

# Scale-dependent processes of community assembly in an African rift lake

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## SUMMARY

1. Ecologists continue to debate whether the assembly of communities of species is more strongly influenced by dispersal limitations or niche-based factors. Analytical approaches that account for both mechanisms can help to resolve controls of community assembly.
2. We compared littoral snail assemblages in Lake Tanganyika at three different spatial scales (5–25 m, 0.5–10 km and 0.5–27 km) to test whether spatial distance or environmental differences are better predictors of community similarity.
3. At the finest scale (5–25 m), snail assemblages shifted strongly with depth but not across similar lateral distances, indicating a stronger response to environmental gradients than dispersal opportunities.
4. At the two larger scales (0.5–27 km), both environmental similarity and shoreline distance between sites predicted assemblage similarity across sites. Additionally, canonical correspondence analysis revealed that snail abundances were significantly correlated with algal carbon-to-nitrogen ratio and wave energy.
5. Our results indicate that the factors governing assemblage structure are scale dependent; niche-based mechanisms act across all spatial scales, whereas community similarity declines with distance only at larger spatial separations.

*Keywords:* community assembly, dispersal, distance decay, gastropods, neutral theory, niche, niche theory

## Introduction

Ecologists have long debated whether communities of species are assembled by chance events, such as random dispersal (MacArthur & Levins, 1967), or through ecologically deterministic processes (MacArthur, 1957; Preston, 1962a,b). Recently, the dispersal-assembly versus niche-assembly debate has been reignited by claims that species distribution and

abundance patterns can be explained purely by ecologically neutral processes (Bell, 2001; Hubbell, 2001; Volkov *et al.*, 2003, 2005). These neutral theories predict that local species assemblages are the result of metacommunity dynamics under random dispersal probabilities, stochastic birth and death processes, and chance speciation. Moreover, neutral theories assert that well-known patterns of species abundance and distributions arise even when all species are ecologically equivalent. This result challenges the large body of research focused on environmentally driven, deterministic influences on ecological communities and has inspired new tests of the neutral

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theories and the dispersal-assembly hypothesis (Chave, 2004). Empirical analyses have focussed on the prediction that dispersal processes, rather than environmental sorting, drive patterns of species distributions across landscapes.

The first challenge in testing these theories is that they make indistinguishable predictions regarding patterns of species abundances and spatial distributions (Chave, Muller-Landau & Levin, 2002; Mouquet & Loreau, 2003). For instance, each set of theories predicts a positive correlation between community similarity and spatial proximity, a pattern known as distance-decay (Gilbert & Lechowicz, 2004; Thompson & Townsend, 2006; Sojininen, McDonald & Hillebrand, 2007), albeit for different reasons. Niche theories assert that neighbouring communities should be the most alike because they are most likely to share similar environments. Dispersal theories predict that adjacent communities will be more similar because they exchange more migrants.

A second problem in comparing niche and dispersal theories is that the operational mechanisms posited by each are not mutually exclusive. Many of the studies designed to assess which set of theoretical predictions best match field data are, in fact, one-sided tests that confirm or refute one theory without simultaneously testing the other. Not surprisingly, this approach has failed to resolve the issue; both niche- and dispersal-assembly have been supported by different studies (Stokes & Archer, 2010).

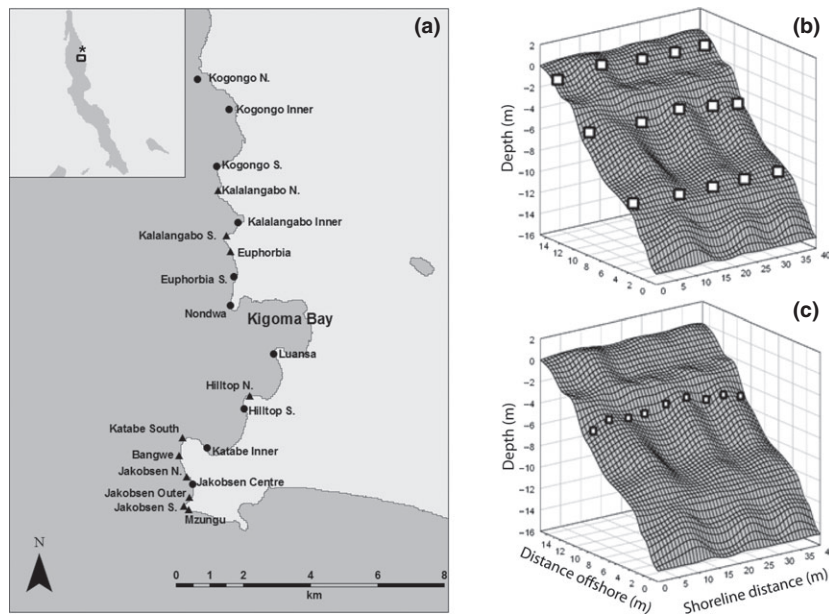
One explanation for why field tests arrive at different conclusions is that the relative influence of dispersal- and niche-assembly could depend upon spatial scale. Some authors maintain that community patterns at local scales are driven by environmental factors, whereas regional patterns are governed by dispersal limitation (Schmida & Wilson, 1985; Cottenie, 2005). From that perspective, organisms are thought to be able to track environmental conditions at small spatial scales, but to be unable to reach favourable environments at greater scales. Other authors have suggested the opposite scenario, and stochastic dispersal processes should dominate patterns at the smallest spatial scales (Gilbert & Lechowicz, 2004). This idea is analogous to predicting positions and distributions of molecules in air; it is hard to know the exact location of molecules because of their rapid random movements, yet deterministic forces create predictable patterns at larger scales. In a

third scenario, theoretical metacommunity models allow both dispersal limitation and environmental sorting to operate across all spatial scales, yielding predictions of their joint effects (Leibold *et al.*, 2004). Given these conflicting hypotheses, there is a need for field studies that test the roles of dispersal- and niche-based processes in community assembly in a spatially explicit way.

In the light of the challenge of simultaneously comparing dispersal and niche-based theories when environmental conditions often show spatial autocorrelation, we designed the present study to disentangle the effects of distance and environment at several spatial scales by focussing on the shoreline of Lake Tanganyika (Fig. 1a), the oldest and largest African rift lake. Shorelines are ideal for testing the effects of dispersal because dispersal along them is constrained to a single dimension. The shoreline of Lake Tanganyika provides an additional advantage, in that it is composed of an irregular mosaic of substrata that form a patchy habitat (Michel *et al.*, 2004). The majority of biodiversity exists on rocky substrata that are separated by sandy areas, and this patchy landscape creates natural units to study at different scales. These rocky patches constitute the smallest spatial scale at which differences in species assemblages can be quantified, and comparisons between such patches can be made at progressively greater distances. In addition, many environmental characteristics are heterogeneous within and between rock patches, meaning that nearby rocky habitats can be very different and distant habitats can have similar environments.

Within a given patch, the effects of distance and environmental change can be tested separately by evaluating how assemblages change as depth increases compared with changes along comparable lateral distances along the shore. The depth gradient is associated with strong shifts in environmental conditions, while the shoreline transect within patches has relatively similar environments despite spatial separation. If niche-based influences prevail, assemblages will change most across depths, whereas if dispersal constraints prevail, then communities should change equally with lateral distance within depth zones and between zones.

The effects of niche and dispersal forces can also be disentangled at larger spatial scales by comparing community compositions of separate rocky patches. Besides substratum, many other environmental



**Fig. 1** Site locations in the Kigoma Bay region (outlined on full lake map) of Tanzania (a) (the dark region is the lake) and sampling strategies (b & c). Local-scale sampling along a depth gradient is displayed in (b). This intensive sampling was performed in 1998 at two sites displayed on the Kigoma map (Hilltop N., Jakobsen S.) as well as two more northerly sites (Mitumba and Mwamgongo) indicated with a star in the full lake map. All 20 sites indicated in (a) were sampled in 2007 according to the quadrat scheme in (c). Triangles in (a) indicate the subset of sites sampled in 2004. Sites from 2004 were sampled according to (c), except that only every other quadrat was sampled (five in total).

characteristics have a heterogeneous distribution. For instance, sites differ widely in hydrology as shoreline curves expose them to varying degrees of wind, current and upwelling from nutrient-rich water from the depths of the lake (Fig. 1a; Corman *et al.*, 2010).

We focussed on littoral snail assemblages in Lake Tanganyika because they satisfy three key assumptions of the neutral theories: close phylogenetic relatedness, similarity in ecological requirements and limited dispersal potential (Hubbell, 2001). Species from as many as five genera coexist on rocky substrata in the littoral zone of Lake Tanganyika, but the species pool is dominated by the endemic *Lavigeria* species flock. Like the famous East African cichlid fish, these snails have speciated extensively, but all are obligate grazers of periphyton (Michel *et al.*, 2004). Their similarities in diet and habitat use suggest that these snails are as close to being ecological equivalents as possible within a clade composed of dozens of syntopic animal species. Their dispersal potential is limited because they produce young by brooding (*Lavigeria* Bourguignat, 1888) or by laying eggs (*Vinundu* Michel, 2004, *Reymondia* Bourguignat, 1885, *Spekia* Bourguignat, 1889, *Paramelania* Giraud, 1885), thereby preventing long-distance dispersal during

early-life stages. Juvenile movement is limited by the need to avoid predators by hiding under the substratum, and adults move slowly relative to the size of habitat patches (Michel, McIntyre & Chan, 2007).

For this study, we hypothesised that the importance of dispersal- and niche-assembly processes are scale dependant and inversely related; therefore, we made quantitative comparisons of assemblage structure across several spatial scales. At local spatial scales, we expected that these animals are able to find their preferred habitat, leading to strong sorting by environment and not spatial distance. In contrast, over larger spatial scales species distributions are less likely to match environmental variation because they are limited by how far individuals can disperse and the likelihood that they will encounter their preferred environment.

## Methods

To determine the spatial domain of niche and dispersal limitation influences, we compared snail assemblage structure at the following three scales: local (5–25 m), subregional (0.5–10 km) and regional (0.5–27 km). We chose overlapping subregional and

regional scales to use a distance matrix approach to test patterns of community composition (statistics discussed later). This approach required a symmetric matrix that includes all site comparisons, rather than just sites spaced >10 km apart. We chose this technique because it is powerful at finding spatial patterns, although one disadvantage is that the results for the regional scale are not fully independent of the subregional scale. However, the influence of the subregional comparisons on the regional result is negligible because there are 2.45 more comparisons made over 10 km in distance than for comparisons less than that 10 km. Field sampling was conducted in July 1998, 2004 and 2007 near Kigoma, Tanzania (see Fig. 1a & Table S1). Local-scale patterns were studied in 1998, while subregional- and regional-scale comparisons were made in 2004 and 2007. Voucher collections of all species were deposited in the Natural History Museum, London.

#### *Local-scale sampling and analysis*

At the local scale, we compared the effects of environmental conditions and spatial distance by characterising snail assemblage composition along a depth gradient. Assemblages were analysed at four separate sites (Hilltop N., Jakobsen S., Mitumba and Mwamgongo) that were separated by 4–30 km (Fig. 1a), each of which was sampled at three depths (1, 5 and 10 m; Fig. 1b). At each depth, five replicate quadrats (4 m<sup>2</sup>) were spaced 5–10 m apart, and all snails were removed from upward-facing rock surfaces by self-contained breathing apparatus. Snails were identified to species and then returned to their sites. Full sampling details are provided by McIntyre *et al.* (2005).

Environmental conditions such as algal biomass and wave energy change rapidly with depth (McIntyre *et al.*, 2005); hence, our sampling design allows evaluation of spatial distance effects with (i.e. at different depths) and without (i.e. along the shore) shifts in environment. We assessed distance and environmental effects by using multivariate approaches to compare species abundances between quadrats within and between depths. First, we tested for distance effects alone by determining whether assemblages in quadrats at the same depth were less similar than randomly generated assemblages. To do this, we generated 1000 randomised assemblages for each site at each depth by resampling the abundances of each species from the

five quadrat samples. We paired randomised assemblages to generate 500 independent pairs and then calculated the frequency distribution of Bray–Curtis similarity scores between randomised assemblages based on the natural log-transformed species abundances (Krebs, 2008). To assess distance effects, we tested whether the similarity of real assemblages from different quadrats was lower than that among randomised assemblages. Second, we quantified whether assemblage similarities decay with distance among quadrats within the same depth and site. The number of transects separating two quadrats was used as the index of distance because the absolute distance between each quadrat was not measured. Assemblage similarities were estimated using Bray–Curtis techniques, and comparisons were repeated separately for all depths and sites. Spearman's rank correlations were used to test whether assemblage similarities decayed with distance between quadrats. This statistical approach provides a rigorous qualitative test of distance effects within each depth (i.e. environmental variation is minimal).

Second, we tested for environmental effects overlaid upon any distance effects by comparing assemblage similarity among depths. The Bray–Curtis index was calculated for all pairs of quadrats within a site, and we used one-way ANOSIM implemented by PAST 1.82 (<http://folk.uio.no/ohammer/past/>) to test whether between-depth comparisons showed lower similarity than within-depth comparisons. This approach distinguished whether the environmental differences between depths decreased community similarity beyond that expected from within-depth variation among quadrats. If distance alone is important, then similarity among assemblages at different depths should be lower than within depths. Conversely, if environmental similarity dictates assemblage structure, then quadrats from different depths should differ strongly. Comparisons were made first within each site, and then results from the four sites were combined using the weighted Z-test (Whitlock, 2005). Similarities in species assemblage structure among quadrats also were visualised using cluster analysis computed by Ward's method using PAST.

#### *Subregional and regional-scale sampling*

In 2007, we studied 20 sites near Kigoma Bay (Fig. 1; Table S1). At each site, divers sampled snails at 5 m



depth, which is considered representative by virtue of having a large potential species pool and relatively high snail densities compared with other depths (Michel, 1994; McIntyre *et al.*, 2005). Nine 1-m<sup>2</sup> quadrats were placed 2–3 m apart along a transect running parallel to the shoreline (Fig. 1c), and every snail >5-mm shell height was collected from upward-facing rock surfaces, identified to species and counted. A total of 3722 individual snails were collected in 2007, representing 11 species (Table S2).

We measured eight environmental variables at each site that were hypothesised *a priori* to influence snail ecology: shoreline aspect, bathymetric slope, wave energy, substratum grain size, rugosity (as a proxy for substratum complexity), inorganic sediment mass, benthic algal biomass and algal carbon to nitrogen ratio (C : N) (Table S3). Shoreline aspect, slope and wave energy are abiotic variables associated with water motion and physical disturbance arising from prevailing winds. Grain size and rugosity were selected to capture the availability and diversity of local-scale microhabitat space to snails. Benthic algal biomass and C : N ratios are assays of food quantity and quality, respectively, and sedimentation mass reflects anthropogenic disturbance (McIntyre *et al.*, 2005). Collectively, these variables describe major physical, biological and human influences on snail ecology.

Aspect was determined by taking a bearing perpendicular to the shoreline at each site using a topographic map. Bathymetric slope was calculated to a depth of 50 m using a bathymetric map (Corman *et al.*, 2010). Substratum grain size was determined by photographing three 1-m<sup>2</sup> quadrats per site, overlaying a four-by-four digital grid, recording the substratum type and size at each of the 16 grid intersections (sand, gravel, cobble or boulders) and calculating mean grain size for each site following Coyer, Steller & Witman (1999). Rugosity was estimated along a 5-m-long transect along the 5-m-depth contour using a small-link chain closely draped over the substratum, and rugosity was calculated by dividing the draped length by the 5-m taut length (Chapman, 2000). Benthic algal biomass (as chlorophyll *a*), algal nitrogen content (as molar C : N) and inorganic sediment mass were measured from four flat cobblestones (10–25 cm diameter) collected from 5 m depth. A plastic cap (15.19 cm<sup>2</sup>) was seated against the top of each stone before the stone was disturbed. The rock was

brought to the surface with the cap held tightly to the rock ensuring that the sediment and algae were not dislodged. The algae around the cap was scrubbed off, purified in a colloidal silica density column (Hamilton *et al.*, 2005), rinsed, dried, acidified and analysed for C : N using an elemental analyser. The algae and sediment protected by the cap were then scrubbed off and saved to make quantitative calculations of sediment and biomass per unit of area. The resulting slurry was divided into two subsamples that were collected on glass fibre filters (Fisherbrand TLLP) and either combusted (2 h, 500 °C) to quantify ash mass as a proxy for sedimentation or extracted in 90% cold ethanol (24 h) for determination of chlorophyll *a* by spectrophotometry.

Wave action was measured at each site as the mean mass of plaster of Paris lost from a 'clod card' over 24 h (Doty, 1971). We placed five clod cards at 2 m intervals along the 5-m-depth contour at each site. Clods of consistent size (*c.* 2 cm<sup>3</sup>) and density were made by pouring a mixture of plaster and water (1.48 : 1 ratio) into a flexible mould. Clods were air-dried for 4 days and sanded smooth before being glued to a plastic base with silicon, weighed to the nearest µg and attached to rocks at each site. Clod cards were collected after 24 h and air-dried for 4 days before their final mass was measured.

A subset of sites and environmental variables were sampled in 2004. Ten of the 2007 sites were studied by surveying snails in five 1-m<sup>2</sup> quadrats at 5 m depth per site (2312 snails representing 11 species in 2004; Table S2). The following six environmental variables were quantified by the methods described earlier: shoreline aspect, slope of the benthos, substratum grain size, environmental complexity, benthic algal biomass and algal C : N.

#### *Regional- and subregional-scale analysis*

We compared distance and environmental effects on snail assemblages in our study area at two scales. The regional-scale analyses included all sites surveyed in 2004 and 2007. To perform analyses at a smaller scale, we split the sites into northern and southern subregions. We considered the Kigoma Bay to be a natural division between the north and south regions because it (*c.* 5 km shoreline distance) acts as a significant biogeographic barrier between the southern and northern portions of the study area because of its

predominantly sandy and muddy substrata (Michel *et al.*, 2004).

To evaluate whether the rocky littoral zone was indeed patchy in terms of the environmental variables measured, we compared a matrix of all pairwise comparisons between site environments to the spatial distance between sites using a Mantel's test. The environmental matrix was constructed by using a Euclidean distance method (in PAST) on Z-score transformed environmental variables. This technique ensured that each environmental variable contributed equally in our determination of how distinct each set of sites was (Legendre, 1998). Spatial distances were estimated using digitised topographical maps (maps used for this analysis and to create Fig. 1a can be found at <http://www.natureearthdata.com> and <http://www.tzgisug.org>). This test was repeated for each year and spatial scale. These four separate sets of results were combined using the weighted Z-score method (Whitlock, 2005).

To test whether snail assemblage patterns were attributable to the effects of spatial distance or environmental characteristics, we adopted a permutation approach using partial Mantel's tests to compare correlations among matrices. This statistical method identifies the variation in assemblage structure that is correlated with environmental versus spatial differences, enabling us to perform balanced, head-to-head comparisons of these alternative influences. To conduct this matrix-based analysis, we generated a matrix of Bray–Curtis pairwise assemblage similarity coefficients between ln-transformed snail densities using PAST and compared that to matrices of shoreline distances and multivariate environmental differences between sites. Tests were performed separately for 2004 and 2007 data using the IBD v1.52 program available at <http://www.bio.sds.edu/pub/andy/IBD.html>. Test statistics and significance were determined by 9999 iterations of the Mantel's test. Results from the 2 years were combined using the Z-score technique (Whitlock, 2005).

To test subregional scale control, we separated the data from northern (north of the Luanza site) and southern sites (south of Luanza) (Fig. 1a) and tested whether shoreline distance or environmental differences were correlated with assemblage similarity within each region. In 2004, only three northern sites were sampled; thus, our subregional scale test is restricted to the seven southern sites. The results of

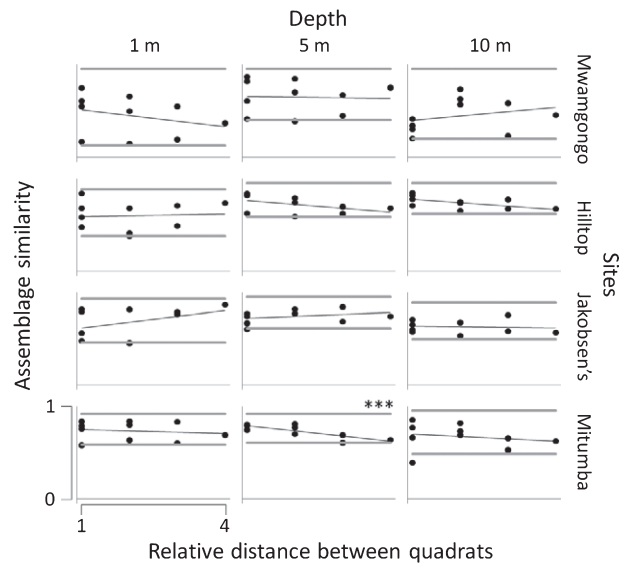


Fig. 2 Effects of distance between quadrats on assemblage similarity. Points represent comparisons of species assemblages between all quadrats from the same site and depth, which are plotted against the relative distance between quadrats. Solid black lines indicate distance-decay patterns based on linear regression; asterisks indicate a significant positive Spearman's rank correlation. The region between the solid grey bands indicates the 95% confidence interval of comparisons between randomised assemblages based on species abundances at each depth and site.

subregional scale analyses in 2007 were pooled with the results from 2004 using the weighted Z-score method.

To assess which environmental variables influenced snail distributions and abundances, we conducted a canonical correspondence analysis (CCA) of the 2007 data using CANOCO v4.5 (Plant Research International, Wageningen, The Netherlands). Stepwise forward selection was used to reduce the number of uninformative environmental variables in the analysis, and a final CCA was run on the resulting significant variables.

## Results

### Local scale

For the majority of sites and depths, there was no evidence that distance *per se* influenced snail assemblage composition at the local scale. Comparisons between actual and randomised assemblages indicated that only 6 of 120 quadrats (5% of comparisons) were less similar than expected based on the 95% confidence

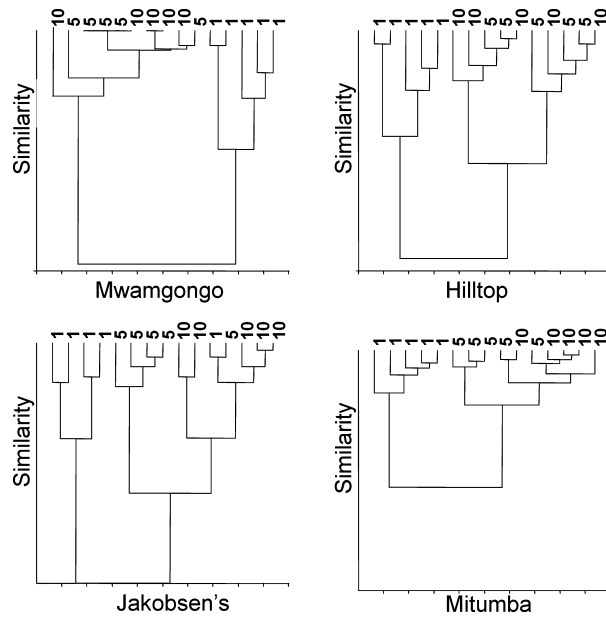


Fig. 3 Similarity of snail assemblages among three depths (1, 5 and 10 m) at each of four sites. Five replicate quadrats were sampled in each depth and site, and assemblage similarity was calculated using Ward's method.

intervals of randomised assemblages (Fig. 2). The test of decreasing assemblage similarity with distance between quadrats indicated a significant pattern in only one of 12 site–depth combinations (Mitumba at 5 m:  $r = -0.71$ ,  $P = 0.029$ ) (Fig. 2; Table S4), although this value is not significant with Bonferroni correction for multiple comparisons ( $n = 12$ ,  $P = 0.004$ ).

In contrast to the lack of effect of distance within a depth, our analyses of local-scale assemblage composition showed strong structuring across depths (ANOSIM: Mwamgongo  $R = 0.56$ ,  $P < 0.001$ ; Hilltop  $R = 0.29$ ,  $P = 0.023$ ; Jakobsen's  $R = 0.70$ ,  $P < 0.001$ ; and Mitumba  $R = 0.73$ ,  $P < 0.001$ ). Samples from 1 m depth were much more similar to each other than to those from other depths (Bonferroni-corrected ANOSIM combined for four sites with the weighted Z-method, 1 versus 5 m:  $Z = -3.17$ ,  $P < 0.001$ ; 1 versus 10 m:  $Z = -2.62$ ,  $P = 0.003$ ). Although, samples from 5 and 10 m depth were not significantly different (5–10:  $Z = 0.15$ ,  $P = 0.984$ ). These patterns were also supported by the cluster analysis (Fig. 3).

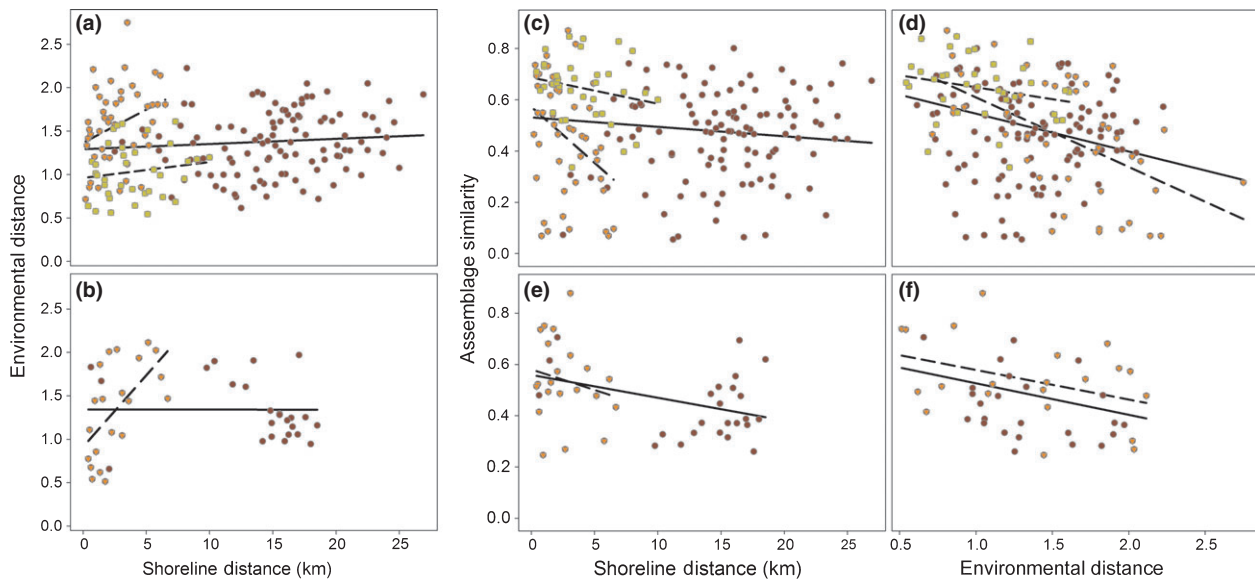
#### Sub-regional and regional scales

Environmental variables were spatially autocorrelated at the subregional scale (north 2007:  $r = 0.14$ ,

$P = 0.250$ ,  $n = 9$  sites; south 2007:  $r = 0.366$ ,  $P = 0.035$ ,  $n = 10$  sites; south 2004:  $r = 0.60$ ,  $P = 0.036$ ,  $n = 7$  sites; combined analysis across regions and years; and weighted Z method  $Z = 2.42$ ,  $P = 0.007$ ), but not at larger distances captured in the regional analysis (2007:  $r = 0.143$ ,  $P = 0.080$ ,  $n = 20$  sites; 2004: sites  $r = -0.002$ ,  $P = 0.394$ ,  $n = 10$  sites; combined analysis across years; and weighted Z method  $Z = 1.37$ ,  $P = 0.085$ ). This discrepancy is exemplified by the sites near Jakobsen's Beach in the south. These sites are both close to each other and have similar environmental characteristics, yet they also show environmental similarities to the Kalalangabo site lying 10 km to the north on the other side of Kigoma Bay. Even at the subregional scale where correlation between environment and distance was significant, certain sites violated this overall pattern (Fig. 4a,b), including Mzungu Beach that is adjacent to Jakobsen's Beach but has a very different environment. Interestingly, Jakobsen's Beach and Kalalangabo shared more snail species than did Jakobsen's Beach with Mzungu, offering anecdotal support for the primacy of environmental sorting over distance effects.

Mantel's tests of assemblage similarity at the sub-regional scale yielded parallel results for 2004 and 2007. Similarity was significantly correlated with multivariate environmental differences (north 2007:  $r = -0.21$ ,  $P = 0.219$ ,  $n = 9$  sites; south 2007:  $r = -0.48$ ,  $P = 0.009$ ,  $n = 10$  sites; south 2004:  $r = -0.34$ ,  $P = 0.083$ ,  $n = 7$  sites; combined analysis across regions and years; and weighted Z method  $Z = 2.65$ ,  $P = 0.004$ ), but not with shoreline distance (north 2007:  $r = -0.19$ ,  $P = 0.212$ ,  $n = 9$  sites; south 2007:  $r = -0.23$ ,  $P = 0.13$ ,  $n = 10$  sites; south 2004:  $r = -0.04$ ,  $P = 0.448$ ,  $n = 7$  sites; combined meta-analysis across regions and years; and weighted Z method  $Z = 2.84$ ,  $P = 0.004$ ) (Fig. 4). When all sites were compared in the regional-scale analysis, similar effects of shoreline distance (2007:  $r = -0.12$ ,  $P = 0.076$ ,  $n = 20$  sites; 2004: sites  $r = -0.42$ ,  $P = 0.018$ ,  $n = 10$  sites; combined analysis across years; and weighted Z method  $Z = 2.09$ ,  $P = 0.013$ ) and environmental similarity (weighted Z method  $Z = 2.52$ ,  $P = 0.011$ ; 2007:  $r = -0.31$ ,  $P = 0.006$ ,  $n = 20$  sites; 2004:  $r = -0.40$ ,  $P = 0.007$ ,  $n = 10$  sites; combined analysis across years; and weighted Z method  $Z = 3.34$ ,  $P < 0.001$ ) were observed (see Fig. 4).

Canonical correspondence analysis showed that the physical characteristics of sites such as slope,



**Fig. 4** Environmental spatial autocorrelation, distance decay of communities and environmental relationship to communities. Positive correlations of spatial distance and environmental differences are given in (a) and (b). The relationship between community similarity and shoreline distance between sites are shown in (c) and (e); the relationship between community similarity and environmental distance is shown in (d) and (f). Sites sampled in 2007 are in (a), (c) and (d), sites sampled in 2004 are displayed in (b), (e), and (f). Values for comparisons between northern sites are depicted as yellow squares, orange triangles indicate values for southern site comparisons and comparisons that traverse Kigoma Bay are indicated by red circles. Dashed lines describe local-scale regressions (shorter dashes are for southern sites), while solid lines portray regional-scale patterns.

substratum grain size and rugosity were correlated with species distributions, although only algal quality (C : N) and wave energy were significantly associated with interspecific differences in shoreline distributions (Fig. 5; Table S5). *Lavigeria* sp. M (open nomenclature *Lavigeria* are referenced in Michel *et al.*, 2003 and in West *et al.*, 2003), *L.* sp. J and *Spekia zonata* (Woodward, 1859) favoured sites with low algal N content, while large-bodied *Lavigeria* species [*L. coronata* Bourguignat, 1888, *L. nassa* (Woodward, 1859), *L. grandis* (Smith, 1881), *L.* sp. W] were found primarily at sites with high-quality food (low C : N). Sites with steep slopes, large boulders and high wave energy were often inhabited by the largest species, *Lavigeria coronata* West *et al.*, 2003;. Conversely, sites with a cobble substratum were dominated by smaller species such as *Lavigeria* sp. L and *Vinundu westae* Michel *et al.*, 2004.

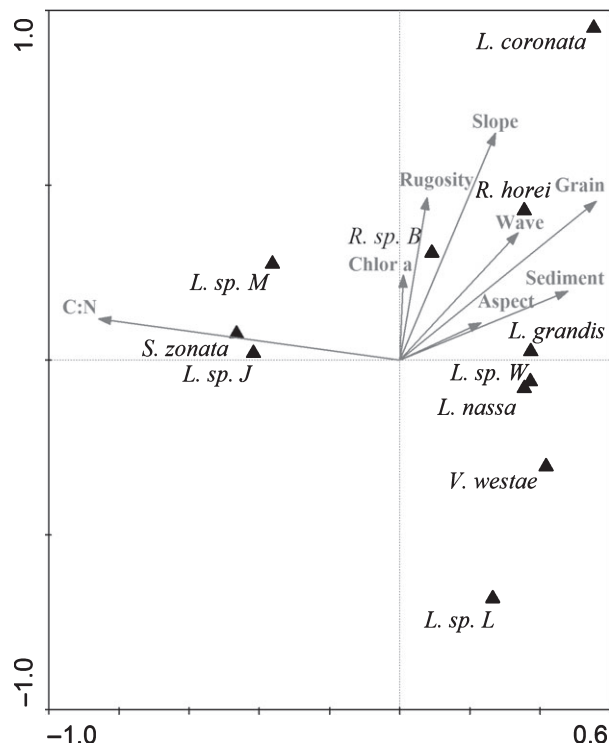
## Discussion

Assemblage patterns at all spatial scales (5 m to 27 km) were explained by variation in environmental conditions. Within sites, assemblages differed dra-

matically across water depths, but changed little across comparable lateral distances (Figs 2 & 3). These comparisons support the importance of niche-based assemblage structure at local spatial scales. Similarly, environmental differences between sites explained more of the variation in snail assemblage structure at a subregional scale than shoreline distance, though both were significant predictors (Fig. 4). At the regional scale, shoreline distance between sites became equally important at the environmental differences between sites (Fig. 4). Thus, our results support Schmidha & Wilson's (1985) and Cottenie's (2005) suggestion that environmental properties are most important for understanding subregional assemblage structure, and that dispersal limitation becomes important for determining species patterns at larger spatial scales.

Many previous empirical studies have also rejected explanations for community assembly based entirely on neutral theory or dispersal limitation. These include tests of whether population dynamics (Clark & McLachlan, 2003), community composition (Dornelas, Connolly & Hughes, 2006), phylogeographic patterns (Webb *et al.*, 2002; Kelly *et al.*, 2008) and





**Fig. 5** Canonical correspondence analysis of environmental variables and species distributions. Species are displayed as point values (triangles), and environmental variables are described as vectors. Species displayed are of the genera *Lavigeria* 'L.', *Reymondia* 'R.' and *Spekia* 'S.'. Environmental variables shown include the amount of inorganic sediment 'Sediment', shoreline aspect 'Aspect', wave energy 'Wave', substratum grain size 'Grain', slope of benthos 'Slope', substratum complexity 'Rugosity', algal quality 'C : N' and algal quantity 'Chlor a'.

distance–decay relationships (Vojtech *et al.*, 2007) conform to neutral predictions. However, none of these studies offered a complimentary test of the explanatory power of niche-based processes. Similarly, studies that have supported neutral theory predictions (Bell, 2001; Hubbell, 2001; Volkov *et al.*, 2005, 2007) have not tested alternative predictions from niche theories. These asymmetries reduce the inferential power of hypothesis tests because niche and neutral theories are not mutually exclusive (Gilbert & Lechowicz, 2004). A strength of the present study is the direct comparison of both hypotheses as a means of disentangling the roles of dispersal- and niche assembly.

Our results add to the growing body of tests of dispersal limitation and environmental sorting over multiple spatial scales for a wide range of taxa and environments. The results of these studies vary, but

most share the finding that environmental differences are important for determining community composition at all spatial scales. Distance between sites did not explain variation at any spatial scale for plant species sampled at local and subregional scales in a Canadian forest (Gilbert & Lechowicz, 2004; Karst, Gilbert & Lechowicz, 2005), similarly for bacterial communities sampled from soils sampled across the Americas (Fierer & Jackson, 2006). However, as in our study on snails, microbes living in European lake sediments are dispersal-limited at larger regional scales (Van der Gucht *et al.*, 2007). Interestingly, a study on rainforest snails found that distance between sites mattered at local through regional scales (Steinitz *et al.*, 2006). Lastly, work on fungal communities spanning all geographical scales was the only study to show no effect of environmental sorting, although, as noted by the authors, their environmental sampling may have been too coarse to detect patterns (Green *et al.*, 2004). Taken together, these divergent results challenge the idea that there are general rules for the overall role and inherent spatial scale of environmental sorting and dispersal limitation in community assembly.

One way forward is to perform meta-analyses spanning a wide range of taxa, environments and scales to test for general patterns. For instance, a recent meta-analysis of 158 datasets representing plants and aquatic animals found strong support for environmental species sorting that was independent of scale, as well as weak support for distance effects that was scale dependant for some taxa (Cottenie, 2005). Although there was no evidence of scale dependence among mobile organisms like the snails we studied, this meta-analysis focussed on much larger spatial scales that often spanned many insular ecosystems (e.g. lakes) between which individuals would be unable to disperse directly. Despite the subtle disagreements, the cross-scale, within-ecosystem approach taken in our study and several earlier ones compliments the meta-analysis approach of Cottenie (2005). Overall, both methodologies provide evidence of scale dependence in the relative influence of environmental conditions and dispersal limitation.

Our empirical tests of niche- and neutral-based predictions across multiple spatial scales also elucidate the environmental factors structuring snail assemblages in Lake Tanganyika. Our local-scale comparisons within sites showed that species abundances were strongly determined by depth. These

snails are unlikely to be dispersal-limited at scales of 10 s of metres because their net travel rate averages *c.* 0.5 m day<sup>-1</sup> (Michel *et al.*, 2007). Thus, we infer that distance *per se* is not a constraint, but rather shifts in assemblage structure with depth must reflect species-specific responses to environmental variation in primary productivity, wave action or other depth-mediated factors.

Beyond simply summarising the aggregate influence of environmental similarity, our analyses revealed the effects of specific environmental characteristics on snail assemblage structure. The wave energy and physical structure of the substratum (rugosity, slope and grain size) were the dominant axes along which snail species appeared to segregate (Fig. 5). The nitrogen content of the algae consumed by these snail species was orthogonal to substratum characteristics and formed the largest component of variation in the second major axis of differentiation, along with deposited sediment and shoreline aspect. Despite the limited segregation of snail species relative to variation in algal C : N, there was a distinct pattern with respect to body size. All of the largest *Lavigeria* species (*L. coronata*, *L. nassa*, *L. grandis*, *L. sp. W*) were associated with high algal N content (expressed as low C : N) and low-sediment load on rocks relative to smaller congeners (*L. sp. M*, *L. sp. J*). This suggests the potential for diet quality to limit the distribution of large snails, but more targeted analyses are required to test this conjecture.

The effects of dispersal limitation on snail community similarity were evident only at the largest spatial scales 0.5–27 km. These snails lack a pelagic juvenile phase (like most freshwater snails, all brood their young or lay eggs), and thus are likely to be dispersal-limited, although not enough to overwhelm the effects of environmental sorting. The importance of dispersal constraints appears to increase when snails are confronted with crossing Kigoma Bay. The littoral substratum of the bay is mainly sand and mud, making it inhospitable to rock-dwelling snails. The role of Kigoma Bay as a barrier to dispersal could reflect fundamental effects of long-term geology or an impact of recent anthropogenic degradation of habitat and water quality. Using molecular methods to assess gene flow and to date population divergences for a number of taxa in this region would help to elucidate the mechanisms underlying dispersal limitation (e.g. Wagner & McCune, 2009).

The statistical approach for comparing dispersal-assembly and niche-assembly theory predictions illustrated in this study is broadly applicable, but several limitations must be recognised. Physical distance between sites constitutes only a rough surrogate for actual dispersal constraints between sites. This problem will arise whenever the habitat characteristics between focal sites vary, such that the challenges of dispersing are not a linear function of distance alone. Nonetheless, shoreline distance is an adequate surrogate for dispersal potential of snails in Lake Tanganyika and other freshwaters because these animals lack a planktonic life stage or potential for airborne dispersal.

A similar limitation applies to our assessment of environmental differences between sites. One of the greatest challenges in evaluating evidence for niche assembly of ecological communities is identifying and quantifying the key environmental variables that influence organismal distributions. We measured a large suite of variables that could potentially influence snail fitness, but we recognise that unmeasured factors such as predation or parasite pressure are also important. In any case, strong tests of how environmental variation affects community structure must be based upon *a priori* selection of ecologically relevant variables, after which multivariate similarity indices provide an integrative measure of the niches available at each site.

In conclusion, our analyses at spatial scales from 5 m to 27 km consistently indicated that assemblage structure of the endemic snails of Lake Tanganyika reflects environmental variation. While niche-based assembly appears to prevail in this system across most spatial scales, dispersal limitation also becomes important at large scales. The limited support for the predictions of dispersal assembly is especially striking given the low dispersal potential and apparent ecological equivalence of these snail species. We conclude that simultaneously testing predictions from dispersal and niche theories across several spatial scales is necessary for robust inferences about mechanisms of community assembly, and these approaches can also enrich understanding of each species' ecology. Although results from a wide variety of taxa and ecosystem types have failed to identify any universal rules, our study and many others indicate that the balance between dispersal- and niche-based structuring of ecological communities is scale dependent.

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### Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Site locations.

**Table S2.** Species abundance by site.

**Table S3.** Average values for environmental variables by site.

**Table S4.** Results of spatial correlations with snail community differences at local scales.

**Table S5.** Loadings on the first two axes from the CCA of 2007 survey data.

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