# STRUCTURAL HETEROGENEITY AND NUTRIENT AVAILABILITY EFFECTS ON SIMULATED BROMELIAD INVERTEBRATE COMMUNITIES

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*Abstract:* Nutrient availability and structural heterogeneity are important regulators of invertebrate communities. We manipulated these effects separately to understand their relative importance on aquatic invertebrate abundance and diversity in simulated bromeliad tanks. We found that both increased structural heterogeneity and nutrient availability increased invertebrate abundance, but had no effect on community diversity. An interaction between these two factors had a marginal influence on community abundance, suggesting that increased structural heterogeneity may allow invertebrates to better utilize high nutrient availability.

*Key Words: aquatic invertebrates, bromeliad tank, phytotelmata*

## INTRODUCTION

Nutrient availability and structural heterogeneity are important determinants of community diversity and abundance. Heterogeneity of structure and nutrients creates unique combinations of habitat and food resources that can be utilized by varied taxa. For aquatic invertebrate communities, organic matter provides both structural heterogeneity and nutrient availability, making it difficult to assess the relative importance of these factors.

We used simulated bromeliad tanks to assess the effects of nutrient availability and structural heterogeneity on invertebrate communities. We hypothesized that different levels of nutrients and structural complexity would influence both the abundance and diversity of aquatic invertebrates. At increased nutrient availability and increased structural heterogeneity levels, we predicted that abundance and diversity of invertebrates would be greatest due to partitioning of nutrients. Similarly, with low levels of nutrients and decreased structural heterogeneity, competitive exclusion for limited resources would increase, and exhibit the lowest abundance and diversity of invertebrates. In intermediate treatments, we expected that high nutrient availability and low structural heterogeneity would yield higher invertebrate abundance with lower diversity because a competitive dominant would monopolize resources and multiply. Finally, low nutrient availability and high structural heterogeneity would yield lower invertebrate abundance but higher diversity because resources would be limited and highly partitioned.

## METHODS

On 21 and 22 January 2005 we applied four treatments to simulated bromeliad tanks: high structural heterogeneity and high nutrient availability, high struc-

tural heterogeneity and low nutrient availability, low structural heterogeneity and high nutrient availability, and low structural heterogeneity and low nutrient availability. We gathered 15 bromeliads from the ground and base of trees close to the Sendero Principal ~300 m northeast of La Estación Biológia Monteverde, in Monteverde, Costa Rica. We collected invertebrates by rinsing the bromeliad leaves with filtered stream water into a homogenized solution. We added 150 mL of this solution to 12 opaque plastic cups with 100 mL of filtered stream water to increase volume.

To create high and low nutrient availability treatments, we cut *Quercus costaricensis* leaves (low nutrient content) and *Ficus* spp. leaves (high nutrient content) (Gonzalez and Seastedt 2001) into 1 $cm^2$ squares. Low nutrient treatments contained 0.3 g of *Ficus* and 3.9 g of *Q. costaricensis* squares and high nutrient treatments contained 3.9 g of *Ficus* and 0.3 g of *Q. costaricensis* squares. To simulate naturally-occurring structural heterogeneity, we added three squares of 5 $cm^2$ nylon mesh to each tank. Treatments of low structural heterogeneity contained three squares of 0.20 mm mesh and high structural heterogeneity treatments contained one piece each of 0.50 mm, 0.20 mm, and 0.04 mm mesh. Three cups were assigned to each treatment.

All treatments were placed uncovered at the base of the Sendero Principal for approximately 24 h. Mesh and leaves from each cup were rinsed with filtered water and removed, leaving a solution containing all surviving invertebrates in 250 mL of water. The solution was homogenized and five microscope counting trays were prepared per tank. We used mean abundance and diversity per tray to quantify invertebrates for each cup and identified the invertebrates to order.

Mean invertebrate abundance and diversity for the four treatments were compared with a two-way ANOVA. Diversity was calculated using a species richness index, Simpson's diversity index, Simpson's evenness index, Shannon diversity index and Shannon evenness index.

## RESULTS

Total invertebrate abundance per cup was increased with higher nutrient level ($F = 10.25$, $df = 3, 8$, $P = 0.01$, Fig. 1) and structural heterogeneity ($F = 14.20$, $df = 3, 8$, $P = 0.006$), and there was a weak interaction between these parameters ($F = 3.63$, $df = 3, 8$, $P = 0.09$).

For the five most abundant invertebrate orders, we tested for effects of nutrient level, structural heterogeneity, and an interaction between these two factors on abundance of five most abundant invertebrate orders (Table 1). Both nutrient level and structural heterogeneity increased abundances of Coleoptera and Nematoda, while only structural heterogeneity increased Copepoda abundance. Nematoda alone showed increases in abundance from an interaction between resource level and structural heterogeneity. Annelida abundance was not affected by any of the treatments.

All measures of richness, diversity,

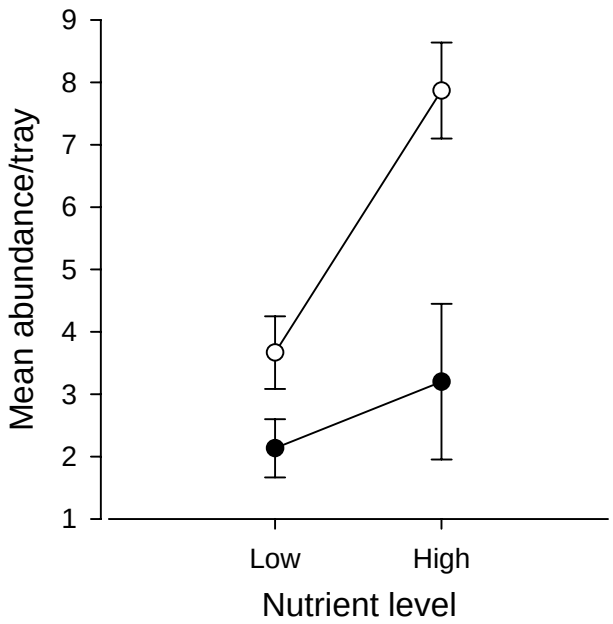


Figure 1. Mean invertebrate abundance per tray increased from low to high nutrient treatments for both low structural heterogeneity (filled circles) and high structural heterogeneity (open circles) treatments. The interaction between these two factors caused a marginally significant increase in invertebrate abundance (see text.)

and evenness showed no effects of nutrients, structural heterogeneity, or an interaction (Table 2).

## DISCUSSION

Our study showed that higher nutrient levels and structural heterogeneity independently increase invertebrate abundance. Higher nutrient availability leads to greater total abundance, while increasing structural heterogeneity may increase resource partitioning and provide refugia from predators or interference competitors. High structural heterogeneity also increased the effect of greater nutrient availability on invertebrate abundance, although the test for an interaction between these factors was only marginally significant. This effect could be due to high structural heterogeneity generating an environment where different taxa can exploit increased nutrient availability.

We propose two possible mechanisms for differing abundances between treatments. First, Nematoda and Copepoda can reproduce several times in a 24 h period, and their reproduction could be stimulated quickly by increased nutrient availability (Pennak 1953). Second, reduced competition as a result of higher nutrient levels and more varied resource niches from greater structural heterogeneity could decrease competitive exclusion and invertebrate mortality.

The trends for the five most abundant invertebrate orders in our samples follow, generally, the trends found for total abundance. However, Annelida, the fifth most abundant order, did not exhibit any effects between treatments. This difference may be due to this order's preferential feeding on particulate substrate at the bottom of stagnant pools (Pennak 1953). If annelids were not feeding on leaf material or migrating through our simulated bromeliad tank, they would not be affected by varied structural heterogeneity or nutrient availability.

Our tests for differences in diversity across treatments showed no significant effects of nutrient level, structural heterogeneity, or an interaction of these two factors. This could be due to our identification being limited to the level of orders, which would mask diversity at a finer taxonomic scale.

Table 1. Two-way ANOVA results for effects of nutrient availability, structural heterogeneity and an interaction between nutrients and structure on abundances on the five most common invertebrate orders (df = 3, 8 for each test). Mean abundance is the number of invertebrates per tray.

| Order | Mean abundance | Effect | F | P |
|---|---|---|---|---|
| Copepoda | 1.59 | | | |
| | | Nutrients | 2.00 | 0.20 |
| | | Structural heterogeneity | 8.22 | 0.02 |
| | | Nutrients * structural heterogeneity | 2.00 | 0.20 |
| Nematoda | 0.81 | | | |
| | | Nutrients | 14.79 | 0.005 |
| | | Structural heterogeneity | 11.46 | 0.01 |
| | | Nutrients * structural heterogeneity | 6.06 | 0.04 |
| Diptera | 0.55 | | | |
| | | Nutrients | 1.76 | 0.22 |
| | | Structural heterogeneity | 3.67 | 0.09 |
| | | Nutrients * structural heterogeneity | 1.76 | 0.22 |
| Coleoptera | 0.43 | | | |
| | | Nutrients | 9.95 | 0.01 |
| | | Structural heterogeneity | 4.98 | 0.06 |
| | | Nutrients * structural heterogeneity | 1.71 | 0.23 |
| Annelida | 0.25 | | | |
| | | Nutrients | 0.16 | 0.70 |
| | | Structural heterogeneity | 0.02 | 0.90 |
| | | Nutrients * structural heterogeneity | 0.45 | 0.52 |

Other potential limitations of our study include predation and colonization that could have occurred during the 24 hours when samples were left uncovered. We left our tanks uncovered to simulate the natural processes occurring in bromeliad tanks, but these effects on our tanks may not be indicative of those in natural systems. Further research including replication with predators could extend the conclusions of our study to natural systems.

## LITERATURE CITED

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Table 2. Two-way ANOVA results for the effects of nutrient availability, structural heterogeneity, and an interaction on richness, diversity and evenness indices, df = 3,8 for each test.

| Diversity index | Effect | F | P |
|---|---|---|---|
| Species richness | | | |
| | Nutrients | 0.57 | 0.47 |
| | Structural | 0.57 | 0.47 |
| | Nutrients * structural heterogeneity | 0.57 | 0.47 |
| Simpson's diversity index | | | |
| | Nutrients | 0.70 | 0.43 |
| | Structural | 0.04 | 0.85 |
| | Nutrients * structural heterogeneity | 0.43 | 0.53 |
| Simpson's evenness index | | | |
| | Nutrients | 0.12 | 0.74 |
| | Structural | 0.61 | 0.46 |
| | Nutrients * structural heterogeneity | 0.08 | 0.79 |
| Shannon diversity index | | | |
| | Nutrients | 0.71 | 0.42 |
| | Structural | 0.27 | 0.62 |
| | Nutrients * structural heterogeneity | 0.33 | 0.58 |
| Shannon evenness index | | | |
| | Nutrients | 0.30 | 0.60 |
| | Structural | 0.40 | 0.55 |
| | Nutrients * structural heterogeneity | 0.02 | 0.89 |