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Ella Arms March 17, 2023

Analysis of the community composition and interactions of invertebrate predators within schistosome-infected temporary and permanent waterbodies in Tanzania

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An abstract of
a thesis submitted to the Faculty of Emory College of Arts and Sciences
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Abstract

Analysis of the community composition and interactions of invertebrate predators within schistosome-infected temporary and permanent waterbodies in Tanzania

By Ella Arms

Community context is an important factor in understanding the ecology of infectious diseases. Hosts and parasites do not exist in isolation, and their interactions can be influenced by the other species in the communities where they reside.

Biocontrol of human parasites, such as schistosomes, has been attempted using predators/competitors of either wildlife reservoir hosts or disease vectors with variable success. Frequently, these attempts have introduced new species into disease transmission sites, rather than using species normally found at these locations. Current thinking in ecology is that disrupting an environment by introducing non-native species can have unintended, and potentially seriously negative, consequences. Therefore, we sought to evaluate potential predators that naturally co-occur with the snails that are schistosome hosts and if snail size/infection status affected their predation. We conducted a field survey around Mwanza, Tanzania, focusing on the parasite *Schistosoma haematobium*, its freshwater snail host *Bulinus nasutus*, and the broader macroinvertebrate communities in waterbodies identified by rural communities as potential transmission sites. We found that two distinct macroinvertebrate communities varied over space and time, one dominated by dragonflies, damselflies, water bugs, and diving beetles, and the other dominated by crabs and backswimmers. Whether the waterbodies dried in the previous year explained a significant amount of variation in abundance for several taxa. We then found that snails were significantly larger and more likely to be infected in communities dominated by the invertebrate backswimmer insect *Notonectidae* and water boatman insect *Corixidae*; two unconfirmed predators of snails. These patterns suggest

natural macroinvertebrate predators could influence schistosome transmission, and a deeper understanding of the factors that influence their abundance and their resulting effects on transmission potential could improve predictions and interventions for schistosomiasis in this region.

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1 Introduction

The interactions between hosts and parasites are not isolated but rather profoundly intertwined in the ecological communities in which they coexist. Therefore, interactions with other species, such as predators and competitors, can potentially affect disease dynamics. For example, *Borrelia burgdorferi,* the bacterium that causes Lyme disease, is vectored by ticks within a complex community of competing hosts, like deer and squirrels, and predators of those species that can alter the abundance of these host populations[1]. There are several well-described mechanisms by which predators exert significant effects on parasite transmission in populations of their prey. Predators kill and consume hosts. Therefore, they can act as "culling agents," mimicking a management intervention often used to stop epidemics[2]. This process is incorporated in the "Healthy Herds" hypothesis, which suggests that predators can reduce disease in a prey species by (1) suppressing the density of the prey species as they target healthy or infected organisms and (2) shortening the average infectious period by consuming individual infected prey. Both effects should reduce transmission potential or disease prevalence in a population. Given the potential of predators to suppress disease transmission, researchers have begun investigating the prospect of biocontrol against parasites, especially those that harm humans, livestock, and species of conservation concern.

Here we investigate the relationship between predator abundance and biodiversity and the transmission potential of human schistosomes, flatworm parasites that cause schistosomiasis, a disease with a significant human health burden. Schistosomiasis is a Neglected Tropical disease that affects over 200 million people worldwide and can manifest, depending on the number of worms infecting a person, as flu-like acute disease or chronic inflammatory and obstructive disease[3]. The life cycle of a schistosome begins through contamination of waterbodies with human excretion that contain schistosome eggs[4]. The eggs hatch into the miracidia that infect snail hosts and subsequently develop into sporocysts. Sporocysts grow into the cercariae that emerge from snails and swim within waterbodies searching for mammalian hosts. Humans become infected via dermal contact. Once inside, the cercariae travel through the bloodstream near the lungs and liver where they develop into mature worms who eventually produce thousands of eggs per day. These eggs either become granulomas within organs, causing inflammation, or pass through the feces or urine, beginning the cycle once more[4]. Schistosomes must infect specific genera of intermediate host snails, which themselves are commonly consumed by vertebrate and invertebrate predators[5–7]. Therefore, schistosome transmission could be powerfully affected by predators in aquatic habitats.

While there is much interest in predatory biocontrol of snails and schistosomiasis, no biocontrol programs have proven successful to date. However, substantial schistosomiasis control has been achieved in the past through molluscicide application to kill snails in freshwater sites, mass drug administration to reduce infection loads in people, and modifications to freshwater habitats or behaviors to reduce human exposure to parasites[8]. Each approach has benefits and weaknesses, suggesting that a multipronged approach will be needed to eliminate or eradicate human schistosomes. Habitat modification, like lining of ponds and canals with concrete, is expensive and has limited applicability[8]. Annual or biennial mass drug treatment of humans with praziquantel, and at times paired with the application of molluscicide, has been shown to control morbidity but often fails to reduce local transmission rates[9]. Mass-scale praziquantel distribution is also unlikely to be a viable and permanent solution due to cost and high reinfection rates[9]. Molluscicides like niclosamide have also been used in endemic regions to kill snails to help reduce human infection rates. The World Health Organization has recommended niclosamide since the 1960s[10], and it has been used throughout the world. However, it is not permanently effective, as snails are observed to recolonize habitats after each application. Moreover, although niclosamide is thought to be minimally toxic to non-target species, scientists are still unsure of the long-lasting environmental effects of the continuous chemical application needed to eradicate schistosomes[11]. For example, niclosamide has been found to harm carp and tilapia, essential dietary protein sources, after its application to rice paddies in the Philippines[10]. Given the strengths and weaknesses of existing programs, understanding the relationships among predators, snails, and schistosomes could improve risk predictions while identifying a potential non-chemical method to stop schistosome transmissions that could be combined with these other imperfect, yet invaluable, interventions.

To date, biocontrol programs have focused on individual predators, with the aim to find a highly selective predator of snails that does not otherwise harm biodiversity or ecosystem function. Early attempts capitalized on the inadvertent introduction of the Louisiana red swamp crayfish to schistosome endemic regions. However, these programs found highly variable success and large environmental catastrophes[5]. Specifically, the crayfish was found to be an extreme generalist and harshly reduced the biodiversity in Eastern Africa after its application in predatory biocontrol[12]. Later focus shifted to regionally native species, such as African cichlids, which demonstrated high rates of snail consumption in laboratory settings[6]. However, this predator proved to be an extreme generalist in field sites, preferring other food sources over the hard-shelled snails[8]. Most recently, focus has shifted yet again to African river prawns, which voraciously consume snails in the laboratory and are native to many estuarine river systems[13]. However, these prawns cannot tolerate the poor water quality characteristic of schistosome transmission sites and either disperse (if uncontained) or die, thus failing to achieve control[14].

We aim to take a fundamentally different approach to the idea of predation control by observing the native communities of macroinvertebrates that are naturally present in community-identified schistosome transmission sites, with the ultimate goal of investigating if we can manipulate these communities and their interactions. Specifically, I explore whether snail predator abundance, size, and/or diversity correlate with host snail abundance, body size, infection prevalence, and/or production rate of schistosome cercariae across waterbodies in an endemic transmission setting. We paired this observational study with experimental predation trials to document the ability of abundant predators to consume snails of different sizes. Assessing the predation rate and size preferences of predators is essential to determine if they are likely to enhance or inhibit schistosome transmission by snail populations[15]. We hypothesize that these predator communities alter disease dynamics of schistosomes through their control over the abundance and traits of the host snail species. There is very little known about the native predators of snails, especially within these temporary waterbodies that permit the transmission of *S. haematobium* by *Bulinus*. Therefore, my study will contribute critical information to evaluate how native biodiversity affects schistome transmission. Identifying patterns between predators, snails, and schistosomes could aid in a better understanding of schistosome disease dynamics and facilitate insight into how predators affect these dynamics.

2 Methods

2.1 *Field study*

We collected data on snail and other macroinvertebrates abundance in 64 waterbodies that had been identified as putative transmission sites by community leaders of 14 villages in the Mwanza region of northwestern Tanzania. Schistosomes are considered hyperendemic in this region, and we focused on *Schistosoma haematobium*, which is transmitted by *Bulinus nasutus* snails in small, often temporary waterbodies. These waterbodies have been created or intentionally enlarged to collect rainwater for domestic and agricultural uses. We sampled snails and predators using the "time-constrained net sampling" approach that is an established method in schistosome research, which can generate relative but not absolute abundance data on macroinvertebrate communities[16]. We searched for snails and potential predators for fifteen-minute time periods, in which team members used nets, tweezers, and falcon tubes to collect organisms. Two researchers collected snails and invertebrate predators, while another two collected only snails. If the snail count surpassed one hundred, the collection period was abbreviated. We recorded the maximal length, width, and depth of each waterbody. If the waterbody was too deep in the center, sampling was restricted to the edge, which is the most relevant snail habitat. The majority of invertebrate predators collected were stored in falcon tubes containing 95% ethanol in order to kill and preserve the organisms. Live pictures were taken in the field of predators too large for the falcon tubes. The falcon tube or an expo marker was used as a size scale in most pictures taken. If a scaling object was missing, the dimensions of the container within the image was used as a scale instead. Larger macroinvertebrates were also brought back to conduct feeding trials in order to determine the predation status of each species.

2.2 *Laboratory processing and trials*

Two members of the team spread the preserved invertebrates out on a pre-measured, laminated grid sheet and took photos. The snails collected that day were also brought back to the lab to test for infection status by placing them into 30-mL glass beakers with 25-mL of clean bottled water for 24 hours to allow any mature parasites to emerge. If parasites emerged from a snail, they were morphologically distinguished as schistosomes or non-schistosomes. The vast majority were identified as virgulate cercaria in the genus *Xiphidioc*

ercaria. Large predators for feeding trials were held in tanks overnight before beginning trials the following day to ensure they would survive. If the macroinvertebrates survived overnight, they were given five snails of varying size, photographed as above on the pre-measured grid sheet. Predators were offered snails across the gradient of snail body size. Snails that were not consumed were photographed on the grid sheet before adding new ones. The number of consumed snails, the date, and the organism type were labeled with expo markers on the grid sheet as well.

2.3 *Digital data collection*

Invertebrates collected from waterbodies were measured and counted using Fiji, an open-source digital image processing package that is based on ImageJ2[17]. Each image was scaled based on a pre-measured grid sheet or pre-measured object, which was captured in the picture. Measuring dimensions were normalized per taxon based on the most consistent and longest measure on the organism's body. Macroinvertebrates were taxonomically identified based on the "Aquatic Invertebrates of South African Rivers Field Guide"[18]. All fifteen taxonomic identifications can be visualized in Table 1. *Ranatra* and *Laccotrephes* were measured by the length of their body without their tails. *Aeshnidae*, *Libellulidae*, *Belostomatidae*, *Dytiscidae* (beetle and larval form), *Hirudinea*, *Naucoridae*, *Coleoptera*, *Notonectidae*, *Gerridae*, *Ecnomidae*, and *Corixidae* were measured by the length of their whole bodies. *Hirudinea*, *Gerridae* and *Ecnomidae* were measured with segmented line measurements due to the non-linear body shapes. *Zygoptera* were measured by the length of their heads, as bodies were sometimes missing. *Potamonautidae* were measured by the shorter length of their shell, from the eyes to the posterior.

2.4 *Multivariate analysis of community composition*

Our analysis had three major goals: (1) characterizing the potential macroinvertebrate predators of *Bulinus*, (2) to understand if relative abundances of macroinvertebrates was affected by time or waterbody drying, and, (3) investigating whether predator communities associated with important snail outcomes like schistosome shedding rates, infection probabilities, or snail sizes. To address the first goal, we fit an unconstrained ordination to visualize the covariation among the species. Unconstrained ordinations, by definition, use no predictors and describe variation in communities, but do not seek to explain it. They result in estimated values of “latent variables” that serve to reduce the dimensionality of biodiversity data sets. Here, we analyzed 15 taxa, i.e., fifteen dimensions, which we sought to reduce to 1-3 dimensions of correlated changes in taxonomic composition. We addressed our second goal by using full-rank regression, to determine how the relative abundance of each taxon changed with time and in waterbodies that do or do not dry. Finally, I addressed the third question by using generalized linear mixed models to determine if snail size and infection rates were correlated with community composition, using each site visit's latent variable scores as predictors representing community composition in this analysis.

The numerical data for each invertebrate taxon from each site visit was organized and analyzed with Tidyverse and stringdist software R packages[19,20]. Taxa that appeared in less than five sites were removed from the analysis as they do not provide reliable information for analyses. These were: "Baetidae", "Gerridae", "Hydropsychidae", "Syrphidae", and "Unknown". There was a labeling error, and we are nearly certain that one picture labeled as "Lambo la Nzengo Matunge" is actually from another body, "Kisima cha Nzengo Matunge." Therefore, we are assigning it to the latter site. We plotted the raw counts of invertebrates over the sampling period, grouping them by waterbody and taxonomic group (Fig 1).

The R package gllvm was used to analyze variation in community composition using generalized linear latent variable models with the negative binomial error distribution appropriate for count data[21]. First, we conducted an unconstrained ordination to describe variation in community composition among the samples (Fig 2). Unconstrained ordination uses latent variables to describe covariation among the species in our samples, but it uses no predictor variables; therefore, it describes but is not intended to explain, variation in community composition. Due to the nature of time-constrained net sampling, our observed counts can be appropriately interpreted as representing relative abundance rather than absolute abundance. Therefore, we incorporated a sample-level random intercept to account for this. We investigated whether the underlying correlation structure of the samples, i.e., how species co-vary in relative abundance across site visits, could be explained using 1-3 latent variables. Latent variables are a dimension-reduction tool that intend to summarize how multiple species covary across site visits with few variables, thereby containing information on cross-species correlations. Two latent variables were used based on observing maximal AIC scores fitting models with 1-3 latent variables. We then visualized correlations among species across the sites using the software package corrplot[22] (Fig 3).

For our second question, we conducted a full-rank multivariate regression using the gllvm function in the gllvm package in order to explain how each taxon changes as a function of (1) whether the waterbody dried at some point in the previous year, and (2) the month of sampling (February, April, or June). This analysis yields parameter estimates for the effect of month and waterbody drying on the relative abundance of each taxon while accounting for the multivariate nature of the dataset. We visualized these parameter estimates with the coefplot function from the gllvm package (Fig 4a & 4b). The baseline comparison for this data is all in reference to the month of April due to alphabetical order.

2.5 *Correlating community composition with snail size and infections*

Last, we investigated relationships between community composition on snail body size (measured as shell length) as well as both infection prevalence and intensity with *Schistosoma haematobium* and all other non-schistosomes. We extracted the scores of latent variables 1 and 2 from the unconstrained ordination for each site visit using the getLV.gllvm function in the gllvm package.

We then aligned these latent variable scores with individual-level data on each snail collected from these same site visits describing snail size and shedding rates of schistosomes and non-schistosomes. We then fit several generalized linear mixed models using the glmmTMB function in the glmmTMB package[23]. In each model, we assessed the fixed effects of the predictors LV1, LV2, their interaction, and the month. Each model also contained a random intercept for the waterbody, to account for the nonindependence of observations. The first model tested for the effects of these predictors on snail length (Table 3a). The remaining models used length as another fixed covariate because we know from previous work that snail size is positively correlated with infection probability and intensity (Table 3b-e). We focused our interpretation on the significance of LV1, LV2, and their interaction, which represent community composition. We used the visreg2d function in the visreg R package[24] to create contour plots from the model outputs (Fig 5-7).

3 Results:

3.1 *Predation trials*

All macroinvertebrates that survived transport back to the laboratory in February were confirmed predators of *Bulinus*, and they are: *Belostoma, Potamonautidae, Libellulidae, Laccotrephes*, and *Dytiscidae*. Refer to Table 1 to visualize identified predators and Table 2 for predation trial outcomes.

3.2 *Dynamics of raw counts of invertebrates*

Invertebrate abundances throughout waterbodies were observed to vary in raw count data (Fig 1) and were further investigated in the full-rank ordination. We observed changes in raw counts of several taxa that we also detected in our analysis of relative abundance (Fig 4a). For example, *Potamonautidae, Aeshnidae,* and *Zygoptera*have significant relative increases in February compared to April, while *Hydrophilidae* and *Coleoptera* have a significant reduction. *Corixidae, Notonectidae, Ranatra*, and *Dytiscidae* have significant increases in relative abundances from April to June, while *Coleoptera* significantly decreases in abundance.

3.3 *Community composition*

The unconstrained ordination indicated that there were strong correlations among two groups of taxa in our sampling. Specifically, the correlation matrix (Fig 3) suggests that community samples were either composed of predominantly *Naucoridae, Aeshnidae, Libellulidae, Hydrophilidae, Ranatra,* and *Zygoptera*, or *Notonectidae, Corixidae*, *Potamonautidae*, and *Bulinus*. However, we note that the correlations among taxa in the second group were slightly weaker than those in the first group. There were generally large negative pairwise correlations when comparing across the two groups, indicating that these communities were largely distinct.

Month and waterbody drying explained significant changes in the relative abundance of several taxa. For example, *Aeshnidae*, *Potamonautidae*, and *Zygoptera* were most abundant in February, and *Corixidae*, *Notonectidae*, *Ranatra*, and *Dytiscidae* were most abundant in June (Fig 4a). Several taxa changed significantly in relative abundance between waterbodies that dried and those that did not. For example, *Potamonautidae* and *Bulinus* were more common in waterbodies that dry, while *Zygoptera*, *Ranatra*, *Naucoridae*, and *Hirudinea* were less common in waterbodies that dry (Fig 4b).

3.4 *Correlating community composition with snail size and infections*

Snail size increased significantly over the season. Compared to April, it was lower in February and higher in June (Table 3a). Additionally, snail size was associated with latent variables 1 and 2 as well as their interaction (Table 3a). Specifically, snails were the largest from samples with high values of LV1 and low values of LV2 (Fig 5). None of the tested factors were significantly associated with the number of cercariae released per snail (Table 3b). However, snails shed more non-schistosome cercariae if they were larger and in June compared to April (Table 3c). The probability of schistosome and non-schistosome infection were both related to community composition. Specifically, schistosome infection probability was significantly related to the LV1*LV2 interaction (Table 3d); the highest infection rates were seen in samples with high LV1 and low LV2 scores (Fig 6). In contrast, non-schistosome infection probability was highest in samples with high LV1 and high LV2 scores (Fig 7), also revealing a significant interaction (Table 3e).

4 Discussion

Community context is an essential factor for understanding infectious disease ecology. We found strong temporal patterns in abundance for several taxa of macroinvertebrates that are potential predators of snails and schistosomes (Fig 1; Fig 4a). For instance, *Coleoptera* was observed to reach maximum relative abundances in April, while *Potamonautidae* was observed to peak in February.

We found that community composition was partially explained by whether or not the waterbody dried within the previous year. Temporary ponds have been known to have different community compositions, inter/intraspecific competition, and predation[25]. The correlation matrix and ordination plots resulting from the unconstrained ordination revealed a block-like structure, in which samples primarily reflected one of two community types: one dominated by *Potamonautidae*, *Bulinus* snails, and *Notonectidae*, and the other dominated by odonates, diving beetles, and water bugs (Fig 3). The full rank regression then revealed that these differences were in part driven by waterbody drying (Fig 4b). We also found a correlation between community composition and snail size and probability of infection, which was consistent with the hypothesis that these putative snail predators can alter transmission potential. Snails were the largest in communities with high LV1 and low LV2, indicating the dominance of *Notonectidae* and *Corixidae* (Fig 5; Fig 2). It is possible that these swimming insects could be restricted to consuming smaller snails due to their own small size or unable to consume snails at all. Past research has determined *Corixidae* to be unable to consume snails due to its small size and limited diet[26]. *Notonectidae* have been seen to be more predatory but remain untested on their abilities to consume snails[27,28]. This could shift snail populations to become dominated by larger individuals that are less vulnerable to predation by these species.

The probability of schistosome infection was also maximized in the same bottom right corner of the LV1-LV2 contour plot (Fig 6). This may reflect that larger/older snails have more time to become exposed and, therefore, are infected with schistosomes. Positive age or size vs. prevalence relationships are extremely common across nearly all disease systems[29]. The smaller average sizes and lower infection probabilities for snails from sites dominated by other species, e.g., *Potamonautidae* (crabs), are consistent with our observation that these species voraciously consumed snails in the laboratory. If these species consume many snails in transmission sites, then they can shift the population to smaller sizes and increase the probability that any given snail dies before the ~1 month developmental period required by schistosomes[30]. Other evaluations of predation by species, such as crabs, dragonflies, diving beetles, and water bugs, should focus on their ability to consume snails across their body size ranges.

We analyzed all non-schistosomes together. While we know that there are at least five morphologically distinct taxa, the vast majority (>90%) are likely to be virgulate cercariae in the genus *Xiphidiocercaria*, which can infect wildlife and livestock[31]. Non-schistosome infection probabilities were found to maximize in the top right corner, with high measures of both latent variables, of its contour plot (Fig 7). The unconstrained ordination biplot revealed that this space is inhabited partially by *Potamonautidae* but mainly by no defined community type (Fig 2). We do not currently know enough about the dynamics of *Xiphidiocercaria* to speculate on an underlying mechanism.

We have demonstrated that there is variation in predator communities and that several species of macroinvertebrates are confirmed predators of *Bulinus* snails. To better understand how different predator communities might impact snail-schistosome dynamics across the entire disease transmission season, we plan to collect and incorporate data for snails and parasites from

January to July in the future. We are also interested in investigating how these community effects might unfold staggered in time. For instance, crabs might affect snail shedding due to their predation, but do they affect shedding in future months rather than within the period of consumption? From our short predation trials, crabs seem to act as nonselective predators in terms of snail sizes, however we did not get to test all sizes of snails. Ultimately, learning about the community dynamics of these permanent and temporary waterbodies in Mwanza can unveil vital information that relays directly to disease transmission of schistosomiasis, specifically in these endemic regions.

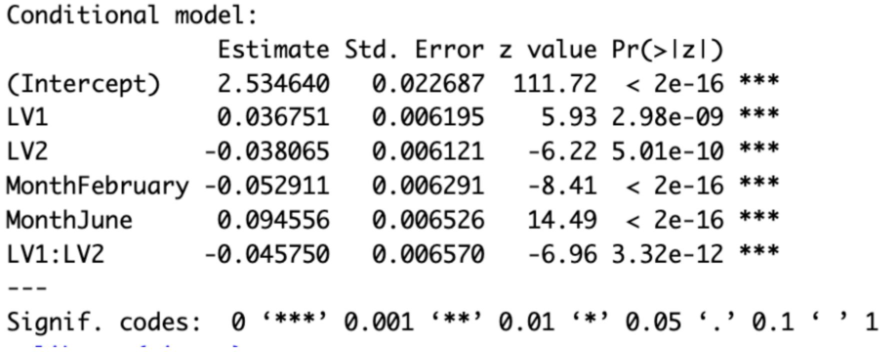
5 Tables

5.1 Table 1: Taxonomic identification table of macroinvertebrates and confirmed predators.

Taxonomic Name	**Taxonomic Level**	**Common Name**	**Photo**
Aeshnidae	Family	Dragonfly nymph	
Coleoptera	Order	Beetle	
Corixidae	Family	Water boatmen	
Ecnomidae	Family	Caseless caddisfly	
Hirudinea	Class	Leech	
Hydrophilidae	Family	Water scavenger beetle	
Naucoridae	Family	Creeping water bug	
Notonectidae	Family	Backswimmer	

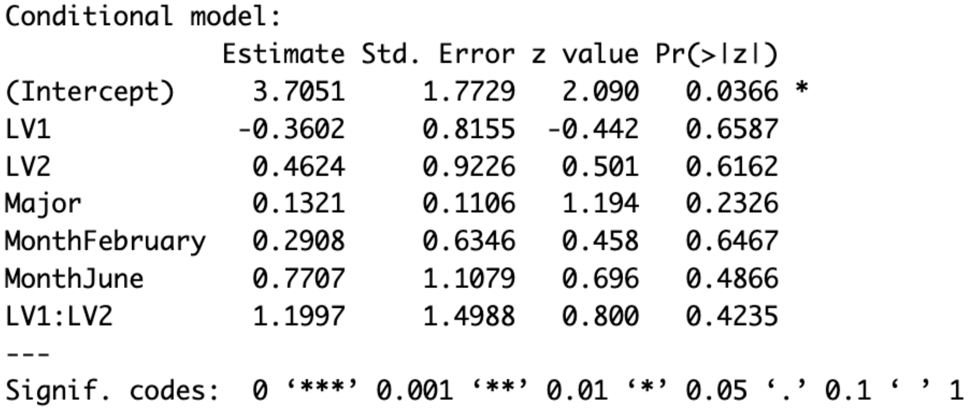
Ranatra	Genus	Water scorpion	
Zygoptera	Suborder	Damselfly larva	
CONFIRMED PREDATORS:	___________________	___________________	___________
Belostomatidae	Family	Giant water bug	
Dytiscidae	Family	Predaceous diving beetle	
Laccotrephes	Genus	Water scorpion	
Libellulidae	Family	Dragonfly larva	
Potamonautidae	Family	Freshwater crab	

5.2 Table 2a: Snail size as a function of latent variables and month.



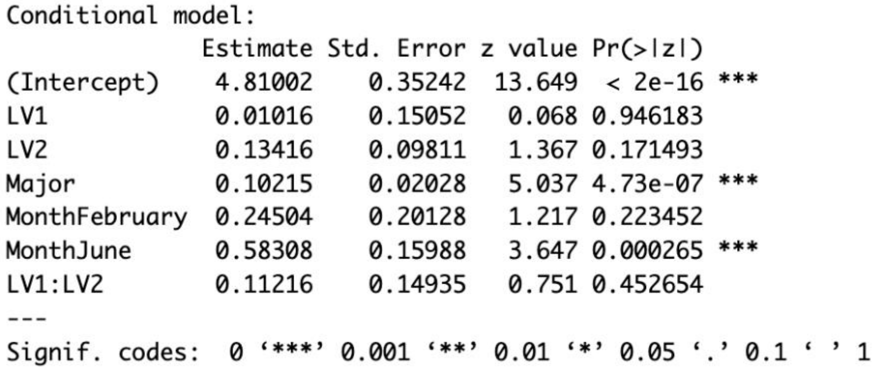
```
Conditional model:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)    2.534640   0.022687  111.72  < 2e-16 ***
LV1            0.036751   0.006195    5.93 2.98e-09 ***
LV2           -0.038065   0.006121   -6.22 5.01e-10 ***
MonthFebruary -0.052911   0.006291   -8.41  < 2e-16 ***
MonthJune      0.094556   0.006526   14.49  < 2e-16 ***
LV1:LV2       -0.045750   0.006570   -6.96 3.32e-12 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

5.3 Table 2b: Number of schistosomes shed as a function of latent variables, snail size, and month.



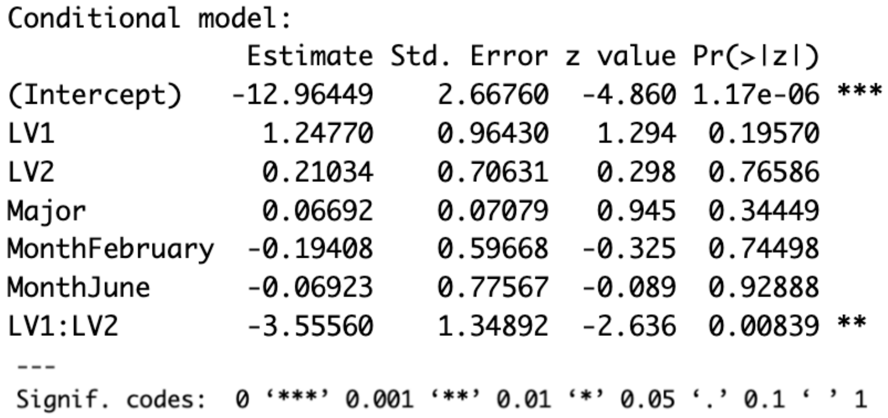
```
Conditional model:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)     3.7051     1.7729   2.090   0.0366 *
LV1            -0.3602     0.8155  -0.442   0.6587
LV2             0.4624     0.9226   0.501   0.6162
Major           0.1321     0.1106   1.194   0.2326
MonthFebruary   0.2908     0.6346   0.458   0.6467
MonthJune       0.7707     1.1079   0.696   0.4866
LV1:LV2         1.1997     1.4988   0.800   0.4235
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

5.4 Table 2c: Number of non-schistosomes shed as a function of latent variables, snail size, and month.



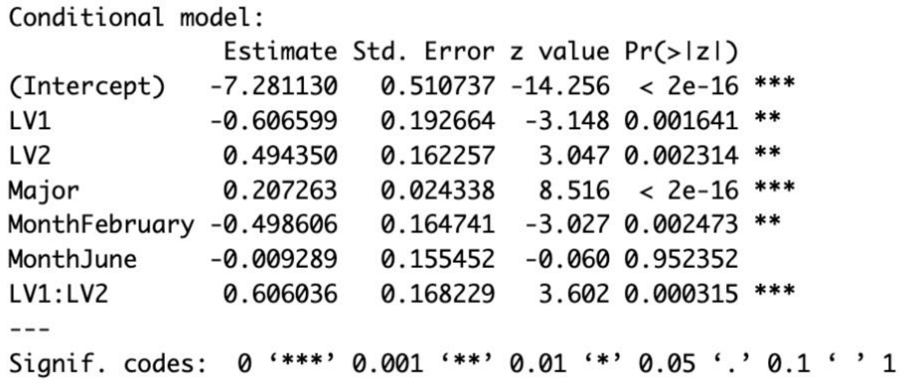
```
Conditional model:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)    4.81002    0.35242  13.649  < 2e-16 ***
LV1            0.01016    0.15052   0.068 0.946183
LV2            0.13416    0.09811   1.367 0.171493
Major          0.10215    0.02028   5.037 4.73e-07 ***
MonthFebruary  0.24504    0.20128   1.217 0.223452
MonthJune      0.58308    0.15988   3.647 0.000265 ***
LV1:LV2        0.11216    0.14935   0.751 0.452654
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

5.5 Table 2d: Probability of schistosome infection as a function of latent variables, snail size, and month.



```
Conditional model:
               Estimate Std. Error z value Pr(>|z|)
(Intercept)   -12.96449    2.66760  -4.860 1.17e-06 ***
LV1             1.24770    0.96430   1.294  0.19570
LV2             0.21034    0.70631   0.298  0.76586
Major           0.06692    0.07079   0.945  0.34449
MonthFebruary  -0.19408    0.59668  -0.325  0.74498
MonthJune      -0.06923    0.77567  -0.089  0.92888
LV1:LV2        -3.55560    1.34892  -2.636  0.00839 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

5.6 Table 2e: Probability of non-schistosome infection as a function of latent variables, snail size, and month.



```
Conditional model:
               Estimate Std. Error z value Pr(>|z|)
(Intercept)   -7.281130   0.510737 -14.256  < 2e-16 ***
LV1           -0.606599   0.192664  -3.148 0.001641 **
LV2            0.494350   0.162257   3.047 0.002314 **
Major          0.207263   0.024338   8.516  < 2e-16 ***
MonthFebruary -0.498606   0.164741  -3.027 0.002473 **
MonthJune     -0.009289   0.155452  -0.060 0.952352
LV1:LV2        0.606036   0.168229   3.602 0.000315 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

6 Figures

6.1 Figure 1

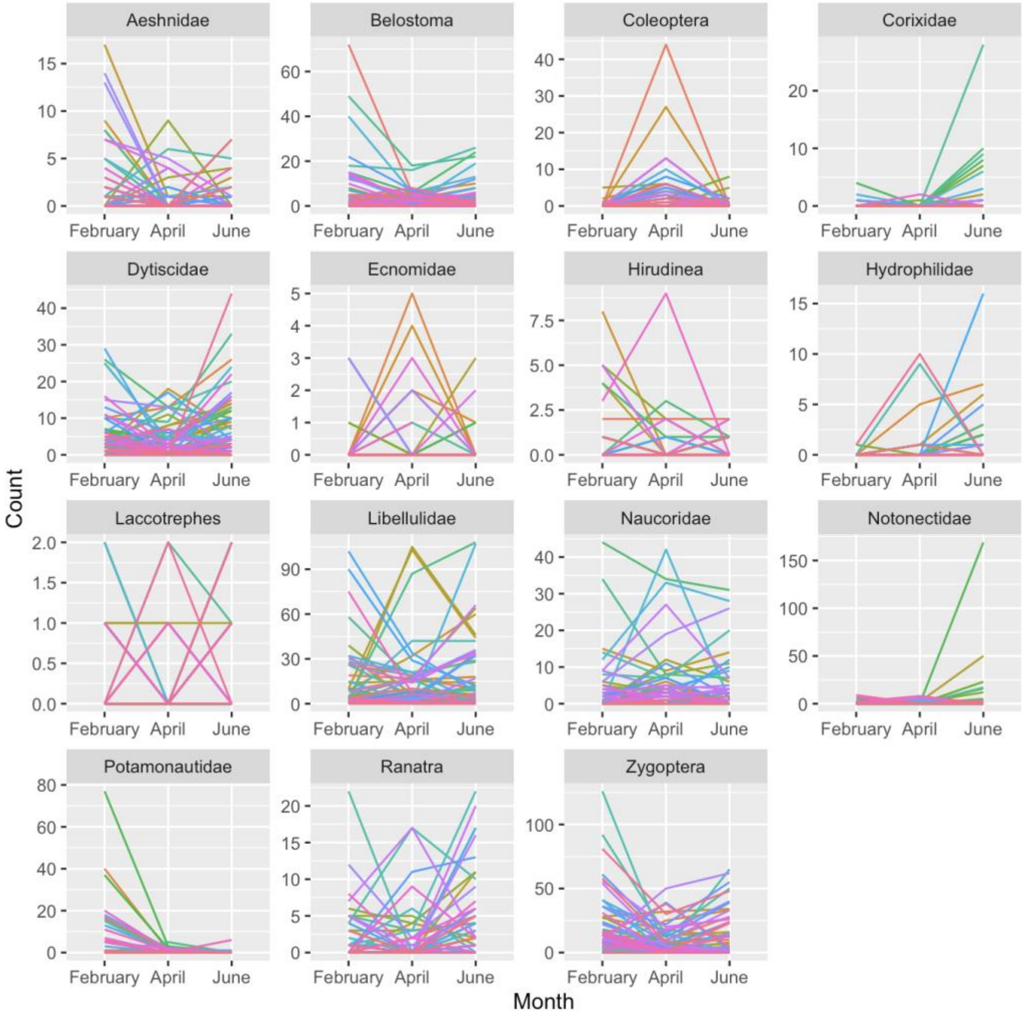


Figure 1: **Plot array of invertebrate predator raw count variations over three months in 64 water bodies.** The linear plots shown use raw count data per waterbody across three months in each taxon. Each graph is a separate taxonomic group while each colored line represents a different waterbody. Sometimes lots of lines overlap. E.g., when a species is rare, lots of lines will have 3 zeroes. There is observed waterbody-to-waterbody variation in the abundance of taxa. A handful of significant taxonomic patterns were observed like with *Aeshnidae*, as they were observed to decrease in count from February to April. *Coleoptera* were found to reach peak relative abundances in June. A test of significance was later completed to quantify any patterns of abundance.

6.2 Figure 2

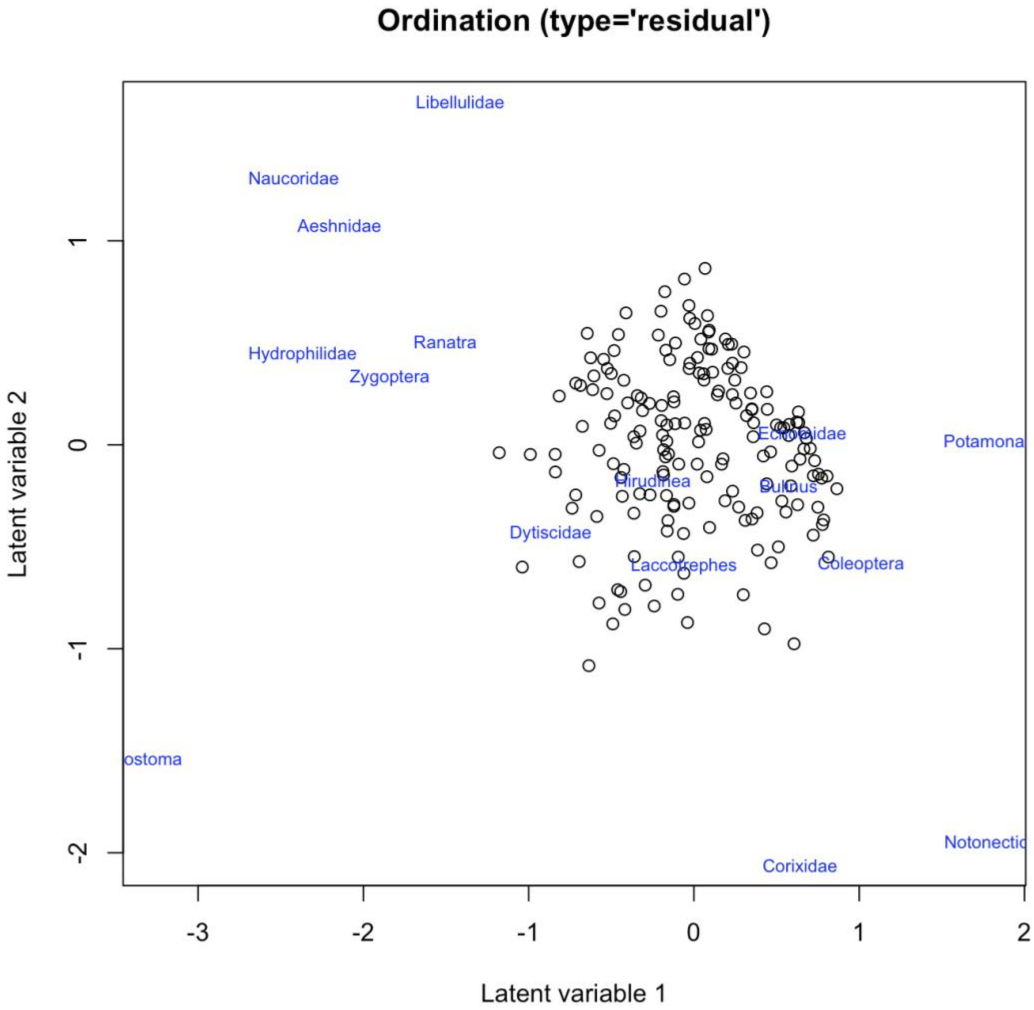


Figure 2: An unconstrained ordination biplot with 17 invertebrate species fitted to the negative binomial GLLVM model. An unconstrained ordination was created using a negative binomial and row level random effect on relative abundances. Blue text in this scatterplot are taxonomic names whose locations are dispersed across the latent variable space. Black, hollow circles represent water bodies across the three months. Axial movement of waterbody positioning describes community composition based on two latent variables. Two latent variables were used based on AIC scores.

6.3 Figure 3

Correlation matrix from the unconstrained ordination using relative counts.

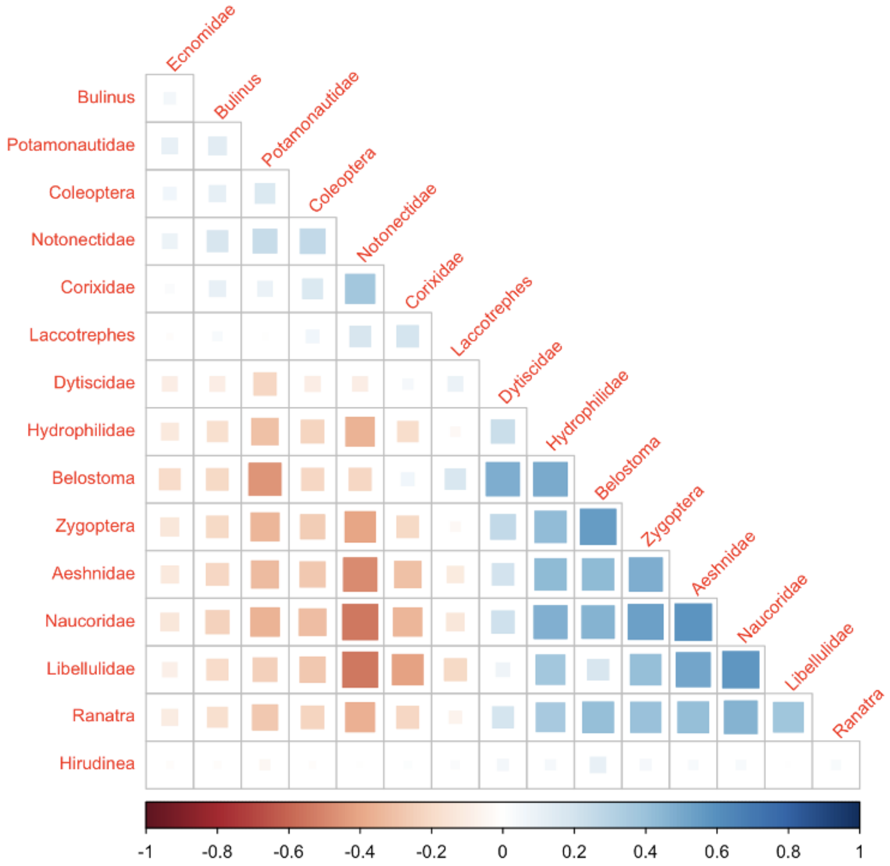


Figure 3: A correlation matrix visualizing an unconstrained ordination revealing two communities. An unconstrained ordination was created using a negative binomial on relative abundances, which was then viewed in a correlation matrix. The plot reveals a coarse, block-like separation of taxonomic groups within the matrix. Blue represents positive correlation while red begets negative correlations. Taxonomic names are printed in red along the left side and the diagonal. A scale is provided on the bottom that deems the degree of positive or negative correlation between taxonomic groups. The splitting of two blue, blocked sections along the diagonal is observed and paired with a red block of negative correlation in between them. This pattern points to two communities present throughout water bodies. The upper block of positive correlating taxa are distinctly weaker than the bottom group's correlations.

6.4 Figure 4a

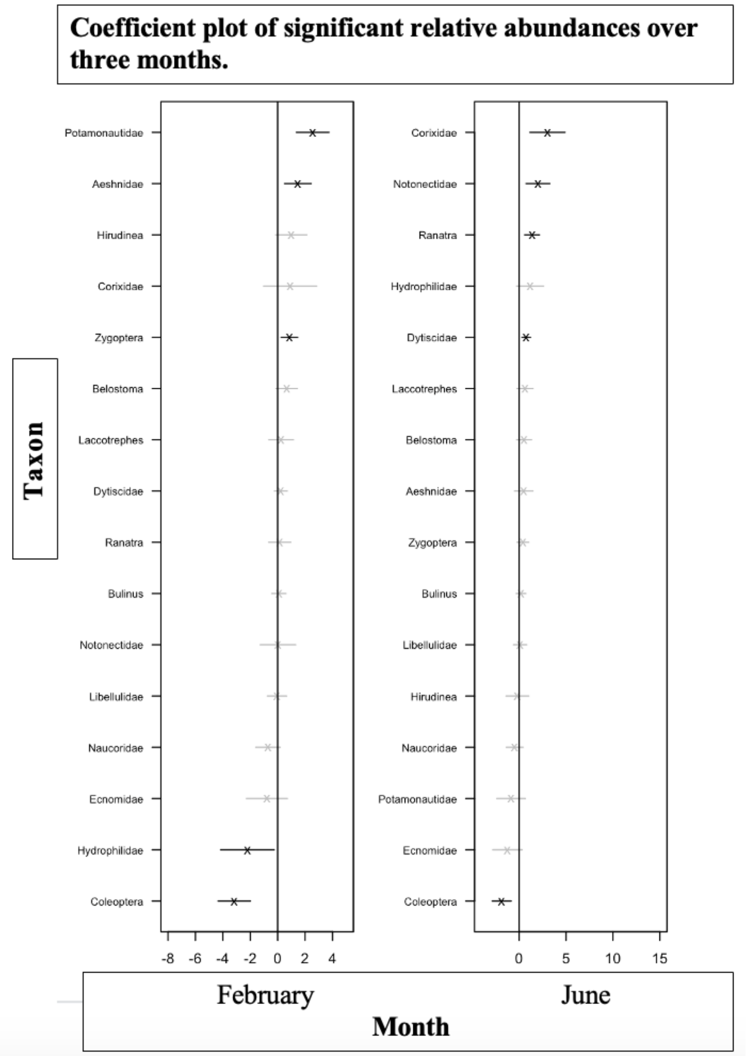


Figure 4a: A 95% confidence interval coefficient plot reveals significant taxonomic abundance patterns. The full-rank ordination was used to create a plot of these coefficients and their confidence intervals at 95%. Taxonomic names are found on the left of each graph. The months are baselined as a comparison to abundances in April. The stars were bolded in black if the taxonomic group revealed significant changes in abundances in comparison to April. Light gray stars are insignificant. *Potamonautidae*, *Aeshnidae*, and *Zygoptera* have significant relative increases from April to February, while *Hydrophilidae* and *Coleoptera* have significant decreases in those months. *Corixidae*, *Notonectidae*, *Ranatra*, and *Dytiscidae*, have significant increases in relative abundances from April to June, while *Coleoptera* decreases with significance.

6.5 Figure 4b

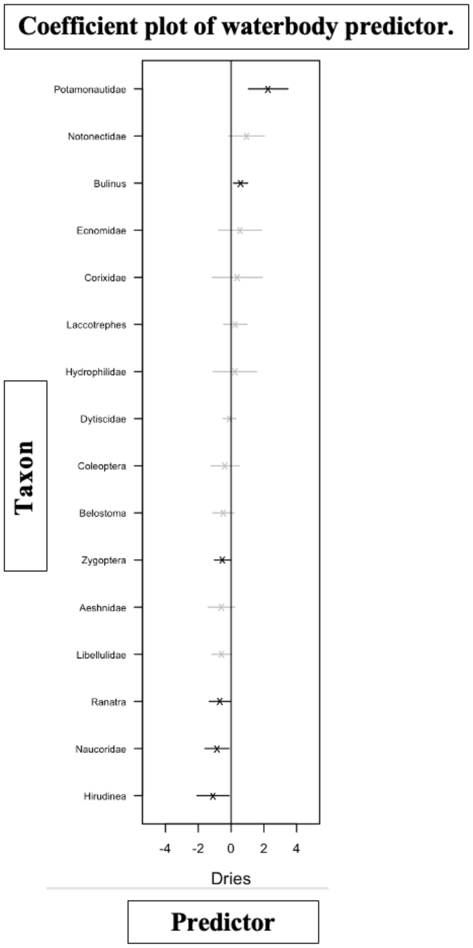


Figure 4b: A 95% confidence interval coefficient plot reveals the effect of the waterbody drying predictor. The full-rank ordination was used to create a plot of these coefficients and their confidence intervals at 95%. Taxonomic names are found on the left of each graph. The stars were bolded in black if the taxonomic group revealed significant changes in abundances in comparison to water bodies that never dries. Organisms in the taxa *Potamonautidae* and *Bulinus* have significant positive correlations with their appearances in water bodies that dry. Invertebrate predators in the taxa *Zygoptera, Ranatra*, *Naucoridae*, and *Hirudinea* relay significant negative correlation with their habitation of water bodies that dry.

6.6 Figure 5

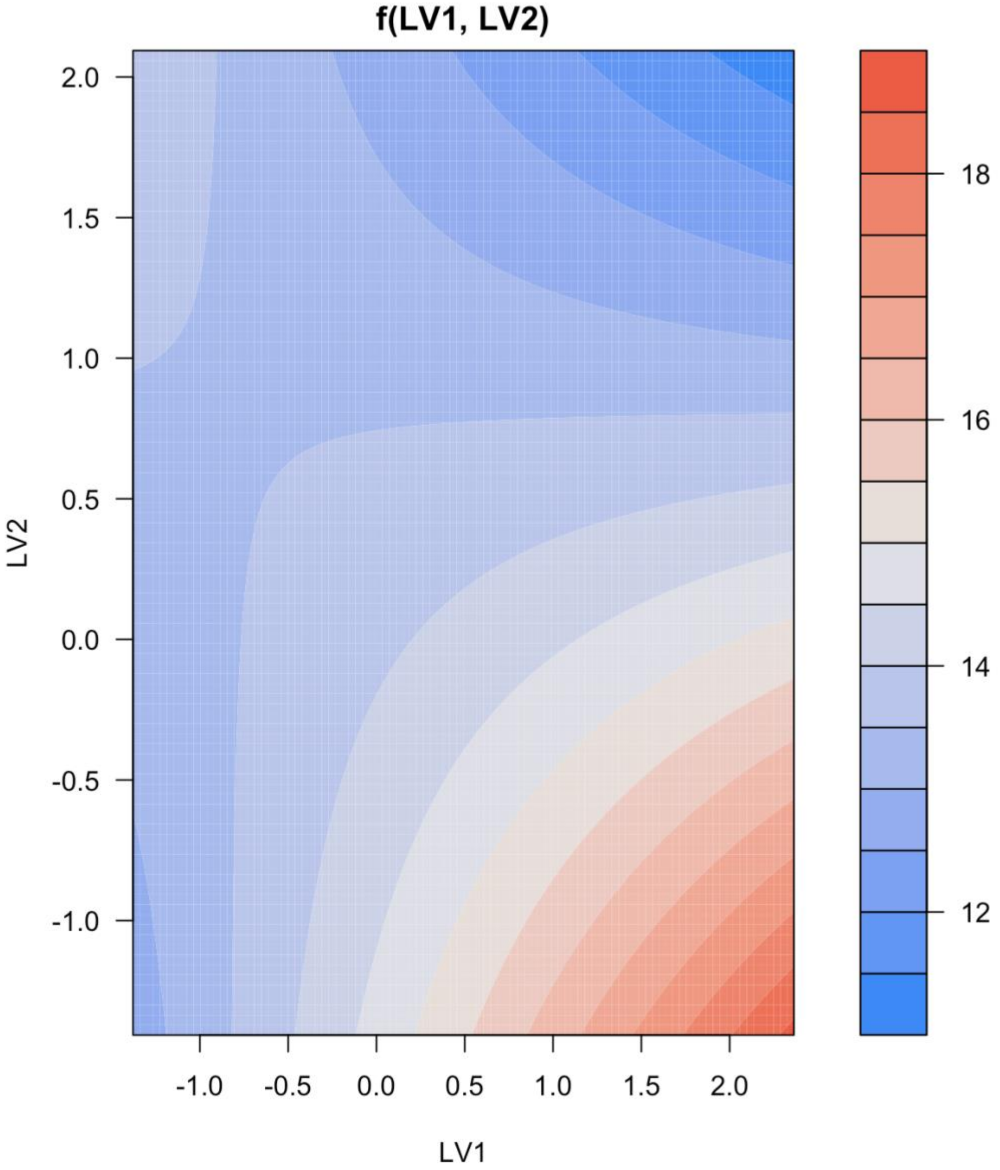


Figure 5: Contour plot of community composition relating to snail size. Snail size is denoted by colors which can be determined using the gradient key besides the graph. Snail size is measured by the maximal length of the snail's shell. Latent variables are plotted on the X and Y axes and represent community composition. Dark red denotes maximal snail sizes while dark blue represents minimal shell sizes. Snail size is maximized when LV2 is low and LV1 is high. Snail size is minimized when both latent variables are high.

6.7 Figure 6

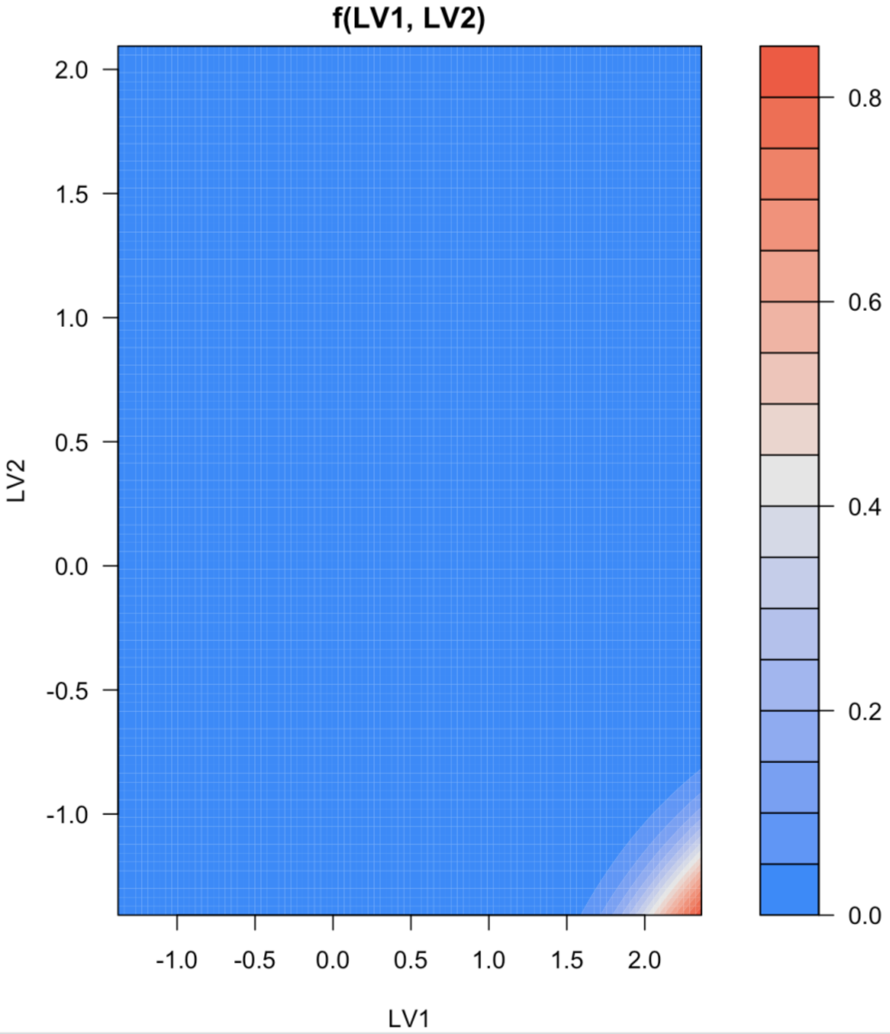


Figure 6: Contour plot of community composition relating to probability of infection by schistosomes. Probability of infection is denoted by colors which can be determined using the gradient key besides the graph. Dark red denotes maximal infection probability while dark blue represents minimal. Latent variables are plotted on the X and Y axes and represent community composition. Probability of infection when LV2 is low and LV1 is high.

5.8 Figure 7

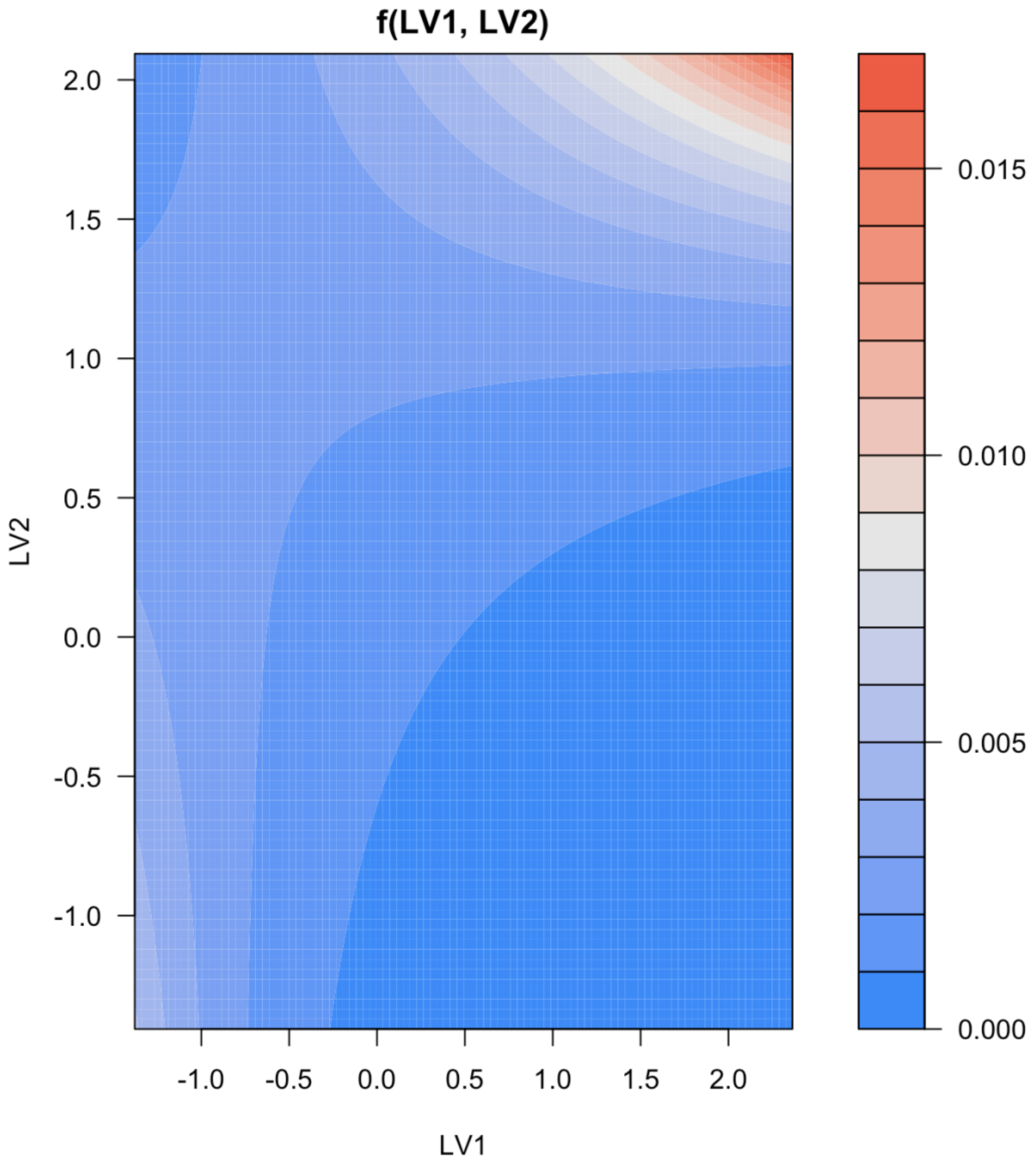


Figure 7: Contour plot of community composition relating to probability of infection by non-schistosomes. Probability of infection is denoted by colors which can be determined using the gradient key besides the graph. Dark red denotes maximal infection probability while dark blue represents minimal. Latent variables are plotted on the X and Y axes and represent community composition. Probability of infection when both latent variables are high. Non-schistosomes are deemed to be virgulate cercariae based on body characteristic observations.

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