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



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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-focused 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 180 km of Tanzanian coastline, sampling 70 cichlid species representing a diverse range of life-histories and trophic groups. Alpha diversity was up to 50% 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.

1. 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 and 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 (Revenga et al., 2005; 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 and Jenkins, 1998). A dominant component of the LT ecosystem are its cichlid fishes (~200 valid species, 97% endemics) that form multiple adaptive radiations (Day et al., 2008). Despite this considerable richness, only 6% of its coastline is protected consisting of four national parks with differing levels of protection (Coulter and Mubamba, 1993, see Appendix S1). 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

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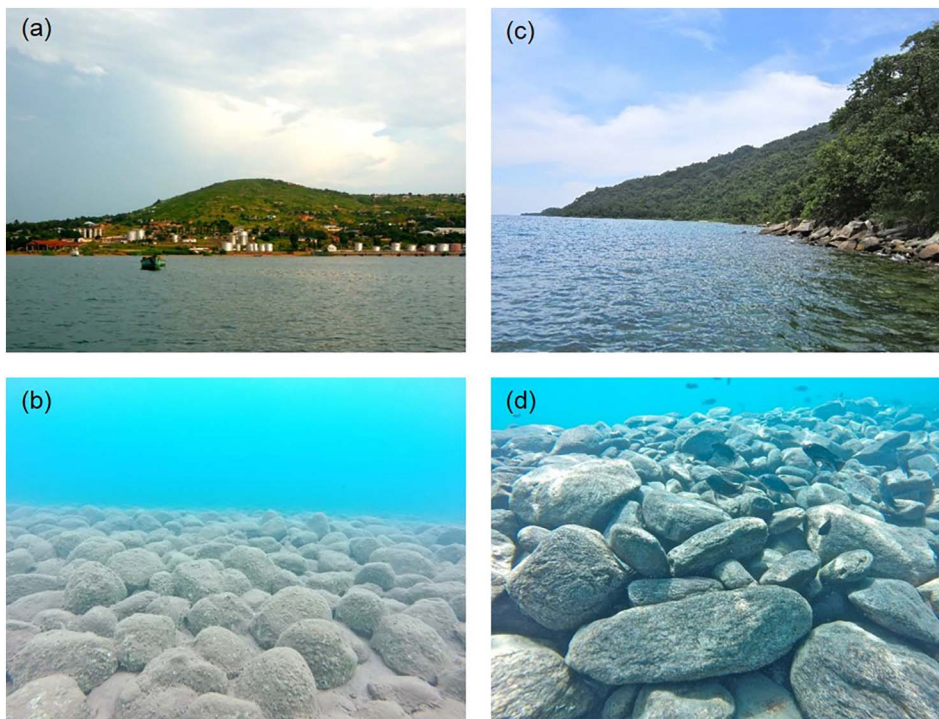


Fig. 1. Photographs showing visible differences between (a) Kigoma Town's urban and deforested shoreline and (b) corresponding disturbed rocky shore, and, (c) Mahale NP's forested shoreline, (d) and corresponding pristine rocky shore. At GPS co-ordinates (a) 4°89.252'S 29°61.593'E, (b) 4°53.518'S 29°36.411'E, (c) 6°05.042'S 29°43.456'E and (d) 6°10.258'S 29°44.251'E.

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., 1993, Alin et al., 2002, McIntyre et al., 2005, see Fig. 1). The detrimental effects of sedimentation on aquatic communities have been widely demonstrated (reviewed in Donohue and 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 and 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 and 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 input 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 et al., 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 its impact has not been quantified.

Previous studies focussing on LT have investigated the effects of human disturbance on the alpha diversity of fish and invertebrate community composition (Cohen et al., 1993; Alin et al., 1999; McIntyre et al., 2005; Sweke et al., 2013) 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 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., 2015) 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 4 km (Ding et al., 2015). 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., 2016).

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, 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, while 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., 2016). The recently developed zeta diversity metric, ζ_i , (Hui and 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,

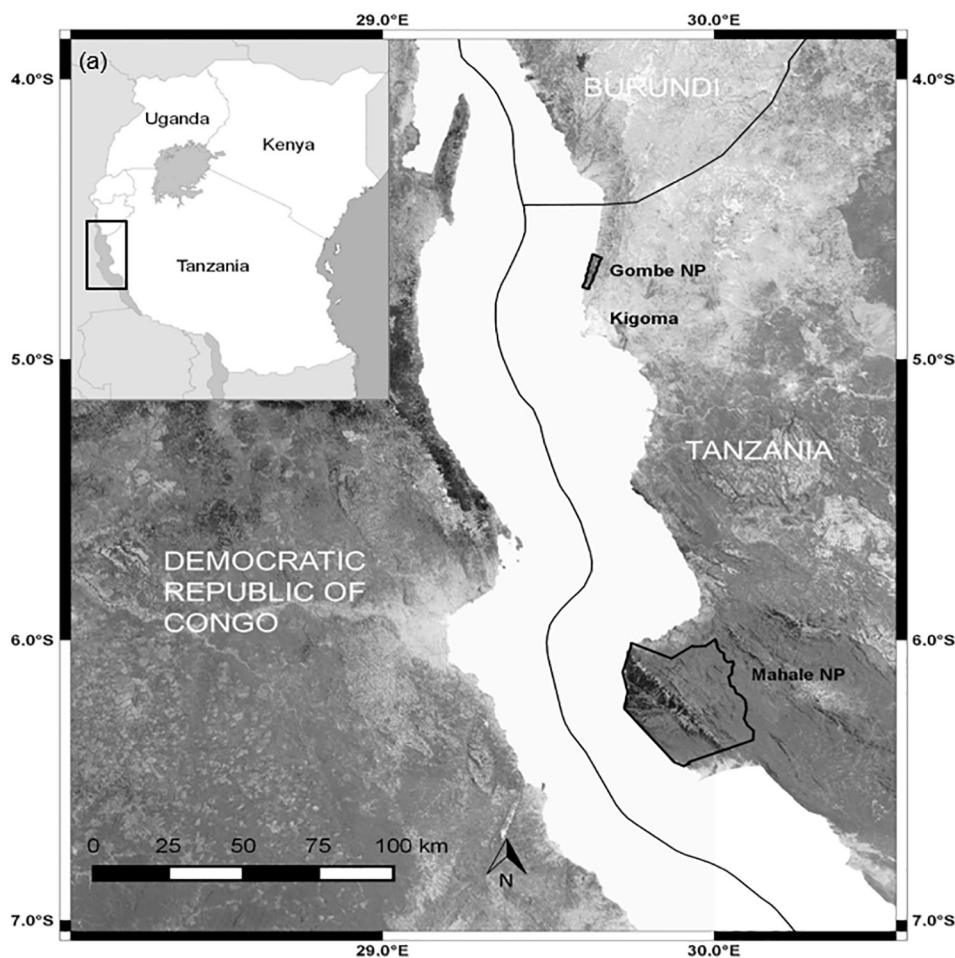
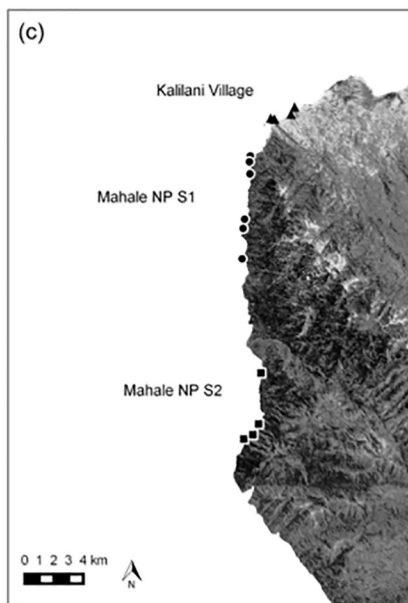
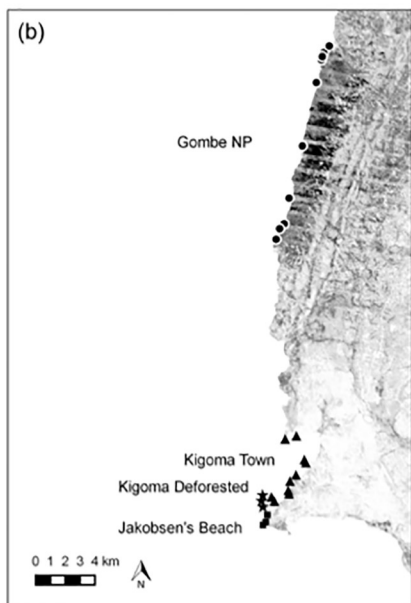


Fig. 2. (a) Map of the Northern and central regions of Lake Tanganyika (LT) highlighting the protected areas (bold black outline), with inset showing the location of LT, and the study location (black box) in East Africa. (b) Northern study localities detailing samples points (Gombe NP, black circles; 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).



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 and 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 and 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. 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 and 10 m (Konings, 1998).

2.1. 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 and Mubamba, 1993). Hence the shoreline exhibits a wide range of disturbance (Fig. 1).

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 and 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 1.6 km off the coast covering an area of 96 km² (Sweke et al., 2013). In contrast Gombe NP is much smaller, protecting 35 km² 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 et al., 2005), with few signs of human disturbance.

The following seven localities spanning 180 km of coastline (Fig. 2) were selected and surveyed between January and April 2015: (1) Kigoma Town, a large town with a human population in excess of 200 000; (2) Kigoma Deforested, an unpopulated stretch of deforested shoreline to the south of Kigoma Town; (3) Jakobsen's Beach, a 1 km

stretch of privately owned uninhabited shoreline with early-stage secondary growth forest, situated 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 12 km stretch of semi-deciduous and evergreen forest 11 km north of Kigoma Town; (6) Mahale NP S1, an uninhabited 7 km 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 5 km stretch of rocky shoreline within the NP and south of Mahale NP S1 (see Appendix S1 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 (iii) terrestrial and (iv) water (no-fishing) protection status. These factors were then combined with equal weighting to produce a HD index (Falcone et al., 2010) on a relative scale of 1 (low disturbance) to 10 (high disturbance) (Appendix S1 and Table S1).

2.2. Data collection

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

SCUBA survey counts of cichlid species and their abundances were conducted using the stationary visual census technique (Bohnsack and Bannerot, 1986), in which fish were given 1 min to settle once divers had reached the survey point, after which all species and individuals observed with a radius of 5 m were counted. Each survey lasted 8 min. 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 was 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); beta-part v1.3 (Baselga and Orme, 2012); and zetadiv v0.1 packages to generate diversity measures (see below).

2.3. 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.

2.3.1. 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. In order 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.

2.3.2. 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 takes into account (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. 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, while the loss/nestedness component describes species loss without replacement (Baselga and 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 accumulate 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 and 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 and McGeoch, 2014). Moreover, when environmental change has a disproportionately 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 and McGeoch, 2014).

2.3.3. 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 et al., 2006).

3. 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 S3). 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 10 m depths (see Tables S4 and S5) 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 (Fig. S2). All community datasets used to generate the results reported here are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.8cs37>.

3.1. Species diversity along a gradient of human disturbance

3.1.1. Alpha diversity

We found a clear negative relationship between disturbance rank and alpha diversity (Table 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).

3.1.2. Beta and zeta diversity

We found only very weak distance decay in similarity within each locality (Table S6), meaning pairs of surveys separated by 20 m were as similar as pairs separated by several km. In contrast, we found a significant positive trend between the Sørensen index and HD ranking (Table 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 to 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 1). Our prediction that the nestedness component of beta diversity would increase with increased HD was thus borne out.

All localities showed a monotonic decline in zeta diversity (ζ_i) with the number of survey sites considered (Fig. 3). Tests for spatial autocorrelation in zeta showed some statistically significant spatial structure, but generally this was very weak apart for Kigoma Deforested (Appendix Fig. S3), 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, 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 S7). To test the hypothesis that an exponential decay in zeta in the disturbed localities might occur due to biased loss of common or rare

Table 1
Correlations between relative HD rank and alpha and beta diversity (all pairs of survey within each locality) values for cichlids at all localities^a.

Locality	Relative human disturbance	Alpha diversity			Beta diversity			Sørensen loss component (%)	Mean Bray-Curtis dissimilarity between survey pairs [± sd]	Bray-Curtis loss component (%)
		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 (%)			
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	
Kaliliani 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*	

^a 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).

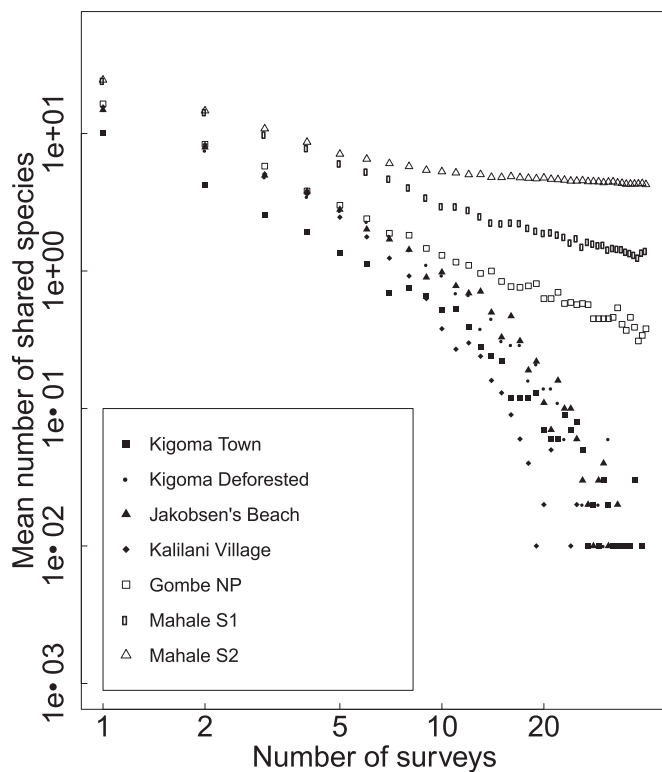


Fig. 3. The relationships between zeta diversity ζ_i (the mean number of species shared between i surveys), and the number of surveys (i). Filled symbols represent degraded localities and are best fit by an exponential function; open symbols represent the Freshwater Protected Areas (FPAs) that are best fit by a power function (AIC values given in Table S4).

species, we constructed a null model (described in Appendix S2) 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 (Fig. S3). 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 (Fig. S4). 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 more sparse community matrix of Kalilani suggesting large drops in species occurrences may be sufficient to produce exponential decays in zeta diversity.

3.2. 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 S3. Overall, we found significant differences in how the tribes and trophic groups responded to locality HD rank.

3.2.1. HD gradient analysis

The median species richness per survey was negatively correlated

Table 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^a.

Group	Alpha diversity			Beta diversity			
	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

^a Statistically significant positive or negative correlation are denoted by * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$. See Table S5 for details of Spearman's Rank Correlation input values.

with the HD gradient for all three tribes (Table 2, full results given in Table S8). 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 S8) 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). 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). 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). 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 S8). 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.

3.3. 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 1 km apart (Table S9). 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 S9). 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 locality, 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 (Fig. S6).

4. Discussion

Here, we specifically investigated the effects of human disturbance (HD) along an environmental gradient focusing on the species rich and ecologically heterogenous LT rocky-shore cichlid communities. By using a variety of alpha, beta and zeta diversity measures, and by focussing on species, functional (trophic group), and 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 et al., 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 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 (Winkler and Hall, 2013; Soininen et al., 2007). We also found a positive correlation between the Sørensen index and locality HD rank (Table 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). 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., 2016). 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). 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 (Fig. 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 S3). 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). However, specific groups appear to be more greatly affected by HD. We showed that herbivore diversity was more affected by HD (Tables 2, S5), and in particular the diversity of specialist herbivores that constitute the Tropheini, compared to other tribes (Tables 2, S8). We argue the loss in specialist herbivores is likely to 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 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.

4.1. 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. Fig. 1). Previous studies (reviewed by Donohue and 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, and 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 S10). 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). 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 (e.g. Yamaoka, 1991; Hata et al., 2015). These results support the findings of Alin et al. (1999) who observed a decline in algivore 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 epilithic and filamentous algae (reviewed in Donohue and Molinos, 2009). It would then be interesting to link studies of diet 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 S3). 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).

5. 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 inter-connection 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 and 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 spillover 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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2017.06.001>.

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