

An evaluation of niche and neutral theories using the gastropod community distribution in Lake Tanganyika

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Introduction

Among ecologists, niche theory is the traditional frontrunner explanation of biodiversity and biogeography. This view supports the perspective that species distributions follow ‘niches’, which are representative of the environmental requirements needed by the species (Molles 2002). With this perspective, the community composition of a site is determined by its environmental conditions. However, because niche theory assumes there can be a better or worse fit of species to their habitat, individuals in different species at that site have a fitness that is influenced by the species-habitat match. In the presence of these fitness discrepancies, strong stabilizing mechanisms are needed in order to account for biodiversity (Adler et al. 2007). According to niche theory, similar environmental conditions predict similar communities.

However, Hubbell’s (2001) Unified Neutral Theory (UNT) challenges the niche portrayal of biogeography. In this model, communities harbor a fixed number of species with “ecologically equivalent” individuals (Hubbell 2001). Neutrality comes into play because all individuals, independent of species membership, are assumed to be equivalent in their chances of reproduction and death (Chave 2004). In contrast to niche theory, the neutral perspective explains biodiversity with the combination of the identical fitness of individuals and weak stabilization forces (Alder et al. 2007). Thus, species similarities, rather than differences, drive high diversities within communities (Bell 2000; Hubbell 2001). The neutral perspective allows for extinction rates to be balanced with speciation in order to account for the diversity of species (Adler et al. 2007). The only factors affecting population dynamics are demographic stochasticity (environmental stochasticity is ignored) and migration, leaving community similarity to be negatively associated with the spatial distance between sites (Adler et al. 2007; Thompson and Townsend 2006). In effect, spatial separation between sites completely trumps environmental variables as a determinant of community composition.

Tests of neutral theory are possible by comparing the fit of community composition to environmental conditions against the fit of community composition to distance between sampled sites. However, this method is only valid when spatial separation and environmental condition are not associated with each other (Thompson & Townsend 2006). Lake Tanganyika is an ideal system to test the neutral theory due to the patchiness of littoral habitats. The littoral zone is also where most biodiversity within the lake is concentrated (Coulter 1991). The shoreline provides environmental heterogeneity with a minimum of actual spatial separation, preventing the overlap of community composition predictions between niche and neutral theory (Meyer 2004).

Even though they are opposing theories, the niche and neutral theories are not mutually exclusive (Chave 2004; Adler et al. 2007). Both processes are likely acting together in nature, possibly on different spatial scales. To accommodate this, we are testing both regional (entirety of sampled sites) and local scales. In this study, we predict that both neutral and niche processes are present in the gastropod communities in the Kigoma region of Lake Tanganyika, with niche theory being the dominant process, as seen by Meyer (2004).

Materials and Methods

Study Sites

We sampled 20 sites in the Kigoma Bay Region of Lake Tanganyika, Tanzania between July 13- 30, 2007. Using Kigoma Bay as a midpoint, we surveyed sites, along 25 km of shoreline, with 9 sites north of the bay, 10 sites south of the bay, and one site inside the bay. We chose 10 of the sites due to previous sampling by Meyer (2004) and Huntington (2004). The 10 remaining sites were selected by choosing intermediate locations between initial sites, and we extended our sample area to the north by 5 km. A hand-held, Garmin Etrex Global Positioning System was used to record latitude and longitude for each site (Table 1). All sites were sampled

using SCUBA at a 5-meter depth. For our study, all sites sampled consisted of rocky substrate, which for our purposes included areas of pebbles, cobbles, boulders, or any combination of the above. Large areas of sandy substrate were avoided, and when sample areas contained patches of sand, rocky areas were chosen to sample whenever possible to keep samples consistent.

At each site, 9 quadrats, placed 2 meters apart, were sampled along a 25 meter transect. Each quadrat was constructed of rope, using sandbags for weight, and measured 1m². To quantify data for gastropod abundance, we collected every gastropod visible on the substrate surface inside of each quadrat. No rocks were overturned and no gastropods were collected that were not visible from above. All gastropods were returned to the lab where they were scrubbed clean of algal materials for species identification. Each snail was measured for height and width. If more than 30 snails of a species were collected from one site, we selected 30 snails of that species at random for measurement.

Measurement of Environmental Variables

We chose 7 environmental variables to be measured at each site. Four variables that change slowly over geological time included: aspect, slope, grain-size, and rugosity. The three remaining variables are likely to show more fluctuation over a short-time range and could therefore influence gastropod communities annually, or seasonally. These included: chlorophyll a, wave energy, and sediment.

Aspect was determined by taking a bearing perpendicular to the shoreline from the sites using a map of the Kigoma region (1978, Series Y742, Sheet 92/3, Edition 1-TSD). We used bathymetric surveys of the Kigoma region (Wheeler 2004, Smith 2005) and measured depth/distance from shoreline to give an estimate of slope. For assessment of substrate grain size, digital photographs were taken of three quadrats at each sample size. We created a sixteen-point intercept grid, which was placed over each photo and substrate type was recorded at each intersection. Four grain-size classes were used, following a modified Wentworth Scale (Table 2), which classifies sand, gravel, cobble, or boulder as relative grain-size (Lane et al. 1947). Relative grain-sizes were recorded at each intersection and averaged. These three quadrat results were then averaged to provide a site estimation of grain-size. To measure levels of substrate homogeneity at each site, a metal chain was laid flush with the substrate contours along a 5-meter rope, which was held taut in a straight line above the substrate level. The chain length was measured and divided by rope length to give a measure of rugosity.

We used chlorophyll *a* measurements to give an estimate of benthic algal productivity. Four rocks, measuring 10 -25 cm maximum diameter were collected from each site. Rocks were chosen at a 5-meter depth by snorkeling. Before each rock was removed from the surrounding substrate, a plastic cap with an area of 15.19 cm was placed over a flat portion of the rock and held in place with rubber bands for transport to the surface. On removal from the water, all areas surrounding the cap were scrubbed clean of sediment and algal material using a toothbrush, and the materials collected were preserved in a Whirl-Pak for future carbon:nitrogen testing. Once the rock surrounding the cap was clean, the plastic cap was removed and sediment was rinsed into a separate Whirl-Pak using a squirt bottle filled with lake water. The algal materials under the cap were also removed using a toothbrush, and placed in the sample bag along with sediment. Samples were kept cool and in shade until processed. At the lab, each sample was placed in a graduated cylinder where it was agitated to uniformly mix sediment and algae. At this point, the sample was divided, and each part was strained separately through a 47mm, Fisherbrand TLLP filter. Samples for chlorophyll *a* analysis were placed in 10ml of 95% ETOH and placed in a freezer for a 24-hour period, at which point the filter was removed and the resulting materials were run on a centrifuge for 15 minutes. A Genesys 20, Thermospectronic spectrophotometer was used to determine wavelengths at 665 nanometers. The sample was then acidified with 0.1ml HCL and ran at 664 nanometers.

To quantify sediment amounts at each site, the unused materials separated from samples in the previous step, were strained through pre-weighed filters and allowed to dry in a Raven drying oven at 60° C for a 24-hour period. Organic materials were removed by combustion of the filter for 2 hours at a temperature of 500° C in a Neycraft Combustion Oven. Filters were then reweighed to determine total inorganic sediments.

To measure wave action, we placed 5 clod cards (Doty 1971) at each site. Clod cards were placed at a depth of 5-meters, and spaced at 2-meter intervals. The cards were made by mixing 400 grams plaster with 270 ml of water, which was then molded in flexible plastic ice-cube trays, and allowed to set for 30 minutes. The cards

were then removed from the trays and allowed to air-dry for four days, at which time each card was weighed and placed onto the underside of a plastic petri dish using silicon sealant. Cards were weighed on the dish, and length and width were measured. At the sample sites, each dish was attached to a rock for added weight and stability. After a 24-hour period, cards were collected and allowed to air-dry for four days before taking final measurements of mass lost and dimensions.

Statistical Analysis

Species abundance data for all sites were summarized into a matrix of Bray-Curtis similarities, representing community similarities. A matrix of Euclidean dissimilarities for the environmental variables was calculated to describe environmental conditions. A distance matrix was created to provide information on spatial separation between sites using GPS points and the shoreline map.

Our distance and environmental matrix were shown to have no correlation of Euclidean distance, as per both statistical prudence and neutral theory as a whole. Mantel tests were used to test correlations between our Bray-Curtis community similarity matrix against both the environmental matrix of Euclidean dissimilarities and the matrix of spatial separation. Both regional (all 20 sites included) and local (segregated by north and south sites) scales were tested with Mantel.

Results

During identification, 11 species of snails were found with the majority (7 species) being in the genus *Lavigeria*. Our Bray-Curtis community similarity matrix and Euclidean environmental matrix were shown to be uncorrelated at both a regional ($r=-.048$) and local scale ($r=.244$, for northern sites and $r=.050$, for southern sites). The community similarity matrix was also uncorrelated to spatial separation at a regional ($r=-.019$). However, a strong correlation was found between spatial separation and community similarity at a local scale ($r=-.408$, for northern sites and $r=-.465$, for southern sites).

Discussion

The lack of a significant correlation between our environmental and community similarity matrices at both scales provides no evidence in favor of niche theory. The correlation between spatial separation and community similarity at the local scale provides strong evidence in favor of neutral processes. This shows that in our sampled areas, neutral processes are dominant over environmentally-determined processes.

Figures 1 and 2 show the spatial clumping of species along both the north and south shorelines. From our species abundance data, a smooth transition between distributions of species on a very local scale can be seen. However at a more coarse scale, as observed by Michel (2003), these distributions appear patchy. This clumping resulting in species patchiness is likely due to the limitation of the dispersal ability of *Lavigeria* (Michel et al. 2003). Our data suggests that Kigoma Bay (the indicator point for north and south sites) may be a historical migration barrier, accounting for the lack of correlation between community similarity and spatial separation at a regional scale.

Even though some of these species are known to have environmental preferences (Huntington 2004; Barrett et al. 2003), their distributions do not reflect them. Niche processes depend on species benefiting from their local adaptations in suitable locales, but this benefit does not exist if they cannot reach suitable locales (Fuentes 2002). More localized dispersal will cause more species to experience random abundance and benefit less from location-specific environmental conditions, leaving processes to become more neutral (Fuentes 2002).

The findings of this study are particularly interesting due to the recent suggestion that neutral theory may only be legitimate at over large geographic areas with great degrees of spatial separation (Alonso and McKane 2004). Perhaps this can open up potential projects that examine the processes of both neutral and niche theory at an even finer scale.

Some caveats on this study include the decision to use shoreline distance, which may not be a good determinate of migration rate; however, we did show a strong spatial correlation. The environmental variables that we collected may not be the best suited for this testing model. That being said, previous studies on this genus have

reported some of the values of the variables as being preferred over others (Huntington 2004; Barrett et al. 2003). Yet some biotic environmental variables that are difficult to quantify, such as predation, and seem important for gastropod environmental preferences (Bisbee and Holzer, this volume) unfortunately remain unquantified. The possibility exists that the environmental variables that we collected were not quantified correctly, but there is low variation in replicate samples and our variables correlate with past studies, making this unlikely.

Conclusions and Suggestions for Further Research

After analysis, our data was strongly neutral with environmental variables having little effect on the community composition of *Lavigeria* species. Within our sampled areas, sites spatially closer maintain a more similar community composition than sites with similar environmental conditions. Hubbell wins this round.

As for further research, we feel that Kigoma Bay may be acting as a historical migration barrier, which would explain why community similarity correlate with spatial separation on a local scale, but not when the entire shoreline is considered. Knowing more about the dispersal ability and methods of the gastropods in Lake Tanganyika would help complete the case for neutral theory in these communities. Furthermore, another aspect that would benefit a study of this type would be the addition of predation effects on the local scale among these endemic gastropods.

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Table 1. Sampled site number, name and GPS coordinates.

| Site | Name | Latitude | Longitude |
|------|-------------------|-------------|--------------|
| 1 | Kogongo North | S 04.48.132 | E 029.35.964 |
| 2 | Kogongo Inner | S 04.48.615 | E 029.36.478 |
| 3 | Kogongo South | S 04.49.528 | E 029.36.275 |
| 4 | Kalalongabo North | S 04.49.916 | E 029.36.296 |
| 5 | Kalalongabo Inner | S 04.50.628 | E 029.36.513 |
| 6 | Kalalongabo South | S 04.50.639 | E 029.36.429 |
| 7 | Euphorbia | S 04.50.900 | E 029.36.497 |
| 8 | Euphorbia South | S 04.51.303 | E 029.36.547 |
| 9 | Nondwa | S 04.51.772 | E 029.36.499 |
| 10 | Luansa | S 04.52.538 | E 029.37.195 |
| 11 | Hilltop North | S 04.53.212 | E 029.36.803 |
| 12 | Hilltop South | S 04.53.426 | E 029.36.718 |
| 13 | Katabe Inner | S 04.54.053 | E 029.36.117 |
| 14 | Katabe South | S 04.53.882 | E 029.35.725 |
| 15 | Bangwe | S 04.54.177 | E 029.35.670 |
| 16 | Jakobsen North | S 04.54.517 | E 029.35.794 |
| 17 | Jakobsen Centre | S 04.54.641 | E 029.35.885 |
| 18 | Jakobsen South | S 04.54.724 | E 029.35.890 |
| 19 | Jakobsen Outer | S 04.54.986 | E 029.35.751 |
| 20 | Mzungu | S 04.55.050 | E 029.35.829 |

Table 2. Grain size for sediment categories.

| Substrate Type | Grain Size |
|----------------|---------------|
| Fine Sediments | .00025-.062mm |
| Sand | .062-2mm |
| Pebbles | 2-64mm |
| Cobble | 64-256mm |
| Boulder | 256-4096mm |

Figure 1. Species abundance by site, showing smooth trends between sites. Northern sites.

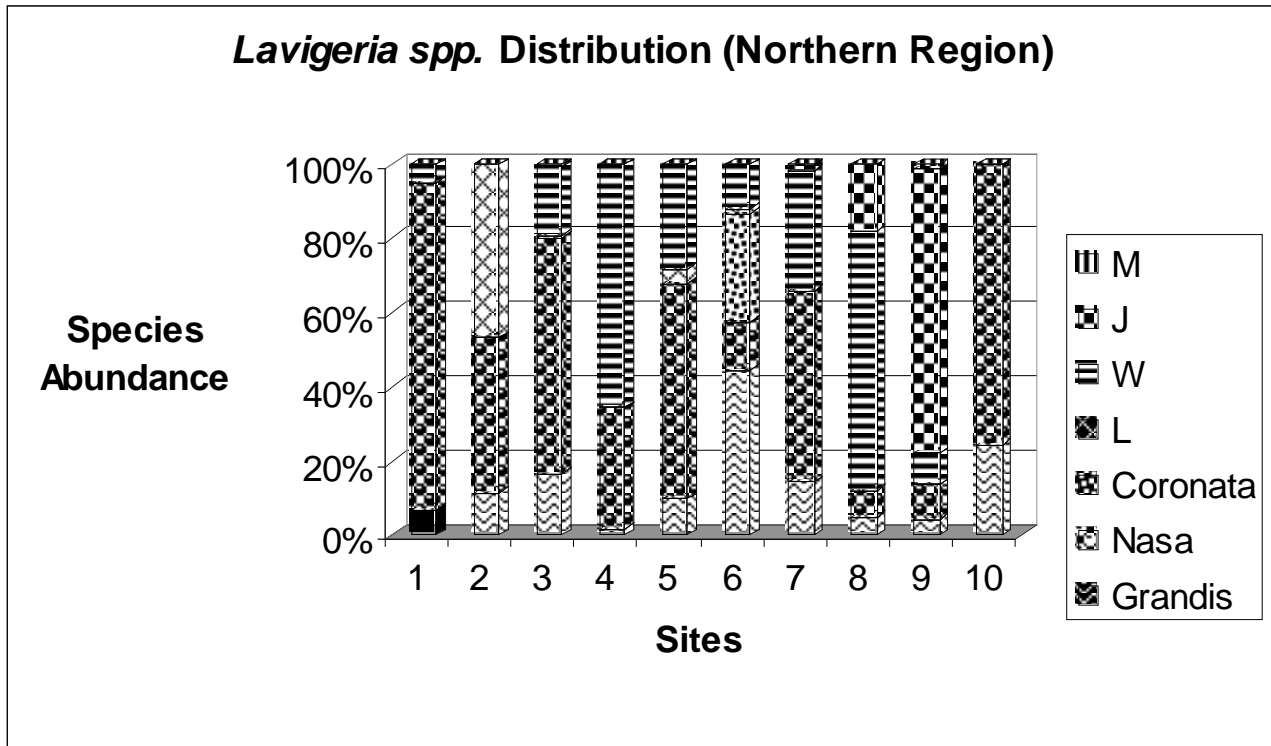


Figure 2. Species abundance by site, showing smooth trends between sites. Southern sites.

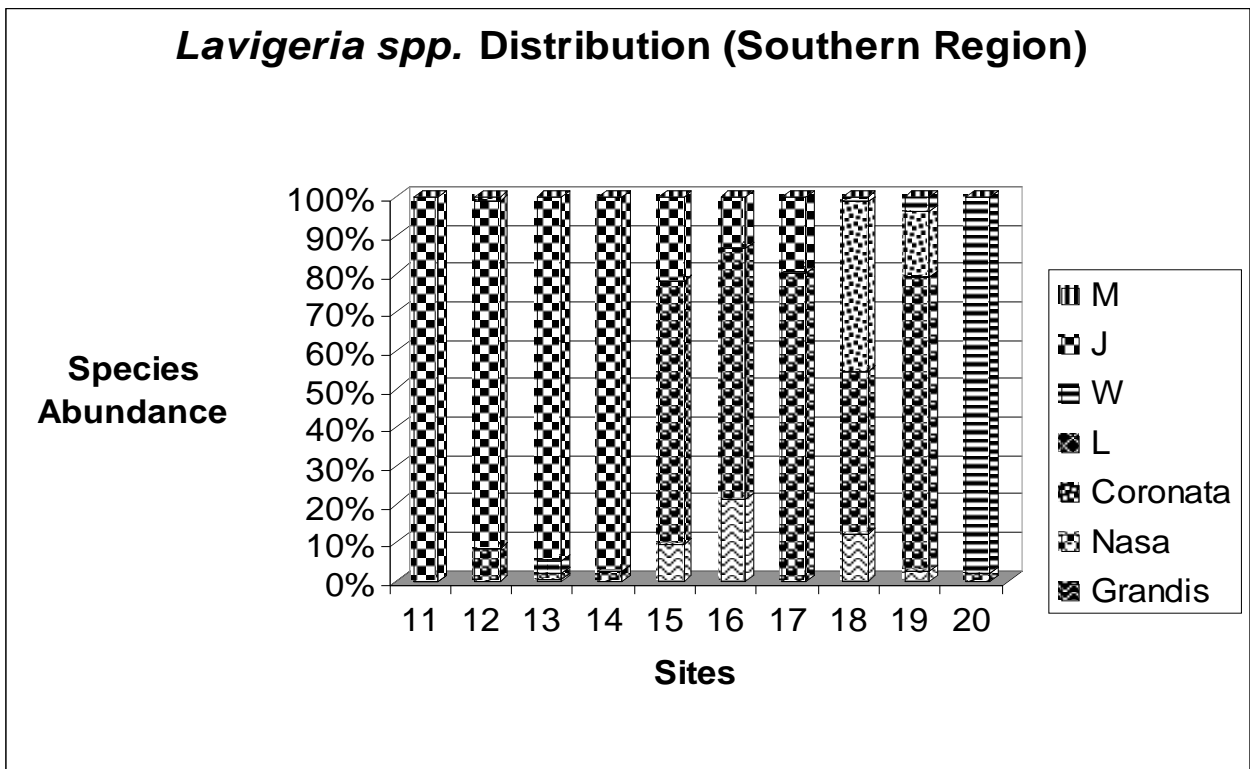
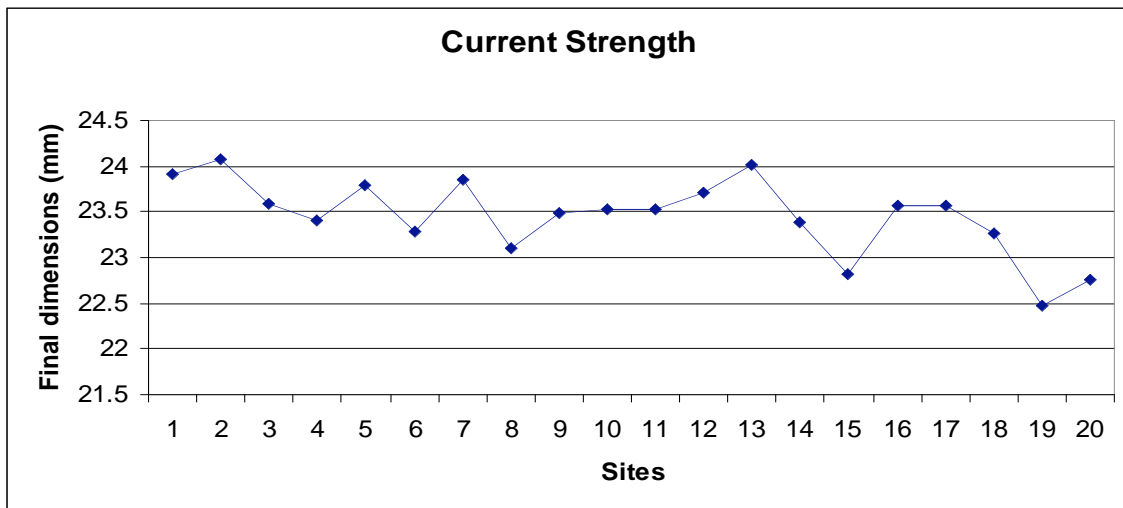
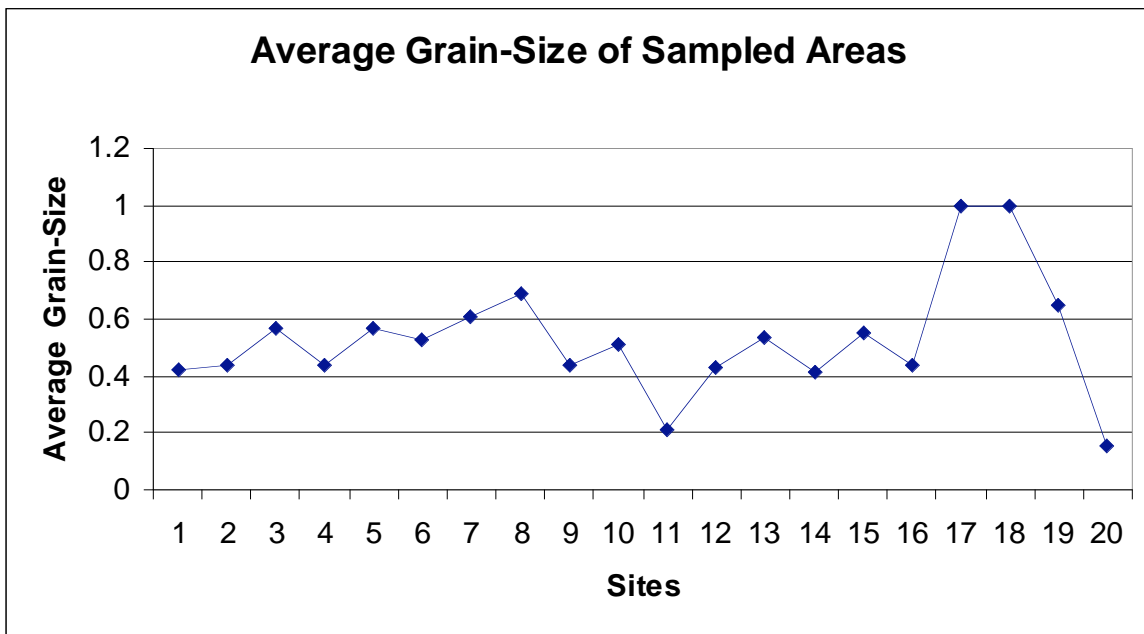
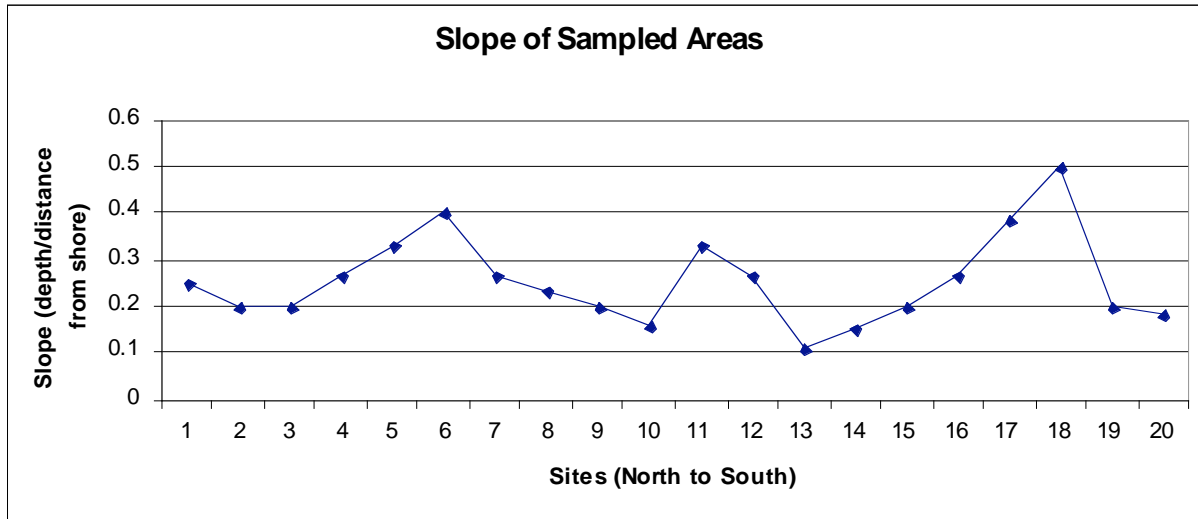
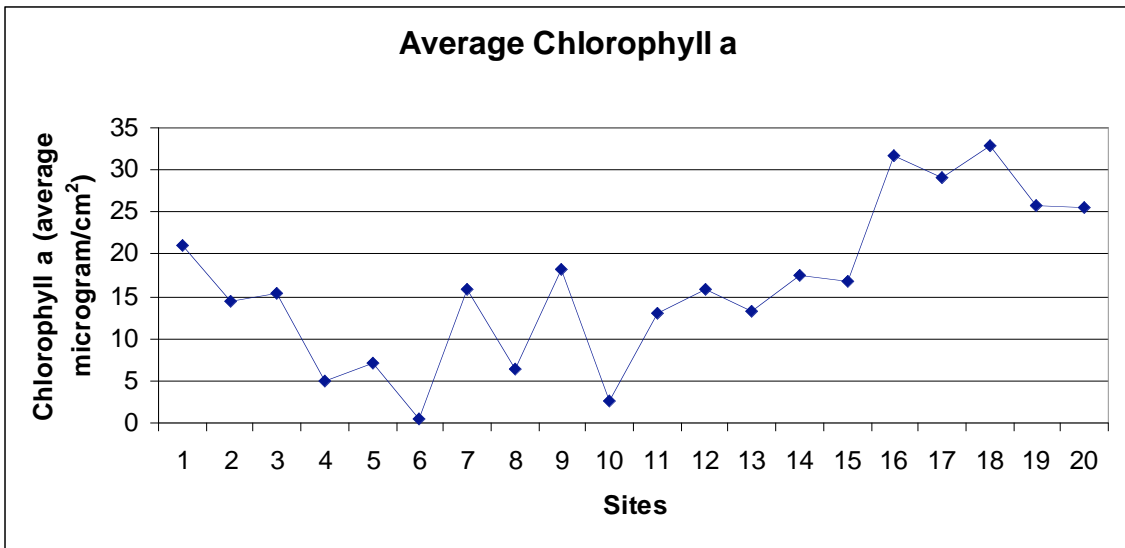
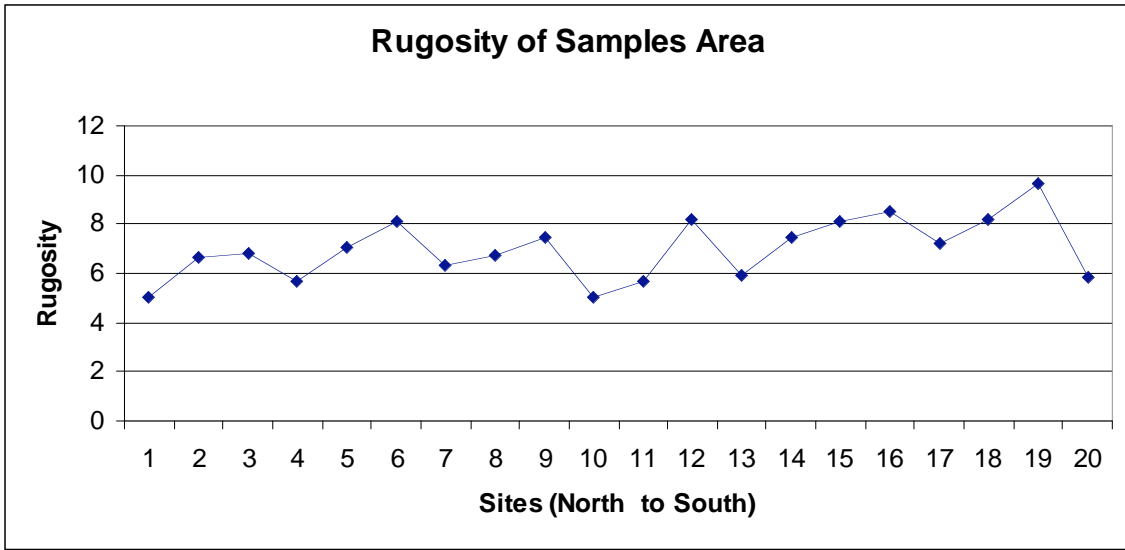
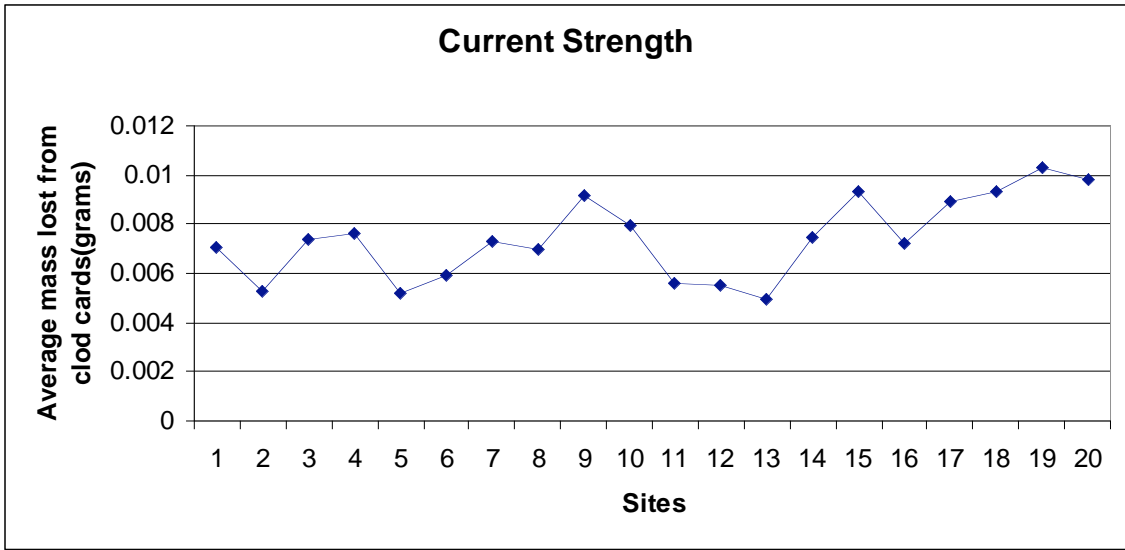
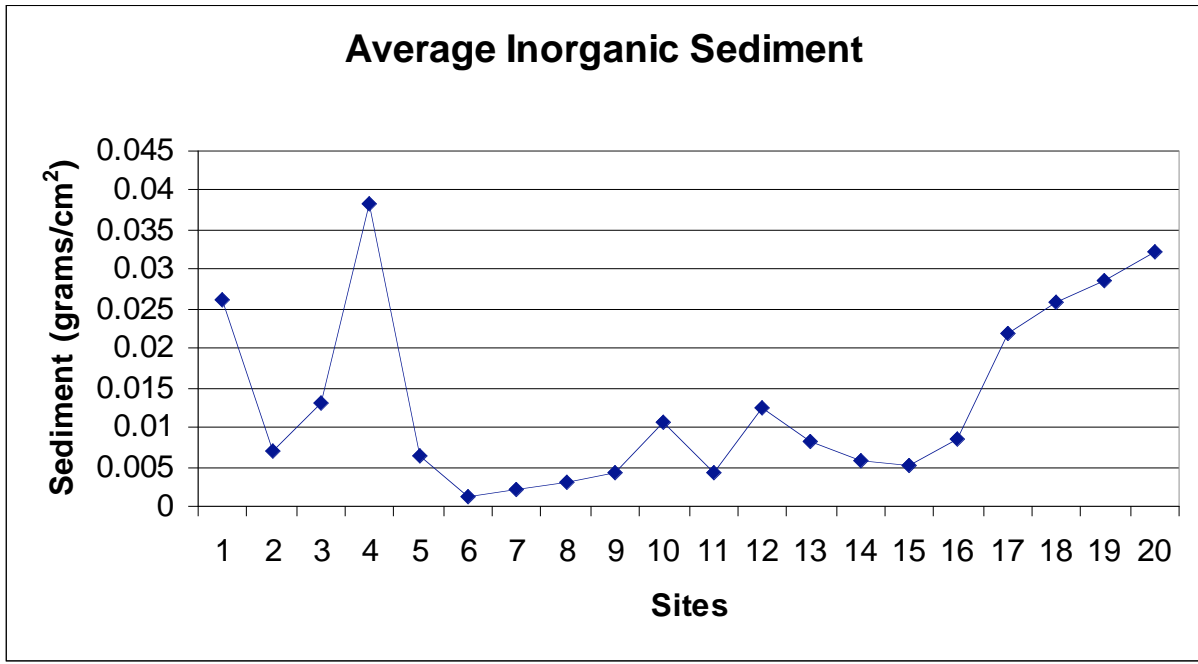


Figure 3. Environmental Variables between Sites







| Site | Name | Aspect |
|------|-------------------|--------|
| 1 | Kogongo North | 253 |
| 2 | Kogongo Inner | 273 |
| 3 | Kogongo South | 295 |
| 4 | Kalalongabo North | 268 |
| 5 | Kalalongabo Inner | 350 |
| 6 | Kalalongabo South | 290 |
| 7 | Euphorbia | 284 |
| 8 | Euphorbia South | 295 |
| 9 | Nondwa | 239 |
| 10 | Luansa | 283 |
| 11 | Hilltop North | 283 |
| 12 | Hilltop South | 311 |
| 13 | Katabe Inner | 83 |
| 14 | Katabe South | 331 |
| 15 | Bangwe | 307 |
| 16 | Jakobsen North | 300 |
| 17 | Jakobsen Centre | 300 |
| 18 | Jakobsen South | 344 |
| 19 | Jakobsen Outer | 223 |
| 20 | Mzungu | 237 |