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Trophic specialization on unique resources despite limited niche divergence in a celebrated example of sympatric speciation

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Abstract

Trophic niche partitioning is observed in many adaptive radiations and is hypothesized to be a central process underlying species divergence. However, patterns of dietary niche partitioning are inconsistent across radiations and there are few studies of niche partitioning in putative examples of sympatric speciation. Here, we conducted the first quantitative study of dietary niche partitioning using stomach contents and stable isotope analyses in one of the most celebrated examples of sympatric speciation: the cichlid radiation from crater lake Barombi Mbo, Cameroon. We found little evidence for trophic niche partitioning among cichlids, including the nine species coexisting in the narrow littoral zone. Stable isotope analyses supported these conclusions of substantial dietary overlap. Our data, however, did reveal that five of eleven species consume rare dietary items, including freshwater sponge, terrestrial ants, and nocturnal foraging on shrimp. Stomach contents of the spongivore (*Pungu maclareni*) were 20% freshwater sponge, notable considering that only 0.04% of all fishes consume sponges. Overall, we conclude that cichlid species in lake Barombi Mbo overlap considerably in broad dietary niches—in part due to the large proportion of detritus in the stomach contents of all species—but there is evidence for divergence among species in their diet specializations on unique resources. We speculate that these species may utilize these additional specialized resources during periods of low resource abundance in support of Liem's paradox.

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AUTHORS' CONTRIBUTION STATEMENT
Conceived and designed the investigation: CHM
Performed field and/or laboratory work: CHM, CDT, LNG, KM
Analyzed the data: JRG, MES
Contributed materials, reagents, and/or analysis tools: CHM
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Keywords

trophic niche partitioning; dietary niche partitioning; dietary specialization; specialization; adaptive radiation; ecological divergence; sympatric speciation; Liem's paradox

INTRODUCTION

Adaptive radiations are a hallmark of evolutionary biology, being among the most celebrated, studied, and charismatic examples of ecological diversity. Much research on these systems centers on uncovering the mechanisms driving diversification (Schluter 2000; Martin & Richards 2019; Stroud & Losos 2020), and there are several hypotheses suggesting that specific temporal, spatial, environmental, and/or genomic factors are necessary for a radiation to proceed (Schluter 2000; Gavrilets & Losos 2009; Richards et al. 2021). Many of these theories highlight the importance of divergence in trophic niche, as dietary niche partitioning can allow for the coexistence of similar species by reducing interspecific competition for limited food resources (Ross 1986; Winemiller & Pianka 1990; Reinthal 1990; Correa & Winemiller 2014; Varghese et al. 2014). For example, the stages hypothesis suggests that adaptation occurs in distinct, ordered stages, and that divergence in habit is followed by divergence in trophic morphology and diet, and finally divergence in traits related to communication (Danley and Streelman 2003). Other hypotheses suggest that divergence in dietary niche may occur early in diversification (Ackerly et al. 2006), and still others suggest that shifts in dietary niche can occur without much phenotypic change (Gavrilets & Losos 2009). Even though multiple hypotheses assume that divergence in trophic niche—as well as divergence in relevant phenotypic traits—are ubiquitous and integral to adaptive radiations, evidence from empirical studies remains conflicting (Gillespie et al. 2020). To fully understand how divergence in dietary niche contributes to diversification in adaptive radiations, we need more empirical evidence documenting the patterns and frequency of trophic niche partitioning in examples in nature.

African cichlids are widely regarded as a model system for studying adaptive radiation and have been especially useful for investigating patterns of dietary niche partitioning. There is great diversity in trophic divergence patterns among closely related cichlid species, with no single solution to how diet relates to diversification. For example, the species flocks of lakes Malawi, Victoria, and Tanganyika contain dietary specialists and closely related species that exhibit varying levels of trophic niche partitioning (Kocher 2004; Martin & Genner 2009; Wagner et al. 2009), providing evidence that divergence in dietary niche is important for adaptive radiations. Yet divergence in these lakes cannot solely be attributed to dietary differences. Habitat partitioning (Albertson 2008; Conith et al. 2020) and sexual selection (McKaye et al. 1993; Taylor et al. 1998; Seehausen 2000; Stauffer et al. 2002; Streelman & Danley 2003; Martin & Genner 2009; Poelstra et al. 2018) are also hypothesized to play an important role in the observed ecological diversity of these lineages. Additionally, many sympatric rock-dwelling Malawi cichlids exhibit differences in trophic morphology, but still show extreme dietary overlap (Ribbink et al. 1983; Reinthal 1990; Genner *et al.* 1999*a*; Genner *et al.* 1999b; Martin & Genner 2009), suggesting that many closely related species can diversify and coexist without strong trophic niche divergence (see also

Stauffer & McKaye 2002; McKaye et al. 2002 for an example of dietary overlap among co-occurring cichlids in Nicaraguan crater lake Xiloá). This phenomenon—where trophic specialists act as "jacks-of-all-trades" able to consume both their narrow food source as well as a more generalist diet despite substantial differences in trophic morphology—is known as "Liem's paradox" (Liem 1980). Contrastingly, there are African cichlid systems in which diet may be the primary driver of ecological divergence, such as the *Alcolapia* species flock of the alkaline Lake Natron (Seegers & Tichy 1999). These three herbivorous species exhibit fine-scale trophic and ecomorphological differences despite limited genomic differentiation, suggesting the importance of trophic niche partitioning in the diversification of this clade (Ford et al. 2016). Continuing to investigate these diverse, unique patterns of dietary divergence will aid in understanding how trophic niche partitioning contributes to ecological diversity in adaptive radiations, especially in systems where diet is hypothesized to play an integral role in divergence.

One such system is the African cichlid radiation in crater lake Barombi Mbo, Cameroon. This adaptive radiation contains 11 endemic cichlid species, including a monophyletic *Stomatepia* clade (*Stomatepia mongo*, *Stomatepia mariae*, and *Stomatepia pindu*), a polyphyletic *Sarotherodon* group (S*arotherodon linnellii, Sarotherodon caroli, Sarotherodon steinbachi,* and *Sarotherodon lohbergeri*), the shallow/deep-water sister species pair of *Konia* (*Konia eisentrauti* and *Konia dikume*), and monotypic genera *Pungu maclareni* and *Myaka myaka* (see Martin et al. 2015 for phylogenetic relationships). The cichlids of Barombi Mbo are an excellent system to investigate patterns of dietary niche partitioning for several reasons. First, the radiation is celebrated as a putative example of sympatric speciation in nature and is responsible for renewing interest in the empirical and theoretical study of this process (Schliewen et al. 1994; Turelli et al. 2001; Schliewen and Klee 2004; Coyne et al. 2004; Bolnick & Fitzpatrick 2007; Martin 2012; Richards et al. 2019). Second, dietary partitioning appears to be the primary axis of divergence in this system (Martin 2012). In a second radiation of *Coptodon* cichlid species endemic to Lake Ejagham, Cameroon—another recognized example of sympatric speciation in nature—olfactory preferences and sexual selection are hypothesized to play a primary role in divergence (Martin 2013; Poelstra et al. 2018), making it difficult to isolate the effects of diet. The cichlid radiation of Barombi Mbo, on the other hand, displays striking differences among sympatric species in trophic morphology and there is no evidence of sexual dimorphism in 10 out of the 11 species in the lake, suggesting that differences in diet may be the primary driver of ecological divergence (Martin 2012). Finally, despite the renewed interest in this system, few studies have documented the dietary niches of each species, nor have they quantitatively identified species that may partake in dietary specialization. Trewavas et al. (1972) provided qualitative descriptions of dietary profiles among species and identified potential specialist species that feed heavily on plants (*K. eisentrauti*) and freshwater sponges (*P. maclareni*). More recently, Martin (2012) investigated trophic position divergence within endemic *Stomatepia spp.* using stable isotope data, finding minimal divergence within the genus but some difference between *Stomatepia spp.* and *P. maclareni.* Still, divergence in dietary components (i.e. stomach contents) and relative trophic position (i.e. stable isotopes) has not been recently assessed for all species. Furthermore, the dietary niche partitioning patterns, especially among generalists and putative specialists, are still unknown.

Here we measured the dietary profiles of all cichlid species from Barombi Mbo. We used stomach content analyses to quantify differences in dietary item proportions, niche width and overlap, and overall dietary composition (9 out of 11 species). We also used stable isotope analyses to investigate relative trophic position and carbon source differences among species over a longer timeframe than the “snapshot” provided by stomach content data (11 out of 11 species). These data allowed us to specifically investigate 1) the extent of dietary niche partitioning and overlap occurring in the system, 2) the existence of any unique or specialized food items, and 3) the extent of tropic specialization—all necessary for furthering our understanding of how dietary divergence contributed to diversification in this system.

METHODS

Study site and sample collection

Barombi Mbo is a 1 Mya volcanic crater lake (Cornen et al. 1992) in southwestern Cameroon. It is roughly circular in shape with a diameter of 2.5 km and a maximum depth of 110 m, but the oxic zone only reaches to 30 m (Trewavas et al. 1972; Cornen et al. 1992; Musilova et al. 2019). We collected samples in December 2009 through January 2010, and in July through December, 2016 from several localities in the lake using a 6 x 2 m seine net with 0.5 cm^2 mesh. *Sarotherodon linnellii* and *K. dikume* were caught by artisanal fishers using gill nets. We collected all 11 cichlid species that are endemic to Barombi Mbo. We euthanized captured fish with an overdose of MS-222 and immediately took a 5 mg muscle tissue sample from the caudal peduncle for stable isotope analysis. Muscle samples were desiccated individually with magnesium perchlorate in airtight vials following Martin (2012; 2013). Specimens were then individually labeled and fixed in 95-100% ethanol. Field procedures followed approved protocols by the Institutional Animal Care and Use Committees of the University of California, Davis and the University of North Carolina at Chapel Hill.

Stomach content analyses

In total, we selected 241 individuals for stomach content analysis, including at least 3 individuals from each species. Nine out of the lake’s 11 endemic species of cichlid were analyzed in this study, all except *S. caroli* and *S. lohbergeri*, which are morphologically and ecologically similar to *S. linnellii* and *S. steinbachi*, respectively (Trewavas et al. 1972). We removed the entire stomach and intestine from each individual and placed stomach contents or a subset of the intestine on a Sedgwick-Rafter cell containing 1 x 1 mm squares for visualization and quantification under a stereomicroscope (following Martin and Wainwright 2013). Dietary proportions were based upon a visual volume estimation method (Hyslop 1980; Manko 2016). We compressed stomach contents to a uniform thickness (approx. 0.5 mm) and estimated the surface area of each prey item by counting the number of 1 mm^2 squares covered by the item (Hyslop 1980; Gelwich & McIntyre 2017). Smaller items were assigned fractions of a square to the nearest 0.1 mm^2. This number was then divided by the total number of squares covered by all diet items for that individual to calculate individual dietary proportions for each item. Proportions were rounded to the nearest 0.001

and are reported as percentages. Individuals with empty stomachs were excluded from all subsequent calculations and statistical analyses (*n* = 38).

We identified all diet items based on partially digested remnants, including exoskeletal remains, plant matter, and sponge spicules; unidentified organic matter was classified as detritus, and inorganic matter—such as particles of sand—was classified as silt. All prey items were grouped into taxa, usually to the level of class or family. Diet categories were comparable to previously identified prey items of the cichlid species described in Trewavas et al. (1972). We used 13 diet categories in total: ants, *Corvospongilla spp.* sponge, Dipteran larvae, Ephemeropteran larvae, Trichopteran larvae, fish, gastropod shell, nematode, plant tissue, shrimp, detritus, silt, and unidentified. Ants were identified by distinct head capsules of species within Formicidae, which likely originated from terrestrial debris that fell into the lake. The sponge category consisted of two members of the genus *Corvospongilla*: *C. thysi*, endemic to Barombi Mbo, and closely related *C. bohmii* (Trewavas et al. 1972). Both species are found in the lake's shallow waters (up to 3-4 m depth), with *C. thysi* typically covering the outer surfaces of rocks and *C. bohmii* found in crevices (Trewavas et al. 1972). Dipteran larvae included larval forms of the midge families Chaoboridae and Chironomidae. Ephemeropteran larvae included larval forms of various mayfly families Baetidae and Caenidae. This category also included larvae of the common burrowing mayfly species *Povilla adusta*, previously identified by Trewavas et al. (1972) to be present on both stones and fallen logs in Barombi Mbo. Trichopteran larvae consisted of caddisflies in their larval form, likely from the genus *Triaenodes*, which has many species endemic to West Africa (Andersen & Holzenthal 2002). The fish category was assigned to portions of fish fins and tissue, as well as to whole fry found in individuals' stomachs (not identifiable to species level at this size). The gastropod shell category consisted of shell remains from various snails, including freshwater limpets from the genus *Ferrissia* (Trewavas et al. 1972). The nematode category contained all roundworms, likely including both terrestrial and aquatic species. The plant tissue category was assigned to all plant material found in individuals' stomachs. This included aquatic species such as *Najas pectinate* and *Potamogeton octandrus* previously documented in Barombi Mbo (Trewavas et al. 1972) and any terrestrial plant leaves. The shrimp category consisted of *Caridina spp.* and *Macrobranchium spp.*, freshwater shrimp genera found in Barombi Mbo and throughout Cameroon (Trewavas et al. 1972). Detritus was used as a catch-all term to describe organic matter that was digested beyond the point of identification. Silt was used as a catch-all to describe inorganic materials, including rocks and sand. Animal remains that could not be clearly identified (e.g. egg-like structures) were grouped into the unidentified category.

We estimated dietary niche breadth of each species by calculating Levins' standardized index (Levins 1968) and Pianka's measure of dietary niche overlap (Pianka 1973) using the *spaa* package (Zhang 2016) in R (version 4.0.2). Both indices have values ranging from 0-1, with increasing values corresponding to increased niche breadth (Levins) and increased niche overlap (Pianka), respectively. Values were set at the following levels for both metrics: high (>0.6), moderate (0.4-0.6), and low (>0.4) following guidelines outlined in other dietary studies on fishes (Grossman 1986; Novakowski et al. 2008; da Silva et al. 2012; Sá-Oliveira et al. 2014; de Oliveira et al. 2021). An assumption adopted for both indices is that all dietary resources are equally available to all species (Grossman 1986, Reinthal 1990, Sá-Oliveira et al. 2014). While we did not collect specific data on dietary resource abundance and variation within Barombi Mbo, this assumption seems reasonable for our system due to the shared lake environment and most species (all except *K. dikume*, *Myaka myaka* and *S. caroli*) coexist in the littoral zone (Trewavas et al. 1972). Previous studies lacking these data have used these matrices and followed this assumption for aquatic systems (Grossman 1986; Novakowski et al. 2008; Sá-Oliveira et al. 2014).

Stable isotope analyses

To assess relative trophic positions of cichlid species in Barombi Mbo, we performed stable isotope analyses for all 11 species (including *S. caroli* and *S. lohbergi*). In limnetic systems, $\delta^{13}C$ isotope ratios offer insight into the ultimate carbon source of prey consumed (Post 2002). Higher $\delta^{13}C$ values indicate a more littoral carbon source, while lower values indicate a more pelagic source (Post 2002). Ratios of $\delta^{15}N$ indicate the relative trophic position of individual consumers (Post 2002). In total, we selected 180 individuals for stable isotope analysis, including at least 6 individuals from each species. Field samples desiccated with magnesium perchlorate in individual vials were subsequently dehydrated at 60° C for at least 24 hours, then 1 mg samples were weighed to the nearest 0.0001 g, packaged into tinfoil capsules, and sent to the UC Davis Stable Isotope Facility. Isotopes of ^{13}C and ^{15}N were measured on a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, U.K.).

Statistical analyses

We performed all statistical analyses in R version 4.0.2 (R Core Team 2020). Our sample size for stomach content analysis was n= 203; the sample sizes for each species are reported in Table 1.

To visualize overall dietary similarity among species, we estimated a non-metric multidimensional scaling (NMDS) plot from a Bray-Curtis dissimilarity matrix of dietary proportions for each individual. To test for differences in diet among species, we used analysis of similarities (ANOSIM) with species designated as the grouping variable (“anosim” function in R *vegan* package version 2.5.6). To determine which dietary components significantly contributed to the stomach contents of each species, we performed an indicator species analysis (“multipatt” function in R *indicspecies* package version 1.7.9) (Defrêne & Legendre 1997; Cácaeres & Legendre 2009). This analysis has traditionally been used to identify one or more species characterizing various habitats or sites in ecological studies (Defrêne & Legendre 1997). More recently, it has been used in dietary studies to identify diet items significantly contributing to differences in stomach contents between groups (Hertz et al. 2017; Lee et al. 2018; Thalmann et al. 2020). These visualizations and analyses were performed in R using the *vegan* (Oksanen et al. 2019) and *indicspecies* (Cáceres & Legendre 2009) packages.

To determine whether individual dietary proportions varied by species, we used linear models (LMs). All LMs were fitted using the stats package in R (R Core Team 2020). Dietary proportions were first transformed using the arcsine (also known as arcsine square root) transformation typical for proportional data. We fit a separate model for each dietary item after arcsine-transformation of the proportions. The independent variable was species with log-transformed standard length (SL) as a covariate. A normal distribution was used for all models. To test the significance of each model, we performed an ANOVA with Type II sum of squares using the *car* package (Fox & Weisberg 2019) in R. For significant models, we used Tukey's HSD post hoc analysis for pairwise comparisons between species. Post-hoc analyses were conducted using the *stats* package in R.

Since volume-based dietary proportions are highly variable depending on prey condition (Buckland et al. 2017), we decided to additionally analyze our stomach content data using a frequency of occurrence approach. To determine whether presence/absence of dietary components varied by species, we fit generalized linear models (GLMs) using a binomial distribution. We converted all proportions into binomial success (proportion > 0) and failure (proportion = 0) data, and then fit all models as described above.

Both our proportional and binomial models indicated that standard length (SL) significantly impacted the proportion of *Corvospongilla* sponge, detritus, fish, and plant tissue in an individual's diet (Tables 5 & 6). We therefore investigated if this relationship was species specific or a more general pattern using LMs. We fitted these models using the *lme4* package (Bates et al. 2015) in R. We ran individual models for each species and food item (when sample size allowed), used the arcsine-transformed proportion of a dietary item consumed (i.e., arcsine-transformed proportion of *Corvospongilla* sponge, detritus, fish, and plant tissue) as the response variable, and log-transformed SL as the predictor variable. A normal distribution was used for all models. We tested the significance of predictor variables using an ANOVA with Type II sum of squares.

To determine whether stable isotope content varied by species, we fit LMs for both δ^{15}N and δ^{13}C. We fit models including all 11 cichlid species, and models including only the three *Stomatepia* species. The response variable for each was δ^{15}N and δ^{13}C, respectively, and the independent variable was species. A normal distribution was used for all models. To test the significance of each model, we performed an ANOVA with Type II sum of squares. We used Tukey's HSD post hoc analysis for pairwise comparisons between species.

RESULTS

Dietary composition, niche breadth, and niche overlap

We found a majority of individuals consumed detritus, plant tissue, and aquatic insects (Fig. 1). Detritus was the majority (>50%) dietary component in all species except for *S. mongo* (Table 1; Fig. 1). Notably, *M. myaka* was the only species with stomach contents consisting of 100% detritus (Table 1; Fig. 1). *Konia eisentrauti* consumed the largest percentage of plant tissue (22.8%) across all species (Table 1; Fig. 1). While *P. maclareni* and all three *Stomatepia* species consumed shrimp (Fig. 2A), *Stomatepia mongo* consumed the greatest proportion of shrimp (62.9%) among all species (Table 1; Fig. 1). Most species also had unidentified material in their stomach contents, although this percentage was typically under 15% on average (Table 1; Fig. 1). *Sarotherodon steinbachi* contained the highest percentage (38.3%) of unidentified material (Table 1; Fig. 1), specifically egg-like structures that could not be identified.

Several dietary components were much rarer and found in only one or two cichlid species. *Sarotherodon linnellii*, the largest species in the radiation, and *Stomatepia mariae* were the only two species to consume fish (Table 1; Fig. 2F). The only species to consume gastropod shells and *Corvospongilla* sponge spicules was *P. maclareni* (Fig. 2D), and sponge spicules comprised about 20% of this species' diet on average (Table 1; Fig. 1). *Stomatepia mariae* was the only species to consume ants (Fig. 2B), comprising about 10% of this species' diet on average (Table 1; Fig. 1). While insect larvae from the orders Ephemeroptera and Diptera were found in the stomach contents of several species (Table 1; Fig. 1), only *Stomatepia pindu* consumed Trichopteran larvae (Fig. 2C), comprising about 14% of this species' diet on average (Table 1; Fig. 1).

All cichlids displayed limited niche breadth, with Levins values below 0.2 for all species (Table 1). *Stomatepia mariae* had the widest niche breadth among all species ($B_A = 0.173$), whereas *M. myaka* had the smallest ($B_A = 0.000$) (Table 1). Many species displayed considerable dietary niche overlap, with Pianka index values typically ranging from 0.8-1 (Table 2). Notably, *S. mongo* showed the lowest niche overlap with other species, with Pianka index values from 0.2-0.4 (Table 2).

Clustering, analysis of similarities, and indicator analyses of overall diet

The NMDS ordination (stress = 0.103) displayed little clustering of species by dietary components, with considerable overlap among species (Fig. 3). There was, however, a statistically significant difference in overall diet among species (ANOSIM: R = 0.06275, $P = 0.0238$).

We identified several dietary items that were significant indicators of species or species groups (Fig. 1). For *K. dikume, M. myaka,* and *S. linnellii*, detritus was a significant indicator (Table 3; indicspecies: Dufrêne-Legendre indicator value = 0.454, $P = 0.0077$). For *K. eisentrauti*, plant tissue was a significant indicator (Table 3; Dufrêne-Legendre Indicator = 0.438, $P = 0.0184$); for *S. mongo*, shrimp was a significant indicator (Table 3; Dufrêne-Legendre Indicator = 0.744, $P = 0.0002$); *Corvospongilla* sponge was a significant indicator of *P. maclareni* (Table 3; indicspecies: Dufrêne-Legendre indicator value = 0.49, $P = 0.013$); ants were a significant indicator of *S. mariae* (Table 3; indicspecies: Dufrêne-Legendre indicator value = 0.405, $P = 0.0458$); and Trichopteran larvae were a significant indicator of *S. pindu* (Table 3; indicspecies: Dufrêne-Legendre indicator value = 0.457, $P = 0.0295$).

Individual dietary components

We found individual diet proportions to vary by species for several items (Fig. 2). All comparisons of relative diet item consumption between species is based on mean surface area proportion. Detritus consumption was significantly different among species (Table 4; ANOVA: $\chi^2 = 36.242$, df = 8, P = 1.585*10-5). In particular, *M. myaka* consumed about 2 times more detritus than *S. mariae* (Table 1; Tukey HSD: $P = 0.044$), and *S. linnellii* consumed about 1.5 times more detritus than *S. mariae* (Table 1; Tukey HSD: $P = 0.021$). Plant tissue consumption varied across species (Table 4; Fig. 2E; ANOVA: $\chi^2 = 49.347$, df = 8, $P = 5.455 * 10^{-8}$), with *K. eistentrauti* consuming at least 5 times more plant tissue than *S. linnellii*, *S. steinbachi*, *P. maclareni*, *S. mariae*, and *S. pindu* (Table 1; Tukey HSD: $P < 0.05$).

Shrimp consumption also varied among species (Table 4; Fig. 2A; ANOVA: $\chi^2 = 116.674$, df = 8, $P < 2*10^{-16}$), with *S. mongo* consuming at least 7 times more shrimp than all other species (Table 1; Tukey HSD: $P < 0.001$). Consumption of unidentified diet items varied among species (Table 4; ANOVA: $\chi^2 = 55.175$, df = 8, $P = 4.082*10^{-9}$), with *S. steinbachi* consuming at least 2 times more than all other species (Table 1; Tukey HSD: $P < 0.05$). *Pungu maclareni* was the only species to consume *Corvospongilla* sponge (Table 4; Fig. 2D; ANOVA: $\chi^2 = 55.461$, df = 8, $P = 3.591*10^{-9}$). *Corvospongilla* spicules made up 21.2% of *P. maclareni's* diet (Table 1; Fig. 1). Similarly, *S. mariae* was the only species to consume ants (Table 4; Fig. 2B; ANOVA: $\chi^2 = 51.806$, df = 8, $P = 1.835*10^{-8}$). Ants made up 9.8% of *S. mariae's* diet (Table 1; Fig. 1). *Stomatepia pindu* was the only species to consume Trichopteran larvae (Table 4; Fig. 2C; ANOVA: $\chi^2 = 58.100$, df = 8, $P = 1.098*10^{-9}$). Trichopteran larvae made up 14.1% of *S. pindu's* diet (Table 1; Fig. 1).

Collapsing these proportional data to presence/absence data of individual dietary components (as described above) yielded similar results. Detritus (Table 6; ANOVA: $\chi^2 = 24.440$, df = 8, $P = 0.002$); plant tissue (Table 6; ANOVA: $\chi^2 = 36.158$, df = 8, $P = 1.643*10^{-5}$); shrimp (Table 6; ANOVA: $\chi^2 = 19.1124$, df = 8, $P = 0.014$); unidentified items (Table 6; ANOVA: $\chi^2 = 45.748$, df = 8, $P = 2.654*10^{-7}$); *Corvospongilla* sponge (Table 6; ANOVA: $\chi^2 = 55.628$, df = 8, $P = 3.333*10^{-9}$); ants (Table 6; ANOVA: $\chi^2 = 51.997$, df = 8, $P = 1.685*10^{-8}$); and Trichopteran larvae (Table 6; ANOVA: $\chi^2 = 17.6528$, df = 8, $P = 0.024$) all varied significantly among species by presence/absence with similar specialists as described above.

Finally, we found a significant relationship between log-transformed SL and arcsine-transformed proportion of certain dietary items for *S. mariae*, *K. eisentrauti*, and *P. maclareni.* For *S. mariae*, we found that larger individuals consumed significantly more fish than smaller individuals (ANOVA: $F = 5.716$, df = 1, $P = 0.022$). For *K. eisentrauti*, we found that smaller individuals consumed more detritus (Fig. 4A; ANOVA: $F = 5.986$, df = 1, $P = 0.02$), while larger individuals consumed more plant tissue (Fig. 4B; ANOVA: $F = 7.24$, df = 1, $P = 0.011$). Similarly, smaller *P. maclareni* consumed more detritus than larger individuals (Fig. 4C; ANOVA: $F = 24.755$, df = 1, $P = 5.621*10^{-6}$), and larger individuals consumed more *Corvospongilla* sponge material than smaller individuals (Fig. 4D; ANOVA: $F = 9.583$, df = 1, $P = 0.003$).

Carbon and nitrogen stable isotopes

We found $\delta^{13}C$ values to be significantly different among species when comparing all 11 cichlid species (Table 6; ANOVA: $\chi^2 = 123.36$, df = 11, $P = 2.2*10^{-16}$). *Sarotherodon lohbergeri* had the highest $\delta^{13}C$ value, significantly more than all other species except *P. maclareni*, *S. caroli*, and *S. steinbachi* (Tukey HSD: $P < 0.01$). Contrastingly, *M. myaka* had the lowest $\delta^{13}C$ value, significantly lower than all other species except *K. dikume*, *K. eisentrauti*, *S. linnellii*, and *S. pindu* (Tukey HSD: $P < 0.05$). *Stomatepia mongo* exhibited significantly higher $\delta^{13}C$ than *S. pindu* in both the model containing all cichlid species (Tukey HSD: $P = 0.041$) and the model containing only *Stomatepia* species (Tukey HSD: $P = 0.005$).

Values of δ^{15}N were also significantly different among species in the model containing all cichlid species (Table 6; ANOVA: $\chi^2 = 67.967$, df = 11, $P = 2.969*10^{-10}$). *Konia dikume* had the highest δ^{15}N value of any species, significantly more than *M. myaka*, *S. caroli*, *S. lohbergeri*, and *S. pindu* (Tukey HSD: $P < 0.05$). *Sarotherodon lohbergeri* had the lowest δ^{15}N value, significantly lower than all other species except *M. myaka*, *S. caroli*, and *S. steinbachi* (Tukey HSD: $P < 0.05$). There were no significant differences in δ^{15}N values among *Stomatepia* species (Table 6). Despite these significant differences in both δ^{13}C and δ^{15}N values among species, there was minimal clustering by species when visualizing stable isotope values (Fig. 5).

DISCUSSION

We measured dietary profiles and relative trophic positions in a celebrated potential of cichlid sympatric speciation and adaptive radiation in crater lake Barombi Mbo using stomach content analyses stable isotope data. We found minimal evidence of trophic niche partitioning among species but documented several specialized dietary items that were consumed by a single or few species within the radiation. In general, our findings align with the major trophic strategies outlined by Trewavas et al. (1972), providing quantitative data for differences in dietary components among species.

Minimal trophic niche partitioning among cichlid species in lake Barombi Mbo in overall dietary niche

Our measurements of niche overlap (Pianka index) and relative trophic position (δ^{13}C and δ^{15}N stable isotope measurements) suggest there is not strong evidence for dietary niche partitioning among cichlid species. We observed Pianka index values of 0.84 (84% similarity) and higher for most species (Table 2), and while we did find significant differences in δ^{13}C and δ^{15}N values among species (Table 6), there was little evidence of clustering by species (Fig. 5). Detritus was the majority (>50%) dietary component in 8 out of 9 species studied (Table 1), which may explain the high niche overlap values observed in this system. For instance, Levins' and Pianka's indices for *M. myaka* are estimated to be 0 and 0.85, respectively, (Tables 1 & 2) suggesting that this species simultaneously exhibits the narrowest niche breadth and 85% similarity in niche with all other species. In contrast, *S. mongo* was both the only species to display relatively low values of niche overlap—26% similarity in niche on average (Table 2)—and to have a majority diet component other than detritus (Fig. 1), perhaps reflecting its nocturnal foraging habits which previously limited successful captures of this species (Musilova et al. 2014).

Limited dietary divergence is not uncommon because short-term coexistence among ecologically similar species can occur even without fine-scale niche partitioning, particularly within speciose African cichlid communities in the great lakes (Liem 1980; Ribbink & Lewis 1982; Martin and Genner 2009). Previous work has also shown that cichlid species may partition the same resources based on functional access, allowing for similarity in dietary profiles but different modes of access. For example, Stauffer & Posner (2006) found that the rock-dwelling cichlid species of Lake Malawi utilized the same dietary items but exhibited habitat partitioning based on the unique feeding kinematics (feeding angles) of each species to reduce competition between groups. This may also be the case for some generalist diet items (detritus, aquatic insects, microalgae) in Barombi Mbo, and further research is needed on the kinematics and functional mechanisms by which these cichlids consume their food to investigate this possibility.

Another explanation for the minimal trophic niche partitioning we observed could lie in undetected seasonal differences. Our data combined specimens collected during both the wet (July-September) and dry (December-January) seasons in Cameroon across multiple years (2009-10, 2016). Prey availability often differs greatly between seasons, especially in tropical systems (Winemiller 1990; Correa & Winemiller 2014); however, dietary profiles of the trophic specialists in Barombi Mbo were generally consistent between seasons and years collected.

Alternatively, dietary niche partitioning may have been obscured by variability in prey condition. Stomach content analyses are highly dependent on prey condition (Baker et al. 2014; Buckland et al. 2017). Soft-bodied organisms are likely to digest more quickly than those with chitinous exoskeletons or other similarly tough external features, potentially leading to an overrepresentation of hard-bodied, less digestible organisms (Randall 1967). Furthermore, there may be finer-scale niche partitioning at lower taxonomic prey levels (i.e. genus, species) than what can be detected by microscopic visual analysis of stomach contents. DNA metabarcoding approaches may aid in identifying these finer-scale patterns (Berry et al. 2015; Harms-Tuohy et al. 2016; Jakubavičiūtė et al. 2017) and can also account for highly digested prey (Carreon-Martinez et al. 2011), though such techniques come with their own suite of challenges and may overestimate the relative importance of certain dietary items (Sakaguchi et al. 2017).

Evidence of trophic niche partitioning via dietary specialization

Although the above summary statistics failed to detect differences in overall dietary niche between species, distinctions are apparent when we examined the proportions of individual dietary items between species. Our indicator species analysis, LMs, and GLMs all suggest that different specialized dietary items are consumed primarily by single species (Tables 4, 5, 6; Fig. 2). Specifically, *K. eisentrauti* consumes the most plant tissue, *P. maclareni* is the only species that consumes sponge tissue, *S. mariae* is the only species to consume ants, *S. mongo*'s diet is primarily shrimp, and *S. pindu* is the only species to consume Trichopteran larvae (Fig. 1 & 2). Herbivory is common among African cichlids (Ribbink & Lewis 1982; Genner & Turner 2005), and *K. eisentrauti* was previously qualitatively described as a plant specialist (Trewavas et al. 1972). Additionally, shrimp (Kohda & Hori 1993; Yuma et al. 1998) and Trichopteran larvae (Kohda & Hori 1993; Kohda & Tanida 1996; Kohda et al. 2008) have been documented in the stomach contents of cichlids from African rift lake Tanganyika, but the remaining dietary items (sponge and ants) are rare among African cichlids.

One of our most exciting findings is evidence of spongivory in *P. maclareni*. A significant proportion (20%) of this species' diet is freshwater sponges (*Corvospongilla spp.*) and it is the only cichlid species from Barombi Mbo to consume this diet item. Spongivory is extremely rare among fishes, with only about 0.04% of all fishes (FishBase) consuming sponges (2 out of a total of 14 of these species are cichlids from Cameroonian crater lakes). In fact, the only freshwater fishes partaking in sponge-eating are cichlids found in African Great Lakes Tanganyika (Kohda & Hori 1993; Awata & Kohda 2004) and Victoria (Bouton et al. 1997), and Cameroonian crater lakes Barombi Mbo (Trewavas et al. 1972) and Bermin (Stiassny et al. 1992; Schliewen 2005). Sponges are a rare diet item among fishes and other vertebrates because they are incredibly hard to consume. Most documented spongivores have evolved morphological adaptations to aid in sponge consumption, including beak-shaped mouths (Witzel 1983; Pritchard & Mortimer 1999; Blumenthal et al. 2009) and multiple rows of tricuspid teeth (Hourigan et al. 1989) used to shear and scrape sponge off its substrate. *P. maclareni* also appears to have adaptations that may aid in sponge-eating, including short robust oral jaws, large epaxial musculature (particularly when compared to other cichlids in Barombi Mbo), and fleshy lips with protruding tricuspid teeth (Trewavas et al. 1972).

Another notable finding of this study was evidence of ant consumption in *S. mariae*. We found that about 10% of this species' diet is ants, and it is the only cichlid species in Barombi Mbo to consume this item. While *S. mariae* has previously been noted to feed on adult terrestrial insects (Trewavas et al. 1972), this is the first study documenting terrestrial ants as a major component of this species' diet. It is interesting that *S. mariae* was the only species to consume ants, as *S. mariae* and *S. pindu* are closely related species, ecologically similar, hybridize in the lab, and represent the extreme tails of a unimodal distribution for all trophic traits measured (Martin 2012, Martin et al. 2015). This divergence in dietary items may be due to the potential sensory adaptations that *S. mariae* uses to detect ants and its shoaling mid-water habitat, whereas *S. pindu* is a solitary benthic species that forages within the leaf-litter (Trewavas et al. 1972). Alternatively, it may be that *S. mariae* is consuming ants incidentally. Terrestrial insects are not uncommon components of fish diets, as they enter lakes and rivers through fallen vegetation. Fish that opportunistically feed near the surface or middle of the water column will take up these insects while foraging, which is likely why terrestrial insects are a major food source of known drift foragers (Resh et al. 1999; Nakano et al. 1999). This species had the highest Levins' index, indicating that it had the widest niche breadth of all cichlids studied and suggests dietary flexibility within the species (Pedreschi et al. 2015; Spencer et al. 2017; Jesmer et al. 2020). Future studies should investigate if *S. mariae* is preferentially seeking out ants or if they are an incidental part of the diet.

Finally, we also document that *S. mongo* consumed the most shrimp out of all cichlid species in lake Barombi Mbo (at least 7 times more than all other species). We only observed and captured this species after twilight hours (beginning around 19:00 hours), yet many individuals had full stomachs. This could suggest that *S. mongo* exhibits a rare hunting strategy for nocturnal shrimp prey, which is notable as nocturnality is extremely rare among African cichlids and has only been documented once in Lake Malawi out of thousands of species (Lloyd et al. 2021). It is also interesting that *S. mongo* is the only cichlid species to have a dietary component other than detritus as its majority component (Fig. 1). Trewavas et al. (1972) were unable to qualitatively describe the stomach contents of *S. mongo* (due to limited catches, small sample size, and empty stomachs), but here we provide quantitative evidence that this species should indeed be considered a dietary specialist of shrimp.

The term ‘specialist’ has a wide range of definitions that often differ among researchers, which can lead to confusion when identifying empirical examples of specialization in nature (see Bolnick et al. 2003 for further discussion on this topic). When discussing dietary niche, the term specialist has been historically used to describe organisms that exploit a relatively narrow breadth of dietary resources compared to other members of their ecological community (Futuyma & Moreno 1988; Sargeant 2007). Recent work, however, suggests that we must broaden the term to include temporal, spatial, environmental, and organizational level (i.e., individual level, species level, community level, etc.) effects on dietary patterns (Bolnick et al. 2003; Shipley et al. 2009; Devictor et al. 2010; Poisot et al. 2011; Pagani-Núñez et al. 2016). Our current data suggests that the above ‘specialist’ species most closely align with the definition of *‘facultative generalist’* from Pagani-Núñez et al. (2016) (also noted as *‘functional specialist’* from Bolnick et al. 2003), where a given group primarily feeds on generalist diet items but can exploit novel resources when necessary. The remaining species in our study (*K. dikume, M. myaka, S. steinbachi,* and *S. linnellii*), neatly align with the definition of *‘obligate generalist’* (Pagani-Núñez et al. 2016; also noted as *‘pure generalist’* from Bolnick et al. 2003), where individuals within a group completely overlap in diet, exploit dietary items that are common in the environment (such as detritus), and exhibit limited foraging innovations.

Our data also suggests that the cichlid radiation of Barombi Mbo may be another example of Liem’s paradox, in which trophic specialists act as “jacks-of-all-trades” able to consume both their specialized resources and more generalist diet items (Liem 1980). One potential explanation for this phenomenon is that trophic specialists will act as opportunistic feeders during periods of high resource availability—closely related species may show minimal or undetectable ecological differentiation during this time—but will consume a specialized diet when resources are scarce (Robinson & Wilson 1998). All specialists appear to be predominantly feeding on common, shared resources (microinvertebrates, microalgae, detritus) while also supplementing their diet with unique resources, but our current data do not allow us to determine if the time periods measured encompass high or low resource availability. Future studies should explicitly measure dietary profiles of species in this system during high and low resource periods, as Liem’s paradox may simultaneously provide explanations for when ecological niche divergence is necessary (e.g., low resources periods) and for why some radiations do not display trophic niche partitioning.

Other modes of trophic niche partitioning

Dietary niche partitioning may be occurring in this system on organizational levels other than between species, such as between individuals of the same species, across developmental time periods, or across different behavioral strategies; our current data supports some of these possibilities. First, many studies incorporate variation in dietary profiles among conspecifics into their definitions of specialization, often termed ‘individual specialization’ (Bolnick et al. 2003; Sargeant 2007; Poisot et al. 2011; Pagani-Núñez et al. 2016). Organisms displaying individual specialization are expected to have minimal overlap in dietary niche with conspecifics and—at the population and species levels—specialist groups are expected to show more variation between individuals (i.e. more individual variation in niche breadth and overlap) than generalist groups (Bolnick et al. 2003). There is some evidence to suggest that this pattern is occurring in the cichlid radiation of Barombi Mbo. Figure 6 depicts density plots of individuals from generalist and specialist species, comparing proportional consumption of detritus and an additional diet item. For specialist species, we display the specialized food items highlighted by our analyses. Since generalist species do not have an obvious specialized diet item for comparison, we display the second most-prevalent item in their dietary profile. While generalist display narrow, unimodal distributions for both detritus and their secondary diet items, specialists display wide, and potentially bimodal, distributions across dietary components (Fig. 6). These bimodal distributions could indicate that niche partitioning is occurring at the individual level or may even suggest that these groups are undergoing further ecological diversification (Schluter 2000; Bolnick et al. 2003; Kusche et al. 2014).

Trophic niche partitioning may also occur across developmental time periods. Previous studies have documented variation in dietary niche partitioning across life history stages in sympatric populations of snappers (Takahashi et al. 2020), drums (Deary et al. 2017), and whitefish (Chouinard & Bernatchez 1998). Differences in diet early in life have also been associated with plastic variation in trophic morphology in species of cichlids (Stauffer & Gray 2004) and could explain why we observe divergent feeding morphology between species despite dietary overlap. While our study does not specifically investigate differences in dietary profiles across age, we do observe some dietary divergence between large and small fish. In general, fish growth is isometric, meaning that standard length or size can be a good proxy for age. For *S. mariae*, *K. eisentrauti*, and *P. maclareni* we observed that larger individuals were more likely to consume the specialized dietary items of fish, plant tissue, and sponge respectively (Fig. 4B, 4D). Furthermore, smaller *K. eisentrauti* and *P. maclareni* were also more likely to consume detritus (Fig. 4A, 4C). This may indicate that that juvenile or small individuals are more easily able to consume a generalist diet—perhaps due to morphological constraints or competition from larger fish. This finding agrees with previous work that suggests niche partitioning at early life stages may not be as important as later in life (Chouinard & Bernatchez 1998), but other studies suggest there can also be fine-scale trophic niche partitioning among larval life stages in fishes (Mcaskill et al. 2021). Future work on this system should explicitly document dietary profiles across the various life stages of cichlids (juvenile, adult, breeding adult) to understand if and how dietary competition differs through ontogeny.

Dietary divergence and speciation

The cichlid radiation in Barombi Mbo is an excellent candidate system for investigating the role of dietary divergence in speciation, due to both the lack of sexual dimorphism and substantial differences in trophic morphology among species (Trewavas et al. 1972; Schliewen et al. 1994; Coyne et al. 2004; Martin 2012; Richards et al. 2018). The current study provides empirical evidence of dietary specialization in 5 out of the 11 cichlid species and ultimately strengthens the above argument by providing potential focal species for future studies to investigate. We still lack many key pieces of information, however, that would provide a clear link between these two processes. For instance, we still lack information on how different trophic morphologies aid, hinder, or play no role in feeding on specialized and generalist diet items, nor do we understand the connection between these morphologies and assortative mating. Understanding temporal and spatial differences in feeding and reproduction is also potentially important. In general, future studies should investigate whether dietary specialization coincides with phenotypic traits under disruptive selection and assortative mating, both of which contribute to ecological speciation in sympatry (Dieckmann & Doebeli 1999; Gavrilets 2004; Gavrilets & Losos 2009; Martin 2013). Examples of this phenomenon include experimental evolution studies (Blount et al. 2008), divergence of insect host races (Nosil 2009), and ecological speciation in classic adaptive radiations (Grant & Grant 2002; Kocher et al. 2004; Lamichhaney et al. 2015; Gillespie et al. 2020). Further study of how dietary specialization in this system contributes to ecological divergence and assortative mating can offer further insight into the mechanisms driving sympatric speciation.

Conclusion

In conclusion, we documented a high level of dietary niche overlap among cichlid species in lake Barombi Mbo, but suggest that this pattern is primarily due to the presences of detritus in the diet of all cichlid species. We also find evidence of dietary specialization in 5 out of the 11 cichlid species and suggest that these species be viewed as functional specialists that utilize specialized dietary items to supplement their otherwise generalist diet, possibly at certain times of the year when resources are scarce. Future work should investigate if specialist species' dietary profiles shift across spatial or temporal scales and investigate how variation in morphology connects to diet and reproductive isolation in the system.

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DATA AVAILABILITY STATEMENT

All data analyzed for this study will be provided upon request.

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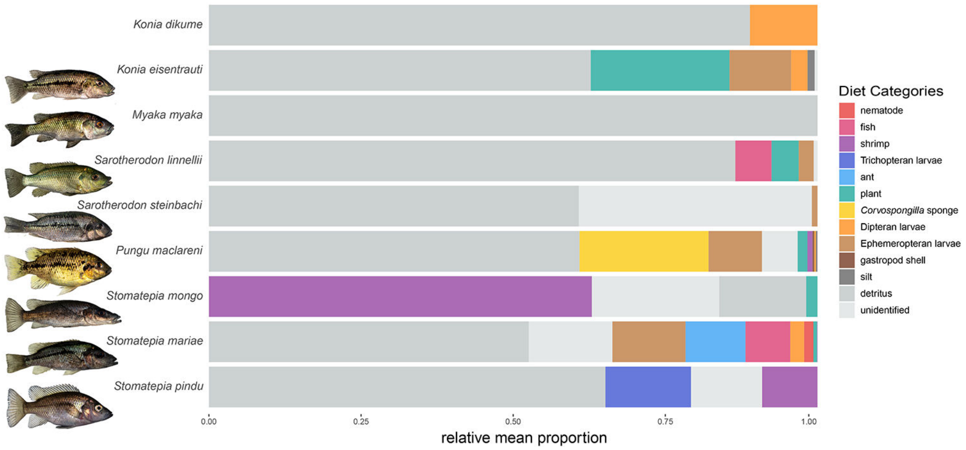

Figure 1:

Dietary profiles of cichlid species from Barombi Mbo by prey item proportion. Each color represents a different dietary component. Bar length is based on the average proportion of each prey item. Representative live photographs of most species reared in a common lab environment are also shown, excluding *K. dikume* which was never successfully recovered alive.

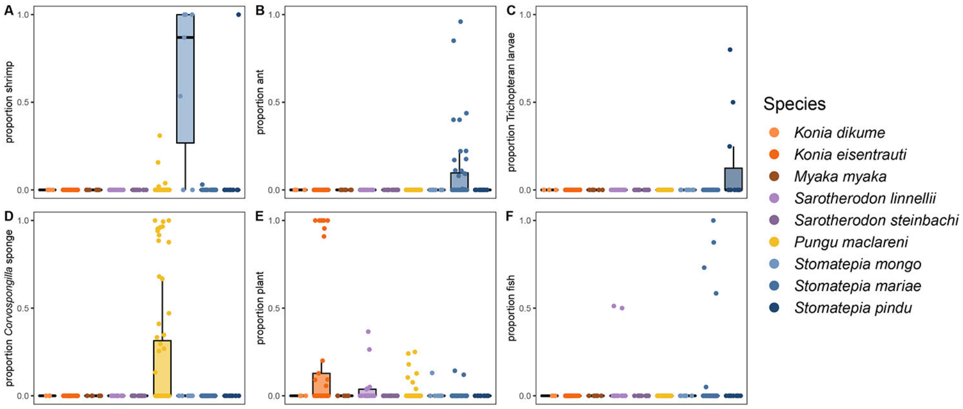

Figure 2:

Box and whisker plots displaying the proportions of A) shrimp B) ants, C) Trichopteran larvae, D) *Corvospongilla* sponge, E) plant tissue, and F) fish found in each species' stomachs. Total sample size was 203 individuals collected in 2010 and 2016 from multiple sites around the lake.

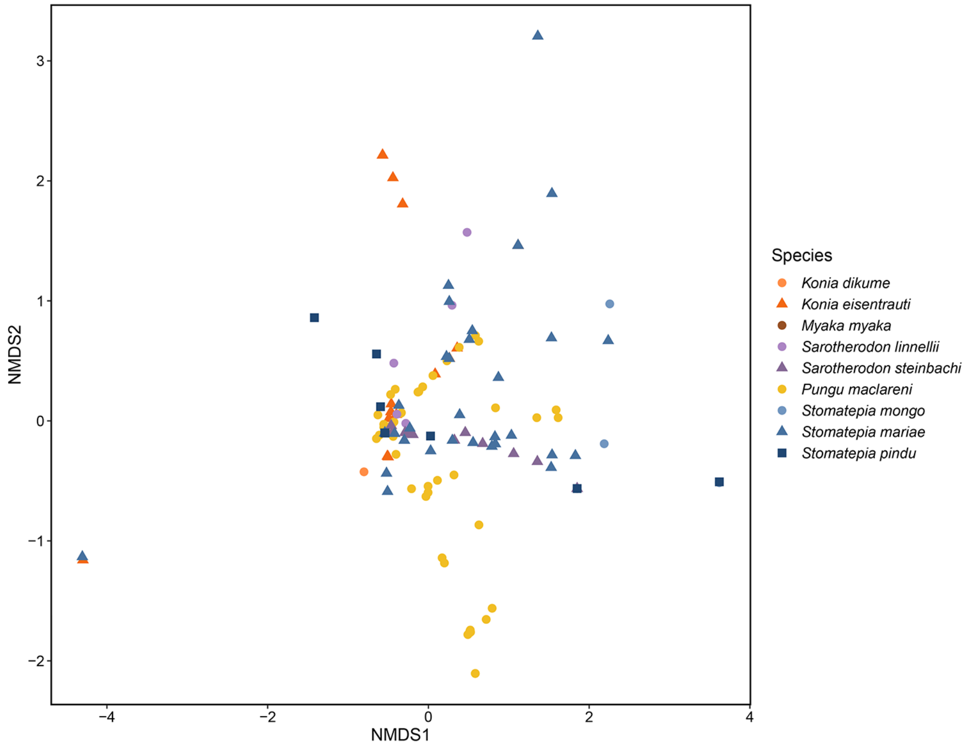

Figure 3:

Non-metric multidimensional scaling (NMDS) ordination of dietary item proportions for nine out of the eleven cichlid species from Barombi Mbo. Ordination is based on Bray-Curtis similarity index (stress = 0.103).

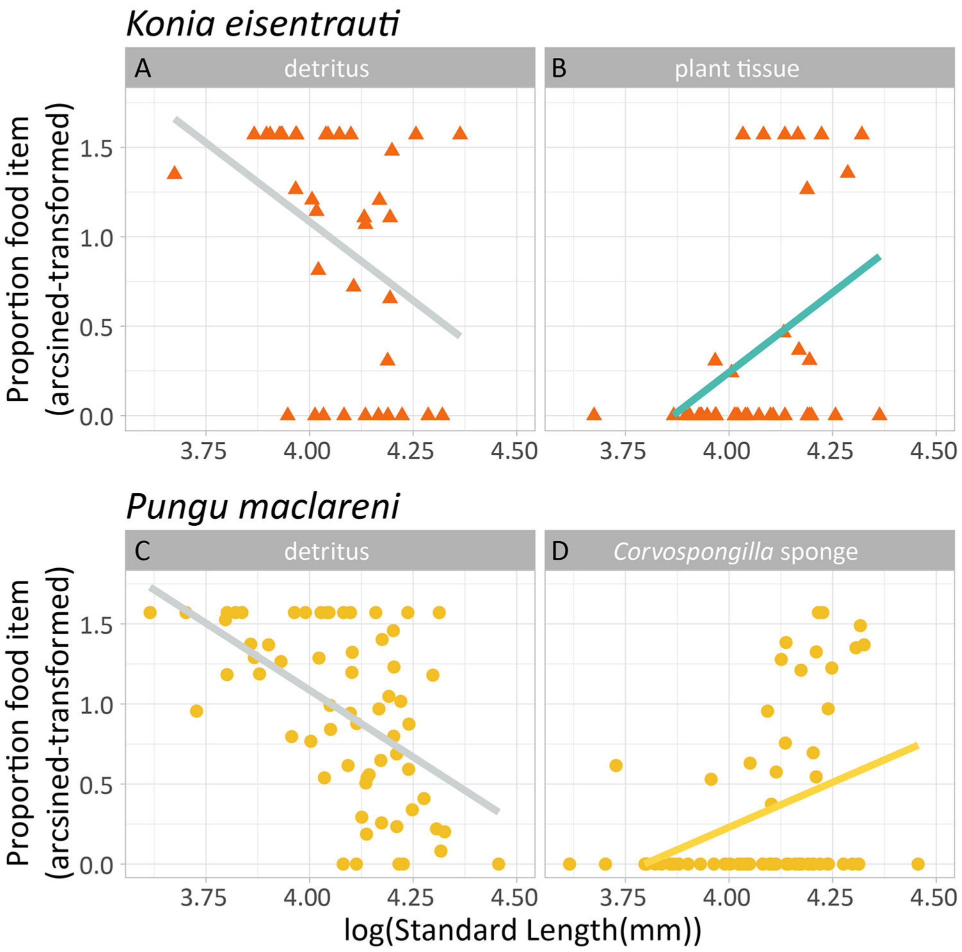

Figure 4:

The diet of large *Konia eisentrauti* and *Pungu maclareni* individuals contains a larger proportion of plant tissue and *Corvospongilla* sponge respectively, while the diets of small *K. eisentrauti* and *P. maclareni* individuals contain a larger proportion of detritus. Graphs display the linear relationship between the log(standard length(mm)) of individual fish and the proportion (arcsine-transformed) of A) detritus and B) plant tissue for *K. eisentrauti*, and C) detritus and D) *Corvospongilla* sponge for *P. maclareni*. Points represent individuals, lines represent the predicted results of a LOESS model with proportion of a diet item as the response variable and log(standard length(mm)) as the predictor variable.

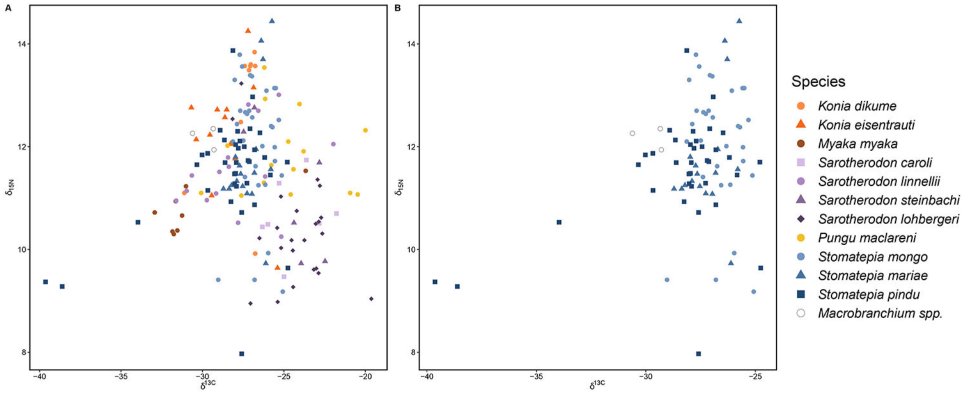

Figure 5:

Scatterplots of $\delta^{13}C$ and $\delta^{15}N$ isotopic values for A) all eleven cichlid species from Barombi Mbo and B) only *Stomatepia* species. $\delta^{13}C$ offers insight into ultimate carbon source (littoral vs pelagic) while $\delta^{15}N$ values describe relative trophic position.

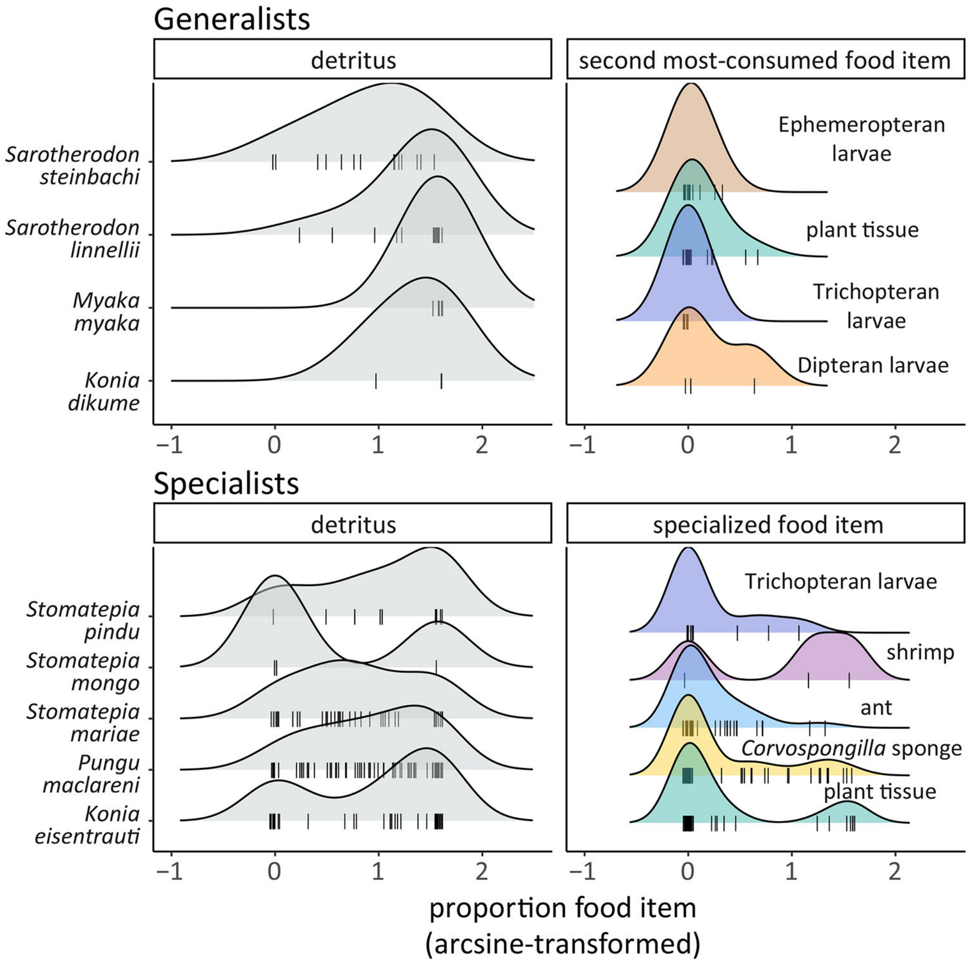

Figure 6:

Individuals that are part of specialist groups exhibit a wider range of detritus in their diets and more individuals consume secondary or specialized diet items. Density plots displaying the number of individuals per species consuming a given proportion (arcsine-transformed) of 1) detritus and 2) the second most-consumed item (generalist species) or their specialized food item (specialist species).

Table 1:

Mean proportion of each dietary component and sample sizes by species. B_A is Levins' standardized index of niche breadth (Levins 1968).

Dietary component	***Konia dikume***	***Konia eisentrauti***	***Myaka myaka***	***Sarotherodon linnellii***	***Sarotherodon steinbachi***	***Pungu maclareni***	***Stomatepia mongo***	***Stomatepia mariae***	***Stomatepia pindu***
Ant	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.098	0.000
***Corvospongilla* Sponge**	0.000	0.000	0.000	0.000	0.000	0.212	0.000	0.000	0.000
Detritus	0.889	0.628	1.000	0.865	0.608	0.609	0.143	0.526	0.651
Dipteran Larvae	0.111	0.027	0.000	0.000	0.000	0.003	0.000	0.023	0.000
Ephemeropteran Larvae	0.000	0.101	0.000	0.025	0.009	0.088	0.000	0.120	0.000
Fish	0.000	0.000	0.000	0.060	0.000	0.000	0.000	0.074	0.000
Gastropod Shell	0.000	0.000	0.000	0.000	0.000	0.003	0.000	0.000	0.000
Nematode	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.015	0.000
Plant Tissue	0.000	0.228	0.000	0.045	0.000	0.016	0.019	0.006	0.000
Shrimp	0.000	0.000	0.000	0.000	0.000	0.008	0.629	0.001	0.091
Silt	0.000	0.012	0.000	0.000	0.000	0.002	0.000	0.000	0.000
Trichopteran Larvae	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.141
Unidentified	0.000	0.005	0.000	0.006	0.383	0.059	0.209	0.137	0.117
n	3	37	6	17	15	63	7	44	11
B_A	0.021	0.099	0.000	0.027	0.078	0.112	0.098	0.173	0.095

Table 2:

Pianka's measure of niche overlap (Pianka 1973) among cichlid species from Barombi Mbo. Values range from 0-1, with 0 being no niche overlap and 1 being complete niche overlap.

	Konia dikume	***Konia eisentrauti***	***Myaka myaka***	***Sarotherodon linnellii***	***Sarotherodon steinbachi***	***Pungu maclareni***	***Stomatepia mongo***	***Stomatepia mariae***
Konia eisentrauti	0.926							
Myaka myaka	0.992	0.928						
Sarotherodon linnellii	0.988	0.946	0.996					
Sarotherodon steinbachi	0.840	0.791	0.846	0.847				
Pungu maclareni	0.925	0.894	0.932	0.934	0.838			
Stomatepia mongo	0.209	0.207	0.211	0.213	0.342	0.236		
Stomatepia mariae	0.919	0.894	0.921	0.935	0.910	0.909	0.270	
Stomatepia pindu	0.947	0.887	0.954	0.951	0.899	0.906	0.377	0.920

Table 3:

Results of indicator species analysis (indicspecies). Each dietary component was assigned a group consisting of either one or multiple species based on its abundance in the data set (Bray-Curtis dissimilarity matrix). Significant indicators ($P < 0.05$) are bolded and denote dietary items that contribute to differences in stomach contents among groups.

Dietary component	Species group associated	Dufrêne-Legendre indicator value	*P*
Ant	***Stomatepia mariae***	**0.405**	**0.0458**
***Corvospongilla* Sponge**	***Pungu maclareni***	**0.49**	**0.013**
Detritus	***Konia dikume*** ***Myaka myaka*** ***Sarotherodon linnellii***	**0.454**	**0.0077**
Dipteran Larvae	*Konia dikume*	0.34	0.0878
Ephemeropteran Larvae	*Konia eisentrauti* Pungu maclareni Stomatepia mariae	0.319	0.141
Fish	Sarotherodon linnellii Stomatepia mariae	0.28	0.212
Gastropod Shell	Pungu maclareni	0.166	0.674
Nematode	Stomatepia mariae	0.209	0.3545
Plant Tissue	***Konia eisentrauti***	**0.438**	**0.0184**
Shrimp	***Stomatepia mongo***	**0.744**	**0.0002**
Silt	*Konia eisentrauti*	0.206	0.4217
Trichopteran larvae	***Stomatepia pindu***	**0.457**	**0.0295**
Unidentified	***Sarotherodon steinbachi*** ***Stomatepia mongo***	**0.413**	**0.0077**

Table 4:

Results of linear models (LMs) investigating variation in dietary component proportions among cichlid species. Table displays results of LMs investigating if individual dietary item proportions vary among species, with log(Standard length) as a covariate. All proportions were transformed using the arcsine square root transformation and a normal distribution was used for all models. Significant predictors ($P < 0.05$) are bolded.

Response	**Predictor**	χ^2	**d.f.**	***P***
Ant	**Species**	**51.806**	**8**	**$1.835*10^{-8}$**
	log(Standard length)	0.448	1	0.503
***Corvospongilla* Sponge**	**Species**	**55.461**	**8**	**$3.591*10^{-9}$**
	log(Standard length)	**5.374**	**1**	**0.02**
Detritus	**Species**	**36.242**	**8**	**$1.585*10^{-5}$**
	log(Standard length)	**15.282**	**1**	**$9.26*10^{-5}$**
Dipteran Larvae	Species	5.569	8	0.695
	log(Standard length)	0.336	1	0.562
Ephemeropteran Larvae	Species	11.772	8	0.162
	log(Standard length)	0.978	1	0.323
Fish	Species	8.299	8	0.405
	log(Standard length)	**7.11**	**1**	**0.00766**
Gastropod Shell	Species	3.445	8	0.903
	log(Standard length)	1.214	1	0.271
Nematode	Species	9.123	8	0.332
	log(Standard length)	0.002	1	0.964
Plant Tissue	**Species**	**49.347**	**8**	**$5.455*10^{-8}$**
	log(Standard length)	**6.317**	**1**	**0.012**
Shrimp	**Species**	**116.674**	**8**	**$<2*10^{-16}$**
	log(Standard length)	0.041	1	0.839
Silt	Species	4.914	8	0.767
	log(Standard length)	0.022	1	0.882
Trichopteran Larvae	**Species**	**58.1**	**8**	**$1.098*10^{-9}$**
	log(Standard length)	0.048	1	0.826
Unidentified	**Species**	**55.175**	**8**	**$4.082*10^{-9}$**
	log(Standard length)	0.341	1	0.559

Table 5:

Results of generalized linear models (GLMs) investigating variation in frequency of occurrence of dietary components among cichlid species. Table displays results of GLMs investigating if individual dietary item presence/absence varies among species, with log(Standard length) as a covariate. All proportions were converted into binomial success (proportion > 0) and failure (proportion = 0) data, and a binomial distribution was used for all models. Significant predictors (*P* < 0.05) are bolded.

Response	**Predictor**	χ^2	**d.f.**	***P***
Ant	**Species**	**51.997**	**8**	**$1.685*10^{-8}$**
	log(Standard length)	0.074	1	0.786
***Corvospongilla* Sponge**	**Species**	**55.628**	**8**	**$3.333*10^{-9}$**
	log(Standard length)	**5.715**	**1**	**0.0168**
Detritus	**Species**	**24.44**	**8**	**0.00193**
	log(Standard length)	**5.537**	**1**	**0.0186**
Dipteran Larvae	Species	8.216	8	0.413
	log(Standard length)	0.0434	1	0.835
Ephemeropteran Larvae	**Species**	**22.971**	**8**	**0.0034**
	log(Standard length)	2.067	1	0.151
Fish	Species	14.411	8	0.0717
	log(Standard length)	**11.178**	**1**	**0.000828**
Gastropod Shell	Species	4.783	8	0.781
	log(Standard length)	1.845	1	0.174
Nematode	Species	9.412	8	0.309
	log(Standard length)	0.102	1	0.75
Plant Tissue	**Species**	**36.158**	**8**	**$1.643*10^{-5}$**
	log(Standard length)	**13.795**	**1**	**0.000204**
Shrimp	**Species**	**19.112**	**8**	**0.0143**
	log(Standard length)	1.384	1	0.239
Silt	Species	4.81	8	0.778
	log(Standard length)	0.604	1	0.473
Trichopteran Larvae	**Species**	**17.653**	**8**	**0.024**
	log(Standard length)	0.268	1	0.605
Unidentified	**Species**	**45.748**	**8**	**$2.654*10^{-7}$**
	log(Standard length)	0.823	1	0.364

Table 6:

Results of linear models (LMs) investigating variation in stable isotope values among 1) all cichlid species and 2) only *Stomatepia spp.* Table displays results of LMs investigating if $\delta^{13}C$ and $\delta^{15}N$ values vary among species. A normal distribution was used for all models. Significant predictors ($P < 0.05$) are bolded.

Model	**Response**	**Predictor**	χ^2	**d.f.**	***P***
ALL species	**$\delta^{13}C$**	**Species**	**123.36**	**11**	**$<2.2*10^{-16}$**
	$\delta^{15}N$	**Species**	**67.967**	**11**	**$2.969*10^{-10}$**
***Stomateptia* ONLY**	**$\delta^{13}C$**	**Species**	**15.534**	**3**	**0.00141**
	$\delta^{15}N$	Species	5.36	3	0.147