The macroecology of rapid evolutionary radiation

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A long-standing debate in ecology addresses whether community composition is the result of stochastic factors or assembly rules. Non-random, over-dispersed patterns of species co-occurrence have commonly been attributed to competition—a particularly important force in adaptive radiation. We thus examined the macroecology of the recently radiated cichlid rock-fish assemblage in Lake Malawi, Africa at a spectrum of increasingly fine spatial scales (entire lake to depth within rock-reef sites). Along this range of spatial scales, we observed a signal of community structure (decreased co-occurrence of species) at the largest and smallest scales, but not in between. Evidence suggests that the lake-wide signature of structure is driven by extreme endemism and micro-allopatric speciation, while patterns of reduced co-occurrence with depth are indicative of species interactions. We identified a 'core' set of rock-reef species, found in combination throughout the lake, whose depth profiles exhibited replicated positive and negative correlation. Our results provide insight into how ecological communities may be structured differently at distinct spatial scales, re-emphasize the importance of local species interactions in community assembly, and further elucidate the processes shaping speciation in this model adaptive radiation.

**Keywords:** species distribution; cichlid; community assembly; null models; adaptive radiation

1. **INTRODUCTION**

A central goal in ecology is to understand the patterns and processes that explain the organization of natural communities. A major focus investigates whether communities form as the result of stochastic processes or are constructed via assembly rules (i.e. competition; [1–3]). The former scenario is attributed to random species colonization, habitat gradients and stochastic environmental effects, while the latter deterministically generates a community with a marked and predictable signature of co-occurrence owing to species interactions [4–6]. Competitive interactions form communities with species that co-occur less often than expected by chance [1], while species that do co-occur may differ significantly in key traits (e.g. body size or trophic morphology) that relax the degree of overlap in resource use [7]. Although competition has been used synonymously with descriptions of structured communities, decreased species co-occurrence can be explained by other mechanisms. For instance, species may not co-occur because of diverged habitat choice; similarly, 'historical checkerboards' can result from biogeography (e.g. dispersal barriers) and evolutionary history (e.g. allopatric speciation; [6]). Recent studies have linked expectations from reduced co-occurrence patterns to empirical verification of species interactions (competition; [8,9]). Studies of community structure have assessed a variety of assemblages including salamanders [9], ants [8,10], desert rodents [11], beetles [12], marine reef fishes [13] and birds [14]. Despite mixed individual results, a meta-analysis of 96 datasets revealed that non-random community structure (lower species co-occurrence) is more common in natural communities than expected [6]. This finding is consistent with the idea that interspecific interactions play an important role in community organization.

While competition is only one possible mechanism producing structured communities, its importance in adaptive radiation is more straightforward [15–17]. It is generally accepted that all adaptive radiations have involved a component of divergence owing to competition for a limiting resource, usually producing disparity in functional characters, and possibly resulting in ecological speciation [18–20]. We reasoned that communities built recently from adaptively radiating species would show the expected signature of assembly rules. We thus examined the macroecology of a textbook rapid adaptive radiation, the cichlid fishes of Lake Malawi (LM), Africa. LM houses some 600–1000 species that have evolved in the last 1–2 Myr, with little to no phylogenetic structure [21–25]. The LM cichlids contain a lineage of rock-dwelling species [23–25], known locally as the ‘mbuna’, characterized by their strict habitat requirements. Mbuna dominate rocky habitats in densely packed communities consisting of dozens of species and hundreds of individuals [26]; these rock-fishes exploit all available niches, thus producing local communities built from a single lineage of closely related species. This condition is unique among assemblages examined for community structure [1,8–14].

The rocky habitats of LM are interspersed by sand flats and deep water, restricting the mbuna to near-zero dispersal and extreme local population genetic structure [27–33]. The rock-reef mbuna thus live an island-like existence—a situation that has been associated with community structure in other systems [1,10,12,34]. Under these conditions, a suite of traits has evolved in the mbuna including aggressive territoriality [23,35–37], colour-based assortative mating [38], high site fidelity

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The distribution and abundance of the mbuna is coupled with minimal interspecific variation in body size but an extensive diversity in oral jaw morphology [26,43,44]. Mbuna ecology and biology imply a propensity for competition between species [23,26,40,45], yet no conclusive manipulative data exist. Based on: (i) the rapidity and extent of the LM cichlid radiation, (ii) the biology and ecology of the mbuna, and (iii) the primacy of competition in adaptive radiations, assembly rules seem obligatory to the formation and maintenance of these communities.

We used null model analyses [4] to test for community structure in the LM mbuna cichlid assemblage. We employed this approach at multiple spatial scales to investigate how structure emerges as geographical resolution increases—a topic that remains unsettled in the literature [8,11,13,46]. We made two central predictions: first, because this is a system where local species interactions are thought to be pervasive and partly responsible for evolutionary diversification, we expected to detect the signature of community structure at the finest scale (depth within sites). Second, because this is a system characterized by extreme endemism and local population structure, we expected to detect the signature of community structure at the broadest scale (lakewide). Indeed, our results demonstrate that the signal of community structure changes with the scale of analysis—as do our inferences of the forces producing this signal. It is only at the finest scale—that of depth within island sites—where we infer that species interactions shape LM cichlid communities. Therefore, assembly rules exist in communities of LM mbuna cichlids, but their influence is extremely localized and does not scale up to broader spatial levels.

2. MATERIAL AND METHODS

(a) The mbuna data

The data used in this study were originally published in a comprehensive survey of the rock-dwelling cichlids of LM [26]. Ribbink et al. [26] made direct counts of species richness and abundance along belt transects at 18 sites throughout the lake and published them as 37 figures of species abundance by depth (kite plots). We estimated the abundance of each species at six discrete depths (1, 2.5, 5, 10, 15 and 20 m) by physically measuring the plots (e.g. electronic supplementary material, figure S1). We selected a vertical segment across each depth and quantified the width of each species’ plot at that point. In this way, we were able to extract (i) species abundance data at six depths that correspond to actual samples from Ribbink et al. [26], as well as (ii) species presence–absence data at all sites. Species abundance data were used in calculations of diversity (see below) and correlations by depth, while presence–absence data were used in the null model analyses of species co-occurrence. Species richness was plotted against depth-structuring within local communities. We used two null models for co-occurrence analyses: a fixed-fixed model and a fixed-proportional model (SIM9 and SIM4 in [5]). SIM9 maintains column sums (i.e. number of species at a site) and row sums (i.e. number of species where a species is found) from the observed matrix when producing each simulated matrix, thus preserving species occurrence frequencies and the number of species at sites. This model is suitable for examining ‘island list’ datasets and exhibits the most robust statistical properties against type I and type II errors [5]. The fixed-proportional model (SIM4) also maintains the total number of site occurrences for each species (row sums); however, the number of species at each site is proportional to the total number of site occurrences at that scale. This model is more sensitive to type I errors than SIM9 but it has been shown to behave robustly in multiple tests. Although site occurrences are not identical to those in the observed matrix, they are proportional to one another, thus maintaining differences between sites [5]. SIM9 was used to analyse co-occurrence at the finest scale (local-vertical) because at this resolution the column proportionality of SIM4 approached an equi-probable model (SIM2; equal occurrence probability). Ten-thousand simulated matrices were produced for each model and scale, using the sequential swap algorithm [48].

Several metrics can be used to test for patterns in the observed matrix, compared with the randomly simulated matrices produced by EcoSim. We chose the checkerboard score (C-score), which measures the average co-occurrence of all species pairs; the C-score has been shown to be robust to type II errors [5,49]. This metric is calculated based on the number of shared sites and the number of unique sites between every species combination. The observed community matrix is scored and the probability of the observed score is calculated directly from the distribution of scores from the simulated (randomized) matrices. A significantly higher observed C-score (than the average from the randomized matrices) indicates less average pairwise species co-occurrence and therefore a structured (non-random) community, while a C-score within the distribution for the simulated matrices indicates a community not different from the null model of random assembly [5]. The EcoSim program returns the observed score, the distribution of simulated matrix scores, the probability of a higher C-score in the observed data and the standardized effect size (SES) for the observed C-score. The SES represents the distance (in standard deviations) that the observed score lies beyond the mean score of the simulated distribution, whereby 95 per cent of the simulated scores fall...
between −2 and 2. Calculating the SES for each separate analysis allows for meaningful comparison of results across spatial scales used in this study, as well as those of other studies where this metric is employed [5].

(c) A 'core' community

LM houses a high number of species endemic to a single site (electronic supplementary material, figure S2; [26]), a characteristic that may complicate investigations of species interactions owing to (already) low levels of co-occurrence [8]. Because we were interested not only in the presence of community structure, but also the forces responsible for shaping communities at multiple scales, we extracted a replicated group of co-occurring species for detailed investigation. Several methods have been employed to discover 'core' and 'satellite' communities in previous studies of other assemblages. Our data did not show certain indicators of a 'core-satellite' assemblage: (i) the abundance-occupancy distribution is unimodal, (ii) there exists no positive correlation between the fraction of sites occupied and the average population size, and (iii) no shift is seen from lognormal to log-series between the 'core' (>50% sites) and 'satellite' (less than three sites) relative abundance distributions [12]. Therefore, we used two approaches to simplify the LM assemblage into a smaller, site-replicated community of species. First, we ranked each species by the total number of site occurrences and added each in order (most sites to single site) to a Shannon diversity index, which uses the relative abundance of each species to quantify a metric representing richness and evenness within an assemblage [50]. At each step, the proportional increase in diversity was calculated and the highest peak was used as a proxy for the selection of a 'core' community. With this approach we generated a species list comprised of the most abundant and frequently occurring species across all sites in the lake, thereby including the majority of possible species interactions in this set. Next we used cluster analysis to examine groupings based on a species-occurrence matrix. A bootstrapped hierarchical cluster (1000 iterations) was used to examine which species were grouped together based on this ecological measure of similarity (Sorensen or Bray distance) (R-package 'pvclust'). Our clustering strategy to identify 'core' species is akin to other network approaches in ecology and evolution [51]. Both methods of choosing the 'core' group of mbuna species produced a condensed target assemblage for closer examination of species interactions and the forces acting in community structuring.

(d) Species abundances by depth

We asked whether there were patterns of species abundances across the depth gradient within the list of 'core' species using iterative correlation analysis. Monte Carlo randomizations of species abundances by depth (summed across sites) allowed us to compare patterns in our observed data to those expected by random chance (1000 iterations). Product-moment correlation coefficients for observed data were compared with the distribution produced from randomized abundances and the tail probability of each observed correlation was calculated from its respective random family [47]. Significant correlations (p < 0.1) of 'core' species abundances were used to construct a network of depth-based relationships between species. A less-conservative significance level was chosen because of the small sample sizes available for this analysis and the fact that many strong, potentially relevant correlations (r > 0.75) would be lost at the traditional threshold (p < 0.05). However, we realize that using a more liberal critical threshold may increase the chance of selecting spurious correlations.

To address repeated patterns of co-occurrence by depth, we analysed each significant pairwise correlation (as above) on a site-by-site basis. Replication of correlation across sites was assessed qualitatively as the ratio of: (i) repeated significant correlations (p < 0.1) between two species, to (ii) the total number of site co-occurrences for that pair. For instance, if two species show strong correlations (p < 0.1) in the same direction at five sites and they co-occur at seven sites, the weight of this interaction would be 5/7 = 0.71, while two species with strong correlations at five sites, but co-occurring at a total of 15 sites have a replication weight of 5/15 = 0.33. In this way, the relative replicated correlation between two species can be examined across multiple sites with the weight of a single network edge. Significant correlations (p < 0.1) by depth between species were used to construct a network, and site-by-site replication was superimposed on this network.

(e) Species richness and depth distribution

To examine the effects of species richness on the depth profile of each 'core' species, we compared patterns in depth distributions at high- and low-richness sites. First, the abundance distributions of each species were examined across all 18 sites in the order of increasing richness using a Jonckheere-Terpstra test. This more powerful analogue to the Kruskal–Wallis test is used when samples have a natural ordering, such as richness among our sites [52]. Next, sites were binned into treatment groups of high and low richness for a pooled test of species distributions (Kolmogorov–Smirnov). Among all 18 sites used in this study, the average species richness was 20; therefore, this value was used as the threshold to separate low- and high-richness sites (n = 10 and 8, respectively). Each species’ depth distribution was tested for differences in shape and shifts in scale (along the depth axis) occurring with variation in community richness (Kolmogorov–Smirnov two-sample test). Changes along the depth axis were analysed using raw depth data while distributional shape differences were examined by mean standardization, thus removing the effects of scale from the shape analysis.

3. RESULTS

(a) The LM cichlid data

We analysed previously published census data; Ribbink et al. [26] compiled observations from 18 sites across the lake, including over 40 000 individuals from 138 cichlid species (14 genera). More than half (53%) of the species found were endemic to only one site, while all are endemic to LM (electronic supplementary material, figure S2; [23,26]). We focused on the rock-dwelling mbuna, which included 134 species and 10 genera. Of the mbuna, only Labeotropheus fuelleborni was observed at all 18 sites, while Metriaclima zebra (found at 12 sites) had the highest overall abundance (6851 individuals, 16.7% of total fish abundance). An average of 20 species (±1.8 s.e.) was found at each site and richness ranged from 9 to 36. Species richness was positively correlated with the available rock-reef area (figure 1; r² = 0.50), with a distribution well fit to the power function known.
(b) Community structure in LM cichlids

We randomized the species presence–absence matrix thousands of times to compare the observed pattern of co-occurrence to the distribution of matrices produced by chance. Mbuna communities showed the signature of community structure (higher C-scores, lower co-occurrence) at both the lakewide and sub-regional (north and south) scales (SES > 3.65, \( p \leq 0.01 \)) with SIM9. Notably, local communities showed compositions no different than random (SES < 2.14, \( p > 0.07 \); table 1). The same pattern was observed with the fixed-proportional model (SIM4), excepting the southern sub-regional analysis—which was no different than null (table 1). A strong signal of community structure was observed at the local-vertical scale (SES = 33.26, \( p < 0.00001 \); table 1). Independent depth-occurrence results for each site further supported this finding, with non-random structure (SES > 4.18, \( p < 0.04 \)) at 13 of 18 sites (72%), after correction for multiple tests.

(c) The ‘core’ community

Because LM mbuna contain a large proportion of narrowly endemic species (above), we sought to identify a ‘core’ assemblage found together throughout the lake. Two approaches converged on the same answer. The highest proportional increases in the Shannon diversity index were observed at the addition of the 4th and 13th species by rank occurrence (7.6% and 6.8% increase, \( p = 0.21, 0.07; \) figure 2). This group of 13 species accounted for a large proportion of fish observations [23,26]. Identification of ‘core’ species found together in various combinations at local reef sites permitted subsequent analysis of fine-scale interactions.

(d) Depth distributions are correlated among species

Dispersal of cichlids from rock-reef to rock-reef is low [27,28,31,33]; therefore each site in this study acts operationally as an independent community. To further investigate our observation of strongly non-random community structure with depth (above), we examined correlations of total abundance by depth between the ‘core’ species. We found both statistically significant positive and negative correlations (figure 3). Because ‘core’ species are represented in varied combinations at sites throughout the lake, we then asked if pairwise abundance by depth correlations were replicated from site to site. Most of the relationships between ‘core’ species (85%) were consistent across multiple sites, indicative of repeated patterns of interaction with depth.

(e) Richness alters species depth distributions

LM cichlid communities differ in species richness. We wanted to know if and how species richness affected the depth distribution of ‘core’ species. Nine of 12 ‘core’ species exhibited significantly different distributions across depth as sites increased in richness (Jonckheere-Terpstra, \( p < 0.05 \)). When sites were binned by richness, the depth profiles of 9 of the 12 ‘core’ species differed significantly (Kolmogorov–Smirnov, \( p < 0.05 \); figure 4). Species shifted to both deeper (e.g. ‘LF’ figure 4) and shallower (e.g. ‘MM’ figure 4) distributions between richness groups. There was no significant difference in fish density between high and low richness groups (Mann–Whitney, \( p = 0.66 \)), thus excluding the effect of total fish abundance on species’ depth distributions.

4. DISCUSSION

Biologists have long used the distributional patterns of species to infer the ecological and evolutionary forces that shape communities [1]. The observation of over-dispersed species co-occurrence has been interpreted as evidence of competition (assembly rules), yet the same signature can be produced by other, quite distinct ecological and demographic factors [6]. Despite the controversy surrounding competition’s role in generating community structure, its importance in adaptive radiation is well accepted [15]. We reasoned that if one could catch an adaptive radiation early in its history of diversification, one should be able to capture the signature of species interactions on community structure. To this end, we asked if we could detect the presence of community

from the theory of island biogeography [53]. The highest abundance of mbuna at any one site was approximately 7300 individuals (36 species at Likoma Island).

Figure 1. Mbuna distributions fit the power function familiar from the theory of island biogeography [53]. \( y = 16.30x^{0.21}, r^2 = 0.50. \)
structure, at hierarchical geographical scales, in the young adaptive radiation of rock-dwelling mbuna cichlids from LM. These species live and breed on rock-reef islands at high densities (e.g. 7 fish m$^{-2}$; [26]), consume effectively the same food items in different ways and essentially do not disperse [23].

We expected to detect the signature of community structure for LM mbuna at the broadest and finest scales of analysis, for different reasons (below). In fact, our results indicate that cichlid communities are under pressure from deterministic processes, and that these are extremely localized interactions that may shape depth distributions similarly across independent sites. Notably, local–vertical interactions do not scale-up, as mbuna communities at the local scale (transects around the perimeter of sites) are assembled no differently than random.

(a) Island biogeography and cichlid communities at broad scales

Mbuna species exhibit high rates of endemism (53% of species were present at only one rock-reef site [26]), and extreme geographical structuring of population genetic variation [29,30,33,54]. At the broadest scales, we expected that (on average) species would co-occur less frequently than observed in random draws, not because they physically interact, but precisely because they do not. Although the simulations we used approximate the species site occupancy and the percentage of endemics in the empirical data, they do not account for the spatially autocorrelated nature of species co-occurrence owing to geographical population structure. We reasoned that if the signature of reduced co-occurrence observed at regional and subregional (north and south) scales was influenced by species interactions, such interactions would necessarily involve the ‘core’ species, whose distributions span multiple sites. However, when we applied the null model co-occurrence analysis to the ‘core’ species only, at both the regional and subregional scales, we could not reject the hypothesis of random assembly (electronic supplementary material, table S1). Thus, there is strong evidence that mbuna communities are indeed structured (i.e. different than random) at the broadest scales within LM (table 1), but that the cause of ‘structure’ is evolutionary and demographic history rather than ecological interaction. Our inference here runs counter to that suggested for Danish avifauna by Gotelli et al. [14], where the signature of species interactions on community structure was apparent even at the regional scale.

(b) Local rock-reef cichlid communities are randomly distributed

Community analyses have traditionally focused on the regional scale [1,3,11], neglecting intermediate scales within locales, perhaps because the data have not been available. Yet, this scale represents an important one, linking (or not) processes that occur at the level of individual territories to patterns apparent across regions [14]. In the mbuna system, this is the broadest scale at which species interactions would probably affect community structure—individuals tend not to disperse from rock-reef island to island, but they will move around the perimeter of contiguous habitat [55]. Notably, our analyses of community structure within two sites failed to detect the signal of decreased co-occurrence ($p > 0.07$), and therefore we cannot reject the hypothesis of random assembly. Of course, there may be species interactions at this scale; however, they are apparently neither strong nor consistent enough to produce exclusion along site perimeters.

Table 1. EcoSim analysis of LM cichlid observed co-occurrence matrix versus 10 000 randomized matrices. (Scale of analysis is in descending order from broad to fine, no. of sites (no. of spp.) denotes the number of sites or depths and species used at each scale, $\text{SES}$ is standardized effect size (see §2) of observed $G$-score compared with the mean of simulated matrices, probability of $C_{\text{obs}} > C_{\text{sim}}$ is the probability of an observed $G$-score being greater than the average of random matrices, result is the determination of random or structured community based on analysis. Listed values correspond to fixed-fixed model (SIM9 in 5), values in parentheses correspond to fixed-proportional model (SIM4 in 5) where they differ. All $p$-values are corrected for multiple tests within a scale.)

<table>
<thead>
<tr>
<th>Scale of analysis</th>
<th>No. of sites (no. of spp.)</th>
<th>SES</th>
<th>Probability of $C_{\text{obs}} &gt; C_{\text{sim}}$</th>
<th>Result</th>
</tr>
</thead>
<tbody>
<tr>
<td>Regional (lake-wide)</td>
<td>18 (154)</td>
<td>9.80 (3.61)</td>
<td>$p &lt; 0.000001$</td>
<td>segregated</td>
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<tr>
<td>Subregion—north</td>
<td>11 (113)</td>
<td>8.05 (2.59)</td>
<td>$p &lt; 0.00004$</td>
<td>segregated</td>
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<tr>
<td>Subregion—south</td>
<td>7 (47)</td>
<td>3.65 (2.38)</td>
<td>$p = 0.01 (p &gt; 0.90)$</td>
<td>segregated</td>
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<td>Local (transect)—north</td>
<td>6 (36)</td>
<td>2.14 (0.33)</td>
<td>$p &gt; 0.07$</td>
<td>null</td>
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<tr>
<td>Local (transect)—south</td>
<td>6 (36)</td>
<td>0.37 (1.37)</td>
<td>$p &gt; 0.30$</td>
<td>null</td>
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<td>Local–vertical (depth)—across sites</td>
<td>6 (134)</td>
<td>33.26 (–)</td>
<td>$p &lt; 0.000001 (–)$</td>
<td>segregated</td>
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<td>Local–vertical (depth)—13/18 sites</td>
<td>6 (14–36)</td>
<td>4.18–22.79</td>
<td>$p &lt; 0.04$</td>
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Figure 2. ‘Core’ community selection based on proportional increase in Shannon diversity calculation with the addition of species in rank order of site occurrences (from most site occurrences to fewest). Arrows indicate the largest proportional increases at 4 and 13 species, respectively.
One of the limitations of the ECOSIM approach is that it revealed by the presence–absence co-occurrence analysis. Causes of the pattern of community structure by depth richness. Characterized by small habitable areas and low species with Bonferoni correction, 94% before correction. The chance between mbuna species was lower than expected by random community structure (table 1). Co-occurrence regime at local sites revealed a striking pattern of non-consistent correlations to total co-occurrences. LF, \( L. \text{fuelleborni}\); LV, \( L. \text{velicaris}\); PG, \( P. \text{genalutea}\); MA, \( M. \text{auratus}\); MV, \( M. \text{vermiculus}\); MM, \( M. \text{melanopterus}\); GM, \( G. \text{meno}\); LT, \( L. \text{trewavasae}\); MZ, \( M. \text{zebra}\); PT, \( P. \text{tridentiger}\); PrT, \( P. \text{taeniolatus}\); TT, \( T. \text{tropheops}\).

\( P. \text{t} r i d e n t i g e r \)

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\( M. \text{zebra} \)

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\( T. \text{tropheops} \)

\( P. \text{genalutea} \)

\( L. \text{fuelleborni} \)

\( G. \text{meno} \)

\( L. \text{trewavasae} \)

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\( M. \text{auratus} \)

\( M. \text{vermiculus} \)

\( M. \text{taeniolata
abundance of silt and debris) vary with depth in LM [36,40,41,43,56,57] and that species segregate by depth with associated, and assumed adaptive jaw morphologies [45]. At any single depth, multiple species are thought to coexist via habitat partitioning, as they exploit the same algal resources with divergent modes of feeding [36,40,45]. Our data, indicative of both positive and negative species interactions, are consistent with the conclusions of these studies.

Alternatively, mbuna cichlids may be segregated by depth because of variation in the light environment. Mbuna feed and breed in their territories, and male colour patterns, filtered through the visual systems of females, are key to mating success [58,59]. The greatest variations in species’ abundances are found in the first 5–10 m at all sites, a result also reported in Ribbink [5–10 m at all sites, a result also reported in Ribbink [5–10 m at all sites, a result also reported in Ribbink variations in species' abundances are found in the first 

5. CONCLUSION

Taken together, our results indicate that: (i) significant and replicated effects of non-random mechanisms shape vertical species distributions within sites, and (ii) that the incredible diversity in the LM mbuna assemblage can be explained by a combination of extremely localized ecological interactions and the unique biogeographic and evolutionary attributes of these fishes. Notably, it is apparent that the forces structuring communities across depth gradients do not persist through broader local and regional scales. Based on our results and the speed and extent of the Malawi cichlid radiation, we suggest that similar patterns may exist in older, less species-rich but more extensively studied ecological systems (e.g. Anolis lizard and Darwin’s finch ecotypes across islands). Indeed, investigations focused on these assemblages might provide additional insight as the implementation of phylogenetic community analyses should be possible.

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