Beta diversity of rock-restricted cichlid fishes in Lake Malawi: importance of environmental and spatial factors

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The rock-restricted cichlid fish assemblages of Lake Malawi exhibit high spatial diversity in their species composition and relative abundance. However the extent to which this is due to the effects of local environmental differences, dispersal limitation of constituent taxa, and the assignment of allopatric populations to species is uncertain. We examined the factors associated with diversity within an assemblage from the north-western shores, encompassing a spatial scale of 170 km. For both the whole assemblage, and all constituent species-complexes, spatial variance in community structure was significantly dependent upon both geographic distances between locations and local habitat variables. Pronounced effects of distance indicate limited dispersal, but our results also show that that the spatial variance explained by geographic distance alone was strongly linked to proportion of allopatric populations within a species-complex with species status. Thus, the taxonomic status of allopatric populations underlies, at least partially, the biogeographical structure of this assemblage. Substrate composition and habitat depth were also significant determinants of community structure, although spatial variance attributed to these variables was less than that associated with distance alone. Substantial unexplained variance may be a consequence of the effects of unmeasured habitat variables, high ecological similarity between co-occurring species, stochastic influences on population abundance, and the effects of local adaptation. Despite low spatial variance explained by the assessed environmental variables, significant environmental influence on cichlid assemblage structure across a wide spatial scale indicates that even slight future environmental changes may have the capacity to significantly alter species composition.

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Explaining the processes that contribute to spatial variability in assemblage structure (beta diversity) remains one of the fundamental themes of contemporary community ecology (Tuomisto et al. 2003). Central to this is the relative contributions to biogeographical structure that are made by: 1) ecological interactions of populations with their environment, 2) stochastic events that influence population abundance within a habitat, and 3) rates of dispersal between habitat patches (Borcard et al. 1992). From a general theoretical standpoint, if the relative contributions of these factors can be quantified, then this will provide a good starting point for determining the underlying mechanisms that generate biogeographical patterns (Tokeshi 1999). At

present few studies have quantified patterns of beta diversity in Africa's great rift lakes, which are hotspots of global aquatic biodiversity, and home to numerous endemic species (Turner et al. 2001, Genner et al. 2004). Preserving the species in Africa's rift lakes requires a comprehensive understanding of beta diversity patterns at large spatial scales.

In freshwater environments fish assemblages can show remarkable levels of spatial variation in species richness and abundance (Oberdorff et al. 1995, 1999). However, due to autocorrelation between purely spatial effects and spatial contrasts in environmental variables, it can be difficult to determine the relative contribution of each to the composition of communities. This is particularly the case in assemblages where spatial clines in species composition are present. One method of overcoming this problem is to partition spatial variance in assemblages into three categories: 1) the variance associated purely with geographic distance; 2) the variance associated with spatially structured environmental variables, and 3) the variance associated purely with contrasting local environments (Borcard et al. 1992). Here we use a variance partitioning technique to investigate the spatial variation in the "mbuna", a group of brightly coloured and largely rock-restricted fishes belonging to the species-rich haplochromine cichlid assemblage of Lake Malawi (Konings 2001, Turner et al. 2001).

The mbuna comprise between 15 and 40% of the estimated 450 to 600 endemic haplochromine species present within Lake Malawi (Genner et al. 2004). Species distributions and population abundances of mbuna have been linked to three processes: 1) Limited dispersal ability. Individual mbuna exhibit strong local habitat fidelity within stretches of continuous habitat, as manifested by intense male territorial aggression (Genner et al. 1999a), female home ranging (Hert 1992), homing after experimental displacement (Hert 1992) and a limited ability for rapid vertical migration (Marsh and Ribbink 1981). Molecular studies have revealed that stretches of sandy lake bottom or deep-water act as strong barriers to gene flow (van Oppen et al. 1997, Arnegard et al. 1999, Markert et al. 1999). This low dispersal has been linked to the evolution of differing breeding coloration in allopatric populations through directional sexual selection (Fryer 1959, Smith and Kornfield 2002, Knight and Turner 2004), and allopatric divergence in ecological characteristics may have taken place by natural selection, as has been proposed for rocky habitat haplochromine cichlids of Lake Victoria (Bouton et al. 1999). 2) Environmental determinism. Despite considerable inter-specific overlap, sympatric species that appear anatomically virtually indistinguishable, but are discernable by breeding coloration, can differ significantly in their ecological characters (Genner et al. 1999b,c). As such, spatial differences in species abundance are likely to be linked to the availability of

resources upon which they depend, and habitat dependent rates of predation and parasitism. Thus, habitat structure variables may be associated with community composition through both direct and indirect biological interactions. In these environments the two most prominent variables are substrate composition and habitat depth (Ribbink et al. 1983). However, many other environmental variables have been linked to cichlid adaptive traits and behaviour, and may also potentially affect community structure, including the slope of substrate (Ribbink et al. 1983), food resource supply (Bouton et al. 1999), local light conditions (Seehausen et al. 1997) and oxygen levels (Bouton et al. 2002). 3) Stochastic events. All mbuna are maternal mouth-brooders and release free-swimming juveniles that take shelter in crevices within the rocks to avoid numerous predators (Trendall 1988). Predation is believed to be very high at this stage in the life history, and allocation of shelter appears to operate on a non-species-specific first-come, first-served basis (Trendall 1988, Hert 1995). Such "priority" effects have a capability to lead to temporal and spatial changes in species abundance that are not linked to fine-scale inter-specific differences in resource use patterns (Chesson 1991, 2000). "Neutral" theory proposes this as one of the major factors contributing to the maintenance of coexistence of ecologically similar taxa (Hubbell 1997).

Estimates of mbuna species richness depend upon the species status of populations that differ in phenotypic traits such as breeding colours and trophic morphology. Both field and laboratory studies have demonstrated that co-occurring taxa with differing breeding colours are reproductively isolated, even if indistinguishable in other phenotypic traits (Knight et al. 1998, van Oppen et al. 1998). Hence, we can be certain that anatomically similar sympatric populations with contrasting breeding colours are good species. Moreover, it has also been shown that anatomically similar populations with adjacent distributions that share breeding colours are on average genetically more closely-related than sympatric populations with different breeding colours on the north-western shores of the lake (Rico et al. 2003). This indicates that parallel evolution of species with adjacent distributions that share male breeding colours has not taken place within that region, and it is reasonable to assume that adjacent allopatric populations sharing the same colour traits and anatomical characters are representatives of the same species. However, although anatomically similar allopatric populations differing in male colours are known to be genetically differentiated (van Oppen et al. 1997), and have on average more genetic divergence than anatomically similar allopatric populations sharing male colours (Rico et al. 2003), at present it is difficult to be certain whether these populations would freely interbreed upon reunification, and thus whether they represent good

biological species (Knight and Turner 2004). This is a significant issue, for "species" with totally allopatric distributions comprise over 70% of the estimated 225 mbuna species present in the lake, and the assignment of such allopatric populations to species could severely affect measures of beta diversity (Genner et al. 2004).

Here we evaluated the relative contribution of these factors to the structuring of the mbuna assemblage of the north-western rocky shores of Lake Malawi. The aims of this study were: 1) to describe biogeographical structuring across a broad spatial scale; 2) to determine the importance of geographic distances between sites on local community structure; 3) to determine the significance of species delimitation of allopatric populations on assemblage biogeography; and 4) to evaluate the importance of prominent environmental variables on local community structure.

Materials and methods

Study organisms

In this study we encountered 44 mbuna species belonging to nine generic and subgeneric groupings, hereafter referred to as "complexes" (Table 1). For most taxa, we used the species classification adopted by Ribbink et al. (1983) or Konings (2001). However, because assigning species status to allopatric populations can be difficult, in this study we were conservative and only when allopatric taxa differed overwhelmingly in colour and appeared to differ in morphological and ecological characteristics were they treated as distinct species. Details are provided in the legend to Table 1.

Survey techniques

The communities present at sixteen rocky habitats on the north-western shore of Lake Malawi were surveyed between 30 September and 18 November 1998 (Fig. 1; Table 1). A stretch of deep water or sandy lake bottom separated adjacent rocky habitats. Co-ordinates of each survey location were obtained from a handheld global positioning system. Using SCUBA, two 25×2 m horizontal transects were laid at each of 3, 6 and 9 m depths where rocky habitat was present. After transects were laid, fish were given five minutes to settle and adults of all mbuna species were counted. After the first count, fish were again given five minutes to settle before a second count was made. A single observer made all fish counts (MJG), and the mean of the two counts for each 25×2 m transect was used in all subsequent analyses. After the first observer had passed, a second observer (MIT) estimated substrate composition. Each transect was divided into five 5×2 m sections, and in each of these sections percentage area cover of

six habitat classifications was assessed (sand, rocks <20 cm, rocks 20–50 cm, rocks 51–150 cm, rocks 151–400 cm and rocks >400 cm diameter). The observer estimated proportional area covered by each of the substrate categories using a points method. Briefly, the technique proceeded as follows, a value of 16 was assigned to the most abundant substrate category, and then a value of 0, 1, 2, 4, 8 or 16 was assigned to each other category in turn using the most abundant category as a reference. Percentage cover of each substrate component in each 5×2 m section of transect was calculated using the equation below. This enabled the average proportion of each substrate category within each 25×2 m transect to be determined.

% cover of component α within subsection

$$= \frac{\text{Points allocated to component } \alpha \text{ within subsection}}{\text{Total points allocated to subsection}}$$

$$\times 100$$

The use of this points method, that is most frequently used to estimate proportions of food categories within fish stomach contents (e.g. Genner et al. 1999b), allowed the rapid visual assessment that was necessary given time restrictions of working with SCUBA. We found that directly estimating percentage area cover by eye was slower and less repeatable.

Analysis of species distributions

To determine the main biogeographic regions in the study area, a species presence-absence similarity matrix was constructed using the Bray-Curtis index (Bray and Curtis 1957), and to illustrate the similarity of communities among sites, a group-average cluster analysis was applied to the matrix. The quantitative Bray-Curtis similarity index is frequently used in ecological work (Clarke and Gorley 2001, Ellingsen 2002, Cleary 2003) and ranked among the best of the similarity indexes studied by Faith et al. (1987). Analyses were conducted in the statistical package Primer 5 (Primer-E, Plymouth, U.K.).

Importance of geographic and environmental variables to assemblage structure

The mean number of individuals present was calculated from the two transects at each depth. These data were then $\log_{10}(x+1)$ transformed. Using Primer 5, the similarity of community composition between all transects was then calculated using the Bray-Curtis index, and the dissimilarity of the measured environmental variables was determined using normalised Euclidean differences between pairs of sites. The normalised Euclidean difference is particularly appropriate for assessing differ-

Table 1. Co-ordinates of study sites and number of total number of species recorded in transects within each depth category. Species included are as follows. *Cynotilapia* complex: *C. afra* (Günther), *C. axelrodi* Burgess and *C.* "mbamba". *Genyochromis* complex: *G. mento* Trewavas. *Labeotropheus* complex: *L. fuelleborni* Ahl and *L. trewavasae* Fryer. *Labidochromis* complex: *L. caeruleus* Fryer, *L. maculicauda* Lewis and *L. gigas* Lewis[1]. *Melanochromis* complex: *M. joanjohnsonae* Johnson, *M. parallellus* Burgess and Axelrod and *M. robustus* Johnson. *Pseudotropheus* (*Maylandia*) complex: *P. callainos* Stauffer and Hert[2], *P. emmiltos* (Stauffer, Bowers, Kellogg, McKaye)[3], *P. zebra* (Boulenger)[4] and *P.* "zebra gold". *Petrotilapia* complex: *P. genalutea* Marsh[5], *P. tridentiger* Trewavas, *P.* "black flank" and *P.* "small blue"[6]. *Pseudotropheus* (*Pseudotropheus*) complex: *P.* "elongatus bee", *P.* "elongatus mpanga", *P.* "elongatus nkhata blue", *P.* "elongatus ruarwe", *P.* "elongatus usisya", *P. fuscus* Trewavas, *P. minutus* Fryer, *Melanochromis perspicax* Trewavas, *P.* "zebra ruarwe", *P. tursiops* Burgess and Axelrod and *P.* "variable kande". *Pseudotropheus* (*Tropheops*) complex: *P.* "band", *P.* "black", *P.* "chilumba", *P. macrophthalmus* Ahl, *P.* "deep", *P. lucerna* Trewavas, *P.* "mauve"[7], *P.* "mauve white dorsal"[8], *P.* "olive", *P.* "orange head"[9], *P.* "red fin, *P.* "rust" and *P.* "weed". Notes.[1] *L.* "gigas mara" and *L.* "gigas chilumba" (Konings 2001) were grouped into *L. gigas*.[2] *P.* "zebra cobalt", *P.* "zebra chitande" and *P.* "zebra pearly" (Ribbink et al. 1983) were grouped into *P. callainos* following Konings (2001).[3] *P. emmiltos* was treated as a distinct species, although Konings (2001) suggests this population might be considered a geographic race of *P. zebra*.[4] *P. zebra* and *P.* "zebra chilumba" (Ribbink et al. 1983) were grouped into *P. zebra*.[5] *P. genalutea* and *P.* "chitande" (Ribbink et al. 1983) were grouped into *P. genalutea*.[6] *P.* "small blue" and *P.* " ruarwe" (Ribbink et al. 1983) were grouped into *P.* "small blue".[7] *P.* "mauve" was present between Ruarwe and Kande Island. Males: body purple with geographic races differing in the amount of yellow on the head. Females: yellow with faint vertical and horizontal markings.[8] *P.* "mauve white dorsal" was present between Ruarwe and Nyathenama. *P.* "mauve" and *P.* "mauve white dorsal" were recorded in sympatry at Ruarwe. Male *P.* "mauve white dorsal" are superficially similar in body coloration to *P.* "mauve", however they have more steeply sloping head, lack yellow on the head region and have prominent white lappets on the dorsal fin. Females are pale brown with yellow/orange pelvic and anal fins, resembling females of *P.* "deep". These two taxa are the cryptic species pair mentioned by Rico et al. (2003), and both were resolved as monophyletic in the nuclear phylogeny of Allender et al. (2003) where they were referred to as *Tropheops* "mauve" yc (yellow chest) and *Tropheops* "mauve" b (all blue).[9] *P.* "orange head" present only at Mphanga Rocks. Males: body dark purple with a red/orange head region; dorsal fin distinctive red/orange. Females: plain dark brown.

Study site	Latitude(s)	Longitude(E)	Number of species in transects			
			3 m	6 m	9 m	All
Nyathenama	10°23.57′	34°15.16′	15	12	11	18
Chitande Island	10°23.86′	34°15.42′	15	15	13	18
Mphanga Rocks	10°25.89′	34°16.68′	13	14	16	17
Lulomo Peninsula	10°26.38′	34°16.09′	16	16	15	18
Katale Island	10°27.38′	34°17.06′	19	18	17	21
Chirwa Island	10°27.83′	34°16.55′	17	14	15	19
Ruarwe	11°06.12′	34°13.50′	17	12	15	21
Mara Rocks	11°14.89′	34°15.35′	19	17	16	21
Chindazowa Point	11°36.18′	34°18.17′	21	14	12	27
Chirundu Point	11°36.48′	34°18.17′	12	12	16	20
Nkukuti Point	11°36.68′	34°18.41′	19	16	9	24
Mwafufu rock	11°37.41′	34°18.48′	16	16	15	22
Nkhwazi Reef	11°53.85′	34°10.21′	10	–	–	10
Mpandikucha Island	11°54.88′	34°11.13′	3	6	–	6
Bandawe Point	11°55.35′	34°10.92′	5	–	–	5
Kande Island	11°58.18′	34°08.08′	10	8	8	12
Total			38	41	40	44

– No rocky habitat present.

ences in the physical environment (Clarke and Gorley 2001). To test the hypothesis that community similarity was dependent upon $\log_{10}(x)$ transformed geographic distance between transects and the environmental variables we quantified, we used stepwise forward multiple matrix regression within the program Permute! 3.4.9 (Casgrain 2001), selecting the option for 999 permutations. The matrix regression is the functional equivalent of a Mantel test, and calculates the probability of the observed regression coefficient arising by chance. In brief, during each permutation, data within one of the matrices are randomised and an expected regression coefficient calculated. The significance of the test is the proportion of expected regression coefficients that are higher than, or equal to, the observed value (for further details see Casgrain 2001). In order to determine the relative variance in community composition explained by geographic distance alone, the environmental vari-

ables alone, and spatial and environmental variables combined, a variance partitioning technique described in Borcard et al. (1992) was used on the results of the matrix regressions. Briefly, the procedure was as follows: first, the community similarity matrix was regressed against the total set of environmental and distance matrices to obtain the variance explained by all $= R_T$. Next, the community similarity matrix was regressed against the environmental matrices to obtain R_E, and the community similarity matrix was also regressed against the distance matrix to obtain R_S. Then it was possible to calculate the purely environmental fraction $R_{PE} = R_T - R_S$, the purely spatial (geographic) fraction $R_{PS} = R_T - R_E$, the spatially structured environmental fraction $R_{SE} = R_E + R_S - R_T$, and the unexplained variation $R_{UN} = 1 - R_T$. All procedures were performed on the whole assemblage, and tests were then repeated for each of the nine complexes independently, grouping indivi-

Fig. 1. (A) Sampling locations on the north-western shores of Lake Malawi. Survey sites were clustered around four areas; 1) Chilumba; 2) Ruarwe; 3) Nkhata Bay and 4) Bandawe. (B) Dendrogram illustrating the similarity of mbuna assemblages at the sampling locations, based on group-average Bray-Curtis similarity of species presence-absence within transects.
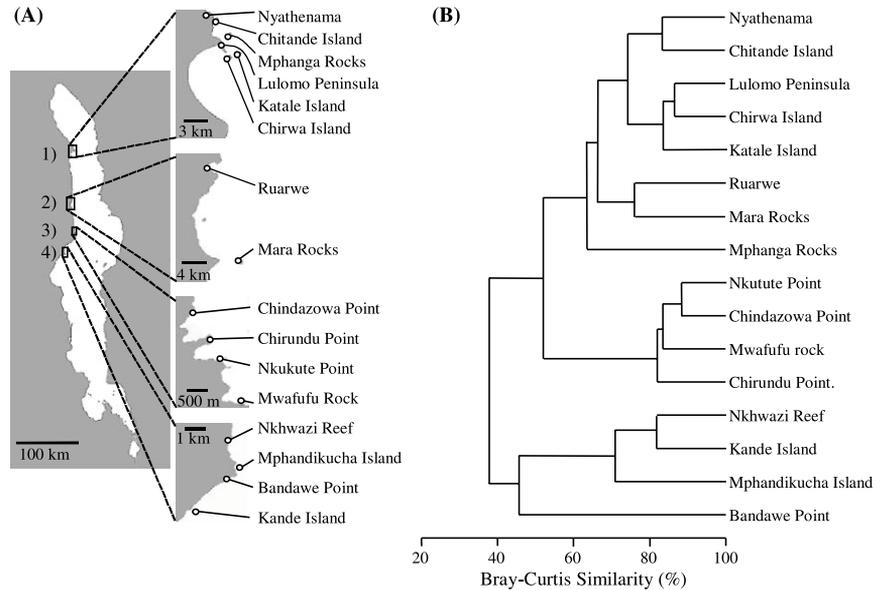
duals by species and including only transects where at least one species belonging to the complex was present.

## Importance of species delimitation of allopatric populations to beta diversity

Minimum species richness is the number of species remaining after the explicit assumption has been made that populations of two currently recognised species are allopatric forms of the same species, unless they co-occur within at least one location. Minimum richness of the complexes was determined using an iterative technique described in Genner et al. (2004). Briefly, the taxon with the largest geographic range (I) is selected and if the next most frequently occurring taxon (II) is sympatric with I, then it is considered to be a distinct species. Otherwise it is considered to be an allopatric population of I, and the distribution of II is added to that of I. Next, species are resorted in descending order by the number of sites at which they were present and the iterative process continued with the next taxon, if present. The process is complete when it has been applied to all taxa within the complex (Fig. 2). Next, a "Sympatry Index" was derived by dividing the minimum species richness of each complex by its "observed species richness" based on present species classifications. Lower values of the sympatry index indicate that proportionally more species within the complex did not co-occur in our study area. Consequently, in order to determine if taxonomic designation was also influencing community similarity, we investigated the following questions: Did the non-monotypic complexes in which more variance was explained by geographic distance alone have: 1) higher observed species richness than other complexes; 2) lower mean geographic range of constituent taxa; and 3) higher proportions of totally allopatric species as indicated by a lower sympatry index?

Results

Across the spatial scale of 170 km three distinct sub-assemblages were present; 1) Chilumba and Ruarwe; 2) Nkhata Bay and 3) Bandawe (Fig. 1b), thus indicating
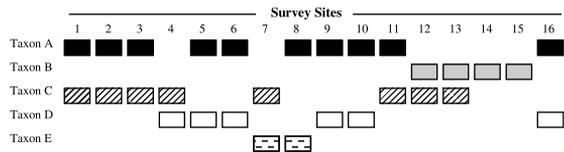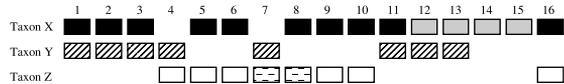

Fig. 2. Example of the procedure for estimating minimum regional species richness within a complex. (A) Here the "observed" regional richness before the procedure has been applied at 16 survey sites is 5 (taxa A to E). (B) After the procedure, the calculated "minimum" regional richness is 3 (taxa X–Z). Note that when the procedure is complete, no two taxa can have totally allopatric ranges. The Sympatry Index of a complex is determined by dividing its minimum by its observed species count.

the restricted ranges of species. The pattern is also evident from the significant decline in community similarity with increasing geographic distance between surveyed sites (Table 2). The total variance explained by the full set of spatial and environmental variables that we measured was 42.8% for the whole assemblage and ranged from 1.2 to 57.8% for the individual complexes.

In total, 34.7% of the variance in whole community similarity among sites was explained by geographic distance. Finer-scale analyses showed decreases in community similarity with geographic distance were also significant for every complex taken separately, with the exception of *Cynotilapia* (Table 2). However, the complexes differed considerably in the amount of spatial variance explained by geographic distance alone (range 0.1–55.4%). Variance explained by geographic distance alone was greatest in the non-monotypic complexes with higher species richness (Pearson's product moment; $N = 8$, $R = 0.879$, 1-tailed $p < 0.01$), in complexes with smaller observed mean geographic ranges of constituent species (Pearson's product moment; $N = 8$, $R = -0.670$, 1-tailed $p < 0.05$), and in complexes where higher proportions of previously designated species were only found in allopatry (i.e. low "Sympatry Indices", Pearson's product moment; $N = 8$, $R = -0.789$, 1-tailed $p < 0.05$).

The variance explained by spatially structured environmental variables was slight (1.7 for the whole assemblage; 0–2.7% for individual complexes). After accounting for this, in total, local substrate and depth similarity explained 5.1% of the variance in community similarity. This indicates that significantly more similar communities were found on more environmentally similar transects (Table 3). Environmental similarity also explained significant proportions of variance in community similarity in all complexes when they were tested independently, with the exception of the monotypic genus *Genyochromis* (Table 3). However, in all of the individual complexes, variance in community struc-

ture explained by the measured environmental variables was small, ranging between 0.6 and 1.9% (Table 3). There were no associations between the variance within complexes explained by distance and measured environmental variables, and the average number of species in transects (Pearson's product moment: distance alone; $N = 9$, $R = 0.49$, $p = 0.17$: environment alone; $N = 9$, $R = 0.50$, $p = 0.17$:), or the average number of individuals in transects (Pearson's product moment: distance alone; $N = 9$, $R = -0.05$, $p = 0.88$: environment alone; $N = 9$, $R = -0.15$, $p = 0.69$), thus indicating that sample sizes were not significantly influencing the within-complex spatial variance explained by these variables (see Wolda 1981).

Discussion

Dispersal limitation

Geographical sub-structuring of the assemblage, and the significant decreases in community similarity with increasing geographic distance are consistent with dispersal limitation of Malawi rock-restricted cichlids, as documented in both biogeographic and genetic studies (Ribbink et al. 1983, van Oppen et al. 1997, Arnegard et al. 1999, Markert et al. 1999, Rico and Turner 2002). Since spatially structured environmental variation was minimal, and the effects of geographical distance alone were more pronounced, our results suggest that limited dispersal has prevented the ubiquitous establishment of populations throughout the survey area, despite the presence of suitable habitat structure.

Limited dispersal ability is also likely to explain the contrasts in sympatric species richness between the four most southern sites (range 5–12 species), and the twelve northern sites (range 17–27). The southern sites are in a gently sloping, shallow region of the lake (ca depth 100–200 m at 10 km offshore) in contrast to the more northerly sites with more steeply shelving habitat and

Table 2. Number of transects and sites species were present, the maximum regional species richness and the minimum regional species richness.

Taxa	Number transects present	Number sites present	Maximum regional species richness	Minimum regional species richness	Mean number species per transect present	Mean number individuals per transect present
All taxa (individuals grouped by species)	86	16	44	28	12.08	217.65
Cynotilapia	68	12	3	3	1.38	79.56
Genyochromis	29	12	1	1	1.00	1.14
Labeotropheus	57	14	2	2	1.26	7.37
Labidochromis	58	14	3	2	1.21	3.55
Melanochromis	31	8	3	3	1.23	3.61
Petrotilapia	74	15	4	3	1.77	6.73
Pseudotropheus (*Maylandia*)	83	15	4	3	1.97	49.42
Pseudotropheus (*Tropheops*)	86	16	13	7	3.59	43.98
Pseudotropheus (*Pseudotropheus*)	75	15	11	4	1.77	14.12

Table 3. Relationship between community dissimilarity in transects and G (geographic distance), S (substrate dissimilarity) and D (depth distance).

Taxa	Total multiple regression model			Percentage of variance explained by factors			
	Variables selected for model	Total R^2	p	Distance	Spatially structured environment	Environment	Unexplained
All taxa (individuals grouped by species)	G+S+D	0.428	<0.001	34.65*	3.03	5.07*	57.25
Cynotilapia	G+D	0.012	<0.001	0.12	0.88	0.12*	98.85
Genyochromis	G+D	0.042	0.002	3.15*	0.21	0.88	95.76
Labeotropheus	G+D	0.080	<0.001	6.57*	0.08	1.32*	92.04
Labidochromis	G+D	0.028	<0.001	2.01*	0.00	0.87*	97.19
Melanochromis	G+D	0.129	<0.001	8.72*	2.74	1.42*	87.12
Petrotilapia	G+D	0.058	<0.001	4.34*	0.19	1.22*	94.25
Pseudotropheus (*Maylandia*)	G+S	0.037	<0.001	1.37*	0.48	1.85*	96.30
Pseudotropheus (*Tropheops*)	G+D	0.353	<0.001	33.28*	0.26	1.75*	64.71
Pseudotropheus (*Pseudotropheus*)	G+D	0.578	<0.001	55.35*	1.88	0.60*	42.17

* indicates statistically significant relationships between community similarity and G alone, and community similarity and the measured environmental variables (S+D) at p <0.001.

deeper inshore waters (ca depth 400–700 m depth at 10 km offshore) (Crul 1997). Of the southern sampling sites, the deepest rocky habitat was at Kande Island, where rocky habitat met sand at a depth of 10 m. At all twelve northern sampling sites the rocky habitat continued much deeper. The southern rocky habitat fauna is likely to be much younger than equivalent faunas at more northerly locations. Lake Malawi has been subject to rapid lake-level changes that would have resulted in the removal and subsequent reformation of rocky habitats and faunal composition in the south of our study area. In comparison the communities of the more steeply sloping northern rocky shores would have been less transitory, with the fauna simply moving up and down the shoreline in response to changing lake-level. The scale and timing of the most recent lake level changes is disputed. Owen et al. (1990) suggest that the lake was 121 m below present day levels within the last 150–500 yr, which would imply remarkably rapid speciation of the cichlid species now endemic to islands in the shallow south of the lake (Owen et al. 1990). However, other reconstructions suggest that during this period the lake was at most only 8–9 m lower than the present day (Nicholson 1998). Moreover, core evidence from the north basin of the lake suggests the most recent major low stands of 100–200 m magnitude occurred much earlier, ca 11 000 yr ago, and between 15 700 and 23 000 yr ago (Johnson et al. 2002). Regardless of the timing of the lake level fluctuations, it is likely that the changes in water level coupled with the complex habitat structure of the Lake Malawi shoreline would have resulted in less time for opportunistic migration and colonisation of at least some of the sites in our study by dispersal limited species, and such a process could have generated observed spatial variability in species richness.

Significance of the species delimitation of allopatric populations

In this study, distance alone explained a 34.7% of variation in whole community similarity. This is generally more than has been found in other systems, for instance, the amount of variation explained by space alone ranged from 12 to 20% for mites, trees and bacteria (Borcard et al. 1992), between 13 and 20% for Amazonian terrestrial plants (Tuomisto et al. 2003), 7% in Panamanian trees (Duivenvoorden et al. 2002) and 1.3–5.3% in South African birds (Githaiga-Mwicigi et al. 2002). Our analyses also showed that spatial variance explained by geographic distance alone varied considerably among complexes (0.1 and 55.4%). This may be because of between-complex differences in the dispersal ability of constituent taxa, but to our knowledge no comparative between-complex analyses of dispersal ability have been undertaken. However, since our analyses showed that the proportions of species that were totally allopatric were greater in complexes where distance explained more spatial variance, the alternative explanation that differences among complexes are largely a consequence of the taxonomic classification of allopatric populations is plausible. Geographically separated populations of haplochromine cichlids have typically been delimited as species on the basis of phenotypic traits such as body shape, tooth, jaw and head morphology, and breeding colours (Ribbink et al. 1983). Differences in these traits are commonplace among allopatric populations of conspecifics, and appear to arise over very short time scales (Ribbink et al. 1983, Stauffer and Hert 1992). To our knowledge the scale of between-species differences among complexes has never been quantified in a comparative manner, so whether some complexes possess more genuine morphological differ-

entiation among allopatric populations is unknown. Moreover, to what extent breeding colours or anatomical traits would need to differ to result in complete prezygotic isolation of taxa should they become united in sympatry is equally unclear (Knight and Turner 2004), and as such whether some complexes have more "good" biological species remains subjective (Turner et al. 2001, Genner et al. 2004). Nevertheless, it seems that taxonomic designation of allopatric populations is strongly related to spatial diversity of the assemblage. Thus, rapid evolution of phenotypic traits in allopatric populations of cichlids may be the reason more variance was explained by distance alone in the whole mbuna assemblage, than has been found in other species groups. Thus, our results emphasise a need to consider taxonomic classification of allopatric populations when interpreting patterns of diversity.

Importance of spatial differences in local environmental variables

In this study spatially structured environmental variables that we measured explained only minimal variation in assemblage composition (whole assemblage, 3.0%; individual complexes, 0–2.7%), indicating that there was only a slight environmental cline in our study area in measured variables. These results contrasts with many other studies where spatially structured environmental variance is typically a more important explanatory component. For example, figures range between 7.8 and 39.8% for mites, trees and bacteria (Borcard et al. 1992); between 12 and 23% in Amazonian terrestrial plants (Tuomisto et al. 2003), 24% in Panamanian trees (Duivenvoorden et al. 2002) and 5.7–16.6% in South African birds (Githaiga-Mwicigi et al. 2002), indicating that in these other studies environment-distance clines were more prominent.

After standardising for the effects of distance and the environment-distance cline, community similarity was significantly greater where more similar environmental conditions prevail. This indicates a degree of dependence of local community structure on the immediate environment. The variance explained by purely local environmental variables that we measured was low (whole assemblage, 5.8%; individual complexes, 0.9–2.7%). Other studies that have used this technique on indices of community similarity have found that proportions of community variance explained by non-spatially structured environment variance have been similar. For example, figures range between 0.3 and 18.8% for mites, trees and bacteria (Borcard et al. 1992); between 2 and 7% in Amazonian terrestrial plants (Tuomisto et al. 2003), 10% in Panamanian trees (Duivenvoorden et al. 2002) and 7.7–21.1% in South African birds (Githaiga-Mwicigi et al. 2002). Taken together, these results

indicate that non-spatially structured environmental variables have a role in determining community composition, but also that it is not unusual to find low amounts of assemblage variability explained by these factors.

Despite the relatively low amount of variance explained by the environmental variables that we measured, the fact that the local habitat variables assessed are significantly associated with community similarity demonstrates empirically that fine-scale differences in environmental regimes do contribute in part to the structure of these cichlid assemblages, rather than assemblages being randomly thrown together aggregations from a common species pool. As such, it would appear that slight environmental change would generate modest, but significant changes in the diversity of the assemblage. Nevertheless, considerable proportions of observed variance remained unexplained, 57.3% for the whole assemblage and between 42.1 and 98.9% for individual complexes. Similar studies have shown that unexplained variation can be substantial, for example 35–78% in birds, mites, bacteria and trees (Borcard et al. 1992, Duivenvoorden et al. 2002, Githaiga-Mwicigi et al. 2002, Tuomisto et al. 2003).

There are several possible explanations for the high levels of unexplained variance in our study. 1) Other variables that were not measured may contribute substantially to mbuna community structure, including habitat area, shoreline slope, the type and abundance of available food resources, substrate heterogeneity, wave action, water clarity, and predator abundance. 2) Sampling may have been carried out over insufficiently large spatial and temporal scales. For example, the sampling strategy may not have accounted for local dispersal away from favoured habitats, thus making associations between species abundance and environment variables difficult to detect. Species assemblages may also respond to environmental variables such as habitat heterogeneity at much larger spatial scales than measured in this study. Developments in remote sensing should make this feasible to address in the near future (Turner et al. 2003). 3) Inter-specific comparisons of resource use patterns have shown that considerable overlap is commonplace; both within and between complexes, despite some significant differences. Generally speaking, most taxa utilise epilithic algae within their diets (Reinthal, 1990, Genner et al. 1999b), are present in waters of 3–5 m and have affinities for medium-size rocks (Ribbink et al. 1983). As such, the same species may have similar abundance responses to contrasting environmental regimes, and the same species composition may be present in both favoured and non-favoured habitats. Thus associations between community similarity and the similarity of environmental variables may be at best weak and hence difficult to detect, even if slight but significant differences are present in micro-distributional resource use patterns. 4) Coexisting species may undergo

unpredictable abundance changes as a consequence of chaotic or stochastic events. Lake Malawi cichlids are most vulnerable at the juvenile stage when >95% are lost to predation (Trendall 1988). To avoid the numerous predators, juveniles occupy refugia in rocks that appear to be allocated on a first-come first-served basis, with subsequent colonisers being aggressively excluded from shelter (Trendall 1988). The lack of species specificity of these priority effects may lead to a high degree of variation in species abundance over space and time that would be unrelated to environmental characters (Sale 1977). 5) Allopatric populations of haplochromine cichlids have been shown to differ morphologically in a pattern consistent with more efficient utilisation of resources within their local environments (Bouton et al. 2002), and this may be a consequence of selection (Albertson et al. 2003). This raises the possibility that allopatric populations of conspecifics may not be functioning as ecological equivalents, and such differences among populations may result in contrasting abundance changes in response to local environmental regimes and inter-specific interactions. Further studies may elucidate the relative contributions of these factors to the observed patterns.

Conclusions

In this study we investigated the effects of geographic distance and environmental similarity on an assemblage of Lake Malawi rock-restricted cichlids. We found significant dependence of cichlid community structure interactions on both the geographical proximity of sites and the local environmental parameters measured at those sites. Our results provide support for both assemblage-wide dispersal limitation and environmental influence on community structure, and indicate a need to consider the species status of allopatric populations when investigating patterns of beta diversity.

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