn cichlids is in line with predictions of biological invasions owing to human modification of ecosystems (Didham *et al.*, 2005, 2007; Bramburger *et al.*, 2017). As reported for many other invasive freshwater fishes (Nico and Fuller, 1999; Gido and Franssen, 2007; Strayer, 2010), Lake Matano's flowerhorns are aggressive, territorial fishes that exhibit pronounced parental care (Nico *et al.*, 2007; Knight, 2010). The stomach content data of the present study characterized Lake Matano's flowerhorns as omnivorous feeders, consuming a considerable amount of fish (Fig. 2d). In contrast to the more specialized sailfin silverside species, adult flowerhorns occupy a wide trophic niche. The potential to exploit multiple resources may contribute to the flowerhorns' invasive success because niche width was previously shown to be positively linked with invasion success (see Vazques, 2006 for a review; Hill *et al.*, 2015). Additionally, flowerhorns consumed large amounts of bivalves and crabs, which were almost absent from the diet of *Telmatherina*. Accordingly, flowerhorns exhibited only low to medium dietary overlap with the native *Telmatherina*, which may have facilitated their successful invasion. Furthermore, the present analyses show that the Matano flowerhorn population exhibits a prominent ontogenetic trophic niche shift. Aquatic insects and ostracods dominate the diet of juveniles, while adults have an omnivorous diet dominated by molluscs, fishes, shrimps, and crabs (Fig. 2d). Ontogenetic shifts in diet composition are common in teleost fishes (Werner and Gilliam, 1984;

Persson, 1988), but have – in contrast to other trophic features – rarely been investigated in the context of invasion success (but see García-Berthou, 2002; Jang *et al.*, 2006; Hasegawa *et al.*, 2012; Hayden *et al.*, 2013).

Theory predicts that ontogenetic niche shifts reduce competition between adults and juveniles (Werner and Gilliam, 1984), which can significantly influence resource availability (Claessen and Dieckmann, 2002). Limited inter- and intraspecific competition may increase the chances for a successful invasion, because resource availability is crucial for the establishment of alien species (Shea and Chesson, 2002). Competition has an effect in particular on the juveniles of predatory fishes, which often compete with their prospective prey, leading to so-called competitive bottlenecks (Persson and Greenberg, 1990; Amundsen *et al.*, 2003). Interestingly, juvenile flowerhorns show only minimal dietary overlap with species of the endemic *Telmatherina* flocks, indicating low interspecific competition for trophic resources (Fig. 3). This finding is in line with the stochastic niche theory (Tilman, 2004), which predicts that limited competition between juvenile invaders and natives markedly enhances the invader's chances of establishment. However, despite the wide array of trophic resources utilized by sailfin silversides, only adult *Telmatherina* were considered here. Hence, it cannot be ruled out that juvenile sailfin silversides or other endemic fish species like gobies, ricefishes or halfbeaks exhibit a greater dietary overlap with juvenile or adult flowerhorns, something which requires further research. Intrinsic factors promoting successful fish invasions reportedly include a generalized diet, aggressiveness, effective reproduction, and a medium to large body size (Nico and Fuller, 1999). Thus, the combination of aggressive territoriality, parental care, omnivorous feeding habits, and limited intraspecific competition between different life stages may explain the high invasive potential of flowerhorns in general. Specifically, low to medium interspecific competition for trophic resources with sailfin silversides may explain the rapid range expansion and very high abundances of flowerhorns around Lake Matano (Herder *et al.*, 2012).

Conclusions

The invasive flowerhorn cichlids occupy a broad trophic niche, but dietary overlap with the endemic sailfin silversides remains limited. A pronounced ontogenetic dietary shift by flowerhorns may have facilitated their successful invasion into Lake Matano, because juvenile flowerhorns neither compete for trophic resources with adult conspecifics, nor with the endemic fish species investigated in this study. In contrast to limited competition with endemic *Telmatherina*, cichlid stomach contents indicate that predation pressure on the endemic fish and invertebrate radiations is significant. Thus, the recent invasion of flowerhorn cichlids constitutes a serious threat to the scientifically, economically, and ecologically valuable – but equally vulnerable – ecosystem of Lake Matano. Although removal of flowerhorns from the lake would appear an impossible task, a sound impact assessment and monitoring programme is necessary to help manage the system. Similarly, education of the public and policy-makers combined with stricter legislation might help reduce the possibility of further alien introductions into this and other aquatic habitats in Sulawesi.

DATA ACCESSIBILITY

The raw stomach content data and exact niche overlaps are available at evolutionary-ecology.com/data/3112Appendix.pdf.

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