

ORIGINAL ARTICLE

The effects of land use disturbance vary with trophic position in littoral cichlid fish communities from Lake Tanganyika

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Abstract

1. Impacts of anthropogenic disturbance are especially severe in freshwater ecosystems. In particular, land use disturbance can lead to increased levels of pollution, including elevated nutrient and sediment loads whose negative impacts range from the community to the individual level. However, few studies have investigated if these impacts are uniform across species represented by multiple trophic levels. To address this knowledge gap, we focused on Lake Tanganyika cichlid fishes, which comprise hundreds of species representing a wide range of feeding strategies. Cichlids are at their most diverse within the near-shore environment; however, land use disturbance of this environment has led to decreasing diversity, particularly in herbivores. We therefore tested if there is a uniform effect of pollution across species and trophic groups within the hyper-diverse rocky shore cichlid fish community.
2. We selected three sites with differing levels of human impact along the Tanzanian coastline and 10 cichlid species, comprising varying taxonomic and trophic groups, common to these sites. Nitrogen and carbon stable isotope values for 528 samples were generated and analysed using generalised linear mixed models. We also estimated stomach contents including sediment proportions.
3. Our study highlights that multiple sources of pollution are having differing effects across species within a diverse fish community. We found that nitrogen stable isotope values were significantly higher at the most disturbed (urbanised) site for benthic feeding species, whereas there was no difference in these isotopes between sites for the water column feeding trophic group. Stomach contents revealed that the elevated $\delta^{15}\text{N}$ values were unlikely to have been caused by differences in diet between sites. However, at the most disturbed site, higher proportions of sediment were present in most herbivores, irrespective of foraging behaviour.
4. It is likely that anthropogenic nitrogen loading is the cause of higher nitrogen stable isotope values since there was no evidence of species shifting trophic levels between sites. Results support our previous study showing herbivore species to

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be most affected by human disturbance and make the link to pollution much more explicit. As lower diversity of consumers can negatively affect ecosystem processes such as stability, alleviating environmental impact through sewage treatment and afforestation programmes should continue to be a global priority for the conservation of aquatic ecosystems, as well as human health.

KEYWORDS

cichlids, nitrogen loading, sedimentation, stable isotopes, stomach contents

1 | INTRODUCTION

The impacts of anthropogenic disturbance are especially severe in freshwater ecosystems because they are subject to a variety of anthropogenic stressors (Søndergaard & Jeppesen, 2007), which, combined with their disproportionately high diversity, results in these ecosystems being some of the most endangered in the world (Dudgeon et al., 2006; Magurran, 2009). In particular, changes in land use can lead to elevated nutrient and sediment loads in some freshwater systems (Saunders, Meeuwig, & Vincent, 2002), with both stressors implicated as threats to freshwater species (Richter, Braun, Mendelson, & Master, 1997).

Anthropogenic impacts have led to higher levels of nitrogen deposition into aquatic ecosystems in the form of domestic, industrial, and agricultural waste products (Camargo & Alonso, 2006). Excess nitrogen is known to have many negative effects on the individual fitness of organisms, including ammonia, nitrite, and nitrate toxicity, in addition to habitat level effects such as eutrophication (Camargo & Alonso, 2006). Anthropogenic nitrogen in the form of sewage has been identified in organisms using nitrogen stable isotope analysis (Fry, 1999), with areas subjected to treated wastewater effluent, and untreated sewage contamination, having higher $\delta^{15}\text{N}$ values (Anderson & Cabana, 2005; Cabana & Rasmussen, 1996; Kelly, Mtimi, McIntyre, & Vadeboncoeur, 2016; Schlacher, Mondon, & Connolly, 2007; Vermeulen, Sturaro, Gobert, Bouquegneau, & Lepoint, 2011). Consequently, $\delta^{15}\text{N}$ values have been proposed as an indicator for detecting anthropogenic nitrogen in aquatic ecosystems (Costanzo, O'Donohue, Dennison, Loneragan, & Thomas, 2001; Lake et al., 2001; Vermeulen et al., 2011). Environmental stress can also increase individual variation in $\delta^{15}\text{N}$ values in invertebrates in controlled conditions, possibly because of more variable growth rates (Gorokhova, 2018). One of the advantages of measuring $\delta^{15}\text{N}$ in fish muscle is that it averages nutrient flux over a period of several months (Trueman, McGill, & Guyard, 2005), compared to measuring anthropogenic nitrogen levels in the water, which can be temporally more variable and therefore may not show any significant differences between polluted and non-polluted sites (Kelly et al., 2016).

Deforestation of near shore habitats and subsequent soil erosion can lead to increased rates of sedimentation and is one of the main threats to aquatic ecosystems (Dudgeon et al., 2006). Increased sediment influx can negatively impact freshwater habitats

by altering light, oxygen, and temperature in the water column (Donohue, Verheyen, & Irvine, 2003) as well as smothering substrata and reducing the nutritional value of periphyton (Graham, 1990). Pollutants such as pesticides and trace metals, as well as being absorbed directly by primary producers and magnifying up the food chain (Gersberg, Elkins, Lyon, & Goldman, 1986), can also be concentrated in sediment (Donohue & Garcia Molinos, 2009), and assimilated through indirect sediment ingestion (Eggleton & Thomas, 2004). Aquatic organisms ingesting sediment have a higher likelihood of physiological and behavioural defects, as well as increased risk of mortality (Donohue & Garcia Molinos, 2009), and by covering breeding and feeding grounds sediment can reduce habitat heterogeneity (Passy & Blanchet, 2007), resulting in more homogenous assemblages (Balata, Piazzini, & Benedetti-Cecchi, 2007).

1.1 | Pollution of a global aquatic hotspot

One of the world's most diverse freshwater ecosystems is East Africa's Lake Tanganyika (LT) with c. 1,470 animal species, which is renowned for its impressive adaptive radiations of cichlids fishes (e.g. Day, Cotton, & Barraclough, 2008). Although the least disturbed of the great lakes (Dobiesz et al., 2010), there have been major increases in anthropogenic stressors around its shores, and the lake is especially vulnerable to pollution due to the slow rate of water renewal in its effectively closed system (Coulter & Mubamba, 1993). This is particularly problematic in near shore urban areas where incorrect treatment and disposal of domestic, agricultural and industrial waste is prevalent (Chale, 2003; Kelly et al., 2016). Increased erosion and sediment transport is also a major threat to the LT ecosystem, primarily caused by deforestation of the lake shore's miombo woodland (Alin et al., 1999; Cohen, Bills, Cocquyt, & Caljon, 1993; Coulter & Mubamba, 1993), particularly in areas with steep rift basins such as around the Kigoma region (Alin et al., 2002; Cohen, Kaufman, & Ogotu-Ohwayo, 1996). Increased sediment loads have been shown to affect the community dynamics of LT benthic invertebrate and fish communities by decreasing species richness and abundance (Donohue et al., 2003); however, the uptake of sediment by cichlids in this region has to our knowledge not been investigated.

A recent study showed the multi-faceted effect of human disturbance on the cichlids with a clear decline in α -diversity with increasing human disturbance, especially among herbivorous species within the Tropheini

tribe. By contrast, there was a positive relationship between (β -diversity) nestedness across surveys and human disturbance implying rare or specialist species were being lost, and the functional form of ζ -diversity (the expected number of species common to n -surveys) was found to be qualitatively different between disturbed and protected sites indicating stochastic processes dominate in the former, but niche processes dominate in the latter (Britton et al., 2017). These results hint that species are being differentially affected by human disturbance, perhaps based upon their feeding behaviour, but how this is occurring, and whether some species are escaping disturbance effects due to diet changes remains an open question.

Previous LT studies have investigated the effect of anthropogenic loading on the $\delta^{15}\text{N}$ values of sediment, and across a variety of taxonomic groups, with mixed results. Alin et al. (2002) reported higher sediment rates, and higher $\delta^{15}\text{N}$ values of sedimentary organic matter from a disturbed site compared to a nearby National Park (Gombe) in the Kigoma region, probably due to increasing inputs of terrestrial organic matter from shoreline erosion through deforestation. Elevated $\delta^{15}\text{N}$ values in gastropods from village shorelines from this region were attributed to anthropogenic nitrogen loading from human waste (Kelly et al., 2016), although these authors found no difference in nutrient concentrations at these sites compared to reference sites. It is likely that nutrients in LT are quickly sequestered by phytoplankton and periphyton (Corman et al., 2010; McIntyre, Michel, & Olsgard, 2006); however, due to the open nature of the littoral zone, phytoplankton are rapidly washed away. In contrast, diversity and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of crab species from Kigoma were similar at sediment impacted and reference sites (Marijnissen, Michel, Cleary, & McIntyre, 2009) with dietary breadth potentially contributing to their resilience to sedimentation, based on the wide range of $\delta^{13}\text{C}$ values from both sites. This study suggested that some species may adapt their feeding behaviour to negate the effects of environmental changes, or that they may be immune to the effects of pollution because of a broad diet. However, it is hard to know whether these mixed results, associated with increased sedimentation, are due to differences in the taxonomic groups or differences in the feeding behaviour. Here, we focus on the cichlid fish community, which is a useful study group to test out these possibilities as they contain a wide range of feeding strategies across multiple trophic levels.

1.2 | Aims and expectations

To answer whether changes in water quality have a uniform effect on the LT cichlid fish community, we characterised the stable isotope signatures of rocky shore littoral cichlids from sites with differing levels of anthropogenic disturbance. Firstly, we asked whether nitrogen stable isotope values differ between urban and non-urban areas, and which taxonomic and trophic groups are most affected. Because high stable nitrogen signatures are used as indicators of anthropogenic impact (Vermeulen et al., 2011), we predicted elevated $\delta^{15}\text{N}$ values and variance in species at urban sites compared to non-urban sites. We expected all cichlids, but particularly benthic herbivores to have higher $\delta^{15}\text{N}$ values, in part

because their diversity has recently been shown to be more affected by human disturbance within this region than the other feeding groups (Britton et al., 2017). Secondly, we investigated possible biological mechanisms causing changes in nitrogen stable isotope values using stomach content analysis. We expected to rule out dietary changes as the cause of higher $\delta^{15}\text{N}$ values, and instead predicted anthropogenic nitrogen input (Vermeulen et al., 2011) to be the principal driver. Based on the higher sedimentation at urban sites, we also predicted higher sediment content in the stomachs of fishes at the urban site compared to the non-urban site.

2 | MATERIALS AND METHODS

2.1 | Study system

Lake Tanganyika's littoral and sublittoral zones contain highly diverse communities of endemic fishes, molluscs and crustaceans (Coulter, 1991; Day et al., 2008). Of these, cichlid fishes are the most diverse animal group (200 species) and dominate the rocky littoral zone (c. 65% of all cichlid species) (Konings, 2015). Upwards of 60 species have been recorded at some rocky-shore locations (Britton et al., 2017) with communities comprising a vast range of feeding strategies and taxonomic groups (Konings, 2015). Based on these attributes, and that rocky-shore cichlids have previously been shown to be affected by human impacts (e.g. Alin et al., 2002; Britton et al., 2017) they were therefore selected as our focal system.

2.2 | Study sites

We focused on three sites, TAFIRI Bay, Kigoma Deforested, and Kalilani Island, in the Kigoma region of Tanzania (Figure 1). These sites were situated within localities surveyed by Britton et al. (2017), and in the absence of baseline stable isotope data before anthropogenic impact (Rowell, Dettman, & Dietz, 2010), were selected due to their differing levels of human disturbance ranking (Britton et al., 2017). An urban site, TAFIRI Bay, was classified as the most disturbed site, followed by the nearby uninhabited but non-urban Kigoma Deforested site, with the more distant largely forested site of Kalilani Island being the least disturbed (Table 1).

TAFIRI Bay is located in the south of Kigoma Bay, on the shores of Kigoma Town, a large urban area with a human population of 215,458 (Tanzania National Bureau of Statistics, 2013), and a population density of over 32 people per 100 m² (Linard, Gilbert, Snow, Noor, & Tatem, 2012). TAFIRI Bay is responsible for the town's water supply, but is also a repository for untreated domestic and industrial waste (Chale, 2003). The area surrounding TAFIRI Bay has been developed considerably resulting in a population density of 56 people per 100 m² (Linard et al., 2012), and a reduction in tree cover to <10% canopy density (Hansen et al., 2013). Two sampling points within TAFIRI Bay were selected, (a) 4°87.879'S, 29°62.169'E in the northern bay; (b) 4°88.652'S, 29°61.566'E, located 900 m south west, in the southern bay.

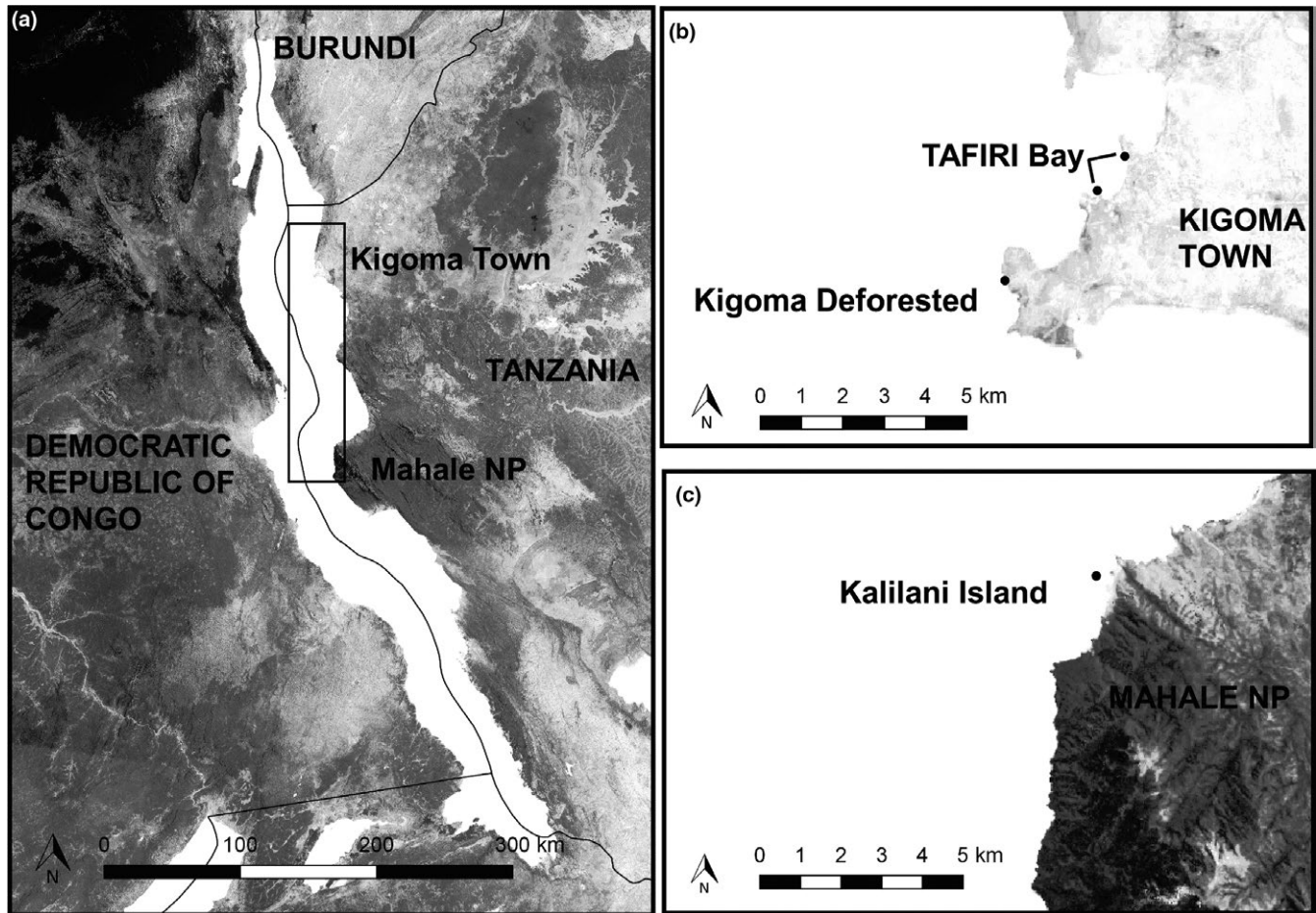


FIGURE 1 (a) Map of Lake Tanganyika, showing study location. (b) TAFIRI Bay and Kigoma Deforested sites from the northern basin. (c) Kalilani Island site from the central basin. The background of all three maps represents tree cover from 0% white–100% black (Hansen et al., 2013)

TABLE 1 Levels of human disturbance at the three study sites. Mean tree canopy and human population density were both quantified in QGIS as the mean raster value per pixel within 1 km of the shoreline of the distance spanning collection sites

Site	Mean tree canopy cover (% per 30 m ²) ^a	Population density (per 100 m ²) ^b
TAFIRI Bay	8.8	56
Kigoma Deforested	9.7	0
Kalilani Island	46.1	0

^aHansen et al. (2013). ^bLinard et al. (2012).

The Kigoma Deforested site (4°90.216'S, 29°59.472'E) is located south of TAFIRI Bay, separated by a 2-km stretch of deforested and uninhabited shoreline. Kigoma Deforested has a tree canopy density of approximately 10% (Hansen et al., 2013), and is uninhabited. The Jakobsen's Beach reserve is 100 m south of this site, encompassing 1 km of shoreline with 16% canopy density (Britton et al., 2017; Hansen et al., 2013).

Kalilani Island (6°02.023'S, 29°74.243'E) is a small 1,000 m² uninhabited island with c. 46% tree canopy density (Hansen et al.,

2013), located 125 km south of Kigoma Town. It is situated approximately 300 m north of the border of Mahale National Park, a pristine area that protects 1,613 km² of lake shore forest (Sweke, Assam, Matsuishi, & Chande, 2013) and 96 km² of the lakes aquatic littoral habitat (West, 2001). It is also situated 200 m west of Kalilani village, a small fishing village covering 2 km of shoreline. Kalilani Village has a tree cover of approximately 25% canopy density (Britton et al., 2017; Hansen et al., 2013), and a population of fewer than three people per 100 m² (Britton et al., 2017; Linard et al., 2012).

2.3 | Sampling

Sampling was conducted from February to March 2015 at TAFIRI Bay and Kalilani Island, and October 2016 at TAFIRI Bay and Kigoma Deforested. The 2016 season was conducted to verify our 2015 cichlid results at TAFIRI Bay in addition to sampling additional baseline species. It also enabled analysis of a non-urbanised deforested site (Kigoma Deforested), which is near to TAFIRI Bay, thereby minimising spatial variation.

To ensure a range of taxonomic and trophic groups were represented, species encompassing benthic herbivores and invertivores, and water column planktivores and piscivores were targeted.

Samples were collected underwater by SCUBA and snorkel at depths of 0–15 m in the rocky littoral zone. Cichlids were caught using a seine net with each species targeted separately. Sampling was random, with several collections made all within a radius of c. 100 m of the GPS coordinates of the anchored boat. Only adult fish were collected, although nitrogen isotopes have been shown to be independent of age in fish and mollusc species (Hobson & Welch, 1995; Kiriluk, Servos, Whittle, Cabana, & Rasmussen, 1995; Minagawa & Wada, 1984). Similar sized individuals were targeted since total individual length has been positively linked to $\delta^{13}\text{C}$, and to a lesser extent $\delta^{15}\text{N}$ values in other labroid fish species (Plass-Johnson, McQuaid, & Hill, 2015), while ontogenetic dietary changes have altered stable isotope signatures in the Lake Malawi cichlid *Pseudotropheus callainos* (Genner, Hawkins, & Turner, 2003). We were only able to determine sex for one cichlid species—*Ophthalmotilapia ventralis*—in the field, and therefore our sampling was indiscriminate. However, sex has not been found to influence stable isotope values in haplochromine cichlids (Genner, Turner, Barker, & Hawkins, 1999).

Upon collection, fish were immediately euthanised with an overdose of clove oil (Neiffer & Stamper, 2009) and preserved in 80% ethanol. Baseline invertebrate species were collected by hand from rocks and benthic substrate, and algae were scraped from multiple (>3) rocks at each site resulting in one multispecies algae sample per site. As comprehensive sample processing could not be conducted on site due to logistical constraints, samples were preserved in ethanol for 2 months before being processed in the laboratory. Therefore, 40 cichlid individuals (including at least one individual of each of the 10 species) across all sites had an additional sample sun dried with the aid of a desiccant (silica gel), and used as controls to allow correction for the effect of ethanol preservation (Correa, 2012).

2.4 | Stable isotope analysis

White muscle tissue from the left dorsal flank of each fish was oven dried at 55°C for 48 hr, along with muscle tissue of mollusc baseline samples and the multispecies algae samples. A subset of the algae samples at each site were acid washed after drying, because of the presence of inorganic carbon in the sediment, and were used to obtain the algae $\delta^{13}\text{C}$ values (Schlacher & Connolly, 2014). Samples were homogenised to a powder using a pestle and mortar for consistency. Fish and invertebrate samples were weighed to c. 0.6 mg and algae samples to c. 3 mg in tin capsules ready for mass spectrometry. The samples were analysed by continuous flow IRMS using an ECS 4010 elemental analyser (Costech instruments, Milan, Italy) coupled to a Delta V Plus Mass Spectrometer (Thermo Fisher Scientific, Bremen, Germany) at the NERC Life Sciences Mass Spectrometry Facility, SUERC, East Kilbride, UK, with four runs in December 2015, and five runs in January 2017. In house laboratory standards—gelatine, alanine, and glycine—were run at the start and the end of the analyses, and after every eight samples, to correct for instrument linearity and drift. In addition, glutamic acid (USGS40) was analysed to compare data quality between runs, with standard deviations of <0.2‰ for

carbon and nitrogen isotope values within all runs. A sample from a benchmark *Gadus morhua* (Gadidae) individual stored at Newcastle University, UK, was analysed on each run to ensure results generated in 2015 and 2017 were comparable (Supporting Information Table S1). Stable isotope ratios are expressed in parts per mil (‰) with the δ symbol using the equation: δ (‰) = $(R_{\text{sample}}/R_{\text{standard}} - 1) \times 1,000$, where $R = {}^{15}\text{N}/{}^{14}\text{N}$ or ${}^{13}\text{C}/{}^{12}\text{C}$.

We aimed to sample 15 individuals of each cichlid species from each site following Ford et al. (2016); however, for a third of species at all sites we obtained fewer individuals due to naturally lower density of certain species during sampling, with eight individuals the minimum analysed. Three to 12 individuals of baseline invertebrate species and three replicates of the multispecies algae sample were analysed at each site. A total of 528 samples were analysed. These included 414 samples from 10 cichlid species: 128 and 43 samples, TAFIRI Bay, 2015, 2016 respectively; 138 samples, Kalilani Island, 2015; 105 samples, Kigoma Deforested, 2016 (Supporting Information Table S2). Sun-dried control samples included: 40 cichlid individuals from nine species, and 62 baseline samples composed of four mollusc species, and 12 multispecies algae samples.

2.5 | Corrections for lipid content and tissue preservation

Due to carbon isotope fractionation during lipid synthesis, a lipid normalisation was applied to the $\delta^{13}\text{C}$ values (Kiljunen et al., 2006). A revised model ($\delta^{13}\text{C}' = \delta^{13}\text{C} + D - [I + 3.9/1 + 287/\text{lipid proportion}]$) modified from McConnaughey and McRoy (1979) with updated parameters applicable to freshwater fish was used for the correction (Kiljunen et al., 2006). The parameters, $D = 7.018 \pm 0.263$ and $I = 0.048 \pm 0.013$, are similar to other cichlid species (Gaye-Siessegger, Focken, Abel, & Becker, 2004), and have been used in one other study of cichlid stable isotope values (Ford et al., 2016). A lipid extraction was not performed because it can change the nitrogen isotopes in an unpredictable way (Kiljunen et al., 2006), and $\delta^{15}\text{N}$ values were not modified because there is very little nitrogen in lipids. The baseline species were also not lipid corrected.

Ethanol preservation can affect $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Correa, 2012). When the $\delta^{13}\text{C}$ values of sun-dried control samples were pooled between the four sites, there was a significant difference with ethanol preserved specimen $\delta^{13}\text{C}$ values, for both raw and lipid-normalised values (Supporting Information Table S3). The pooled, lipid-corrected, ethanol-preserved $\delta^{13}\text{C}$ values and lipid-corrected, air-dried $\delta^{13}\text{C}$ values were plotted and a linear correction was applied to all cichlid ethanol-preserved $\delta^{13}\text{C}$ values using the data fitted equation: $\delta^{13}\text{C}_{\text{corrected}} = 1.0387 \times \delta^{13}\text{C}_{\text{ethanol}} + 0.3758$ (Bicknell et al., 2011; Bugoni, McGill, & Furness, 2008; Kelly, Dempson, & Power, 2006). However, it has been reported that $\delta^{13}\text{C}$ values decrease by over 1‰ in fish muscle tissue preserved in ethanol for 6 weeks, and longer preservation might increase variation (Arrington & Winemiller, 2002). Therefore, the corrections applied to $\delta^{13}\text{C}$ mean fine scale differences

in stable isotope values (<2‰) will not be used to make ecological inferences in this study, although $\delta^{13}\text{C}$ values can be used to differentiate between larger scale differences in habitats (e.g. Piola, Moore, & Suthers, 2006). In terms of $\delta^{15}\text{N}$, there were no systematic difference between pooled $\delta^{15}\text{N}$ values of ethanol preserved and air-dried tissues (mean difference of 0.212‰, with a paired *t*-test, $t = 1.8833$, $p = 0.0668$), so no ethanol correction was applied to $\delta^{15}\text{N}$, and raw $\delta^{15}\text{N}$ values were used for downstream analysis. Furthermore, baseline samples were not used to correct cichlid $\delta^{15}\text{N}$ values and standardise between site comparisons because the presence of inorganic carbonates prevented reliable baseline stable isotope values being obtained in 2015 (Woodcock et al., 2012), and the large variation in some baseline species $\delta^{15}\text{N}$ values between sites prevented a reliable normalisation (Supporting Information Table S4).

2.6 | Data analysis

To assess if the effects of land use disturbance vary with trophic position, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures were investigated with a global analysis. $\delta^{15}\text{N}$ values were analysed with a generalised linear mixed model (GLMM) with trophic group, sampling site and body size as fixed predictors, and species as a random variable. These analyses were performed in the R package lme4 v1.1-19 (Bates, Mächler, Bolker, & Walker, 2015). To investigate if trophic group $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures differ between sites, the estimated mean trophic group $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were compared between all sites with a multiple comparison Tukey post hoc test in the emmeans R package v1.2.4 (Lenth, Singmann, Love, Buerkner, & Herve, 2018), using Bonferroni-adjusted *p*-values.

To further explore variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures between sites, a species level analysis of stable isotope values was conducted with a generalised linear model with site as the fixed main predictor variable, and body size as a covariate, in the base library of R v3.1.3 (R Core Team, 2015; Supporting Information Table S5). Additionally, the estimated mean species $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values between sites were compared with a multiple comparison Tukey post hoc test, using Bonferroni-adjusted *p*-values to assess which sites differ in terms of a species stable isotope values.

For all GLMM and generalised linear model analyses, diagnostic plots of the residuals confirmed that the γ -distribution was most appropriate choice for the link function for the $\delta^{15}\text{N}$ analyses whereas the Gaussian distribution was most appropriate for the $\delta^{13}\text{C}$ analyses.

2.7 | Stomach content analysis

To identify areas with higher rates of sedimentation and diet shifts, stomach content analysis was used to allow quantification of diet (e.g. Davis, Blanchette, Pusey, Jardine, & Pearson, 2012; Malins et al., 1985, 1987), although we note that it provides only a temporal snapshot of each individual's intake (Polito et al., 2011; Wagner, McIntyre, Buels, Gilbert, & Michel, 2009). Stomach contents of a subset of fish, totalling 187 specimens, collected at TAFIRI Bay and

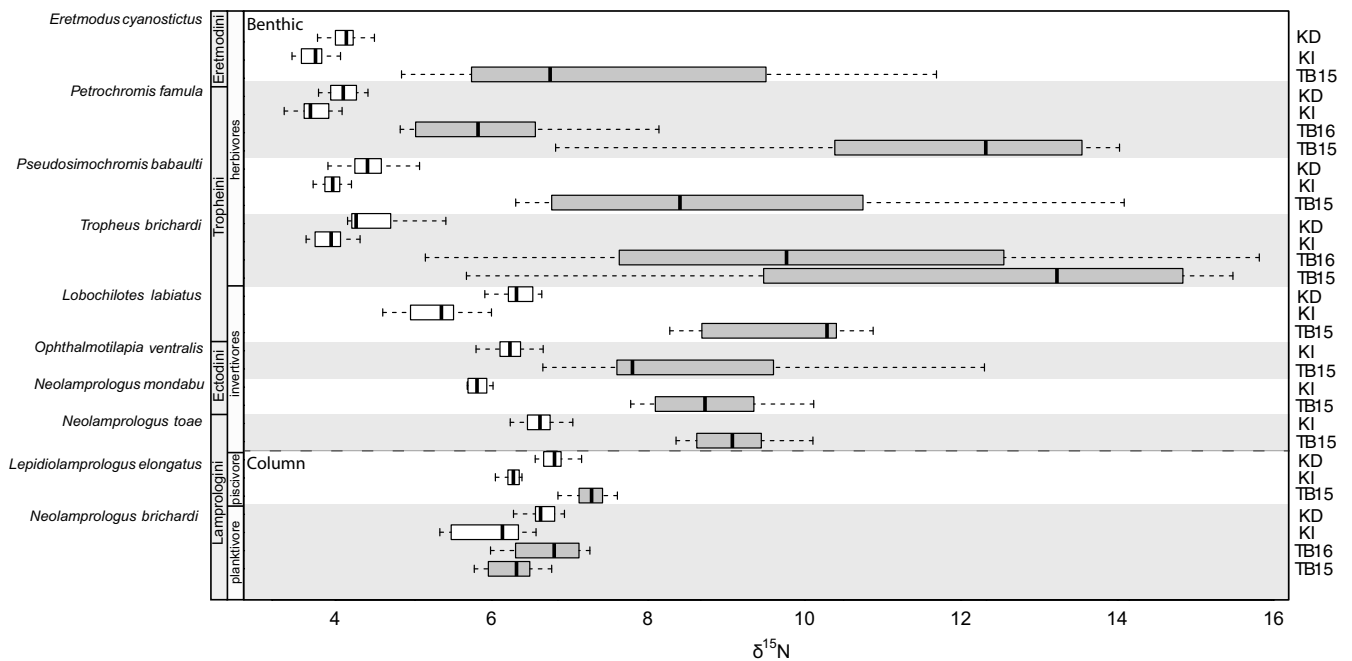
Kalilani Island in 2015 were analysed to identify actual diet (see Supporting Information Tables S6 and S7) with 8–12 individuals selected per site. Stomachs and intestines were removed with a ventral incision in the body wall and measured, before being dissected under a Leica L2 dissection microscope. The poor preservation condition of the intestines and their frequent disintegration upon removal meant that only stomachs were analysed. As contents were too small to weigh, a modified version of the points method of (Hynes, 1950) and (Hyslop, 1980) was used (Genner et al., 1999). Items were sorted and split into the broad categories: (1) sediment; (2) algae; (3) fish scales; (4) insects; (5) crustaceans; (6) gastropods; (7) fish; (8) plankton. Fish scales were included as a separate category from *fish* as they are reported within the stomachs of non-piscivorous cichlids species, and inferred to be ingested through aggressive territorial behaviour (Kohda, 1995). The categories were allocated points based on their proportional value. The category with the largest volume was given 16 points and, if other categories were present, they were sequentially awarded 8, 4, 2, 1 or 0 points, in descending order of volume relative to the most abundant category (Genner et al., 1999). Total points were counted and the volume contribution of each category was calculated as a percentage, and averaged for the species at each site. Pairwise comparison of dietary composition between each species at both study sites were performed using Schoener's dietary overlap index (Schoener, 1970) with the equation $SI = 1 - 0.5(|\sum P_{iA} - \sum P_{iB}|)$ where P_{iA} is the proportion of food category *i* in the diet of fish population A, and P_{iB} is the proportion of food category *i* in the diet of fish population B. Values varied between 0, when no food items are shared, and 1, indicating complete dietary overlap, with values ≥ 0.6 considered to indicate high diet similarity and overlap (Langton, 1982). Additionally, dietary overlaps were visualised with multidimensional scaling in the base library of R v3.1.3 (R Core Team, 2015) to identify groups based on diet. To compare proportions of individual dietary components between sites, Fisher's least significant difference tests were performed on arcsine transformed sediment proportions of individual specimens for each of the eight species with sediment present in their stomachs. As multiple comparisons were conducted a Bonferroni-adjusted *p*-value was used. To further explore the variation in the organic components of diet, an analysis of similarity (ANOSIM) with 999 permutations and Bray–Curtis distance metric was conducted in the R package vegan v2.3-0 (Oksanen et al., 2015). The ANOSIM compared the similarity of stomach contents (excluding the non-organic category sediment) between species and between sites.

3 | RESULTS

3.1 | Nitrogen stable isotopes

All but one benthic feeding cichlid species, as well as the water column feeding cichlid piscivore *Lepidolamprologus elongatus*, display significantly different mean $\delta^{15}\text{N}$ values between the urban site of TAFIRI Bay and the less disturbed sites (i.e. the non-urban sites

(a) Nitrogen stable isotopes



(b) Carbon stable isotopes

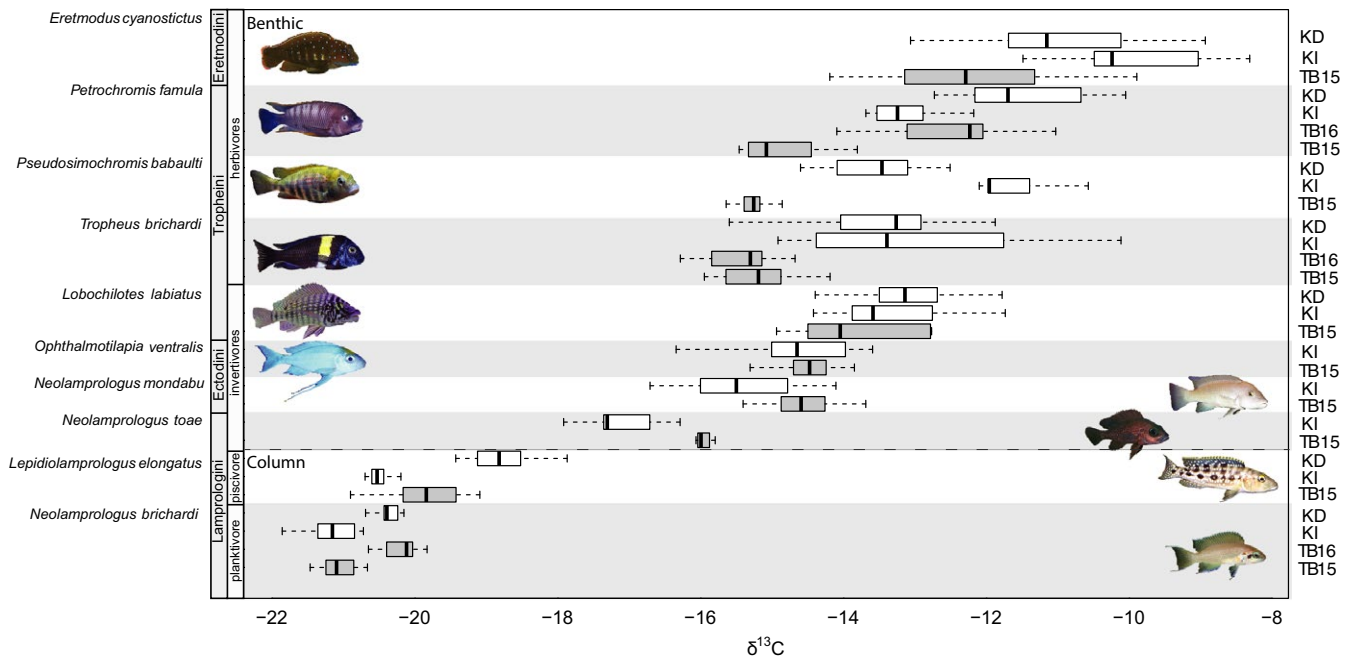


FIGURE 2 (a) The median $\delta^{15}\text{N}$ values and ranges of cichlid species collected in 2015 from TAFIRI Bay (TB15) and Kalilani Island (KI), and in 2016 from TAFIRI Bay (TB16) and Kigoma Deforested (KD). (b) The median $\delta^{13}\text{C}$ values and ranges of cichlid species collected from TAFIRI Bay and Kalilani Island in 2015, and TAFIRI Bay and Kigoma Deforested in 2016. Interquartile ranges for the urban site TAFIRI Bay are shaded grey, and Kalilani Island and Kigoma Deforested interquartile ranges are unshaded

of Kigoma Deforested, and the forested Kalilani Island; Figure 2a and Table 2). In contrast, the water column feeding planktivore *Neolamprologus brichardi* and benthic invertivore *O. ventralis* are the only species to show no difference in $\delta^{15}\text{N}$ values between TAFIRI Bay and both non-urban sites (Table 2). When $\delta^{15}\text{N}$ values are analysed by trophic group there are significant differences in estimated

mean $\delta^{15}\text{N}$ values between TAFIRI Bay and the non-urban sites for benthic herbivores and invertivores with a Tukey post hoc test, but not for water column feeders (Table 3).

The difference in $\delta^{15}\text{N}$ at urban and non-urban sites reveals a similar pattern for the baseline species, with benthic feeders more affected than filter feeders (Supporting Information Table S4).

TABLE 2 Results of generalised linear model Tukey's post hoc tests to compare $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values between sites for each species

$\delta^{15}\text{N}$	Estimate	SE	z	p
<i>Eretmodus cyanostictus</i>				
Kigoma Deforested–Kalilani Island	-0.045	0.014	-3.216	0.0037
Kigoma Deforested–TAFIRI Bay 2015	0.108	0.01	10.614	<0.0001
Kalilani Island–TAFIRI Bay 2015	0.153	0.013	11.397	<0.0001
<i>Lepidiolamprologus elongatus</i>				
Kigoma Deforested–Kalilani Island	-0.015	0.002	-8.131	<0.0001
Kigoma Deforested–TAFIRI Bay 2015	0.013	0.002	7.857	<0.0001
Kalilani Island–TAFIRI Bay 2015	0.028	0.002	14.939	<0.0001
<i>Lobochilotes labiatus</i>				
Kigoma Deforested–Kalilani Island	-0.036	0.006	-5.631	<0.0001
Kigoma Deforested–TAFIRI Bay 2015	0.064	0.007	9.422	<0.0001
Kalilani Island–TAFIRI Bay 2015	0.1	0.007	13.749	<0.0001
<i>Neolamprologus brichardi</i>				
Kigoma Deforested–Kalilani Island	0.018	0.003	-6.412	<0.0001
Kigoma Deforested–TAFIRI Bay 2015	-0.006	0.003	-1.953	0.2059
Kigoma Deforested–TAFIRI Bay 2016	0.006	0.003	2.136	0.1416
Kalilani Island–TAFIRI Bay 2015	0.013	0.003	4.166	0.0002
Kalilani Island–TAFIRI Bay 2016	0.025	0.003	8.897	<0.0001
TAFIRI Bay 15–TAFIRI Bay 2016	0.012	0.003	4.365	0.0001
<i>Neolamprologus mondabu</i>				
Kalilani Island–TAFIRI Bay 2015	0.06	0.008	7.315	<0.0001
<i>Neolamprologus toae</i>				
Kalilani Island–TAFIRI Bay 2015	0.042	0.002	19.116	<0.0001
<i>Ophthamotilapia ventralis</i>				
Kalilani Island–TAFIRI Bay 2015	-0.011	0.004	-2.907	0.0036
<i>Petrochromis famula</i>				
Kigoma Deforested–Kalilani Island	-0.043	0.027	-1.553	0.4057
Kigoma Deforested–TAFIRI Bay 2015	0.13	0.013	10.167	<0.0001
Kigoma Deforested–TAFIRI Bay 2016	0.075	0.014	5.526	<0.0001
Kalilani Island–TAFIRI Bay 2015	0.173	0.026	6.639	<0.0001
Kalilani Island–TAFIRI Bay 2016	0.117	0.026	4.442	0.0001
TAFIRI Bay 2015–TAFIRI Bay 2016	-0.056	0.01	-5.377	<0.0001
<i>Pseudosimochromis babaulti</i>				
Kigoma Deforested–Kalilani Island	-0.015	0.015	-0.98	0.5894
Kigoma Deforested–TAFIRI Bay 2015	0.106	0.013	7.956	<0.0001
Kalilani Island–TAFIRI Bay 2015	0.12	0.009	13.045	<0.0001
<i>Tropheus brichardi</i>				
Kigoma Deforested–Kalilani Island	-0.05	0.035	-1.436	0.4767
Kigoma Deforested–TAFIRI Bay 2015	0.134	0.016	8.549	<0.0001
Kigoma Deforested–TAFIRI Bay 2016	0.112	0.016	6.821	<0.0001
Kalilani Island–TAFIRI Bay 2015	0.184	0.032	5.676	<0.0001
Kalilani Island–TAFIRI Bay 2016	0.162	0.033	4.94	<0.0001
TAFIRI Bay 2015–TAFIRI Bay 2016	-0.022	0.011	-2.079	0.1598

(Continues)

TABLE 2 (Continued)

$\delta^{13}\text{C}$	Estimate	SE	z	p
<i>E. cyanostictus</i>				
Kigoma Deforested—Kalilani Island	-0.44	0.242	-1.816	0.1797
Kigoma Deforested—TAFIRI Bay 2015	0.116	0.285	0.408	0.9125
Kalilani Island—TAFIRI Bay 2015	0.557	0.308	1.807	0.1826
<i>L. elongatus</i>				
Kigoma Deforested—Kalilani Island	1.778	0.164	10.812	<0.0001
Kigoma Deforested—TAFIRI Bay 2015	0.619	0.163	3.801	0.0014
Kalilani Island—TAFIRI Bay 2015	-1.158	0.173	-6.677	<0.0001
<i>L. labiatus</i>				
Kigoma Deforested—Kalilani Island	0.683	0.273	2.498	0.0457
Kigoma Deforested—TAFIRI Bay 2015	1.349	0.473	2.851	0.021
Kalilani Island—TAFIRI Bay 2015	0.667	0.469	1.421	0.3425
<i>N. brichardi</i>				
Kigoma Deforested—Kalilani Island	0.965	0.115	8.399	<0.0001
Kigoma Deforested—TAFIRI Bay 2015	0.659	0.112	5.886	<0.0001
Kigoma Deforested—TAFIRI Bay 2016	-0.08	0.118	-0.682	0.9036
Kalilani Island—TAFIRI Bay 2015	-0.306	0.116	-2.638	0.0521
Kalilani Island—TAFIRI Bay 2016	-1.045	0.121	-8.612	<0.0001
TAFIRI Bay 2015—TAFIRI Bay 2016	0.739	0.119	-6.233	<0.0001
<i>Neolamprologus mondabu</i>				
Kalilani Island—TAFIRI Bay 2015	0.142	0.577	0.247	0.8074
<i>Neolamprologus toae</i>				
Kalilani Island—TAFIRI Bay 2015	-1.006	0.148	6.972	<0.0001
<i>Ophthamotilapia ventralis</i>				
Kalilani Island—TAFIRI Bay 2015	-0.018	0.356	0.518	0.6106
<i>Petrochromis famula</i>				
Kigoma Deforested—Kalilani Island	1.267	0.43	-2.946	0.0261
Kigoma Deforested—TAFIRI Bay 2015	2.2	0.317	6.953	<0.0001
Kigoma Deforested—TAFIRI Bay 2016	0.603	0.281	2.147	0.1556
Kalilani Island—TAFIRI Bay 2015	0.934	0.456	2.046	0.1882
Kalilani Island—TAFIRI Bay 2016	-0.664	0.432	-1.536	0.4259
TAFIRI Bay 2015—TAFIRI Bay 2016	-1.598	0.32	-4.999	0.0001
<i>Pseudosimochromis babaulti</i>				
Kigoma Deforested—Kalilani Island	-1.22	0.357	-3.416	0.0037
Kigoma Deforested—TAFIRI Bay 2015	1.822	0.374	4.872	<0.0001
Kalilani Island—TAFIRI Bay 2015	3.041	0.28	10.857	<0.0001
<i>T. brichardi</i>				
Kigoma Deforested—Kalilani Island	-0.639	0.557	-1.447	0.6623
Kigoma Deforested—TAFIRI Bay 2015	0.143	0.42	2.724	0.0426
Kigoma Deforested—TAFIRI Bay 2016	1.382	0.414	3.335	0.0085
Kalilani Island—TAFIRI Bay 2015	1.782	0.586	3.041	0.019
Kalilani Island—TAFIRI Bay 2016	2.021	0.582	3.471	0.0058
TAFIRI Bay 2015—TAFIRI Bay 2016	0.239	0.453	0.528	0.9519

Kalilani Island was sampled in 2015 and Kigoma Deforested was sampled in 2016, whereas urban site TAFIRI Bay was sampled in both 2015 and 2016, as indicated in the table. Post hoc test *p*-values highlighted bold indicate a significant difference with a Bonferroni-adjusted *p*-value of 0.0015.

Additionally, the differences between baseline and cichlid $\delta^{15}\text{N}$ values ranged between 4‰ and 9‰ within trophic groups per site.

3.2 | Carbon stable isotopes

There are clear differences between the mean $\delta^{13}\text{C}$ values of benthic and water column species (Figure 2b). All trophic group $\delta^{13}\text{C}$ values are significantly different at TAFIRI Bay in 2015 compared to less disturbed non-urban sites, whereas there is no difference in trophic group $\delta^{13}\text{C}$ values at TAFIRI Bay in 2016 compared to the non-urban sites (Table 3). In terms of the species level analysis, there are no consistent differences in mean $\delta^{13}\text{C}$ values between sites (Table 2), suggesting that, unlike nitrogen isotopes, differences in carbon isotopes are not linked to human disturbance.

Algae $\delta^{13}\text{C}$ values range between approximately -10‰ and -15‰ $\delta^{13}\text{C}$, which is reflected in similar values for algivorous molluscs, the gastropods *Lavigeria grandis* and *Lavigeria nassa*, and herbivorous cichlid *Tropheus brichardi* (Figure 3a, c). In detritus-feeding mollusc *Neothauma tanganyicense* (Viviparidae), filter-feeding mollusc *Pleiodon speki* (Iridinidae), and water column-feeding cichlid *N. brichardi*, $\delta^{13}\text{C}$ values range between approximately -20 and -25‰ (Figure 3b, d). The $\delta^{13}\text{C}$ values differ slightly within sites for the benthic cichlid and baseline species but as the differences are not consistently $> 2\text{‰}$ they were not considered large enough to make ecological inferences (Arrington & Winemiller, 2002).

3.3 | Stomach content analysis

Variation in dietary overlap broadly mirrored the differences in $\delta^{15}\text{N}$ values where species with the highest $\delta^{15}\text{N}$ values show the greatest dietary overlap, and vice versa (Figure 4 and Table S8). All cichlid species showed considerable dietary overlap between sites, apart from the benthic-feeding *Neolamprologus toae* and water column-feeding *L. elongatus* and *N. brichardi*. However, as the latter two species had the smallest differences in $\delta^{15}\text{N}$ values, we can assume that diet did not play a role in the increased $\delta^{15}\text{N}$ values at TAFIRI Bay. When these differences are visualised, multidimensional scaling shows clustering of herbivores and clustering of non-herbivores (Supporting Information Figure S1), however within the herbivores the species cluster by site. In terms of individual dietary components (Supporting Information Tables S6 and S7) a significantly higher proportion of sediment was found in the stomachs of four cichlid species at TAFIRI Bay compared to Kalilani Island in 2015 (Supporting Information Table S8). These species included three of the four herbivores, encompassing multiple behavioural adaptations for harvesting algae: *Eretmodus cyanostictus* (scraper), *Petrochromis famula* (grazer), *T. brichardi* (browser) as well as the planktonic column feeding *N. brichardi* (Supporting Information Table S8). *Pseudosimochromis babaulti* (browser) had a higher proportion of sediment in its stomach at Kalilani Island than the other herbivores, probably because it often feeds in sediment-rich areas of the rocky shore (Koblmüller, Egger, Sturmbauer, & Sefc, 2010). We suggest that it is the extra stomach sediment in the urban site that leads to the herbivores clustering out according to site (Supporting Information

Figure S1). We also found significant differences in stomach contents between the species (ANOSIM, $R = 0.547$, $p = 0.01$), but not between sites (ANOSIM, $R = 0.001$, $p = 0.064$) when the non-organic sediment category was removed from the ANOSIM.

4 | DISCUSSION

Nitrogen stable isotopes have been shown to be a highly sensitive tool for monitoring anthropogenic allochthonous sources of nitrogen in freshwater and marine ecosystems (Anderson & Cabana, 2005; Kelly et al., 2016; Vermeulen et al., 2011), as well as an indicator of stress (Gorokhova, 2018). We utilised this method to investigate the effect of land-use disturbance in a species rich lacustrine tropical fish community and revealed significantly higher and more variable $\delta^{15}\text{N}$ values in individuals sampled from an urban area than those at non-urban areas (Figures 2 and 3, and Tables 2 and 3). Notably, this finding is not uniform across species examined from the urbanised site as we showed that benthic feeding species, particularly herbivores, were more affected than species feeding in the water column (Figures 2 and 3, and Tables 2 and 3). Nitrogen isotope values for benthic feeders at the urban site are far higher than those for *L. elongatus*, which as a carnivore would hold a higher trophic position in a typical food web of this species rich community. The increase in nitrogen stable isotopes appears to be robust because it is large, consistent across years, and reflects long-term assimilation. These results support a previous study of freshwater habitats in North America where more variable $\delta^{15}\text{N}$ values were reported in benthic feeding fish species than pelagic species (Lake et al., 2001).

Cichlid fishes have been shown to change their food source in response to ecological pressures, as reported in Lake Victoria cichlids responding to increased predation (Katunzi, Zoutendijk, Goldschmidt, Wanink, & Witte, 2003), and changing resource availability (Njiru, Okeyo-Owuor, Muchiri, & Cowx, 2004), while reduction of habitat availability is suggested to have caused dietary change in the Arctic charr, *Salvelinus alpinus* (Salmonidae) from Lake Windermere (Corrigan, Winfield, Hoelzel, & Lucas, 2011). However, we could rule out dietary shifts as the cause of elevated $\delta^{15}\text{N}$ values, since aside from an intra-trophic level shift in *N. toae* (Supporting Information Tables S6 and S7) there were no differences in stomach content of benthic feeders between sites apart from an elevated sediment content in TAFIRI Bay. The switch of major dietary component from crustaceans to benthic gastropods observed in *N. toae* at TAFIRI Bay (Supporting Information Tables S6 and S7) could, however be responsible for the higher $\delta^{15}\text{N}$ values found at this site.

Urban areas with higher human populations are subjected to inputs of anthropogenic waste nitrogen (Camargo & Alonso, 2006), and primary producers in these environments incorporate human sewage with elevated $\delta^{15}\text{N}$ (Vermeulen et al., 2011). The higher $\delta^{15}\text{N}$ values that we identify in the benthic food web at our urban site (TAFIRI Bay), and absence of a trophic level dietary shift in benthic feeding cichlid species, indicate that algae is the likely source of the elevated nitrogen stable isotopes. As reported in other lacustrine systems benthic algae absorb increased anthropogenic nitrogen input, and $\delta^{15}\text{N}$ is subsequently biomagnified up the food chain (Cabana & Rasmussen, 1996).

TABLE 3 Results of generalised linear mixed model (GLMM) and Tukey's post hoc tests to compare $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values between sites for each trophic group

$\delta^{15}\text{N}$	Estimate	SE	t	p
GLMM				
Benthic herbivores (intercept)	1.544	0.084	18.466	<0.0001
Benthic invertivores	-0.625	0.01	-6.267	<0.0001
Column feeders	-0.624	0.109	-5.723	<0.0001
TAFIRI Bay 2015	-0.905	0.037	-24.353	<0.0001
TAFIRI BAY 2016	-0.685	0.044	-15.662	<0.0001
Kalilani Island	0.208	0.053	3.947	<0.0001
Standard length	0.141	0.053	2.661	0.008
Post hoc test	Estimate	SE	z	p
Benthic herbivores				
Kigoma Deforested–Kalilani Island	-0.208	0.053	-3.947	0.005
Kigoma Deforested–TAFIRI Bay 2015	0.905	0.037	24.353	<0.0001
Kigoma Deforested–TAFIRI Bay 2016	0.685	0.044	15.662	<0.0001
Kalilani Island–TAFIRI Bay 2015	1.113	0.044	25.496	<0.0001
Kalilani Island–TAFIRI Bay 2016	0.893	0.05	17.969	<0.0001
TAFIRI Bay 2015–TAFIRI Bay 2016	-0.22	0.031	-7.158	<0.0001
Benthic invertivores				
Kigoma Deforested–Kalilani Island	-0.132	0.058	-2.268	0.4994
Kigoma Deforested–TAFIRI Bay 2015	0.0267	0.058	4.644	0.0002
Kalilani Island–TAFIRI Bay 2015	0.4	0.032	12.556	<0.0001
Water column feeders				
Kigoma Deforested–Kalilani Island	-0.091	0.045	-2.014	0.6838
Kigoma Deforested–TAFIRI Bay 2015	0.002	0.043	0.048	1
Kigoma Deforested–TAFIRI Bay 2016	0.019	0.058	0.33	1
Kalilani Island–TAFIRI Bay 2015	0.019	0.007	2.739	0.662
Kalilani Island–TAFIRI Bay 2016	0.11	0.059	1.851	0.7892
TAFIRI Bay 2015–TAFIRI Bay 2016	0.017	0.057	0.297	1
$\delta^{13}\text{C}$	Estimate	SE	t	p
GLMM				
Benthic herbivores (Intercept)	-12.952	0.708	-18.295	<0.0001
Benthic invertivore	-1.867	0.884	-2.113	0.0721
Column feeders	-7.259	1.077	-6.74	0.0003
TAFIRI Bay 2015	-1.147	0.153	-7.477	<0.0001
TAFIRI Bay 2016	-0.651	0.213	-3.052	0.0024
Kalilani Island	0.604	0.171	3.532	0.0042
Standard length	0.008	0.004	1.751	0.0807
Post hoc test	Estimate	SE	z	p
Benthic herbivores				
Kigoma Deforested–Kalilani Island	0.427	0.148	2.882	0.1472
Kigoma Deforested–TAFIRI Bay 2015	1.147	0.153	7.477	<0.0001
Kigoma Deforested–TAFIRI Bay 2016	0.651	0.213	3.052	0.094
Kalilani Island–TAFIRI Bay 2015	0.721	0.138	5.216	<0.0001
Kalilani Island–TAFIRI Bay 2016	0.224	0.212	1.059	0.9962
TAFIRI Bay 2015–TAFIRI Bay 2016	-0.496	0.207	-2.396	0.4088

(Continues)

TABLE 3 (Continued)

Post hoc test	Estimate	SE	z	p
Benthic invertivores				
Kigoma Deforested–Kalilani Island	0.427	0.148	2.882	0.4994
Kigoma Deforested–TAFIRI Bay 2015	1.147	0.153	7.477	<0.0001
Kalilani Island–TAFIRI Bay 2015	0.224	0.212	1.059	0.9962
Water column feeders				
Kigoma Deforested–Kalilani Island	0.427	0.148	2.882	0.1472
Kigoma Deforested–TAFIRI Bay 2015	1.147	0.153	7.477	<0.0001
Kigoma Deforested–TAFIRI Bay 2016	0.651	0.213	3.052	0.094
Kalilani Island–TAFIRI Bay 2015	0.721	0.138	5.216	<0.0001
Kalilani Island–TAFIRI Bay 2016	0.224	0.212	1.059	0.9962
TAFIRI Bay 2015–TAFIRI Bay 2016	-0.496	0.207	-2.396	0.4088

Kalilani Island was sampled in 2015 and Kigoma Deforested was sampled in 2016, whereas urban site TAFIRI Bay was sampled in both 2015 and 2016, as indicated in the table. Post hoc test *p*-values highlighted bold indicate a significant difference with a Bonferroni-adjusted *p*-value of 0.0033.

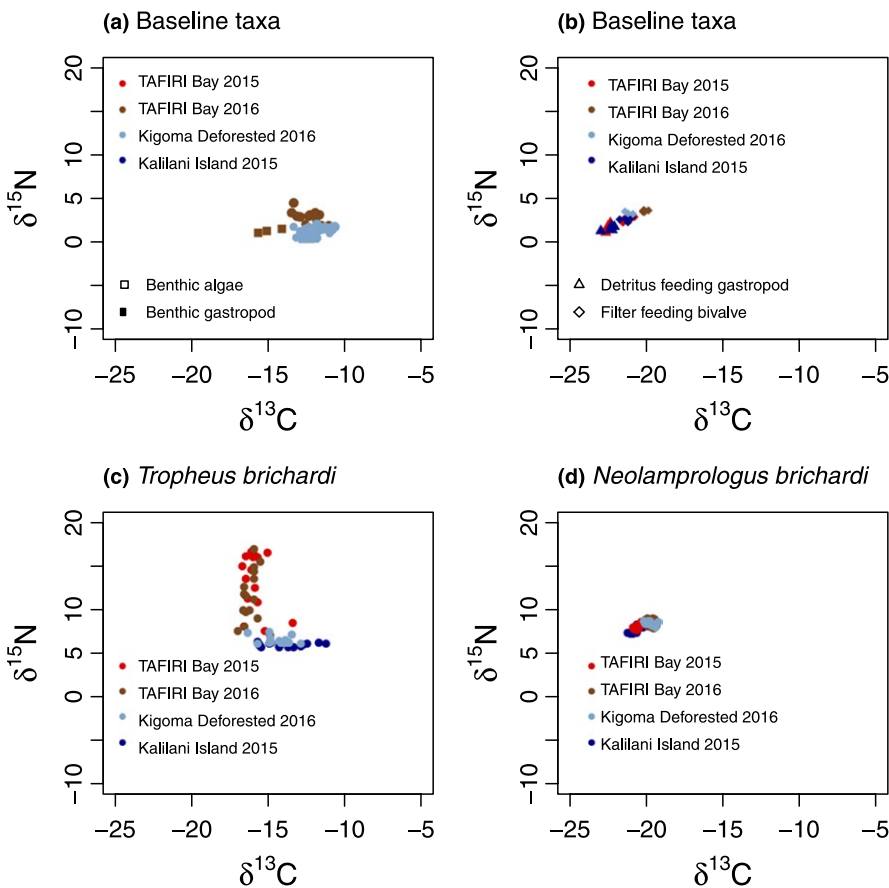


FIGURE 3 Stable isotope values for species collected at sites in 2015 and 2016. (a) Baseline samples including, benthic feeding species *Lavigeria grandis* and *Lavigeria nassa*, and benthic algae. (b) Baseline samples including, detritus feeding *Neothauma tanganyicense* and filter feeding *Pleiodon spekkii*. (c) *Tropheus brichardi* (Tropheini), feeds on benthic algae. (d) *Neolamprologus brichardi* (Lamprologini), feeds on zooplankton in the water column

We suggest that the elevated $\delta^{15}\text{N}$ is from anthropogenic nitrogen loading, and probably reflects the high $\delta^{15}\text{N}$ of human sewage, as reported in other studies focused on a variety of aquatic systems (Cabana & Rasmussen, 1996; Schlacher, Liddell, Gaston, & Schlacher-Hoenlinger, 2005; Vermeulen et al., 2011). While subsistence agriculture is practiced along the shores of LT close to villages (Kelly et al., 2016), only our urbanised site identified elevated $\delta^{15}\text{N}$ values, and by

sampling during non-wet periods we also accounted for substantial nutrient runoff. Other pathways, such as fishery inputs, which are common practice in the focal region (i.e. fish processing on beaches) could also affect $\delta^{15}\text{N}$ in aquatic systems; however, we did not encounter this activity at our urban site (Britton and Doble, personal observation). Notably, anthropogenic nitrogen loading is not restricted to densely populated areas, as Kelly et al. (2016) showed significant

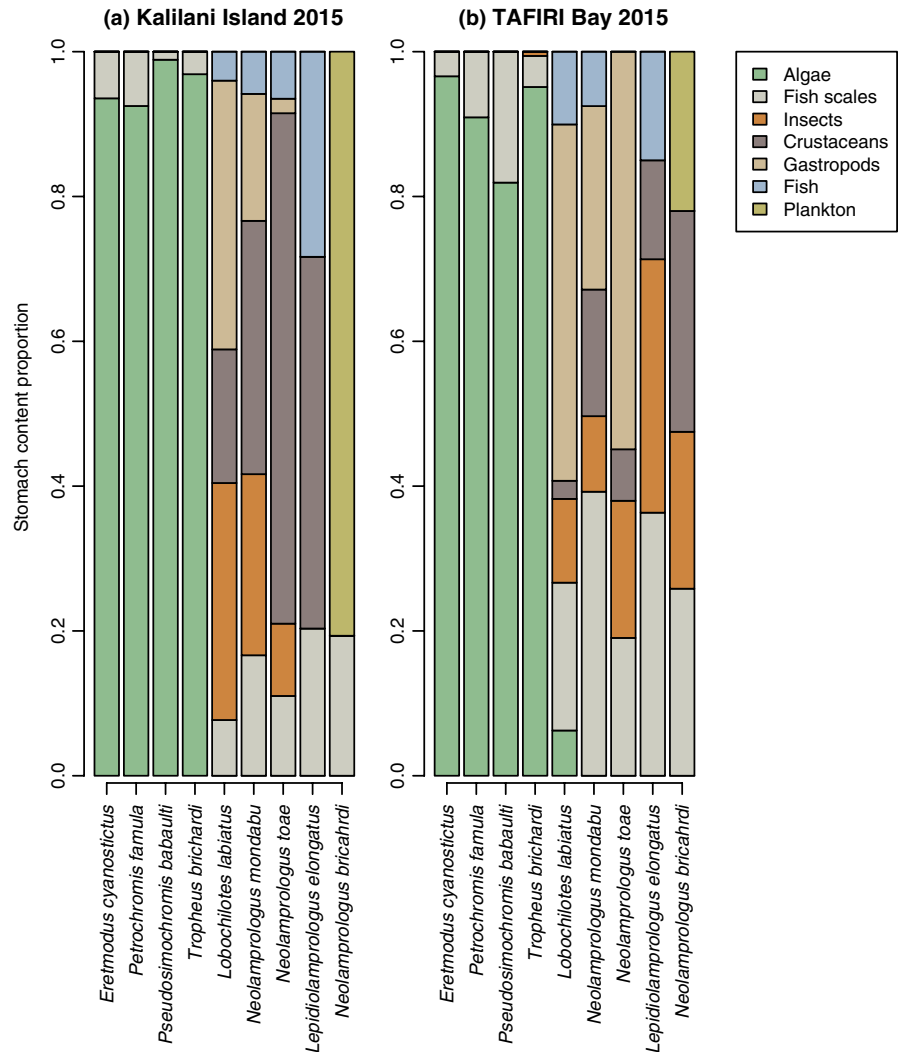


FIGURE 4 Stomach content proportions for the nine species sampled at (a) Kalilani Island 2015 and (b) TAFIRI Bay 2015. Stomach contents include all organic items, and exclude the sediment category

differences in LT gastropod nitrogen stable isotopes values and village population size and village area (north of Kigoma Town), suggesting nutrient loading from villages.

We also showed that herbivorous cichlids, in an area of high human disturbance and with reported higher sedimentation rates (Marijnissen et al., 2009; McIntyre et al., 2005), have higher proportions of sediment in their stomachs, irrespective of foraging behaviour, than at a low human disturbance site, demonstrating that species at this trophic level are also particularly sensitive to high sediment pollution. Previous studies have shown that cichlid diversity decreases with increasing human disturbance (Britton et al., 2017; Cohen et al., 1993; Sweke et al., 2013). In particular, the results presented here are in broad agreement with Britton et al. (2017) who identified that α -diversity and abundance of benthic species, particularly herbivores that are members of the Tropheini, were more greatly affected than other trophic guilds or tribes. This highlights a potential causal link between the extent of human disturbance and the change in community diversity of the cichlids, but clearly more work is required to establish which aspects of life-history (survival, reproduction, growth) are being most affected. Sediment pollution suspended in the water column can cause negative health impacts in fish such as gill clogging (Bruton, 1985), in which resultant gill

hypertrophy has been linked to decreased growth rate, possibly from respiratory impairment (Sutherland & Meyer, 2007). Environmental stress can place a limit on the energy available for growth (Smolders, Bervoets, De Coen, & Blust, 2004), and we found some evidence for this as two herbivorous species (*T. brichardi* and *P. lamula*) were smaller at the urban disturbed site than the non-urban sites (unpublished results), although a detailed study is needed to test this.

Results from our study also raise questions regarding the accuracy of applying stable nitrogen isotopes to trophic level descriptions in areas of human disturbance. Isotopic niche is commonly used to compare differences between species ecological niche (e.g. Ford et al., 2016; Hata, Shibata, Omori, Kohda, & Hori, 2015; Muschick, Indermaur, & Salzburger, 2012). However, we did not calculate isotopic niche because the anthropogenically elevated nitrogen stable isotope values overwhelmed the ecological $\delta^{15}\text{N}$ signature relating to trophic position. In the pristine habitat, benthic herbivores had lower $\delta^{15}\text{N}$ values than invertivores and piscivores, but in the disturbed site the highest $\delta^{15}\text{N}$ values were found in benthic herbivore species, even though there was no detectable change in diet. Given the number of stable isotope studies in the vicinity of disturbed areas of LT (e.g. Campbell, Verburg, Dixon, & Hecky, 2008; Hata et al., 2015; Kelly et al., 2016;

Muschick et al., 2012; Wagner et al., 2009), this study demonstrates that care should be taken when associating isotopic niche to ecological niche (Jackson, Inger, Parnell, & Bearhop, 2011). Unfortunately, little is known about the effects of spatial variation in nitrogen loading since the influence of a local source of nitrogen on $\delta^{15}\text{N}$ values will be the result of both physical (water movement) and biological (movement of individuals) factors. Therefore, systematic spatial sampling, sufficient intra-specific sampling (c. 15), and adequate baseline sampling are recommended as good practice to prevent biasing results.

Our findings, combined with the considerably lower diversity of herbivores previously identified at Kigoma Bay (Britton et al., 2017), suggest that habitat degradation through deforestation causing sedimentation, and water pollution including nitrogen deposition due to human disturbance, are possible causes contributing to negative changes in community composition and diversity of cichlids in this region (Britton et al., 2017). While consumer effects on prey are well known, the role of consumer diversity in affecting community structure or ecosystems is not particularly well understood, although Burkepile and Hay (2008) demonstrated that herbivorous fish species richness is critical for preserving coral reefs. Herbivores also form an important component of communities in the African Great Lakes (Hata & Ochi, 2016), and their decline may have serious implications for these systems. For example, the decrease in diversity of Lake Victoria herbivorous haplochromine cichlids after the introduction of the Nile perch (*Lates niloticus*) could have led to trophic cascades in this ecosystem (Goldschmidt, Witte, & Wanink, 1993).

5 | CONCLUSIONS

It is likely that the various forms of pollution identified are affecting the health of lake cichlids, and other fish groups, but several questions remain regarding how pollution is affecting individual fish and community structure. Elevated $\delta^{15}\text{N}$ has been shown to reflect a host of negative health impacts in fish species, including a range of pathological tissue changes such as abnormalities in most major organs (e.g. Schlacher et al., 2007). As well as investigating histopathology, future studies of Great Lake cichlids could consider investigating transcriptome level changes related to increased human driven environmental stress to provide a better understanding of genes and biochemical pathways affected. Our study supports previous work on other aquatic ecosystems that anthropogenic nitrogen loading and sedimentation are major threats to aquatic biodiversity (Dudgeon et al., 2006; Gangloff, Edgar, & Wilson, 2016; Islam & Tanaka, 2004). As such, alleviating pollution through afforestation programmes (Deng, Shanguan, & Li, 2012) and the effective treatment and disposal of waste (Eggen, Hollender, Joss, Schärer, & Stamm, 2014) should continue to be a global priority for the conservation of aquatic ecosystems, as well as human health.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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