A Biodiversity Atlas for Lake Malawi

Version 3.0

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Biodiversity Atlas Executive Summary

Paul Cooley, Editor

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Evidence emerging from the Lake Malawi Biodiversity Conservation Project (1996 - 2000), a 5-year study of the lake and watershed, has shown many new insights into this marvelous system. For the first time in the African great lakes lake wide scale patterns of coastal habitat and intralacustrine endemism and diversity have been demonstrated. The composition of the rocky dwelling mbuna fauna has a strong regional component that reflects strongly the tectonic framework of the basin. For the sandy shore haplochromines, this research program has shown with large temporal sampling that abrupt changes in the species composition occur above and below the mud boundary usually found between 60 and 80 m water depth in the lakeshore plains. On the sandy shores haplochromine rarity is very high in less than 30 m of water and decreases with increasing water depth, as does species richness. On islands, the relationship between species number and sample number for the mbuna and non-mbuna is strongly asymptotic. On the mainland coasts, the sandy shore and offshore (i.e. mud) haplos have strongly non-asymptotic species accumulation curves.

This research program has provided a basic framework that shows species composition changes regionally within the lake, and also with increasing water depth. While the study of the extensive sandy shore and offshore fishes is mostly ahead, the available information suggests that conservation planning/fisheries management zones could be structured based on the tectonic framework of the basin. The ecology of the fishes suggest the mbuna would benefit from smaller more frequently placed reserves, whereas management zones for the sandy shore and offshore fishes would be much larger.

The Coastal and Littoral Zone

Lake Malawi has 1, 649 kms of coast and can be divided into three main types based on geomorphologic classification of rift structures. The tectonic framework of the Malawi rift is the principal control of the distribution, slope, and length of coastal habitat at regional and local scales. Rock or sand and sand/vegetated shores alternate at up to 110 km spacing and reflect the dip polarity of half graben units comprising the rift. Border faults along the edge of rift scarps form rock coasts whereas the shoaling margin of half grabens in the lakeshore plains is mainly sand or sand/vegetation. Large sandy platforms, river deltas, or rocky outcrops form discontinuities in the main habitat. Rocky habitats are structured hierarchically with abrupt discontinuities at regional and local scales. Sandy habitats extend deeper and appear continuous at the half graben scale.

Border fault coasts have characteristics that suggest habitat availability and connectivity during lake level variation is greatest and so are areas most likely to provide temporal refuge. Shoaling margins of half grabens have rocky coasts that are spaced farther apart and suggest lateral shifts in mbuna populations (i.e. divergence) are more likely during periods of lake level variation. Some very isolated rocky shores in the lakeshore plains are easily desiccated and are temporally unstable. In such areas, temporal stability in habitat seems too low for allopatric speciation to persist and so immigration of species seems more plausible.

The 1500-1850 lake recession-refilling cycle with stands 120 m below present is a contentious issue. If low lake stands occurred recently as reported, it would have not only desiccated most of the southern basin, but also exposed several other low slope areas around the lake. Under this scenario, like the well-documented southern basin, many of these areas could now contain immigrants from adjacent areas where temporal stability is high, or may be areas low in species (but maybe higher in endemism) due to desiccation. Better temporal resolution on historic lake level variation may clarify the relative importance of rate of lateral movement of mbuna (voluntary divergence) vs. shifting habitat availability during periods of water level variation (involuntary divergence). Preliminary study of lake wide mbuna distributions by Jos Snoeks, see below, does not show such a pattern. If the low lake stands was actually thousands of years ago as seems to be the growing consensus, it follows that the most recent form of allopatry in the lake has been shore sequential (voluntary dispersal) rather than one moderated by lake level variation.

Lakeshore Communities

Aerial surveys of the coast at about 400 m above water level documented coastal habitat and lakeshore community attributes including the number of dwellings/houses, boats/canoes, and fish drying racks. This information was mapped and divided into three ordinal classes based on frequency (low, medium, and high). Such data serve as a static snapshot in time to contrast to identify patterns and to compare to future patterns of habitation and fishing activity.

The southern basin has by far the largest lakeshore communities and density of dwellings and canoes. This finding is not new. However, observations contrasting the types of locations where habitation and fishing are most common revealed some straightforward patterns, and identified areas where fishing is actively being undertaken but in topography where habitation typically is avoided.

In the lakeshore plains physiographic region where abundant low slope and sandy shores are present most communities are found in areas away from river deltas, and in larger aggregations. In other areas of the Lake along rift scarps, the only low slope areas available are river deltas and in most cases each river delta has a small community, even if only a single dwelling. Fishing effort appears to be significant north of Makanjilla to about the Mozambique border. In this region, many dwellings and fish drying racks are evident on hilly ground that typically is avoided in all other areas of the lake suggesting

good catches or political boundaries influence this lakeshore habitation. The video record also demonstrates that habitation on steep slopes occurs on sections of all rift scarps surrounding the lake. The most notable habitation begins South of Matema on the Livingstone Mountains, and is also present in several sections along the Usisya rift scarp.

Most lakeshore communities are comprised of less than 15 huts (n = 130) and less than 10% of the locations observed had frequencies greater than 60 dwellings, indicating most habitation is small and dispersed along the coast. The distribution of lakeshore habitation around the lake is centered on the southeast arm where density is high and also on the rift scarp north of Usisya but frequencies are low or moderate. Many areas of the Tanzania and Mozambique lakeshore are uninhabited. Fish drying racks are most abundant on the east shore of the southern basin south of Gome to the Shire River, and at Nankumba. In these areas, several locations have between 100 and 250 fish drying racks, including Chembe Beach. Canoes had a generally similar pattern to dwellings but concentrations of canoes were also evident on the northeast shore between Lupembe to Kaporo, and also at Itungi. There are several large sandy platforms on the east side of the lake that appear to be under exploited relative to the southern basin.

The southwest arm contains a stretch of vegetated shoreline about 60 km long with abundant macrophytes in the shallow littoral, and is unique to the lake. This region is essentially uninhabited and likely has an unexploited shallow water fish community that has not received any scientific study.

Seasonal Variation in Species Richness and Abundance of Sandy Shore Fishes

The shallow sandy shore fishes are the most accessible and understudied fisheries resource found on Lake Malawi. Sandy habitats make up most of the littoral of the lake and frequently are close to rivers exporting sediments from agricultural watersheds. The shallow and sandy littoral (0-15 m) is a temporally unstable habitat with differences observed in response to suspended sediment by season and depth strata. Rainy season concentrations at beach seine sites (0-5m) exceeded dry season values and were statistically different. A total of 197 species comprising of cichlids and non-cichlids were collected during eight months of replicate sampling within 32 km of the Linthipe River, with total cumulative species richness ranging 32 – 98. This level of richness exceeds published richness numbers for the mbuna, or the non-mbuna caught with trawls in this project (see below).

As expected, statistical correlations between species richness and abundance for the Haplochromine are weak, reflecting the dynamic nature of the suspended sediment regime and the apparent shifting nature of the community. Haplochromine species richness did not differ statistically between the rainy season and dry, but qualitative declines were evident, as was a trend of decreasing richness towards the river mouth. In beach seine catches abundance tended to decrease with distance from the river mouth during the dry season but increased with distance from the river mouth during the rainy season. A notable increase in the abundance of non-cichlids was evident near the river

mouth during the rainy season. Non-cichlids demonstrated the opposite trend during both seasons. Species richness and abundance was greatest near the river mouth and declined with increasing distance from the river mouth. At some distance the perceived negative effect of high concentrations of suspended sediments diminishes and the small enrichment appears to have a positive effect on Haplochromine abundance. Given the wave climate and turbulent nature of these featureless habitats and the ephemeral character of sediment plumes, it appears that sandy shore fishes are more mobile and eurytopic than the more stenotopic rocky dwelling mbuna.

The effect of Space, Time, and Environment on, and the temporal variation of, haplochromine cichlids in rock, sand, and mud habitats

Freshwater parks/fisheries management zones in Lake Malawi are needed but deficiencies in the underlying science prevents their design and implementation. We examine how space, time, and environment (depth, substratum, temperature, total suspended solids), interact to influence the composition of haplochromine cichlids in rock, sand, and mud habitats in the southern basin of Lake Malawi. We studied 23 sites (0 – 125 m) using biweekly or monthly sampling for up to one year, using Correspondence Analysis (CA) Canonical Correspondence Analysis (CCA), and hierarchical clustering. We also documented the frequency and magnitude of temporal variation of the samples.

The composition of the mbuna species is influenced strongly by Space and Depth, and accounted for 31% and 15% of the variance in species composition. In contrast, Space explained less variance (< 9%) for the sandy shore (0 - 5 m) and the offshore samples (10 - 125 m)(0.4 - 3%) suggesting these species are more widely distributed. Depth appears to be the main explanatory variable for large changes in the composition of the offshore haplochromine species where dramatic differences in assemblage composition was observed between 50 – 75 m, and is coincident with the upper edge of the offshore depositional basin. Time explained little variance for the mbuna (0.4%) suggesting a stable assemblage but increased 8 x for the sandy shore (3.1%), and 17x for the offshore samples (6.9%). Accordingly, temporal variation of the sandy and offshore fishes was 1.7 – 2.0 x the magnitude of the mbuna. The frequency of occurrence over time was markedly lower for fishes of the smooth bottomed habitats. Both imply a shifting assemblage. In general, the composition of the cichlid assemblages reflects persistent habitat characteristics rather than ephemeral influences, including TSS. Rarity in the sandy shallows (<30 m) is rampant and exceeds that of the rock dwelling mbuna. Rarity is very low in the offshore zone. Our results support the hypothesis that stenotopy of the rocky dwelling mbuna is high and is comparatively low for the sand and mud species. This implies much larger reserves/fisheries management zones are needed for the haplochromines of the smooth bottomed habitats. We identify a major deficiency in understanding of dispersal abilities of rare haplochromines over shallow sand habitats.

Species Accrual of Haplochromine Cichlids in Rock, Sand, and Mud Habitats

The accrual of haplochromine cichlid fishes of rock, sand, and mud substratum habitats was studied in the southern basin of Lake Malawi from 0 – 125 m depth using 6 nonparametric estimators to better understand the relationship between sample size and species richness. The mbuna and non-mbuna of rocky shore species live in habitats of finite scale and provide asymptotic species accumulation curves where all models are highly convergent on the estimated species number. Assemblages sampled over expansive sand and mud habitats show no evidence of an asymptote; in this case most estimators of richness were positively biased. Site richness is a concept that is readily accommodated by rocky shore mbuna species because the temporal stability of the count statistics is high. In contrast, site richness over sand and mud habitats varies widely in space and time, suggesting a shifting assemblage. According to the tenet of habitat based sampling the sampling of species at smooth bottomed sites appears to be incomplete, suggesting local richness is supported by a geographically large species pool.

Species Richness and Distribution of the Mbuna and Non-mbuna

Mbuna Species richness was investigated using the mbuna data of Konings (1996) and an earlier version of the coastal data of Cooley (this volume). As shown above, the distribution of the rocky dwelling mbuna clearly reflect the physical composition of the shoreline. Interpreted from mean species richness values and visual assessment of pattern, highest levels of diversity appear in predominant but not continuously rocky coasts or where rocks and sand coasts are about equally important. As established by others previously and confirmed here, high levels of endemicity and diversity characterize the large islands. It is suggested that islands have higher isolation and habitat diversity than adjacent coastal areas. Point diversity observed seems the result of several intrinsic factors including stenotopy of the rocky dwelling mbuna, and the physical composition of the shoreline.

There is a negative correlation between non-mbuna species richness and depth for trawl sampling as well as for gill nets. A 37% or 18% decline in species numbers was observed between 5 and 150 m using trawls and gill nets, respectively. In general, the loss of non-mbuna species with depth is gradual. Non-mbuna species diversity is not distributed equally around the lake. Many areas had low or variable numbers, like Domira Bay or the southern basin. In Chiwanga and Chilola on the eastern central area of the lake were predominantly high. Highest non-mbuna species number was observed in Nkhotakota above 120 m. Amongst soft-bottom substrata, fine sand habitats tend to have higher species numbers.

Ichthyogeographic Regions

Intralacustrine endemism of the non-mbuna is at least several factors smaller than the mbuna, indicating these taxa are less stenotopic and less constraint by geographic barriers than the mbuna. Information on these taxa is new and less populous than the mbuna so geographic regions are difficult to interpret. The three large depositional basins are suggested as ichthyogeographic regions, but evidence is preliminary and inconclusive.

The information of Konings (1996) for the mbuna allows a more strictly defined set of Ichthyogeographic regions to be defined. In general, the regions identify the main isolated islands (Likoma, Chisumulu, Mbenji, Thumbi West, Chinya, and the three Maleri Islands) supporting the work of Ribbink et al. (1983) and the long held recognition of the importance of isolation in speciation. On the main coast, most Ichthyogeographic regions closely resemble the regional distribution of rocky habitats where sections of rocky coast with few discontinuities are separated most often by large sand platforms. This strengthens support for the contention that regional signals in the distribution of the mbuna are imparted by the tectonic structure of the basin. In some cases, however, the geographic barriers are subtler and like the case south of Cobwe a transition exists where erosional relief changes to depositional relief with short and infrequent stretches of rocky coast. In general, islands can be considered hotspots of diversity and are important for the mbuna and non-mbuna that frequent rocky habitats. Several smaller areas appear to be better conservation or management units than fewer large to preserve species numbers.