ADVANCES IN CICHLID RESEARCH

Habitat complexity predicts the community diversity of rock-dwelling cichlid fish in Lake Malawi, East Africa

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Abstract Understanding the factors that regulate species diversity remains an important goal in ecology, conservation and evolutionary biology. Speciose communities, like the cichlid fishes in the East African Great Lakes, offer useful opportunities to examine these factors. For example, Lake Malawi supports well over 700 cichlid fish species which likely descended from a common ancestor within the past 2–4 million years. One consequence of this remarkable radiation is the high species diversity of Lake Malawi's cichlid communities. However, the factors facilitating the assembly and maintenance of species rich cichlid communities have yet to be fully identified. In this study, we examine the diversity of Lake Malawi's rock-dwelling cichlid communities and investigate the roles that several environmental variables have played in maintaining such high diversity. We surveyed 82 quadrats spanning seven sites and observed 54 species from 12 genera. Most environmental variables that we measured varied significantly within, but did not differ significantly among sampled sites, suggesting that habitat heterogeneity is locally high, but at the lake-wide scale habitats are uniformly heterogeneous. Community diversity was strongly influenced by habitat complexity, while community similarity was strongly dependent on the geographical distance between communities. At the genus level, no relationship between geographic distance and community similarity was found, but community composition was also determined by habitat complexity. Our findings demonstrate that habitat complexity predicts both cichlid species diversity and functional diversity, whereas geographic separation determines the similarities among communities at the species but not at the generic level.

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Introduction

Understanding the factors regulating species diversity is a central goal in ecology, conservation biology and macroevolutionary biology. A variety of factors can influence species diversity including historical events (Ricklefs & Schluter, 1993; Wiens & Donoghue, 2004), immigration and extinction (MacArthur & Wilson, 1963; Rosenzweig, 1995), latitudinal gradients (Willig et al., 2003), area size and productivity (Wright, 1983), rate and degree of disturbance (Petraitis et al., 1989), competition (Vandermeer, 1970) and habitat complexity (Ricklefs & Schluter, 1993; Huston, 1994). Among these factors, the relationship between habitat complexity and species diversity seems universal (Kovalenko et al., 2012). First quantified by MacArthur and MacArthur in their study of tropical birds (MacArthur & MacArthur, 1961), this association was later confirmed in a variety of organisms, including insects (Whitmore et al., 2002; Lassau & Hochuli, 2004) and other invertebrates (Kohn & Leviten, 1976; Heck & Wetstone, 1977; Parr et al., 2010), reptiles (Petren & Case, 1998; D'cruze & Kumar, 2011), fish (Roberts & Ormond, 1987; Ferreira et al., 2001; Brian & Martin, 2005; Gratwicke & Speight, 2005; Willis et al., 2005) and small mammals (August, 1983; Williams et al., 2002). Although the relationship between habitat complexity and species diversity has been well documented in many aquatic systems (Cunha et al., 2012), it is still poorly understood in lakes, except in the context of anthropogenic disturbance and restoration (Tews et al., 2004).

Here, we examine the role of several environmental factors, particularly habitat complexity, in shaping the cichlid fish diversity in Lake Malawi. The lake supports well over 700 haplochromine cichlid fish species, all of which likely descended from a single common ancestor within the past 2–4 million years (Koblmüller et al., 2008; Danley et al. 2012). The rock-dwelling cichlids, or mbuna, are among the most diverse lineages in the lake. They are represented by several hundred species, many of which are locally endemic. At any given rocky habitat, 30 or more species may co-exist and utilize this habitat for feeding, shelter and reproduction (Ribbink et al., 1983). These large numbers of sympatric species provide an excellent opportunity to elucidate the mechanisms that contribute to the distribution and maintenance of species diversity.

A number of factors have been suggested to account for the remarkable diversity of Lake Malawi's cichlid fish. The great depth of the lake, for example, is believed to have allowed cichlid fish to persist through the East African megadroughts (Danley et al., 2012) and the long and heterogeneous shoreline likely facilitated the divergence of even geographically proximate populations (Danley et al., 2000; Genner et al., 2004). Throughout the lake, species richness negatively correlates with water depth (Ribbink et al., 1983; Genner & Turner, 2005; Albertson, 2008; Parnell & Streelman, 2011). Biotic factors such as trophic partitioning (Ribbink et al., 1983; Albertson, 2008), mate choice (Van Oppen et al., 1998), dispersal rates (Trendall, 1988), migration (Danley et al., 2000), extinction (Seehausen et al., 1997) and anthropogenic translocation (Trendall, 1988; Genner et al., 2006) can all influence mbuna diversity. However, despite this extensive work, the relationship among habitat complexity, spatial scale and cichlid diversity still remains poorly quantified in Lake Malawi.

To identify the major environmental factors determining the diversity of mbuna communities, we quantified the relationship between mbuna diversity and a variety of environmental variables at different sampling sites across the lake. To quantify the similarities of mbuna communities at different spatial scales, we further generated community similarity matrices across the lake at both the species and functional levels and examined how different environmental variables predict the similarities among different communities.

Materials and methods

Community survey

To investigate the relationship between environmental features and mbuna diversity, seven sites with rocky substrate were studied in Lake Malawi between 14 May and 13 June 2010 (Table 1; Fig. 1). A nested sampling design using a large range of distances within and between sites was employed to investigate large-, intermediate-, and fine-scale spatial patterns. To investigate large-scale diversity patterns, we sampled cichlid communities greater than 100 km apart. Cichlid communities separated by 1–100 km were sampled to investigate the effects of intermediate

Table 1 Coordinates and number of species of each transect in the study

Study site	Latitude(S) (°)	Longitude(E) (°)	Number of observed species
Boadzulu Island 1	14.15004	35.08506	7
Boadzulu Island 2	14.15950	35.08546	10
Chiofu Bay 1	13.31941	34.52013	8
Chiofu Bay 2	13.32033	34.51884	10
Maleri Island 1	13.53729	34.37130	11
Maleri Island 2	13.53633	34.37164	5
Nakantenga 1	13.54987	34.38568	13
Nakantenga 2	13.54949	34.38626	15
Thumbi West Island 1	14.01438	34.49437	16
Thumbi West Island 2	14.01434	34.49397	14
Otter Point 1	14.02366	34.49338	1
Otter Point 2	14.02321	34.49375	2
Nkhata Bay 1	11.36522	34.18057	7
Nkhata Bay 2	11.36418	34.18197	18

geographic distances. Analysis at the fine spatial scale included transects less than 100 m apart at the same site.

At each site, we established two 20 m long transect lines running perpendicular to the shoreline. Along each transect, three positions at randomly selected distances from the shoreline were chosen. On both sides of these three positions a 2 m × 2 m quadrat was placed on the substrate perpendicular to the transect line. These quadrats, with centres 2 m from the transect line, defined the area of data collection. Thus, 12 quadrats were sampled at each site except for Chiofu Bay, where only 10 quadrats were sampled (at Chiofu Bay transect 1, six

quadrats were sampled; at Chiofu Bay transect 2, four were sampled).

To document the mbuna community in each quadrat, a diver placed the quadrat on the substrate and moved away to allow fish to acclimate for 10 min. The diver then returned to the quadrat and allowed the fish to acclimate to the diver's presence for an additional 5 min. After acclimation, the diver recorded the number of adult individuals of each mbuna species entering from the left side of the quadrat during a 10 min observation period to avoid repeat counting. Species identification and classification followed Konings (2007) and Ribbink et al. (1983). Water samples were taken at the centre of each quadrat at the depth of the substrate, and water temperature, conductivity, pH, and salinity were measured with a YSI 556 Multiparameter System Probe (DBA Instrumart, South Burlington, VT, USA). Lateral Secchi distance was used to estimate turbidity at each quadrat. Lateral Secchi distance was measured as the distance at which a diver, located at the quadrat, could no longer distinguish black from white on a horizontally displaced Secchi disc. The depth of the quadrat centre was measured with a dive computer (Subgear XP-10, Wendelstein, Germany).

Two variables quantifying habitat complexity were used: rock complexity and rugosity. Rock complexity of the substrate was quantified at each quadrat using the Shannon–Wiener index, similar to the methods established by Willis et al. (2005). Six strings spanning opposing sides of the quadrat created a 4 × 4 grid of 0.5 × 0.5 m cells with nine cross string nodes. At each node, the underlying substrate was categorized as (1) sand, (2) pebble (<20 cm along its long axis), (3) cobble (20–50 cm along its long axis), (4) boulder (50–150 cm along its long axis) or (5) bedrock (>150 cm along its long axis). To generate relative frequencies for substrate types in each quadrat, the number of occurrences of each substrate type in a quadrat was summed and divided by nine.

Rugosity, the topographic complexity of the substrate within the quadrat (Shumway et al., 2007), was measured by draping a flexible metal chain across the quadrat, keeping the chain parallel to the lake shore and cautiously following the contour of the substrate such that all chain links were in contact with the substrate. The chain length required to span the quadrat was divided by the linear distance (2 m). This process was repeated three times at 50 cm intervals,
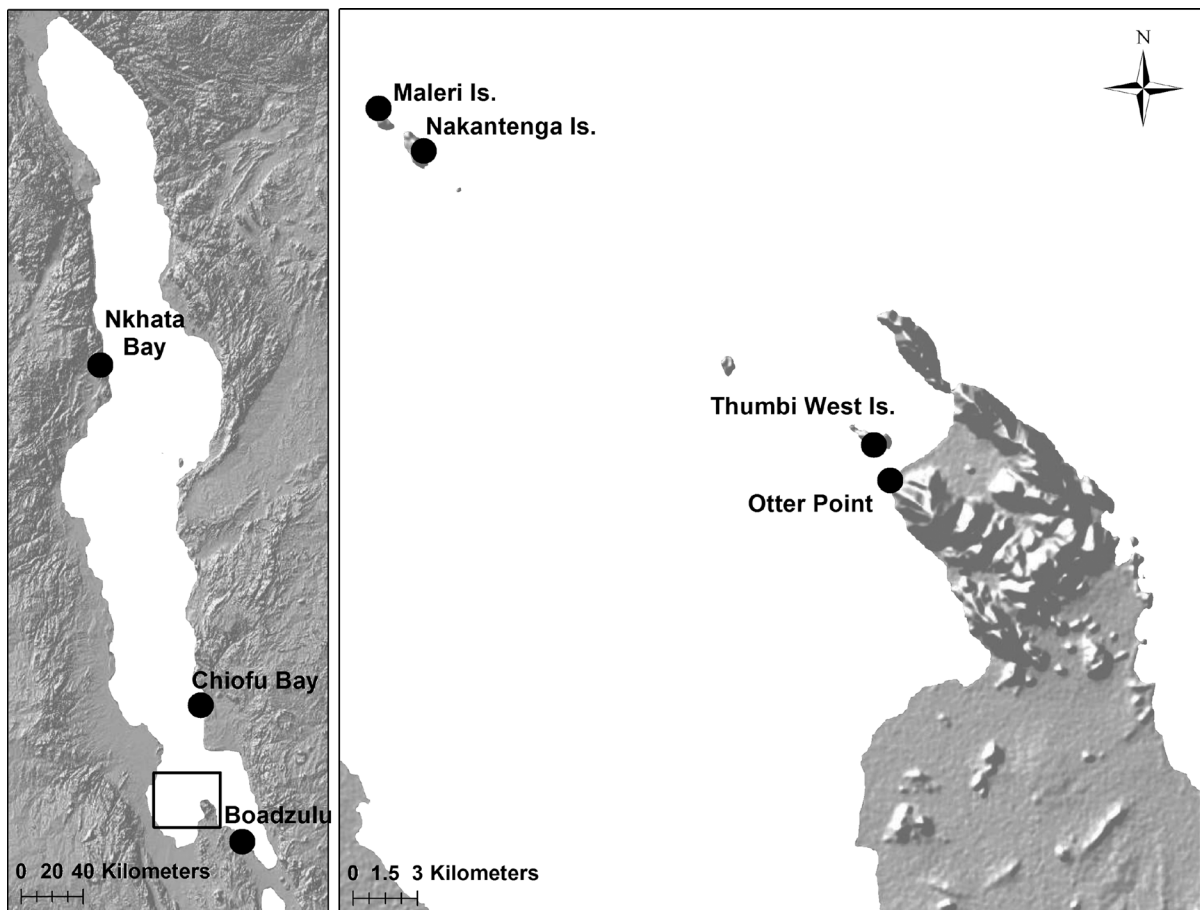
Fig. 1 Lake Malawi showing the seven sampling sites covering both large and small geographical distances

and the mean of these three values was used to quantify the quadrat's rugosity. A rugosity value of 1.0 describes a flat substrate and rugosity increases with increasing irregularity of the substrate.

Data analysis

To test the similarity of the measured environmental variables across all sample sites, a mixed-model nested analysis of variance (ANOVA) was used. Rugosity, hydrochemical measurements and species count data were $\log_{10}(x + 1)$ transformed to improve normality of the data. The significance of pairwise correlations between different environmental variables was examined with a t test.

The Simpson's index was calculated to describe mbuna diversity (Simpson, 1949). We used classification and regression tree analysis (CART) to identify the major environmental variables which affect mbuna diversity (Rejwan et al., 1999). CART divides the dataset recursively into increasingly homogenous subsets with respect to the defined groups and provides a regression tree with an associated dichotomous key to sort samples into statistically significant different groups (McCune et al., 2002). After tree construction, cross-validation ($n = 1,000$) procedures were used to prune the tree and avoid over fitting the variables in the model. The analysis is implemented in the mvpart library in the statistical package R (Therneau et al., 2012). The same analysis was applied to test the relationships between environmental variables and cichlid diversity at the functional (generic) level (see below).

The Bray–Curtis dissimilarity index was calculated for each transect to evaluate how communities varied across different geographical scales. For each transect,

we pooled the counts of each species from the 6 local quadrats to allow for comparisons between transects while discarding within transect variation. Geographical distances were calculated from GPS coordinates with the distGPS function in the SoDA package (Chambers, 2008) in R. We then generated linear and nonlinear regression models to estimate the relationship between spatial distance and community divergence across the study transects. The best models for both linear and nonlinear regression were determined by utilizing a least-squares approach. Having identified the best linear and nonlinear models, a lack-of-fit test was performed for model selection using ANOVA with two arguments: the nonlinear regression fit as the first argument and the linear fit as the second argument.

Mbuna genera are distinguished by unique trophic structures that reflect genus specific adaptations to different food sources (Ribbink et al., 1983). Therefore, genera can be regarded as functional groups in the mbuna. To determine how environmental variables affect the differences of cichlid fish communities at the functional level, species data were collapsed to the level of genera. Hierarchical agglomerative cluster analysis was utilized to determine the similarity of functional groups in each community (Lavorel et al., 1997; Hooper et al., 2002). An indicator species analysis (Dufrene & Legendre, 1997) was used to assign clusters into statistically significant groups. These groups were evaluated based on the calculation of the indicator value (IndVal) of genera in each cluster. To visualize these groups, nonmetric multidimensional scaling (NMDS) was used. Environmental variables correlated with community similarities at the generic level were determined using linear correlation. All analyses were performed in R statistical package (R Development Core Team, 2012).

Results

Community surveys and environmental variables

We sampled a total of 82 quadrats at seven locations across the lake. Within these 82 quadrats, 54 mbuna species belonging to 12 genera were observed (Appendix 1 in Supplementary Material). *Maylandia* (synonymous with *Metriaclima*) *zebra* was present at 45 of 82 quadrats (54.9%) and was the most frequently observed species. In contrast, most species were restricted to a limited number of quadrats. Species richness was the highest at Nkhata Bay, where as many as 15 species were recorded in a single quadrat. Otter Point had the lowest species richness with only two species observed across all quadrats. However, it is important to note that these data represent only the numbers of species recorded during our observation periods and, therefore, are not a complete record of the species at each site.

Mixed-model nested analysis of variance indicates that the majority of environmental parameters varied significantly within sites, but not differ among sites (Table 2). Rugosity, rock complexity, salinity, pH and lateral Secchi distance all varied significantly within sites, but did not differ among sites. Only temperature and depth differed significantly among sites. Temperature varied within sites, but depth did not. Conductivity showed no significant difference at either level. The pairwise correlations between different environmental variables were examined (Supplemental Fig. 1). Water depth and secchi distance were significantly correlated ($P < 0.001$). Salinity was significantly correlated with pH ($P = 0.006$) and conductivity ($P < 0.001$). Water temperature was significantly correlated with the distance to the lake shore ($P = 0.003$) and depth ($P < 0.001$). No other significant correlations were identified.

Cichlid diversity correlates with habitat complexity

CART analysis revealed that rugosity was significantly positively correlated with mbuna diversity at the species ($r^2 = 0.14$, $P < 0.01$) and functional level ($r^2 = 0.12$, $P < 0.01$). At the species level, a habitat with a rugosity greater than 1.18 supported a more diverse community (mean Simpson index = 0.79, Fig. 2a), whereas when rugosity was less than 1.18, less diverse communities were supported (mean Simpson index = 0.58). At the functional level, as with the species analysis, a habitat with higher rugosity (≥ 1.24) supported a more diverse functional group community (mean Simpson index = 0.245, Fig. 2b). When rugosity was less than 1.24, less diverse functional groups were supported (mean Simpson index = 0.196). No other environmental variables were found to significantly influence species or functional group diversity at the studied sites.

Table 2 Results of mixed-model nested analysis of variance (ANOVA) with 1,000 permutations on selected environmental variables across sampling sites

Environmental variables	Among sites				Within sites	
	d.f	F	Pr(>F)	d.f	F	Pr(>F)
Rugosity	6	2.6832	0.1149	7	6.8967	**0.0010**
Rock complexity	6	2.6220	0.1419	7	3.5603	**0.0190**
Salinity	6	1.0305	0.4325	7	1.9376	**0.0070**
pH	6	1.3456	0.3367	7	4.4054	**0.0040**
Lateral Secchi distance	6	4.5580	0.0550	7	3.4060	**0.0150**
Temperature	6	6.1810	**0.0080**	7	3.2950	**0.0360**
Depth	6	5.6215	**0.0240**	7	1.7889	0.1386
Conductivity	6	0.6620	0.6980	7	1.4960	0.0850

Environmental variables with significant among and within site variation are indicated with bold *p* values

Fig. 2 Scatterplots of Simpson diversity and rugosity at **a** the species and **b** the functional levels. Each point represents a sampled quadrat. The *dotted line* shows the partitioning of species diversity into two groups as identified by the classification and regression tree analysis. Rugosity values to the right of the line support a more diverse community, those to the left support a less diverse community
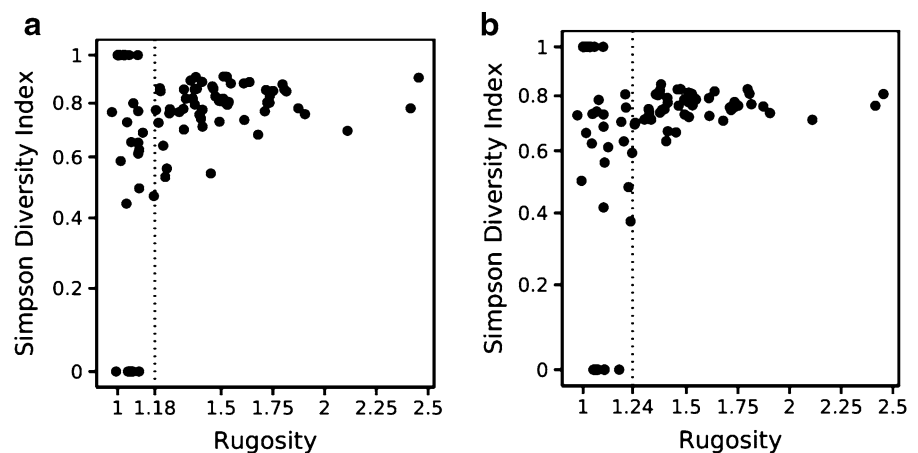
Community similarity decays rapidly across limited spatial distance

We examined the relationship between geographic distance (*n*) and community composition (*S(n)*). The lack-of-fit test was highly statistically significant ($F = 31.518$, $d.f = 1$, $P < 0.001$), indicating that the nonlinear model better reflected the relationship between geographic distance and community dissimilarity. Our nonlinear regression showed a significant correlation between the two ($F = 18.9$, $d.f = 89$, $P < 0.001$, adjusted $r^2 = 0.29$). The estimated model was

$$S(n) = -0.028/n + 0.816.$$

This relationship (solid line in Fig. 3) demonstrated that, across small geographic distances (less than ~4 km), community dissimilarity increased with distance, but for more widely spaced communities, dissimilarity was not correlated with geographic distance.

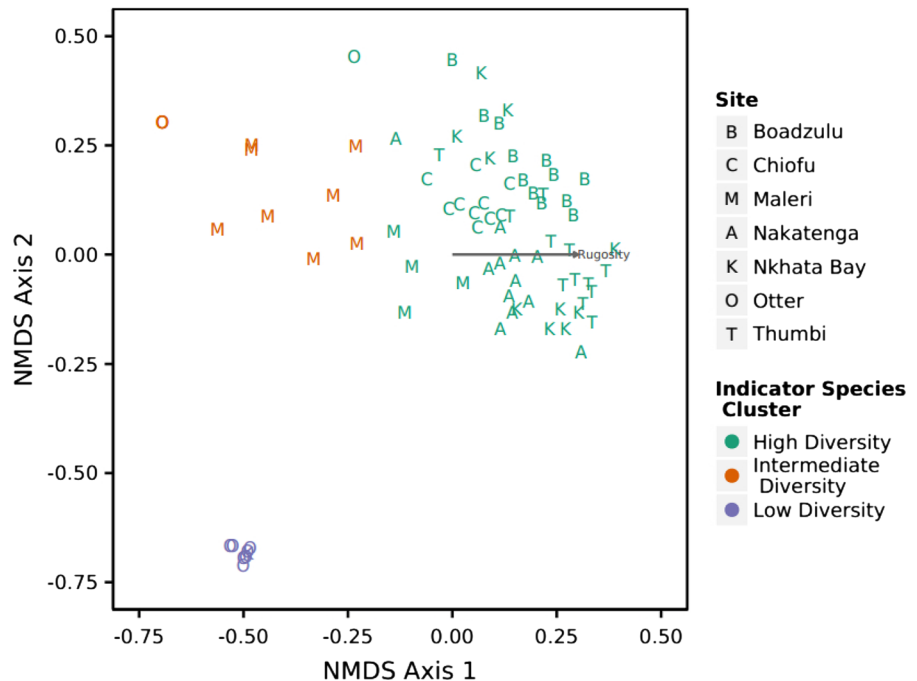## Habitat complexity predicts functional diversity of cichlid fish

The cluster analysis of the functional group diversity in each quadrat showed a less distinct geographic pattern. As visualized on an NMDS plot (Fig. 4), the hierarchical agglomerative cluster analysis indicated that quadrats from different sites grouped together (Supplemental Fig. 2). The indicator species analysis identified three significantly differentiated groups from the quadrats analysed at the functional level (IndVal = 293.31, Supplemental Fig. 3). The first was a large group comprising samples from all sampling sites with high diversity of genera (mean
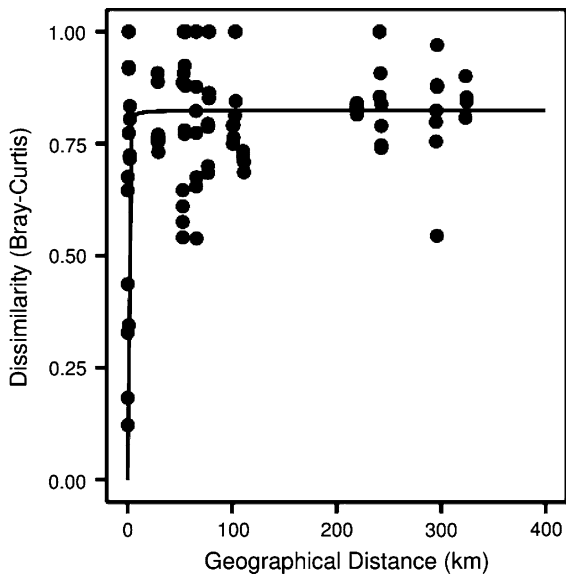
Fig. 3 Relationship of community dissimilarity and geographic distance modelled with nonlinear regression

of the Simpson index = 1, SD = 0) (Fig. 4). The second was a smaller cluster consisting of samples from Maleri Island, Otter Point and Nkhata Bay (mean of the Simpson index = 0.74, SD = 0.06) (Fig. 4). The third comprised quadrats from Otter Point/Nkhata

Bay (mean of the Simpson index = 0.26, SD = 0.28) (Fig. 4). Rugosity showed a positive correlation with community diversity at the functional level: as the rugosity increases, the functional diversity of the community also increases. It accounted for the greatest amount of variance ($r^2 = 0.38$, $P < 0.01$).

Discussion

Species diversity

Our analysis suggests that within the rocky habitats most abiotic variables are homogeneous across all sampled sites, but highly heterogeneous within sites. The inshore habitats of Lake Malawi consist of a heterogeneous patchwork of rocky, sandy and marshy stretches. The heterogeneous nature of the shoreline (Ribbink et al., 1983), combined with the highly lithophilic nature of the mbuna (Markert et al., 1999), has resulted in the evolution of species that consist of highly fragmented populations with very low levels of gene flow between them (Arnegard et al., 1999). Thus, the heterogeneous nature of Lake Malawi's shoreline is believed to have played an important role in the diversification of its cichlids.

Fig. 4 Scatter plot of sites relative to the first and second MDS (multidimensional scaling) axes. Three groups were identified: *1* a low diversity cluster comprised primarily of quadrats from Otter Point, *2* an intermediate diversity cluster comprised quadrats from Maleri Island, Otter Point and Nkhata Bay and *3* a high diversity cluster comprising the rest of the quadrats. *Arrow* shows regressed rugosity ($r^2 = 0.38$) with length scaled to r^2

Although many environmental variables significantly varied within each site, only rugosity was a robust predictor of mbuna community diversity. As rugosity increases, so did the species richness in a community. High rugosity might provide a variety of benefits for mbuna. For example, increasing rugosity may increase the amount of epilithic algae, the primary food for many mbuna (Ribbink et al., 1983). Also, the number of caves, which provide mbuna with shelter and breeding areas (Ribbink et al., 1983), likely increases with increasing habitat complexity. In addition, the number of microhabitat types increases with rising structural heterogeneity allowing for higher species diversity as observed in the pattern of microhabitat partitioning for cichlid fish of Lake Victoria (Seehausen & Bouton, 1998) and Lake Malawi (Husemann et al., 2014). Furthermore, increasing habitat complexity may reduce cichlid aggressive behaviour and decrease the size of individual territories, thereby permitting the co-existence of a greater number of individuals (Danley, 2011). It is noteworthy that some unexamined biological factors might play an important role in mediating species co-existence and maintaining diversity as well. In Lake Tanganyika, for example, the interaction among different species can significantly facilitate an increase in species diversity (Hori et al., 1993).

A second measure of habitat complexity, rock composition, did not show a statistically significant correlation with community diversity in this or some lineages of mbuna of a previous study (Genner et al., 2004). The inadequate predictive ability of rock composition in both studies highlights the importance of using multiple measurements of habitat complexity when identifying the environmental factors influencing community composition and diversity (Kovalenko et al., 2012).

Surprisingly, depth was not informative in our study. Previous studies have shown that most mbuna species dwell between 2 and 7 m, with a progressive diminution in species diversity below this depth and very few species occurring below 20 m (Fryer, 1959; Hill & Ribbink, 1978; Marsh & Ribbink, 1981; Ribbink et al., 1983; Albertson, 2008; Parnell & Streelman, 2011). Our sampling strategy limited quadrats to be within 20 m of the shore, and given the gently sloping nature of the lake bed at most sites, the majority of our quadrats were between 0.8 and 15.2 m deep. Hence, our sampling limited the variation in depth within each sampling site and consequently reduced our ability to detect the effect of depth on species diversity.

Similarity among communities decays as geographical distance increases

Nonlinear regression analysis revealed a strong geographical effect on community similarity. Our model indicated that when the distance between two transects is less than 4 km, the divergence of communities increases dramatically as the geographical distance increases. When the distance between sites is greater than 4 km, communities are equivalently different from each other, regardless of distance. The similarities of communities that are found among spatially distant sites are likely due to few shared cosmopolitan species (e.g. *M. zebra* and *Labeotropheus fuelleborni*). This result is consistent with the highly restricted distribution pattern of most mbuna species (Genner et al., 1999; Markert et al., 1999; Danley et al., 2000), supports previous ecological and population genetic studies (Ribbink et al., 1983; Markert et al., 1999; Genner et al., 2004), and agrees with the distance–decay relationship observed in many other communities (Morlon et al., 2008; Astorga et al., 2012). The breakdown of community similarity even across small geographic distances reflects both the fragmented nature of Lake Malawi's shoreline and the philopatric nature of the mbuna (Albertson et al., 1999; Danley et al., 2000; Genner et al., 2004).

Functional diversity

The analysis of community similarity at the functional (generic) level yielded three distinct clusters and no geographic structure was detected. The similarity of many quadrats found at the generic level across a variety of spatial scales suggests that most sampled sites throughout the lake harbour functionally equivalent communities. The similarity of the communities at the functional level and the great differentiation at the species level suggests that many communities include ecologically equivalent endemic species that replace other members of the same genus at different sites.

When analysed at the generic level, rugosity was positively related to functional group diversity. A highly complex environment tended to accommodate

greater functional diversity at any given rocky habitat. Since each cichlid genus possesses unique jaws and the variation of the jaws is believed to be directly linked to resource exploitation and ecological performance, different jaw shapes can be applied as surrogates for niche attributes (Wainwright & Reilly, 1994). This suggests that in cichlid communities, as in many other fish communities, greater rugosity increases the number of available niches in a habitat (Willis et al., 2005).

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