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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-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 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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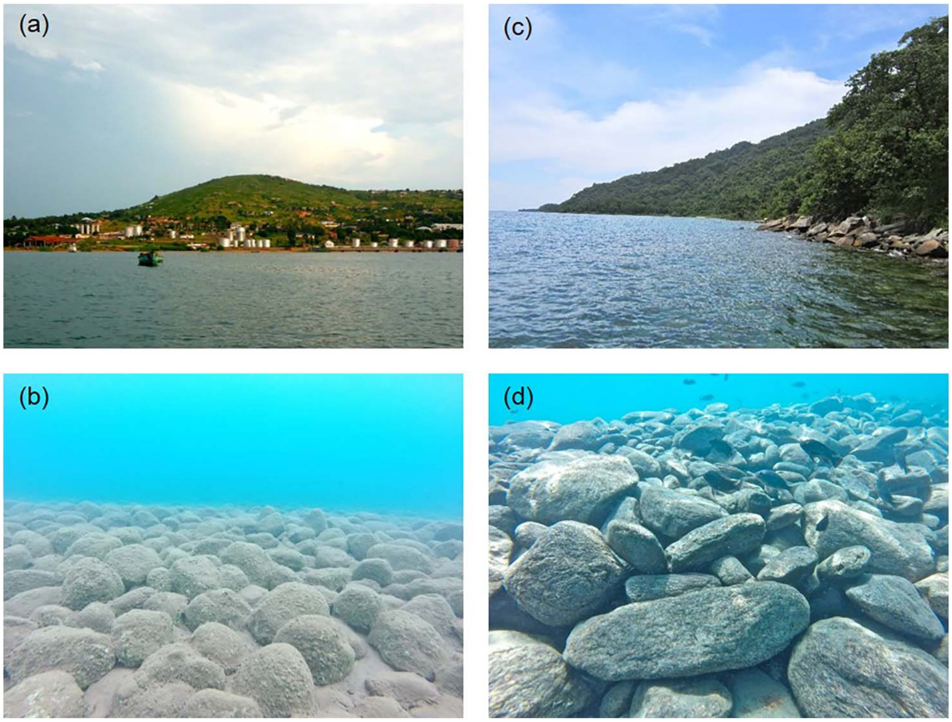

Fig. 1. Photographs showing visible differences between (a) Kigoma Town's urban and deforested shoreline and (b) corresponding disturbed rocky shore, and, (c) Mahale NP's forested shoreline, (d) and corresponding pristine rocky shore. At GPS co-ordinates (a) 4°89.252′S 29°61.593′E, (b) 4°53.518′S 29°36.411′E,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