Assessing human impacts on Lake Tanganyika cichlid fish communities

---

Adam William Britton

University College London

A thesis submitted for the degree of Doctor of Philosophy

February 2019

Declaration

I, Adam William Britton, confirm the work presented in this thesis is my own. Where information has been derived from other sources, I confirm this has been indicated in the thesis.

Adam William Britton
Candidate

Statement of authorship

I conducted field work in the Tanzanian section of Lake Tanganyika in 2015 to collect community composition data used in Chapters two and three, and to collect specimens used in Chapter four. Chris Doble collected extra specimens used in Chapter four in 2016 because my research permit was delayed whilst I was in Tanzania.

Chapter two has been published in Biological Conservation with co-authors Julia Day, David Murrell, Chris Carbone, Kirsty Kemp, Chris Doble and Ben Ngatunga (Britton *et al.*, 2017). I collected and analysed the data and wrote the first draft of the manuscript. Comments from Julia Day and David Murrell were incorporated into the text prior to publication. Reviewer's comments regarding zeta diversity analysis in Chapter 2 supporting information Appendix S2.2 and S2.3, and Figure S2.3, S2.4 and S2.5 were carried out and added to the text by David Murrell.

Morphological data in Chapter three was collected by myself at the British Natural History Museum and the Royal Museum of Central Africa in Belgium.

Stable isotope analysis of samples from Chapter four was conducted at the Scottish Universities Environmental Research Centre (SUERC), Life Science Mass Spectrometry Facility in 2015 and 2016. I prepared and measured all samples and received training from Rona McGill (SUERC) to run sample on the mass spectrometer. Stomach content data was collected during the course of a Master's research project that I oversaw (Calum Ramage, 2017). Chapter four is in press at Freshwater Biology, I wrote the first draft of the manuscript, and comments from Julia Day and David Murrell were incorporated into the text prior to submission.

Abstract

This thesis assesses the human impacts on rocky shore cichlid fish communities from the biodiversity hotspot Lake Tanganyika, by comparing the diversity of its protected and unprotected areas. Chapters two and three use cichlid community composition data collected from a range of localities in the Tanzanian section of Lake Tanganyika, to investigate whether human impact is negatively affecting their species, functional, and phylogenetic diversity, and to assess whether protected areas are conserving these components of diversity. In terms of species diversity, alpha diversity was higher in protected areas than adjacent unprotected localities, and the pattern of beta and zeta diversity in protected areas indicate a more even community composition. Additionally, benthic feeding herbivores were the most affected trophic group. Functional diversity, which was defined as the shape variation of geometric morphometric landmarks reflecting key traits, was also higher in protected areas than adjacent unprotected localities, as was phylogenetic diversity. Furthermore, functional and phylogenetic diversity were both linked to species richness, possibly due to a lack of variation in species uniqueness. Chapter four investigates the possible reasons for changes in cichlid diversity in unprotected areas using stable isotope and stomach content analysis. Benthic feeding species from the most disturbed locality had significantly higher nitrogen stable isotopes and stomach sediment proportions than a less disturbed locality, which may contribute to the lower species diversity of this trophic group. In conclusion, protection from human disturbance prevents a reduction in the core components of cichlid fish diversity in Lake Tanganyika, and therefore the network of freshwater and terrestrial protected areas should be increased. Moreover, protection of species appears to be an effective conservation strategy for the core components of biodiversity, so species richness could be used as a surrogate for biodiversity assessments in other systems.

Impact Statement

Assessing human impacts on fish communities in aquatic habitats is vital to ensure biodiversity is conserved and ecosystems are providing essential services such as a clean water source for all life. Conservationists have started to quantify different components of biodiversity to enable a more holistic protection of species and habitats. For instance, protecting functional diversity can improve the resilience of an ecosystem to change. Protected areas are a widely used strategy for conserving marine and terrestrial species, however, there are a lack of freshwater protected areas to conserve the numerous endangered freshwater species and habitats. Furthermore, the ability of protected areas to conserve morphological diversity and ecosystem functions is often not investigated. Cichlid fishes represent the most species rich group in biodiversity hotspot Lake Tanganyika, comprising 250 species, but like many freshwater systems, only a small proportion of Lake Tanganyika is formally protected. Despite this, there are few studies investigating how anthropogenic activities have impacted LT cichlid fish diversity, and whether they are conserved in the current protected area network. The research in this thesis provides a comprehensive diversity assessment of Lake Tanganyika cichlid fish communities, by investigating whether the current network of protected areas in Tanzania is conserving the core components of biodiversity. This thesis also provides a possible link to lower diversity encountered in human impacted sites. Academic outputs from this thesis include a peer-reviewed publication, with another under review. The publication is freely available online, and the data is on open access digital repository Dryad. Research has been presented at the British Ecological Society Annual Meeting and the Student Conference on Conservation Science. Samples collected will be vouchered at the British Natural History Museum for future use. The impact of the thesis also has policy implications. By demonstrating Tanzanian protected areas are conserving the core components of diversity this thesis provides recommendations for increasing Lake Tanganyika's protected area network. The thesis also demonstrates that protecting species conserves other aspects of biodiversity, which can be used to inform conservation policy globally.

Acknowledgements

First and foremost, thanks go to my supervisors at UCL Julia Day and David Murrell who have provided amazing support and guidance throughout my research project. Thanks to my co-supervisors Chris Carbone and Kirsty Kemp who always made me feel very welcome at the Zoological Society of London. Thanks to Chris Doble and Jane Hallam in the Day lab for their friendship along the way, and past members Antonia Ford and Claire Peart for all their help. Also, to Masters students Calum Ramage and Ana Da Silva. Thanks also to members of the Goswami lab for their help and friendship, Andrew Cuff, Thomas Halliday, Marcela Randau, Carla Bardua, Ryan Felice and Aki Watanabe.

Several collaborators were instrumental to this research project. George Kazumbe from Kigoma in Tanzania for his help in the field. Ben Ngatunga from the Tanzania Fisheries Research Institute, for his help obtaining research permits from the Tanzania Commission for Science and Technology. Rona McGill at the Scottish Universities Environmental Research Centre (SUERC), Life Sciences Mass Spectrometry Facility was very helpful with training and guidance for stable isotope analysis. James Maclaine and Oliver Crimmen at the British Natural History Museum, and Emanuel Vreven at the Royal Museum of Central Africa for letting me photograph specimens.

Funding is acknowledged from NERC for a case industrial studentship (NE/L009005/1), and a NERC grant in kind for use of the Life Sciences Mass Spectrometry Facility at East Kilbride. Also, a small research grant from the Fisheries Society of the British Isles.

Lastly, thank you friends and family who have been so supportive over the last four years. Especially my parents, Esther, Ped, Dom, Mike, Liz, Dave, and most importantly Lilly, who has been so supportive of me every single day.

Table of Contents

List of abbreviations

Abbreviation	**Full name**
FBeta	Beta functional diversity
FD	Functional diversity
FDis	Functional dispersion
FEve	Functional evenness
FPA	Freshwater protected area
FRic	Functional richness
HD	Human disturbance
LT	Lake Tanganyika
PC	Principal components
PD	Phylogenetic diversity
SES	Standard effect size
SIA	Stable isotope analysis
SL	Standard length
SR	Species richness

List of Figures

List of Tables

1 Introduction

1.1 Biodiversity

Documenting existing patterns of biological diversity is central to understanding the responses of biodiversity to environmental change (Gaston, 2000). Broad scale patterns such as the latitudinal diversity gradient (Fischer, 1960) are thought to be influenced by factors such as climate (Pianka, 1966), while factors such as habitat variability have an influence on which species survive and proliferate at local scales (Huston, 1979). At the community level there has been debate about whether patterns of diversity can be explained by niche processes such as competition (Diamond & Gilpin, 1982), or by null models indicating a random community assembly (Connor & Simberloff, 1979). Research into patterns of community assembly is ongoing (Ulrich, 2004; Pavoine & Bonsall, 2011), and the hope is that with more research a unified theory of biodiversity incorporating different elements might be proposed (Rosindell, Hubbell & Etienne, 2011). More recently, anthropogenic forces have had a remarkable impact on altering existing patterns of biodiversity and shaping new biotic communities (Purvis & Hector, 2000; Ellis & Ramankutty, 2008; Ellis, 2011). Rapid human population growth has increased species extinction rates from 100 to 1000 times their pre human level (Pimm *et al.*, 1995), predominantly driven by habitat loss (Fahrig, 1997; Brooks *et al.*, 2002). This has resulted in global biodiversity declines and homogenised ecosystems with a fewer number of specialist species (Mckinney & Lockwood, 1999; Newbold *et al.*, 2015).

Measuring biodiversity is fundamental to assessing the impact of human activity on ecosystems and enabling conservation effort to be targeted to protecting areas of high diversity. However, there is often an absence of reliable baseline biodiversity data before the human disturbance event (Collen *et al.*, 2008), so instead of a time series approach - a space for time substitute - is often adopted (Franca *et al.*, 2016). A space for time approach compares the diversity of sites in protected areas with sites of comparable habitat in neighbouring unprotected areas, with protected areas providing a control for human impact (Christie, 2005; Guidetti *et al.*, 2005; Claudet *et al.*, 2006; Tittensor *et al.*, 2007). However, it should be noted that a space for time approach assumes the control site represents diversity pre-disturbance, and can underestimate the impacts of humans on a community because of spatial heterogeneity in biodiversity (Johnson & Miyanishi, 2008; Franca *et al.*, 2016).

Biodiversity can be measured in a variety of ways (Purvis & Hector, 2000), therefore it is important to use appropriate biological indicators to assess anthropogenic impact (Keough & Quinn, 1991; Balmford *et al.*, 2005). Broadly, biodiversity can be measured at the regional scale (gamma diversity), at the local scale (alpha diversity), and within or between communities at the local alpha scale (beta diversity) (Fisher, Corbet & Williams, 1943; Whittaker, 1960; Sepkoski, 1988). Alpha diversity is the primary data collected at the survey level and can also be calculated across multiple surveys to calculate the average alpha diversity of a locality, providing a different perspective to the total gamma diversity of the region. There is evidence that alpha diversity deceases with anthropogenic impact across a range of ecosystems (Mckinney & Lockwood, 1999; Newbold *et al.*, 2015), but the responses of beta diversity also need to be considered (Socolar *et al.*, 2015; Newbold *et al.*, 2016). Beta diversity measures the dissimilarity between survey pairs within a locality but can also more simply measure the difference between localities in a region. Furthermore, a new measure, zeta diversity, has recently been proposed, which estimates the mean number of shared species across all surveys rather than just survey pairs (Hui & McGeoch, 2014).

Biodiversity is multi-dimensional concept with three core components; species, functional and phylogenetic diversity (Figure 1.1), each comprising a variety of metrics (Swenson, 2011; Swenson *et al.*, 2012). Most commonly a species centric view of diversity is taken (Devictor *et al.*, 2010; Swenson *et al.*, 2012), despite the fact human impact is decreasing functional and phylogenetic diversity, as well as species diversity (Naeem, Duffy & Zavaleta, 2012). Species richness is the most common measure of species diversity (Lyashevska & Farnsworth, 2012), and is an informative universal indicator because species descriptions are standardised and only presence absence data is required (Gotelli & Colwell, 2001). Furthermore species richness is often correlated to the other core components of diversity, phylogenetic (PD) and functional (FD) (Swenson, 2009; Strecker *et al.*, 2011). However, although species richness is sensitive to human impact (Bhat & Magurran, 2006), identical weighting is given to all species in a community, regardless of their abundances. Therefore calculating species abundances gives a more complete picture of the species diversity of a community, and when combined give a measure of evenness (Hill, 1973). A community dominated by many species with a similar abundance is considered to be more diverse than one in which a few species dominate (Stirling *et al.*, 2001). Species abundances are often unequal in nature (Scheffer *et al.*, 2017), and of the species diversity metrics, the Shannon Index is able to meaningfully partition diversity into its components when community weights differ (Jost, 2007). The Shannon index also does not place as much importance on rare or dominant species, and can be transformed to a measure of true diversity; the effective number of species (Jost, 2006; Tuomisto, 2010). Nevertheless, sometimes communities with high species diversity can have lower functional PD than communities with less species (Devictor *et al.*, 2010), and conserving PD is not always successful for protecting FD (Mazel *et al.*, 2017), so it is important to consider other components of biodiversity.

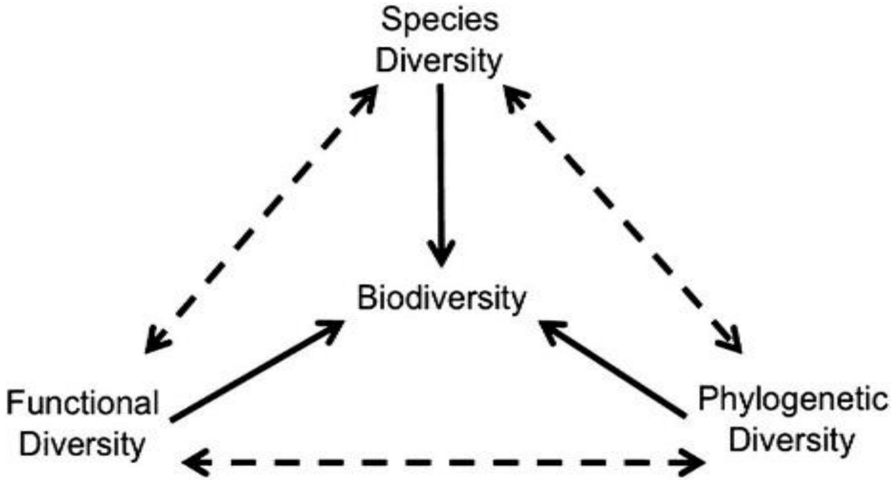


Figure 1.1. The three main components of biodiversity. Source: (Swenson, 2011).

Species diversity metrics treat all species as ecologically equivalent (Swenson *et al.*, 2012), and do not measure the range of functions performed by organisms in a community (Petchey & Gaston, 2006). Morphological variation in a community is often used as a measure of functional diversity (Petchey & Gaston, 2006; Schneider *et al.*, 2017), giving an indication of ecosystem performance. The higher the extent of functional differences within a community, the more traits are available to ensure the provisioning of goods and services in response to human impact (Díaz *et al.*, 2007). Originally, functional diversity was measured as the number of functional groups in a community (Naeem & Li, 1997; Tilman *et al.*, 2001). A more widely used measure utilising a trait matrix of continuous variables such as morphological measurements was then proposed (Petchey & Gaston, 2002). The trait matrix is converted to a functional dendrogram with a distance matrix of species pairs, and community branch lengths are summed in a similar way to Faiths phylogenetic diversity (Faith, 1992). More recently morphometric measurements have been used to calculate community FD from multidimensional functional space, using the minimum convex hull volume of all species to give a measure of functional richness (Mason *et al.*, 2005; Villéger, Mason & Mouillot, 2008; Mouillot *et al.*, 2013; Legras, Loiseau & Gaertner, 2018). Alternatively the convex hull volume of a community in morphospace can be calculated directly from geometric morphometric coordinate data (Fontaneto *et al.*, 2017), which assesses shape variation using landmarks based on morphological traits.

Functional traits are often clustered within phylogenies, consequently functional diversity can be congruent with phylogenetic diversity (Weiher, 2011). Phylogenetic diversity is the total evolutionary branch length of a community phylogenetic tree, and was originally proposed as a way of maximising feature diversity to prioritise conservation in reserve selection (Faith, 1992). Community phylogenies can reveal the evolutionary relationships between co-existing species (Webb *et al.*, 2002), an aspect of diversity species metrics do not consider. Phylogenetic community ecology links long term global processes to short term local processes, providing an insight into what is driving community assembly (Cavender-Bares *et al.*, 2009). Local processes such as environmental filtering may result in the clustering of communities, whereas competitive exclusion between closely related species could result in the phylogenetic over dispersion of communities (Graham & Fine, 2008). However, there is empirical evidence for the coexistence of closely related species with similar competitive abilities (Cahill *et al.*, 2008), possibly because some phylogenetically conserved traits provide a fitness benefit (Mayfield & Levine, 2010). Therefore, the competition-relatedness hypothesis may not always explain the assembly patterns in phylogenetically over dispersed communities, and niche differences should also be considered (Mayfield & Levine, 2010). Analysing species diversity assumes all species have the same conservation value, whereas analysing PD reveals species whose extinction would result in a higher loss of phylogenetic diversity (Rodrigues & Gaston, 2002a). Thus conserving PD could be a crucial conservation strategy for providing options in an uncertain future (Forest *et al.*, 2007), and analysing different components of diversity can expand our knowledge of the human impacts on biological communities.

Worldwide, areas of high species endemism that are subjected to habitat loss have been classified as biodiversity hotspots for prioritisation to minimize loss of diversity (Brooks *et al.*, 2006). As there is only a finite amount of resources to conserve existing biodiversity (Myers *et al.*, 2000), areas within hotspots can be targeted with protection. Protected areas if managed properly, are an effective way of safeguarding a habitat against anthropogenic change (Ferraro, Hanauer & Sims, 2011), and conserving species diversity (Gray *et al.*, 2016). However, there are deficiencies in protected area management (Leverington *et al.*, 2010), with the key management tool of detailed monitoring often not incorporated. Monitoring biodiversity in protected areas, using a temporal comparison of species diversity data, or a space for time comparison to a neighbouring unprotected area, allows decision makers to assess whether protected areas are working (Yoccoz, Nichols & Boulinier, 2001; McClanahan & Graham, 2005; McClanahan *et al.*, 2007; Carrillo, Wong & Cuarón, 2008). Protected areas can conserve all three core components of biodiversity (Thuiller *et al.*, 2015; Campos *et al.*, 2017), because globally, species richness is often linked to functional and phylogenetic diversity (Safi *et al.*, 2011). However, biodiversity hotspots and protected areas do not always conserve multiple aspects of diversity (Forest *et al.*, 2007; Mouillot *et al.*, 2011; Guilhaumon *et al.*, 2015; Brum *et al.*, 2017; Pardo *et al.*, 2017). For example, there is a lack of congruence between global biodiversity hotspot species richness and endemism (Orme *et al.*, 2005). Therefore targeting species rich areas should be complemented with an integrated approach to biodiversity conservation that protects different components (Devictor *et al.*, 2010; Mouillot *et al.*, 2011; Tucker & Cadotte, 2013).

1.2 Freshwater ecosystems

Terrestrial and marine protected areas are relatively numerous compared to freshwater protected areas (Saunders, Meeuwig & Vincent, 2002; Chape *et al.*, 2005), and often freshwater ecosystems are only protected incidentally within terrestrial national parks (Herbert *et al.*, 2010). Consequently protection is frequently inadequate for freshwater species (Herbert *et al.*, 2010; Hermoso *et al.*, 2015), despite the fact freshwater habitats and species are more endangered than their terrestrial equivalents (Abell, 2002). Additionally, freshwater ecosystems may be the most endangered in the world (Dudgeon *et al.*, 2006; Holland, Darwall & Smith, 2012), with amphibians and freshwater fishes thought to be the two most endangered vertebrate groups (Bruton, 1995). Freshwater ecosystems are also disproportionately diverse, covering less than 1% of the Earth but containing 6% of all species (Dudgeon *et al.*, 2006). However, there is a lack of assessment of freshwater species, with nearly half of all freshwater megafauna species lacking population data, and of the species with known population trends, nearly three-quarters are in decline (He *et al.*, 2018). Furthermore, there is a lack of congruence in the global diversity of species richness, endemism and threat between different freshwater groups, so the designation of freshwater protected areas should be carefully considered (Collen *et al.*, 2014).

Freshwater ecosystems are a focus of human impact, and face multiple threats, including habitat degradation, water pollution, overexploitation and species invasions (Dudgeon *et al.*, 2006). These threats can lead to catastrophic environmental consequences, as evidenced when overexploitations and species invasions combined to result in the extinction of around 200 endemic Lake Victoria cichlid species in under a decade (Goldschmidt, Witte & Wanink, 1993). Furthermore, climate change has caused a higher amount of local extinctions of freshwater biodiversity than in terrestrial and marine habitats, with a higher frequency in tropical species (Wiens, 2016). Work has been conducted to identify key freshwater biodiversity areas, based on irreplaceability and vulnerability (similar to the criteria used for Important Bird Areas and Biodiversity Hotspots) (Holland *et al.*, 2012). However, there is contrasting evidence about whether freshwater protected areas work (Chessman, 2013), because when freshwater biodiversity is conserved within protected areas, management is rarely targeted towards freshwater biodiversity (Darwall *et al.*, 2011). For example, the diversity of fish species in North American lakes bordering terrestrial protected areas is no higher than in unprotected lakes, although there is a higher abundance of small fish outside protected areas (Chu, Ellis & de Kerckhove, 2017).

Freshwater fish species (12,740 spp.) comprise around a quarter of living vertebrates, and nearly half the total fish species currently described (Lévêque *et al.*, 2008). They have a global distribution with the highest diversity found in South America (4,035 spp. in 74 families), Asia (3,553 spp. in 85 families), and Africa (2,945 spp. in 48 families) (Toussaint *et al.*, 2016). Higher functional diversity is concentrated in the Neotropics, however functional vulnerability is spread around the globe (Toussaint *et al.*, 2016), and over 30% of freshwater fish species are thought to be threatened (Abell, 2002). In terms of species, some of the most diverse and vulnerable freshwater fish faunas in the world are found in the Great Lakes of East Africa; Lake Victoria, Lake Malawi and Lake Tanganyika (Fryer, 1972; Lowe-McConnell, 1993), of which only a small percentage of water is protected. Combined, these three lakes contain over 1500 fish species, most of which are endemic (Salzburger, Van Bocxlaer & Cohen, 2014). Of the three lakes, Tanganyika has the highest genus-level diversity, with over 100 fish genera (Salzburger *et al.*, 2014) (Figure 1.2).

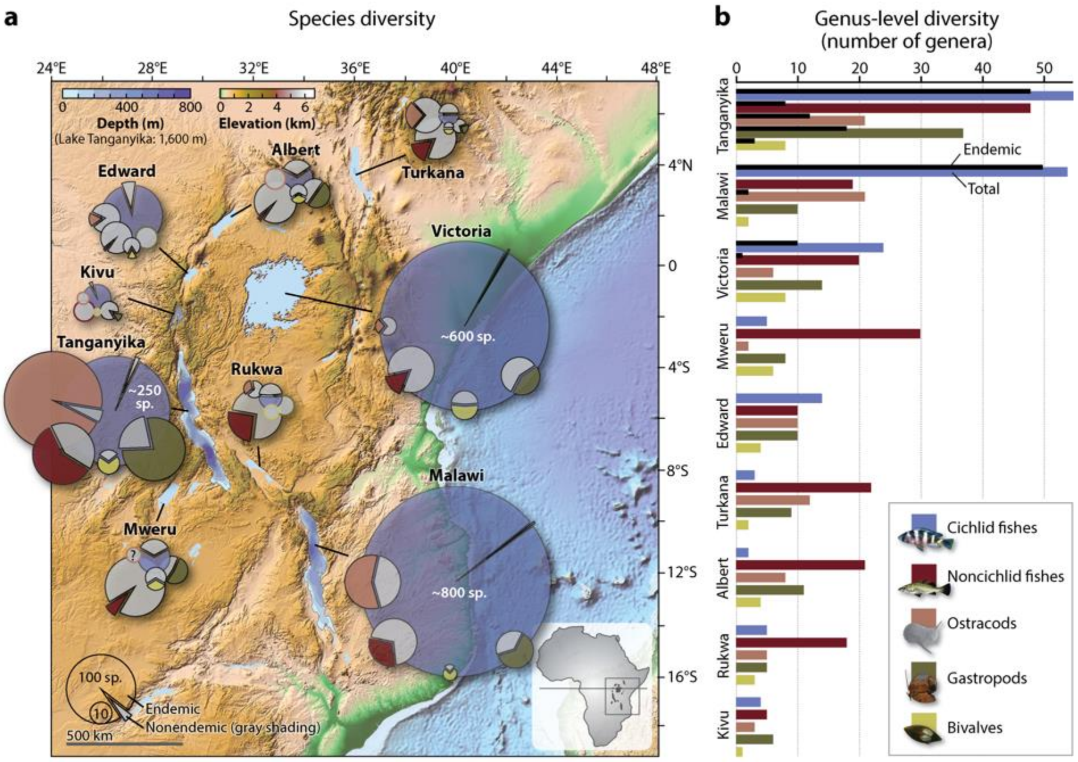


Figure 1.2. Map of East African Great Lakes detailing a) Species diversity, and b) Genus diversity, black bars indicate endemic genera for each animal group. Source: (Salzburger *et al.*, 2014).

1.3 Lake Tanganyika

Lake Tanganyika (LT), situated within the Eastern Afromontane biodiversity hotspot (Brooks *et al.*, 2006), is the longest, second oldest and second deepest lake in the world (after Lake Baikal) (Cohen, Soreghan & Scholz, 1993b; Cohen *et al.*, 1997; Rüber, Verheyen & Meyer, 1999; Sturmbauer *et al.*, 2008; Niyonkuru, Isumbisho & Moreau, 2015). Lake Tanganyika is bordered by four countries – Tanzania, Zambia, Burundi and the Democratic Republic of Congo (DRC). It is internationally recognized for its biodiversity, comprising one of the most diverse freshwater ecosystems in the world (Groombridge & Jenkins, 1998). It is the oldest of the rift lakes (9-12 Mya) in the region (Cohen *et al.*, 1993b) with the central basin forming between 9 and

12 Mya, the northern 7-8 Mya, and the southern 2-4 Mya (Cohen et al. 1993). This complex geological history has undoubtedly led to LT rich diversity, with estimates suggesting LT contains around 1470 animal species (Coulter, 1991; Groombridge & Jenkins, 1998), of which approximately 600 are endemic (Groombridge & Jenkins, 1998; Snoeks, 2000). Besides the cichlid fishes that form multiple radiations (e.g. Day, Cotton & Barraclough 2008), there is a diverse array of independent endemic radiations including multiple fish radiations e.g. various catfishes (e.g. Day & Wilkinson 2006; Peart *et al.* 2014), and mastacembelid spiny-eels (Brown *et al.*, 2010), as well as invertebrate radiations such as crab (Marijnissen *et al.*, 2006), and gastropods (West & Michel, 2000).

Increasing population density around LT means over one million people rely on its resources (Lake Tanganyika Authority, 2012), and development of the lake shore for agriculture and urbanisation has resulted in much of the lake being increasingly threatened from anthropogenic activities. There are however four national parks on the shores of LT; Nsumbu in Zambia, Rusizi in Burundi, and Gombe and Mahale in Tanzania that protect both terrestrial and aquatic habitat. In the Tanzanian section of LT, the shore area with the largest human population is found in the Kigoma region on the eastern side of the lake (Worldpop, 2013). Much of this 200km stretch, both terrestrial and aquatic, between Burundi and Mahale Mountain National Park is unprotected (Allison, 2000) and has been subject to varied anthropogenic impacts (Global Forest Watch, 2000). Human settlements along this shoreline vary in size from isolated fishing communities, to small villages, to the large urban area of Kigoma Town.

1.4 Cichlid fishes

A dominant component of the LT ecosystem are the cichlid fishes (Lowe-McConnell, 1993) with ~ 250 species (Snoeks, 2000; Day *et al.*, 2008; Brawand *et al.*, 2015; Salzburger, 2018) in over 50 genera (Meyer, Matschiner & Salzburger, 2015). Along with the cichlid radiations from the other East African great lakes, Lakes Malawi and Victoria, these lake cichlids represent the most diverse extant vertebrate radiations (Seehausen, 2006) (Figure 1.3). The majority of LT species (97%) are endemic (Coulter, 1991), and although LT has fewer cichlid species than Lakes Malawi and Victoria, LT has the highest number of endemic cichlid genera (Meyer *et al.*, 2015), and the cichlids of this lake have higher familial diversity (Coulter, 1991; Lowe-McConnell, 1993). Lake Tanganyika also has higher morphological and ecological diversity, possibly because of LT's greater age (Fryer & Iles, 1972; Chakrabarty, 2005). High morphological diversity means LT cichlids species are reasonably easily identifiable and combined with being diurnal, stenotopic and not secretive, makes LT cichlids a usefull target group to study with self-contained underwater breathing apparatus (SCUBA) (Figure 1.4). LT cichlid species belong to the subfamily Pseudocrenilabrinae, which currently comprises 14 tribes (Meyer *et al.*, 2015), the three most diverse being Lamprologini (Poll, 1986) (92 spp. (Eschmeyer, 2015)) Tropheini (Poll, 1986) (24 spp. (Eschmeyer, 2015)), and Ectodini (Poll, 1986) (34 spp. (Eschmeyer, 2015)). Lake Tanganyika cichlids represent several independent adaptive radiations that colonised habitats after LT was formed (e.g. Day, Cotton & Barraclough 2008). However, major diversification within the lineages coincides with the establishment of full lacustrine conditions 5–6 Mya (Cohen *et al.*, 1993b), possibly driven by environmental conditions (Day *et al.*, 2008), and the development of certain traits under ecological and sexual selection (Salzburger, 2009; Wagner *et al.*, 2009; Takahashi & Koblmüller, 2011).

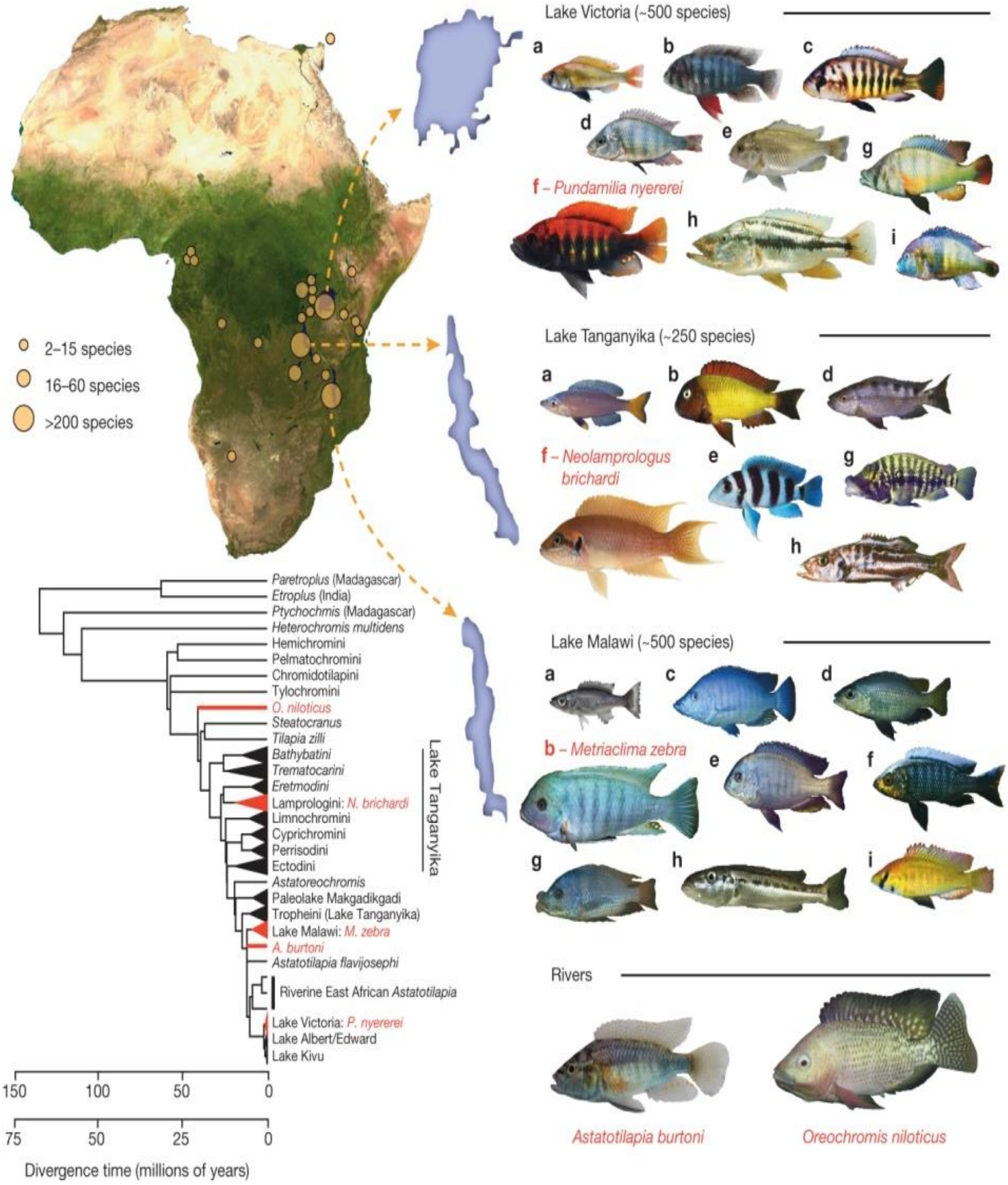


Figure 1.3. An overview of the species diversity in the Great Lakes of East Africa. Including a tribal level phylogeny of Lake Tanganyika cichlids (Brawand *et al.*, 2015).

Figure 1.4. SCUBA surveys in Lake Tanganyika. Photo credit: Kirsty Kemp.

Around a quarter of LT cichlid species are found at depths between zero and ten metres in the rocky shore littoral zone (Konings, 1998) with community composition analogous to that of coral reefs (Coulter, 1991). The littoral zone consists of sloping rocky stretches that are interspersed with sandy patches (Takeuchi *et al.*, 2010). The complex rocky littoral habitat is not homogenous regarding substrate, and comprises boulders, rocks, rubble and stones (Hori *et al.*, 1993) providing a range of microhabitats for LT cichlids. Within the rocky littoral zone several tribes are present, and are characterised by differing life histories (Hori *et al.*, 1993). LT cichlids have a variety of methods of giving care to their offspring, the main two being substrate and mouth brooding (Konings, 1998). Substrate brooding is thought to be the primitive state (Barlow, 1991), with mouth brooding evolving in several different tribes (Koblmüller, Sefc & Sturmbauer, 2008). Lamprologini, the most species rich tribe, are substrate brooders that thrive in the complex micro habitats of the rocky shore (Sturmbauer *et al.*, 2010). Lamprologini species encompass vastly different dietary niches, and have highly specialised pharyngeal jaw morphology (Takahashi & Koblmüller, 2011) allowing them to develop an array of feeding strategies including as planktivores, piscivores, egg-eaters, invertebrate-eaters and scale-eaters (Hori *et al.*, 1993). In contrast the maternally mouth brooding (derived condition) Tropheini tribe are specialist herbivores that are restricted to feeding on periphyton growing on rocks in the littoral zone (Sturmbauer *et al.*, 2003). Species of the maternal and bi-parental mouth brooding tribe Ectodini also have varied diets and are found in a range of habitats, meaning they are not rock restricted in the same way as Tropheini and Lamprologini (Koblmüller *et al.*, 2008). The high diversity in the rocky littoral zone means LT cichlids are particularly sensitive to human impacts on the lake shore, that destroy their feeding and breeding grounds (Craig, 1992; Lowe-McConnell, 1993).

1.5 Threats to Lake Tanganyika rocky shore cichlid fishes

There are three main threats to the LT ecosystem; sedimentation, overfishing, and pollution (Coulter & Mubamba, 1993). Deforestation increases watershed sedimentation in aquatic systems (Rogers, 1990; Ryan, 1991), and LT’s tropical climate coupled with intense periodic rainfall makes areas of the lake bordering deforested areas particularly susceptible to regular inundations of sediment. Sediment core data from LT has revealed deforested areas have a higher rate of sediment accumulation than forested watersheds (Cohen *et al.*, 2005). Sediment can directly impact a whole host of aquatic organisms including primary producers, invertebrates and fishes (Wood & Armitage, 1997; Busch *et al.*, 2018), and has been reported to degrade the habitat of rocky shore cichlid fishes (Rusuwa, Maruyama & Yuma, 2006). Sediment settles on submerged rocks, detrimentally affecting habitat quality and heterogeneity, foraging and reproductive success (Henley *et al.*, 2000). Suspended sediment has been reported to negatively affect aquatic ecosystems by increasing turbidity and degrading water quality (Newcombe & Macdonald, 1991). Growing human population density on the lakeshore has also increased the demand for dietary protein, resulting in overfishing becoming a threat to the larger species of fish in the lake (Kimirei, Mgaya & Chande, 2008). Additionally, demand for smaller cichlid species in European ornamental markets has encouraged overfishing (Craig, 1992; Mölsä *et al.*, 1999). Fishing methods include beach seining, which uses non selective gear and, although prohibited in Tanzania, is still carried out illegally (Kimirei *et al.*, 2008). Finally, the rate of urban and industrial waste input into LT is increasing, with pollution being a major concern given the slow rate of water renewal in the virtually closed basin (Coulter & Mubamba, 1993). This has been illustrated by gastropod species in unprotected areas of LT displaying elevated nitrogen stable isotopes as a result of increased nitrogen pollution (Kelly *et al.*, 2016).

The two protected areas in the Tanzanian section of the lake differ in terms of size and protection status; Mahale NP protects 1,613 square km of forest (Sweke *et al.*, 2013), with a 96 square km fishing exclusion zone stretching 1.6km into the lake along the parks 60km shoreline (West, 2001), whereas Gombe NP protects a 35 square km strip of forest (Pusey *et al.*, 2007), and its waters have been fished by local villages until a no take zone was trialled in 2015. Both were primarily designated to protect terrestrial wildlife, and are successful for the conservation of chimpanzees (Pusey *et al.*, 2007; Sweke *et al.*, 2016). However, the capacity of both the national parks to protect cichlid fish is yet to be investigated. The steep gradient of human impact throughout the Kigoma region makes it particularly suitable for studies investigating the effect of human disturbance on LT rocky shore cichlid fishes. However, despite the opportunity LT cichlids provide as a study system to investigate the generation and maintenance of biological diversity, the majority of previous focus has been in an evolutionary context (e.g. Nishida 1991; Sturmbauer & Meyer 1992; Day, Cotton & Barraclough 2008; Muschick, Indermaur & Salzburger 2012; Winkelmann *et al.* 2014; Meyer, Matschiner & Salzburger 2015), and there are few studies that have investigated the impacts of anthropogenic activities on their community ecology. The fact that the IUCN Red List states all LT cichlid species conservation status needs updating, further illustrates the lack of assessment of human impacts on their diversity (International Union for Conservation of Nature and Natural Resources., 2018).

Long term studies on LT cichlids involving behavioural observations, dietary analysis, and population census have been conducted (Hori *et al.*, 1993; Takeuchi *et al.*, 2010), but did not consider how humans have impacted cichlid fish diversity. Previous studies investigating the effects of human disturbance on community composition in LT focused on the comparison of sites over a large spatial scale, where the effect of geographic distance was not taken into account (Cohen *et al.*, 1993a; Alin *et al.*, 1999). Additionally, although Cohen *et al.* (1993) and Alin *et al.* (1999) focused on areas of differing human disturbance, they did not address how protected areas differ from disturbed. A study focusing on cichlids in protected areas and outside found there was higher alpha species diversity inside the protected area (Sweke *et al.*, 2013), but Sweke *et al.* (2013) did not analyse beta diversity - an important measure for comparing the species variation between sites (Legendre, Borcard & Peres-Neto, 2005). Results from a study of the beta diversity of rocky shore Lake Malawi cichlid fishes (Genner *et al.*, 2004) demonstrated geographic distance has an effect on community composition, highlighting that spatial variation must be considered when testing for an effect of human impact. Habitat complexity was also found to predict community composition in Lake Malawi cichlids (Ding *et al.*, 2014), so sites with comparable habitat should similarly be considered when investigating human impacts on cichlid community composition. Additionally in this study, higher FD was reported at sites with complex habitats, however generic level diversity was used as a proxy for FD (Ding *et al.*, 2014). A morphometric study investigating cichlids in the southern LT basin suggested neutral processes were responsible for community assembly across a range of environments, however the response of community composition to human impacts were not assessed (Janzen *et al.*, 2017). Therefore, research investigating different components of LT cichlid fish diversity in response to a gradient of human disturbance is required to assess the effectiveness of the current protected area network. Thereby increasing the body of evidence assessing the effectiveness of protected areas globally, to ensure they are conserving different aspects of biodiversity.

1.6 Aims

The overall aim of this thesis is to assess human impacts on LT cichlid fish and elucidate if protected areas are conserving their diversity. This will be achieved primarily using cichlid fish community composition data collected from a range of rocky shore localities, subject to differing levels of human disturbance. The study is focused in the Kigoma region of LT, selected because it offers a gradient of human impact, political stability (compared to DRC and Burundi) and relatively safe waters from wildlife (e.g. crocodiles, hippos are prevalent in Nsumbu National Park, Zambia). Chapter two investigates whether LT cichlid species alpha, beta and zeta diversity differs along a gradient of human disturbance, and whether protected areas have higher species diversity than their neighbouring unprotected localities. Furthermore, the species diversity of different trophic and tribal groups is assessed to investigate if human disturbance is affecting particular functional groups. In Chapter three the functional and phylogenetic diversity of rocky shore cichlids are investigated in response to human impact to test if LT protected areas are conserving other components of biodiversity. The relationship between species richness, FD and PD is also investigated to assess if neutral or functional pressures are influencing community composition. Chapter four uses stable isotope and stomach content analysis to investigate possible individual level changes in cichlid species from the most degraded sites, compared to control sites. Intra specific differences between sites could provide a link to differences in diversity investigated in chapters two and three. Finally, Chapter five summarises the main conclusions from the thesis and outlines future directions based on the research conducted.

2 Terrestrial-focused protected areas are effective for conservation of freshwater fish diversity in Lake Tanganyika

2.1 Abstract

Freshwater protected areas are rarely designed specifically for this purpose and consequently their conservation benefit cannot be guaranteed. Using Lake Tanganyika as a test case we investigated the benefits of terrestrial-focussed protected areas on the alpha and beta taxonomic and functional diversity of the diverse endemic rocky-shore cichlid fishes. Lake Tanganyika has limited protected shorelines and continued human population growth in its catchment, which has potential for negative impacts on habitat quality and key biological processes. We conducted 554 underwater surveys across a gradient of human disturbance including two protected areas, along 180km of Tanzanian coastline, sampling 70 cichlid species representing a diverse range of life-histories and trophic groups. Alpha diversity was up to 50 per cent lower outside of protected areas, and herbivores appeared most affected. Turnover dominated within-locality variation in beta diversity, but the nestedness component was positively related to human disturbance indicating an increase in generalist species outside of protected areas. Within protected areas the decline in zeta diversity (the expected number of shared species across multiple surveys) was best described by power law functions, which occur when local abundance is predicted by regional abundance; but declined exponentially in unprotected waters indicating a dominance of stochastic assembly. Despite not being designed for the purpose, the protected areas are clearly benefitting cichlid taxonomic and functional diversity within Lake Tanganyika, probably through local reduction in sediment deposition and/or pollution, but as cichlids can be poor dispersers protected area coverage should be expanded to benefit isolated communities.

2.2 Introduction

The impact of anthropogenic disturbance has been particularly acute across freshwater ecosystems, exceeding that of their terrestrial counterparts (Abell, 2002), and is of particular concern due to the disproportionately high contribution that these habitats make to global biodiversity (Strayer & Dudgeon, 2010). As focal points of human development, freshwater ecosystems face multiple anthropogenic stressors including habitat loss, the introduction of invasive species, pollution, sedimentation, and species exploitation (Dudgeon *et al.*, 2006). Freshwater ecosystems therefore represent hotspots of endangerment (Dudgeon *et al.*, 2006) and improvement in our knowledge of how their communities respond both to anthropogenic pressures, and to management strategy is required. Freshwater protected areas (FPAs) are potentially one key conservation management tool, but they are rarely designed specifically with freshwater diversity in mind, and the few attempts to quantify their impact have produced mixed results (Chessman, 2013; Adams *et al.*, 2015).

Here, we focused on one of the world's most diverse freshwater ecosystems, Lake Tanganyika (LT) containing ~1470 animal species (Groombridge & Jenkins 1998). A dominant component of the LT ecosystem are its cichlid fishes (~250 valid species, 97% endemics) that form multiple adaptive radiations (Day *et al.*, 2008; Salzburger, 2018). Despite this considerable richness, only 6% of its coastline is protected, consisting of four national parks with differing levels of protection (Coulter & Mubamba 1993, see Appendix S2.1). None of these protected areas were assigned specifically to target freshwater diversity protection, and therefore their benefit to the aquatic diversity remains an open question. However, anthropogenic stressors have led to increased threats to the LT ecosystem (Alin *et al.*, 2002), so testing the efficacy of the protected areas is a pressing concern.

Along with climate change (Cohen *et al.*, 2016), possibly the most severe threat to the biota of LT is sedimentation from watershed deforestation (Cohen *et al.*, 1993a; Alin *et al.*, 2002; McIntyre *et al.*, 2005) (see Figure 2.1). The detrimental effects of sedimentation on aquatic communities have been widely demonstrated (reviewed in Donohue & Molinos 2009), and include negative impacts on habitat quality and heterogeneity, foraging and reproductive success (Henley *et al.*, 2000), as well as increased turbidity and degraded water quality (Newcombe & Macdonald, 1991). The rate of urban and industrial waste input into LT is also increasing, which is a major concern given the slow rate of water renewal in this virtually closed basin (Coulter & Mubamba, 1993). For example, industrial chlorinated pesticides and polychlorinated biphenyls, used for agricultural and industrial purposes in Africa, have been found in fat cells of LT cichlid fishes in areas of high human disturbance (Manirakiza *et al.*, 2002), and can cause a host of negative physiological effects that reduce fitness (Napit, 2013). Locally, eutrophication of LT in Kigoma Town area from domestic waste is also increasing turbidity of the water in the bay to over double that of offshore water (West, 2001; Chale, 2003). Decreasing water clarity has been demonstrated to indirectly affect Lake Victoria cichlids by constraining colour vision and reducing diversity in sexually dichromatic species (Seehausen, van Alphen & Witte 1997). Furthermore, the growing human population density is likely to increase the demand for dietary protein leading to heightened fishing pressure of pelagic species (Mölsä *et al.*, 1999), while cichlid species have been exploited for the aquarium trade, although the impact of fishing has yet to be quantified.

Previous studies focussing on LT have investigated the effects of human disturbance on the alpha diversity of fish and invertebrate community composition (Alin *et al.*, 1999; McIntyre *et al.*, 2005; Sweke *et al.*, 2013, 2016) and have shown that sites of high disturbance have fewer species (i.e. lower alpha diversity), although we note that Marijnissen *et al.* (2009) showed that crab density and species incidence was largely unaffected by sedimentation. However, conservation management needs to consider regional scale gamma diversity, and how this accumulates from inter-site differences between local species assemblages (beta diversity). For example, alpha diversity (e.g. the number of species per survey) might remain constant, or even increase in the face of disturbance, yet beta diversity (diversity amongst surveys) could decline as homogenization leads to an increase in generalists at the expense of specialist species, and ultimately this would lead to a reduction in large-scale gamma diversity. Little is known about cichlid fish beta diversity within LT, let alone how disturbance may affect it. At large spatial scales, prior studies of rocky shore Lake Malawi cichlid fishes (Genner *et al.*, 2004; Ding *et al.*, 2014) found geographic distance (limiting dispersal between sites) and differences in habitat complexity (depth) to be important explanatory variables for community dissimilarity between pairs of sites, although most of the decay in community similarity occurred within sites separated by 4km (Ding *et al.*, 2014). Despite this, there are very few studies of HD induced changes in beta diversity in aquatic ecosystems, and it remains an open question as to whether there are general patterns that can inform and guide conservation management (Socolar *et al.*, 2015).

Beta diversity can be partitioned into two opposing phenomena: (1) species turnover resulting from species replacement; and (2) nestedness of local assemblages caused by species loss (Baselga, 2010, 2013). Changes to the relative dominance of these two components of beta diversity can indicate important effects of disturbance on biological diversity. For example, Gutiérrez-Cánovas *et al.* (2013) found macroinvertebrates on natural stress gradients showed a stronger turnover component, whilst increased anthropogenic stress led to an increased nestedness component of beta diversity. This confirmed predictions that natural environmental stress (e.g. changes in elevation) leads to an increase in species that are specialised to the local environmental conditions (leading to high spatial turnover in species diversity), whereas anthropogenic stressors lead to an increase in generalist species with wide ranges and the loss of specialists with narrow ranges (leading to high nestedness component).

Most beta diversity indices estimate the dissimilarity of pairs of surveys. However, to gain potentially important information about the spatial scaling between alpha and gamma (regional) diversity, higher order patterns of co-occurrence need to be taken into account (Socolar *et al.*, 2015). The recently developed zeta diversity metric, ζ_i, (Hui & McGeoch, 2014) fills this gap by estimating the mean number of species found in all *i* surveys. So, for example, ζ_3 is the expected number of species found in any three surveys. As *i* increases ζ_i inevitably declines, but the rate at which it does so, and the functional form of the relationship between ζ_i and *i* are thought to be indicative of important biological processes. A review of available data suggests that most ecological communities exhibit either a power law, or exponential decline in zeta diversity with sample number (Hui & McGeoch, 2014). A power law decline occurs when the local abundance is correlated to the regional abundance, and this is found in null models where species have different site or habitat preferences. In contrast, exponential declines occur when all species have the same probability of occurring in the survey, regardless of overall abundance such as when community assembly is purely stochastic (Hui & McGeoch, 2014). If HD acts to change the relative importance of niche and stochastic processes in community assembly then a shift from power law to exponential decline in zeta diversity (or vice versa) is likely to occur, but this has yet to be tested and consequently the usefulness to conservation management of the zeta diversity metric has yet to be explored.

To address these gaps in knowledge we sought to answer a number of questions regarding the conservation value of the protected areas and effects of human disturbance on LT cichlids. Firstly, we asked whether a gradient of increasing human disturbance corresponds to a decline in cichlid fish diversity, and if the non-specific FPAs benefit cichlid taxonomic and functional diversity? Secondly, we asked if fine scale beta diversity (how diversity is structured within a locality) is affected by human disturbance, and if turnover or nestedness dominates in LT. Here we expected nestedness to increase with increasing HD as implied by Gutiérrez-Cánovas *et al.* (2013). Thirdly, we asked if the functional form of decline in zeta diversity with sample number differed qualitatively along the gradient of HD. Changes in the functional form of zeta could highlight changes in community structure that are caused by different assembly processes dominating and/or biased loss of species in the disturbed areas. We expected disturbed areas to show an exponential decline in zeta if generalists dominate, but a power law if the disturbed areas are dominated by a different set of specialists to the protected areas. Finally, as cichlids constitute a diverse range of life histories, we asked if there are particular taxonomic and trophic groups that are more affected by the human disturbance gradient than others. In this case we expected specialist groups to suffer more than generalists. In answering these questions using a variety of alpha and beta diversity metrics we not only catalogued the effects of HD and the benefits of FPAs on cichlid diversity, but also uncovered some of the key ecological processes that are underpinning the different diversity patterns within protected and unprotected waters.

2.3 Materials and methods

We focussed on rocky-shore (littoral zone) cichlids, the most diverse assemblage within LT, in which ~25% of all species occur between 0-10 metres (Konings, 1998).

2.3.1 Study localities

The Tanzania shoreline was selected as it includes several Freshwater Protected Areas (FPAs), although the majority of this coast (as with the rest of the lake) is unprotected regarding both terrestrial and aquatic habitats (Allison, 2000) and has been subject to varied anthropogenic impacts (Coulter & Mubamba, 1993). Hence the shoreline exhibits a wide range of disturbance (Figure. 2.1).

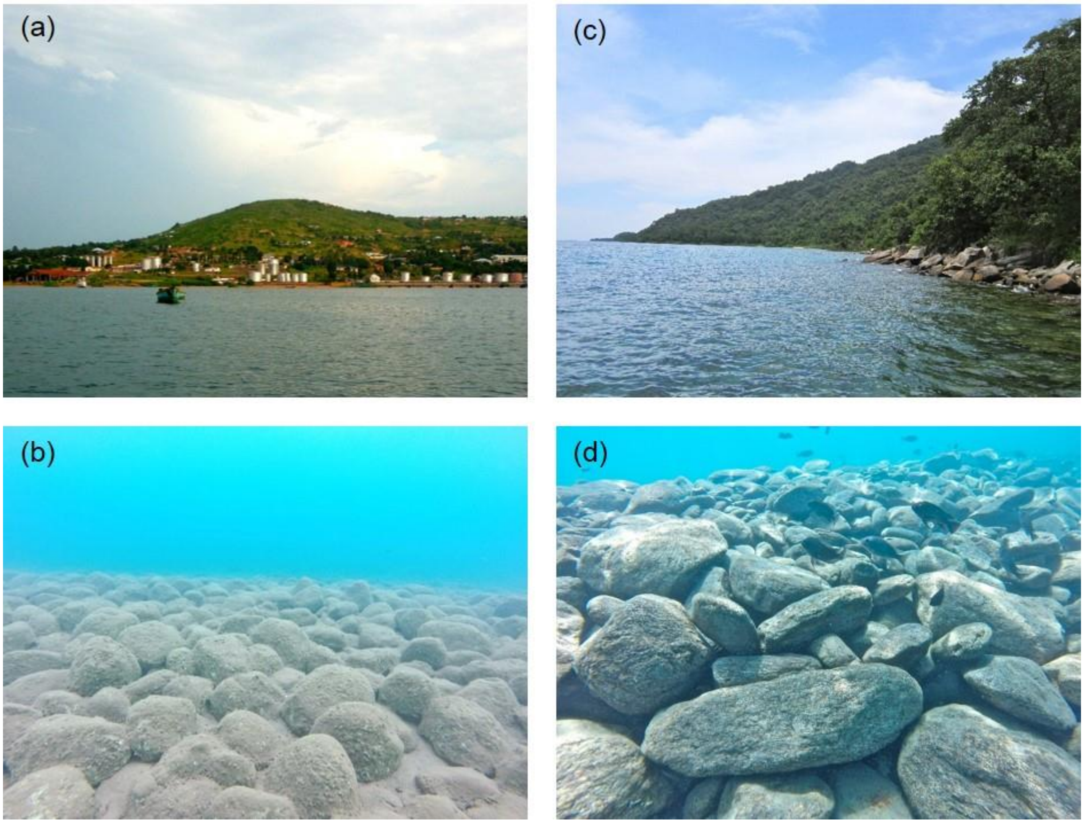


Figure 2.1. Photographs showing visible differences between (a) Kigoma Town's urban and deforested shoreline and (b) corresponding disturbed rocky shore, and, (c) Mahale NP's forested shoreline, (d) and corresponding pristine rocky shore. At GPS co-ordinates (a) 4°89.252'S 29°61.593'E, (b) 4°53.518'S 29°36.411'E, (c) 6°05.042'S 29°43.456'E and (d) 6°10.258'S 29°44.251'E.

Human settlements along the selected shoreline vary in size from isolated fishing communities, small villages, to the large urban area of Kigoma Town, which holds the largest human population on the eastern side of the lake (Worldpop, 2013). Two protected areas in the Kigoma region that conserve both the lakeshore Miombo woodland and littoral zone (Coulter & Mubamba, 1993) include Gombe Stream National Park (Gombe NP) and Mahale Mountain National Park (Mahale NP) (West, 2001). However, the scale and level of protection varies greatly, with Mahale NP representing the largest area of protected coastline containing a no take fishing zone that extends 1.6km off the coast covering an area of 96km^2 (Sweke *et al.*, 2013). In contrast Gombe NP is much smaller, protecting 35km^2 of forest, and provided no protection until 2015 when a no take zone was introduced. Gombe NP's size makes it vulnerable to edge effects at the borders, and the waters north of the park are particularly at risk because of the presence of a large fishing village (McIntyre *et al.*, 2005). On the other hand Mahale NP scores highly on a qualitative scale of conservation success (Struhsaker, Struhsaker & Siex, 2005), with few signs of human disturbance.

The following seven localities spanning 180km of coastline (Figure 2.2) were selected and surveyed between January and April 2015: (1) Kigoma Town, a large town with a human population in excess of 200,00; (2) Kigoma Deforested, an un populated stretch of deforested shoreline to the south of Kigoma Town; (3) Jakobsen's Beach, a 1km stretch of privately owned uninhabited deforested shoreline to the south of Kigoma Deforested; (4) Kalilani Village, a small fishing village with low population density and 25% tree canopy coverage; (5) Gombe NP, a 12km stretch of semi-deciduous and evergreen forest 11km north of Kigoma Town; (6) Mahale NP S1, an uninhabited 7km of shoreline near the northern border of the NP that was established in 1985 and includes a fishing exclusion zone; and (7) Mahale NP S2, a 5km stretch of rocky shoreline within the NP and south of Mahale NP S1 (see Appendix S2.1 for detailed locality descriptions).

Since we do not have data on how biodiversity within localities has changed with changing disturbance intensity we chose localities that were close to the protected area in order to minimise variation in sites caused by factors other than disturbance. Localities were given a ranking of their relative human disturbance (HD) considering (i) percentage of forest canopy and (ii) human population density along the shoreline; and the binary factors (ii) terrestrial and (iv) water (no-fishing) protection status. These factors were then combined with equal weighting to produce a HD index (Falcone, Carlisle & Weber, 2010) on a relative scale of 1 (low disturbance) to 10 (high disturbance) (Appendix S2.1 and Table S2.1).

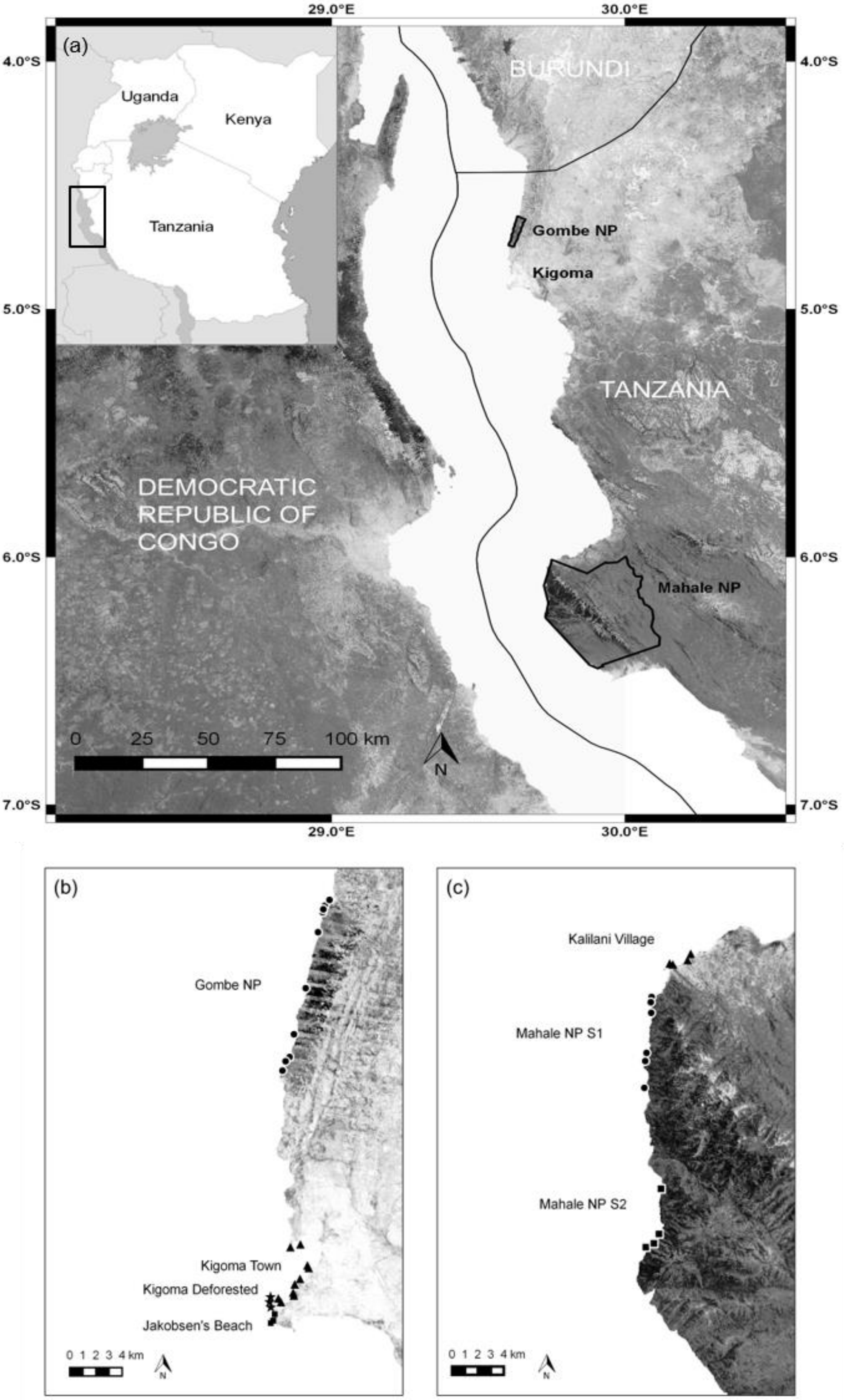


Figure 2.2. (a) Map of the Northern and central regions of Lake Tanganyika (LT) highlighting the protected areas (bold black outline), with inset showing the location

of LT, and the study location (black box) in East Africa. (b) Northern study localities detailing samples points (Gombe NP, black circles; Kigoma Town, black triangles; Kigoma Deforested, black stars; Jakobsen's Beach, black squares). (c) Southern study localities detailing sample points (Kalilani Village, black triangles; Mahale NP S1, black circles; Mahale NP S2, black squares). The background to all three maps represents tree cover as a percentage from 0% tree cover (white) to 100% cover (black). Data generated from (Hansen *et al.*, 2013) in QGIS (Quantum GIS Development Team, 2015).

2.3.2 Data collection

We used a nested study design incorporating the following hierarchy: localities – sites – surveys (Figure S2.1). Sites were selected within each locality following a visual inspection from the surface to ensure comparable (~75% rock) 200m stretches of 0-10m depth rocky littoral habitats were surveyed (for survey nomenclature see Figure S2.1). We endeavored to keep sites approximately 1km apart, however this was not always possible because the rocky habitat was not uniform at each locality. Therefore, over 200m Euclidean distance was maintained between sites to ensure the outer surveys of each site did not overlap. Due to the size variation of localities a differing number of sites were surveyed at each: Kigoma Town (10 sites); Kigoma Deforested (3); Jacobsen's Beach (3); Kaliliani Village (4); Gombe NP (10); Mahale NP S1 (6); Mahale NP S2 (4). The coordinates of each site, given in Table S2.2, were recorded on a handheld global positioning system (Garmin eTrex Summit). At each site a nested survey design (Marsh & Ewers, 2013), at intervals of 20, 50 and 100 metres to the left and right of a central survey (also the GPS position of the site), was employed at five and ten metre depths, resulting in 14 survey counts per site (Figure S2.1). The slope of the rocky littoral habitat surveyed rarely exceeded a 60% gradient so there was no overlap in surveys at 5m and 10m depths.

SCUBA survey counts of cichlid species and their abundances were conducted using the stationary visual census technique (Bohnsack & Bannerot, 1986), in which fish were given one minute to settle once divers had reached the survey point, after which all species and individuals observed with a radius of five metres were counted. Each survey lasted eight minutes. Individuals were identified to species level in the field and any colour morphs were classified only to species level. Two experienced SCUBA divers conducted these surveys. Survey data was collected by George Kazumbe (with over 20 years' experience of cichlid fish identification in the field) and Adam Britton (an experienced Divemaster). Video and survey data were used to check for discrepancies between diver data to ensure robust data collection.

The cumulative number of species recorded at each locality was plotted against sampling effort to create species accumulation curves for all localities. Community composition data was analysed in R v3.1.3 (R Core Team, 2015) using vegan v2.3-0 (Oksanen *et al.*, 2015); betapart v1.3 (Baselga & Orme, 2012); and zetadiv v0.1 packages to generate diversity measures (see below).

2.3.3 Species diversity along a gradient of human disturbance

We first asked how the degree of HD alters patterns of local species diversity and turnover within a locality by comparing measures of alpha, beta and zeta diversity across our seven localities.

2.3.3.1 Alpha diversity

Species richness and pooled abundance values were quantified for each survey count. The Shannon index was used to estimate the effective number of species per locality, thereby quantifying differences in true diversity between localities (Jost 2006). The effective number of species is the number of equally abundant species necessary to produce the observed value of diversity and is analogous to the effective population size in genetics. To test the hypothesis that evenness decreases with increasing HD we computed Pielou's J for each locality, pooling all survey data together. We then performed a Spearman's rank correlation to test for a relationship between locality HD rank and each alpha diversity metric.

2.3.3.2 Beta and zeta diversity

Beta and zeta diversity measures estimate how diversity changes with spatial scale or number of surveys and are important to estimate the degree of turnover in each locality. Mean dissimilarity between all survey pairs within localities was calculated using the Sørensen index and the Bray-Curtis index. Since the Sørensen index only considers (binary) presence-absence data, it gives extra weighting to rare species. In contrast, the Bray-Curtis index is an abundance based index so rare species receive a lower weighting (Baselga, 2013). Both indices can be decomposed into the contributions to dissimilarity from turnover and nestedness. In the Sørensen index the turnover component is increased when a species in one site is replaced by a different species in another site, whilst the loss/nestedness component describes species loss without replacement (Baselga & Orme 2012). Similarly, the Bray-Curtis index can be broken down into a balanced turnover of individuals, whereby reductions in one species is balanced by increases in another species, and the loss/nestedness components where all species suffer some reduction in abundance (Baselga 2013). As for the alpha diversity measures we used Spearman rank correlation tests to investigate the relationship between locality HD rank and both within locality dissimilarity and turnover component.

The Sørensen and the Bray-Curtis indices evaluate the community similarity of pairs of surveys/samples, and consequently they do not link directly to larger scales patterns of diversity that occur from aggregates of lots of surveys. The recently developed zeta diversity metric, ζ_i, does this by estimating the mean number of species occurring in all *i* surveys (Hui & McGeoch, 2014). As *i* increases, so ζ_i should decline and the functional form of this decline is indicative of different community assembly processes. A power law decline occurs when the probability that a species occurs in a particular survey is predicted by its regional (locality) abundance. An exponential decay is expected when local occurrences are no longer linked to regional abundances (Hui & McGeoch, 2014). Moreover, when environmental change has a disproportionally detrimental effect on rare species, the slope of zeta diversity decline will become shallower and will be steeper if common species are more severely affected (Hui & McGeoch, 2014).

2.3.4 Taxonomic and trophic group comparisons

Species diversity is not the only important measure of biological diversity to monitor and we also estimated the effect of the HD on taxonomic tribes and trophic guilds. We focussed on the three most species-rich tribes occurring in the rocky-shore zone: Ectodini, Lamprologini, and Tropheini that encompass different intrinsic traits (i.e. breeding behaviour, diet). We further compared the following trophic groups: invertivores, herbivores, and piscivores that encompass all tribes occurring in the rocky-shore zone. For both tribes and trophic groups, we estimated alpha and beta diversity measures within localities; and tested for correlation with the HD gradient as described above. Breaking up the cichlid fish into taxonomic and trophic groups necessarily results in smaller number of species and to counteract beta diversity analyses where both pairs of surveys had no species of the particular group present, we used the zero adjusted Sørensen and Bray-Curtis indices (Clarke, Somerfield & Chapman, 2006).

2.4 Results

A total of 554 surveys were conducted (technical issues caused six surveys to be aborted early and the resultant data was not analysed), in which a total of 70 cichlid species from 12 tribes were observed (see Table S2.3). A total of 138 surveys were conducted at Kigoma Town, 42 at Kigoma Deforested, 42 at Jakobsen’s Beach, 56 at Kalilani Village, 138 at Gombe NP, 83 at Mahale NP S1, and 55 at Mahale NP S2. There were no differences between community composition data at 5 and 10m depths (see Tables S2.4 and S2.5) so species data were pooled across both depths for each locality. The species accumulation curves for all localities approached an asymptote early in the sampling effort (gradient of slope ≤0.02 between 30 and 40 surveys for all localities) indicating sampling was sufficient to capture the majority of species at each locality and with no bias along the disturbance gradient (Figure S2.2).

2.4.1 Species diversity along a gradient of human disturbance

2.4.1.1 Alpha diversity

We found a clear negative relationship between disturbance rank and alpha diversity (Table 2.1). Localities with lower HD had significantly higher median species richness per survey and effective number of species per locality, but there was no correlation of locality HD with median logged abundance per survey or Pielou’s J (diversity evenness).

Table 2.1. Correlations between relative HD rank and alpha and beta diversity (all pairs of survey within each locality) values for cichlids at all localities[*].

		ALPHA DIVERSITY				*BETA DIVERSITY*			
Locality	Relative human disturbance	Median species richness per survey [interquartile range]	Median log abundance per survey [interquartile range]	Pielou's evenness index (all surveys pooled)	Effective number of species (all surveys pooled)	Mean Sørensen dissimilarity between survey pairs [±sd]	Sørensen loss component (%)	Mean Bray-Curtis dissimilarity between survey pairs [±sd]	Bray-Curtis loss component (%)
Kigoma Town	10	10.0 [6]	2.1 [0.49]	0.68	13.1	0.55 [±0.17]	25	0.77 [±0.16]	30
Kigoma Deforested	7.5	12.0 [5.75]	2.3 [0.62]	0.55	7.9	0.53 [±0.13]	23	0.76 [±0.19]	27
Jakobsen's Beach	7.25	15.0 [5.75]	2.3 [0.31]	0.55	7.7	0.49 [±0.13]	18	0.63 [±0.18]	33
Kalilani Village	7	15.5 [4]	1.9 [0.34]	0.72	15.7	0.48 [±0.11]	14	0.7 [±0.14]	20
Gombe NP	4	16.0 [5]	2.1 [0.34]	0.76	20.0	0.48 [±0.14]	21	0.69 [±0.14]	26
Mahale S1	1	24.0 [4]	2.6 [0.26]	0.73	21.8	0.41 [±0.11]	12	0.71 [±0.15]	12
Mahale S2	1	21.0 [4]	2.5 [0.39]	0.74	21.0	0.45 [±0.11]	12	0.71 [±0.16]	18
Rho value		-0.991	-0.514	-0.473	-0.847	0.982	0.891	0.345	0.847
P value		<0.001***	0.238	0.284	0.016*	<0.001***	0.007**	0.448	0.016*

[*] Rho and p values are given for Spearman's rank correlation of alpha and beta diversity values across the human disturbance gradient. Asterisks indicate a significant positive or negative correlation (* P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001).

2.4.1.2 Beta and zeta diversity

We found only very weak distance decay in similarity within each locality (Table S2.6), meaning pairs of surveys separated by 20 m were as similar as pairs separated by several km's. In contrast, we found a significant positive trend between the Sørensen index and HD ranking (Table 2.1), indicating HD acts as a heterogenizing force within the rocky shore cichlid fish communities. This trend was not found in the Bray-Curtis analysis suggesting the increase in beta diversity is mainly due to effects on the rare species (that are given a higher weighting in the Sørensen index). Indeed, repeating the analysis but for each locality removing any species with just one individual leads to the disappearance of the correlation of the Sørensen index and HD ranking (unpublished results). The turnover component dominated both beta diversity measures at all localities (explaining from 67-88% of the beta diversity), and this indicates most survey pair dissimilarity is due to the appearance of new species. However, we also found a significant positive correlation between HD rank and the loss (nestedness) components of both indices (Table 2.1). Our prediction that the nestedness component of beta diversity would increase with increased HD was thus borne out.

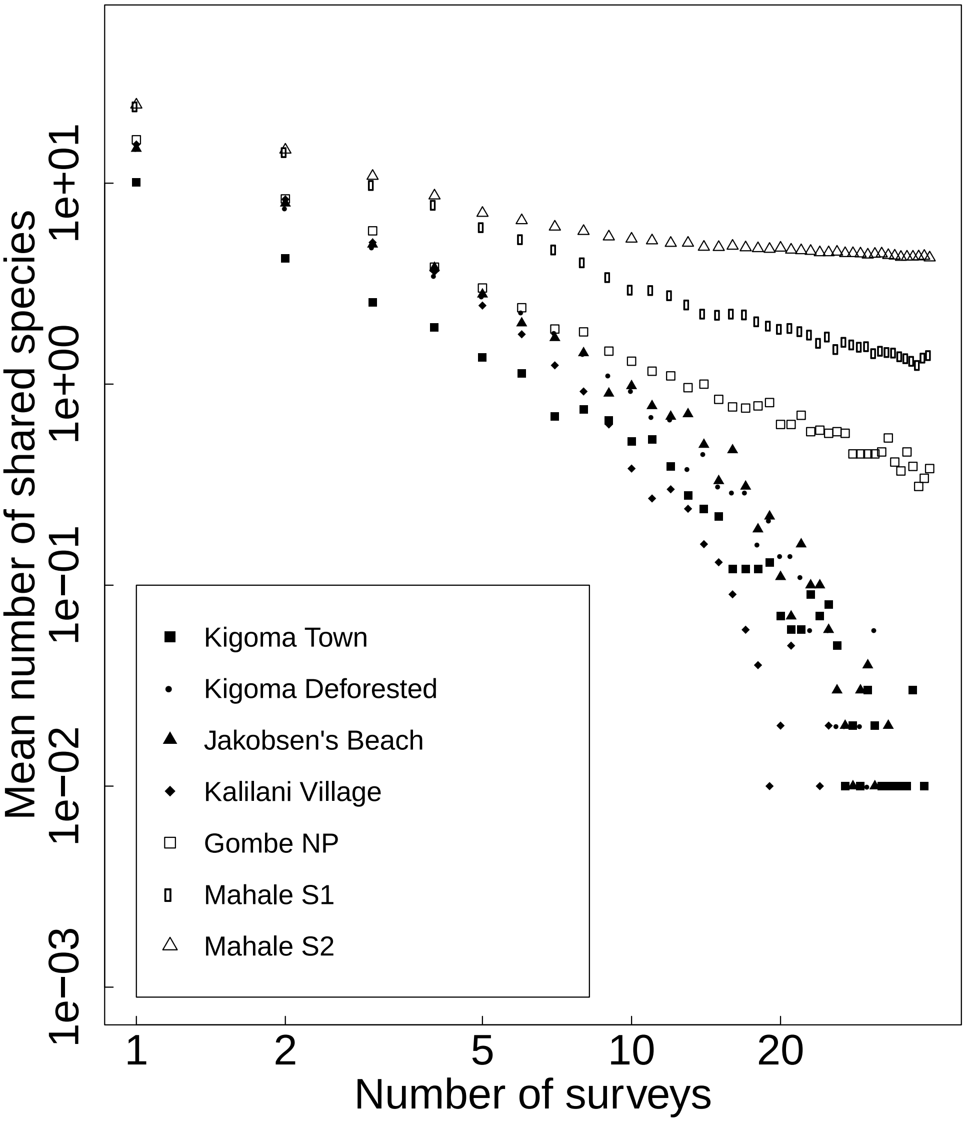


Figure 2.3. The relationships between zeta diversity ζi (the mean number of species shared between i surveys), and the number of surveys (i). Filled symbols represent degraded localities and are best fit by an exponential function; open symbols represent the Freshwater Protected Areas (FPAs) that are best fit by a power function (AIC values given in Table S2.4).

All localities showed a monotonic decline in zeta diversity (ζ_i) with the number of survey sites considered (Figure 2.3). Tests for spatial autocorrelation in zeta showed some statistically significant spatial structure, but generally this was very weak apart for Kigoma Deforested (Appendix S2.2 and Figure S2.3), confirming our results for spatial decline in beta diversity. However, we found the functional form of decline in ζ_i differed between the freshwater protected areas (FPAs: Gombe, Mahale S1, S2), and the unprotected areas (Kigoma Town, Kigoma Deforested, Kalilani Village, and Jakobsen’s Beach). In line with our expectations the power law function showed the best fit in the FPAs, whereas the exponential function was the best fit in unprotected areas (AIC scores given in Table S2.7). To test the hypothesis that an exponential decay in zeta in the disturbed localities might occur due to biased loss of common or rare species, we constructed a null model (described in Appendix S2.3) where species’ occurrences in surveys are removed with a probability that is dependent on their starting occurrence (and including the special case where there is no bias). Starting from the Gombe NP dataset and reducing the number of occurrences down to the Kigoma Town community matrix we found that biasing loss to either originally common or rare species led to an increase in frequency of exponential decay in zeta (Figure S2.3). However, biasing towards the loss of common species led to unrealistically high zeta decay rates, whereas unbiased loss, or biasing towards the loss of rare species led to zeta decay rates that are commensurate with that observed in Kigoma Town (Figure S2.4). In contrast when we reduced the community occurrence matrix from Mahale NP S1 to that observed in Kalilani village we found the empirical relationship observed in Kalilani was most likely to occur when there was a weak bias towards the loss of common species. However, in both cases the neutral loss of species could also produce a zeta diversity decay that appeared similar to that observed in the unprotected site, and we note that an exponential decay was easier to produce for the sparser community matrix of Kalilani suggesting large drops in species occurrences may be sufficient to produce exponential decays in zeta diversity.

2.4.2 Taxonomic and trophic group comparisons

The following number of species were observed within the tribes: Ectodini (15), Lamprologini (26), Tropheini (16), and trophic groups: invertivore (32), herbivore (25), and piscivore (9) see Table S2.3. Overall, we found significant differences in how the tribes and trophic groups responded to locality HD rank.

2.4.2.1 HD gradient analysis

The median species richness per survey was negatively correlated with the HD gradient for all three tribes (Table 2.2, full results given in Table S2.8). Additionally, both Lamprologini and Tropheini show a negative correlation of HD rank and effective species number per locality; and the Tropheini and Ectodini both show a negative relationship between locality HD rank and median log survey abundance. The difference in effective species number per locality between the most disturbed locality and least disturbed locality was much bigger for Tropheini than Lamprologini (Table S2.8) and on this basis we argue the Tropheini are more sensitive to the HD gradient. The Tropheini also showed a positive relationship of beta diversity with HD gradient in both incidence- and abundance-based metrics (Table 2.2). This indicates HD acts as a heterogenizing process in the Tropheini and because we also observe fewer species in more disturbed localities, this is likely due to loss of some common and wide-ranging species. Lamprologini also show a positive relationship albeit only for the Sørensen index, indicating changes in beta diversity caused by HD are probably acting through changes to rare species occupancies. In contrast, the Ectodini show a negative relationship between HD gradient and within-locality Bray-Curtis dissimilarity (Table 2.2). The latter result indicates HD acts to spatially homogenize Ectodini within localities of high disturbance.

Trophic groups showed a similar degree of heterogeneity in their response. Herbivores showed the most negative response to the HD gradient with median species richness per survey, median log abundance per survey and effective species number per locality all being negatively related to locality HD ranking (Table 2.2). Piscivores showed a negative correlation of HD with median species richness per survey and median log abundance per survey, but not effective species number per locality. The effective species number per survey for herbivores in the least disturbed locality was approximately 100% larger than for the most disturbed localities, whereas for piscivores the increase was approximately 50% implying herbivores are more sensitive to the HD gradient (Table S2.8). In contrast, invertivores showed the weakest response to disturbance, with only species richness per survey being negatively correlated to locality HD ranking. We found fewer correlations between beta diversity and trophic groups, but herbivores did display a positive effect of HD on Sørensen dissimilarity, and like the Tropheini and Lamprologini this indicates HD acts to heterogenize herbivores within localities.

Table 2.2. Spearman's Rank Correlation Rho-values of alpha, and beta diversity (comparison between all pairs of surveys within each locality) measures with human disturbance rank across all seven localities for the three main tribes and trophic groups[*].

	ALPHA DIVERSITY			*BETA DIVERSITY*			
Group	Median species richness per survey	Median log abundance per survey (all species pooled)	Effective number of species per locality	Sørensen dissimilarity value within locality	Sørensen loss component (%)	Bray-Curtis dissimilarity within locality	Bray-Curtis loss component (%)
Lamprologini	-0.850*	-0.595	-0.793*	0.847*	0.743	-0.054	0.847*
Tropheini	-0.860*	-0.883**	-0.865*	0.865*	0.883**	0.775*	0.505
Ectodini	-0.905**	-0.793*	-0.559	-0.703	0.288	-0.829*	0.491
Invertivores	-0.954***	-0.450	-0.505	0.667	0.523	-0.216	0.754
Herbivores	-0.963***	-0.883**	-0.883**	0.829*	0.739	0.414	0.736
Piscivores	-0.874*	-0.827*	0.739	0.164	0.464	0.432	0.345

[*] Statistically significant positive or negative correlation are denoted by * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$). See Table S2.5 for details of Spearman's Rank Correlation input values.

2.4.3 Robustness of results

In order to correct for possible biases in our results due to sampling differences between localities, we standardized the number of samples per locality, in all localities using the same number of surveys, and the same spatial extent as the smallest and least sampled localities (Kigoma Deforested and Jakobsen's Beach). Therefore, the surveys chosen to check for potential biases in each locality were limited to sites that were approximately 1km apart (Table S2.9). Repeating the analyses described above produced the same correlations between the HD gradient and the alpha and beta diversity measures, apart from evenness and mean Sørensen dissimilarity (Table S2.9). In addition, we compared the alpha diversity measures of two pairs of localities (i) Gombe NP vs. Kigoma Town; and (ii) Mahale S1 vs. Kalilani Village. These pairs were chosen because they are adjacent to one another, thereby minimising the intrinsic differences between localities, but still allow the comparison of a protected area with a highly degraded counterpart. This is important since the effects of FPAs on diversity can be confounded by other factors, such as large-scale habitat variability, and trends such as a latitudinal gradient in diversity (Adams *et al.*, 2015). As before, we found a statistically significant decline in alpha diversity (median survey abundance, mean survey species richness, and mean Shannon index) in the highly disturbed localities compared to the protected localities (Figure S2.6).

2.5 Discussion

Here, we specifically investigated the effects of human disturbance (HD) along an environmental gradient focusing on the species rich and ecologically heterogeneous LT rocky-shore cichlid communities. By using a variety of alpha, beta and zeta diversity measures, and by focussing on taxonomic diversity we were able to show a clear benefit of FPAs on all aspects of cichlid diversity. In particular, we detected a clear decrease in alpha diversity with increasing HD, especially for herbivore species. The general negative effect of disturbance on alpha diversity agrees with previous studies across various groups within Lake Tanganyika including molluscs, ostracods, and fish (Alin *et al.*, 1999; Donohue, Verheyen & Irvine, 2003; Sweke *et al.*, 2013). We extend these analyses by including Gombe NP; focussing on the changes in functional and taxonomic diversity, as well as showing how beta diversity is affected by the disturbance gradient. Our predictions of a positive relationship between the nestedness component of beta diversity and HD, and the qualitative difference in zeta diversity between protected and unprotected localities were both supported by our analyses.

We also found turnover with replacement is the main component of beta diversity within localities, and this reflects the common pattern identified in aquatic, especially freshwater, systems (Soininen & Hillebrand, 2007; Winkler & Hall, 2013). We also found a positive correlation between the Sørensen index and locality HD rank (Table 2.1), implying the HD acts as a heterogenizing process in the cichlid communities within LT. This relationship was repeated when we considered the Tropheini, Lamprologini, and herbivores separately (Table 2.2). Such an increase in beta diversity could occur if common and wide ranging species are most affected by disturbance, and/or if disturbance leads to lots of species occurring at low abundances (Socolar *et al.*, 2015). Our re-analyses suggest the latter occurred since discounting species with only one individual within a locality removed the correlation. However, a stronger positive relationship was found between locality HD ranking and percentage of dissimilarity explained by loss of species/individuals without replacement (nestedness) (Table 2.2). This finding is consistent with a previous study on freshwater macroinvertebrates that showed local communities under higher anthropogenic stress are expected to have a higher loss/nestedness component of beta diversity due to the loss of specialist over generalist species (Gutiérrez-Cánovas *et al.*, 2013). As we discuss below, the key group of specialist cichlids being lost appears to be within the herbivores and especially the Tropheini, which are specialist herbivores.

The zeta diversity measure has been developed to provide a link between the pairwise beta diversity indices and the regional (gamma) diversity (Hui & McGeoch, 2014). We found the three protected localities to have a power-law relationship between ζ_i (the expected number of shared species in i sites) and i (Figure 2.3). Power-law relationships occur when the probability of finding a species within a survey is correlated to its regional abundance and implies niche processes such as competition and habitat filtering are important in structuring these communities. In contrast the unprotected localities showed a decline in ζ_i, that is best described by an exponential function, and this occurs when the probability that a particular species is found in a local survey is independent of its regional abundance, implying a greater role for stochastic community assembly (Hui & McGeoch, 2014). However, we also found the unprotected area zeta diversity decay could be produced by the unbiased loss of species from the protected areas (Appendix S2.3). To our knowledge this is the first time such an effect of HD on zeta diversity has been described.

Our findings show that there is a significant negative correlation between per survey species diversity and HD ranking across all taxonomic and trophic groups, despite the differing biology of these groups e.g. substrate brooding (Lamprologini) vs. mouthbrooding (Tropheini, Ectodini), and trophic ecology (Table 2.2). However, specific groups appear to be more greatly affected by HD. We showed that herbivore diversity was more affected by HD (Tables 2.2, S5), and in particular the diversity of specialist herbivores that constitute the Tropheini, compared to other tribes (Tables 2.2, S8). We argue the loss in specialist herbivores is likely to be one of the driving forces behind the increased nestedness component of beta diversity, and also why HD has a mild heterogenizing effect on the total within-locality beta diversity (Table 2.1). In direct contrast, the invertivore group was much less affected by HD even though previous studies have highlighted the decline in invertebrate diversity and abundance within LT (Alin *et al.*, 1999; Donohue *et al.*, 2003; McIntyre *et al.*, 2005).

Like many other assessments of impacts of disturbance on biodiversity we have employed a space-for-time substitution. That is to say, in the absence of a long-time series that includes ecological surveys before and after shoreline forest has been removed and urban area expanded we have used comparisons of protected/undisturbed localities with unprotected/disturbed localities under the assumption that the FPAs are able to act as unbiased reference points for the disturbed localities. Recent analyses of the effects of logging on tropical forest diversity has shown the space-for-time substitution can underestimate the effects of disturbance (Franca *et al.*, 2016). In the absence of suitable temporal data, we are unable to make this comparison in LT but note that our differences are already large, and we were careful to exclude biases due to major environmental differences beyond the disturbance status of our localities. None-the-less, it would be fruitful to see if the qualitative and quantitative differences between the disturbed and protected areas continue to get larger, and it would also be interesting to track the effect of a no-fishing policy that was implemented in Gombe NP waters in 2015.

2.5.1 Biological mechanisms

Although we argue for a strong relationship between alpha, beta and zeta diversity of cichlid fish and the degree of human disturbance, our analyses were restricted to correlations. As such a number of open questions remain regarding the processes that lead to these changes. For instance, does human disturbance lead to a reduction in survival, or a reduction in fertility? If so, what are the mechanisms? Is predation and/or parasitism higher in disturbed than undisturbed localities? Most animals are able to adapt to disturbance in the first instance by altering their behaviour, so does this mean human disturbance leads to greater dispersal away from these localities?

One of the most obvious environmental differences between the localities was the increased sedimentation in the unprotected sites (e.g. Figure 2.1). Previous studies (reviewed by Donohue & Molinos 2009) have shown there is a high potential for sedimentation to disrupt lake community diversity and structure of bacteria, primary producers, zooplankton, benthic invertebrates and fish via a variety of mechanisms. However, the response of different functional and taxonomic groups to the HD gradient is likely to depend on differences in life history. For example, in an experiment where a one-time high sediment load was added to quadrats within LT, Donohue *et al.* (2003) found a long-lasting negative effect of sedimentation on benthic invertebrate diversity. In contrast, there were few clear signals in the fish community response. The authors suggest the lack of response of the fish community could be due to the relatively small spatial scale of the experiment in combination to emigration and immigration leading to a high turnover of species, persistent long-term sedimentation may be required to show an effect in the fish community. Donohue *et al.* (2003) did however observe sand dwelling species begin nesting in the sediment treated quadrats. This raises the possibility that rocky dwelling species are replaced by species able to inhabit sandy areas, but we failed to find evidence for this functional replacement (Table S2.10). This may not be surprising given Sweke *et al.* (2013) also found sandy habitat had lower cichlid species richness and abundance in unprotected areas outside compared to inside Mahale NP, implying a very general negative effect of disturbance on cichlid diversity.

We did however find a difference between the Ectodini and Tropheini and their relationship to disturbance (Table 2.2). The majority of Tropheini are grazers and browsers of epilithic algae growing on rocks in close proximity to the shore, whereas non-Tropheini herbivores tend to be less specialist in their feeding habits, also consuming detritus and plankton (Hata *et al.*, 2015). These results support the findings of Alin *et al.* (1999) who observed a decline in algivorous fish dominance as disturbance increased, and Donohue *et al.* (2003) who found a short-term negative response of algivores to artificial sedimentation. Future work should investigate the effect of sedimentation on algal diversity within our localities since sedimentation leads to increased water turbidity, lower rates of photosynthesis and can negatively affect the biomass of epithilic and filamentous algae (reviewed in Donohue & Molinos, 2009). It would then be interesting to link studies of diet niche breadth in protected and unprotected areas and to see if species that are found in the disturbed areas have changed their diets compared to individuals that are found in the protected areas.

In contrast, the Ectodini appear to have been least affected by HD. This tribe is highly diverse ecologically and, unlike the other focal tribes examined, are not restricted to the rocky-shore with some species also occurring exclusively in the sandy-shore, and both the rocky and sandy-shore zones (Konings, 1998, Table S2.3). Some of these species also have more generalist diets, for example, some species feed on both aufwuchs (surface growth) and detritus, while many may feed on various invertebrates (Yamaoka, 1991), and we found the invertivores were generally less affected by HD. This greater plasticity in habitat preference and diet may explain why the Ectodini are not as affected by human disturbance compared to other more specialised tribes. Similarly, a previous study on crabs, the major component of invertebrate biomass within LT could find no effect of sedimentation on their density or incidence, and this was attributed to their large diet breadth that enables them to adapt to local changes in the biomass of algal, detrital and invertebrate food resources (Marijnissen *et al.*, 2009).

2.5.2 Conclusions

Our results showed a decline of taxonomic and functional diversity outside of the protected waters in LT even though the protected areas were terrestrially focussed. It is likely that multiple mechanisms are driving this pattern, but we suspect the increased sedimentation in disturbed areas is an important factor behind the decline in diversity, although we stress this has yet to be shown. Moreover, there are other important effects of HD, such as fishing (Mölsä *et al.*, 1999) and climate change (Cohen *et al.*,

2016) and the relative importance of, and interaction of these with sedimentation pollution needs to be unravelled before we can fully understand the causes of the declines in diversity outside of the protected areas. Unfortunately, only a small percentage of the LT shoreline is formally protected (Coulter & Mubamba, 1993), and given the generally low dispersal ability of rocky-shore cichlid fishes, the reserves might be too isolated to act as a source for less diverse areas of the lake. Future studies should therefore investigate the spill over effects of the FPA’s to see whether and how far their positive effects on diversity reach beyond their borders and investigate whether their beneficial effects extend beyond their protection from high sedimentation rates. In the meantime, our results imply management strategies that decrease sedimentation and pollution entering the lake are likely to greatly benefit the biodiversity within the waters of LT.

3 Higher cichlid species diversity in Lake Tanganyika's protected areas is consistent with higher functional and phylogenetic diversity

3.1 Abstract

Protected areas are frequently selected for their high levels of endemic species richness (SR), however, the amount of morphological variation and ecosystem functions conserved is often unknown. In response, conservationists are questioning whether national parks conserving species diversity are adequately protecting functional diversity (PD) and phylogenetic diversity (FD).

Focusing on the highly diverse communities of rocky-shore cichlids from Lake Tanganyika (LT), we tested whether protected areas with higher species diversity, have higher FD and PD than neighbouring unprotected areas. We also explore whether the patterns of FD and PD are connected to SR using null model simulations.

We demonstrated protected areas contain higher FD and PD than unprotected areas. Additionally, FD and PD in both protected and unprotected areas are not higher than expected given SR, suggesting the different measures of diversity are linked. This is supported by a significant positive linear relationship between SR, and FD and PD regardless of protection status. By demonstrating the congruence between the core components of biodiversity in a low taxonomic level group in a species rich lake system, we add to the seemingly idiosyncratic nature of the relationship between SR and FD across ecosystems and regions.

We also showed that for LT rocky shore cichlids, pressures have to be more extreme than the observed anthropogenic impact on surveyed communities, for FD to differ from expected given SR. Only when the most functionally unique species are strongly biased against do we see a consistently different FD than expected given SR, most likely because most LT cichlid species have similar uniqueness values, so as species are lost so is FD.

Our work highlights that the current protected area network in LT is likely protecting cichlid FD and PD as well as species diversity. However, the lack of functional redundancy means a loss of species could result in a loss of ecosystem

functions. Based on our results, management of the existing protected areas should continue, in addition to targeting species rich areas of the lake not already protected with conservation effort.

We suggest that protected areas successfully conserving species could also protect morphological variation and ecosystem functions. Ideally all protected areas chosen for high levels of endemic SR would be assessed for FD and PD, however, given limited conservation resources, species diversity should continue to be used as a surrogate.

3.2 Introduction

Protected areas are frequently selected for their high levels of endemic species richness (SR) and rarity (Myers *et al.*, 2000; Rodrigues & Gaston, 2002b), and can be effective at conserving taxonomic diversity (Rodrigues *et al.*, 2004b; González-Maya *et al.*, 2015; Britton *et al.*, 2017). However, less is known about the effectiveness of protected areas at conserving species morphological variation and functional traits (Thuiller *et al.*, 2015). Targeting taxonomic diversity has been proposed as a way of also conserving ecosystem functions (Garcia & Martinez, 2012). However, ecosystem function may be more closely related to the measure functional diversity (FD), because FD can be linked to niche complementarity (Frund *et al.*, 2013; Comte *et al.*, 2016; Hiraiwa & Ushimaru, 2017). FD can be quantified using morphological information, as well as by measuring phylogenetic diversity (PD), which assumes species features are phylogenetically conserved (Forest *et al.*, 2007; Faith, 2015). Thus, FD and PD are related, and both can reveal patterns of ecosystem functioning and in a community (Srivastava *et al.*, 2012; Brocchieri, 2016). Therefore there is much overlap of taxonomic, functional and phylogenetic diversity (Pool, Grenouillet & Villéger, 2014), and protection of one measure can conserve another (Quan *et al.*, 2018). However, there is sometimes a lack of congruence between taxonomic diversity, FD and PD (Devictor *et al.*, 2010; Mouillot *et al.*, 2011; D’Agata *et al.*, 2014), possibly because the relationships between taxonomic, FD and PD can be specific to the community’s location, size, evolutionary history, and disturbance (Forest *et al.*, 2007; Devictor *et al.*, 2010; Mayfield *et al.*, 2010; Tucker & Cadotte, 2013). Therefore conservationists have started to quantify FD and PD as well as taxonomic diversity to assess the effectiveness of protected areas at conserving all aspects of diversity (Devictor *et al.*, 2010; Mouillot *et al.*, 2011; Cottee-Jones *et al.*, 2015; Quan *et al.*, 2018).

There is a broad consensus that increasing human disturbance causes a decline in SR (Bhat & Magurran, 2006; Flynn *et al.*, 2009; Biswas & Mallik, 2011; Britton *et al.*, 2017; Chapman *et al.*, 2018), which is often mirrored by a decline in the related measures of FD and PD (Micheli & Halpern, 2005; Magnan *et al.*, 2010; Luck, Carter & Smallbone, 2013; Matsuzaki, Sasaki & Akasaka, 2013; D'Agata *et al.*, 2014; Schmera *et al.*, 2017). A linear relationship with a steep slope results in low functional redundancy, so if a species is lost, so is its unique set of functions. Therefore communities with low functional redundancy, possibly due to non-random community assembly (Halpern & Floeter, 2008), are less resilient to increased human disturbance, (Bellwood *et al.*, 2004; Micheli & Halpern, 2005). Conversely, if a species is lost from a community with high functional redundancy, there are other species to replace the FD lost. Nevertheless, even in a functionally redundant ecosystem, a lack of consistency in redundancy across communities can result in low functional redundancy at the local scale (Mouillot *et al.*, 2014).

On the other hand, the responses of SR, FD and PD to human disturbance are not always congruent. For example, the relationship between SR and FD is not uniform at differing levels of disturbance in temperate plant communities (Biswas & Mallik, 2011; Pakeman, 2011). Furthermore fish community SR and FD can remain fixed as human disturbance increases, or SR can increase whilst FD decreases (Villéger *et al.*, 2010). Consequently, to assess whether the relationship between human disturbance, and FD and PD are linked to human impacts on SR, null models have been utilised to build simulated communities with fixed SR from the species pool, to calculate differences between mean simulated and observed diversity values (Mason *et al.*, 2013). However, it should be acknowledged that the ability of null models to discriminate between observed and expected FD is dependent on the magnitude of the community FD, which can be influenced by the size of the community sample pool, because higher SR is linked to higher FD (de Bello, 2012).

The relationship between SR and FD in response to human disturbance appears to be idiosyncratic, even within the same taxonomic clade or ecoregion. In terrestrial systems, FD is as expected given SR in temperate and tropical plant communities (Flynn *et al.*, 2009) and sub-tropical forest bird communities (Luck *et al.*, 2013; Cottee-Jones *et al.*, 2015). Conversely, FD is more clustered than expected from the SR in UK woodland and farmland plant communities (Pakeman, 2011), but more dispersed than expected in Malaysian tropical forest bird communities (Chapman *et al.*, 2018). In a meta-analysis of temperate and tropical bird and mammal communities (Flynn *et al.*, 2009), the FD of some communities were consistent with that expected given SR, but in the majority FD is both more clustered and dispersed than expected given SR. There is a similar pattern in aquatic systems, with patterns of FD as expected given SR in tropical coral reef fish communities (Plass-Johnson *et al.*, 2016), whereas FD is more dispersed than expected given SR in Japanese freshwater fish communities (Matsuzaki *et al.*, 2013). These studies illustrate how the relationship between SR and FD is probably reliant on factors specific to the community of interest, as well as the definition of FD used (Halpern & Floeter, 2008). However, less is known about the relationship between SR and FD in protected areas. Bird communities in protected sub-tropical forests FD can be linked to SR (Luck *et al.*, 2013; Cottee-Jones *et al.*, 2015), but to our knowledge this relationship has yet to be investigated in aquatic protected areas. Additionally, considering protected and unprotected areas means a departure from the null model may be more likely to be detected, because there is likely to be a biased composition of species in the unprotected community.

Here, we focused on Lake Tanganyika (LT), one of the world's most diverse freshwater ecosystems (~1300 animal species, Coulter 1991). Cichlid fishes (~250 valid species, 97% endemics (Salzburger *et al.*, 2014; Salzburger, 2018)) dominate the diverse rocky shore zone of LT (Coulter, 1991), comprising higher morphological diversity than any other East African Great Lake (Chakrabarty, 2005). Despite these high levels of diversity, only 6% of Tanganyika’s shoreline is protected within national parks, which were primarily designated to protect terrestrial biodiversity (Coulter and Mubamba, 1993). Recent studies in the Tanzanian region of LT found protected areas have higher cichlid fish species diversity than unprotected areas (Sweke *et al.*, 2013, 2016; Britton *et al.*, 2017). However, their metrics of species diversity considered all species as ecologically and evolutionarily equivalent (Swenson *et al.*, 2012), and did not measure phylogenetic diversity (Vellend *et al.*, 2011), or the range of morphologies and functions performed by organisms in a community (Petchey & Gaston, 2006), although Britton *et al.* (2017) investigated trophic groups as a proxy for FD.

Recently methods have been developed to calculate FD from multidimensional functional space, generated from traditional morphometric measurements and trait ratios (Mouillot *et al.*, 2013). However, a more direct way to calculate multidimensional space is to use coordinate data from geometric morphometric analysis (Klingenberg, 2016). Geometric morphometric methods have been successfully used to measure diversity of fish communities (Farré *et al.*, 2013), and are considered better at capturing shape diversity in cichlid fish than traditional morphometric methods (Maderbacher *et al.*, 2008). We therefore investigated LT cichlid morphological diversity based on shape analysis of geometric morphometric landmarks and define FD as the shape diversity of the key morphological areas captured. These areas include functionally significant features such as the jaws, eyes, fins and overall body shape, which are relevant to feeding, locomotion and habitat use (Claverie & Wainwright, 2014), although we acknowledge that morphological diversity is not always tightly coupled to FD (Wainwright, 2007).

Within the East African Great Lakes, higher FD, defined as generic level diversity rather than morphological diversity, has been reported in Lake Malawi at sites with complex habitats (Ding *et al.*, 2014), however, generic diversity is more of a proxy of PD instead of FD, and protected areas were not assessed by Ding *et al.* (2014). A study of trait diversity of cichlids in the southern LT basin using traditional morphometric methods found neutral processes were responsible for community assembly across a range of environments, but human impacts were not investigated (Janzen *et al.*, 2017). Geometric morphometric methods have been applied to LT cichlids from an evolutionary perspective to study the role of ecology in adaptive radiation e.g. (Clabaut *et al.*, 2007). Yet despite the range of ecological studies on LT cichlids (Hori *et al.*, 1993; Kocher *et al.*, 1993; Rüber & Adams, 2001; Chakrabarty, 2005; Arbour & López-Fernández, 2014), no assessment of the FD and PD of LT freshwater protected areas has been conducted.

Given a recent study by Britton *et al.* (2017) found higher species diversity of rocky shore cichlids in LT in protected areas than urban localities, we investigated whether LT cichlid FD and PD follow a similar pattern. The reason for measuring both FD and PD was to give a more complete picture of ecosystem functioning than measuring species diversity alone. We also tested whether species diversity was linked to FD and PD and considered whether anthropogenic pressures in unprotected areas were strong enough to cause FD to differ from expected given SR. Firstly we measured the FD of all rocky shore cichlid species in LT and compared total FD to locality and survey level FD found in three protected areas, as well as four unprotected localities. Furthermore, using a null model we investigated if these changes in FD are expected given SR at each locality, and compared null models to biased simulated communities to test if FD could consistently differ from the null expectation. We also tested if SR is correlated to FD at the survey level, in addition to investigating dissimilarity in FD between surveys within localities. Secondly, we investigated if PD is higher in protected areas at the locality and survey level, and whether these results are expected given SR, as well as assessing beta PD within localities to test if protected and unprotected areas differ.

3.3 Materials and methods

3.3.1 Study localities and community data collection

Seven localities, described in Britton *et al.* (2017), were used in this study (for descriptions see Chapter two supporting information Appendix S2.1). The localities span 180km of the east coastline of LT in the Kigoma region of Tanzania, including two national parks (NP). The northern third of the larger national park Mahale NP was split into two localities – Mahale NP S1 to the north and Mahale NP S2 to the south, and the whole of Gombe NP was defined as one locality. The four unprotected localities included Kigoma Town, Kigoma Deforested and Jakobsen's Beach located near Gombe NP in the northern basin of the lake, and Kalilani Village, located near Mahale NP in the central basin of the lake (see Briton *et al.* 2017 and Figure 2.2 for map). The localities were surveyed with SCUBA between January and April 2015 as described in Britton *et al.* (2017) (see Chapter two supporting information Figure S3.1) with the following number of surveys per locality: Mahale NP S1 – 83, Mahale NP S2 – 55, Gombe NP – 138, Kalilani Village – 56, Jakobsen's Beach – 42, Kigoma Deforested – 42, Kigoma Town – 138. A total of 70 species were recorded with the following number of species present at each locality: Mahale NP S1 (67 spp.), Mahale NP S2 (60 spp.), Gombe NP (51 spp.), Kalilani Village (47 spp.), Jakobsen's Beach (42 spp.), Kigoma Deforested (42 spp.), Kigoma Town (43 spp.). Sampling was sufficient at each locality to survey the majority of species since the asymptote of the species accumulation curve at all localities reached a gradient of ≤0.02 between 30 and 40 surveys (Britton *et al.*, 2017) (see Chapter two supporting information Figure

S3.2). Therefore, diversity at the locality level was analysed in addition to diversity at the survey level.

3.3.2 Photo data collection

To quantify intra and inter specific morphological differences, digital photographs (Canon EOS 2OD DS126061 camera with Macro lens EF 100m 1:2.8 USM) were taken of the lateral left side of 91 cichlid species (n= 887 individuals) found in the rocky shore zone of LT (Konings, 2015). Specimens were photographed from the Natural History Museum, London, UK (BMNH), which includes our recent collections, and the Royal Museum of Central Africa, Belgium (RMCA). Specimens were sampled throughout LT from the shores of Tanzania, Zambia, Burundi and the Democratic Republic of Congo. We aimed to photograph ten adult individuals of each species (Tixier, 2012), however due to specimen availability some species had fewer individuals, with a minimum of five photographed per species. External sexing based on colour was generally not possible due to sample preservation in alcohol, however as the majority of LT cichlid species do not display extreme sexual dimorphism (Konings, 1998), and no difference in body shape has been found in other East African lake cichlids (e.g. Ford *et al.* (2016) and (Kassam, Mizoiri & Yamaoka, 2004)), fish were analysed without regard to sex.

3.3.3 Geometric morphometrics

Landmark based geometric morphometrics were used to analyse shape variation (Webster & Sheets, 2010), which is highly suitable for fishes with compressed body shapes (Cardini, 2014). Landmarking also leads directly to coordinate measures for a principal component analysis, rather than having to transform categorical variables (Schleuter *et al.*, 2010). This method has provided a better representation of overall body shape in LT cichlids species than traditional morphometric measurements because landmarks cover the geometry of the whole organism, as demonstrated in the *Tropheus moorii* species complex (Maderbacher *et al.*, 2008). Fourteen homologous landmarks found in every individual were modified from Chakrabarty (2005), Claverie & Wainwright (2014) and Ford *et al.* (2016) to capture a range of body regions and functions such as eye size and position, oral gape size and position, pectoral fin position, caudal peduncle size, body elongation, and standard length (Figure S3.1). The digital photographs were uploaded into tpsUtil64 v 1.74 (Rohlf, 2015), and the x and y coordinates of the landmarks were subsequently digitised tpsDig2 v 2.3 (Rohlf, 2015). Landmarks were not weighted. A subset of 30 randomly chosen individuals were landmarked twice (blind replication) and the variation in landmark position analysed to ensure landmarks were not variable. There were no significant differences between the first and second replicate of landmarks (paired t test, p=1), therefore the rest of the individual digital photographs were landmarked once by AB.

3.3.4 Procrustes superimposition

Differences in orientation, size and position were removed with a Procrustes analysis, and shape data was extracted in R (R Core Team, 2015) using the package geomorph v3.0.5 (Adams & Otárola-Castillo, 2013). Individuals were sorted into species and checked for individual outliers by measuring Procrustes distance from the mean shape of each species. Forty-one individual outliers, whose Procrustes distance from the mean shape of their species fell above the upper quartile due to sample preservation, were removed from the dataset leaving 846 individuals from 91 species (Table S3.1). Additionally, a consensus of x and y coordinates of the 14 landmarks was calculated for each species using the mean of its individuals, and the consensus was used to assess the effect of phylogeny.

3.3.5 Phylogenetic correction

The effect of phylogeny was assessed in geomorph using a densely sampled LT cichlid dated phylogenetic tree including 160 species (Day *et al.*, 2008). The consensus tree based on the fossil calibrated timescale from that study was imported into R and pruned to a subset of 69 species (69 of the 91 species sampled were present in the phylogeny) with the ape package v5 (Paradis, Claude & Strimmer, 2004). A phylogenetic least squares regression ANOVA was performed between the Procrustes aligned coordinates, centroid size and the phylogeny. The branch lengths were found not to be influencing shape after resampling 999 random iterations (p=0.985). The lack of relationship between phylogeny and geometric morphometric data may be due to the cichlids recent radiation, which has been previously reported in LT cichlids (Clabaut *et al.*, 2007), and East African soda lake cichlids (Ford *et al.*, 2016).

3.3.6 Size correction

Procrustes superimposition overlays specimens and aligns coordinates by holding constant variation in their shape (Adams & Otárola-Castillo, 2013), however allometric shape variation due to ontogenetic effects may still need correcting for in morphological and taxonomic studies (Klingenberg, 2016). A regression of centroid size and shape was used to check if individuals needed to be corrected for allometry (Klingenberg, 2016). Size had a significant effect on shape explaining 4.4% of the shape variation (1000 permutation test, p=0.001), therefore the residuals of the allometric regression were used for downstream analysis (Ford *et al.*, 2016). A consensus of x and y coordinates of the 14 landmarks was calculated for each species using the mean of its individuals. The mean size corrected residual coordinates for each species were visualised along shape axes with Principal Component (PC) analysis in geomorph. Axis one explained 44% of the variance, axis two explained 14% (58% cumulative), axis three explained 12% (70%), axis four explained 9% (79%), axis five explained 7% (86%) and axis six explained 5% (90%).

Additionally, the standard length of each individual (cm) was measured, and a principal coordinate analysis was performed on the data in the base library of R (Villéger *et al.*, 2008). These coordinates were added to the landmark data and an additional consensus of x and y coordinates were calculated for each species. The PC axes of this body size and landmark dataset, as well as the landmark only dataset, was then used for FD analysis.

3.3.7 Alpha FD analysis

FD was calculated at the locality and survey level using multidimensional indices (Villéger *et al.*, 2008) from the first four PC axes (79% of the variation) of the landmark only dataset, and the first six PC axes (80% of the variation) of the landmark and body size dataset. Functional richness (FRic) is defined as the minimum convex hull that includes all species in niche space, and takes into account only presence absence data so is the functional equivalent of SR. Functional richness was chosen because it can compare FD across gradients (Mouillot *et al.*, 2013; Plass-Johnson *et al.*, 2016), and calculates proportions of morphospace at each locality compared to the regional species pool. To take abundance into account functional dispersion (FDis) was also calculated, FDis weights species by relative abundance and measures the mean distance to the assemblage centroid (Weiher, 2011). Additionally, functional evenness (FEve), the regularity of relative abundance in multidimensional functional space (Mouillot *et al.*, 2013), was also calculated. As FD is linked to SR (Petchey & Gaston, 2002) FRic was compared to SR at the survey level to standardise FD comparisons between localities. This included a Pearson correlation and linear regression between median survey SR and median survey FRic, and as FRic values are proportions they were arcsine transformed. Coefficients of variation were also calculated for survey SR and FRic, which helped inform the beta diversity analysis.

3.3.8 Functional uniqueness

After converting the species coordinates of the first four PC axes of the landmark only dataset, and the first six axes of the landmark and body size dataset, into a pairwise distance matrix, the R package adiv v1.1 (Ricotta *et al.*, 2016) was used to calculate each species functional dissimilarity (uniqueness). For both datasets, species uniqueness was quantified over all PC axes for each locality and the species pool. Additionally, to check if a landmark with low variation was reducing overall species uniqueness in both datasets, the the highest axis uniqueness values were quantified for each species at every locality.

3.3.9 Measuring expected FD

As in other studies we used null models to test whether observed FD differs from simulated FD given the same SR of the community (Flynn *et al.*, 2009; Luck *et al.*, 2013; Mason *et al.*, 2013; Plass-Johnson *et al.*, 2016; Toussaint *et al.*, 2016; Schmera *et al.*, 2017). For each locality we simulated 999 communities where the observed species abundances were retained, but where the species assigned to each observed abundance was drawn at random (without replacement) from the regional (91) species pool of LT rocky shore cichlids. Hence, both the total number of individuals, and the species abundance distributions were held constant. Simulations were conducted in R v3.1.3 (R Core Team, 2015) using vegan v2.3-0 (Oksanen *et al.*, 2015), with the quasiswap algorithm. Standardised effect size was calculated using the equation ((observed FD – mean expected FD)/expected standard deviation) (Gotelli & McCabe, 2002). The standard effect size of FRic (SES FRic) is recommended as a measure of functional richness, the standard effect size of FDis (SES FDis) is recommended as a measure of functional divergence, in addition to the standard effect size of FEve (SESFEve) (Mason *et al.*, 2013). Additionally the observed communities were ranked within the simulated 999, and a two sided 95% confidence interval was used to check if observed community FD was significantly higher or lower than expected given SR (Pakeman, 2011).

To investigate whether it was possible for observed FRic to differ from the null model, a power test was conducted on the landmark only dataset, with biased communities (rather than observed) based on feeding groups and overall uniqueness to. Biased communities were simulated 200 times and ranked within the null communities. The community composition from the most degraded locality Kigoma Town (38 spp.), and the two protected areas (Mahale NP S1 – 60 spp., Gombe NP – 45 spp.) were used. To replicate community niche assembly, species were grouped into herbivores and non-herbivores, in which the herbivores were weighted to be 100 times less likely to be selected (thereby replicating species diversity effect found by Britton *et al.*, 2017). Additionally, to further test the power of our null model, the most functionally extreme communities were generated when the most or least unique species were more likely to be included in the community. In this case species were weighted by their uniqueness rank so the most functionally unique species was 91 times more or less likely to be selected than the least. Finally, we tested if the number of species in a community influences whether FRic is more or less likely to differ from the random expectation given SR. Two hundred communities biased towards and against the most unique species ranked in the regional pool were generated for a variety of SR, and ranked within 999 simulations of the null expectation of the species pool given the SR.

3.3.10 Beta FD analysis

Due to computational time Beta FD (FBeta) was calculated only from the first three PC axes of the landmark only dataset (explaining 70% of the variation) (Villéger, Grenouillet & Brosse, 2013). At each locality mean functional dissimilarity between all survey pairs was calculated from survey species occurrence data using R package Betapart v1.4.1 (Baselga & Orme, 2012). Additionally, the mean locality turnover and nestedness of FBeta between survey pairs was also calculated to identify if dissimilarity was caused by replacement of species morphospace (turnover), or loss of species morphospace (nestedness).

3.3.11 Taxonomic and feeding group analysis

Patterns of alpha FD were further assessed by investigating the most species-rich tribal groups of the rocky-shore: Lamprologini, Ectodini and Tropheini, and feeding groups: invertivores, herbivores and piscivores, to identify if a particular group was driving the pattern of FRic at localities. FRic was calculated for each group at each locality from the four PC axes of the landmark only dataset. To calculate SES FRic, 999 communities were selected for each locality for each group, with SR of each locality and group fixed. Species were chosen from the LT rocky shore pool for each group at the localities allowing us to check if a particular group has higher FRic than expected given SR at a locality.

3.3.12 Phylogenetic diversity analysis

Of the 70 rocky shore LT cichlid species observed at all localities by Britton *et al.* (2017), 58 were present in the Day *et al.* (2008) densely sampled cichlid phylogenetic tree. To ensure that the PD analysis was as complete as possible, we therefore added the 12 remaining species to this phylogenetic tree using the R package addTaxa (Miller, 2017). Species were added as sister taxa to corresponding species in their genus based on the latest Catalog of Fishes classification (Eschmeyer, 2015) (Figure S3.2). To ensure branch lengths were not artificially increased in the 70 species tree, PD was also calculated for the 58 species trees, and both trees yielded similar PD values (Table S3.2). Community SR data (Britton *et al.*, 2017) was used to calculate PD in R package picante v1.6.2 (Kembel *et al.*, 2010). SR data was used to calculate

PD by summing the total phylogenetic branch lengths of each locality (Faith, 1992). Species abundance data was used to calculate the mean phylogenetic pairwise distance (MPD) separating taxa at each locality, and the mean nearest taxon phylogenetic distance (MNTD) at each locality (Webb, 2000). To quantify whether PD is greater or less than expected given SR, the net relatedness index (NRI) and the nearest taxon index (NTI) were used (Webb, 2000; Swenson, 2009; Graham *et al.*, 2009; Chapman *et al.*, 2018). Positive NRI and NTI values indicate phylogenetic clustering which could signify environmental filtering, whereas negative values indicate phylogenetic over dispersion which could signify the effects of competition (Graham *et al.*, 2009). However, empirical evidence supporting this is mixed, and there is some evidence that competition can favour closely related species (Mayfield & Levine, 2010), therefore NRI and NTI values should be interpreted carefully because it is hard to determine the processes underlying phylogenetic dispersion. Again, as with the FD analysis we used a two-sided 95% confidence interval to check if observed community NRI and NTI was significantly higher or lower than expected given SR. To calculate NTI and NRI the observed MPD and MNTD were compared to the expected values at each locality using a null model of 999 replicates generated with the independent swap algorithm, the effect sizes calculated are then converted to the NTI (-1 SES MNTD) and the NRI (-1 SES MPD) (Kembel *et al.*, 2010). NRI is weighted to basal dispersion in the phylogeny and NTI is weighted to terminal taxa dispersion (Swenson *et al.*, 2012). PD was also calculated at the survey level at each locality to ensure a few highly diverse surveys did not bias the overall locality PD. Additionally to test whether SR was influencing PD at the survey level Pearson correlations and linear regressions were performed at each locality between median survey SR and median survey PD. Beta PD was calculated within localities using the mean pairwise MPD and MNTD separating all species across survey pairs weighted by abundance (Webb, 2000; Swenson, 2009).

3.4 Results

3.4.1 Functional diversity

The proportion of landmark only morphospace (FRic) occupied by rocky shore cichlids in protected areas is 78-83% of the morphospace of all LT rocky shore cichlids, whereas the morphospace occupied by unprotected localities ranges between 43% and 64% (Table 3.1a and Figure 3.1). Similarly, when body size is considered, rocky shore cichlids in protected areas occupy over 70% of LT rocky shore morphospace, whereas unprotected areas occupy under 70% (Table 3.1b). At all localities, regardless of protection status, community size and body size there is no statistically significant difference between the observed FRic and the null expectation given the SR of the locality (Tables 3.1a and 3.2b). There is also no difference between the observed and null expectation of abundance weighted FDis and FEve at all localities and the FDis values show little variation regardless of locality protection status (Tables 3.1a and 3.1b). However, FEve values tend to be lower in protected areas (Tables 3.1a and 3.1b). At the survey level FRic is again higher in protected areas with surveys at the Mahale NP localities containing on average between 15% and 18% of the landmark only morphospace occupied by all rocky shore cichlids, whereas Kigoma localities contain on average ≤5% of the morphospace (Table 3.1a). Kigoma localities also contain ≤5% of the morphospace per survey when body size is considered, whereas Mahale NP localities occupy between 28% and 35% morphospace (Table 3.1b). Furthermore, survey FRic is positively correlated with survey SR at all localities with a significant linear relationship (Table 3.1 and Figures 3.2a and 3.2b). The survey SR and FRic coefficients of variation are generally lower at the protected areas signifying a consistently higher diversity at protected areas, which may go some way to explaining why FEve and FBeta are higher in unprotected areas (Table 3.2), although the beta FD at each locality is composed from similar amounts of turnover and loss.

Table 3.1a. Landmark data four-dimensional locality and survey level functional richness (FRic) and functional dispersion (FDis) values calculated from a pool of all 90 rocky shore cichlid species, with standardised effect size calculated from 999 random simulations, with no significant effect sizes reported. Number of surveys per locality, locality species richness (SR) and survey SR are also indicated. As well as Pearson correlation coefficients between median survey SR and FRIC (SR FRic) with significant relationships from linear regressions starred, and survey SR and FRIC coefficients of variation (CV).

		Locality level							*Survey level*				
	Surveys	**SR**	**FRic**	**SES FRic**	**FDis**	**SES FDis**	**FEve**	**SES FEve**	**SR**	**SR CV**	**FRic**	**FRic CV**	**FRic SR**
Mahale NP S1	83	60	0.83	1.19	0.44	-0.7	0.38	0.43	22	0.13	0.18	0.39	0.47*
Mahale NP S2	55	54	0.81	1.67	0.52	0.58	0.43	-0.21	20	0.15	0.15	0.42	0.46*
Gombe NP	138	45	0.78	2.35	0.43	-0.88	0.35	0.03	15	0.27	0.09	0.59	0.81*
Kalilani Village	56	43	0.64	1.27	0.49	0.29	0.41	-1.74	15	0.19	0.09	0.59	0.60*
Jakobsen's Beach	42	37	0.59	1.51	0.38	-0.05	0.57	-0.44	14	0.26	0.05	0.7	0.77*
Kigoma Deforested	42	36	0.43	0.03	0.29	-1	0.45	0.24	12	0.32	0.04	0.91	0.86*
Kigoma Town	138	38	0.58	1.43	0.47	0.1	0.46	0.95	10	0.32	0.04	0.92	0.90*

Table 3.2b. Landmark and body size data four-dimensional locality and survey level functional richness (FRic) and functional dispersion (FDis) values calculated from a pool of all 90 rocky shore cichlid species, with standardised effect size calculated from 999 random simulations, with no significant effect sizes reported. Number of surveys per locality, locality species richness (SR) and survey SR are also indicated. As well as Pearson correlation coefficients between median survey SR and FRIC (SR FRic) with significant relationships from linear regressions starred, and survey SR and FRIC coefficients of variation (CV).

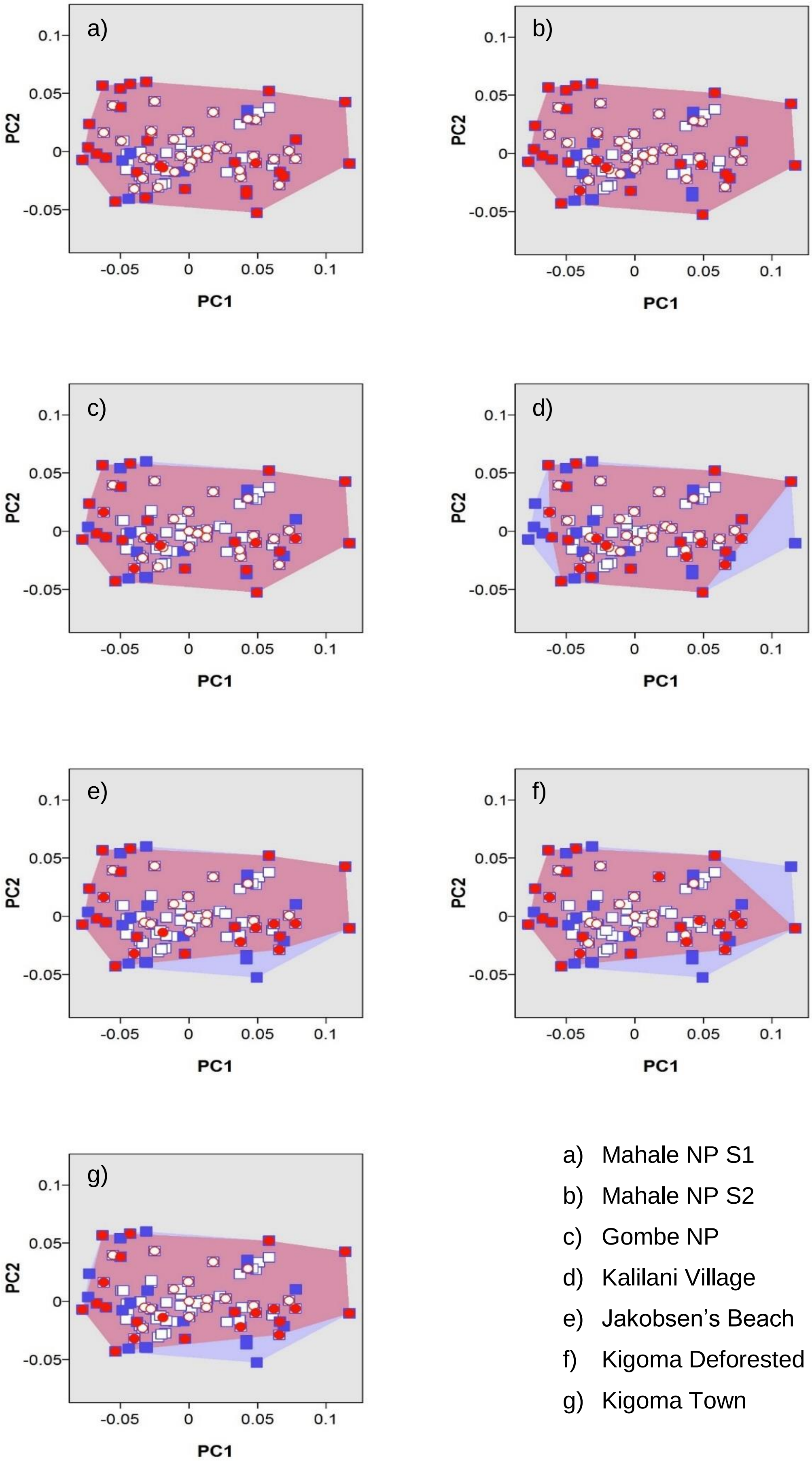
		Locality level							*Survey level*				
	Surveys	**SR**	**FRic**	**SES FRic**	**FDis**	**SES FDis**	**FEve**	**SES FEve**	**SR**	**SR CV**	**FRic**	**FRic CV**	**FRic SR**
Mahale NP S1	83	60	0.83	0.37	0.72	-1.71	0.19	-2.17	22	0.13	0.35	0.31	0.65*
Mahale NP S2	55	54	0.77	0.1	0.77	-0.56	0.23	-1.82	20	0.15	0.28	0.41	0.76*
Gombe NP	138	45	0.7	0.44	0.79	-0.51	0.15	-1.79	15	0.27	0.1	0.84	0.88*
Kalilani Village	56	43	0.69	0.49	0.76	-0.37	0.76	0.75	15	0.19	0.12	0.63	0.81*
Jakobsen’s Beach	42	37	0.55	-0.24	0.7	1.14	0.51	0.6	14	0.26	0.09	0.8	0.77*
Kigoma Deforested	42	36	0.5	-0.55	0.65	0.62	0.41	0.5	12	0.32	0.03	2.61	0.86*
Kigoma Town	138	38	0.58	-0.02	0.8	0.7	0.42	0.96	10	0.32	0.04	1.38	0.82*

Table 3.3. Three-dimensional mean beta functional diversity (FBeta) within localities, with proportions of turnover and loss.

	Surveys	**FBeta**	**Turnover**	**Loss**
Mahale NP S1	83	0.339	0.53	0.47
Mahale NP S2	55	0.439	0.51	0.49
Gombe NP	136	0.545	0.48	0.52
Kalilani Village	56	0.517	0.54	0.46
Jakobsen’s Beach	42	0.615	0.63	0.37
Kigoma Deforested	42	0.753	0.56	0.44
Kigoma Town	129	0.736	0.51	0.49

To test if there were biases in our results due to differences in locality size and number of surveys per locality we standardised the number and extent of sites at each locality for the landmark only dataset (see Britton *et al.*, 2017 and Chapter two). Results were similar to complete locality FD, with protected areas having higher diversity than unprotected areas (see Table S3.3), but again, we found no significant differences between FD and that expected from the null model, confirming our earlier result that patterns of FD are consistent with that expected given SR.

All species in our landmark only dataset have functional uniqueness values of at least 0.05 over all the PC axes (Table S3.4a), therefore FD is possibly not being replaced when a species is lost, which may explain why FRic declines between protected and unprotected areas, as well as the positive relationship between survey FD and SR. Additionally in terms of functional uniqueness the species are quite interchangeable as the values only range between 0.05-0.15, which could be contributing to the observed FRic being as expected given SR at all localities. In terms of the highest uniqueness across the PC axes, values are similar to over all the PC axes; ranging between 0.02-0.13 for each locality (Table S3.4b). Additionally, when body size is considered, overall species uniqueness values increase to between 0.6-1.86 (Table S3.4c), and highest uniqueness values across PC axes increase to between 0.34 and 1.34 (Table S3.4d). Futhermore, larger species having higher uniqueness values, possibly because body size is more variable in coordinate space than an individual landmark.



a) Mahale NP S1
b) Mahale NP S2
c) Gombe NP
d) Kalilani Village
e) Jakobsen’s Beach
f) Kigoma Deforested
g) Kigoma Town

Figure 3.1. Four-dimensional functional richness (FRic) values for all seven localities. Plots of the first two dimensions of morphospace indicate the site in red compared to the total LT rocky shore cichlid morphospace in blue. White dots indicate species not contributing to 4D morphospace.

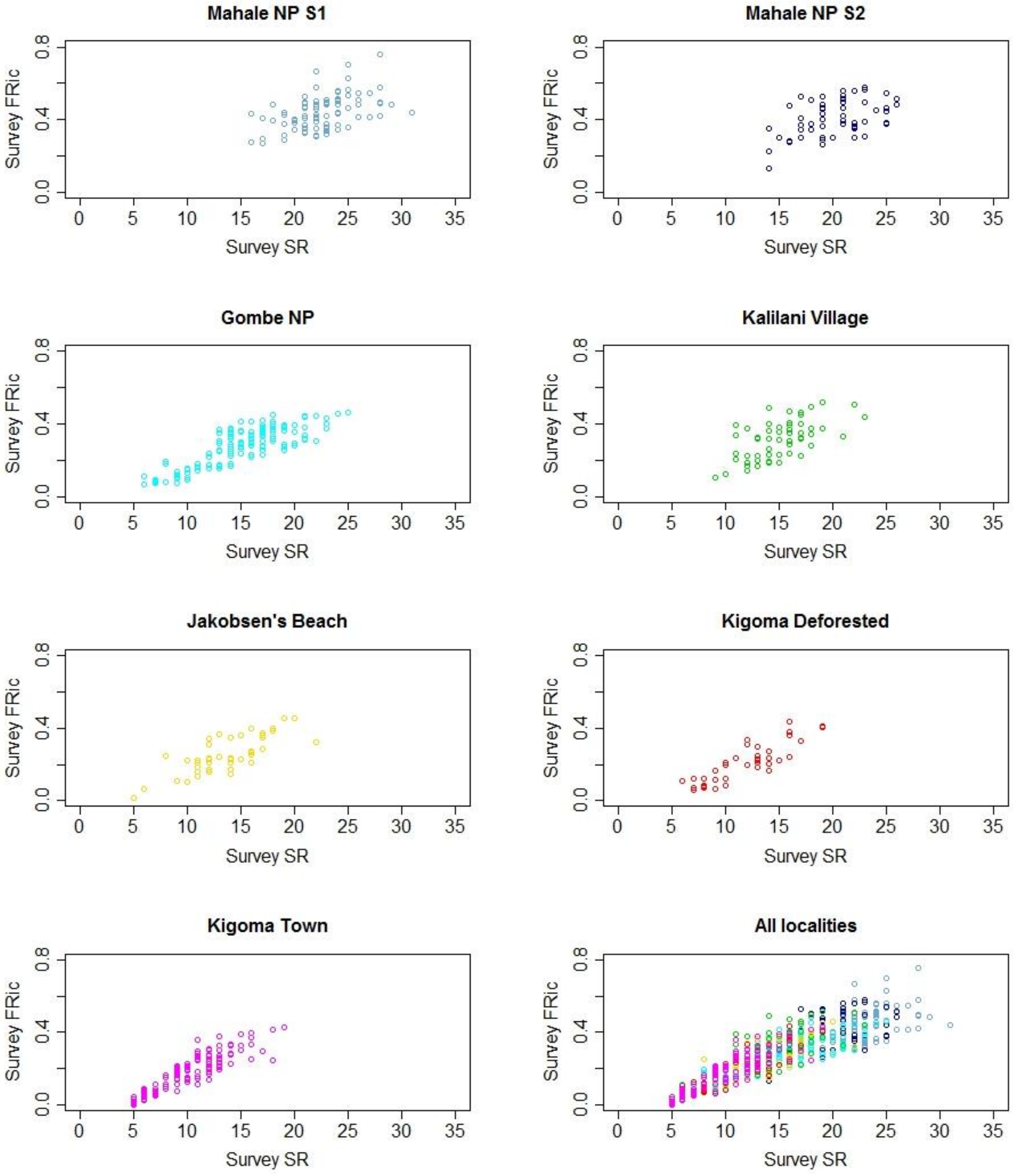


Figure 3.2a. Relationship between survey species richness and survey landmark only functional richness for all localities.

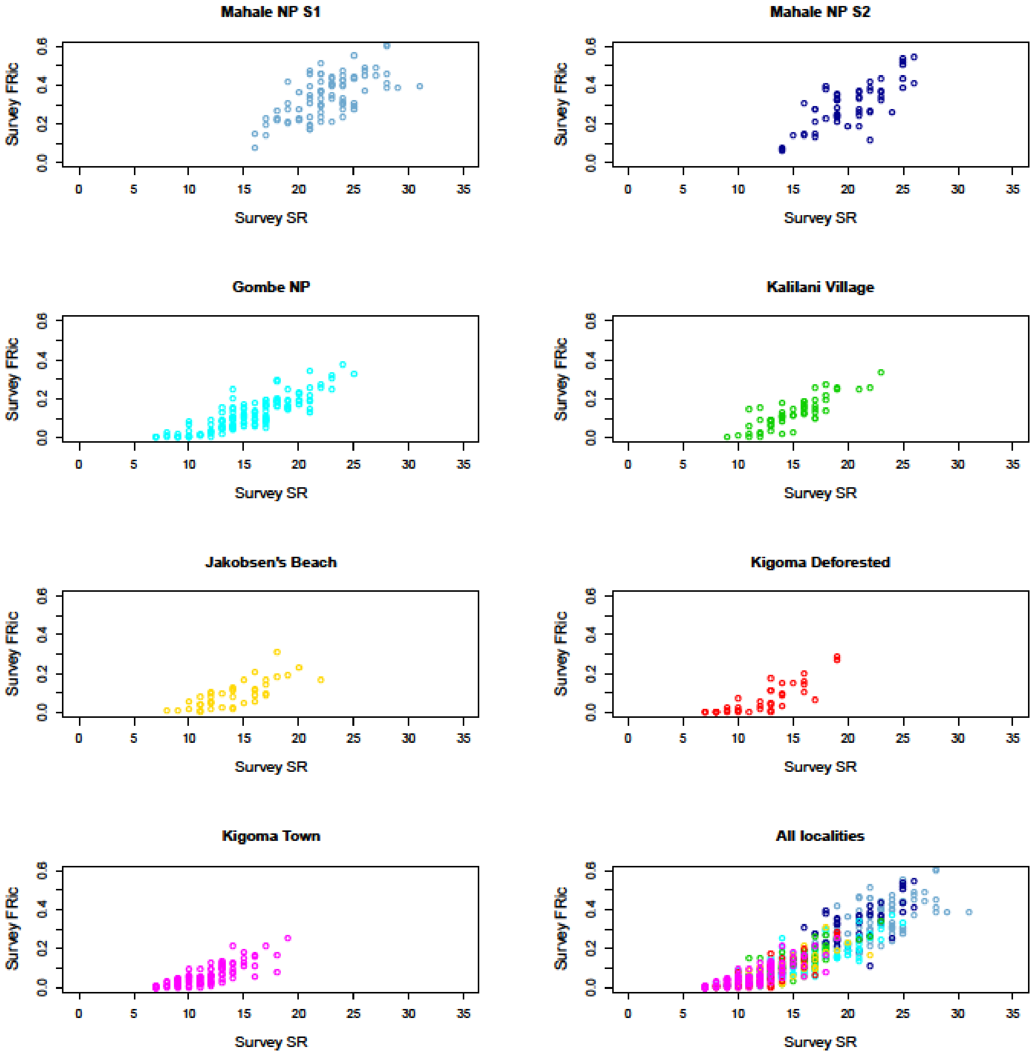
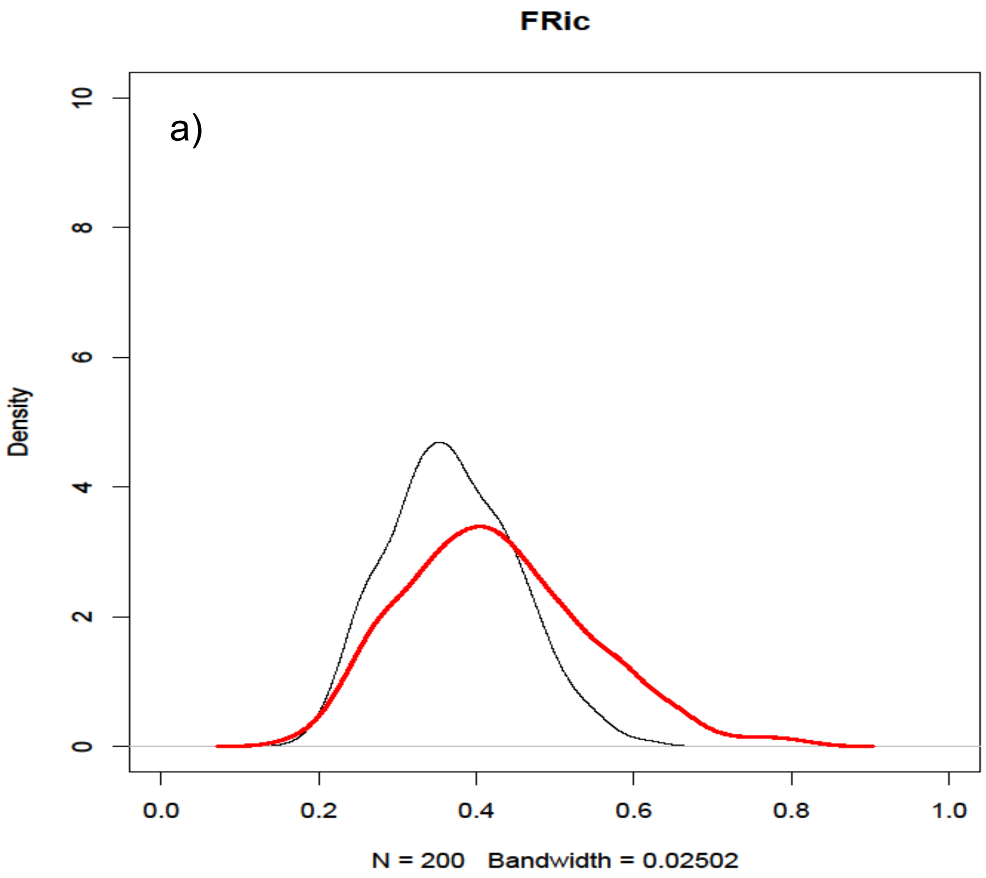
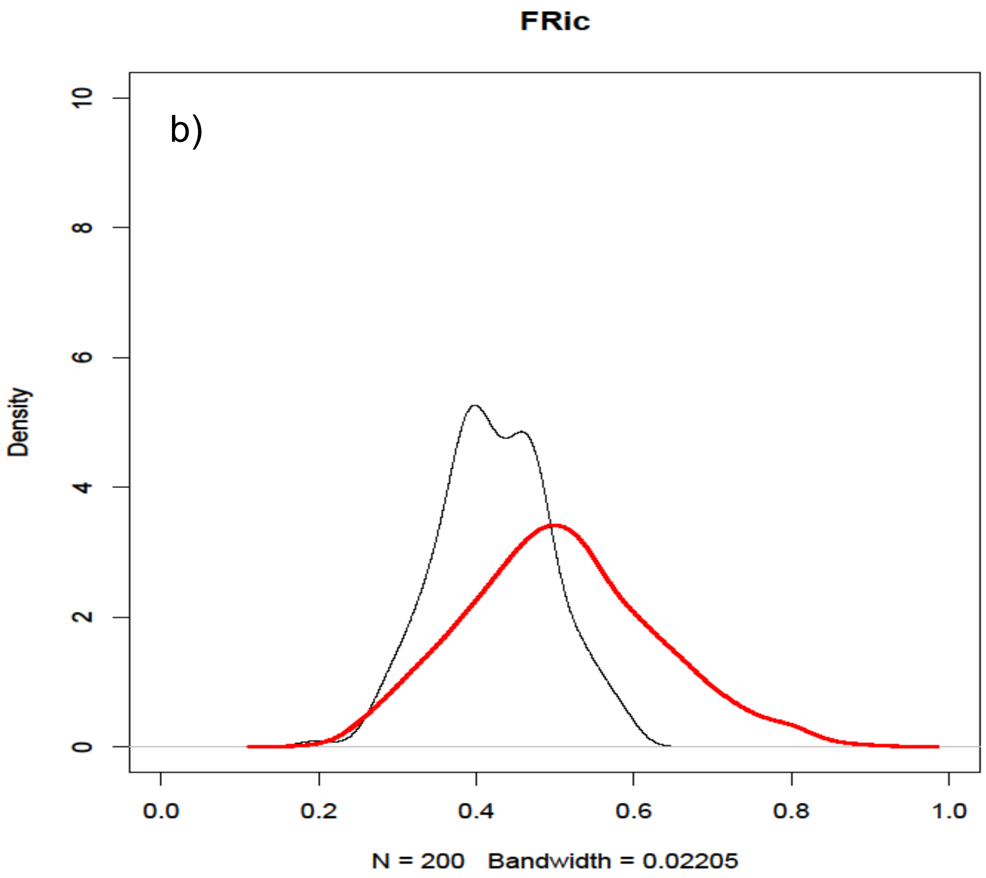


Figure 3.3b. Relationship between survey species richness and survey landmark and body size functional richness for all localities.

When community composition at each locality was split into feeding and tribal groups the landmark only FRic values of all groups were no different to the null expectation at all localities (Table S3.5 and S3.6). Therefore, particular tribal or feeding groups do not appear to be driving the overall locality FRic results. In terms of feeding groups, when the power test was simulated against herbivores, only 1.5 - 3.5% of biased communities could be distinguished from the null model in Kigoma Town, Gombe NP and Mahale NP S1 (Figure 3.3). Therefore, it seems a pressure against herbivores (as seen outside national park with species diversity) results in similar FRic as if there was neutral community assembly at the three localities. With regards to uniqueness, when the communities were weighted by ranking biased for and against the most unique species over all landmark only PC axes, a much higher percentage of communities had higher and lower FRic than random community assembly. When biased towards functional uniqueness, 42% of communities in Kigoma Town, 44.5% of communities in Gombe NP, and 67% of communities in Mahale NP S1 had higher FRic than expected. When biased against functional uniqueness, 92.5% of communities in Kigoma Town, 85.5% of communities in Gombe NP, and 99% of communities in Mahale NP S1 had lower FRic than expected. Therefore, the power test suggests it is possible for community FRic to differ from random, but only if an extreme weighting is applied based on the inclusion or exclusion of the most unique species. Additionally, the number of species in a community can influence whether uniqueness (over all landmark only PC axes) biased FRic is more or less likely to differ from the random expectation given SR (Table S3.7), with community FRic more likely to differ from random at higher species richness when biased both towards and against uniqueness rank.


FRic
a)
Density
0
2
4
6
8
10
0.0
0.2
0.4
0.6
0.8
1.0
N = 200   Bandwidth = 0.02502


FRic
b)
Density
0
2
4
6
8
10
0.0
0.2
0.4
0.6
0.8
1.0
N = 200   Bandwidth = 0.02205

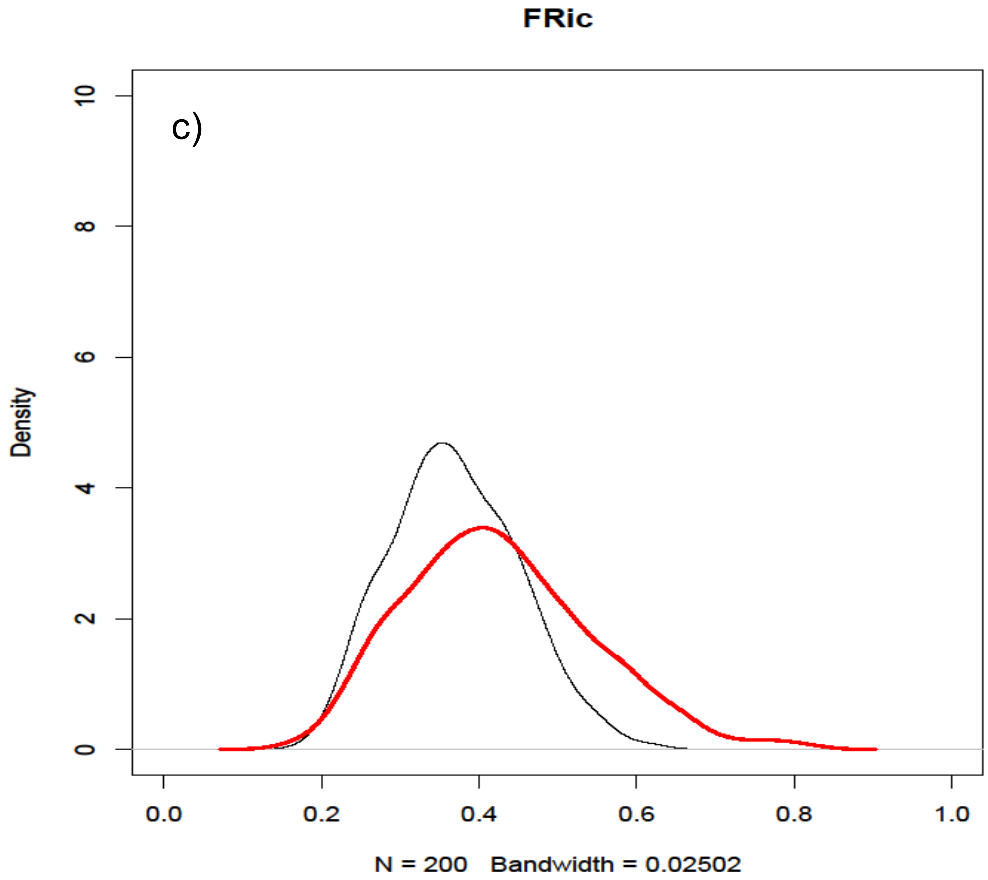


Figure 3.4. Density distribution of FRic biased against herbivore species compared to null FRic for a) Mahale NP S1, b) Gombe NP, and c) Kigoma Town. Red lines indicate the biased simulations and black lines indicate the null model.

3.4.2 Phylogenetic diversity

At the locality level PD is higher in protected areas than unprotected (Table 3.3). Additionally, at the locality level the net relatedness and nearest taxon index are as expected at all localities given SR, however, although not significant, protected areas appear more phylogenetically dispersed than unprotected areas (Table 3.3). At the survey level PD is similarly higher in protected areas than unprotected, especially at Mahale NP, and survey SR is strongly correlated to survey PD (Table 3.3 and Figure

3.4). When PD was compared across surveys within localities the abundance weighted mean pairwise and nearest taxon phylogenetic distance were very similar at all localities. Consequently, there was no difference in the mean species phylogenetic distances between survey pairs among localities, as well as no difference in the mean phylogenetic distance from each species to its closest relative between survey pairs among localities.

Table 3.4. Phylogenetic diversity (PD) indices calculated from the 70 species tree at all localities, with the number of surveys, locality species richness (SR), and mean survey SR indicated. Locality alpha PD includes Faith's PD, the net relatedness index (NRI) the nearest taxon index (NTI). NRI and NTI are calculated from the standardised effect sizes of the mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) from 999 random simulations, with no significantly phylogenetically clustered (positive values) or dispersed (negative values) values reported. Survey alpha diversity includes the mean survey Faiths PD and Pearson correlations coefficient with survey SR (Survey SR PD), with significant relationships from linear regressions starred. Beta FD was calculated within localities based on survey species abundance, using MPD and MNTD indices.

				ALPHA					*BETA*	
	Surveys	**SR**	**Survey SR**	**PD**	**NRI (SES**	**NTI (SES)**	**Survey PD**	**Survey SR PD**	**MPD**	**MNTD**
Mahale NP S1	83	67	24	264	-0.72	-0.08	118	0.73*	15.2	3.23
Mahale NP S2	55	60	22	239	-0.57	-1.41	111	0.89*	15.7	3.28
Gombe NP	138	51	16	212	-0.73	1.53	83	0.90*	15.4	3.35
Kalilani Village	56	47	16	204	0.28	0.42	83	0.92*	15.2	2.88
Jakobsen's Beach	42	42	15	184	0.40	-0.63	80	0.86*	14.8	3.3
Kigoma Deforested	42	42	13	175	0.82	-1.08	71	0.96*	15.6	5.08
Kigoma Town	134	43	10	194	1.63	1.35	56	0.95*	13.1	4.6

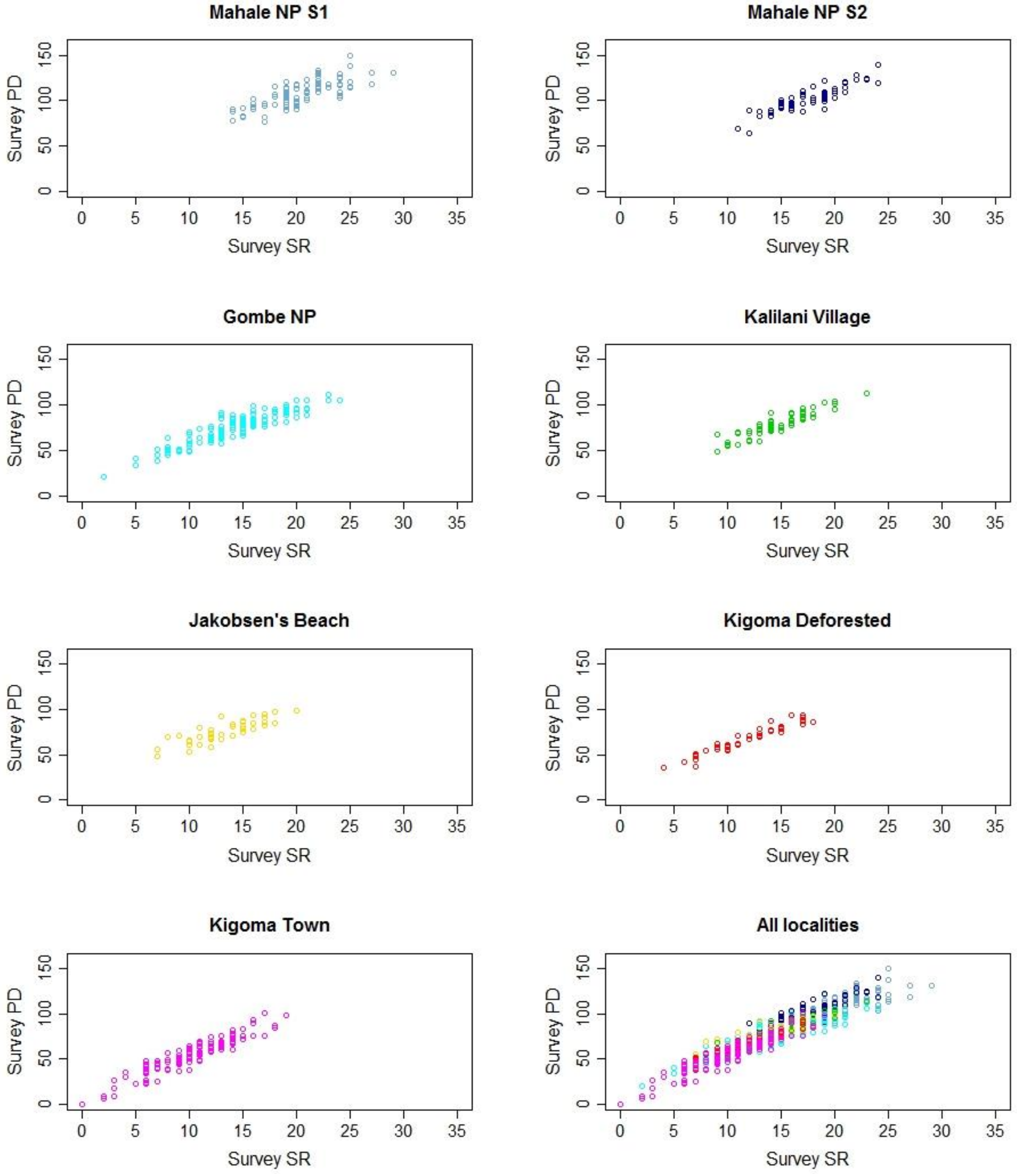


Figure 3.5. Relationship between survey species richness and survey phylogenetic diversity for all localities.

3.5 Discussion

Here we show protected areas contain between 78-83% of LT rocky shore cichlid FD (or between 70-83% when body size is considered), as well as higher FD and PD than unprotected areas. Additionally, due to SR influencing FD and PD at all localities regardless of protection status, protected areas have higher FD and PD because they have more species. Correspondingly unprotected areas have lower FD and PD because human impact is reducing species. Consequently, protecting LT cichlid species diversity appears to be conserving morphological diversity and likely ecosystem functions.

3.5.1 The relationship of species diversity with other components of biodiversity

Our FD results are similar to the species diversity results reported by Britton *et al.* (2017) with higher diversity at protected localities and surveys, most likely because SR is linked to FRic. Additionally, the species and functional diversity abundance-based measures show a similar pattern, with FDis and FEve not higher in protected areas, possibly because abundance is a more variable measure. The beta functional diversity results differ from beta species diversity, with the proportion of loss similar at all localities, regardless of protection, although FBeta is higher in unprotected areas, which is comparable to the pattern found with species diversity. Furthermore, human impact is affecting PD in the same way as functional and species diversity, by reducing species. Locality PD patterns are consistent with those expected given locality SR, which is similar to FD results. Although PD in protected areas is more dispersed, possibly because niche processes such as competitive exclusion may be in some way contributing to community composition. These results mirror the zeta species diversity results reported in Britton *et al.* (2017) with possible niche processes contributing to community assembly in protected areas. However, attributing community assembly to niche processes such as competition may not be accurate because there is evidence that competition can lead to both closely and distantly related taxa being excluded (Mayfield & Levine, 2010). To our knowledge this is the first time the FD and PD of a protected, species rich tropical lake system has been investigated. However, we surveyed just rocky shore cichlids, and results may differ if other fish radiations in the lake such as catfish and mastacembelid eels were considered. Furthermore, analysing the FD and PD of invertebrate radiations of LT gastropods and ostracods could result in different relationships between the facets of diversity.

All species analysed for FD have similar uniqueness values of between 0.05 and 0.15 (when analysed across PC's and without body size), resulting in a lack of functional redundancy, which could explain why SR is linked to FRic. The lack of redundancy may be due to the fact that we only analysed data at the sub family level of a recently diverged group, whereas surveying at higher taxonomic levels is likely to yield a greater range of functional uniqueness values, which may cause FD not to be linked to SR. This has been demonstrated in taxonomically diverse communities (Flynn *et al.*, 2009; Pakeman, 2011; Chapman *et al.*, 2018), however patterns of FD consistent with those expected given SR do occur in taxonomically diverse bird communities in protected sub-tropical forests (Luck *et al.*, 2013; Cottee-Jones *et al.*, 2015). Furthermore, neutral processes could be responsible for community assembly in LT cichlids (Janzen *et al.*, 2017), which may explain why in our study community composition based on morphology was no more likely than a random community composition with the same SR. However, our power test with biased models demonstrate that even with a pressure, such as biasing against herbivores, only a handful of the 200 simulated communities have higher FRic than expected given SR. Therefore, null models may not be good at detecting non-neutral signal in cichlid communities, based on a realistic pressure in LT. Nevertheless, it is possible for FRic in our communities to differ from the null expectation given SR, however the community has to be weighted by rank in favour of the most or least unique species. Then only when the most unique species are not selected, do the biased communities FD consistently differ from those expected given SR.

3.5.2 LT protected areas have higher cichlid diversity

We demonstrated the current protected area network in LT which conserves species diversity (Britton *et al.*, 2017) is successful for conserving FD and PD, and identifying other areas of high species diversity would be a positive move to conserve all three components of LT rocky shore cichlid diversity. A high level of congruence between freshwater fish taxonomic diversity, PD and FD in areas of conservation priority has been demonstrated before (Strecker *et al.*, 2011). However, not all studies show protected areas are effective at conserving different aspects of biodiversity. A study of European bird taxonomic diversity, PD and FD, found taxonomic diversity is overrepresented in protected areas, whereas FD is under represented (Devictor *et al.*, 2010). In Mediterranean fish communities the current protected area network is sometimes no better than a random designation at conserving species diversity, as well as FD and PD (Guilhaumon *et al.*, 2015). Furthermore hotspots of Mediterranean fish taxonomic diversity are congruent with the current protected area network, but hotspots of functional and phylogenetic diversity are not (Mouillot *et al.*, 2011). In a range of modelled communities, under certain biological scenarios, targeting PD can protect less FD than random, so the relationship between FD and PD could be an avenue for further study (Mazel *et al.*, 2017). Therefore, targeting SR is not suitable for conserving FD and PD in all ecosystems, and ideally comprehensive biodiversity assessments should be carried out when selecting new protected areas.

Although protected areas in LT are conserving FD, the low variation in functional uniqueness values indicate a lack of redundancy, which means LT FD is vulnerable if species are lost. In contrast, Touissant *et al.* (2016) concluded temperate freshwater fish are more vulnerable than tropical species, however their study was at the global scale so analysed one individual per species and used traits instead of geometric morphometrics to define FD. Additionally, their conclusions have been examined by Vitule *et al.* (2017), who state conservation action should be focused in vulnerable tropical freshwater regions. Therefore, due to a lack of functional redundancy in LT's protected areas, they should be considered functionally vulnerable and continue to be protected.

3.5.3 Limitations

In this study we define FD as the 2D shape diversity of key morphological landmarks that reflect traits, however these traits may not always directly relate to the functions performed in a complex ecosystem like LT. Detailed 3D measurements of cichlid morphology such as the oral and pharyngeal jaws (Janzen *et al.*, 2017), in addition to traits such as feeding behaviour (Yamaoka, 1983), may be needed to identify a morphological signal where FD differs from what is expected given SR. Moreover, the interpretation of FD influences its relationship with SR (Halpern & Floeter, 2008); we calculate FD as FRic convex hull which is closely linked to SR (Villéger *et al.*, 2008) and may not be the best proxy for FD because this method is more sensitive to extreme morphologies (Legras *et al.*, 2018). Additionally other studies that have found FD to differ from what is expected given SR have been measured over a larger spatial scale (Flynn *et al.*, 2009), whereas our study assesses one LT coastline. However, we note that intra species differences in cichlid FD are possible, even while focusing just on LT (Maderbacher *et al.*, 2008). Finally the validity of null models in detecting assembly in observed communities has been questioned, due to differing species pools affecting the magnitude of FD (de Bello, 2012). Our results demonstrate there is a higher chance of FD differing from the null expectation in 200 uniqueness biased communities at higher species richness. However, in our study we have one pooled observation for species rich localities, therefore a time series of repeated observations at a locality may be needed to identify a signal where FD differs from the null expectation.

3.5.4 Conclusions

The current protected area network in LT is conserving cichlid FD and PD because SR is being protected, nevertheless a loss of species could result in a loss of ecosystem functions, so management of the existing protected areas should continue. Consequently, it is also important to protect other species rich areas of the lake not in national parks, to ensure the extraordinary diversity of cichlid fishes in Lake Tanganyika are not lost. Additionally, although our results are specific to LT cichlids, we demonstrate protected areas successfully conserving species can also protect other components of biodiversity such as morphological variation and functional diversity. Therefore, our results indicate in the absence of a comprehensive biodiversity assessment given limited conservation resources, SR should continue to be used as an indicator of biodiversity.

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

4.1 Abstract

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 cichlid fishes from a biodiversity hotspot, Lake Tanganyika, which comprises 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 different trophic groups and feeding strategies within the hyper-diverse rocky shore cichlid fish community, by determining nitrogen and carbon stable isotope values, and estimating stomach sediment proportions at three sites with differing levels of human impact.

We found clear differences in the carbon stable isotopes values between benthic and column feeding species across all sites. Nitrogen stable isotope values were significantly higher at the most disturbed (urbanised) site for benthic feeding species, whereas there was no difference in nitrogen stable isotopes between sites for the water column feeding trophic group. Stomach contents revealed the elevated δ15N values were unlikely 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.

This study highlights that multiple sources of pollution are having differing effects across species within a diverse fish community. Results support our previous study showing herbivore species to be most affected by human disturbance and make the link to pollution much more explicit.

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. As elevated δ15N values at disturbed sites suggest isotopic niche is not always comparable to ecological niche, we highlight that care needs to be taken when selecting data for evolutionary studies.

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.

4.2 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 *et al.*, 2002), with both stressors implicated as threats to freshwater species (Richter *et al.*, 1997).

Anthropogenic impacts over the last half century have led to higher levels of nitrogen deposition into aquatic ecosystems (Vitousek *et al.*, 1997) 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 (Camargo & Alonso, 2006), in addition to habitat level effects such as eutrophication (Smith, 2003).

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 δ^{15}N values (Cabana & Rasmussen, 1996; Anderson & Cabana, 2005; Schlacher, Mondon & Connolly, 2007; Vermeulen *et al.*, 2011; Kelly *et al.*, 2016). Consequently δ^{15}N values have been proposed as an indicator for detecting anthropogenic nitrogen in aquatic ecosystems (Costanzo *et al.*, 2001; Lake *et al.*, 2001; Vermeulen *et al.*, 2011). Environmental stress can also increase individual variation in δ^{15}N values in invertebrates in controlled conditions, possibly because of more variable growth rates (Gorokhova, 2018). One of the advantages of measuring δ^{15}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 *et al.*, 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 *et al.*, 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, Piazzi & Benedetti-Cecchi, 2007).

4.2.1 Pollution of a global aquatic hotspot

One of the world's most diverse freshwater ecosystems is East Africa's Lake Tanganyika (LT), which has seen major increases in anthropogenic stressors around its shores. The lake is host to high levels of biodiversity (~1470 animal species) and endemicity, in which evolutionary radiations of multiple lineages have diversified in situ (e.g. Day, Cotton & Barraclough, 2008; Meyer, Matschiner & Salzburger, 2015). Lake Tanganyika is the main source of income and nutrition for many human communities (Mölsä *et al.*, 1999; Tierney *et al.*, 2010), who are heavily concentrated around its shores, and populations in this region are suggested to be amongst the fastest growing in the world (Cohen, Kaufman & Ogutu-Ohwayo, 1996). Although still the least disturbed of the great lakes of the world (Dobiesz *et al.*, 2010), Lake Tanganyika is especially vulnerable to pollution due to the slow rate of water renewal in its effectively closed system (Coulter & Mubamba, 1993), which 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). Higher levels of chlorophyll *a* and nitrogen are reported in waters from disturbed areas of the lake (Chale, 2003; McIntyre *et al.*, 2005), and eutrophication has been reported in Kigoma Bay (Chale, 2003). Various pollutants with trace metals such as lead, mercury and arsenic have also been found in water, sediment and fish samples (Sindayigaya *et al.*, 1994; Chale, 2002; Campbell *et al.*, 2008), and toxic contaminants such as organochlorine pesticides and polychlorinated biphenyls have also been identified in several cichlid fish species (Manirakiza *et al.*, 2002).

Increased erosion and sediment transport is a major threat to the LT ecosystem, primarily caused by deforestation of the lake shore's miombo woodland (Cohen *et al.*, 1993a; Coulter & Mubamba, 1993; Alin *et al.*, 1999), but this also occurs via deforestation along rivers draining into the lake (Eggermont & Verschuren, 2003). Large-scale deforestation has been caused by increases in agricultural land-use and burning of wood for fuel. This, combined with poor infrastructure and lack of erosion control measures have greatly increased sediment discharge into the lake, particularly in regions with steep rift basins such as around the Kigoma region in the northern lake basin (Cohen *et al.*, 1996; Alin *et al.*, 2002). 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.

Lake Tanganyika's littoral and sublittoral zones contain highly diverse communities of endemic fishes, molluscs and crustaceans (e.g. West & Michel, 2000; Day & Wilkinson, 2006; Marijnissen *et al.*, 2006; Day *et al.*, 2008; Brown *et al.*, 2010; Peart *et al.*, 2014). Cichlid fishes, the most diverse animal group, dominate the rocky littoral zone (~65% of all cichlid species), with upwards of 60 species recorded at some locations (Britton *et al.*, 2017). This high diversity in the near shore zone exposes many cichlid species to human impacts on the lake shore (Alin *et al.*, 2002; Britton *et al.*, 2017). A recent study showed the multi-faceted effect of human disturbance on the cichlids with a clear decline in alpha diversity with increasing human disturbance, especially among herbivorous species within the Tropheini tribe. On the other hand there was a positive relationship between (beta diversity) nestedness across surveys and human disturbance implying rare or specialist species were being lost, and the functional form of zeta 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 $\delta^{15}N$ values of sediment, and across a variety of taxonomic groups, with mixed results. Alin *et al.* (2002) reported higher sediment rates, and higher $\delta^{15}N$ values of sedimentary organic matter from a disturbed site compared to a nearby National Park (Gombe) in the Kigoma region, likely due to increasing inputs of terrestrial organic matter from shoreline erosion through deforestation. Elevated $\delta^{15}N$ values in gastropods from village shorelines from this region was 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 (McIntyre, Michel & Olsgard, 2006; Corman *et al.*, 2010), however due to the open nature of the littoral zone, phytoplankton are rapidly washed away. In contrast, diversity and $\delta^{13}C$ and $\delta^{15}N$ values of crab species from Kigoma were similar at sediment impacted and reference sites (Marijnissen *et al.*, 2009) with dietary breadth potentially contributing to their resilience to sedimentation, based on the wide range of $\delta^{13}C$ 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 as they contain a wide range of feeding strategies across multiple trophic levels.

4.2.2 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 $\delta^{15}N$ values and variance in species at urban sites compared to non-urban sites. We expected all cichlids, but particularly benthic herbivores to have higher $\delta^{15}N$ 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 $\delta^{15}N$ 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.

4.3 Materials and methods

4.3.1 Study sites

We focused on three sites, TAFIRI Bay, Kigoma Deforested, and Kalilani Island, in the Kigoma region of Tanzania (Figure 4.1). 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 4.1).

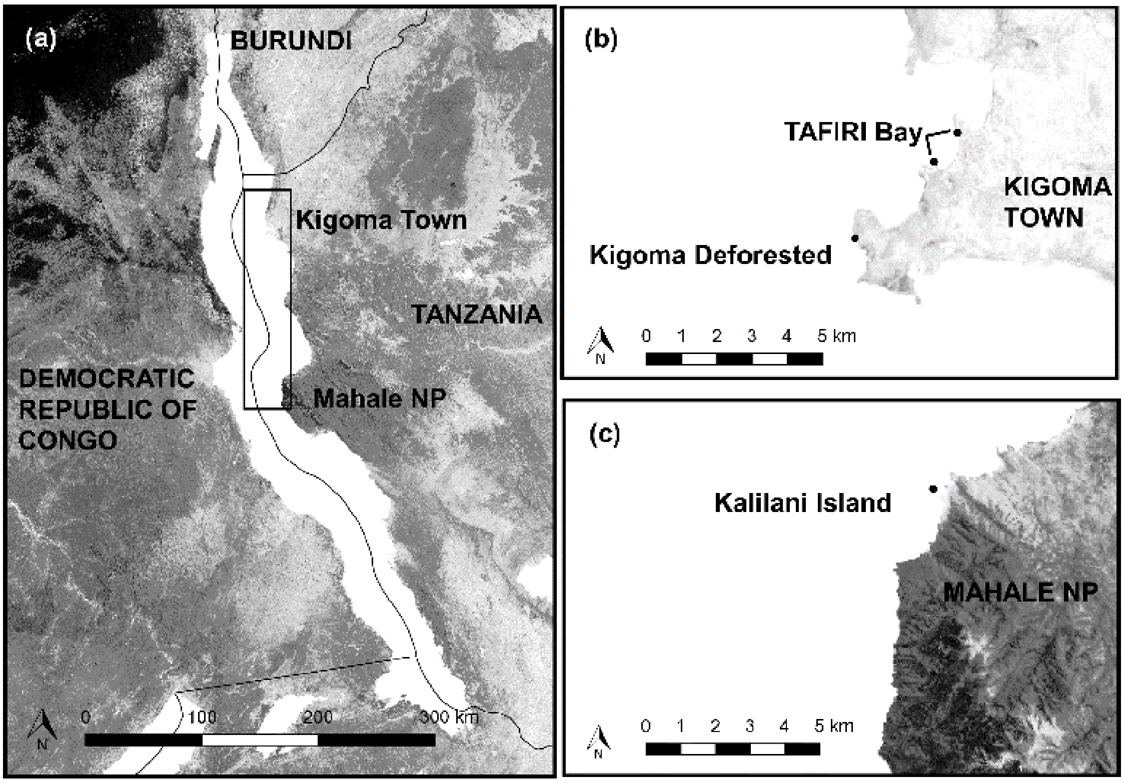


Figure 4.1. (a) Map of Lake Tanganyika, showing study location. (b) TAFIRI Bay and Kigoma Deforested sites from the northern basin. (c) Kalilani Island site from the central basin. The background of all three maps represents tree cover from 0% white - 100% black (Hansen *et al.*, 2013).

Table 4.1. 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 1km of the shoreline of the distance spanning collection sites. †(Hansen *et al.*, 2013); ‡(Linard *et al.*, 2012)

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

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 100m^2 (Linard *et al.*, 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 100m^2 (Linard *et al.*, 2012), and a reduction in tree cover to less than 10% canopy density (Hansen *et al.*, 2013). Two sampling points within TAFIRI Bay were selected, 1) 4°87.879'S, 29°62.169'E in the northern bay; 2) 4°88.652'S, 29°61.566'E, located 900m south west, in the southern bay.

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

Kalilani Island (6°02.023'S, 29°74.243'E) is a small 1 square km uninhabited island with ~46% tree canopy density (Hansen *et al.*, 2013), located 125km south of Kigoma Town. It is situated approximately 300m north of the border of Mahale National Park, a pristine area that protects 1,613 square km of lake shore forest (Sweke *et al.*, 2013) and 96 square km of the lakes aquatic littoral habitat (West, 2001). It is also situated 200m west of Kalilani village, a small fishing village covering 2km of shoreline. Kalilani Village has a tree cover of approximately 25% canopy density (Hansen *et al.*, 2013; Britton *et al.*, 2017), and a population of less than three people per 100m^2 (Linard *et al.*, 2012; Britton *et al.*, 2017) (see Chapter two supporting information Table S2.1).

4.3.2 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 clades 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 0-15m 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 c100 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 (Minagawa & Wada, 1984; Hobson & Welch, 1995; Kiriluk *et al.*, 1995). Similar sized individuals were targeted since total individual length has been positively linked to $\delta^{13}C$, and to a lesser extent $\delta^{15}N$ 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 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 *et al.*, 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 two months before being processed in the lab. Therefore, 40 cichlid individuals (including at least one individual of each of the ten 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).

4.3.3 Stable isotope analysis

White muscle tissue from the left dorsal flank of each fish was oven dried at 55°C for 48 hours, 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 $\delta^{13}C$ values (Schlacher & Connolly, 2014). Samples were homogenised to a powder using a pestle and mortar for consistency. Fish and invertebrate samples were weighed to ~0.6mg and algae samples to ~3mg 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 8 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* individual stored at Newcastle University, UK was analysed on each run to ensure results generated in 2015 and 2017 were comparable. Stable isotope ratios are expressed in parts per mil (‰) with the δ symbol using the equation: δ (‰) = (R sample/R standard – 1) x 1000, where R = $^{15}N/^{14}N$ or $^{13}C/^{12}C$.

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 ten cichlid species: 128 and 43 samples, TAFIRI Bay, 2015, 2016 respectively; 138 samples, Kalilani Island, 2015; 105 samples, Kigoma Deforested, 2016 (Table S4.1). Sun dried control samples included: 40 cichlid individuals from 9 species, and 62 baseline samples composed of 4 mollusc species, and 12 multispecies algae samples.

4.3.4 Corrections for lipid content and tissue preservation

Due to carbon isotope fractionation during lipid synthesis, a lipid normalisation was applied to the $\delta^{13}C$ values (Kiljunen *et al.*, 2006). A revised model [$\delta^{13}C' = \delta^{13}C + D$ x

(I + (3.9/1+287/Lipid proportion)] modified from McConnaughey & McRoy (1979) with updated parameters applicable to freshwater fish was used for the correction (Kiljunen *et al.*, 2006). The parameters, D = 7·018 ± 0·263 and I = 0·048 ± 0·013, are similar to other cichlid species (Gaye-Siessegger *et al.*, 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 $\delta^{15}N$ values were not modified because there is very little nitrogen in lipids. The baseline species were also not lipid corrected.

Ethanol preservation can affect $\delta^{13}C$ and $\delta^{15}N$ values (Correa, 2012). When the $\delta^{13}C$ values of sun-dried control samples were pooled between the four sites, there was a significant difference with ethanol preserved specimen $\delta^{13}C$ values, for both raw and lipid normalised values (Table S4.2). The pooled, lipid corrected, ethanol preserved $\delta^{13}C$ values and lipid corrected, air dried $\delta^{13}C$ values were plotted and a linear correction was applied to all cichlid ethanol preserved $\delta^{13}C$ values using the data fitted equation: $\delta^{13}C$ corrected = 1.0387 x $\delta^{13}C$ ethanol + 0.3758 (Kelly, Dempson & Power, 2006; Bugoni, McGill & Furness, 2008; Bicknell *et al.*, 2011). Post correction there was no difference in corrected $\delta^{13}C$ values and non-ethanol preserved $\delta^{13}C$ values (Table S4.2). As there was no systematic difference between pooled $\delta^{15}N$ values of ethanol preserved and air-dried tissues (mean difference of 0.212‰, with a paired t-test (t= 1.8833, p=0.0668), no ethanol correction was applied to $\delta^{15}N$, and raw $\delta^{15}N$ values were used for downstream analysis.

There was no systematic difference in *Gadus morhua* $\delta^{13}C$ values between 2015 and 2017, and only a small difference (0.116‰) between the mean $\delta^{15}N$ values of *G. morhua* (Table S4.3), suggesting stable isotope results are comparable between years. However, it has been reported $\delta^{13}C$ values decrease by over 1‰ in fish muscle tissue preserved in ethanol for six weeks, and longer preservation might increase variation (Arrington & Winemiller, 2002). Therefore the corrections applied to $\delta^{13}C$ mean fine scale differences in stable isotope values (<2‰) will not be used to make ecological inferences in this study, though $\delta^{13}C$ values can be used to differentiate between larger scale differences in habitats (e.g. Piola, Moore, & Suthers, 2006). Furthermore, baseline samples were not used to correct cichlid $\delta^{15}N$ 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 δ^{15}N values between sites prevented a reliable normalisation (Table S4.4).

4.3.5 Statistical analysis

To assess if the effects of land use disturbance varies with trophic position, δ^{15}N and δ^{13}C signatures were investigated with a global analysis. δ^{15}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, 2018). To investigate if trophic group δ^{15}N and δ^{13}C signatures differ between sites, the estimated mean trophic group δ^{15}N and δ^{13}C values were compared between all sites with a multiple comparison Tukey post-hoc tests in the emmeans R package v1.2.4 (Lenth *et al.*, 2018).

To further explore variation in δ^{15}N and δ^{13}C signatures between sites, a species level analysis of stable isotope values was conducted with a Generalised Linear Model (GLM) 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) (Table S4.5). Additionally, the estimated mean species δ^{15}N and δ^{13}C values between sites were compared with a multiple comparison Tukey post-hoc tests to assess which sites differ in terms of a species stable isotope values.

For all GLMM and GLM analyses, diagnostic plots of the residuals confirmed that the Gamma distribution was most appropriate choice for the link function for the δ^{15}N analyses whereas the Gaussian distribution was most appropriate for the δ^{13}C analyses.

4.3.6 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. Malins *et al.*, 1985, 1987; Davis *et al.*, 2012), although we note that it provides only a temporal snapshot of each individual's intake (Wagner *et al.*, 2009; Polito *et al.*, 2011). 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 Table S4.6 and S4.7) 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: (i) sediment; (ii) algae; (iii) fish scales; (iv) insects; (v) crustaceans; (vi) gastropods; (vii) fish; (viii) 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 $SI = 1 - 0.5(\sum|P_iA\text{-}P_iB|)$ 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 (LSD) 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.

4.4 Results

4.4.1 Nitrogen stable isotopes

All benthic feeding species and the water column feeding piscivore *Lepidiolamprologus elongatus* display significantly different mean δ^{15}N values between the urban site of TAFIRI Bay and the less disturbed sites (i.e. the non-urban sites of Kigoma Deforested, and the forested Kalilani Island) (Figure 4.2a and Table 4.2). In contrast the water column feeding planktivore *Neolamprologus brichardi* is the only species to show no difference in δ^{15}N values between TAFIRI Bay and both non-urban sites (Table 4.2). When δ^{15}N values are analysed by trophic group there are significant differences in estimated mean δ^{15}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 4.3).

The difference in δ^{15}N at urban and non-urban sites reveals a similar pattern for the baseline species, with benthic feeders more affected than filter feeders (Table S4.4). Additionally, the differences between baseline and cichlid δ^{15}N values ranged between 4‰ and 9‰ within trophic groups per site.

Table 4.2. Results of GLM Tukey's post-hoc tests to compare δ^{15}N and δ^{13}C values between sites for each species. 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 which is indicated in the table. P values highlighted bold indicate a significant difference.

δ^{15}N	**Estimate**	**SE**	**z**	***p***
Eretmodus cyanostictus				
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**
Lepidiolamprologus elongatus				
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**

Lobochilotes labiatus				
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**
Neolamprologus brichardi				
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**
Neolamprologus mondabu				
Kalilani Island - TAFIRI Bay 2015	0.06	0.008	7.315	**<0.0001**
Neolamprologus toae				
Kalilani Island - TAFIRI Bay 2015	0.042	0.002	19.116	**<0.0001**
Ophthamotilapia ventralis				
Kalilani Island - TAFIRI Bay 2015	-0.011	0.004	-2.907	**0.0036**
Petrochromis famula				
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**
Pseudosimochromis babaulti				
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**
Tropheus brichardi				
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
$\delta^{13}C$	**Estimate**	**SE**	**z**	***p***
Eretmodus cyanostictus				
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
Lepidiolamprologus elongatus				
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**
Lobochilotes labiatus				
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
Neolamprologus brichardi				
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**
Neolamprologus mondabu				
Kalilani Island - TAFIRI Bay 2015	0.142	0.577	0.247	0.8074
Neolamprologus toae				
Kalilani Island - TAFIRI Bay 2015	-1.006	0.148	6.972	**<0.0001**
Ophthamotilapia ventralis				

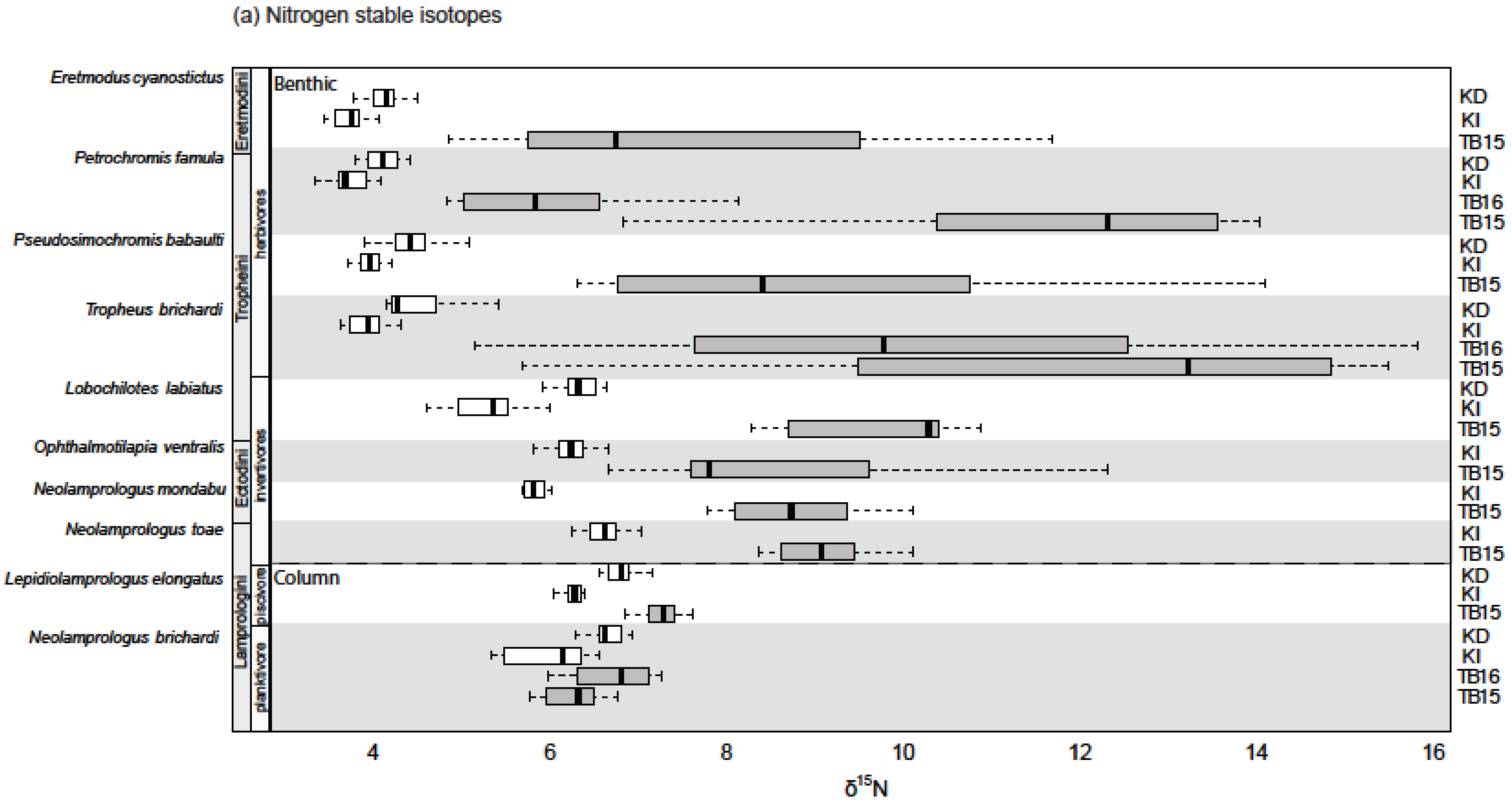
Kalilani Island - TAFIRI Bay 2015	-0.018	0.356	0.518	**0.6106**
Petrochromis famula				
Kigoma Deforested - Kalilani Island	1.267	0.43	-2.946	**0.0261**
Kigoma Deforested - TAFIRI Bay 2015	2.2	0.317	6.953	**<0.0001**
Kigoma Deforested - TAFIRI Bay 2016	0.603	0.281	2.147	0.1556
Kalilani Island - TAFIRI 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**
Pseudosimochromis babaulti				
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**
Tropheus brichardi				
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

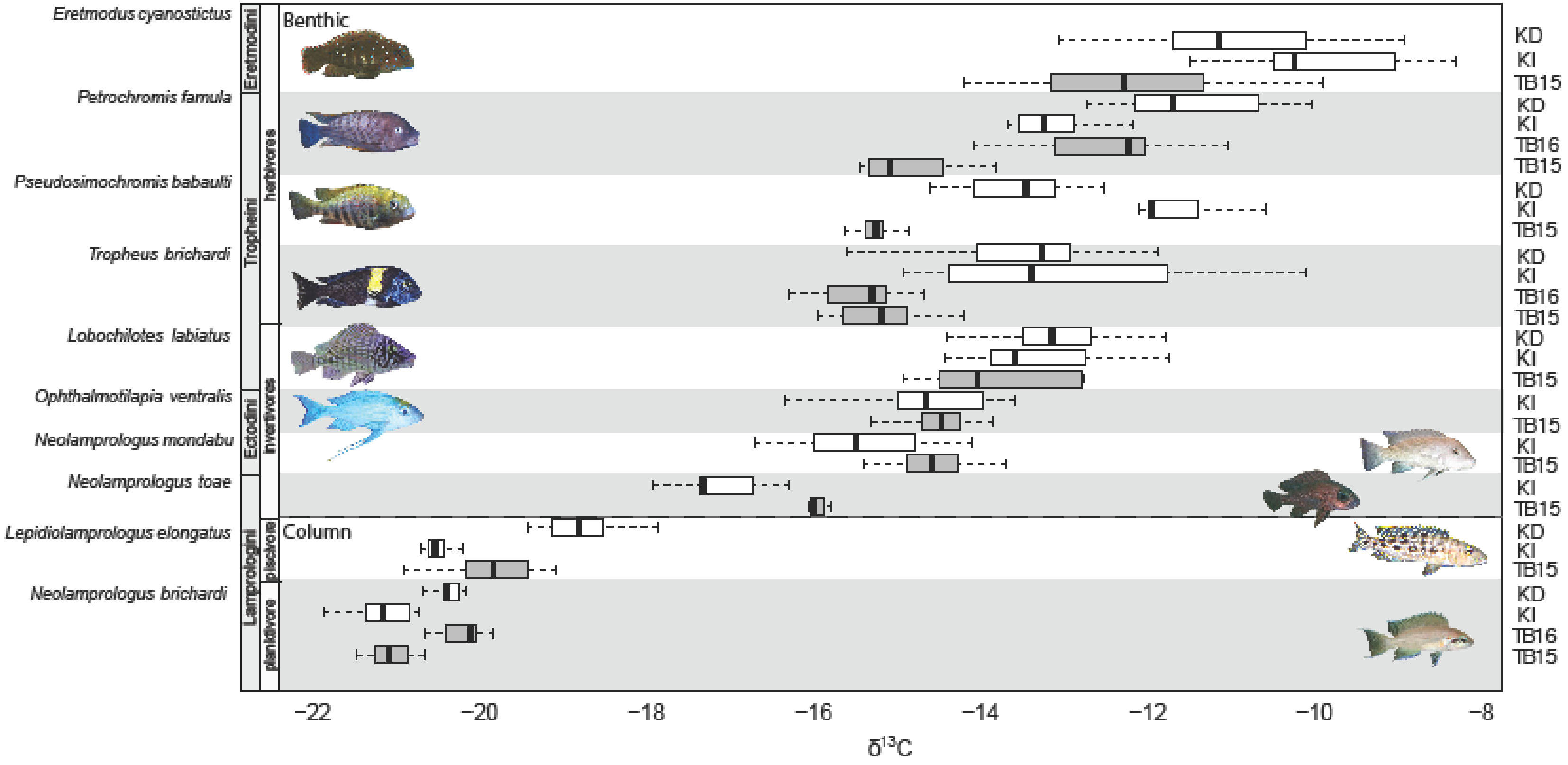
Table 4.3. Results of GLMM and Tukey's post-hoc tests to compare δ^{15}N and δ^{13}C values between sites for each trophic group. Kalilani Island was sampled in 2015 and Kigoma Deforested was sampled in 2016, whereas urban site TAFIRI Bay was sampled in both 2015 and 2016 which is indicated in the table. P-values highlighted bold indicate a significant difference.

$\delta^{15}N$	**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
δ^{13}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
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


(a) Nitrogen stable isotopes
Benthic
Column
Eretmodus cyanostictus
Petrochromis famula
Pseudosimochromis babaulti
Tropheus brichardi
Lobochilotes labiatus
Ophthalmotilapia ventralis
Neolamprologus mondabu
Neolamprologus toae
Lepidiolamprologus elongatus
Neolamprologus brichardi
Eretmodini
Tropheini
Ectodini
Lamprologini
herbivores
invertivores
piscivore
planktivore
KD
KI
TB15
KD
KI
TB16
TB15
KD
KI
TB15
KD
KI
TB16
TB15
KD
KI
TB15
KI
TB15
KI
TB15
KI
TB15
KD
KI
TB15
KD
KI
TB16
TB15
4
6
8
10
12
14
16
δ15N



(b) Carbon stable isotopes

Figure 4.2. (a) The median $\delta^{15}N$ 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 $\delta^{13}C$ 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 (IQR's) for the urban site TAFIRI Bay are shaded grey, and Kalilani Island and Kigoma Deforested IQR's are unshaded.

4.4.2 Carbon stable isotopes

There are clear differences between the mean δ^{13}C values of benthic and water column species (Figure 4.2b). All trophic group δ^{13}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 δ^{13}C values at TAFIRI Bay in 2016 compared to the non-urban sites (Table 4.3). In terms of the species level analysis, there are no consistent differences in mean δ^{13}C values between sites (Table 4.2), suggesting, unlike nitrogen isotopes, differences in carbon isotopes are not linked to human disturbance.

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

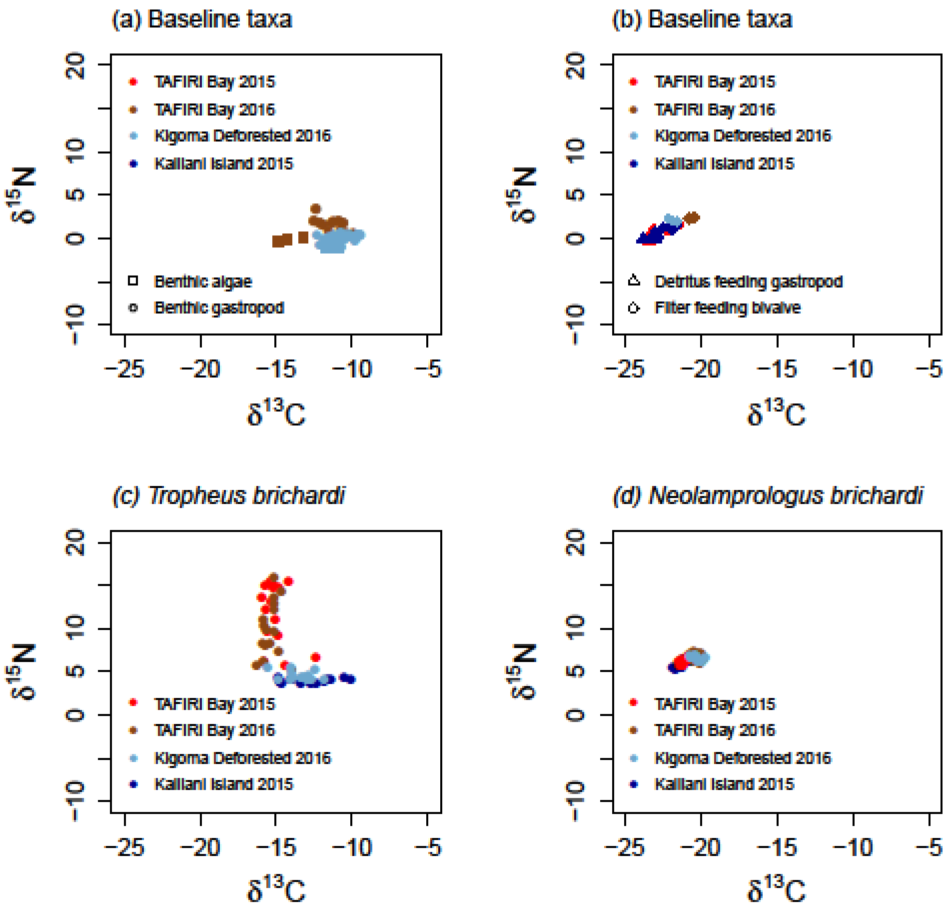


Figure 4.3. Stable isotope values for species collected at sites in 2015 and 2016. (a) Baseline samples including, benthic feeding species *Lavigeria grandis* and *Lavigeria nassa*, and benthic algae. (b) Baseline samples including, detritus feeding *Neothauma tanganyicense* and filter feeding *Pleiodon spekii*. (c) *Tropheus brichardi* (Tropheini), feeds on benthic algae. (d) *Neolamprologus brichardi* (Lamprologini), feeds on zooplankton in the water column.

4.4.3 Stomach content analysis

Variation in dietary overlap broadly mirrored the differences in δ^{15}N values where species with the highest δ^{15}N values show the greatest dietary overlap, and vice versa (Figure 4.4 and Table S4.8). 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

δ^{15}N values we can assume that diet did not play a role in the increased δ^{15}N values at TAFIRI Bay. When these differences are visualised, multidimensional scaling shows clustering of herbivores and clustering of non-herbivores (Figure S4.1), however within the herbivores the species cluster by site. In terms of individual dietary components (Table S4.6 and S4.7) a significantly higher proportion of sediment was found in the stomachs of four cichlid species at TAFIRI Bay compared to Kalilani Island in 2015 (Table S4.8). These species included three of the four herbivores, encompassing multiple behavioural adaptations for harvesting algae: *Eretmodus cyanostictus* (“scraper”), *P. famula* (“grazer”), *T. brichardi* (“browser”) as well as the planktonic column feeding *N. brichardi* (Table S4.8). *Pseudosimochromis babaulti* (“browser”) had a higher proportion of sediment in its stomach at Kalilani Island than the other herbivores, likely because it often feeds in sediment-rich areas of the rocky shore (Koblmüller *et al.*, 2010). We suggest it is the extra stomach sediment in the urban site that leads to the herbivores clustering out according to site (Figure S4.1). 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 Analysis of Similarities.

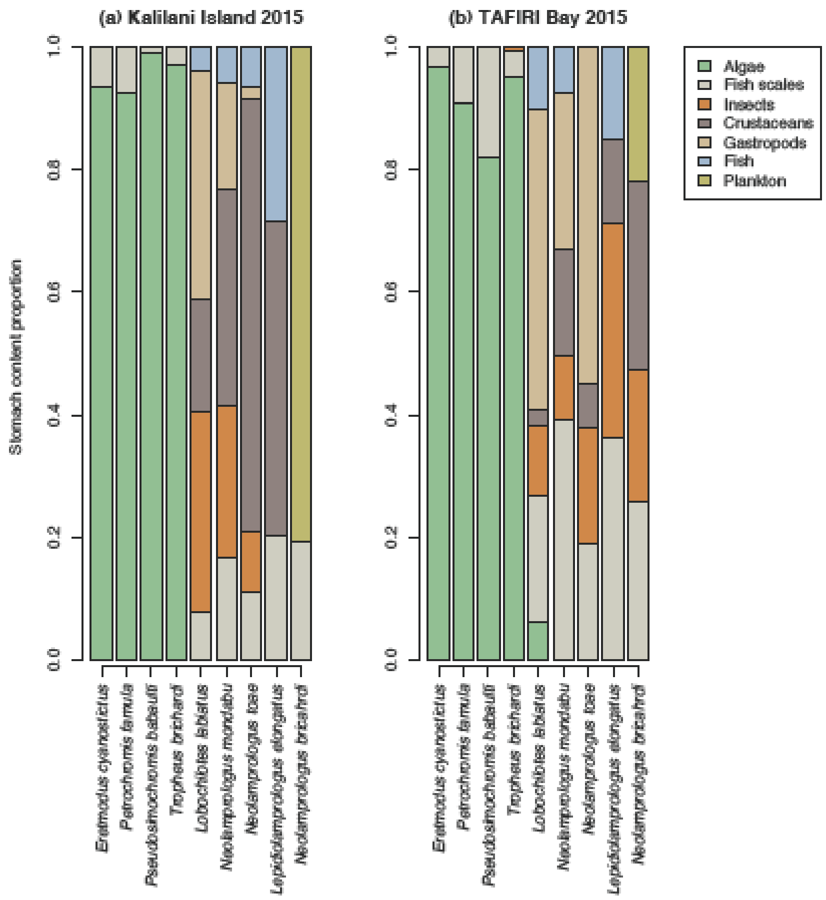


Figure 4.4. Stomach content proportions for the nine species sampled at (a) Kalilani Island 2015 and (b) TAFIRI Bay 2015. Stomach contents include all organic items and exclude the sediment category.

4.5 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; Vermeulen *et al.*, 2011; Kelly *et al.*, 2016), 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 $\delta^{15}N$ values in individuals sampled from an urban area than those at non-urban areas (Figures 4.2 and 4.3, and Tables 4.2 and 4.3). 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 4.2 and 4.3, and Tables 4.2 and 4.3). 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 $\delta^{15}N$ 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 *et al.*, 2003), and changing resource availability (Njiru *et al.*, 2004), while reduction of habitat availability is suggested to have caused dietary change in the Arctic charr (*Salvelinus alpinus*) from Lake Windermere (Corrigan *et al.*, 2011). However, we could rule out dietary shifts as the cause of elevated $\delta^{15}N$ values, since aside from an intra trophic level shift in *N. toae* (Tables S4.6 and S4.7) 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 (Tables S4.6 and S4.7) could however be responsible for the higher $\delta^{15}N$ 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 $\delta^{15}N$ (Vermeulen *et al.*, 2011). The higher $\delta^{15}N$ 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 $\delta^{15}N$ is subsequently biomagnified up the food chain (Cabana & Rasmussen, 1996).

We suggest that the elevated $\delta^{15}N$ is from anthropogenic nitrogen loading, and likely reflects the high $\delta^{15}N$ of human sewage, as reported in other studies focused on a variety of aquatic systems (Cabana & Rasmussen, 1996; Schlacher *et al.*, 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 $\delta^{15}N$ 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 $\delta^{15}N$ in aquatic systems, however, we did not encounter this activity at our urban site (Britton and Doble pers. obs.). Notably, anthropogenic nitrogen loading is not restricted to densely populated areas, as Kelly *et al*. (2016) showed significant 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 (McIntyre *et al.*, 2005; Marijnissen *et al.*, 2009), have higher proportions of sediment in their stomachs, irrespective of foraging behaviour, than at a low human disturbance site, demonstrating 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 (Cohen *et al.*, 1993a; Sweke *et al.*, 2013; Britton *et al.*, 2017). In particular, the results presented here are in broad agreement with Britton *et al.* (2017) who identified that alpha 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 *et al.*, 2004), and we found some evidence for this as two herbivorous species (*T. brichardi* and *P. famula*) 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. Muschick, Indermaur & Salzburger, 2012; Hata *et al.*, 2015; Ford *et al.*, 2016). However, we did not calculate isotopic niche because the anthropogenically elevated nitrogen stable isotope values overwhelmed the ecological $\delta^{15}N$ signature relating to trophic position. In the pristine habitat, benthic herbivores had lower $\delta^{15}N$ values than invertivores and piscivores; but in the disturbed site the highest $\delta^{15}N$ 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 *et al*., 2008; Hata *et al*., 2015; Kelly *et a*l., 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 *et al.*, 2011). Unfortunately, little is known about the effects of spatial variation in nitrogen loading since the influence of a local source of nitrogen on $\delta^{15}N$ values will be the result of both physical (water movement) and biological (movement of individuals) factors. Therefore, systematic spatial sampling, sufficient intraspecific sampling (n~15), and adequate baseline sampling is recommended as good practice to prevent biasing results.

4.5.1 Conclusions

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 & 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 *et al.*, 1993).

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 $\delta^{15}N$ 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 (Islam & Tanaka, 2004; Dudgeon *et al.*, 2006; Gangloff, Edgar & Wilson, 2016). As such, alleviating pollution through afforestation programmes (Deng, Shangguan & Li, 2012) and the effective treatment and disposal of waste (Eggen *et al.*, 2014) should continue to be a global priority for the conservation of aquatic ecosystems, as well as human health.

5 Conclusions

5.1 Summary

This thesis provides the first assessment of human impacts on the three core components of rocky shore cichlid fish diversity in Lake Tanganyika, and in doing so investigates the effectiveness of multiple protected areas in Lake Tanganyika at conserving rocky shore cichlid fishes. Three central questions are addressed: a) does a gradient of human disturbance affect alpha, beta and zeta cichlid diversity, b) are protected areas effective at conserving functional and phylogenetic diversity, and c) do the stable nitrogen stable isotope values and stomach contents of cichlids differ at degraded sites? Though answering these questions, novel assessments of the lake's cichlid species, functional and phylogenetic diversity across different levels of protection are made, and potential mechanisms driving these patterns in degraded areas are identified. Cichlid community composition data collected from localities with differing levels of human disturbance, including two protected areas in the Tanzanian region of LT, provides the basis for this assessment, in addition to individual level sampling of a subset of species from these localities.

The results of Chapter two demonstrate a negative impact of human disturbance on cichlid fish species diversity with higher alpha diversity, a lower loss component of beta diversity and a different pattern of zeta diversity in protected areas. Chapter three also finds differences between protected and unprotected areas, with higher FD and PD in protected areas. Furthermore, FD and PD are linked to SR, and for FD to differ from what is expected given SR, biases have to be extreme. No particular taxonomic or trophic group are driving the increases in FD and PD in protected areas, however the species diversity of herbivores in the Tropheini tribe were most affected by human disturbance. Chapter four investigates this relationship further and finds benthic feeding herbivores in Tropheini have higher nitrogen isotope values and stomach sediment proportions in a degraded site compared to a less disturbed area. Therefore, this indicator of human disturbance may be linked to the lower species diversity found.

The results support the general pattern that alpha species diversity is higher in protected areas compared to unprotected (Rodrigues *et al.*, 2004b; González-Maya *et al.*, 2015; Gray *et al.*, 2016), and that human impact is having a detrimental effect on taxonomic diversity (Bhat & Magurran, 2006; Flynn *et al.*, 2009; Biswas & Mallik, 2011; Chapman *et al.*, 2018). This thesis also adds to the more limited investigations of human impacts on beta diversity, which suggest patterns of beta diversity can differ between protected and unprotected areas across taxa and ecosystems (e.g. Hiley, Bradbury & Thomas, 2016). Beta diversity was found to be lower in unprotected areas, but in human impacted areas the loss component was higher, as has been found in other freshwater ecosystems (Gutiérrez-Cánovas *et al.*, 2013). These results support the theory that beta diversity is a useful tool for investigating human impacts and assessing the effectiveness of protected areas (Socolar *et al.*, 2015). This is also one of the first studies to apply the zeta diversity metric to assess human impacts on diversity and protected area effectiveness (Hui & McGeoch, 2014), and potentially extends the use of this index to show a difference in pattern of zeta diversity between protected and unprotected areas.

Additionally, it was shown that protected areas are effective at conserving FD and PD. Previous studies show some protected areas conserve multiple components of biodiversity (Luck *et al.*, 2013; Quan *et al.*, 2018), whereas others do not (Mouillot *et al.*, 2011; Guilhaumon *et al.*, 2015). This raises the question of congruence between core components of biodiversity, and the relationship between species, functional and phylogenetic diversity is likely to be taxon and region specific (Devictor *et al.*, 2010; Mouillot *et al.*, 2011; D'Agata *et al.*, 2014; Pool *et al.*, 2014). This thesis demonstrates that patterns of FD and PD are consistent with those expected given SR, and at a low taxonomic level it is extremely hard for the measures of FD used in this thesis to differ from SR using null models. However, although null models can distinguish patterns between random and non-random community assembly (Mason *et al.*, 2013), they may not be a 'magic wand' for explaining community assembly (de Bello, 2012) because it is likely to also be taxon and region specific.

Overall the thesis adds to the growing body of research on the assessment of the three core components of diversity across multiple protected areas (Mouillot *et al.*, 2011; Guilhaumon *et al.*, 2015; Brum *et al.*, 2017; Saraiva *et al.*, 2018), and supports the current evidence that protected areas are effective for conserving terrestrial and aquatic species, functional and phylogenetic diversity (Thuiller *et al.*, 2015; Campos *et al.*, 2017). Through considering the multiple components of diversity this thesis builds on the limited research assessing the effectiveness of freshwater protected areas (Adams *et al.*, 2015), and expands the current literature to include a hyper-diverse endemic lake system. Furthermore, Chapter two was also one of the first studies to show the effectiveness of terrestrial protected areas for freshwater lake fish communities. Conversely a more recent study comparing terrestrial protected and unprotected North American lakes found fish diversity was not affected by human impact (Chu *et al.*, 2017). However, the North American lakes studied had lower fish diversity than the cichlids of LT, so the results may be expected to differ.

5.2 Conservation

By demonstrating LT protected areas conserve the three core components of rocky shore cichlid diversity, as well as highlighting the importance of protecting both terrestrial and aquatic habitat, this thesis can be used as evidence to increase the network of protected areas for this endemic group. The Tanzanian section of LT currently consists of two IUCN category II protected areas - Mahale NP and Gombe NP. Both were designated primarily to protect their ecosystems and promote ecotourism (Boitani *et al.*, 2008), therefore the next step could be to increase the size and connectivity of Mahale NP and Gombe NP. Data from Chapters two and three provide evidence of possible areas for formal protection, such as Jakobsen’s Beach and Kalilani Village, which would contribute to the future conservation of LT rocky shore cichlids. In terms of logistics these two localities would be easier to target with protection because they are located near Gombe NP and Mahale NP. The new protected areas could be managed with aquatic no take zones, which can increase fish biomass, and therefore enhance local fisheries (Sala & Giakoumi, 2018). Aquatic reserves can also generate local job opportunities through ecotourism, with SCUBA divers being attracted to the abundant aquatic life (Sala *et al.*, 2016). Terrestrial habitat could be managed with a reforestation programme, which have been predicted to reduce sediment loads and nutrient runoff into freshwater habitats (Ouyang, Leininger & Moran, 2013).

In terms of the whole lake, there are two other protected areas in LT. Rusizi National Park in Burundi is an IUCN category IV protected area, which requires more management interventions than a category II protected area (Boitani *et al.*, 2008). Category IV protection might be more suitable for newly designated protected areas in LT which will need a more active management approach. The ~238km Zambian section of LT has been designated a wetland of international importance under the RAMSAR convention, including Nsumbu National Park (Ramsar Convention, 2000). Extending this international level of protection to the other national parks of LT would increase their profile, and possibly attract more funding for conservation.

Lake Tanganyika is home to ~1500 animal species of which ~600 are endemic (Groombridge & Jenkins, 1998). A United Nations funded Lake Tanganyika Biodiversity Project in the 1990s found high species richness of all fish groups in LT protected areas (West, 2001), therefore all animal species should also be considered in FPA designation. Data from the United Nations project and other LT diversity data is being compiled by The Nature Conservancy (The Nature Conservancy, 2018) to nominate Key Biodiversity Areas based on International Union for Conservation of Nature Red List (International Union for Conservation of Nature and Natural Resources., 2018). However, the majority of the LT cichlid Red List is based on data from 2006 and needs updating, for example 12 species in LT are listed as data deficient. Also, only 12 species are listed as threatened, despite the fact that the majority of species are endemic with restricted ranges and are found in the vulnerable near shore zone. A more comprehensive Red List assessment may lead to more species listed as threatened, and therefore warrant a Key Biodiversity Area in their habitat. Additionally, accurate red listing would open up further avenues of study, such as testing if rarity is conserved within the

LT rocky shore cichlid phylogeny and morphospace. Therefore a better plan to designate protected areas would involve a gap analysis to identify diverse unprotected areas (Rodrigues *et al.*, 2004a), taking into account all animal species, as well as all three core components of biodiversity.

This thesis provides baseline data for time series based future monitoring of LT cichlids in protected areas to assess their ongoing effectiveness, as well as in unprotected areas to assess their future degradation. Monitoring species diversity would be effective for FD and PD, and can be carried out relatively quickly in terms of data collection and analysis compared to monitoring FD and PD (Gotelli & Colwell, 2001). Continued monitoring is also important to ensure an adaptive management approach is developed which can adjust to potential drops in species diversity (Leverington *et al.*, 2010). These adaptations could include expanding the boundaries of the protected areas or enforcing stricter protection and more severe penalties for illegal activity like fishing and logging.

Lake Tanganyika is a key freshwater ecosystem so there are wider policy implications for this research. As well as nominating Key Biodiversity Areas, The Nature Conservancy is also linking research between the North American and African Great Lakes. The conclusions from this study could be used to justify increased protection of the North American Great Lakes, however it should be noted they are less diverse than the African Great Lakes. This study, like others (Edgar *et al.*, 2014), demonstrates aquatic protected areas can work, and provides evidence that more should be designated globally, because protection is likely have positive effects on species, functional and phylogenetic diversity of fish groups. Additionally, the impact of protected terrestrial habitat bordering aquatic protected areas should not be underestimated and an integrated management strategy should include both terrestrial and freshwater conservation because they are inextricably linked.

In terms of global conservation policy, this thesis demonstrates species conservation can be successful for conserving species, as well as morphological diversity and ecosystem functions. Ideally a robust survey of the key aspects of diversity should be carried out in all protected areas to assess their congruence, and in unprotected areas to find localities conserving all three. However, with limited resources a complete assessment of the three core components may not be possible, therefore assessing species diversity as a biodiversity surrogate would be an informative conservation strategy.

5.3 Future directions

5.3.1 Species diversity

The last comprehensive assessment of animal species diversity in LT protected areas was the United Nations funded Lake Tanganyika Biodiversity Project conducted in the 1990s (West, 2001). This thesis only focuses on Tanzanian rocky shore cichlids but provides compelling evidence to rapidly assess the species diversity of other animals throughout the lake. Sandy and deep dwelling LT cichlid species diversity were not considered in this study, and it would be informative to see if herbivorous sandy species diversity is being affected the most outside protected areas, as was the case rocky shore species. Surveying and monitoring the species diversity of other LT fish groups may also reveal a pattern of higher diversity in protected areas. Furthermore, expanding the protected areas assessment to include all animal groups throughout the lake, would significantly increase the conservation value of LT national parks by including higher taxonomic levels.

Increasing the amount of species surveyed may call for new survey methods that are potentially quicker, or better at identifying species that are more secretive than LT cichlids. Video surveys require less person hours in the field because numerous cameras can be deployed at multiple survey stations. Identifying species from videos does require more analysis time, although automated identification, which has been used on Lake Malawi cichlids (Joo *et al.*, 2013) could be explored. Environmental (e)DNA surveys are a useful tool for the identification of cryptic and rare species (Drummond *et al.*, 2015; Thomsen & Willerslev, 2015), however, as eDNA surveys are a relatively new method, community composition data would still be needed to verify the results. The stationary visual census method with a 5m radius could be used to verify diurnal species, because it has been demonstrated to provide greater precision in density estimates of sedentary species (Samoilys & Carlos, 2000). However, nocturnal species would need to be verified with seine net sampling, and cryptic species with SCUBA searches.

Another avenue for further research is to assess rocky shore cichlid species diversity from a larger proportion of the lake. In this study the northern third of Mahale NP was considered, as well as Kalilani Village – a diverse locality bordering the north of Mahale NP. Surveying throughout the protected areas would enable an assessment of the localities bordering the southern park boundary, resulting in a more complete assessment of whether reserve spill-over effects are occurring (Halpern, Lester & Kellner, 2009), and whether a buffer zone is present outside the borders of this large national park. Sandy stretches on the shoreline of the northern and southern borders of Gombe NP means a buffer zone assessment of rocky shore cichlid species diversity is not possible. However, if sandy species were assessed maybe population extinctions caused by human induced edge effects (Woodroffe *et al.*, 2007) would be reducing species diversity across the borders of this smaller national park.

The assessment of protected area species diversity should be expanded to include the other diverse African Great Lakes, such as Malawi and Victoria, as well as the American Great Lakes. Additionally the impact of this thesis could also be extended to assessing the effectiveness of marine protected areas, as many lack a comprehensive monitoring programme (Gill *et al.*, 2017). It is particularly vital to assess species rich marine protected areas because the results from this thesis predicts they may be harbouring high amounts of FD and PD. After an initial species diversity assessment, monitoring programmes can be initiated to ensure an adaptive management approach is adopted.

5.3.2 Functional diversity

Functional diversity was calculated using geometric morphometric methods to measure the morphological variation of key landmarks, relating to a variety of traits relevant to ecosystem functioning. This method was chosen because of LT cichlids compressed body shape (Cardini, 2014), however, the morphological variation of landmarks may not reflect ecosystem functioning in LT. Therefore, other measures of FD could be investigated and compared to geometric morphometric methods, such as traditional morphometric methods. However, it should be noted to calculate FD over multiple dimensions traditional morphometric measurements need to be transformed through a distance matrix (Schleuter *et al.*, 2010), whereas geometric morphometric data is already in coordinate format. Alternative geometric morphometric measures of FD could be calculated to increase species functional information. For example semi landmarks can identify differences between populations of LT cichlid species *Tropheus moorii* (Maderbacher *et al.*, 2008). Additionally, 3D measurements of specific features such as the lips, which can vary greatly between species e.g. *Lobochilotes labiatus*, can show more shape variation than 2D landmarks (Buser, Sidlauskas & Summers, 2018).

Additionally, as patterns of FD are as expected given SR in this study, maybe the measure of FD used in this thesis does not produce the variation needed to differ from SR. However, these results may change if the sample pool included species from higher taxonomic levels, such as all LT fish species. There are a range of diverse fish groups in radiations in the lake, including spiny-eels and catfishes (Day & Wilkinson, 2006; Brown *et al.*, 2010; Peart *et al.*, 2014), and the inclusion of fish with different body shapes and sizes may cause FD to not be so closely linked to SR. Although the link between SR and FD may be due to the measure of FD used (Halpern & Floeter, 2008). Furthermore, a different measure of FD would be needed to quantify LT mastacembelid spiny-eel FD because their body shape is not as flat as LT cichlids. In terms of the future of FD as an indicator of biodiversity, a more universal measure would need to be produced to become as widely used as SR. However, as mentioned, one measure may not be applicable to all taxonomic groups and ecoregions.

5.3.3 Phylogenetic diversity

While work has been conducted on LT cichlid phylogenetics, there are still ambiguous relationships at the genus level, for example *Neolamprolgus* species are polyphyletic (Day *et al.*, 2008). Currently a genome wide phylogeny is being conducted (European Commission, 2014), therefore the PD analysis could be repeated when this is completed. However the tribal relationships in LT cichlids are well established (Meyer *et al.*, 2015), and due to the improbability of species shifting tribes and vastly increasing PD values, the PD results are unlikely to change significantly with a new phylogeny.

5.3.4 Stable isotope analysis

Finally, in terms of future directions for investigating the spatial effects of pollution, stable isotope analysis could focus on one species of human impacted benthic herbivore. The species would be sampled in a systematic way at 20 metre intervals throughout Kigoma Bay, enabling the identification of point sources of pollution. Additionally, a long term monitoring programme to assess anthropogenic pressures affecting water quality has been proposed (Plisnier *et al.*, 2018), and would enable the identifications of pollutants such, as mercury (Campbell *et al.*, 2008), pesticides (Manirakiza *et al.*, 2002), and nitrogen based pollutants (Kelly *et al.*, 2016).

Chapter two supporting information

Appendix S2.1: Study locality descriptions and disturbance ranking

Here we give detailed descriptions of the seven localities we surveyed as well as the details of the way each was ranked for human disturbance.

Kigoma Town: HD rank 10.

Kigoma, the capital of the Kigoma region, has a human population of 215,458 (GeoHive, 2012), and serves as the largest transit port for people and goods on LT (Lake Tanganyika Authority, 2012). Rural to urban migration and refugee immigration has increased Kigoma Town's population dramatically (National Bureau of Statistics, 2011), resulting in a population density of over 32 people per 100m^2 (Linard *et al.*, 2012). Increased watershed deforestation has caused a reduction in tree cover to less than 10% canopy density (Hansen *et al.*, 2013), and consequently increased runoff into the lake, where visible layers of sediment now covers rocks in the littoral zone (McIntyre *et al.*, 2005). In addition, the rising population has increased fishing effort in Kigoma Bay for subsistence and commercial purposes (Kimirei *et al.*, 2008). The shoreline of Kigoma Town is ~8km and encompasses underwater cliffs, large boulders, rocky patches and bedrock, intercepted by three small sandy bays.

Kigoma Deforested: HD rank 7.5.

To the south of Kigoma Town the urban area gives way to an unpopulated 1km of deforested shoreline (Linard *et al.*, 2012). Tree canopy density is approximately 10% (Hansen *et al.*, 2013), and because of the areas close proximity to Kigoma Town, fishing pressures are high (Kimirei *et al.*, 2008). The littoral zone is rocky, comprising large boulders, smaller rocky patches and bedrock.

Jakobsen's Beach: HD rank 7.25.

Jakobsen's Beach, directly south of the Kigoma Deforested locality, is a private reserve covering 1km of shoreline, with no permanent human population (Linard *et al.*, 2012). Reforestation has resulted in scrubby tree cover of approximately 16% canopy density (Hansen *et al.*, 2013). Similarly to Kigoma Deforested, fishing pressure is high due to the areas close proximity to Kigoma Town (Kimirei *et al.*, 2008). The littoral zone has two small sandy bays and large rocky areas including large boulders and smaller rocky patches.

Kalilani Village: HD rank 7.

Kalilani Village, immediately north of Mahale NP, is a small fishing village encompassing 2km of shoreline, with a low human population (Linard *et al.*, 2012). Basic human habitation and small scale agriculture has resulted in a reduction in tree cover to approximately 25% canopy density (Hansen *et al.*, 2013). Artisanal fisheries dominate due to the nature of the small human population although fishing effort has increased since the exclusion zone was established in Mahale NP (Allison, 2000). The littoral zone is made up of rocky areas with large boulders and smaller rocky patches interspersed with small sand patches.

Gombe NP: HD rank 4.

Gombe Stream NP (IUCN category 2) is a protected 35 square km strip of semi-deciduous and evergreen forest, thicket and grassland (Pusey *et al.*, 2007) stretching along 12km of lake shore, 11km north of Kigoma Town (Allison, 2000). Gombe was declared a National Park in 1968 (Pusey *et al.*, 2007), however, the park boundary ends 100 metres short of the shoreline so forest has been cleared (Allison, Lubchenco & Carr, 1998), contributing to the park having approximately 50% tree canopy cover (Hansen *et al.*, 2013). A small number of park staff and tourists enter the park daily, but it is essentially uninhabited (Pusey, Wilson & Anthony Collins, 2008). The northern littoral zone includes underwater cliffs, large boulders, rocky patches and bedrock, whilst rocky shores are interspersed with sand through the middle of the park, before turning rocky from the shore to a depth of five metres in the south.

Mahale Mountain NP

Mahale Mountain National Park (IUCN category 2) was established in 1985 and lies 140km south of Kigoma Town (Pusey *et al.*, 2007) and protects 1,613 square km of forest (Sweke *et al.*, 2013). The majority of the park has a tree canopy density of approximately 75% (Hansen *et al.*, 2013). There is a 96 square km fishing exclusion zone stretching 1.6km into the lake along the parks 60km shoreline (West, 2001) that represents half of the total protected water in LT (Allison *et al.*, 2000). The parks' inaccessibility and high penalties for fishing ensures that the littoral zone is well protected (Allison, 2000). The park is uninhabited apart from a small number of park staff and tourists (Kaur *et al.*, 2008). Within Mahale NP there are patches of sand interspersed between large distances of rocky shore. As large discontinuities of rocky habitat can be a barrier to LT cichlid dispersal (e.g. Sefc *et al.* 2007; Wagner & McCune, 2009) Mahale NP was split into two localities; Mahale NP 1 (Mahale S1) and Mahale NP 2 (Mahale S2) due to the presence of sandy patch between them.

Mahale S1: HD rank 1.

Mahale S1 covers 7km of shoreline near the northern border of the park, its littoral zone is comprised of underwater cliffs, large boulders and rocky patches interspersed with small sandy bays.

Mahale S2: HD rank 1.

Mahale S2 lies 6km directly south of Mahale S1, separated by a 4km stretch of sand interspersed with small rocky patches. The locality covers 5km of shoreline and its littoral zone is very similar to Mahale S1, with underwater cliffs, large boulders and rocky patches, but with fewer sandy bays.

Human Disturbance (HD) ranking

A modified unweighted range-standardize scoring system was used to rank seven localities on their relative amount of human disturbance, with four factors standardised to range from 0 (low disturbance) to 10 (high disturbance) (Falcone *et al.*, 2010). First, tree cover data within a kilometre of the lake shore was used to indicate the health of the terrestrial habitat at each locality. Percentage tree canopy cover was quantified for each locality in QGIS v2.8.2 (Quantum GIS Development Team, 2015) as the mean estimate of maximum tree canopy cover per 30m x 30m Landsat pixel (Hansen *et al.*, 2013), spanning all sites. Tree canopy cover of 0-10% was scored as 10 points and continued sequentially to canopy cover of 70-80% scoring 3 points, 100% canopy cover would have scored 0 points. Next, each locality was awarded a binary protection status for both their aquatic and terrestrial habitats: protected areas were scored as 0 (low disturbance), and unprotected areas as 10 (high disturbance). At the time of the study Mahale NP's terrestrial and aquatic habit had been protected for 30 years, and Gombe NP's terrestrial habitat had been protected for 47 years (Pusey *et al.*, 2007). Finally mean human population density per 100m^2 (Linard *et al.*, 2012) was quantified for each locality in QGIS as the mean number of humans per 100mx100m pixel, within a kilometre of the lake shore spanning all sites. Unpopulated localities scored 0, and the most populated locality scored 10.

Table S2.1. Human disturbance (HD) factors with their standardised point scores in brackets, and relative rank for each locality on a scale of 0 (low disturbance) to 10 (high disturbance).

Locality	Mean tree canopy cover (% per 30m^2)*	Water protection (0 = not protected, 1 = protected)†	Terrestrial protection (0 = not protected, 1 = protected) ‡	Mean human population density (per 100m^2)¶	Relative HD rank
Kigoma Town	6.3 (10)	0 (10)	0 (10)	32 (10)	10
Kigoma Deforested	9.7 (10)	0 (10)	0 (10)	0 (0)	7.5
Jakobsen's Beach	15.9 (9)	0 (10)	0 (10)	0 (0)	7.25
Kalilani Village	26.1 (8)	0 (10)	0 (10)	0 (0)	7
Gombe NP	52.3 (5)	0 (10)	1 (0)	0.02 (1)	4
Mahale S1	72.6 (3)	1 (0)	1 (0)	0.03 (1)	1
Mahale S2	79.2 (3)	1 (0)	1 (0)	0.04 (1)	1

*****(Hansen *et al.*, 2013)**;** **†**(Allison, 2000)**;** **‡**(Coulter & Mubamba, 1993)**;** ¶(Linard *et al.*, 2012)

Mean tree canopy and human population density were both quantified in QGIS as the mean raster value per pixel within 1km of the shoreline of the distance spanning all sites at each locality.

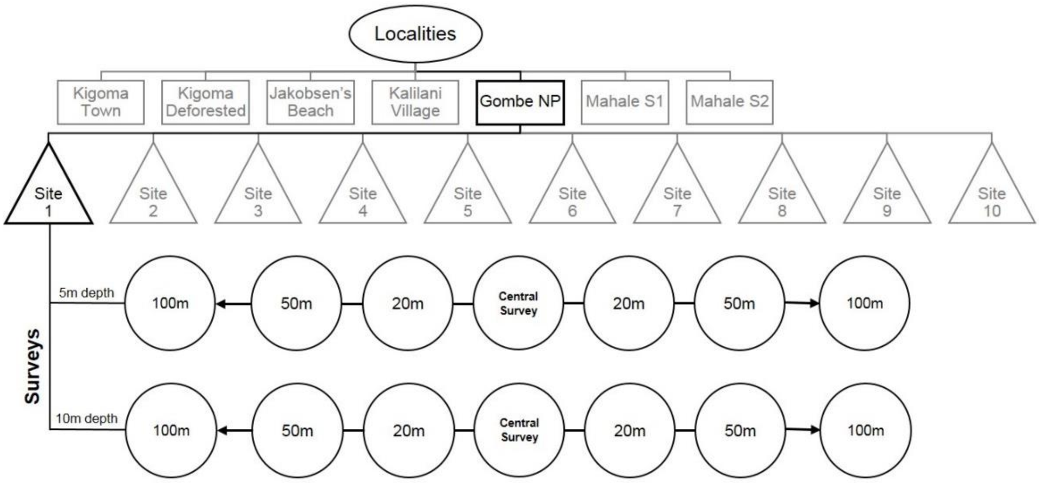


Figure S2.1. Sampling design and associated nomenclature highlighting nested survey design at Gombe NP site 1.

Table S2.2. GPS coordinates of each site. Site coordinates marked in bold were used for robustness of results test.

Locality	Latitude	Longitude
Kigoma Town 1	-4.89971065	29.60077797
Kigoma Town 2	**-4.89572346**	**29.61097154**
Kigoma Town 3	**-4.88626231**	**29.61569734**
Kigoma Town 4	-4.87706153	29.62076319
Kigoma Town 5	**-4.89007624**	**29.61203311**
Kigoma Town 6	-4.86445502	29.60906155
Kigoma Town 7	-4.87879939	29.62169937
Kigoma Town 8	-4.90227166	29.60257203
Kigoma Town 9	-4.8977352	29.61141268
Kigoma Town 10	-4.8625173	29.61593069
Kigoma Deforested 1	**-4.90589691**	**29.5955449**
Kigoma Deforested 2	**-4.90227166**	**29.5947246**
Kigoma Deforested 3	**-4.89881312**	**29.59538908**
Jakobsen’s Beach 1	**-4.91672231**	**29.59556443**
Jakobsen’s Beach 2	**-4.91496873**	**29.59717928**
Jakobsen’s Beach 3	**-4.91070561**	**29.59825384**
Kalilani Village 1	**-6.01632709**	**29.7464034**
Kalilani Village 2	-6.01691818	29.74863365
Kalilani Village 3	**-6.01391997**	**29.75892378**
Kalilani Village 4	**-6.00951947**	**29.76112629**
Gombe NP 1	**-4.62950097**	**29.63271562**
Gombe NP 2	**-4.63390935**	**29.63128173**
Gombe NP 3	-4.64763137	29.62809845

Gombe NP 4	-4.73357714	29.60851816
Gombe NP 5	-4.74293143	29.60360259
Gombe NP 6	**-4.62543952**	**29.63598515**
Gombe NP 7	-4.63187448	29.63174005
Gombe NP 8	-4.73649119	29.60575674
Gombe NP 9	-4.71793408	29.61150966
Gombe NP 10	-4.68621855	29.61961932
Mahale S1 1	**-6.03971151**	**29.73378151**
Mahale S1 2	-6.07880009	29.73022423
Mahale S1 3	-6.0845106	29.72932745
Mahale S1 4	**-6.04336987**	**29.73322897**
Mahale S1 5	**-6.0507897**	**29.73353072**
Mahale S1 6	-6.10324373	29.72870467
Mahale S2 1	**-6.21466991**	**29.7297017**
Mahale S2 2	**-6.21203581**	**29.73538295**
Mahale S2 3	**-6.20542374**	**29.7389228**
Mahale S2 4	-6.17382606	29.74031311

Table S2.3. Cichlid species observed across all surveys detailing taxonomy, diet, habitat and brooding-type. Tribal classsification based on Meyer *et al.* (2015), and species classification according to Eschmeyer (2015) with names in parenthesis denoting possible future taxonomic revision (Konings, 2015). Trophic groups: I, invertivore; H, herbivore; P, piscivore, for each species were assigned where possible based on stomach contents containing >50% of items of that dietary group (data taken from the literature). Where stomach content information was not available the major dietary component stated in the literature was used to assign trophic group. Three species were not assigned a group as they were scale-eaters.

Species	**Major dietary components**	**Trophic group**	**Water column habitat**[c]	**Substrate habitat**[c]
LAMPROLOGINI				
Altolamprologus compressiceps	Crustaceans[a,b]	I	Benthic	Rock
Chalinochromis brichardi	Invertebrates[c]	I	Benthic	Rock
Chalinochromis popelini	Invertebrates[c]	I	Benthic	Rock
Julidochromis regani	Sponges[b]	I	Benthic	Rock
Lamprologus callipterus	Crustaceans, insect larvae[a,b]	I	Benthic	Sand, rock
Lamprologus lemairii	Fish, fry[b]	P	Water column	Rock, sand
Lepidiolamprologus attenuatus	Fish[c]	P	Water column	Rock, sand
Lepidiolamprologus elongatus	Fish, fry[b]	P	Water column	Rock
Lepidiolamprologus profundicola	Fish, fry[b]	P	Water column	Rock
Neolamprologus brichardi	Invertebrates[b]	I	Water column	Rock
Neolamprologus cunningtoni	Fish[c]	P	Water column	Sand, rock
Neolamprologus falcicula	Invertebrates[c]	I	Water column	Rock
Neolamprologus fasciatus	Fish, fry[b]	P	Water column	Rock
Neolamprologus furcifer	Crustaceans, insect larvae[a,b]	I	Benthic	Rock
Neolamprologus gracilis	Invertebrates[c]	I	Water column	Rock
Neolamprologus leleupi	Crustaceans, insect larvae[a,b]	I	Benthic	Rock
Neolamprologus modestus	Crustaceans, insect larvae, gastropods[a,b]	I	Benthic	Sand, rock

Neolamprologus mondabu	Gastropods, insect larvae[a,b]	I	Benthic	Sand, rock
Neolamprologus niger	Crustaceans, insect larvae, gastropods[a,b]	I	Benthic	Sand, rock
Neolamprologus savoryi	Invertebrates, plankton[b]	I	Water column	Rock
Neolamprologus tetracanthus	Gastropods, insect larvae[a,b]	I	Benthic	Sand, rock
Neolamprologus toae	Crustaceans, insect larvae[b]	I	Benthic	Rock
Neolamprologus tretocephalus	Gastropods[b]	I	Benthic	Rock
Telmatochromis bifrenatus	Aufwuchs, unicellular algae[e]	H	Benthic	Rock
Telmatochromis dhonti	Fish, fry[c]	P	Water column	Sand, rock
Telmatochromis temporalis	Aufwuchs browser, filamentous algae[d,e]	H	Benthic	Rock
TROPHEINI				
Gnathochromis pfefferi	Crustaceans[b]	I	Benthic	Rock, mud
Limnotilapia dardennii	Invertebrates, detritus[a,b,f]	I	Benthic	Rock
Lobochilotes labiatus	Crustaceans, insect larvae[g]	I	Benthic	Rock
Petrochromis famula	Aufwuchs grazer, unicellular algae[d,e]	H	Benthic	Rock
Petrochromis fasciolatus	Aufwuchs grazer, unicellular algae[d,e]	H	Benthic	Rock, sand
Petrochromis macrognathus	Aufwuchs grazer[d]	H	Benthic	Rock
Petrochromis orthognathus	Aufwuchs grazer, unicellular algae[e,h]	H	Benthic	Rock
Petrochromis polyodon	Aufwuchs grazer, unicellular algae[d,e]	H	Benthic	Rock
Petrochromis trewavasae	Aufwuchs grazer, unicellular algae[d,e]	H	Benthic	Rock
Pseudosimochromis babaulti	Aufwuchs browser[f]	H	Benthic	Rock
Pseudosimochromis curvifrons	Aufwuchs browser, filamentous algae[d,e]	H	Benthic	Rock, sand

Simochromis diagramma	Aufwuchs browser, filamentous algae[d,e]	H	Benthic	Rock
Tropheus annectens	Aufwuchs browser[c]	H	Benthic	Rock
Tropheus brichardi	Aufwuchs browser[c]	H	Benthic	Rock
Tropheus duboisi	Aufwuchs browser[c]	H	Benthic	Rock
Tropheus moorii	Aufwuchs browser, filamentous algae[d,e]	H	Benthic	Rock
ECTODINI				
Asprotilapia leptura	Aufwuchs, unicellular and Filamentous algae, phytoplankton[e]	H	Benthic	Rock
Aulonocranus dewindti	Invertebrates, plankton[c]	I	Water column	Sand, rock
Callochromis macrops	Crustaceans[c]	I	Benthic	Sand, rock
Cyathopharynx foae	Aufwuchs, phytoplankton, detritus[c]	H	Water column	Rock, sand
Cyathopharynx furcifer	Aufwuchs, phytoplankton, detritus[c]	H	Water column	Rock, sand
Ectodus descampsii	Invertebrates[c]	I	Water column	Sand, rock
Enantiopus melanogenys	Invertebrates[c]	I	Benthic	Sand, rock
Grammatotria lemairii	Molluscs, zoobenthos[c]	I	Benthic	Sand, rock
Microdontochromis tenuidentatus	Invertebrates[c]	I	Benthic	Rock
Ophthalmotilapia nasuta	Aufwuchs, unicellular algae[e]	H	Water column	Rock, sand
Ophthalmotilapia ventralis	Aufwuchs, phytoplankton, detritus[e]	H	Water column	Rock
Xenotilapia flavipinnis	Invertebrates[c]	I	Benthic	Sand, rock
Xenotilapia papilio	Aufwuchs scooper[d]	H	Benthic	Rock
Xenotilapia sima	Diptera[b]	I	Benthic	Sand, rock
Xenotilapia spilopterus	Invertebrates[c]	I	Benthic	Sand, rock

PERISSODINI				
Haplotaxodon microlepis	Zooplankton[c]	I	Water column	Rock
Perissodus microlepis	Fish scales[i]		Water column	Rock
Perissodus paradoxus	Fish scales[c]		Water column	Rock, sand
Perissodus straeleni	Fish scales, eggs[j]		Water column	Rock
ERETMODINI				
Eretmodus cyanostictus	Aufwuchs scraper, filamentous algae[d,e]	H	Benthic	Rock
Spathodus marlieri	Aufwuchs scraper[k]	H	Benthic	Rock
Tanganicodus irsacae	Aufwuchs, filamentous algae[e]	H	Benthic	Rock
BATHYBATINI				
Bathybates ferox	Fish[k]	P	Water column	Rock
BENTHOCHROMINI				
Benthochromis tricoti	Zooplankton[c]	I	Water column	Rock, mud
BOULENGEROCHROMINI				
Boulengerochromis microlepis	Fish[k]	P	Water column	Sand, rock
CYPRICHROMINI				
Cyprichromis leptosoma	Zooplankton[k]	I	Water column	Rock
CYPHOTILAPIINI				
Cyphotilapia frontosa	Fish[k]	P	Water column	Rock
TILAPIINI				
Oreochromis tanganicae	Plants, detritus[d]	H	Benthic	Sand, rock

[a]Yamaoka, K. (1991); [b](Hori *et al.*, 1993); [c](Brichard, 1989); [d](Hata *et al.*, 2014); [e](Takamura, 1984); [f](Sturmbauer *et al.*, 2003); [g](Kohda & Tanida, 1996); [h](Sturmbauer, Mark & Dallinger, 1992); [i](Nshombo, Yanagisawa & Nagoshi, 1985); [j](Yanagisawa *et al.*, 1990); [k](Wagner *et al.*, 2009)

Table S2.4. Differences between species richness per survey at 5m and 10m depths at the seven localities using a Mann-Whitney-Wilcoxon test.

	Mann-Whitney-Wilcoxon test	
	W value	*P* value
Locality	2549	0.4729
Kigoma Town 10m & Kigoma Town 5m	182.5	0.3439
Kigoma Deforested 10m & Kigoma Deforested 5m	215.5	0.9092
Jakobsen's Beach 10m & Jakobsen's Beach 5m	442.5	0.4097
Kalilani Village 10m & Kalilani Village 5m	2177.5	0.3827
Gombe NP 10m & Gombe NP 5m	1001	0.2011
Mahale S1 10m & Mahale S1 5m	409.5	0.5982

Table S2.5. Bray-Curtis dissimilarity between 5m and 10m depths at the seven localities.

	Mean dissimilarity between depths	Turnover component	Loss component
Kigoma Town	0.241	0.096	0.146
Kigoma Deforested	0.274	0.173	0.101
Jakobsen's Beach	0.285	0.165	0.120
Kalilani Village	0.261	0.224	0.037
Gombe NP	0.318	0.260	0.059
Mahale S1	0.257	0.241	0.016
Mahale S2	0.248	0.159	0.089

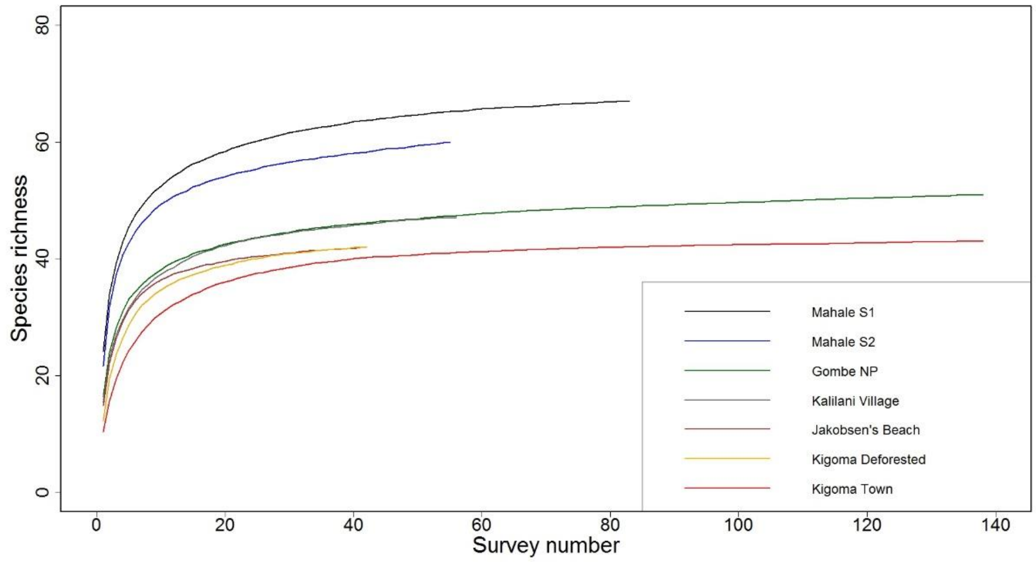


Figure S2.2. Species accumulation curves for all localities generated by plotting the cumulative number of species recorded at each locality against sampling effort (Gombe NP, Kigoma Town, 138 surveys each; Mahale S1, 83 surveys; Kalilani Village, 56 surveys; Mahale S2, 55 surveys; Jakobsen's Beach, Kigoma Deforested, 42 surveys each).

Table S2.6. The distance decay in dissimilarity within each of the seven main localities surveyed. Distance was calculated as the Euclidean distance between surveys from latitude-longitude GPS data. Mantel test values for significance of correlation between log-transformed Sørensen and Bray-Curtis dissimilarity and geographic distance between surveys within all localities. Bold *p*-values indicate significant ($p < 0.05$) distance decay relationships.

	Sørensen index		**Bray- Curtis index**	
Locality	Pearson correlation	*P* value	Pearson correlation	*P* value
Kigoma Town	0.055	**0.043**	0.026	0.162
Kigoma Deforested	0.140	**0.001**	0.134	**0.002**
Jakobsen's Beach	0.060	0.096	0.079	**0.040**
Kalilani Village	0.211	**0.001**	0.165	**0.001**
Gombe NP	0.040	0.154	0.017	0.213
Mahale S1	0.320	**0.001**	0.278	**0.001**
Mahale S2	0.228	**0.001**	0.267	**0.001**

Appendix S2.2. Spatial autocorrelation in zeta diversity

As for the case of classical beta diversity measures, tests for spatial autocorrelation in zeta diversity are accounted for by estimating how the mean number of shared species in *i* surveys changes as a function of distance. We investigated this for all localities and for *i* = (2, 10) surveys, using the *Zeta.ddecays* function in the R library *zetadiv* (v0.1), noting the estimate for the slope of the linear regression between the mean distance between *i* surveys and the expected number of shared species.

As shown in Figure S3.3 we observed little spatial autocorrelation in zeta diversity, and where statistically significant the slope was shallow. However, we found that Kigoma Deforested showed consistent spatial decay in zeta at all number of sites tested. Overall, this supports the earlier results that showed little or no spatial autocorrelation in beta diversity and highlights the fact that the similarity between surveys does not change greatly with the distance.

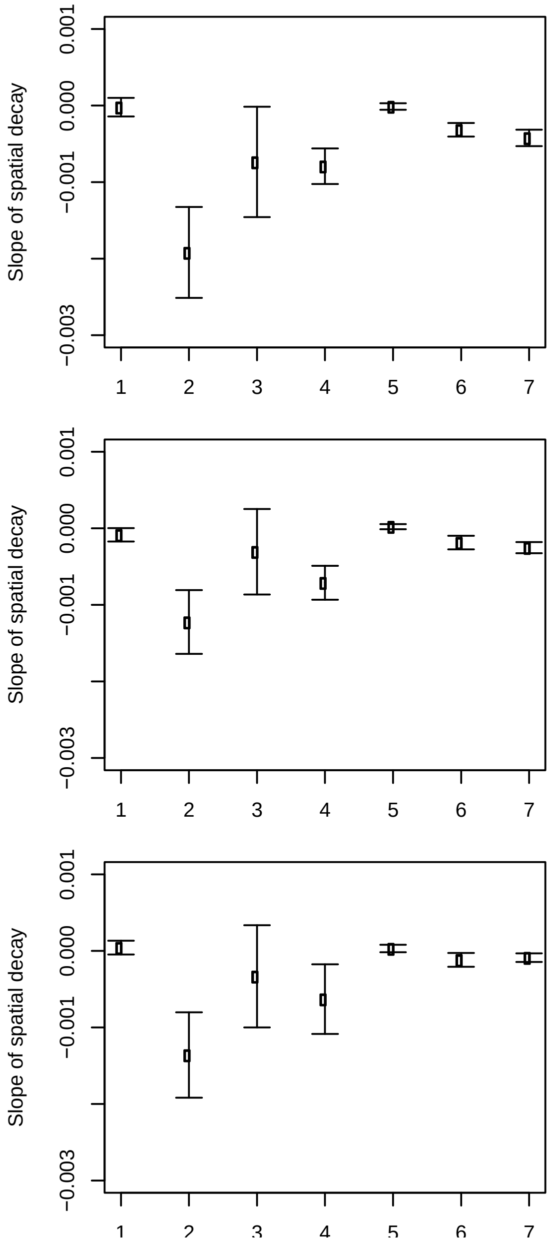


Figure S2.3. The test for spatial autocorrelation in zeta diversity for each of the localities for (top panel) 2; (middle panel) 4; and (bottom panel) 8 surveys. Shown are the slope of the linear model for zeta value with distance (in metres) with 95% confidence interval for Localities are indexed by numbers: (1) Kigoma Town; (2) Kigoma Deforested; (3) Jacobsen’s Beach; (4) Kalilani Village; (5) Gombe NP; (6) Mahale NP S1; (7) Mahale NP S2.

Table S2.7. AIC values for all locality zeta diversity decline model comparisons shown in Figure 3. With lower AIC values highlighted in bold for each locality to show best fitting model in every comparison.

	AIC Value	
Locality	**Exponential model**	**Power law model**
Kigoma Town	**-18.0**	4.95
Kigoma Deforested	**-29.5**	21.9
Jakobsen's Beach	**-32.3**	22.8
Kalilani Village	**7.14**	21.8
Gombe NP	-15.9	**-124.3**
Mahale S1	-34.8	**-158.1**
Mahale S2	-58.1	**-108.4**

Appendix S2.3. Zeta decay null model analysis

Our analyses of the site data showed a clear dichotomy in zeta diversity decay (the expected number of shared species across all surveys as survey number *i* increases): protected localities showed a power law decay with *i*, whereas the disturbed localities exhibit an exponential decay (Figure 2). Here we detail a null model approach to investigate if this change in the functional form of decay could be simply due to non-biased losses in species in the degraded sites. We use the Gombe NP and Mahale NP S1 localities as the pristine communities and the nearby Kigoma Town and Kaliliani Village localities as the degraded communities (Figure 1). Gombe NP surveys returned a total of 2248 species occurrences (the sum across all species of the number of surveys a species was observed), whereas there were 1388 species occurrences recorded in the Kigoma Town site. We observed 1359 species occurrences in Mahale NP S1 whereas Kalilani Village returned 852 species occurrences. Both locality-pairs were surveyed to the same intensity (i.e. had the same number of surveys).

For simplicity we assume that Gombe NP (Mahale NP S1) is representative of the Kigoma Town (Kalilani Village) community before human disturbance affected the cichlid diversity. Secondly, the model assumes that only species losses have occurred due to disturbance. It is likely that some species have increased in occurrence in Kigoma Town and Kalilani Village, and that some species have been lost/gained through emigration/immigration, but overall there is a net decline in diversity, abundance, and species occurrences (see Table 1). With these assumptions in mind the null model proceeds by taking the Gombe NP (Mahale NP S1) community matrix and randomly removing species occurrences from individual surveys until the overall species occurrences matches the Kigoma Town (Kalilani Village) species occurrences (a total of 860 survey ‘extinctions’ for Gombe-Kigoma and 507 for Mahale-Kalilani). The degraded community zeta diversity is then analysed as before to investigate the functional form of decline in zeta with number of surveys. Specifically, we are testing whether the declines in zeta diversity in Gombe NP and Mahale NP S1 can be changed from a power law to exponential decay by unbiased loss of species, or whether this change is more likely if species' losses are biased towards commonly/rarely occurring species. The probability that a species is chosen to have an occurrence removed is weighted by raising its total occurrence across all surveys to an exponent B. When $B = 0$, all species are equally likely to be chosen regardless of total occurrence; $B < 0$ increasingly biases loss towards species with low occurrences, and $B > 0$ increasingly biases loss towards species with high occurrences. Reductions in occurrences are independent of one another and biases towards rare/common species use the species' occurrences at the start of the experiment rather than re-compute biases based upon the transient occurrences (after each occurrence removal). The biological interpretation of this is that rare/common species continue to be more affected by habitat degradation, even as they become rare.

Each simulation proceeds by choosing a species at random based upon the implemented bias, and then selecting an individual occurrence of that species to be removed with equal probability (i.e. if a species has two occurrences, then each occurrence has probability of 0.5 to be removed if that species is chosen). Species can only be chosen if they still have at least one occurrence across the site, but as explained above the probability of being chosen is always based upon the occurrence of that species in the original community. We investigated $-2 < B < 2$, and for each bias value 100 simulated communities were sampled. From these 100 communities we then computed the frequency of simulations where an exponential decay in zeta was the best fitting model (see main text), and also recorded the decay parameter for each of these cases. R code for this null model analysis can be found at https://github.com/djmurrell/Zeta-diversity-null-model.

Results

Removing species occurrences from both pristine cichlid communities resulted in a higher frequency of exponential declines in zeta diversity (Figures S4a, S5a). For Gombe NP, exponential decays in zeta had higher frequency when either rare or commonly occurring species were more likely to be selected to be lost from individual surveys (Figure S3.4a). Loss that is neutral with respect to original occurrence led to the lowest frequency of exponential decay in zeta. Increasing the bias towards common species resulted in the highest frequency of exponential decay, and the frequency of exponential decay peaked at intermediate bias for rare species. Taken in isolation, this implies the functional form of zeta decay in Kigoma Town could have been caused by the biased loss of previously common species, however we note that the rate of decay in zeta is much higher than observed in the data when species loss is biased toward commonly occurring species (Figure S3.4b). This is because removing commonly occurring species leads to a lower expected number of species shared between *i* surveys, leaving only the rare species and the chances of sharing no species between all *i* surveys is much more likely for even intermediate numbers of *i*. Our null model analysis therefore implies that the switch from power law decay in zeta in Gombe NP to exponential decay in Kigoma Town could be driven by the biased loss of species that are rare.

In contrast, for Mahale NP S1, all types of bias in species loss resulted in a high frequency of exponential decline in zeta diversity, although there was a slight increase in frequency for the biased loss of rare species. However, the rate of zeta diversity decay observed in Kalilani Village was matched only for neutral loss or mild bias towards common species. We therefore conclude that the exponential decline in zeta diversity observed in Kalilani Village could have occurred via loss of common species, and this results in the more rapid decay in expected shared species as the number of surveys increases.

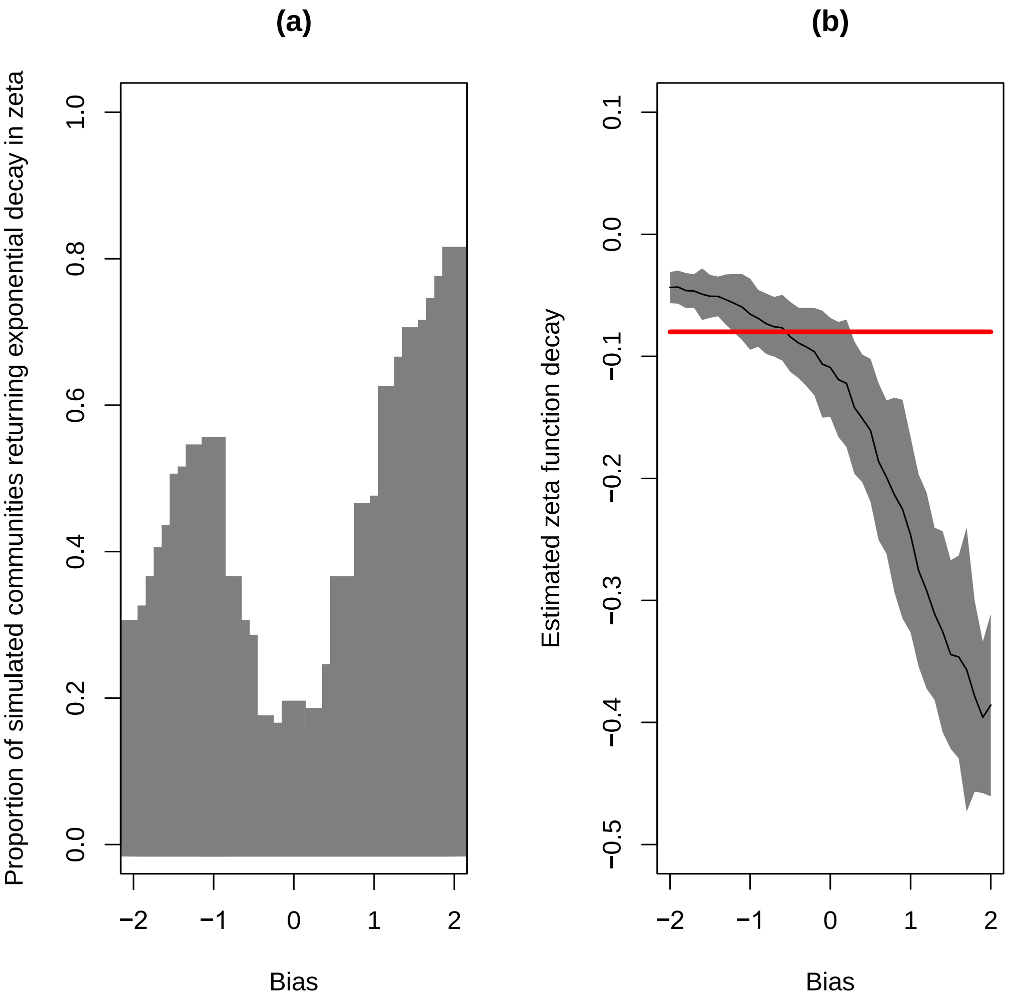


Figure S2.4. Zeta diversity null model results for Gombe NP. Species' survey occurrences are removed at random from the Gombe NP community but with bias towards those with high/low occupancies in the pristine community until the total occurrences matches the number observed in the Kigoma Town community. An increasingly negative bias means species with low occupancy are more likely to be chosen to be removed; large positive bias values means common species are selected. In (a) the proportion of simulated communities that return an exponential decay in zeta diversity is shown as a function of the bias parameter. In (b) the rate of decay from only those communities displaying exponential decay in zeta diversity is shown. The black line represents the mean decay rate and the shaded region the 95% confidence interval. The bold line indicates the estimated decay rate in zeta diversity from the Kigoma Town community (see Figure 2). Results in both panels are taken from 100 simulations of the null model.

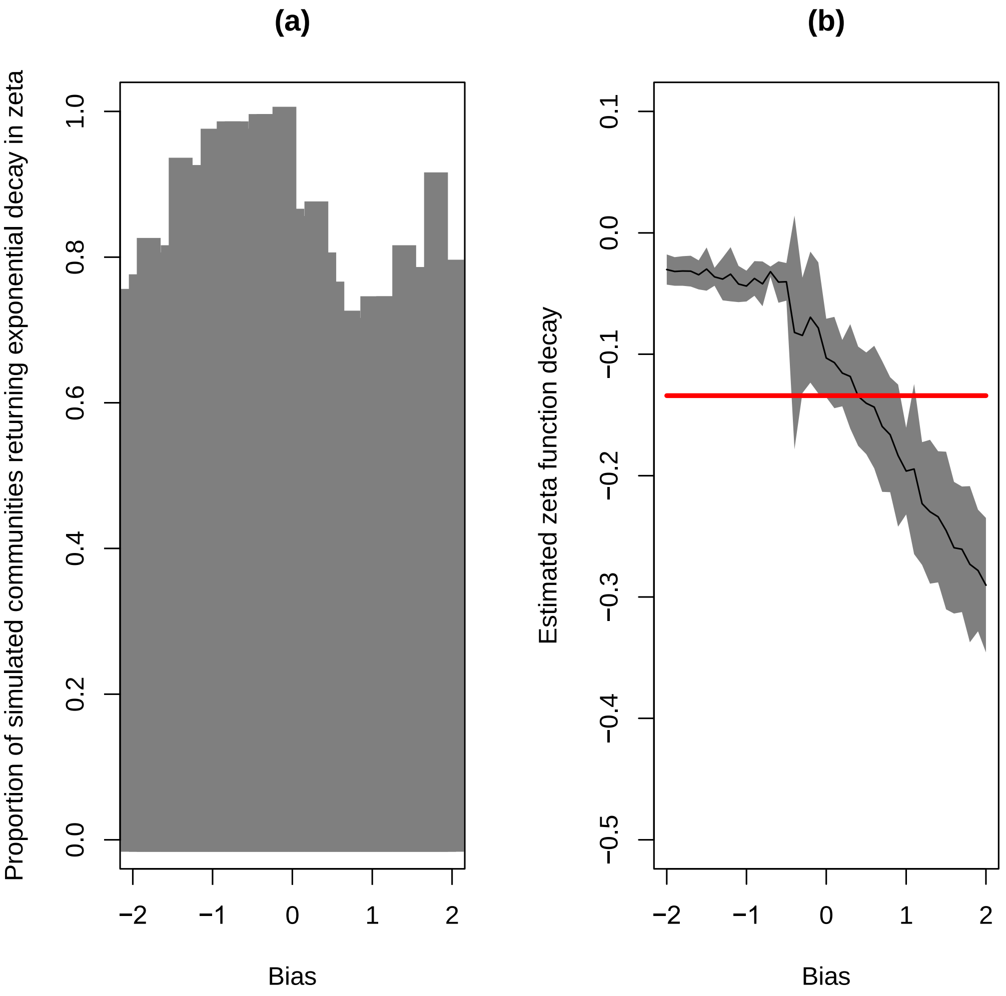


Figure S2.5. Zeta diversity null model results for Mahale NP S1. Species' survey occurrences are removed at random from the Mahale NP S1 community but with bias towards those with high/low occupancies in the pristine community until the total occurrences matches the number observed in the Kalilani Village cichlid community. An increasingly negative bias means species with low occupancy are more likely to be chosen to be removed; large positive bias values means common species are selected. In (a) the proportion of simulated communities that return an exponential decay in zeta diversity is shown as a function of the bias parameter. In (b) the rate of decay from only those communities displaying exponential decay in zeta diversity is shown. The black line represents the mean decay rate and the shaded region the 95% confidence interval. The bold line indicates the estimated decay rate in zeta diversity from the Kalilani Village community (see Figure 2). Results in both panels are taken from 100 simulations of the null model.

Table S2.8. Correlations between relative HD rank and alpha and beta diversity values for the three largest cichlid tribes and selected trophic groups at all localities. Rho and p values are given for Spearman's Rank Correlation of alpha and beta diversity values. Asterisks indicate a significant positive or negative correlation (* *P* ≤ 0.05, ** *P* ≤ 0.01, *** *P* ≤ 0.001).

		ALPHA DIVERSITY				*BETA DIVERSITY*			
LAMPROLOGINI	**Relative human disturbance rank**	**Median species richness per survey**	**Median log abundance per survey (all species pooled)**	**Effective number of species per locality (all surveys pooled)**	**Pielou's evenness index per locality (all surveys pooled**	**Mean Sørensen dissimilarity value between survey pairs**	**Sørensen loss component (%)**	**Mean Bray-Curtis dissimilarity value between survey pairs**	**Bray-Curtis loss component (%)**
Kigoma Town	10	6	1.81	6.13	0.63	0.413	39	0.717	47
Kigoma Deforested	7.5	7	1.96	4.57	0.54	0.388	36	0.667	42
Jakobsen's Beach	7.25	6	1.97	3.22	0.42	0.398	37	0.546	52
Kalilani Village	7	7	1.59	6.68	0.62	0.403	34	0.672	40
Gombe NP	4	7	1.89	7.81	0.68	0.366	37	0.584	41
Mahale S1	1	12	2.42	9.32	0.69	0.335	30	0.673	25
Mahale S2	1	9	2.24	7.49	0.65	0.345	34	0.694	34
Rho value		**-0.850**	-0.595	**-0.793**	-0.685	**0.847**	0.743	-0.054	**0.847**
***P* value**		0.016*	0.159	0.033*	0.09	0.0162*	0.0556	0.908	0.0162*

		ALPHA DIVERSITY				*BETA DIVERSITY*			
TROPHEINI	**Relative human disturbance rank**	**Median species richness per survey**	**Median log abundance per survey (all species pooled)**	**Effective number of species per locality (all surveys pooled)**	**Pielou's evenness index per locality (all surveys pooled**	**Mean Sørensen dissimilarity value between survey pairs**	**Sørensen loss component (%)**	**Mean Bray-Curtis dissimilarity value between survey pairs**	**Bray-Curtis loss component (%)**
Kigoma Town	10	2	0.78	4.67	0.67	0.451	74	0.664	73
Kigoma Deforested	7.5	3	1	4.01	0.58	0.442	55	0.62	58
Jakobsen's Beach	7.25	5	1.19	7.66	0.85	0.415	40	0.577	26
Kalilani Village	7	4	0.98	7.42	0.87	0.379	39	0.542	36
Gombe NP	4	5	1.22	8.17	0.85	0.399	46	0.648	46
Mahale S1	1	6	1.43	7.71	0.74	0.298	36	0.523	43
Mahale S2	1	5	1.32	8.18	0.82	0.382	21	0.535	29
Rho value		**-0.860**	**-0.883**	**-0.865**	-0.345	**0.865**	**0.883**	**0.775**	0.505
***P* value**		0.013*	0.008**	0.012*	0.448	0.012*	0.0085**	0.041*	0.248

		ALPHA DIVERSITY				*BETA DIVERSITY*			
ECTODINI	**Relative human disturbance rank**	**Median species richness per survey**	**Median log abundance per survey (all species pooled)**	**Effective number of species per locality (all surveys pooled)**	**Pielou's evenness index per locality (all surveys pooled**	**Mean Sørensen dissimilarity value between survey pairs**	**Sørensen loss component (%)**	**Mean Bray-Curtis dissimilarity value between survey pairs**	**Bray-Curtis loss component (%)**
Kigoma Town	10	0	0	4.29	0.66	0.304	76	0.57	80
Kigoma Deforested	7.5	2	1.17	3.98	0.63	0.399	39	0.738	39
Jakobsen's Beach	7.25	2	1.06	2.82	0.47	0.408	43	0.614	45
Kalilani Village	7	2	0.7	4.58	0.78	0.375	41	0.62	55
Gombe NP	4	2	1.29	3.92	0.62	0.395	50	0.77	55
Mahale S1	1	3	1.39	8.5	0.81	0.463	36	0.798	34
Mahale S2	1	3	1.26	5.25	0.67	0.431	45	0.763	41
Rho value		**-0.905**	**-0.793**	-0.559	-0.468	-0.703	0.288	**-0.829**	0.491
***P* value**		0.005**	0.033*	0.193	0.289	0.0782	0.531	0.021*	0.263

		ALPHA DIVERSITY				*BETA DIVERSITY*			
INVERTIVORES	**Relative human disturbance rank**	**Median species richness per survey**	**Median log abundance per survey (all species pooled)**	**Effective number of species per locality (all surveys pooled)**	**Pielou's evenness index per locality (all surveys pooled**	**Mean Sørensen dissimilarity value between survey pairs**	**Sørensen loss component (%)**	**Mean Bray-Curtis dissimilarity value between survey pairs**	**Bray-Curtis loss component (%)**
Kigoma Town	10	5.5	1.82	7.17	0.64	0.468	37	0.776	41
Kigoma Deforested	7.5	6	2.09	4.1	0.46	0.423	30	0.751	36
Jakobsen's Beach	7.25	7	2.19	4.14	0.47	0.429	29	0.639	41
Kalilani Village	7	7	1.41	10.26	0.73	0.465	22	0.704	23
Gombe NP	4	7	1.72	10.22	0.74	0.457	27	0.706	29
Mahale S1	1	11	2.34	13.01	0.75	0.402	17	0.788	14
Mahale S2	1	9	2.33	6.81	0.58	0.413	32	0.755	32
Rho value		**-0.954**	-0.450	-0.505	-0.541	0.667	0.523	-0.216	0.745
***P* value**		0.0008***	0.310	0.248	0.210	0.102	0.229	0.641	0.054

		ALPHA DIVERSITY				*BETA DIVERSITY*			
HERBIVORES	**Relative human disturbance rank**	**Median species richness per survey**	**Median log abundance per survey (all species pooled)**	**Effective number of species per locality (all surveys pooled)**	**Pielou's evenness index per locality (all surveys pooled**	**Mean Sørensen dissimilarity value between survey pairs**	**Sørensen loss component (%)**	**Mean Bray-Curtis dissimilarity value between survey pairs**	**Bray-Curtis loss component (%)**
Kigoma Town	10	2	1.17	5.21	0.64	0.469	59	0.733	59
Kigoma Deforested	7.5	4	1.19	5.89	0.67	0.522	38	0.78	41
Jakobsen's Beach	7.25	6	1.41	7.46	0.76	0.460	39	0.636	35
Kalilani Village	7	6	1.18	9.08	0.86	0.396	35	0.586	31
Gombe NP	4	6	1.59	6.65	0.68	0.426	46	0.726	45
Mahale S1	1	7	1.72	10.13	0.74	0.375	25	0.643	30
Mahale S2	1	7	1.64	12.04	0.83	0.416	31	0.67	31
Rho value		**-0.963**	**-0.883**	**-0.883**	-0.577	**0.829**	0.739	0.414	0.736
***P* value**		0.0005***	0.008**	0.008**	0.175	0.0211*	0.0579	0.355	0.059

		ALPHA DIVERSITY				*BETA DIVERSITY*			
PISCIVORES	**Relative human disturbance rank**	**Median species richness per survey**	**Median log abundance per survey (all species pooled)**	**Effective number of species per locality (all surveys pooled)**	**Pielou's evenness index per locality (all surveys pooled**	**Mean Sørensen dissimilarity value between survey pairs**	**Sørensen loss component (%)**	**Mean Bray-Curtis dissimilarity value between survey pairs**	**Bray-Curtis loss component (%)**
Kigoma Town	10	2	1.18	2.19	0.44	0.271	63	0.531	65
Kigoma Deforested	7.5	2	1.04	1.59	0.26	0.264	57	0.562	72
Jakobsen's Beach	7.25	2	0.85	2.69	0.55	0.300	60	0.454	43
Kalilani Village	7	2	1.29	2.12	0.39	0.249	66	0.609	73
Gombe NP	4	3	1.43	2.51	0.42	0.264	56	0.451	65
Mahale S1	1	4	2.09	2.87	0.48	0.236	47	0.593	60
Mahale S2	1	3	1.43	3.23	0.56	0.303	60	0.617	58
Rho value		**-0.874**	**-0.827**	-0.739	-0.468	0.164	0.464	-0.432	0.345
***P* value**		0.01*	0.021*	0.058	0.289	0.726	0.295	0.333	0.448

Table S2.9. Correlations between relative HD rank and alpha and beta diversity for cichlids where all localities are standardised to 42 surveys and approximately 1km shoreline distance. Rho and p values are given for Spearman’s Rank Correlation of alpha and beta diversity values. Asterisks indicate a significant positive or negative correlation (* *P* ≤ 0.05, ** *P* ≤ 0.01, *** *P* ≤ 0.001, **** *P* ≤ 0.0001).

		ALPHA DIVERSITY				*BETA DIVERSITY*			
	Relative human disturbance rank	**Median species richness per survey [interquartile range]**	**Median log abundance per survey [interquartile range]**	**Pielou’s evenness index per locality (all surveys pooled)**	**Effective number of species per locality (all surveys pooled)**	**Mean Sørensen dissimilarity between survey pairs** [±sd]	**Sørensen loss component (%)**	**Mean Bray-Curtis dissimilarity between survey pairs** [±sd]	**Bray-Curtis loss component (%)**
Kigoma Town	10	10 [3.75]	2.2 [0.75]	0.61	8.7	0.51 [±0.20]	28	0.76 [±0.18]	41
Kigoma Deforested	7.5	12 [5.75]	2.3 [0.62]	0.55	7.9	0.53 [±0.13]	23	0.76 [±0.19]	28
Jakobsen’s Beach	7.25	15 [5.75]	2.3 [0.31]	0.55	7.9	0.49 [±0.13]	18	0.63 [±0.18]	33
Kalilani Village	7	15 [3]	1.9 [0.44]	0.69	14.2	0.49 [±0.11]	14	0.71 [±0.14]	21
Gombe NP	4	16 [6.5]	2.1 [0.35]	0.78	19.1	0.53 [±0.17]	21	0.68 [±0.17]	22
Mahale S1	1	24 [5]	2.7 [0.21]	0.72	18.7	0.39 [±0.11]	16	0.69 [±0.17]	12
Mahale S2	1	22 [4]	2.5 [0.32]	0.72	18.9	0.45 [±0.12]	12	0.69 [±0.18]	18
Rho value		**-0.982**	-0.436	**-0.771**	**-0.764**	0.793	**0.793**	0.514	**0.919**
***P* value**		<0.0001****	0.328	0.043*	0.046*	0.120	0.033*	0.238	0.003**

Table S2.10. Correlations between relative HD rank and alpha diversity for cichlids that occur in both sand and rock habitats at all localities. Rho and p values are given for Spearman's Rank Correlation of alpha diversity values.

		ALPHA DIVERSITY					
	Relative human disturbance rank	**Median species richness per survey [interquartile range]**	**Median log abundance per survey [interquartile range]**	**Pielou's evenness index per locality (all surveys pooled)**	**Effective number of species per locality (all surveys pooled)**	**Proportion of sand + rock species per locality (all surveys pooled)**	**Proportion of sand + rock individuals per locality (all surveys pooled)**
Kigoma Town	10	2 [2]	1.29 [0.50]	0.70	6.3	0.26	0.19
Kigoma Deforested	7.5	2 [1.75]	1.35 [0.71]	0.67	5.3	0.21	0.11
Jakobsen's Beach	7.25	2 [1]	1.02 [0.60]	0.64	5.2	0.24	0.07
Kalilani Village	7	2 [2]	0.81 [0.56]	0.67	6.1	0.21	0.08
Gombe NP	4	2 [1]	1.27 [0.43]	0.68	6.3	0.22	0.14
Mahale S1	1	4 [1.75]	1.53 [0.63]	0.75	10.2	0.22	0.13
Mahale S2	1	2 [2]	1.00 [0.70]	0.82	7.1	0.18	0.06
Rho value		-0.515	0.126	-0.523	-0.595	0.505	0.360
***P* value**		0.237	0.788	0.229	0.159	0.248	0.427

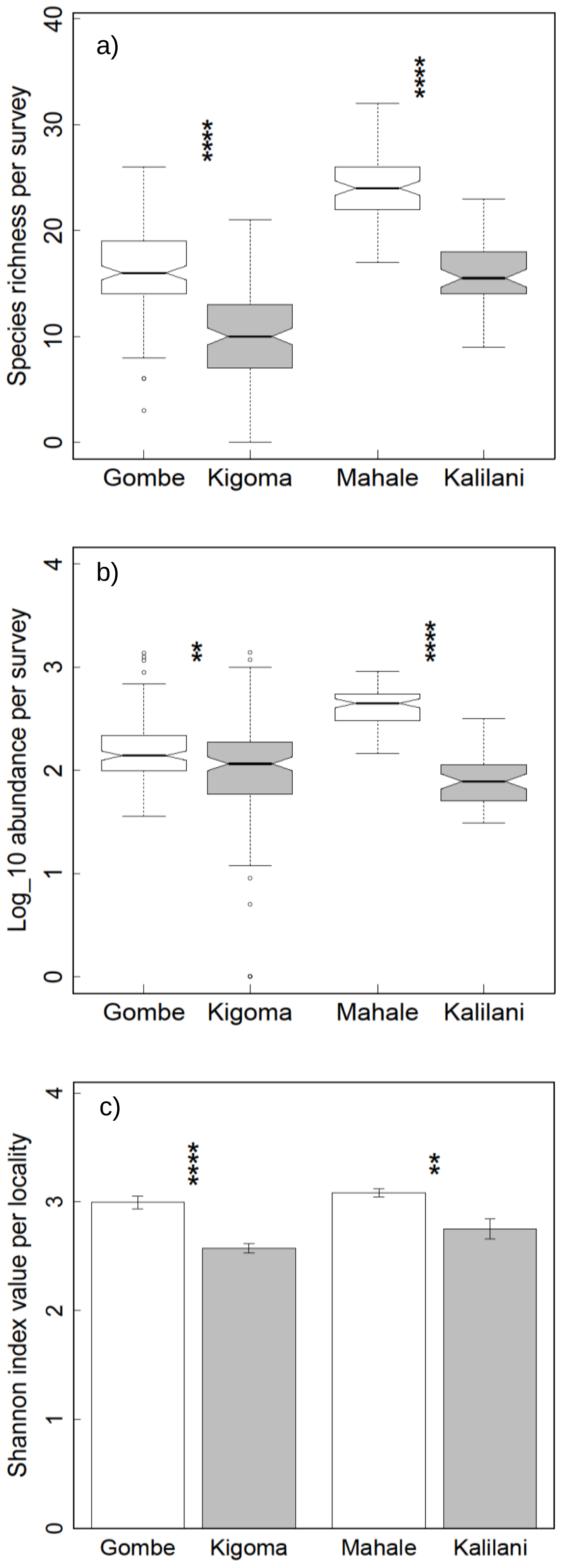

a)
Species richness per survey
0
10
20
30
40
****
****
Gombe
Kigoma
Mahale
Kalilani
b)
Log_10 abundance per survey
0
1
2
3
4
**
****
Gombe
Kigoma
Mahale
Kalilani
c)
Shannon index value per locality
0
1
2
3
4
****
**
Gombe
Kigoma
Mahale
Kalilani

Figure S2.6. Pairwise comparisons of alpha diversity values between protected (white) and unprotected (grey) localities, for (a) Species richness per survey, (b) Abundance per survey and (c) Shannon index per locality Asterisks indicate a significant difference (** $P \leq 0.01$, **** $P \leq 0.0001$) between locality pairs using a Mann Whitney Wilcoxon test (species richness and abundance), and a Hutcheson's t-test (Shannon index).

Chapter three supporting information

1. Anterior insertion of dorsal fin
2. Posterior insertion of dorsal fin
3. Dorsal insertion of caudal fin
4. Ventral base of caudal fin
5. Posterior insertion of anal fin
6. Anterior insertion of anal fin
7. Anterior insertion of pelvic fin
8. Lower insertion of pectoral fin
9. Upper insertion of pectoral fin
10. Posterior extremity of operculum
11. Posterior point of mouth cleavage
12. Lip juncture (anterior snout tip)
13. Centre of the orbit
13. Dorsal margin of the eye

Figure S3.1. The fourteen homologous landmarks used.

Table S3.1. List of 91 species used for FD analysis, with number of individuals indicated after the removal of outliers.

Species	**Individuals**	**Tribe**
Altolamprologous calvus	10	Lamprologini
Altolamprologus compressiceps	9	Lamprologini
Aulonocranus dewindti	10	Ectodini
Bathybates ferox	9	Bathybatini
Benthochromis tricoti	10	Benthochromini
Boulengerochromis microlepis	9	Boulengerochromini
Callochromis macrops	10	Ectodini
Callochromis melanostigma	9	Ectodini
Callochromis pleurospilous	10	Ectodini
Chalinochromis brichardi	10	Lamprologini
Chalinochromis popelini	10	Lamprologini
Ctenochromis horei	10	Tropheini
Cunningtonia longiventralis	8	Lamprologini
Cyathopharynx foae	10	Ectodini
Cyathopharynx furcifer	12	Ectodini
Cyphotilapia frontosa	10	Cyphotilapini
Cyprichromis leptosoma	10	Cyprochromini
Gnathochromis permaxillaris	10	Tropheini
Gnathochromis pfefferi	7	Tropheini
Haplotaxodon microlepis	10	Perrissodini
Julidochromis dickfeldi	10	Lamprologini
Julidochromis marlieri	9	Lamprologini
Julidochromis ornatus	8	Lamprologini
Julidochromis regani	9	Lamprologini
Julidochromis transcriptus	10	Lamprologini
Lamprologus callipterus	10	Lamprologini
Lamprologus leleupi	9	Lamprologini
Lamprologus lemairii	10	Lamprologini
Lepidiolamprologus attenuatus	8	Lamprologini
Lepidiolamprologus cunningtoni	10	Lamprologini
Lepidiolamprologus elongatus	10	Lamprologini
Lepidiolamprologus pleuromaculatus	10	Lamprologini
Lepidiolamprologus profundicola	10	Lamprologini
Limnotilapia dardenii	9	Tropheini

Lobochilotes labiatus	10	Tropheini
Microdontochromis rotundiventralis	10	Ectodini
Microdontochromis tenuidentatus	10	Ectodini
Neolamprologus caudopunctatus	10	Lamprologini
Neolamprologus christyi	9	Lamprologini
Neolamprologus falcicula	9	Lamprologini
Neolamprologus fasciatus	10	Lamprologini
Neolamprologus furcifer	10	Lamprologini
Neolamprologus gracilis	6	Lamprologini
Neolamprologus marunguensis	5	Lamprologini
Neolamprologus modestus	10	Lamprologini
Neolamprologus mondabu	9	Lamprologini
Neolamprologus mustax	10	Lamprologini
Neolamprologus niger	9	Lamprologini
Neolamprologus obscurus	10	Lamprologini
Neolamprologus savoryi	10	Lamprologini
Neolamprologus sexfasciatus	9	Lamprologini
Neolamprologus splendens	10	Lamprologini
Neolamprologus tetracanthus	10	Lamprologini
Neolamprologus toae	8	Lamprologini
Neolamprologus tretrocephalus	9	Lamprologini
Ophthalmotilapia boops	8	Ectodini
Ophthalmotilapia heterodonta	10	Ectodini
Ophthalmotilapia nasutus	10	Ectodini
Ophthalmotilapia ventralis	6	Ectodini
Oreochromis tanganicae	10	Tilapini
Paracyprichromis brieni	8	Cyprochromini
Perissodus microlepis	9	Perrissodini
Petrochromis famula	8	Tropheini
Petrochromis fasciolatus	9	Tropheini
Petrochromis macrognathus	6	Tropheini
Petrochromis orthognathus	10	Tropheini
Petrochromis polyodon	9	Tropheini
Petrochromis trewavasae	10	Tropheini
Plecodus paradoxus	10	Perrissodini
Plecodus straelini	10	Perrissodini
Pseudosimochromis babaulti	10	Tropheini
Pseudosimochromis curvifrons	9	Tropheini
Pseudosimochromis diagramma	9	Tropheini

Spathodus erythrodon	9	Eretmodini
Spathodus marlieri	8	Eretmodini
Tanganicodus irsacae	8	Eretmodini
Telmatochromis bifrenatus	10	Lamprologini
Telmatochromis caninus	10	Lamprologini
Telmatochromis dhonti	9	Lamprologini
Telmatochromis temporalis	10	Lamprologini
Telmatochromis vittatus	10	Lamprologini
Tropheus annectens	10	Tropheini
Tropheus brichardi	5	Tropheini
Tropheus duboisi	10	Tropheini
Tropheus moorii	10	Tropheini
Variabilichromis moorii	9	Lamprologini
Xenotilapia flavipinnis	10	Ectodini
Xenotilapia leptura	10	Ectodini
Xenotilapia melanogenys	9	Ectodini
Xenotilapia nasus	9	Ectodini
Xenotilapia spilopterus	10	Ectodini

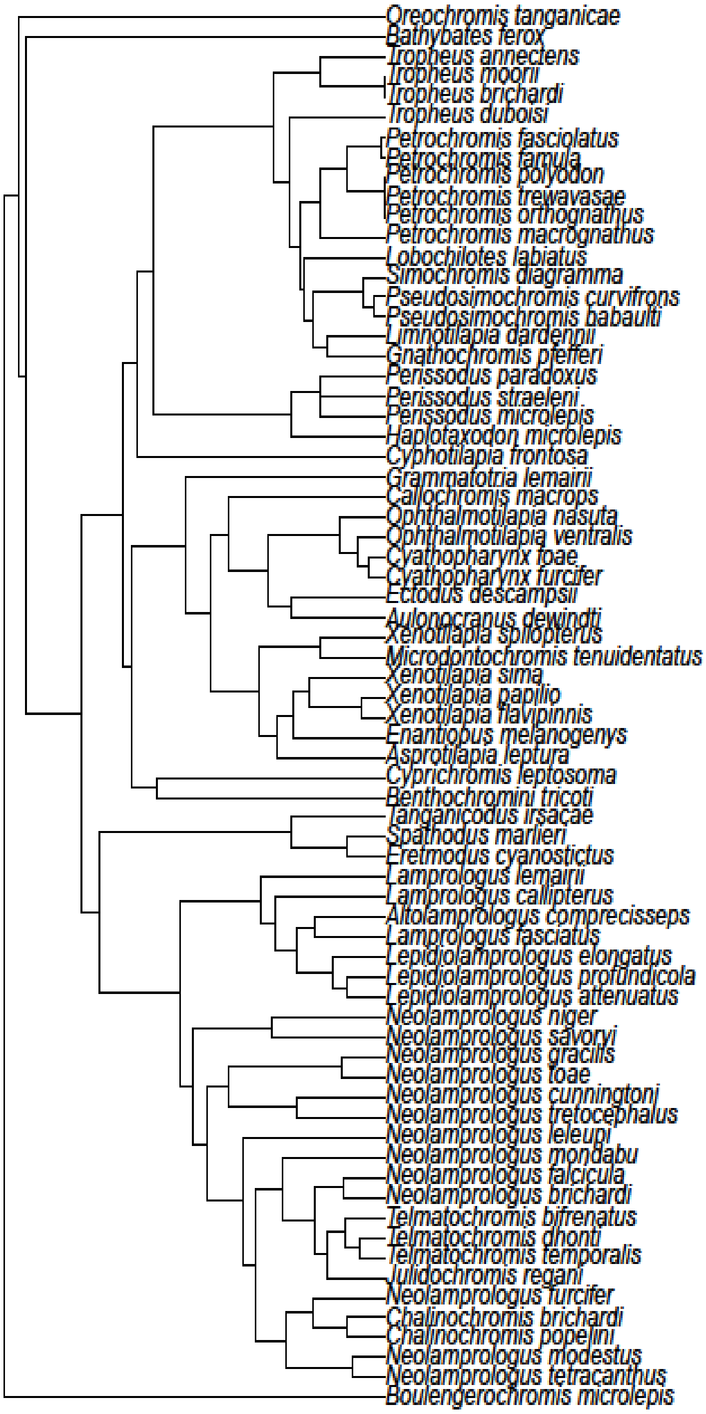

Oreochromis tanganicae
Bathybates ferox
Tropheus annectens
Tropheus moorii
Tropheus brichardi
Tropheus duboisi
Petrochromis fasciolatus
Petrochromis famula
Petrochromis polyodon
Petrochromis trewavasae
Petrochromis orthognathus
Petrochromis macrognathus
Lobochilotes labiatus
Simochromis diagramma
Pseudosimochromis curvifrons
Pseudosimochromis babaulti
Limnotilapia dardennii
Gnathochromis pfefferi
Perissodus paradoxus
Perissodus straeleni
Perissodus microlepis
Haplotaxodon microlepis
Cyphotilapia frontosa
Grammatotria lemairii
Callochromis macrops
Ophthalmotilapia nasuta
Ophthalmotilapia ventralis
Cyathopharynx foae
Cyathopharynx furcifer
Ectodus descampsii
Aulonocranus dewindti
Xenotilapia spilopterus
Microdontochromis tenuidentatus
Xenotilapia sima
Xenotilapia papilio
Xenotilapia flavipinnis
Enantiopus melanogenys
Asprotilapia leptura
Cyprichromis leptosoma
Benthochromini tricoti
Tanganicodus irsacae
Spathodus marlieri
Eretmodus cyanostictus
Lamprologus lemairii
Lamprologus callipterus
Altolamprologus comprecisseps
Lamprologus fasciatus
Lepidiolamprologus elongatus
Lepidiolamprologus profundicola
Lepidiolamprologus attenuatus
Neolamprologus niger
Neolamprologus savoryi
Neolamprologus gracilis
Neolamprologus toae
Neolamprologus cunningtoni
Neolamprologus tretocephalus
Neolamprologus leleupi
Neolamprologus mondabu
Neolamprologus falcicula
Neolamprologus brichardi
Telmatochromis bifrenatus
Telmatochromis dhonti
Telmatochromis temporalis
Julidochromis regani
Neolamprologus furcifer
Chalinochromis brichardi
Chalinochromis popelini
Neolamprologus modestus
Neolamprologus tetracanthus
Boulengerochromis microlepis

Figure S3.2. The 70 species used for PD analysis. 12 species: *Cyathopharynx foae, Neolamprologus cunningtoni, Neolamprologus gracilis, Perissodus paradoxus, Petrochromis famula, Petrochromis fasciolatus, Petrochromis polyodon, Petrochromis trewavasae, Pseudosimochromis curvifrons, Spathodus marlieri, Telmatochromis dhonti, Xenotilapia papilio* were added to the Day *et al.* (2008) phylogeny.

Table S3.2. Phylogenetic diversity (PD) indices at all localities calculated from the 58 species tree, with the number of surveys, locality species richness (SR), and mean survey SR indicated. Locality alpha PD includes Faith’s PD, the net relatedness index (NRI) the nearest taxon index (NTI). NRI and NTI are calculated from the standardised effect sizes of the mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) from 999 random simulations, with no significantly phylogenetically clustered (positive values) or dispersed (negative values) values reported. Survey alpha diversity includes the mean survey Faiths PD and Pearson correlations coefficient with survey SR (Survey SR PD), with significant relationships from linear regressions starred. Beta FD was calculated within localities based on survey species abundance, using MPD and MNTD indices.

				ALPHA					*BETA*	
	Surveys	**SR**	**Survey SR**	**PD**	**NRI (SES**	**NTI (SES)**	**Survey PD**	**Survey SR PD**	**MPD**	**MNTD**
Mahale NP S1	83	56	20	253	-0.56	-0.19	109	0.77*	15.1	4.04
Mahale NP S2	55	49	18	225	-0.37	-1.00	101	0.88*	15.3	3.78
Gombe NP	138	44	15	206	-0.76	1.66	77	0.91*	15.3	3.52
Kalilani Village	56	41	14	194	0.35	0.04	77	0.91*	15.1	2.90
Jakobsen’s Beach	42	38	13	180	0.32	-0.38	74	0.85*	14.7	3.35
Kigoma Deforested	42	38	11	171	0.53	-0.72	65	0.96*	15.6	5.09
Kigoma Town	134	40	10	189	1.58	1.57	54	0.95*	13.0	4.52

Table S3.3. Standardised four-dimensional locality and survey level functional richness (FRic) and functional dispersion (FDis) values calculated from 42 surveys.

	Locality level			*Survey level*		
	SR	**FRic**	**FDis**	**SR**	**FRic**	**FDis**
Mahale NP S1	53	0.79	0.4	23	0.24	0.37
Mahale NP S2	52	0.66	0.51	21	0.19	0.48
Gombe NP	38	0.48	0.48	14	0.12	0.42
Kalilani Village	41	0.51	0.47	15	0.11	0.42
Jakobsen's Beach	36	0.47	0.39	14	0.09	0.38
Kigoma Deforested	36	0.44	0.3	12	0.04	0.31
Kigoma Town	31	0.42	0.45	10	0.05	0.35

Table S3.4a. Landmark data four-dimensional overall axes species functional uniqueness values at each locality, and for the whole species pool.

Species	**All**	**Mahale NP S1**	**Mahale NP S2**	**Gombe NP**	**Jakobsen's Beach**	**Kalilani Village**	**Kigoma Deforested**	**Kigoma Town**
	0.08	0.07	0.09	0.07	0.08	0.08	0.06	0.08
Altolamprologous calvus	0.10							
Altolamprologus compressiceps	0.13	0.14	0.14	0.14	0.14	0.15	0.15	0.15
Aulonocranus dewindti	0.08	0.08	0.08				0.09	
Bathybates ferox	0.09	0.08	0.07	0.08	0.08		0.08	
Benthochromis tricoti	0.09	0.07	0.07					
Boulengerochromis microlepis	0.08	0.06	0.06	0.07	0.06	0.06	0.06	
Callochromis macrops	0.09	0.09	0.09			0.11		0.11
Callochromis melanostigma	0.08							
Callochromis pleurospilous	0.07							
Chalinochromis brichardi	0.07	0.07	0.07	0.07	0.06	0.07	0.07	0.07
Chalinochromis popelini	0.08	0.07	0.07	0.08				
Ctenochromis horei	0.06							
Cunningtonia longiventralis	0.07							
Cyathopharynx foae	0.06	0.06	0.06	0.06			0.06	
Cyathopharynx furcifer	0.06				0.06	0.07		0.06
Cyphotilapia frontosa	0.09	0.11	0.11	0.10	0.11	0.13		0.13
Cyprichromis leptosoma	0.09	0.07	0.07	0.08	0.08	0.08	0.07	0.06
Gnathochromis permaxillaris	0.07							
Gnathochromis pfefferi	0.06	0.07	0.07	0.07	0.07	0.09	0.08	0.09
Haplotaxodon microlepis	0.10	0.09	0.08	0.09	0.09	0.07	0.08	0.07
Julidochromis dickfeldi	0.08							

Julidochromis marlieri	0.09							
Julidochromis ornatus	0.08							
Julidochromis regani	0.08	0.07	0.06	0.07	0.06	0.06	0.07	0.06
Julidochromis transcriptus	0.07							
Lamprologus callipterus	0.08	0.07	0.06	0.07	0.07	0.05	0.07	0.05
Lamprologus leleupi	0.06	0.07	0.06	0.07			0.07	
Lamprologus lemairii	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08
Lepidiolamprologus attenuatus	0.10	0.08	0.08	0.09	0.08	0.06	0.08	0.05
Lepidiolamprologus cunningtoni	0.08							
Lepidiolamprologus elongatus	0.07	0.07	0.06	0.08	0.07	0.06	0.07	0.05
Lepidiolamprologus pleuromaculatus	0.07							
Lepidiolamprologus profundicola	0.07	0.06	0.05		0.06		0.06	0.04
Limnotilapia dardenii	0.06	0.06	0.06	0.07	0.06	0.08	0.07	0.08
Lobochilotes labiatus	0.08	0.10	0.10	0.09	0.09	0.12	0.10	0.12
Microdontochromis rotundiventralis	0.07							
Microdontochromis tenuidentatus	0.09	0.07	0.07	0.08				
Neolamprologus caudopunctatus	0.07							
Neolamprologus christyi	0.06							
Neolamprologus falcicula	0.08	0.08	0.08	0.09	0.08	0.09	0.09	
Neolamprologus fasciatus	0.09	0.08	0.08		0.08			
Neolamprologus furcifer	0.08	0.07	0.07	0.07	0.07	0.07	0.07	0.06
Neolamprologus gracilis	0.06	0.06	0.06	0.06			0.06	
Neolamprologus marunguensis	0.07							
Neolamprologus modestus	0.06	0.06		0.07				

Neolamprologus mondabu	0.06	0.06	0.05	0.06	0.05	0.06	0.06	0.06
Neolamprologus mustax	0.06							
Neolamprologus niger	0.07	0.07	0.07		0.07			
Neolamprologus obscurus	0.06							
Neolamprologus savoryi	0.07	0.08	0.08	0.07	0.07		0.08	0.09
Neolamprologus sexfasciatus	0.08							
Neolamprologus splendens	0.06							
Neolamprologus tetracanthus	0.06	0.05	0.05	0.06			0.05	
Neolamprologus toae	0.08	0.09	0.09	0.09	0.08	0.10	0.10	0.10
Neolamprologus tretrocephalus	0.07	0.08	0.08	0.08	0.08	0.10	0.08	0.10
Ophthalmotilapia boops	0.07							
Ophthalmotilapia heterodonta	0.06							
Ophthalmotilapia nasutus	0.06	0.06	0.06	0.06			0.07	
Ophthalmotilapia ventralis	0.06	0.06	0.06	0.06	0.06	0.07		0.07
Oreochromis tanganicae	0.10	0.11	0.12	0.11				
Paracyprichromis brieni	0.08							
Perissodus microlepis	0.09	0.07	0.07	0.08	0.08	0.06	0.07	0.05
Petrochromis famula	0.08	0.10	0.10	0.10	0.09	0.12	0.11	0.12
Petrochromis fasciolatus	0.07	0.08	0.08		0.07			
Petrochromis macrognathus	0.07	0.09	0.09	0.08			0.09	
Petrochromis orthognathus	0.08	0.10	0.10	0.09	0.09	0.12	0.10	0.12
Petrochromis polyodon	0.08	0.10	0.10	0.10	0.09	0.12		0.13
Petrochromis trewavasae	0.09	0.11	0.11	0.11	0.10	0.13		0.14
Plecodus paradoxus	0.10	0.08	0.08	0.09			0.08	

Plecodus straelini	0.08	0.09	0.09	0.09	0.08		0.10	
Pseudosimochromis babaulti	0.08	0.10	0.10	0.10	0.09	0.12	0.10	0.12
Pseudosimochromis curvifrons	0.06	0.07	0.07	0.07				
Pseudosimochromis diagramma	0.07	0.08	0.08	0.08	0.08	0.10	0.09	0.10
Spathodus erythrodon	0.07							
Spathodus marlieri	0.12	0.12		0.12	0.12		0.13	
Tanganicodus irsacae	0.06	0.07	0.07	0.07				
Telmatochromis bifrenatus	0.09							
Telmatochromis caninus	0.07							
Telmatochromis dhonti	0.07	0.07	0.06	0.07	0.07			
Telmatochromis temporalis	0.06	0.06	0.06	0.07	0.06	0.07	0.07	0.07
Telmatochromis vittatus	0.10	0.09	0.09	0.09	0.09	0.08	0.09	0.08
Tropheus annectens	0.09	0.10	0.10	0.10				
Tropheus brichardi	0.09	0.10	0.11	0.10	0.10	0.12	0.11	0.13
Tropheus duboisi	0.10	0.11	0.12	0.11	0.11	0.14	0.12	0.14
Tropheus moorii	0.09	0.11	0.11	0.10				
Variabilichromis moorii	0.08							
Xenotilapia flavipinnis	0.08	0.06	0.06		0.07	0.05	0.06	0.05
Xenotilapia leptura	0.14	0.12	0.12	0.13	0.13	0.11	0.12	
Xenotilapia melanogenys	0.14	0.13	0.12	0.13	0.13	0.10		0.09
Xenotilapia nasus	0.07							
Xenotilapia spilopterus	0.06	0.05	0.05	0.06	0.05	0.06	0.06	0.06

Table S3.4b. Landmark data four-dimensional highest axes species functional uniqueness values at each locality.

Species	Mahale NP S1	Mahale NP S2	Gombe NP	Jakobsen's Beach	Kalilani Village	Kigoma Deforested	Kigoma Town
Altolamprologous calvus							
Altolamprologus compressiceps	0.08	0.08	0.08	0.1	0.09	0.11	0.08
Aulonocranus dewindti	0.06				0.06		
Bathybates ferox	0.05	0.05	0.05		0.05		
Benthochromis tricoti	0.04						
Boulengerochromis microlepis	0.04	0.05	0.04	0.03	0.04		0.04
Callochromis macrops	0.06			0.09		0.09	0.06
Callochromis melanostigma							
Callochromis pleurospilous							
Chalinochromis brichardi	0.04	0.04	0.04	0.05	0.04	0.05	0.04
Chalinochromis popelini	0.04	0.05					
Ctenochromis horei							
Cunningtonia longiventralis							
Cyathopharynx foae	0.04	0.04			0.05		
Cyathopharynx furcifer			0.04	0.05		0.06	0.04
Cyphotilapia frontosa	0.1	0.09	0.09	0.12		0.13	0.1
Cyprichromis leptosoma	0.05	0.06	0.05	0.02	0.05	0.02	0.05
Gnathochromis permaxillaris							
Gnathochromis pfefferi	0.06	0.06	0.06	0.08	0.06	0.09	0.05
Haplotaxodon microlepis	0.05	0.06	0.05	0.05	0.05	0.05	0.05
Julidochromis dickfeldi							
Julidochromis marlieri							

Julidochromis ornatus							
Julidochromis regani	0.04	0.05	0.04	0.05	0.04	0.05	0.04
Julidochromis transcriptus							
Lamprologus callipterus	0.04	0.05	0.04	0.03	0.04	0.03	0.04
Lamprologus leleupi	0.05	0.05			0.05		
Lamprologus lemairii	0.05	0.04	0.05	0.06	0.05	0.06	0.06
Lepidiolamprologus attenuatus	0.06	0.07	0.06	0.03	0.05	0.03	0.06
Lepidiolamprologus cunningtoni							
Lepidiolamprologus elongatus	0.04	0.05	0.04	0.03	0.04	0.02	0.04
Lepidiolamprologus pleuromaculatus							
Lepidiolamprologus profundicola	0.04		0.04		0.04	0.03	
Limnotilapia dardenii	0.05	0.05	0.04	0.06	0.05	0.07	0.04
Lobochilotes labiatus	0.08	0.08	0.08	0.11	0.09	0.11	0.08
Microdontochromis rotundiventralis							
Microdontochromis tenuidentatus	0.05	0.06					
Neolamprologus caudopunctatus							
Neolamprologus christyi							
Neolamprologus falcicula	0.05	0.05	0.05	0.07	0.06		0.04
Neolamprologus fasciatus	0.04		0.04				
Neolamprologus furcifer	0.04	0.05	0.05	0.05	0.04	0.04	0.06
Neolamprologus gracilis	0.04	0.04			0.04		
Neolamprologus marunguensis							
Neolamprologus modestus		0.04					
Neolamprologus mondabu	0.04	0.04	0.04	0.05	0.05	0.05	0.04
Neolamprologus mustax							
Neolamprologus niger	0.05		0.05				

Neolamprologus obscurus							
Neolamprologus savoryi	0.06	0.06	0.06		0.07	0.09	0.05
Neolamprologus sexfasciatus							
Neolamprologus splendens							
Neolamprologus tetracanthus	0.04	0.04			0.04		0.04
Neolamprologus toae	0.07	0.06	0.06	0.09	0.07	0.09	0.06
Neolamprologus tretrocephalus	0.06	0.05	0.05	0.08	0.06	0.08	0.05
Ophthalmotilapia boops							
Ophthalmotilapia heterodonta							
Ophthalmotilapia nasutus	0.05	0.04			0.05		
Ophthalmotilapia ventralis	0.04	0.04	0.04	0.05		0.06	0.04
Oreochromis tanganicae	0.1	0.09					
Paracyprichromis brieni							
Perissodus microlepis	0.05	0.06	0.06	0.03	0.05	0.03	0.06
Petrochromis famula	0.09	0.08	0.08	0.11	0.09	0.11	0.08
Petrochromis fasciolatus	0.06		0.05				
Petrochromis macrognathus	0.07	0.07			0.08		
Petrochromis orthognathus	0.07	0.07	0.07	0.1	0.08	0.1	0.07
Petrochromis polyodon	0.09	0.08	0.08	0.11		0.12	0.09
Petrochromis trewavasae	0.1	0.09	0.09	0.12		0.12	
Plecodus paradoxus	0.06	0.07			0.05		
Plecodus straelini	0.05	0.05	0.05		0.06		
Pseudosimochromis babaulti	0.08	0.07	0.07	0.1	0.08	0.11	0.07
Pseudosimochromis curvifrons	0.06	0.05					
Pseudosimochromis diagramma	0.06	0.05	0.05	0.07	0.06	0.08	0.05
Spathodus erythrodon							

Spathodus marlieri		0.09	0.08		0.09		
Tanganicodus irsacae	0.06	0.05					
Telmatochromis bifrenatus							
Telmatochromis caninus							
Telmatochromis dhonti	0.04	0.04	0.04				
Telmatochromis temporalis	0.04	0.04	0.04	0.05	0.05	0.06	0.04
Telmatochromis vittatus	0.06	0.06	0.05	0.07	0.05	0.07	0.06
Tropheus annectens	0.07	0.07					
Tropheus brichardi	0.07	0.06	0.06	0.09	0.07	0.1	0.06
Tropheus duboisi	0.09	0.08	0.08	0.11	0.09	0.12	0.08
Tropheus moorii	0.07	0.07					
Variabilichromis moorii							
Xenotilapia flavipinnis	0.04		0.05	0.02	0.04	0.02	0.05
Xenotilapia leptura	0.09	0.1	0.1	0.07	0.09		0.1
Xenotilapia melanogenys	0.09	0.1	0.1	0.07		0.06	0.1
Xenotilapia nasus							
Xenotilapia spilopterus	0.04	0.04	0.04	0.05	0.05	0.05	0.04

Table S3.4c. Species functional uniqueness values based on landmark and body size data over all six PC axes at each locality and for the whole species pool.

Species	**All**	**Mahale NP S1**	**Mahale NP S2**	**Gombe NP**	**Jakobsen's Beach**	**Kalilani Village**	**Kigoma Deforested**	**Kigoma Town**
Altolamprologous calvus	1.24							
Altolamprologus compressiceps	1.24	1.18	1.16	1.17	1.31	1.09	1.36	1.27
Aulonocranus dewindti	1.29	0.96				1.18		
Bathybates ferox	1.3	1.34	1.2	1.22		1.38		
Benthochromis tricoti	1.3	1.38						
Boulengerochromis microlepis	1.77	1.76	1.83	1.78	1.57	1.86		1.81
Callochromis macrops	1.25	1.02			1.27		1.26	1.26
Callochromis melanostigma	1.33							
Callochromis pleurospilous	1.31							
Chalinochromis brichardi	1.36	1.5	1.56	1.53	1.45	1.44	1.41	1.45
Chalinochromis popelini	1.28	1.39	1.42					
Ctenochromis horei	1.22							
Cunningtonia longiventralis	1.28							
Cyathopharynx foae	1.3	1.33	1.19			1.37		
Cyathopharynx furcifer	1.33			1.07	1.36		1.36	1.11

Cyphotilapia frontosa	1.48	1.23	1.37	1.41	1.04		0.99	1.44
Cyprichromis leptosoma	1.37	1.04	1.25	1.33	0.67	1.29	0.6	1.35
Gnathochromis permaxillaris	1.26							
Gnathochromis pfefferi	1.25	1.03	1.06	1.16	1.28	0.97	1.27	1.26
Haplotaxodon microlepis	1.27	1.37	1.29	1.16	1.41	1.24	1.51	1.19
Julidochromis dickfeldi	1.26							
Julidochromis marlieri	1.26							
Julidochromis ornatus	1.36							
Julidochromis regani	1.31	1.44	1.45	1.42	1.47	1.31	1.46	1.4
Julidochromis transcriptus	1.29							
Lamprologus callipterus	1.31	1.37	1.31	1.35	1.41	1.36	1.44	1.41
Lamprologus leleupi	1.3	1.37	1.19			1.38		
Lamprologus lemairii	1.3	1.28	1.16	1.08	1.4	1.32	1.4	1.03
Lepidiolamprologus attenuatus	1.29	1.06	1.12	1.17	1.12	1.12	1.08	1.2
Lepidiolamprologus cunningtoni	1.23							
Lepidiolamprologus elongatus	1.23	0.95	0.99	1.12	1.21	0.9	1.18	1.23
Lepidiolamprologus pleuromaculatus	1.24							

Lepidiolamprologus profundicola	1.32	1.31		1.28		1.33	1.3	
Limnotilapia dardenii	1.25	1.35	1.35	1.25	1.26	1.34	1.31	1.23
Lobochilotes labiatus	1.26	1.41	1.43	1.35	1.31	1.38	1.33	1.3
Microdontochromis rotundiventralis	1.39							
Microdontochromis tenuidentatus	1.32	1.45	1.46					
Neolamprologus caudopunctatus	1.27							
Neolamprologus christyi	1.28							
Neolamprologus falcicula	1.32	1.31	1.16	1.11	1.46	1.34		0.98
Neolamprologus fasciatus	1.31	1.12		1.21				
Neolamprologus furcifer	1.26	0.95	1.13	1.22	0.74	1.16	0.67	1.24
Neolamprologus gracilis	1.22	0.9	1.07			1.02		
Neolamprologus marunguensis	1.33							
Neolamprologus modestus	1.25		1.18					
Neolamprologus mondabu	1.24	1.33	1.26	1.12	1.34	1.22	1.45	1.16
Neolamprologus mustax	1.29							
Neolamprologus niger	1.25	1.43		1.34				
Neolamprologus obscurus	1.36							

Neolamprologus savoryi	1.25	1.37	1.29	1.34		1.27	1.52	1.37
Neolamprologus sexfasciatus	1.3							
Neolamprologus splendens	1.31							
Neolamprologus tetracanthus	1.31	1.28	1.17			1.33		1.05
Neolamprologus toae	1.33	1.13	1.17	1.23	1.24	1.15	1.21	1.24
Neolamprologus tretrocephalus	1.25	0.93	1.11	1.2	0.77	1.13	0.7	1.23
Ophthalmotilapia boops	1.26							
Ophthalmotilapia heterodonta	1.24							
Ophthalmotilapia nasutus	1.23	1.13	1.14			1.08		
Ophthalmotilapia ventralis	1.22	1.3	1.23	1.1	1.32		1.42	1.14
Oreochromis tanganicae	1.43	1.51	1.58					
Paracyprichromis brieni	1.35							
Perissodus microlepis	1.3	1.43	1.44	1.42	1.45	1.31	1.44	1.4
Petrochromis famula	1.23	1.3	1.24	1.31	1.37	1.25	1.37	1.36
Petrochromis fasciolatus	1.28	1.36		1.33				
Petrochromis macrognathus	1.31	1.33	1.21			1.38		
Petrochromis orthognathus	1.32	1.27	1.19	1.07	1.35	1.34	1.34	1.11

Petrochromis polyodon	1.31	1.08	1.15	1.2	1.14		1.1	1.23
Petrochromis trewavasae	1.33	1	1.2	1.29	0.71		0.65	
Plecodus paradoxus	1.36	1.06	1.23			1.22		
Plecodus straelini	1.22	1.13	1.13	1.15		1.06		
Pseudosimochromis babaulti	1.21	1.29	1.23	1.1	1.3	1.19	1.4	1.14
Pseudosimochromis curvifrons	1.26	1.42	1.36					
Pseudosimochromis diagramma	1.36	1.46	1.51	1.44	1.32	1.47	1.32	1.41
Spathodus erythrodon	1.4							
Spathodus marlieri	1.35		1.49	1.47		1.35		
Tanganicodus irsacae	1.23	1.31	1.25					
Telmatochromis bifrenatus	1.36							
Telmatochromis caninus	1.31							
Telmatochromis dhonti	1.3	1.28	1.16	1.08				
Telmatochromis temporalis	1.2	0.9	1.06	1.14	0.82	1.06	0.75	1.16
Telmatochromis vittatus	1.21	0.9	1.05	1.14	1.08	1	1.04	1.19
Tropheus annectens	1.27	1.05	1.08					
Tropheus brichardi	1.22	1.16	1.14	1.15	1.28	1.07	1.34	1.25
Tropheus duboisi	1.29	1.38	1.31	1.18	1.42	1.26	1.53	1.21
Tropheus moorii	1.22	1.36	1.32					

Variabilichromis moorii	1.27							
Xenotilapia flavipinnis	1.4	1.56		1.57	1.54	1.48	1.49	1.47
Xenotilapia leptura	1.3	1.41	1.43	1.41	1.41	1.31		1.4
Xenotilapia melanogenys	1.27	1.35	1.28	1.35	1.41		1.41	1.4
Xenotilapia nasus	1.31							
Xenotilapia spilopterus	1.32	1.3	1.16	1.11	1.45	1.33	1.45	1

Table S3.4d. Species functional uniqueness values based on landmark data for the highest value PC axes at each locality.

Species	**Mahale NP S1**	**Mahale NP S2**	**Gombe NP**	**Jakobsen's Beach**	**Kalilani Village**	**Kigoma Deforested**	**Kigoma Town**
Altolamprologous calvus							
Altolamprologus compressiceps	0.72	0.74	0.7	0.76	0.65	0.81	0.74
Aulonocranus dewindti	0.38				0.51		
Bathybates ferox	0.64	0.49	0.42		0.5		
Benthochromis tricoti	0.46						
Boulengerochromis microlepis	1.25	1.29	1.28	1.06	1.32		1.34
Callochromis macrops	0.52			0.61		0.62	0.62
Callochromis melanostigma							
Callochromis pleurospilous							
Chalinochromis brichardi	0.68	0.52	0.43	0.71	0.54	0.78	0.34
Chalinochromis popelini	0.51	0.4					
Ctenochromis horei							
Cunningtonia longiventralis							
Cyathopharynx foae	0.63	0.48			0.49		
Cyathopharynx furcifer			0.44	0.58		0.63	0.4

Cyphotilapia frontosa	0.46	0.44	0.52	0.43		0.37	0.61
Cyprichromis leptosoma	0.41	0.57	0.7	0.39	0.55	0.32	0.78
Gnathochromis permaxillaris							
Gnathochromis pfefferi	0.52	0.55	0.56	0.61	0.48	0.62	0.62
Haplotaxodon microlepis	0.78	0.74	0.7	0.8	0.66	0.87	0.74
Julidochromis dickfeldi							
Julidochromis marlieri							
Julidochromis ornatus							
Julidochromis regani	0.55	0.42	0.41	0.61	0.43	0.67	0.34
Julidochromis transcriptus							
Lamprologus callipterus	0.54	0.56	0.54	0.61	0.58	0.66	0.6
Lamprologus leleupi	0.73	0.56			0.58		
Lamprologus lemairii	0.56	0.42	0.42	0.62	0.45	0.67	0.36
Lepidiolamprologus attenuatus	0.4	0.37	0.43	0.56	0.46	0.55	0.47
Lepidiolamprologus cunningtoni							
Lepidiolamprologus elongatus	0.49	0.52	0.55	0.59	0.46	0.59	0.65
Lepidiolamprologus pleuromaculatus							

Lepidiolamprologus profundicola	0.68		0.7		0.74	0.7	
Limnotilapia dardenii	0.74	0.58	0.54	0.77	0.6	0.83	0.54
Lobochilotes labiatus	0.84	0.68	0.55	0.86	0.69	0.93	0.46
Microdontochromis rotundiventralis							
Microdontochromis tenuidentatus	0.55	0.42					
Neolamprologus caudopunctatus							
Neolamprologus christyi							
Neolamprologus falcicula	0.59	0.44	0.41	0.65	0.45		0.34
Neolamprologus fasciatus	0.55		0.52				
Neolamprologus furcifer	0.36	0.5	0.62	0.4	0.47	0.33	0.71
Neolamprologus gracilis	0.4	0.57			0.55		
Neolamprologus marunguensis							
Neolamprologus modestus		0.77					
Neolamprologus mondabu	0.74	0.75	0.70	0.76	0.66	0.83	0.74
Neolamprologus mustax							
Neolamprologus niger	0.94		0.65				
Neolamprologus obscurus							

Neolamprologus savoryi	0.57	0.43	0.41		0.43	0.68	0.34
Neolamprologus sexfasciatus							
Neolamprologus splendens							
Neolamprologus tetracanthus	0.55	0.42			0.46		0.37
Neolamprologus toae	0.59	0.55	0.55	0.77	0.51	0.76	0.49
Neolamprologus tretrocephalus	0.36	0.49	0.61	0.4	0.46	0.33	0.7
Ophthalmotilapia boops							
Ophthalmotilapia heterodonta							
Ophthalmotilapia nasutus	0.68	0.7			0.62		
Ophthalmotilapia ventralis	0.72	0.74	0.69	0.75		0.81	0.73
Oreochromis tanganicae	0.72	0.75					
Paracyprichromis brieni							
Perissodus microlepis	0.54	0.41	0.42	0.6	0.44	0.65	0.35
Petrochromis famula	0.47	0.47	0.45	0.56	0.49	0.59	0.51
Petrochromis fasciolatus	0.58		0.52				
Petrochromis macrognathus	0.59	0.44			0.45		
Petrochromis orthognathus	0.5	0.39	0.43	0.58	0.47	0.62	0.39

Petrochromis polyodon	0.43	0.39	0.42	0.59		0.58	0.48
Petrochromis trewavasae	0.4	0.56	0.69	0.39		0.32	
Plecodus paradoxus	0.55	0.72			0.7		
Plecodus straelini	0.71	0.73	0.68		0.64		
Pseudosimochromis babaulti	0.72	0.74	0.69	0.76	0.65	0.81	0.74
Pseudosimochromis curvifrons	0.96	0.8					
Pseudosimochromis diagramma	0.72	0.61	0.6	0.75	0.64	0.81	0.66
Spathodus erythrodon							
Spathodus marlieri		0.42	0.41		0.43		
Tanganicodus irsacae	0.49	0.41					
Telmatochromis bifrenatus							
Telmatochromis caninus							
Telmatochromis dhonti	0.57	0.43	0.42				
Telmatochromis temporalis	0.34	0.44	0.57	0.4	0.42	0.34	0.66
Telmatochromis vittatus	0.38	0.52	0.65	0.43	0.5	0.4	0.74
Tropheus annectens	0.52	0.54					
Tropheus brichardi	0.72	0.74	0.69	0.76	0.65	0.81	0.74
Tropheus duboisi	0.77	0.77	0.73	0.79	0.68	0.85	0.77
Tropheus moorii	0.88	0.71					

Variabilichromis moorii							
Xenotilapia flavipinnis	0.74		0.44	0.76	0.59	0.82	0.36
Xenotilapia leptura	0.51	0.39	0.43	0.58	0.47		0.38
Xenotilapia melanogenys	0.49	0.52	0.51	0.57		0.61	0.56
Xenotilapia nasus							
Xenotilapia spilopterus	0.59	0.44	0.42	0.64	0.45	0.7	0.36

Table S3.5. Four-dimensional feeding and tribal group SR and FRic values for all localities based on proportions of the group at each locality compared to the total lakewide FRic of each group.

	SR	Inv	Herb	Pisc	Lamp	Troph	Ecto
Mahale NP S1	60	27 / 0.70	21 / 0.39	8 / 1.00	23 / 0.58	16 / 0.93	10 / 0.67
Mahale NP S2	54	23 / 0.54	21 / 0.68	6 / 0.56	21 / 0.51	15 / 0.67	7 / 0.14
Gombe NP	45	19 / 0.52	15 / 0.55	8 / 1.00	19 / 0.57	12 / 0.73	6 / 0.06
Kalilani Village	43	21 / 0.41	12 / 0.31	6 / 0.04	19 / 0.49	10 / 0.39	6 / 0.03
Jakobsen’s Beach	37	18 / 0.56	12 / 0.18	5 / 0.08	14 / 0.48	11 / 0.53	7 / 0.23
Kigoma Deforested	36	18 / 0.45	11 / 0.07	5 / 0.04	15 / 0.37	11 / 0.53	6 / 0.04
Kigoma Town	38	20 / 0.56	11 / 0.14	5 / 0.08	16 / 0.48	10 / 0.45	7 / 0.23

Table S3.6. Four-dimensional localities SES FRic and p values for each feeding and tribal group based on 999 random simulations with locality specific fixed feeding and tribal group SR from the pool of each group.

	Inv	Herb	Pisc	Lamp	Troph	Ecto
SR	46	26	10	41	17	18
Mahale NP S1	1.1 / 0.33	-1.3 / 0.24	0 / 1	0.46 / 0.67	0.22 / 0.94	2.41 / 0.06
Mahale NP S2	0.73 / 0.47	0.14 / 0.94	1.39 / 0.24	0.41 / 0.7	-1.4 / 0.23	-0.63 / 0.61
Gombe NP	1.45 / 0.19	1.21 / 0.33	0 / 1	1.51 / 0.15	1.46 / 0.16	0.36 / 0.35
Kalilani Village	0.18 / 0.81	0.51 / 0.52	-0.86 / 0.32	0.8 / 0.45	0.18 / 0.81	-0.2 / 0.54
Jakobsen’s Beach	2.28 / 0.05	-0.42 / 0.86	0.46 / 0.42	2.56 / 0.05	0.6 / 0.52	1.79 / 0.12
Kigoma Deforested	1.29 / 0.23	-1/ 0.23	-0.19 / 0.8	1 / 0.33	0.61 / 0.53	-0.07 / 0.64
Kigoma Town	1.58 / 0.15	-0.42 / 0.83	0.43 / 0.41	1.78 / 0.11	0.78 / 0.4	2.04 / 0.09

Table S3.7. Percentage of FRic of n species from 200 uniqueness rank biased simulations from the regional species pool differing to n species from 999 random simulations of the regional species pool.

SR	% biased towards uniqueness rank	% biased against uniqueness rank
10	25	30.5
20	22	49.5
30	36	79.5
40	47	93
50	49	94.5
60	66	98.5
70	78	98
80	89	99.5

Chapter four supporting information

Table S4.1. Number of individuals of all cichlid and baseline species sampled at the four sites. Numbers starred indicates species that were sampled but the presence of inorganic carbonates prevented reliable baseline stable isotope values being obtained.

	Species	Feeding type	TAFIRI Bay February 2015	Kalilani Island March 2015	TAFIRI Bay October 2016	Kigoma Deforested October 2016
Cichlidae						
Eretmodini	*Eretmodus cyanostictus*	Benthic herbivore	15	15		15
Tropheini	*Petrochromis famula*	Benthic herbivore	13	8	13	15
	Pseudosimochromis babaulti	Benthic herbivore	15	13		15
	Tropheus brichardi	Benthic herbivore	15	15	15	15
	Lobochilotes labiatus	Benthic invertivore	9	15		15
Ectodini	*Ophthalmotilapia ventralis*	Benthic invertivore	9	15		
Lamprologini	*Neolamprologus mondabu*	Benthic invertivore	11	14		
	Neolamprologus toae	Benthic invertivore	11	13		
	Lepidiolamprologus elongatus	Column piscivore	15	15		15
	Neolamprologus brichardi	Column invertivore	15	15	15	15

Baselines						
	Pleiodon spekii	Column feeder	5	4	5	3
	Neothauma tanganyicense	Column feeder	4	5		
	Lavigeria grandis	Benthic herbivore	3*	3*	5	12
	Lavigeria nassa	Benthic herbivore	3*	3*	7	12
	Multi-species algae		1*	1*	1	1

Table S4.2. Difference between carbon isotope values of a subset of ethanol preserved samples and their corresponding air-dried samples pooled between sites. P values highlighted bold indicate a significant difference in δ^{13}C values with a paired t-test.

	t value	P value
Raw ethanol preserved samples vs sun dried samples	3.3836	**0.0016**
Lipid normalised ethanol preserved samples vs sun dried samples	4.3437	**0.0001**
Ethanol preservation corrected ethanol preserved samples vs sun dried samples	0.0135	0.9893

Table S4.3. Difference between stable isotope values of the *Gadus morhua* sample University of Newcastle, UK. P values highlighted bold indicate a significant difference in δ^{13}C values with an unpaired t-test.

	Difference	t value	P value
δ^{13}C	0.047	1.5747	0.1366
δ^{15}N	0.116	2.8219	**0.01377**

Table S4.4. Baseline species mean δ^{15}N values and standard deviations at all sites.

	Algae	*Lavigeria grandis*	*Lavigeria nassa*	*Neothauma tanganyicense*	*Pleiodon spekii*
		Benthic herbivore	Benthic herbivore	Detritus feeder	Filter feeder
TAFIRI Bay 2015				0.43 ± 0.51	1.28 ± 0.26
Kalilani Island 2015				0.17 ± 0.27	1.29 ± 0.26
TAFIRI Bay 2016	-0.12 ± 0.24	1.03 ± 0.56	2.05 ± 0.60		2.33 ± 0.10
Kigoma Deforested 2016	-1.08 ± 0.05	-0.20 ± 0.42	0.07 ± 0.44		2.09 ± 0.16

Table S4.5. Results of Generalised Linear Model testing the effects of site, and covariate body size, on species $\delta^{15}N$ and $\delta^{13}C$ values. 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 which is indicated in the table. P values highlighted bold indicate a significant relationship.

$\delta^{15}N$	**Estimate**	**SE**	**T**	***p***
Neolamprologus toae				
Kalilani Island (Intercept)	0.1965	0.0184	10.68	**<0.0001**
Body size	-0.0006	0.0024	-2.478	**0.0228**
TAFIRI Bay 2015	-0.0388	0.026	-1.494	0.1517
Body size: TAFIRI Bay 2015	-0.0001	0.0003	-0.141	0.8896
Neolamprologus mondabu				
Kalilani Island (Intercept)	0.2017	0.0397	5.086	**<0.0001**
Body size	-0.0004	0.0005	-0.746	0.463
TAFIRI Bay 2015	-0.0711	0.0471	-1.51	0.145
Body size: TAFIRI Bay 2015	0.0003	0.0006	0.401	0.692
Neolamprologus brichardi				
Kigoma Deforested (Intercept)	0.1834	0.0153	11.986	**<0.0001**
Body size	-0.0005	0.0002	-2.165	**0.0352**
Kalilani Island	0.0257	0.0218	1.18	0.2437
TAFIRI Bay 2015	0.0207	0.023	0.898	0.3736
TAFIRI Bay 2016	0.0272	0.0194	1.401	0.1674
Body size: Kalilani Island	-0.0001	0.0003	-0.363	0.7181
Body size: TAFIRI Bay 2015	-0.0003	0.0004	-0.66	0.5125
Body size: TAFIRI Bay 2015	-0.0006	0.0003	-1.763	0.0839
Lobochilotes labiatus				
Kigoma Deforested (Intercept)	0.1499	0.0181	8.268	**<0.0001**
Body size	0.0001	0.0001	0.277	0.7837
Kalilani Island	0.0811	0.0331	2.454	**0.0197**

TAFIRI Bay 2015	-0.0092	0.0258	-0.357	0.7235
Body size: Kalilani Island	-0.0005	0.0004	-1.467	0.1521
Body size: TAFIRI Bay 2015	-0.0006	0.0003	-1.992	0.055
Lepidiolamprologus elongatus				
Kigoma Deforested (Intercept)	0.1748	0.0067	25.941	**<0.0001**
Body size	0.0003	0.0001	-4.082	**0.0002**
Kalilani Island	0.0207	0.0111	2.346	**0.0242**
TAFIRI Bay 2015	-0.0207	0.0089	-2.324	**0.0255**
Body size: Kalilani Island	-0.0001	0.0001	-1.075	0.289
Body size: TAFIRI Bay 2015	0.0001	0.0001	0.88	0.3841
Ophthalmotilapia ventralis				
Kalilani Island (Intercept)	0.1361	0.0247	5.516	**<0.0001**
Body size	0.0002	0.0003	0.658	0.5186
TAFIRI Bay 2015	-0.1202	0.0422	2.848	**0.0107**
Body size: TAFIRI Bay 2015	-0.0014	0.0005	-2.595	**0.0183**
Tropheus brichardi				
Kigoma Deforested (Intercept)	0.1935	0.1736	1.114	0.27
Body size	0.0004	0.0023	0.156	0.876
Kalilani Island	0.1911	0.291	0.657	0.514
TAFIRI Bay 2015	-0.1556	0.1813	-0.858	0.395
TAFIRI Bay 2016	-0.1362	0.1845	-0.885	0.381
Body size: Kalilani Island	-0.0019	0.0036	-0.532	0.597
Body size: TAFIRI Bay 2015	0.0003	0.0024	0.12	0.905
Body size: TAFIRI Bay 2015	0.0007	0.0025	0.281	0.78
Eretmodus cyanostictus				
Kigoma Deforested (Intercept)	0.1852	0.0629	2.942	**0.0058**
Body size	0.001	0.0011	0.898	0.3755
Kalilani Island	0.2261	0.0934	2.422	**0.0209**
TAFIRI Bay 2015	-0.13	0.0671	-1.933	0.0617

Body size: Kalilani Island	-0.003	0.0015	-2.062	**0.0469**
Body size: TAFIRI Bay 2015	0.0004	0.0012	0.306	0.7617
Petrochromis famula				
Kigoma Deforested (Intercept)	0.1866	0.0655	2.849	**0.0068**
Body size	0.0006	0.0007	0.847	0.4019
Kalilani Island	0.1934	0.1693	1.142	0.2599
TAFIRI Bay 2015	-0.118	0.0696	-2.603	**0.0128**
TAFIRI Bay 2016	-0.0018	0.0018	-1.01	0.3183
Body size: Kalilani Island	-0.0018	0.0018	-1.01	0.3183
Body size: TAFIRI Bay 2015	0.0006	0.0008	0.746	0.4598
Body size: TAFIRI Bay 2015	0.0005	0.0009	0.575	0.5683
Pseudosimochromis babaulti				
Kigoma Deforested (Intercept)	0.1401	0.112	1.251	0.217
Body size	0.0011	0.0014	0.755	0.454
Kalilani Island	0.1367	0.1177	1.161	0.251
TAFIRI Bay 2015	-0.0174	0.1168	-0.149	0.882
Body size: Kalilani Island	-0.0017	0.0015	-1.116	0.27
Body size: TAFIRI Bay 2015	-0.0012	0.0015	-0.811	0.421
δ^{15}N	**Estimate**	**SE**	**T**	***p***
Neolamprologus toae				
Kalilani Island (Intercept)	-14.941	1.088	-13.729	**<0.0001**
Body size	-0.0309	0.0145	-2.139	**0.0457**
TAFIRI Bay 2015	-2.9242	1.7822	-1.641	0.1173
Body size:TAFIRI Bay 2015	0.0529	0.024	2.205	**0.04**
Neolamprologus mondabu				
Kalilani Island (Intercept)	-11.917	2.938	-4.056	**0.0005**
Body size	-0.0508	0.039	-1.303	0.2054
TAFIRI Bay 2015	-1.6224	4.0428	-0.401	0.6919
Body size: TAFIRI Bay 2015	0.0201	0.0544	0.37	0.7149

Neolamprologus brichardi				
Kigoma Deforested (Intercept)	-19.698	0.6425	-30.656	**<0.0001**
Body size	-0.0114	0.0103	-1.11	0.2724
Kalilani Island	-3.531	0.8892	-3.971	**0.0002**
TAFIRI Bay 2015	-3.553	0.9564	-3.715	**0.0005**
TAFIRI Bay 2016	-0.1785	0.8202	-0.218	0.8286
Body size: Kalilani Island	0.0413	0.0141	2.93	**0.0051**
Body size: TAFIRI Bay 2015	0.0461	0.0161	2.866	**0.0061**
Body size: TAFIRI Bay 2015	0.0032	0.0137	0.23	0.8188
Lobochilotes labiatus				
Kigoma Deforested (Intercept)	-10.162	0.8691	-11.692	**<0.0001**
Body size	-0.0347	0.0089	-3.908	**0.0005**
Kalilani Island	-2.3613	1.38	-1.711	0.0967
TAFIRI Bay 2015	-2.4068	1.59	-1.511	0.1405
Body size: Kalilani Island	0.0194	0.0148	1.306	0.2009
Body size: TAFIRI Bay 2015	0.0122	0.0213	0.574	0.5701
Lepidiolamprologus elongatus				
Kigoma Deforested (Intercept)	-0.1903	0.6468	-29.423	**<0.0001**
Body size	0.0006	0.0068	0.086	0.9318
Kalilani Island	-1.549	0.9947	-1.557	0.1275
TAFIRI Bay 2015	-3.821	0.8831	-4.327	**0.0001**
Body size: Kalilani Island	-0.0024	0.001	-0.244	0.8089
Body size: TAFIRI Bay 2015	0.0341	0.0097	3.523	**0.0011**
Ophthalmotilapia ventralis				
Kalilani Island (Intercept)	-15.3756	2.351	-6.54	**<0.0001**
Body size	-0.0454	0.0289	-1.569	0.1342
TAFIRI Bay 2015	-6.9188	3.806	-1.818	0.0858
Body size: TAFIRI Bay 2015	0.0865	0.0487	1.776	0.0927
Tropheus brichardi				

Kigoma Deforested (Intercept)	-20.574	3.269	-6.294	**<0.0001**
Body size	0.0854	0.0428	1.994	0.0516
Kalilani Island	3.7818	4.909	0.77	0.4447
TAFIRI Bay 2015	2.3075	4.264	0.541	0.5908
TAFIRI Bay 2016	4.2664	4.174	1.022	0.3116
Body size: Kalilani Island	-0.0427	0.0614	-0.695	0.49
Body size: TAFIRI Bay 2015	-0.0469	0.0585	-0.802	0.4262
Body size: TAFIRI Bay 2015	-0.0768	0.0572	-1.341	0.186
Eretmodus cyanostictus				
Kigoma Deforested (Intercept)	-19.8364	1.2579	-15.769	**<0.0001**
Body size	0.1411	0.0211	6.684	**<0.0001**
Kalilani Island	4.4127	1.726	2.557	**0.0152**
TAFIRI Bay 2015	1.612	1.581	1.02	0.3151
Body size: Kalilani Island	-0.066	0.0274	-2.407	**0.0216**
Body size: TAFIRI Bay 2015	-0.0287	0.0279	-1.028	0.311
Petrochromis famula				
Kigoma Deforested (Intercept)	-0.1501	1.141	-13.158	**<0.0001**
Body size	0.0326	0.0126	2.593	**0.0131**
Kalilani Island	2.362	2.705	0.873	0.3875
TAFIRI Bay 2015	-5.195	1.545	-3.362	**0.0017**
TAFIRI Bay 2016	-0.574	1.589	-0.361	0.7198
Body size: Kalilani Island	-0.043	0.0028	-1.512	0.1382
Body size: TAFIRI Bay 2015	0.0355	0.0019	1.893	0.0654
Body size: TAFIRI Bay 2015	0.0003	0.0018	-0.019	0.9851
Pseudosimochromis babaulti				
Kigoma Deforested (Intercept)	-13.157	2.7533	-4.779	**<0.0001**
Body size	-0.0122	0.0352	-0.345	0.7314
Kalilani Island	0.5888	2.8656	0.205	0.8381
TAFIRI Bay 2015	-7.5404	3.1517	-2.392	**0.0208**

Body size: Kalilani Island	0.0088	0.037	0.238	0.813
Body size: TAFIRI Bay 2015	0.0798	0.0414	1.927	0.0601

Table S4.6. Mean volume (%) and standard deviations (%) of stomach contents of all cichlid species collected from Kalilani Island in 2015.

Species	sample size	(i) sediment	(ii) algae	(iii) fish scales	(iv) insects	(v) crustaceans	(vi) gastropods	(vii) fish	(viii) plankton
Eretmodus cyanostictus	10	2 [0]	91.56 [12.1]	6.44 [11.2]	0	0	0	0	0
Petrochromis famula	8	0	92.5 10.4]	7.5 [0]	0	0	0	0	0
Pseudosimochromis babaulti	10	12.15 [14.7]	86.94 [18.4]	0.91 [0]	0	0	0	0	0
Tropheus brichardi	10	0	96.89 [6.9]	3.11 [6.3]	0	0	0	0	0
Lobochilotes labiatus	10	1.6 [0]	0	7.62 [9.1]	31.51 [30]	18.45 [11.8]	36.81 [16.2]	4 [0]	0
Neolamprologus mondabu	10	4.72 [2]	0	16.43 [26.1]	24.28 [19.9]	33.51 [22.8]	15.23 [18.9]	5.83 [5.9]	0
Neolamprologus toae	10	0	0	11.02 [8.6]	9.98 [3.1]	70.94 [15.2]	2 [0]	6.5 [10.6]	0
Lepidiolamprologus elongatus	10	0	0	20.33 [22]	0	51.33 [33.6]	0	28.33 [21]	0
Neolamprologus brichardi	10	0	0	19.33 [18.1]	0	0	0	0	80.67 [21.4]

Table S4.7. Mean volume (%) and standard deviations (%) of stomach contents of all cichlid species collected from TAFIRI Bay in 2015.

Species	sample size	(i) sediment	(ii) algae	(iii) fish scales	(iv) insects	(v) crustaceans	(vi) gastropods	(vii) fish	(viii) plankton
Eretmodus cyanostictus	10	21.22 [21.5]	76.1 [22.2]	2.68 [2]	0	0	0	0	0
Petrochromis famula	8	31.85 [20.3]	64.63 [22.8]	3.52 [4.8]	0	0	0	0	0
Pseudosimochromis babaulti	12	22.16 [23.3]	63.53 [30.7]	14.3 [27.9]	0	0	0	0	0
Tropheus brichardi	10	20.57 [16.7]	75.12 [20.1]	3.97 [7]	0.3 [0]	0	0	0	0
Lobochilotes labiatus	8	9.92 [20.6]	5.56 [0]	20.25 [24.2]	10.38 [26.5]	2.5 [0]	41.94 [13.6]	9.45 [13.1]	0
Neolamprologus mondabu	11	12.5 [35.4]	0	30.89 [35.7]	8.35 [9.9]	17.49 [39.4]	23.25 [24.4]	7.52 [30.5]	0
Neolamprologus toae	10	1.38 [0]	0	18.79 [25.1]	18.92 [36.3]	7 [11]	53.9 [22.4]	0	0
Lepidiolamprologus elongatus	10	0	0	36.33 [30]	35 [25]	13.67 [23.6]	0	15 [35.4]	0
Neolamprologus brichardi	10	18 [12.2]	0	22.67 [31]	18.16 [18]	22.49 [26]	0	0	18.68 [29.2]

Table S4.8. Intraspecific Schoener's Index of dietary overlap, and comparisons of the amount of sediment in stomach contents between Kalilani Island and TAFIRI Bay in 2015. Schoener's index values highlighted in bold indicates significant dietary overlap between both sites at ≥ 0.6, and p-values highlighted in bold indicate a significant higher proportion of sediment at TAFIRI Bay with a Fisher's LSD test (Bonferroni adjusted p-value of 0.00625). Species names are followed by feeding type abbreviation, benthic herbivore (BH), benthic invertivore (BI), column piscivore (CP) and column invertivore (CI).

Species	**Trophic type**	**Kalilani Island sample size**	**TAFIRI Bay sample size**	**Schoener's Index**	**Sediment p-value**
Eretmodus cyanostictus	BH	10	10	**0.81**	**0.001**
Petrochromis famula	BH	8	8	**0.68**	**<0.001**
Pseudosimochromis babaulti	BH	10	12	**0.77**	0.152
Tropheus brichardi	BH	10	10	**0.78**	**0.001**
Lobochilotes labiatus	BI	10	8	**0.63**	0.149
Neolamprologus mondabu	BI	10	11	**0.68**	0.380
Neolamprologus toae	BI	10	10	0.30	0.645
Lepidiolamprologus elongatus	CP	10	10	0.49	-
Neolamprologus brichardi	CI	10	10	0.38	**<0.001**

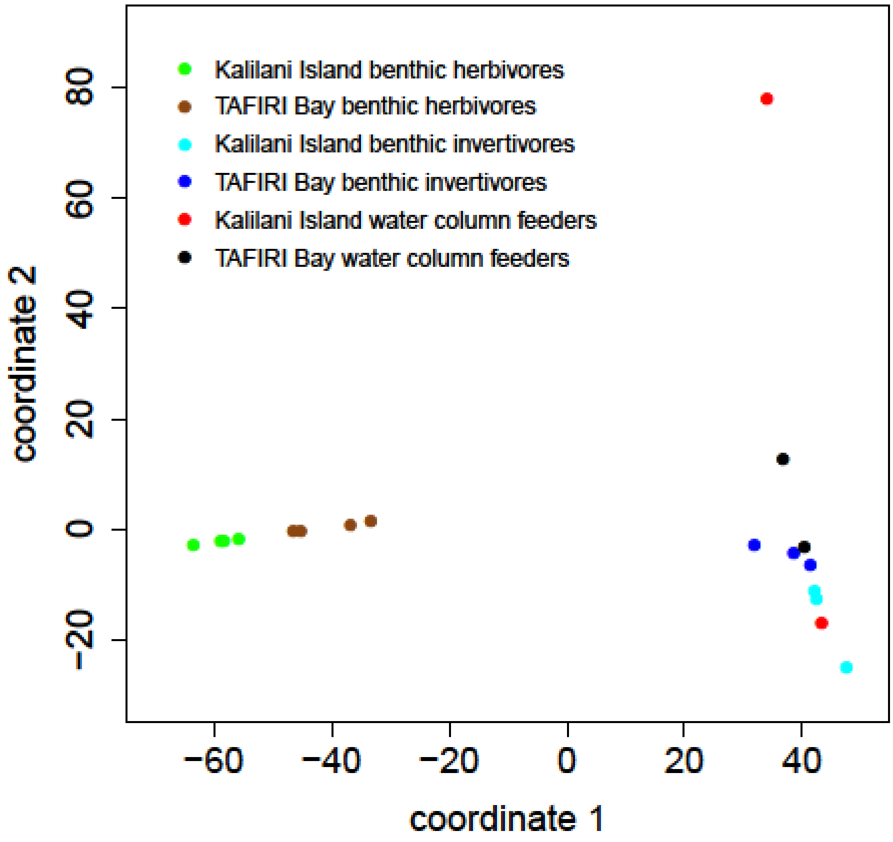


Figure S4.1. Multidimensional scaling plot of distance matrix of species mean proportions of each stomach content item displayed in Tables S4.6 and S4.7.

References

Abell R. (2002) Conservation biology for the biodiversity crisis: A freshwater follow-up. *Conservation Biology* **16**, 1435–1437.

Adams D.C. & Otárola-Castillo E. (2013) Geomorph: An R package for the collection and analysis of geometric morphometric shape data. *Methods in Ecology and Evolution* **4**, 393–399.

Adams V.M., Setterfield S.A., Douglas M.M., Kennard M.J. & Ferdinands K. (2015) Measuring benefits of protected area management: Trends across realms and research gaps for freshwater systems. *Philosophical Transactions of the Royal Society B: Biological Sciences* **370**, 20140274.

Alin S.R., Cohen A.S., Bills R., Gashagaza M.M., Michel E., Tiercelin J.-J., *et al.* (1999) Effects of landscape disturbance on animal communities in Lake Tanganyika, East Africa. *Conservation Biology* **13**, 1017–1033.

Alin S.R., O'Reilly C.M., Cohen A.S., Dettman D.L., Palacios-Fest M.R. & McKee B.A. (2002) Effects of land-use change on aquatic biodiversity: a view from the paleorecord at Lake Tanganyika, East Africa. *Geology* **30**, 1143–1146.

Allison E.H. (2000) Fishing practices special study (FPSS) final situation report: Fishing in the waters adjoining the national parks bordering Lake Tanganyika. United Nations Development Programme.

Allison E.H., Paley R.G.T., Ntakimazi G., Cowan V.J.C. & West K. (2000) Biodiversity assessment and conservation in Lake Tanganyika: BIOSS final technical report. United Nations Development Programme.

Allison G.W., Lubchenco J. & Carr M.H. (1998) Marine reserves are necessary but not sufficient for marine conservation. *Ecological Applications* **8**, 79–92.

Anderson C. & Cabana G. (2005) δ15N in riverine food webs: effects of N inputs from agricultural watersheds. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 333–340.

Arbour J.H. & López-Fernández H. (2014) Adaptive landscape and functional diversity of Neotropical cichlids: implications for the ecology and evolution of Cichlinae (Cichlidae; Cichliformes). *Journal of Evolutionary Biology* **27**, 2431–2442.

Arrington D.A. & Winemiller K.O. (2002) Preservation effects on stable isotope analysis of fish muscle. *Transactions of the American Fisheries Society* **131**, 337–342.

Balata D., Piazzi L. & Benedetti-Cecchi L. (2007) Sediment disturbance and loss of beta diversity on subtidal rocky reefs. *Ecology* **88**, 2455–2461.

Balmford A., Bennun L., Brink B., Cooper D., Côté I.M., Crane P., *et al.* (2005) The Convention on Biological Diversity's 2010 Target. *Science* **307**, 212–213.

Barlow G.W. (1991) Mating systems among cichlid fishes. In: *Cichlid Fishes: Behaviour, Ecology and Evolution*. (Ed. M. Keenleyside), pp. 173–190.

Baselga A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* **19**, 134–143.

Baselga A. (2013) Separating the two components of abundance-based dissimilarity: Balanced changes in abundance vs. abundance gradients. *Methods in Ecology and Evolution* **4**, 552–557.

Baselga A. & Orme C.D.L. (2012) Betapart: An R package for the study of beta diversity. *Methods in Ecology and Evolution* **3**, 808–812.

Bates D. (2018) Package lme4. 1–19.

de Bello F. (2012) The quest for trait convergence and divergence in community assembly: Are null-models the magic wand? *Global Ecology and Biogeography* **21**, 312–317.

Bellwood D.R., Hughes T.P., Folke C. & Nyström M. (2004) Confronting the coral reef crisis. *Nature* **429**, 827–833.

Bhat A. & Magurran A.E. (2006) Taxonomic distinctness in a linear system: A test using a tropical freshwater fish assemblage. *Ecography* **29**, 104–110.

Bicknell A.W.J., Campbell M., Knight M.E., Bilton D.T., Newton J. & Votier S.C. (2011) Effects of formalin preservation on stable carbon and nitrogen isotope signatures in Calanoid copepods: Implications for the use of continuous plankton recorder survey samples in stable isotope analyses. *Rapid Communications in Mass Spectrometry* **25**, 1794–1800.

Biswas S.R. & Mallik A.U. (2011) Species diversity and functional diversity relationship varies with disturbance intensity. *Ecosphere* **2**, 1–10.

Bohnsack J.A. & Bannerot S.P. (1986) *A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. NOAA Technical Report NMFS 41*.

Boitani L., Cowling R.M., Dublin H.T., Mace G.M., Parrish J., Possingham H.P., *et al.* (2008) Change the IUCN protected area categories to reflect biodiversity outcomes. *PLoS Biology* **6**, 0436–0438.

Brawand D., Wagner C.E., Li Y.I., Malinsky M., Keller I., Fan S., *et al.* (2015) The genomic substrate for adaptive radiation in African cichlid fish. *Nature* **513**, 375–381.

Brichard P. (1989) *Cichlids and all other fishes of Lake Tanganyika*. T. F. H., New Jersey.

Britton A.W., Day J.J., Doble C.J., Ngatunga B.P., Kemp K.M., Carbone C., *et al.* (2017) Terrestrial-focused protected areas are effective for conservation of freshwater fish diversity in Lake Tanganyika. *Biological Conservation* **212**, 120–129.

Brocchieri L. (2016) Functional and Phylogenetic Diversity. *Journal of Phylogenetics & Evolutionary Biology* **04**.

Brooks T.M., Mittermeier R.A., da Fonseca G.A.B., Gerlach J., Hoffmann M., Lamoreux J.F., *et al.* (2006) Global biodiversity conservation priorities. *Science* **313**, 58–61.

Brooks T.M., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A.B., Rylands A.B., Konstant W.R., *et al.* (2002) Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology* **16**, 909–923.

Brown K.J., Rüber L., Bills R. & Day J.J. (2010) Mastacembelid eels support Lake Tanganyika as an evolutionary hotspot of diversification. *BMC Evolutionary Biology* **10**, 188.

Brum F.T., Graham C.H., Costa G.C., Hedges S.B., Penone C., Radeloff V.C., *et al.* (2017) Global priorities for conservation across multiple dimensions of mammalian diversity. *Proceedings of the National Academy of Sciences* **114**, 7641–7646.

Bruton M. (1995) Have fishes had their chips? The dilemma of threatened fishes. *Environmental Biology of Fishes* **43**, 1–27.

Bruton M. (1985) The effects of suspendoids on fish. *Hydrobiologia* **125**, 221–241.

Bugoni L., McGill R.A.R. & Furness R.W. (2008) Effects of preservation methods on stable isotope signatures in bird tissues. *Rapid Communications in Mass Spectrometry* **22**, 2457–2462.

Burkepile D.E. & Hay M.E. (2008) Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proceedings of the National Academy of Sciences* **105**, 16201–16206.

Busch J., Soreghan M., de Beurs K., McGlue M., Kimirei I., Cohen A., *et al.* (2018) Linking watershed disturbance with nearshore sedimentation and the shell beds of Lake Tanganyika (Mahale Mountains, Tanzania). *Environmental Earth Sciences* **77**, 514.

Buser T.J., Sidlauskas B.L. & Summers A.P. (2018) 2D or not 2D? Testing the utility of 2D vs. 3D landmark data in geometric morphometrics of the Sculpin Subfamily Oligocottinae (Pisces; Cottoidea). *Anatomical Record* **301**, 806–818.

Cabana G. & Rasmussen J.B. (1996) Comparison of aquatic food chains using nitrogen isotopes. *Proceedings of the National Academy of Sciences of the United States of America* **93**, 10844–10847.

Cahill J.F., Kembel S.W., Lamb E.G. & Keddy P.A. (2008) Does phylogenetic relatedness influence the strength of competition among vascular plants? *Perspectives in Plant Ecology, Evolution and Systematics* **10**, 41–50.

Camargo J.A. & Alonso Á. (2006) Ecological and toxicological effects of inorganic nitrogen pollution in aquatic ecosystems: A global assessment. *Environment International* **32**, 831–849.

Campbell L., Verburg P., Dixon D.G. & Hecky R.E. (2008) Mercury biomagnification in the food web of Lake Tanganyika (Tanzania, East Africa). *Science of the Total Environment* **402**, 184–191.

Campos F.S., Lourenço-de-Moraes R., Llorente G.A. & Solé M. (2017) Cost-effective conservation of amphibian ecology and evolution. *Science Advances* **3**, 1–10.

Cardini A. (2014) Missing the third dimension in geometric morphometrics: How to assess if 2D images really are a good proxy for 3D structures? *Hystrix* **25**, 73–81.

Carrillo E., Wong G. & Cuarón A.D. (2008) Monitoring mammal populations in Costa Rican protected areas under different hunting restrictions. *Conservation Biology* **14**, 1580–1591.

Cavender-Bares J., Kozak K.H., Fine P.V.A. & Kembel S.W. (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters* **12**, 693–715.

Chakrabarty P. (2005) Testing conjectures about morphological diversity in cichlids of Lakes Malawi and Tanganyika. *Copeia* **2**, 359–373.

Chale F.M.M. (2003) Eutrophication of Kigoma Bay, Lake Tanganyika, Tanzania. *Tanzania Journal of Science* **29**, 17–24.

Chale F.M.M. (2002) Trace metal concentrations in water, sediments and fish tissue from Lake Tanganyika. *Science of the Total Environment* **299**, 115–121.

Chape S., Harrison J., Spalding M. & Lysenko I. (2005) Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. *Philosophical Transactions of the Royal Society B:*

Biological Sciences **360**, 443–455.

Chapman P.M., Tobias J.A., Edwards D.P. & Davies R.G. (2018) Contrasting impacts of land-use change on phylogenetic and functional diversity of tropical forest birds. *Journal of Applied Ecology*, 1–11.

Chessman B.C. (2013) Do protected areas benefit freshwater species? A broad-scale assessment for fish in Australia's Murray-Darling Basin. *Journal of Applied Ecology* **50**, 969–976.

Christie P. (2005) Observed and perceived environmental impacts of marine protected areas in two Southeast Asia sites. *Ocean & Coastal Management* **48**, 252–270.

Chu C., Ellis L. & de Kerckhove D.T. (2017) The effectiveness of terrestrial protected areas for lake fish community conservation. *Conservation Biology* **32**, 607–618.

Clabaut C., Bunje P.M.E., Salzburger W. & Meyer A. (2007) Geometric morphometric analyses provide evidence for the adaptive character of the Tanganyikan cichlid fish radiations. *Evolution* **61**, 560–578.

Clarke K.R., Somerfield P.J. & Chapman M.G. (2006) On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. *Journal of Experimental Marine Biology and Ecology* **330**, 55–80.

Claudet J., Pelletier D., Jouvenel J.Y., Bachet F. & Galzin R. (2006) Assessing the effects of marine protected area (MPA) on a reef fish assemblage in a northwestern Mediterranean marine reserve: Identifying community-based indicators. *Biological Conservation* **130**, 349–369.

Claverie T. & Wainwright P.C. (2014) A morphospace for reef fishes: Elongation is the dominant axis of body shape evolution. *PLoS ONE* **9**.

Cohen A.S., Bills R., Cocquyt C. & Caljon A.G. (1993a) The impact of sediment pollution on biodiversity in Lake Tanganyika. *Conservation Biology* **7**, 667–677.

Cohen A.S., Gergurich E.L., Kraemer B.M., McGlue M.M., McIntyre P.B., Russell J.M., *et al.* (2016) Climate warming reduces fish production and benthic habitat in Lake Tanganyika, one of the most biodiverse freshwater ecosystems. *Proceedings of the National Academy of Sciences USA* **113**, 9563–9568.

Cohen A.S., Kaufman L. & Ogutu-Ohwayo R. (1996) Anthropogenic threats, impacts and conservation strategies in the African Great Lakes: A review. In: *The Limnology Climatology and Paleoclimatology of the East African Lakes*. (Eds E.O. Odada & T.C. Johnson), pp. 575–624. Gordon and Breach, Newark, NJ.

Cohen A.S., Lezzar K.E., Tiercelin A J.J. & Soreghan M. (1997) New palaeogeographic and lake-level reconstructions of Lake Tanganyika: Implications for tectonic, climatic and biological evolution in a rift lake. *Basin Research* **9**, 107–132.

Cohen A.S., Palacios-Fest M.R., McGill J., Swarzenski P.W., Veschuren D., Sinyinza R., *et al.* (2005) Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: IV. Lacustrine paleoecology. *Journal of Paleolimnology* **34**, 51–71.

Cohen A.S., Soreghan M. & Scholz C. (1993b) Estimating the age of formation of lakes: an example from Lake Tanganyika, East African Rift system. *Geology* **21**, 511–514.

Collen B., Ram M., Zamin T. & McRae L. (2008) The tropical biodiversity data gap: Addressing disparity in global monitoring. *Tropical Conservation Science* **1**, 75–88.

Collen B., Whitton F., Dyer E.E., Baillie J.E.M., Cumberlidge N., Darwall W.R.T., *et al.* (2014) Global patterns of freshwater species diversity, threat and endemism. *Global Ecology and Biogeography* **23**, 40–51.

Comte L., Cucherousset J., Boulêtreau S. & Olden J.D. (2016) Resource partitioning and functional diversity of worldwide freshwater fish communities. *Ecosphere* **7**, 1–13.

Connor E.F. & Simberloff D. (1979) The assembly of species communities: Chance or competition? *Ecology* **60**, 1132.

Corman J.R., McIntyre P.B., Kuboja B., Mbemba W., Fink D., Wheeler C.W., *et al.* (2010) Upwelling couples chemical and biological dynamics across the littoral and pelagic zones of Lake Tanganyika, East Africa. *Limnology and Oceanography* **55**, 214–224.

Correa C. (2012) Tissue preservation biases in stable isotopes of fishes and molluscs from Patagonian lakes. *Journal of Fish Biology* **81**, 2064–2073.

Corrigan L.J., Winfield I.J., Hoelzel A.R. & Lucas M.C. (2011) Dietary plasticity in Arctic charr (Salvelinus alpinus) in response to long-term environmental change. *Ecology of Freshwater Fish* **20**, 5–13.

Costanzo S.D., O'Donohue M.J., Dennison W.C., Loneragan N.R. & Thomas M. (2001) A new approach for detecting and mapping sewage impacts. *Marine Pollution Bulletin* **42**, 149–156.

Cottee-Jones H.E.W., Matthews T.J., Bregman T.P., Barua M., Tamuly J. & Whittaker R.J. (2015) Are protected areas required to maintain functional diversity in human-modified landscapes? *PLoS ONE* **10**, 1–22.

Coulter G.W. (1991) *Lake Tanganyika and its life*. Oxford University Press, London, UK.

Coulter G.W. & Mubamba R. (1993) Conservation in Lake Tanganyika, with special reference to underwater parks. *Conservation Biology* **7**, 678–685.

Craig J.F. (1992) Human-induced changes in the composition of fish communities in the African Great Lakes. *Reviews in Fish Biology and Fisheries* **2**, 93–124.

D'Agata S., Mouillot D., Kulbicki M., Andréfouët S., Bellwood D.R., Cinner J.E., *et al.* (2014) Human-mediated loss of phylogenetic and functional diversity in coral reef fishes. *Current Biology* **24**, 555–560.

Darwall W.R.T., Holland R.A., Smith K.G., Allen D., Brooks E.G.E., Katarya V., *et al.* (2011) Implications of bias in conservation research and investment for freshwater species. *Conservation Letters* **4**, 474–482.

Davis A.M., Blanchette M.L., Pusey B.J., Jardine T.D. & Pearson R.G. (2012)

Gut content and stable isotope analyses provide complementary understanding of ontogenetic dietary shifts and trophic relationships among fishes in a tropical river. *Freshwater Biology* **57**, 2156–2172.

Day J.J., Cotton J.A. & Barraclough T.G. (2008) Tempo and mode of diversification of lake Tanganyika cichlid fishes. *PLoS ONE* **3**, e1730.

Day J.J. & Wilkinson M. (2006) On the origin of the Synodontis catfish species flock from Lake Tanganyika. *Biology Letters* **2**, 548–552.

Deng L., Shangguan Z. & Li R. (2012) Effects of the grain-for-green program on soil erosion in China. *International Journal of Sediment Research* **27**, 120–127.

Devictor V., Mouillot D., Meynard C., Jiguet F., Thuiller W. & Mouquet N. (2010) Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: The need for integrative conservation strategies in a changing world. *Ecology Letters* **13**, 1030–1040.

Diamond J.M. & Gilpin M.E. (1982) Examination of the “Null” model of Connor and Simberloff for species co-occurrences on islands. *Oecologia* **52**, 64–74.

Díaz S., Lavorel S., de Bello F., Quétier F., Grigulis K. & Robson T.M. (2007) Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 20684–20689.

Ding B., Curole J., Husemann M. & Danley P.D. (2014) Habitat complexity predicts the community diversity of rock-dwelling cichlid fish in Lake Malawi, East Africa. *Hydrobiologia* **748**, 133–143.

Dobiesz N.E., Hecky R.E., Johnson T.B., Sarvala J., Dettmers J.M., Lehtiniemi M., *et al.* (2010) Metrics of ecosystem status for large aquatic systems - A global comparison. *Journal of Great Lakes Research* **36**, 123–138.

Donohue I. & Garcia Molinos J. (2009) Impacts of increased sediment loads on the ecology of lakes. *Biological Reviews* **84**, 517–531.

Donohue I., Verheyen E. & Irvine K. (2003) In situ experiments on the effects of increased sediment loads on littoral rocky shore communities in Lake Tanganyika, East Africa. *Freshwater Biology* **48**, 1603–1616.

Drummond A.J., Newcomb R.D., Buckley T.R., Xie D., Dopheide A., Potter B.C.M., *et al.* (2015) Evaluating a multigene environmental DNA approach for biodiversity assessment. *GigaScience* **4**.

Dudgeon D., Arthington A.H., Gessner M.O., Kawabata Z.-I., Knowler D.J., Lévêque C., *et al.* (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* **81**, 163–182.

Edgar G.J., Stuart-Smith R.D., Willis T.J., Kininmonth S., Baker S.C., Banks S., *et al.* (2014) Global conservation outcomes depend on marine protected areas with five key features. *Nature* **506**, 216–20.

Eggen R.I.L., Hollender J., Joss A., Schärer M. & Stamm C. (2014) Reducing the discharge of micropollutants in the aquatic environment: The benefits of upgrading wastewater treatment plants. *Environmental Science and Technology* **48**, 7683–7689.

Eggermont H. & Verschuren D. (2003) Impact of soil erosion in disturbed tributary drainages on the benthic invertebrate fauna of Lake Tanganyika, East Africa. *Biological Conservation* **113**, 99–109.

Eggleton J. & Thomas K. V. (2004) A review of factors affecting the release and bioavailability of contaminants during sediment disturbance events. *Environment International* **30**, 973–980.

Ellis E.C. (2011) Anthropogenic transformation of the terrestrial biosphere. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* **369**, 1010–1035.

Ellis E.C. & Ramankutty N. (2008) Putting people in the map: Anthropogenic biomes of the world. *Frontiers in Ecology and the Environment* **6**, 439–447.

Eschmeyer W.N. (2015) Catalog of Fishes.

https://www.calacademy.org/scientists/projects/cat.

European Commission (2014) An integrative approach towards the understanding of an adaptive radiation of East African cichlid fishes | Projects | FP7-IDEAS-ERC | CORDIS | European Commission.

Fahrig L. (1997) Relative effects of habitat loss and fragmentation on population extinction. *The Journal of Wildlife Management* **61**, 603–610.

Faith D. (2015) Phylogenetic diversity and extinction: avoiding tipping points and worst-case losses from the tree of life. *Philosophical Transactions of the Royal Society B* **370**, 20140011.

Faith D.P. (1992) Conservation evaluation and phylogenetic diversity. *Biological Conservation* **61**, 1–10.

Falcone J.A., Carlisle D.M. & Weber L.C. (2010) Quantifying human disturbance in watersheds: Variable selection and performance of a GIS-based disturbance index for predicting the biological condition of perennial streams. *Ecological Indicators* **10**, 264–273.

Farré M., Tuset V.M., Maynou F., Recasens L. & Lombarte A. (2013) Geometric morphology as an alternative for measuring the diversity of fish assemblages. *Ecological Indicators* **29**, 159–166.

Ferraro P.J., Hanauer M.M. & Sims K.R.E. (2011) Conditions associated with protected area success in conservation and poverty reduction. *Proceedings of the National Academy of Sciences of the United States of America* **108**, 13913–8.

Fischer A.G. (1960) Latitudinal variations in organic diversity. *Evolution* **14**, 64–81.

Fisher R.A., Corbet A.S. & Williams C.B. (1943) The number of animals in a random sample of an animal population. *Journal of Animal Ecology* **12**, 42–58.

Flynn D.F.B., Gogol-Prokurat M., Nogeire T., Molinari N., Richers B.T., Lin B.B., *et al.* (2009) Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters* **12**, 22–33.

Fontaneto D., Panisi M., Mandrioli M., Montardi D., Pavesi M. & Cardini A. (2017) Estimating the magnitude of morphoscapes: how to measure the morphological component of biodiversity in relation to habitats using geometric morphometrics. *The Science of Nature* **104**, 55.

Ford A.G.P., Rüber L., Newton J., Dasmahapatra K.K., Balarin J.D., Bruun K., *et al.* (2016) Niche divergence facilitated by fine-scale ecological partitioning in a recent cichlid fish adaptive radiation. *Evolution* **70**, 2718–2735.

Forest F., Grenyer R., Rouget M., Davies T.J., Cowling R.M., Faith D.P., *et al.* (2007) Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature* **445**, 757–60.

Franca F., Louzada J., Korasaki V., Griffiths H., Silveira J.M., Barlow J., *et al.* (2016) Do space-for-time assessments underestimate the impacts of logging on tropical biodiversity? An Amazonian case study using dung beetles. *Journal of Applied Ecology* **53**, 1098–1105.

Frund J., Dormann C.F., Holzschuh A. & Tscharntke T. (2013) Bee diversity effects on pollination depend on functional complementarity and niche shifts. *Ecology* **94**, 2042–2054.

Fry B. (1999) Using stable isotopes to monitor watershed influences on aquatic trophodynamics. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 2167–2171.

Fryer G. (1972) Conservation of the Great Lakes of East Africa: A lesson and a warning. *Biological Conservation* **4**, 256–262.

Fryer G. & Iles T.D. (1972) *The cichlid fishes of the great lakes of Africa: Their biology and evolution*. T.H.F. Publications Inc, Neptune City, New Jersey.

Gangloff M.M., Edgar G.J. & Wilson B. (2016) Imperilled species in aquatic ecosystems: Emerging threats, management and future prognoses. *Aquatic Conservation: Marine and Freshwater Ecosystems* **26**, 858–871.

Garcia D. & Martinez D. (2012) Species richness matters for the quality of ecosystem services: a test using seed dispersal. *Proceedings of The Royal Society B* **279**, 3106–3113.

Gaston K.J. (2000) Global patterns in biodiversity. *Nature* **405**, 220–7.

Gaye-Siessegger J., Focken U., Abel H. & Becker K. (2004) Dietary lipid content influences the activity of lipogenic enzymes in the liver and on whole body δ13C values of Nile tilapia, Oreochromis niloticus (L.). *Isotopes in environmental and health studies* **40**, 181–190.

Genner M.J., Hawkins S.J. & Turner G.F. (2003) Isotopic change throughout the life history of a Lake Malawi cichlid fish. *Journal of Fish Biology* **62**, 907–917.

Genner M.J., Taylor M.I., Cleary D.F.R., Hawkins S.J., Knight M.E. & Turner G.F. (2004) Beta diversity of rock-restricted cichlid fishes in Lake Malawi: Importance of environmental and spatial factors. *Ecography* **27**, 601–610.

Genner M.J., Turner G.F., Barker S. & Hawkins S.J. (1999) Niche segregation among Lake Malawi cichlid fishes? Evidence from stable isotope signatures. *Ecology Letters* **2**, 185–190.

GeoHive (2012) Tanzania population statistics. http://www.geohive.com/cntry/tanzania.aspx.

Gersberg R.M., Elkins B. V, Lyon S.R. & Goldman C.R. (1986) Role of aquatic plants in wastewater treatment by artificial wetlands. *Water Research* **20**, 363–368.

Gill D.A., Mascia M.B., Ahmadia G.N., Glew L., Lester S.E., Barnes M., *et al.* (2017) Capacity shortfalls hinder the performance of marine protected areas globally. *Nature* **543**, 665–669.

Global Forest Watch (2000) Tree Cover. http://www.globalforestwatch.org/map/9/-5.57/29.77.

Goldschmidt T., Witte F. & Wanink J. (1993) Cascading effects of the introduced Nile Perch on the detritivorous/phytoplanktivorous species in the sublittoral areas of Lake Victoria. *Conservation Biology* **7**, 686–700.

González-Maya J.F., Víquez-R L.R., Belant J.L. & Ceballos G. (2015) Effectiveness of protected areas for representing species and populations of terrestrial mammals in Costa Rica. *PLoS ONE* **10**, 1–16.

Gorokhova E. (2018) Individual growth as a non-dietary determinant of the isotopic niche metrics. *Methods in Ecology and Evolution* **9**, 269–277.

Gotelli N.J. & Colwell R.K. (2001) Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* **4**, 379–391.

Gotelli N.J. & McCabe D.J. (2002) Species co-occurrence: A meta-analysis of J . M. Diamond's assembly rules model. *Ecology* **83**, 2091–2096.

Graham A.A. (1990) Siltation of stone-surface periphyton in rivers by clay-sized particles from low concentrations in suspention. *Hydrobiologia* **199**, 107–115.

Graham C.H. & Fine P.V.A. (2008) Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time. *Ecology Letters* **11**, 1265–77.

Graham C.H., Parra J.L., Rahbek C. & McGuire J.A. (2009) Phylogenetic structure in tropical hummingbird communities. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 19673–8.

Gray C.L., Hill S.L.L., Newbold T., Hudson L.N., Boïrger L., Contu S., *et al.* (2016) Local biodiversity is higher inside than outside terrestrial protected areas worldwide. *Nature Communications* **7**.

Groombridge B. & Jenkins M.D. (1998) *Freshwater Biodiversity: a preliminary global assessment*. UNEP-WCMC. Cambridge.

Guidetti P., Verginella L., Viva C., Odorico R. & Boero F. (2005) Protection effects on fish assemblages, and comparison of two visual-census techniques in shallow artificial rocky habitats in the northern Adriatic Sea. *Journal of the Marine Biological Association of the UK* **85**, 247–255.

Guilhaumon F., Albouy C., Claudet J., Velez L., Ben Rais Lasram F., Tomasini J.-A., *et al.* (2015) Representing taxonomic, phylogenetic and functional diversity: new challenges for Mediterranean marine-protected areas. *Diversity and Distributions* **21**, 175–187.

Gutiérrez-Cánovas C., Millán A., Velasco J., Vaughan I.P. & Ormerod S.J. (2013) Contrasting effects of natural and anthropogenic stressors on beta diversity in river organisms. *Global Ecology and Biogeography* **22**, 796–805.

Halpern B.S. & Floeter S.R. (2008) Functional diversity responses to changing species richness in reef fish communities. *Marine Ecology Progress Series* **364**, 147–156.

Halpern B.S., Lester S.E. & Kellner J.B. (2009) Spillover from marine reserves and the replenishment of fished stocks. *Environmental Conservation* **36**, 268–276.

Hansen M.C., Potapov P. V, Moore R., Hancher M., Turubanova S.A., Tyukavina A., *et al.* (2013) High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850–854.

Hata H. & Ochi H. (2016) Depth and substratum differentiations among coexisting herbivorous cichlids in Lake Tanganyika. *Royal Society Open Science* **3**, 160229.

Hata H., Shibata J., Omori K., Kohda M. & Hori M. (2015) Depth segregation and diet disparity revealed by stable isotope analyses in sympatric herbivorous cichlids in Lake Tanganyika. *Zoological Letters* **1**, 015.

Hata H., Tanabe A.S., Yamamoto S., Toju H., Kohda M. & Hori M. (2014) Diet disparity among sympatric herbivorous cichlids in the same ecomorphs in Lake Tanganyika: amplicon pyrosequences on algal farms and stomach contents. *BMC Biology* **12**, 90.

He F., Bremerich V., Zarfl C., Geldmann J., Langhans S.D., David J.N.W., *et al.* (2018) Global freshwater megafauna biodiversity: patterns, status, and threats. *Global Ecology and Biogeography*, 1–10.

Henley W.F., Patterson M.A., Neves R.J. & Lemly A.D. (2000) Effects of sedimentation and turbidity on lotic food webs: A concise review for natural resource managers. *Reviews in Fisheries Science* **8**, 125–139.

Herbert M.E., Mcintyre P.B., Doran P.J., Allan J.D. & Abell R. (2010) Terrestrial reserve networks do not adequately represent aquatic ecosystems. *Conservation Biology* **24**, 1002–1011.

Hermoso V., Filipe A.F., Segurado P. & Beja P. (2015) Effectiveness of a large reserve network in protecting freshwater biodiversity: a test for the Iberian Peninsula. *Freshwater Biology* **60**, 698–710.

Hiley J.R., Bradbury R.B. & Thomas C.D. (2016) Impacts of habitat change and protected areas on alpha and beta diversity of Mexican birds. *Diversity and Distributions* **22**, 1245–1254.

Hill M. (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology* **54**, 427–432.

Hiraiwa M.K. & Ushimaru A. (2017) Low functional diversity promotes niche changes in natural island pollinator communities. *Proceedings of the Royal Society B: Biological Sciences* **284**.

Hobson K.A. & Welch H.E. (1995) Cannibalism and trophic structure in a high Arctic lake: insights from stable-isotope analysis. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 1195–1201.

Holland R.A., Darwall W.R.T. & Smith K.G. (2012) Conservation priorities for freshwater biodiversity: The Key Biodiversity Area approach refined and tested for continental Africa. *Biological Conservation* **148**, 167–179.

Hori M., Gashagaza M.M., Nshombo M. & Kawanabe H. (1993) Littoral fish communities in Lake Tanganyika: Irreplaceable diversity supported by intricate interactions among species. *Conservation Biology* **7**, 657–666.

Hui C. & McGeoch M.A. (2014) Zeta diversity as a concept and metric that unifies incidence-based biodiversity patterns. *The American Naturalist* **184**, 684–694.

Huston M. (1979) A general hypothesis of species diversity. *The American Naturalist* **113**, 81–101.

Hynes H. (1950) The food of freshwater sticklebacks (Gasterosteus aculeatus and Pygosteus pungitius), with a review of methods used in studies of the food of fishes. *Journal of Animal Ecology* **19**, 36–58.

Hyslop E.J. (1980) Stomach contents analysis - a review of methods and their application. *Journal of Fish Biology* **17**, 411–429.

International Union for Conservation of Nature and Natural Resources. (2018) The IUCN red list of threatened species. Version 2018 - 1.

Islam M.S. & Tanaka M. (2004) Impacts of pollution on coastal and marine ecosystems including coastal and marine fisheries and approach for management: A review and synthesis. *Marine Pollution Bulletin* **48**, 624–649.

Jackson A.L., Inger R., Parnell A.C. & Bearhop S. (2011) Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. *The Journal of Animal Ecology* **80**, 595–602.

Janzen T., Alzate A., Muschick M., Maan M.E., van der Plas F. & Etienne R.S. (2017) Community assembly in Lake Tanganyika cichlid fish: quantifying the contributions of both niche-based and neutral processes. *Ecology and Evolution* **7**, 1057–1067.

Johnson E.A. & Miyanishi K. (2008) Testing the assumptions of chronosequences in succession. *Ecology Letters* **11**, 419–431.

Joo D., Kwan Y., Song J., Pinho C., Hey J. & Won Y.-J. (2013) Identification of cichlid fishes from Lake Malawi using computer vision. *Plos One* **8**, e77686.

Jost L. (2006) Entropy and diversity. *Oikos* **113**, 363–375.

Jost L. (2007) Partitioning diversity into independent alpha and beta components. *Ecology* **88**, 2427–2439.

Kassam D., Mizoiri S. & Yamaoka K. (2004) Interspecific variation of body shape and sexual dimorphism in three coexisting species of the genus petrotilapia (Teleostei: Cichlidae) from Lake Malawi. *Ichthyological Research* **51**, 195–201.

Katunzi E.F.B., Zoutendijk J., Goldschmidt T., Wanink J.H. & Witte F. (2003) Lost zooplanktivorous cichlid from Lake Victoria reappears with a new trade. *Ecology of Freshwater Fish* **12**, 237–240.

Kaur T., Singh J., Tong S., Humphrey C., Clevenger D., Tan W., *et al.* (2008) Descriptive epidemiology of fatal respiratory outbreaks and detection of a human-related metapneumovirus in wild chimpanzees (Pan troglodytes) at Mahale Mountains National Park, Western Tanzania. *American Journal of Primatology* **70**, 755–765.

Kelly B., Dempson J.B. & Power M. (2006) The effects of preservation on fish tissue stable isotope signatures. *Journal of Fish Biology* **69**, 1595–1611.

Kelly B., Mtiti E., McIntyre P.B. & Vadeboncoeur Y. (2016) Stable isotopes reveal nitrogen loading to Lake Tanganyika from remote shoreline villages. *Environmental Management* **59**, 264–273.

Kembel S.W., Cowan P.D., Helmus M.R., Cornwell W.K., Morlon H., Ackerly D.D., *et al.* (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**, 1463–1464.

Keough M.J. & Quinn G.P. (1991) Causality and the choice of measurements for detecting human impacts in marine environments. *Australian Journal of Marine and Freshwater Research* **42**, 539–554.

Kiljunen M., Grey J., Sinisalo T., Harrod C., Immonen H. & Jones R.I. (2006) A revised model for lipid-normalizing δ13C values from aquatic organisms, with implications for isotope mixing models. *Journal of Applied Ecology* **43**, 1213–1222.

Kimirei I.A., Mgaya Y.D. & Chande A.I. (2008) Changes in species composition and abundance of commercially important pelagic fish species in Kigoma area, Lake Tanganyika, Tanzania. *Aquatic Ecosystem Health & Management* **11**, 29–35.

Kiriluk R.M., Servos M.R., Whittle D.M., Cabana G. & Rasmussen J.B. (1995) Using ratios of stable nitrogen and carbon isotopes to characterize the biomagnification of DDE, mirex, and PCB in a Lake Ontario pelagic food web. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 2660–

2674.

Klingenberg C.P. (2016) Size, shape, and form: concepts of allometry in geometric morphometrics. *Development Genes and Evolution* **226**, 113–137.

Koblmüller S., Egger B., Sturmbauer C. & Sefc K.M. (2010) Rapid radiation, ancient incomplete lineage sorting and ancient hybridization in the endemic Lake Tanganyika cichlid tribe Tropheini. *Molecular Phylogenetics and Evolution* **55**, 318–334.

Koblmüller S., Sefc K.M. & Sturmbauer C. (2008) The Lake Tanganyika cichlid species assemblage: recent advances in molecular phylogenetics. *Hydrobiologia* **615**, 5–20.

Kocher T.D., Conroy J.A., McKaye K.R. & Stauffer J.R. (1993) Similar morphologies of cichlid fish in Lakes Tanganyika and Malawi are due to convergence. *Molecular Phylogenetics and Evolution* **2**, 158–165.

Kohda M. (1995) Territoriality of male cichlid fishes in Lake Tanganyika. *Ecology of Freshwater Fish* **4**, 180–184.

Kohda M. & Tanida K. (1996) Overlapping territory of the benthophagous cichlid fish, Lobochilotes labiatus, in Lake Tanganyika. *Environmental Biology of Fishes* **45**, 13–20.

Konings A. (1998) *Tanganyika cichlids in their natural habitat*, 2nd edn. Cichlid Press, El Paso.

Konings A. (2015) *Tanganyika cichlids in their natural habitat*, 3rd edn. Cichlid Press, El Paso.

Lake J.L., Mckinney R.A., Osterman F.A., Pruell R.J., Kiddon J., Ryba S.A., *et al.* (2001) Stable nitrogen isotopes as indicators of anthropogenic activities in small freshwater systems. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 870–878.

Lake Tanganyika Authority (2012) *The strategic action programme for the sustainable management of Lake Tanganyika. United Nations Development Programme*.

Langton R.W. (1982) Diet overlap between Atlantic Cod, Gadus Morhua, Silver Hake, Merluccius Bilinearis, and fifteen other Northwest Atlantic finfish. **80**, 745–759.

Legendre P., Borcard D. & Peres-Neto P. (2005) Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monographs* **75**, 435–450.

Legras G., Loiseau N. & Gaertner J.C. (2018) Functional richness: Overview of indices and underlying concepts. *Acta Oecologica* **87**, 34–44.

Lenth R., Singmann H., Love J., Buerkner P. & Herve M. (2018) Package “emmeans”. Version 1.2.3.

Lévêque C., Oberdorff T., Paugy D., Stiassny M.L.J. & Tedesco P.A. (2008) Global diversity of fish (Pisces) in freshwater. *Hydrobiologia* **595**, 545–567.

Leverington F., Costa K.L., Pavese H., Lisle A. & Hockings M. (2010) A global analysis of protected area management effectiveness. *Environmental Management* **46**, 685–698.

Linard C., Gilbert M., Snow R.W., Noor A.M. & Tatem A.J. (2012) Population distribution, settlement patterns and accessibility across Africa in 2010. *PLoS ONE* **7**, e31743.

Lowe-McConnell R.H. (1993) Fish faunas of the African Great Lakes: Origins, diversity, and vulnerability. *Conservation Biology* **7**, 634–643.

Luck G.W., Carter A. & Smallbone L. (2013) Changes in bird functional diversity across multiple land uses: Interpretations of functional redundancy depend on functional group identity. *PLoS ONE* **8**.

Lyashevska O. & Farnsworth K.D. (2012) How many dimensions of biodiversity do we need? *Ecological Indicators* **18**, 485–492.

Maderbacher M., Bauer C., Herler J., Postl L., Makasa L. & Sturmbauer C. (2008) Assessment of traditional versus geometric morphometrics for discriminating populations of the Tropheus moorii species complex (Teleostei: Cichlidae), a Lake Tanganyika model for allopatric speciation.

Journal of Zoological Systematics and Evolutionary Research **46**, 153–161.

Magnan P., Pool T.K., Olden J.D., Whittier J.B. & Paukert C.P. (2010) Environmental drivers of fish functional diversity and composition in the Lower Colorado River Basin. *Canadian Journal of Fisheries and Aquatic Sciences* **67**, 1791–1807.

Magurran A.E. (2009) Threats to freshwater fish. *Science* **325**, 1215–1216.

Malins D.C., Krahn M.M., Myers M.S., Rhodes L.D., Brown D.W., Krone C.A., *et al.* (1985) Toxic chemicals in sediments and biota from a creosote-polluted harbor relationships with hepatic neoplasms and other hepatic lesions in English Sole (Parophrys vetulus). *Carcinogenesis* **6**, 1463–1469.

Malins D.C., McCain B.B., Brown D.W., Varanasi U., Krahn M.M., Myers M.S., *et al.* (1987) Sediment-associated contaminants and liver-diseases in bottom-dwelling fish. *Hydrobiologia* **149**, 67–74.

Manirakiza P., Covaci A., Nizigiymana L., Ntakimazi G. & Schepens P. (2002) Persistent chlorinated pesticides and polychlorinated biphenyls in selected fish species from Lake Tanganyika, Burundi, Africa. *Environmental Pollution* **117**, 447–455.

Marijnissen S.A.E., Michel E., Cleary D.F.R. & McIntyre P.B. (2009) Ecology and conservation status of endemic freshwater crabs in Lake Tanganyika, Africa. *Biodiversity and Conservation* **18**, 1555–1573.

Marijnissen S.A.E., Michel E., Daniels S.R., Erpenbeck D., Menken S.B.J. & Schram F.R. (2006) Molecular evidence for recent divergence of Lake Tanganyika endemic crabs (Decapoda: Platythelphusidae). *Molecular Phylogenetics and Evolution* **40**, 628–634.

Marsh C.J. & Ewers R.M. (2013) A fractal-based sampling design for ecological surveys quantifying β-diversity. *Methods in Ecology and Evolution* **4**, 63–72.

Mason N.W.H., De Bello F., Mouillot D., Pavoine S. & Dray S. (2013) A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *Journal of Vegetation Science* **24**, 794–806.

Mason N.W.H., Mouillot D., Lee W.G. & Wilson J.B. (2005) Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos* **111**, 112–118.

Matsuzaki S. ichiro S., Sasaki T. & Akasaka M. (2013) Consequences of the introduction of exotic and translocated species and future extirpations on the functional diversity of freshwater fish assemblages. *Global Ecology and Biogeography* **22**, 1071–1082.

Mayfield M.M., Bonser S.P., Morgan J.W., Aubin I., McNamara S. & Vesk P.A. (2010) What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. *Global Ecology and Biogeography* **19**, 423–431.

Mayfield M.M. & Levine J.M. (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters* **13**, 1085–1093.

Mazel F., Mooers A.O., Riva G.V.D. & Pennell M.W. (2017) Conserving phylogenetic diversity can be a poor strategy for conserving functional diversity. *Systematic Biology* **66**, 1019–1027.

McClanahan T. & Graham N. (2005) Recovery trajectories of coral reef fish assemblages within Kenyan marine protected areas. *Marine Ecology Progress Series* **294**, 241–248.

McClanahan T.R., Graham N.A.J., Calnan J.M. & MacNeil M.A. (2007) Toward pristine biomass: Reef fish recovery in coral reef marine protected areas in Kenya. *Ecological Applications* **17**, 1055–67.

McConnaughey T. & McRoy C.P. (1979) Food-web structure and the fractionation of carbon isotopes in the Bering Sea. *Marine Biology* **53**, 257–262.

McIntyre P.B., Michel E., France K., Rivers A., Hakizimana P. & Cohen A.S. (2005) Individual and assemblage level effects of anthropogenic sedimentation on snails in Lake Tanganyika. *Conservation Biology* **19**, 171–181.

McIntyre P.B., Michel E. & Olsgard M. (2006) Top-down and bottom-up controls on periphyton biomass and productivity in Lake Tanganyika. *Limnology and Oceanography* **51**, 1514–1523.

Mckinney M.L. & Lockwood J.L. (1999) Biotic homogenization : a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution* **14**, 450–453.

Meyer B.S., Matschiner M. & Salzburger W. (2015) A tribal level phylogeny of Lake Tanganyika cichlid fishes based on a genomic multi-marker approach. *Molecular Phylogenetics and Evolution* **83**, 56–71.

Micheli F. & Halpern B.S. (2005) Low functional redundancy in coastal marine assemblages. *Ecology Letters* **8**, 391–400.

Miller E. (2017) addTaxa: An R package for adding missing taxa to phylogenies.

Minagawa M. & Wada E. (1984) Stepwise enrichment of 15N along food chains: Further evidence and the relation between δ15N and animal age. *Geochimica et Cosmochimica Acta* **48**, 1135–1140.

Mölsä H., Reynolds J.E., Coenen E.J. & Lindqvist O. V. (1999) Fisheries research towards resource management on Lake Tanganyika. *Hydrobiologia* **407**, 1–24.

Mouillot D., Albouy C., Guilhaumon F., Ben Rais Lasram F., Coll M., Devictor V., *et al.* (2011) Protected and threatened components of fish biodiversity in the Mediterranean sea. *Current Biology* **21**, 1044–50.

Mouillot D., Graham N.A.J., Villeger S., Mason N.W.H. & Bellwood D.R. (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution* **28**, 167–177.

Mouillot D., Villeger S., Parravicini V., Kulbicki M., Arias-Gonzalez J.E., Bender M., *et al.* (2014) Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proceedings of the National Academy of Sciences* **111**, 13757–13762.

Muschick M., Indermaur A. & Salzburger W. (2012) Convergent evolution within an adaptive radiation of cichlid fishes. *Current Biology* **22**, 2362–2368.

Myers N., Mittermeier R.A., Mittermeier C.G., Fonseca G.A.B. & Kent J. (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858.

Naeem S., Duffy J.E. & Zavaleta E. (2012) The functions of biological diversity in an age of extinction. **336**, 1401–1407.

Naeem S. & Li S. (1997) Biodiversity enhances ecosystem reliability. *Nature* **390**, 507–509.

Napit M.K. (2013) The effect of pesticides on fish fauna of Bhopal lower lake (M. P.). *African Journal of Environmental Science and Technology* **7**, 725–727.

National Bureau of Statistics (2011) *Basic facts and figures on human settlements: Tanzania mainland 2009. Dar es Salaam Ministry of Finance*.

Neiffer D.L. & Stamper M.A. (2009) Fish sedation, analgesia, anesthesia, and euthanasia: considerations, methods, and types of drugs. *Institute for Laboratory Animal Research Journal* **50**, 343–360.

Newbold T., Hudson L.N., Hill S.L., Contu S., Lysenko I., Senior R.A., *et al.* (2015) Global effects of land use on local terrestrial biodiversity. *Nature* **520**, 45-.

Newbold T., Hudson L.N., Hill S.L.L., Contu S., Gray C.L., Scharlemann J.P.W., *et al.* (2016) Global patterns of terrestrial assemblage turnover within and among land uses. *Ecography*, 1–13.

Newcombe C.P. & Macdonald D.D. (1991) Effects of suspended sediments on aquatic ecosystems. *North American Journal of Fisheries*

Management **11**, 72–82.

Nishida M. (1991) Lake Tanganyika as an evolutionary reservoir of old lineages of East African cichfid fishes: Inferences from allozyme data. *Experientia* **47**, 974–979.

Niyonkuru C., Isumbisho P. & Moreau J. (2015) Growth, mortality rates and exploitation of cichlids in anthropological coastal zone in the north of Lake Tanganyika. *Journal of Agriculture and Life Sciences* **2**, 84–94.

Njiru M., Okeyo-Owuor J., Muchiri M. & Cowx I. (2004) Shifts in the food of Nile tilapia, Oreochromis niloticus (L.) in Lake Victoria, Kenya. *African Journal of Ecology* **42**, 163–170.

Nshombo M., Yanagisawa Y. & Nagoshi M. (1985) Scale-eating in Perissodus microlepis (Cichlidae) and change of its food habits with growth. *Japanese Journal of Ichthyology* **32**, 66–73.

Oksanen A.J., Blanchet F.G., Kindt R., Legendre P., Minchin P.R., Hara R.B.O., *et al.* (2015) Community ecology package: Vegan. Version 2.3-0.

Orme C.D.L., Davies R.G., Burgess M., Eigenbrod F., Pickup N., Olson V. a, *et al.* (2005) Global hotspots of species richness are not congruent with endemism or threat. *Nature* **436**, 1016–1019.

Ouyang Y., Leininger T.D. & Moran M. (2013) Impacts of reforestation upon sediment load and water outflow in the Lower Yazoo River Watershed, Mississippi. *Ecological Engineering* **61**, 394–406.

Pakeman R.J. (2011) Functional diversity indices reveal the impacts of land use intensification on plant community assembly. *Journal of Ecology* **99**, 1143–1151.

Paradis E., Claude J. & Strimmer K. (2004) APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–290.

Pardo I., Roquet C., Lavergne S., Olesen J.M., Gomez D. & Garcia M.B. (2017) Spatial congruence between taxonomic, phylogenetic and functional hotspots: true pattern or methodological artefact? *Diversity* *and Distributions* **23**, 209–220.

Passy S.I. & Blanchet F.G. (2007) Algal communities in human-impacted stream ecosystems suffer beta-diversity decline. *Diversity and Distributions* **13**, 670–679.

Pavoine S. & Bonsall M.B. (2011) Measuring biodiversity to explain community assembly: A unified approach. *Biological Reviews* **86**, 792–812.

Peart C.R., Bills R., Wilkinson M. & Day J.J. (2014) Nocturnal claroteine catfishes reveal dual colonisation but a single radiation in Lake Tanganyika. *Molecular Phylogenetics and Evolution* **73**, 119–128.

Petchey O.L. & Gaston K.J. (2006) Functional diversity: back to basics and looking forward. *Ecology Letters* **9**, 741–58.

Petchey O.L. & Gaston K.J. (2002) Functional diversity (FD), species richness and community composition. *Ecology Letters* **5**, 402–411.

Pianka E.R. (1966) Latitudinal gradients in species diversity: A review of concepts. *The American Naturalist* **100**, 33–46.

Pimm S.L., Russell G.J., Gittleman J.L. & Brooks T.M. (1995) The future of biodiversity. *Science* **269**, 347–350.

Piola R.F., Moore S.K. & Suthers I.M. (2006) Carbon and nitrogen stable isotope analysis of three types of oyster tissue in an impacted estuary. *Estuarine, Coastal and Shelf Science* **66**, 255–266.

Plass-Johnson J.G., Mcquaid C.D. & Hill J.M. (2015) The effects of tissue type and body size on δ13C and δ15N values in parrotfish (Labridae) from Zanzibar, Tanzania. *Journal of Applied Ichthyology* **31**, 633–637.

Plass-Johnson J.G., Taylor M.H., Husain A.A.A., Teichberg M.C. & Ferse S.C.A. (2016) Non-random variability in functional composition of coral reef fish communities along an environmental gradient. *Plos One* **11**, e0154014.

Plisnier P.D., Nshombo M., Mgana H. & Ntakimazi G. (2018) Monitoring climate change and anthropogenic pressure at Lake Tanganyika.

Journal of Great Lakes Research, https://doi.org/10.1016/j.jglr.2018.05.019.

Polito M.J., Trivelpiece W.Z., Karnovsky N.J., Ng E., Patterson W.P. & Emslie S.D. (2011) Integrating stomach content and stable isotope analyses to quantify the diets of Pygoscelid penguins. *PLoS ONE* **6**, e26642.

Poll M. (1986) *Classification des Cichlidae du lac Tanganika: tribus, genres et espèces*. Academie Royale de Belgique. Classe des Sciences. Memoires 45.

Pool T.K., Grenouillet G. & Villéger S. (2014) Species contribute differently to the taxonomic, functional, and phylogenetic alpha and beta diversity of freshwater fish communities. *Diversity and Distributions* **20**, 1235–1244.

Purvis A. & Hector A. (2000) Getting the measure of biodiversity. *Nature* **405**, 212–9.

Pusey A.E., Pintea L., Wilson M.L., Kamenya S. & Goodall J. (2007) The contribution of long-term research at Gombe National Park to chimpanzee conservation. *Conservation Biology* **21**, 623–634.

Pusey A.E., Wilson M.L. & Anthony Collins D. (2008) Human impacts, disease risk, and population dynamics in the chimpanzees of Gombe National Park, Tanzania. *American Journal of Primatology* **70**, 738–744.

Quan Q., Che X., Wu Y., Wu Y., Zhang Q., Zhang M., *et al.* (2018) Effectiveness of protected areas for vertebrates based on taxonomic and phylogenetic diversity. *Conservation Biology* **32**, 355–365.

Quantum GIS Development Team (2015) Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org/en/site/.

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/.

Ramsar Convention (2000) The Ramsar List. http://archive.ramsar.org/cda/en/ramsar-documents-.

Richter B.D., Braun D.P., Mendelson M.A. & Master L.L. (1997) Threats to imperilled freshwater fauna. *Conservation Biology* **11**, 1081–1093.

Ricotta C., de Bello F., Moretti M., Caccianiga M., Cerabolini B.E.L. & Pavoine S. (2016) Measuring the functional redundancy of biological communities: a quantitative guide. *Methods in Ecology and Evolution* **7**, 1386–1395.

Rodrigues A. & Gaston K.J. (2002a) Maximising phylogenetic diversity in the selection of networks of conservation areas. *Biological Conservation* **105**, 103–111.

Rodrigues A.S.L., Akcakaya H.R., Andleman S.J., Bakarr M.I., Boitani L., Brooks T.M., *et al.* (2004a) Global gap analysis: Priority regions for expanding the global protected-area network. *BioScience* **54**, 1092.

Rodrigues A.S.L., Andleman S.J., Bakarr M.I., Boitani L., Brooks T.M., Cowling R.M., *et al.* (2004b) Effectiveness of the global protected area network in representing species diversity. *Nature* **428**, 9–12.

Rodrigues A.S.L. & Gaston K.J. (2002b) Rarity and conservation planning across geopolitical units. *Conservation Biology* **16**, 674–682.

Rogers C. (1990) Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series* **62**, 185–202.

Rohlf F.J. (2015) The tps series of software. *Hystrix* **26**, 1–4.

Rosindell J., Hubbell S.P. & Etienne R.S. (2011) The Unified Neutral Theory of Biodiversity and Biogeography at age ten. *Trends in Ecology and Evolution* **26**, 340–348.

Rowell K., Dettman D.L. & Dietz R. (2010) Nitrogen isotopes in otoliths reconstruct ancient trophic position. *Environmental Biology of Fishes* **89**, 415–425.

Rüber L. & Adams D.C. (2001) Evolutionary convergence of body shape and trophic morphology in cichlids from Lake Tanganyika. *Journal of Evolutionary Biology* **14**, 325–332.

Rüber L., Verheyen E. & Meyer A. (1999) Replicated evolution of trophic specializations in an endemic cichlid fish lineage from Lake Tanganyika. *Proceedings of the National Academy of Sciences of the United States of America* **96**, 10230–10235.

Rusuwa B., Maruyama A. & Yuma M. (2006) Deterioration of cichlid habitat by increased sedimentation in the rocky littoral zone of Lake Malawi. *Ichthyological Research* **53**, 431–434.

Ryan P.A. (1991) Environmental effects of sediment on New Zealand streams: A review. *New Zealand Journal of Marine and Freshwater Research* **25**, 207–221.

Safi K., Cianciaruso M. V., Loyola R.D., Brito D., Armour-Marshall K. & Diniz-Filho J.A.F. (2011) Understanding global patterns of mammalian functional and phylogenetic diversity. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366**, 2536–2544.

Sala E., Costello C., De Bourbon Parme J., Fiorese M., Heal G., Kelleher K., *et al.* (2016) Fish banks: An economic model to scale marine conservation. *Marine Policy* **73**, 154–161.

Sala E. & Giakoumi S. (2018) No-take marine reserves are the most effective protected areas in the ocean. *ICES Journal of Marine Science* **75**, 1166–1168.

Salzburger W. (2009) The interaction of sexually and naturally selected traits in the adaptive radiations of cichlid fishes. *Molecular Ecology* **18**, 169–185.

Salzburger W. (2018) Understanding explosive diversification through cichlid fish genomics. *Nature Reviews Genetics*.

Salzburger W., Van Bocxlaer B. & Cohen A.S. (2014) Ecology and evolution of the African Great Lakes and their faunas. *Annual Review of Ecology, Evolution, and Systematics* **45**, 519–545.

Samoilys M.A. & Carlos G. (2000) Determining methods of underwater visual census for estimating the abundance of coral reef fishes. *Environmental Biology of Fishes* **57**, 289–304.

Saraiva D.D., Santos A.S. dos, Overbeck G.E., Giehl E.L.H. & Jarenkow J.A. (2018) How effective are protected areas in conserving tree taxonomic and phylogenetic diversity in subtropical Brazilian Atlantic Forests? *Journal for Nature Conservation* **42**, 28–35.

Saunders D.L., Meeuwig J.J. & Vincent A.C.J. (2002) Freshwater protected areas: Strategies for conservation. *Conservation Biology* **16**, 30–41.

Scheffer M., van Bavel B., van de Leemput I.A. & van Nes E.H. (2017) Inequality in nature and society. *Proceedings of the National Academy of Sciences* **114**, 13154–13157.

Schlacher T.A. & Connolly R.M. (2014) Effects of acid treatment on carbon and nitrogen stable isotope ratios in ecological samples: a review and synthesis. *Methods in Ecology and Evolution* **5**, 541–550.

Schlacher T.A., Liddell B., Gaston T.F. & Schlacher-Hoenlinger M. (2005) Fish track wastewater pollution to estuaries. *Oecologia* **144**, 570–584.

Schlacher T.A., Mondon J.A. & Connolly R.M. (2007) Estuarine fish health assessment: Evidence of wastewater impacts based on nitrogen isotopes and histopathology. *Marine Pollution Bulletin* **54**, 1762–1776.

Schleuter D., Daufresne M., Massol F. & Argillier C. (2010) A user’s guide to functional diversity indices. *Ecological Monographs* **80**, 469–484.

Schmera D., Heino J., Podani J., Erős T. & Dolédec S. (2017) Functional diversity: a review of methodology and current knowledge in freshwater macroinvertebrate research. *Hydrobiologia* **787**, 27–44.

Schneider F.D., Morsdorf F., Schmid B., Petchey O.L., Hueni A., Schimel D.S., *et al.* (2017) Mapping functional diversity from remotely sensed morphological and physiological forest traits. *Nature Communications* **8**, 10.1038/s41467-017-01530-3.

Schoener T. (1970) Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* **51**, 408–418.

Seehausen O. (2006) African cichlid fish: a model system in adaptive radiation research. *Proceedings of The Royal Society B* **273**, 1987–98.

Seehausen O. (1997) Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* **277**, 1808–1811.

Sepkoski J.J.J. (1988) Alpha, Beta, or Gamma: Where does all the diversity go? *Paleobiology* **14**, 221–234.

Sindayigaya E., Cauwenbergh R. Van, Robberecht H. & Deelstra H. (1994) Copper, zinc, manganese, iron, lead, cadmium, mercury and arsenic in fish from Lake Tanganyika, Burundi. *The Science of the Total Environment* **144**, 103–115.

Smith V.H. (2003) Eutrophication of freshwater and coastal marine ecosystems a global problem. *Environmental Science and Pollution Research* **10**, 126–139.

Smolders R., Bervoets L., De Coen W. & Blust R. (2004) Cellular energy allocation in zebra mussels exposed along a pollution gradient: Linking cellular effects to higher levels of biological organization. *Environmental Pollution* **129**, 99–112.

Snoeks J. (2000) Ancient lakes: Biodiversity, ecology and evolution. *Advances in Ecological Research* **31**, 17–38.

Socolar J.B., Gilroy J.J., Kunin W.E. & Edwards D.P. (2015) How should beta-diversity inform biodiversity conservation? *Trends in Ecology & Evolution* **31**, 67–80.

Soininen J. & Hillebrand H. (2007) Disentangling distance decay of similarity from richness gradients: Response to Baselga (2007). *Ecography* **30**, 842–844.

Søndergaard M. & Jeppesen E. (2007) Anthropogenic impacts on lake and stream ecosystems, and approaches to restoration. *Journal of Applied Ecology* **44**, 1089–1094.

Srivastava D.S., Cadotte M.W., MacDonald A.W.M., Marushia R.G. & Mirotchnick N. (2012) Phylogenetic diversity and the functioning of ecosystems. *Ecology Letters* **15**, 637–648.

Stirling G., Wilsey B., Stirling G. & Wilsey B. (2001) Empirical relationships between species richness, evenness, and proportional diversity. *The American Naturalist* **158**, 286–299.

Strayer D.L. & Dudgeon D. (2010) Freshwater biodiversity conservation: recent progress and future challenges. *Journal of the North American Benthological Society* **29**, 344–358.

Strecker A., OLden J.D., Hittier J.B. & Paukert C.P. (2011) Defining conservation priorities for freshwater fishes according to taxonomic , functional , and phylogenetic diversity. *Ecological Applications* **21**, 3002–3013.

Struhsaker T.T., Struhsaker P.J. & Siex K.S. (2005) Conserving Africa's rain forests: Problems in protected areas and possible solutions. *Biological Conservation* **123**, 45–54.

Sturmbauer C., Fuchs C., Harb G., Damm E., Duftner N., Maderbacher M., *et al.* (2008) Abundance, distribution, and territory areas of rock-dwelling Lake Tanganyika cichlid fish species. *Hydrobiologia* **615**, 57–68.

Sturmbauer C., Hainz U., Baric S., Verheyen E. & Salzburger W. (2003) Evolution of the tribe Tropheini from Lake Tanganyika: synchronized explosive speciation producing multiple evolutionary parallelism. *Hydrobiologia* **500**, 51–64.

Sturmbauer C., Mark W. & Dallinger R. (1992) Ecophysiology of aufwuchs-eating cichlids in Lake Tanganyika: Niche separation by trophic specialization. *Environmental Biology of Fishes* **35**, 283–290.

Sturmbauer C. & Meyer A. (1992) Genetic divergence, speciation and morphological stasis in a lineage of African cichlid fishes. *Nature* **358**, 417–421.

Sturmbauer C., Salzburger W., Duftner N., Schelly R. & Koblmüller S. (2010) Evolutionary history of the Lake Tanganyika cichlid tribe Lamprologini (Teleostei: Perciformes) derived from mitochondrial and nuclear DNA data. *Molecular Phylogenetics and Evolution* **57**, 266–84.

Sutherland A.B. & Meyer J.L. (2007) Effects of increased suspended sediment on growth rate and gill condition of two southern Appalachian minnows. *Environmental Biology of Fishes* **80**, 389–403.

Sweke E.A., Assam J.M., Chande A.I., Mbonde A.S., Mosha M. & Mtui A. (2016) Comparing the performance of protected and unprotected areas in conserving freshwater fish abundance and biodiversity in Lake Tanganyika, Tanzania. *International Journal of Ecology* **2016**, 1–7.

Sweke E.A., Assam J.M., Matsuishi T. & Chande A.I. (2013) Fish diversity and abundance of Lake Tanganyika: Comparison between protected area (Mahale Mountains National Park) and unprotected areas. *International Journal of Biodiversity* **2013**, 1–10.

Swenson N.G. (2009) Phylogenetic resolution and quantifying the phylogenetic diversity and dispersion of communities. *Plos One* **4**, e4390.

Swenson N.G. (2011) The role of evolutionary processes in producing biodiversity patterns, and the interrelationships between taxonomic, functional and phylogenetic biodiversity. *American Journal of Botany* **98**, 472–480.

Swenson N.G., Erickson D.L., Mi X., Bourg N.A., Forero-Montana J., Ge X., *et al.* (2012) Phylogenetic and functional alpha and beta diversity in temperate and tropical tree communities. *Ecology* **93**, 112–125.

Takahashi T. & Koblmüller S. (2011) The adaptive radiation of cichlid fish in lake tanganyika: a morphological perspective. *International Journal of Evolutionary Biology* **2011**, 1–14.

Takamura K. (1984) Interspecific relationships of aufwuchs-eating fishes in Lake Tanganyika. *Environmental Biology of Fishes* **10**, 225–241.

Takeuchi Y., Ochi H., Kohda M., Sinyinza D. & Hori M. (2010) A 20-year census of a rocky littoral fish community in Lake Tanganyika. *Ecology of Freshwater Fish* **19**, 239–248.

Tanzania National Bureau of Statistics (2013) *Population distribution by age and sex: The United Republic of Tanzania*.

The Nature Conservancy (2018) Potential Lake Tanganyika Key Biodiversity Areas. http://tnc.maps.arcgis.com/apps/MapSeries/index.ht.

Thomsen P.F. & Willerslev E. (2015) Environmental DNA - An emerging tool in conservation for monitoring past and present biodiversity. *Biological Conservation* **183**, 4–18.

Thuiller W., Maiorano L., Mazel F., Guilhaumon F., Ficetola G.F., Lavergne S., *et al.* (2015) Conserving the functional and phylogenetic trees of life of European tetrapods. *Philosophical Transactions of the Royal Society B: Biological Sciences* **370**, 20140005.

Tierney J.E., Mayes M.T., Meyer N., Johnson C., Swarzenski P.W., Cohen A.S., *et al.* (2010) Late-twentieth-century warming in Lake Tanganyika unprecedented since AD 500. *Nature Geoscience* **3**, 422–425.

Tilman D., Reich P.B., Knops J., Wedin D., Mielke T. & Lehman C. (2001) Diversity and productivity in a long-term grassland experiment. *Science* **294**, 843–845.

Tittensor D.P., Micheli F., Nyström M. & Worm B. (2007) Human impacts on the species-area relationship in reef fish assemblages. *Ecology Letters* **10**, 760–72.

Tixier M.S. (2012) Statistical approaches to assess intraspecific variations of morphological continuous characters: The case study of the family phytoseiidae (acari: Mesostigmata). *Cladistics* **28**, 489–502.

Toussaint A., Charpin N., Brosse S. & Villeger S. (2016) Global functional diversity of freshwater fish is concentrated in the Neotropics while functional vulnerability is widespread. *Scientific Reports* **6**, 1–9.

Trueman C.N., McGill R.A.R. & Guyard P.H. (2005) The effect of growth rate on tissue-diet isotopic spacing in rapidly growing animals. An experimental study with Atlantic salmon (Salmo salar). *Rapid Communications in Mass Spectrometry* **19**, 3239–3247.

Tucker C.M. & Cadotte M.W. (2013) Unifying measures of biodiversity: Understanding when richness and phylogenetic diversity should be congruent. *Diversity and Distributions* **19**, 845–854.

Tuomisto H. (2010) A consistent terminology for quantifying species diversity? Yes, it does exist. *Oecologia* **164**, 853–860.

Ulrich W. (2004) Species co-occurrence and neutral models: reassessing J.M. Diamond’s assembly rules. *Oikos* **107**, 603–609.

Vellend M., Cornwell W.K., Magnuson-Ford K. & Mooers A.Ø. (2011) Measuring phylogenetic biodiversity. In: *Biological Diversity: Frontiers in measurement and assessment*, 1st edn. (Eds A.E. Magurran & B.J. McGill), pp. 194–207. Oxford University Press, Oxford, UK.

Vermeulen S., Sturaro N., Gobert S., Bouquegneau J.M. & Lepoint G. (2011) Potential early indicators of anthropogenically derived nutrients: A multiscale stable isotope analysis. *Marine Ecology Progress Series* **422**, 9–22.

Villéger S., Grenouillet G. & Brosse S. (2013) Decomposing functional β-diversity reveals that low functional β-diversity is driven by low functional turnover in European fish assemblages. *Global Ecology and Biogeography* **22**, 671–681.

Villéger S., Mason N.W.H. & Mouillot D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **89**, 2290–2301.

Villéger S., Miranda J.R., Hernández D.F. & Mouillot D. (2010) Contrasting changes in taxonomie vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications* **20**, 1512–1522.

Vitousek P.M., Aber J.D., Howarth R.H., Likens G.E., Matson P.A., Schindler D.W., *et al.* (1997) Human alteration of the global nitrogen cycle: Source and consequences. *Ecological Applications* **7**, 737–750.

Vitule J.R.S., Agostinho A.A., Azevedo-Santos V.M., Daga V.S., Darwall W.R.T., Fitzgerald D.B., *et al.* (2017) We need better understanding about functional diversity and vulnerability of tropical freshwater fishes. *Biodiversity and Conservation* **26**, 757–762.

Wagner C.E., McIntyre P.B., Buels K.S., Gilbert D.M. & Michel E. (2009) Diet predicts intestine length in Lake Tanganyikas cichlid fishes. *Functional Ecology* **23**, 1122–1131.

Wainwright P.C. (2007) Functional versus morphological diversity in macroevolution. *Annual Review of Ecology, Evolution, and Systematics* **38**, 381–401.

Webb C.O. (2000) Exploring the phylogenetic structure of ecological communities: An example for rain forest trees. *The American Naturalist* **156**, 145–155.

Webb C.O., Ackerly D.D., McPeek M.A. & Donoghue M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics* **33**, 475–505.

Webster M. & Sheets H.D. (2010) A practical introduction to landmark-based geometric morphometrics. *Quantitative Methods in Paleobiology* **16**, 163–188.

Weiher E. (2011) A primer of trait and functional diversity. In: *Biological Diversity: Frontiers in measurement and assessment*, 1st edn. (Eds A.E. Magurran & B.J. McGill), pp. 175–193. Oxford University Press, Oxford, UK.

West K. (2001) *Lake Tanganyika: Results and experiences of the UNDP/GEF conservation initiative (RAF/92/G32) in Burundi, D.R. Congo, Tanzania, and Zambia.* Lake Tanganyika Biodiversity Project. Kent, UK.

West K. & Michel E. (2000) The dynamics of endemic diversification: Molecular phylogeny suggests an explosive origin of the Thiarid gastropods of Lake Tanganyika. *Advances in Ecological Research* **31**, 331–354.

Whittaker R.. H.. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* **30**, 279–338.

Wiens J.J. (2016) Climate-related local extinctions are already widespread among plant and animal species. *PLoS Biology* **14**, 1–18.

Winkelmann K., Genner M.J., Takahashi T. & Rüber L. (2014) Competition-driven speciation in cichlid fish. *Nature Communications* **5**, 3412.

Winkler D.W. & Hall C. (2013) The community structure of coral reef fishes. *The American Naturalist* **130**, 526–543.

Wood P. & Armitage P. (1997) Biological effects of fine sediment in the lotic environment. *Environmental Management* **21**, 203–17.

Woodcock P., Edwards D.P., Newton R.J., Edwards F.A., Khen C.V., Bottrell S.H., *et al.* (2012) Assessing trophic position from nitrogen isotope ratios: Effective calibration against spatially varying baselines. *Naturwissenschaften* **99**, 275–283.

Woodroffe R., Ginsberg J.R., Series N. & Jun N. (2007) Edge effects and the extinction of populations inside protected areas. *Science* **280**, 2126–2128.

Worldpop (2013) Tanzania population density data. http://www.worldpop.org.uk/data/summary/?contselec.

Yamaoka K. (1991) Cichlid Fishes, Behaviour, Ecology and Evolution. (Ed. M. Keenleyside, H), pp. 151–172. Chapman & Hall, London.

Yamaoka K. (1983) Feeding behaviour and dental morphology of algae scraping cichlids (Pisces: Teleostei) in Lake Tanganyika. *African Study Monographs* **4**, 77–89.

Yanagisawa Y., Nshombo M., Nishida M. & Niimura Y. (1990) Sexual dichromatism and feeding habits of the scale-eater *Plecodus straeleni* (Cichlidae, Teleostei) in Lake Tanganyika. *Journal of Ethology* **8**, 25–28.

Yoccoz N.G., Nichols J.D. & Boulinier T. (2001) Monitoring of biological diversity in space and time. *Trends in Ecology & Evolution* **16**, 446–453.