



Elevation Structures Aquatic Microfaunal Communities of Bromeliad Phytotelmata in a Costa Rican Cloud Forest



Jeremy Madden — September 2026

Cloudbridge Nature Reserve

Abstract

Tropical montane cloud forests are rare, structurally complex ecosystems facing uncertain change under a warming climate. Epiphytic bromeliads are keystone species in these systems, enhancing biodiversity and ecosystem complexity through the formation of water-filled reservoirs (phytotelmata) (Tsuda & Castellani, 2016). These structures accumulate rainwater and organic detritus that feed the host plant and support self-contained aquatic habitats occupied by vertebrates and microorganisms. Phytotelm microfauna have been proposed as early indicators of environmental change, since many groups have short generation times and respond rapidly to shifts in tank temperature and resource availability (Kratina et al., 2017; Progênio et al., 2023). However, the structure of these communities and the factors that shape them remain poorly understood, particularly in higher-elevation cloud forests.

Using microscopy and morphological identification, phytotelm community composition was analyzed across an environmental gradient in Cloudbridge Nature Reserve, Costa Rica, and tested associations between community structure and tank volume, canopy cover, elevation, water temperature, largest leaf area, and well number. Across 100 sampled bromeliads, 128,789 individuals spanning 20 morphospecies were documented, with motile ciliates and *Euglena* together accounting for 91% of all individuals recorded.

Environmental variables jointly explained a small but significant proportion of variation in community composition (PERMANOVA $R^2 = 0.124$, adjusted $R^2 = 0.058$, $p = 0.003$), with elevation the strongest individual correlate (envfit $r^2 = 0.200$, $q = 0.0014$). Host bromeliad species identity was also significantly associated with composition ($R^2 = 0.193$, adjusted $R^2 = 0.116$, $p = 0.0001$), an effect that persisted when sparsely sampled host species were excluded. Both associations were significant, but each left most compositional variation unexplained. Ostracoda was the most environmentally responsive taxon: although present in only 12 of 100 bromeliads, its occurrence was strongly structured by elevation, with all records above 1,951 m and the odds of occurrence increasing 1.32-fold per 100 m (95% CI 1.12–1.55) and halving with each degree of tank temperature.

These findings provide a baseline characterization of bromeliad phytotelm microfauna in a Costa Rican cloud forest. The habitat variables measured here explain a small but significant amount of variation in whole-community composition, with elevation the one clear structuring gradient; structural variables — tank volume, largest leaf area, and well number — are best interpreted as correlated proxies for plant size rather than independent drivers. Establishing this baseline is a necessary precondition for detecting future compositional shifts and can inform conservation strategies in montane cloud forests.

Keywords: Bromeliaceae, Phytotelmata, Tropical Montane Cloud Forest, Ostracoda

Introduction

Tropical montane cloud forests (TMCFs) are rare and critical ecosystems in conservation science due to their exceptional endemism and critical role in regional water cycle regulation. Despite accounting for ~2.5% of tropical forest area (Bubb et al., 2004) or 0.4% of global land coverage, they are home to over 3,700 species of birds, mammals, amphibians, and plants — 15% of global diversity in these groups — nearly half of which are endemic (Karger et al., 2021). TMCFs are distinguished from other tropical forests by frequent periods of cloud and fog immersion, which supplies a significant portion of available water through leaf interception (Brujinzeel & Veneklaas, 1998). These ecosystems are heavily dependent on cloud-derived moisture, are particularly sensitive to climate-driven shifts in precipitation and temperature, changes expected to intensify as global warming progresses (Foster, 2001). As a result, these ecosystems face substantial threat from ongoing climate change with recent projections suggesting 57–80% of Neotropical cloud forests may shrink or disappear within the next 25 years (Helmer et al., 2019).

Monitoring ecological change in TMCFs is notoriously difficult because the dominant biological signal of canopy tree composition and structure responds slowly to shifting climate, often delaying measurable ecosystem-level responses by decades (Ramírez-Barahona et al., 2025). Large-scale climate monitoring of TMCFs faces a similar constraint: detecting significant trends requires extensive networks of monitoring stations and two to four decades of continuous data (Los et al., 2021). Efforts to establish long-term monitoring in TMCFs are underway, but many networks remain in early stages, meaning robust data sets are not yet available for a majority of cloud forest sites (Sánchez et al., 2024). Identifying smaller, faster-responding subsystems within TMCFs may therefore offer a more practical means of detecting ecological change in the short term.

Tank-forming bromeliads (Bromeliaceae) have been proposed as one such subsystem (Males et al., 2023). In TMCFs their tightly overlapping leaves intercept rain and fog and capture fallen debris, forming discrete water-filled pools known as phytotelmata (Tsuda & Castellani, 2016). These reservoirs can range from a few milliliters up to several liters of water and support biota across all trophic levels making them a crucial component of TMCF ecosystems (Romero et al., 2020; Benzing, 2023). Leaf litter and organic matter accumulating within these phytotelmata fuel detritus-based food webs composed of diverse microfaunal assemblages that drive decomposition and nutrient cycling (Figure 1), with each bromeliad tank supporting a structurally distinct community shaped by its own local conditions (Carrias et al., 2022).

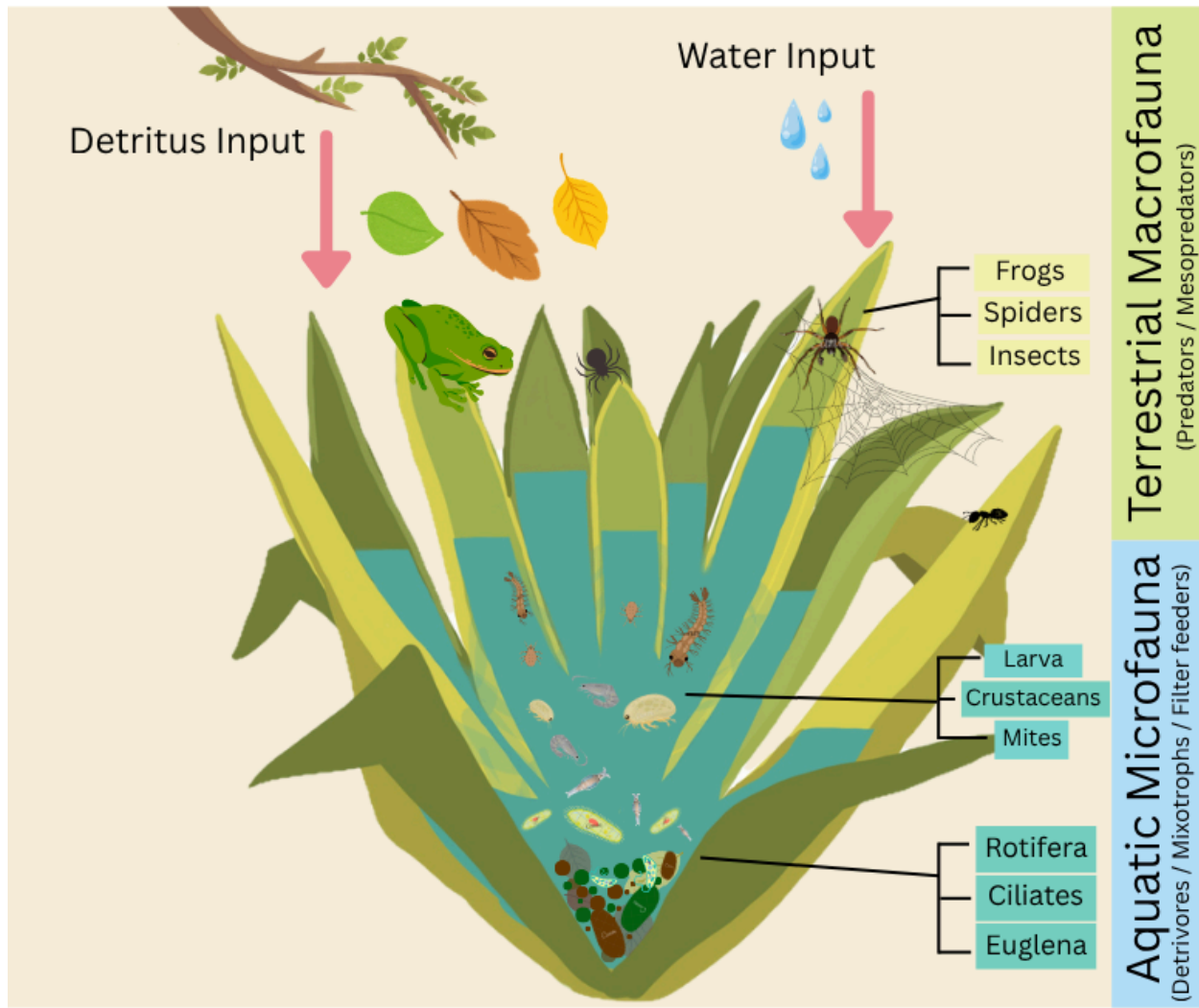


Figure 1. Diagram of a tank bromeliad depicting terrestrial and aquatic habitats and the fauna of their associated trophic groups (figure adapted from Lienau, 2024).

Phytotelmata ecosystems operate on much shorter timescales than the surrounding forest, with community composition changing measurably across wet and dry seasons (Séguigne et al., 2025). Due to the small volumes of water, they are highly sensitive to meteorological shifts compared to the forest (Romero et al., 2016). This rapid turnover makes them useful systems for studying how environmental stress moves through complex food webs (Amundrud & Srivastava, 2016). This, combined with their high distribution density throughout a forest, has led researchers to propose bromeliad-associated microfaunal communities as early bioindicators of broader ecological and climatic change throughout the forest (Penna et al., 2025; Progenio et al., 2023).

Prior work investigating the relationships between habitat variables and bromeliad microfauna found that measurable habitat variables can predict community structure, with mixed results. In northern Costa Rican tank bromeliads (Estación Biológica Pitilla, Guanacaste; Petermann et al., 2015) it was found that resource availability, not abiotic conditions or predator presence, was the strongest driver of microfaunal community composition: as detrital input increased, communities shifted predictably toward assemblages dominated by flagellates and ciliates. This suggests that measurable habitat variables can meaningfully structure microfaunal communities, but which variables matter most likely depends on the specific site and taxa examined.

Despite ongoing bromeliad research more broadly, microfaunal communities remain comparatively overlooked relative to macroinvertebrates and plant-hydrology topics (Carrias et al., 2022; Rangel et al., 2017). Existing surveys of bromeliad microfauna are also disproportionately concentrated in Brazil and South America, with comparatively few studies based in Central America and fewer still from high elevation TMCs specifically, where microclimatic conditions can differ substantially from the lowland systems (Lopes et al., 2023). While preliminary studies have been conducted in Monteverde, Costa Rica (Kellogg, 2020), no published study has characterized bromeliad phytotelmata microfaunal communities within Costa Rica's Talamanca Mountains. This is significant because establishing a baseline understanding of community composition is necessary before any future shifts can be measured.

This study characterizes microfaunal communities inhabiting bromeliad phytotelmata in Cloudbridge Nature Reserve on the Pacific slope of the Talamanca Mountains, Costa Rica (1,550–2,100 m elevation) by collecting water samples from individual plants and analyzing them using microscopy. The goals of this project are to (1) evaluate what influence, if any, environmental (e.g., elevation, canopy cover) and structural (e.g., tank volume, largest leaf area, well number) variables have on community composition and (2) document community composition and abundance, in order to identify potential taxa of interest for future monitoring efforts. It was predicted that tank volume and temperature and canopy cover would be the most influential variables structuring community structure consistent with prior findings that habitat size and detrital input are among the strongest predictors of invertebrate richness and abundance across bromeliad systems (Petermann et al., 2015; Jocqué & Field, 2014).

Objectives

Primary objective:

- Characterize the composition of microfaunal communities in bromeliad phytotelmata.

Secondary objectives:

- Determine which structural and environmental variables influence community composition.
- Identify taxon-specific associations with environmental variables.

Materials & Methods

Study Site

This study was conducted within Cloudbridge Nature Reserve, a 444-acre (~180ha) private reserve located on the Pacific slope of the Talamanca Mountains in southern Costa Rica (Figure 2). The reserve lies adjacent to Chirripó National Park and covers an elevation range of 1,550–2,100 m. Forest coverage is a mix of old growth, naturally regenerated, and planted forest, the latter two resulting from ongoing pasture reclamation efforts beginning in 2002. To ensure adequate water availability in sampled tanks all sampling for this study was conducted during the rainy season, between June and October 2025 (Table 1).

Table 1. Average values for temperature, precipitation, and humidity in Cloudbridge from 2014 to 2024 (Instituto Costarricense de Acueductos y Alcantarillados, 2024)

Month	T °C (min)	T °C (max)	T °C (avg)	Precip. (mm)	Humidity (%)
Jan	13.56	22.63	17.02	33.3	86.08
Feb	13.77	24.09	17.69	19.9	79.55
March	14.17	24.35	17.89	84.2	81.91
April	14.82	23.41	17.88	217.9	88.29
May	15.29	22.77	17.86	389.6	92.51
June	15.06	22.27	17.55	311.7	93.36
July	14.86	21.89	17.41	192.3	93.23
Aug	14.82	21.97	17.35	264.6	93.25
Sept	14.65	21.80	17.17	374.5	92.73
Oct	14.64	21.33	16.95	467.1	94.49
Nov	14.46	21.10	16.80	307.9	95.87
Dec	13.86	21.72	16.88	92.1	91.66

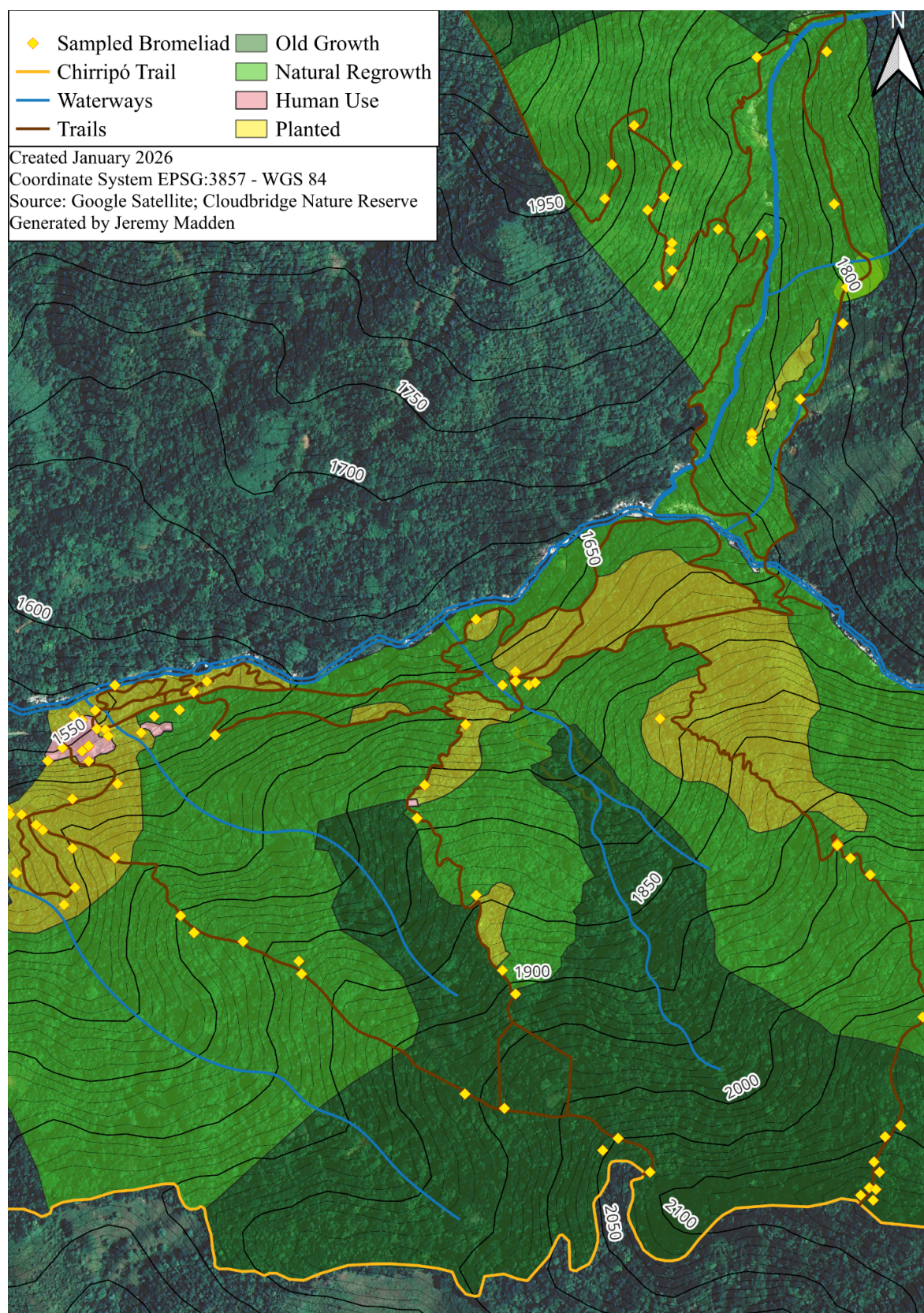


Figure 2. Map of Cloudbridge Nature Reserve with the locations of sampled bromeliads indicated.

Bromeliad Selection & Sampling

During each week of this project, every trail within the reserve was surveyed for bromeliads meeting the sampling criteria: reachable height of less than 2 m above ground, <3 m off trail, and containing >10 mL water. Upon identification of a qualifying individual the following variables were recorded:

- Largest leaf area (length * width of largest leaf)
- Tank volume (width/depth * height of rosette)
- Number of leaves
- Number of phytotelmata

Photographs were taken from multiple angles for documentation and future identification. Water temperature was measured by inserting an OXO Precision Digital Instant Read Thermometer into the deepest tank and allowed to stabilize for one minute. Canopy cover above each individual was measured using fish-eye lens imagery processed through imageJ. Geographic position was recorded using a Garmin GPSMAP 64sx and later processed in QGIS to obtain elevation data for each sampling location.

Once all environmental data was collected, a sterile pipette was inserted into the base of a well and ~2 mL of water and detritus was collected. Samples were collected from multiple wells per individual and pooled together in a screw-top vial until a total of 10 mL was obtained. The sample was then sealed and either immediately returned to the lab, or held until all sampling for that day was completed. To prevent cross-contamination, pipettes were swapped and the thermometer probe was sanitized using a fresh alcohol wipe between each bromeliad.

Sample Analysis

Upon returning to the lab, each water sample was gently shaken to ensure even distribution of organisms. Then, a subsample was pipetted onto a glass microscope slide as three separate drops each of them was covered with a glass coverslip (Figure 3). Slides were examined under a compound microscope using a systematic sweeping pattern at 40× magnification, with organisms identified at higher magnifications when required to resolve morphological detail. A total of 5 slides per sample were examined equating to 15 squares. Identification was carried out to the level of taxonomic morphospecies group using a combination of: Fresh Water Macroinvertebrates of Costa Rica I (Springer et al., 2010), and A User-Friendly Guide to the Ciliates (Foissner & Berger, 1996). *All* individuals within each subsample were quantified in their entirety and entered into a database for each corresponding sample. To minimize double counting across extended observation periods, organisms were distinguished through a combination of morphological characteristics and movement patterns, allowing for differentiation between previously counted and newly encountered individuals.

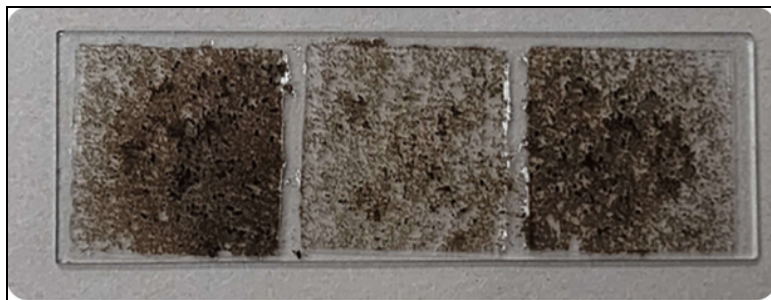


Figure 3. *Glass microscope slide with 3 subsample squares*

Statistical Analysis

Field and laboratory data were compiled in Microsoft Excel and analyzed in R version 4.4.1. Community ordination and multivariate tests were performed using the *vegan* package (version 2.7-3), and figures were produced using *ggplot2* (version 4.0.3). Statistical significance was assessed at $\alpha = 0.05$. Where multiple comparisons were performed, p-values were adjusted using the Benjamini-Hochberg false discovery rate procedure and are reported throughout as q-values.

Sampling completeness was assessed with a species accumulation curve of cumulative morphospecies richness against sample number, with 95% confidence intervals estimated by jackknife resampling. Morphospecies occurring in fewer than 10% of samples were excluded, and the remaining abundances were Hellinger-transformed to limit the influence of the two numerically dominant taxa. A single Bray-Curtis dissimilarity matrix was created from the transformed data and used for all community-level analyses: ordination, both PERMANOVA models, and the test of multivariate dispersion. A three-dimensional NMDS solution (stress = 0.118) was retained, and environmental vectors were fitted across all three axes.

Two permutational multivariate analyses of variance (PERMANOVA; *adonis2*, 9999 permutations) were used to test compositional differences: the first tested the effect of host bromeliad species identity on community composition, and the second tested the joint effect of the seven measured environmental and structural variables (canopy cover, elevation, largest leaf area, tank temperature, total leaves, total wells, and tank volume). Because PERMANOVA R^2 is unadjusted and therefore sensitive to both sample size and model degrees of freedom, adjusted R^2 values are reported alongside raw values wherever models are compared. Multivariate homogeneity of group dispersions was tested for the host species model using *betadisper*. Individual environmental variables were fitted to the NMDS ordination as vectors using *envfit* (9999 permutations).

Taxon-specific relationships between abundance and environmental variables were examined using two complementary approaches. First, Spearman rank correlations were calculated between the abundance of each of the 20 morphospecies and each of the seven variables (140 pairwise comparisons), providing marginal associations that make no distributional assumptions. Second, negative binomial generalized linear models were fitted separately for each morphospecies using the glmmTMB package (version 1.1.14), with all seven environmental variables entered as predictors in a single model per taxon

- Elevation (m)
- Leaf area (cm²)
- Tank temperature (°C)
- Tank volume (cm³)
- Canopy cover (%)
- Total leaves
- Total wells

Coefficients from these models therefore represent partial effects, conditional on the remaining six predictors. Predictors were centered and scaled prior to fitting to improve numerical conditioning, given the wide disparity in measurement scales among variables; coefficients are reported on both the standardized and original scales.

Ostracod was retained in the Spearman analysis but excluded from the GLM framework and analyzed separately. Negative binomial models for this taxon failed to converge, and because Poisson regression assumes equality of mean and variance (Pearson dispersion = 13.50; χ^2 test, $p < 0.001$), Ostracod abundance was instead analyzed as presence/absence using logistic regression (see below).

Results

One hundred bromeliads were sampled during the 107-day collection period, yielding a total of 128,789 individuals across 20 morphospecies (Table 2). Sampled bromeliads spanned eight identifiable host species, with *Tillandsia leiboldiana* the most frequently sampled ($n = 42$). Motile Ciliates were the most abundant morphospecies overall, with 69,910 individuals (54% of all individuals recorded), followed by *Euglena* with 47,975 individuals (37%) and Bdelloid Rotifers with 2,814 individuals (2%); together these three morphospecies accounted for 93.7% of all individuals documented. The least abundant morphospecies were Tardigrades (6 individuals), Flatworms (20 individuals), and Gastrotricha (57 individuals).

Table 2. Summary of microfauna morphospecies documented across 100 sampled bromeliads ($n = 128,789$ total individuals). Relative abundance expresses each taxon's count as a percentage of total abundance. Occurrence frequency indicates the number of samples (out of 100) in which each morphospecies was detected.

Morphospecies	Total Count	Relative Abundance (%)	Occurrence Frequency (# of samples present /100)
<i>Lecane</i> (Rotifer)	653	0.51	56
<i>Euglena</i>	47975	37.25	70
<i>Paramecium</i>	2297	1.78	50
Motile Ciliates	69910	54.28	100
Bdelloid Rotifer	2814	2.19	90
Algae	1108	0.86	74
Nematode	238	0.19	55
Mosquito Larva	281	0.22	65
Diptera Larva	157	0.12	65
Unknown Larva	86	0.07	42
<i>Aeolosoma</i> Worm	72	0.06	18
Mite	294	0.23	44
Ostracod	258	0.20	12
Gastrotrich	57	0.04	18
Nauplius Larva	801	0.62	53
Copepod	888	0.69	54
Oligochaete	244	0.19	31
Tardigrade	6	0.005	6
<i>Euplotes</i>	630	0.49	46
Flatworm	20	0.02	12
Total	128789	100	

Motile Ciliates and Bdelloid Rotifers were also the most widely distributed morphospecies, occurring in 100 and 90 of the 100 sampled bromeliads respectively, while Ostracod and Flatworm were each detected in only 12 samples. Per-sample morphospecies richness ranged from 4 to 15 (mean = 9.6) of the 20 possible morphospecies, and total abundance per sample was highly right-skewed, ranging from 21 to 18,235 individuals (mean = 1,288; median = 431).

Morphospecies Accumulation

To assess whether sampling efforts were sufficient to capture the observed community diversity, a species accumulation curve was generated by plotting cumulative morphospecies richness against the number of samples, with 95% confidence intervals estimated via jackknife resampling. The curve rose steeply over the first 10–15 samples, capturing the majority of observed richness at the taxonomic resolution used, before gradually plateauing at 20 morphospecies by approximately sample 60–70 and remaining flat through the full sample of 100 bromeliads (Figure 4).

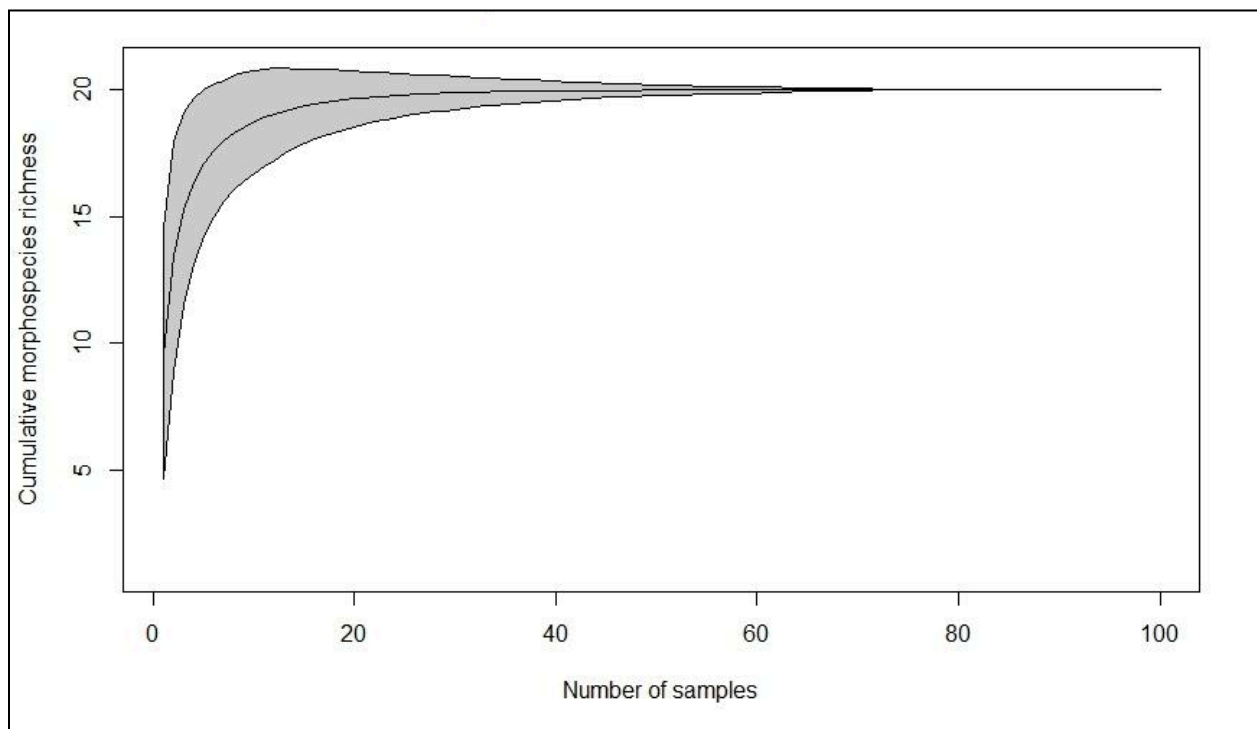


Figure 4. Species accumulation curve of cumulative morphospecies richness as a function of sampling across 100 sampled bromeliads. The solid line represents cumulative richness with 95% confidence interval estimated via jackknife resampling shaded.

Community Composition by Host Bromeliad Species

Sampled bromeliads spanned eight identifiable host species; the 19 individuals that could not be identified to species were excluded from this analysis ($n = 81$). *Tillandsia leiboldiana* was the most frequently sampled host ($n = 42$, 52% of identified individuals), while several species were represented by only a small number of individuals. A PERMANOVA testing the effect of host species identity on community composition was statistically significant ($F_{7,73} = 2.50$, $R^2 = 0.193$, adjusted $R^2 = 0.116$, $p = 0.0001$). Multivariate dispersions also differed among host species (betadisper, $F_{7,73} = 5.41$, $p < 0.001$), with *T. leiboldiana*, the most heavily sampled host, more dispersed than the overall mean (mean distance to spatial median 0.336 versus 0.304). The NMDS ordination showed broad overlap among all host species, with no clear separation of any group in ordination space (Figure 5). Because PERMANOVA is conservative in unbalanced designs when the larger group carries the greater dispersion (Anderson & Walsh, 2013), this pattern works against detection rather than inflating it. The compositional effect remained significant when host species represented by single individuals were excluded ($R^2 = 0.166$, $p = 0.0002$) and when analysis was restricted to species with $n \geq 5$ ($R^2 = 0.140$, $p = 0.0001$).

NMDS of Microfaunal Communities by Bromeliad Species

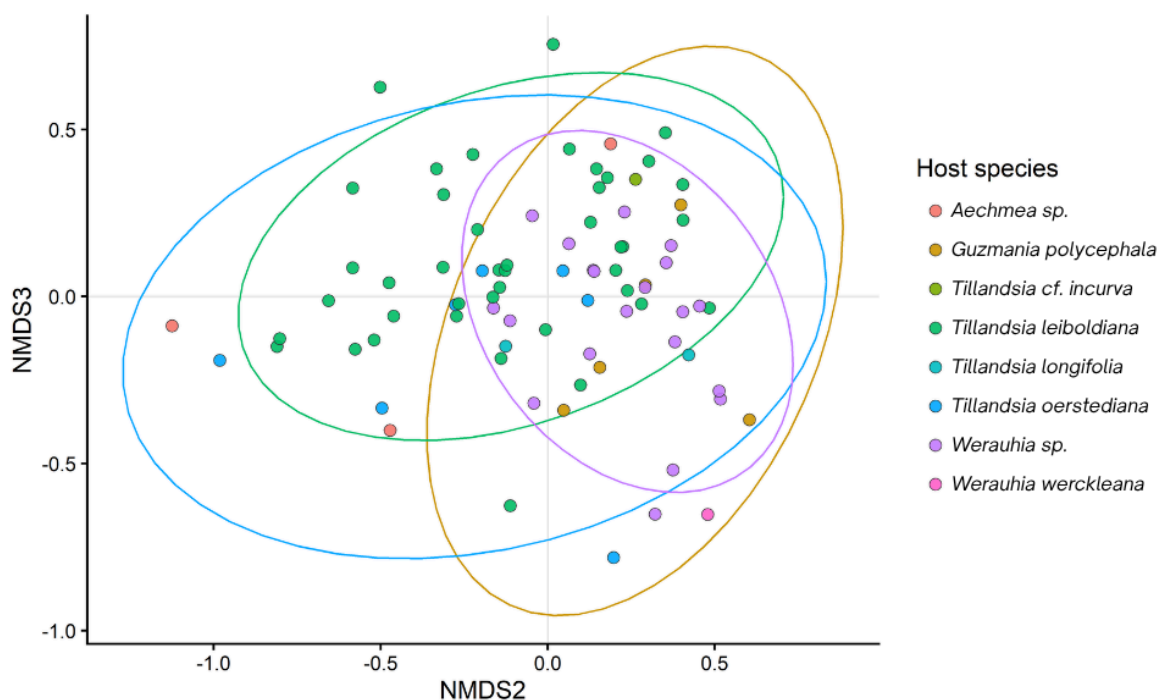


Figure 5. NMDS ordination of bromeliad phytotelm microfaunal communities (Hellinger-transformed abundances, three-dimensional solution, stress = 0.118), coloured by host bromeliad species. Points represent individual bromeliad tanks ($n = 81$); the 19 plants that could not be identified to species are excluded.

Community-Level Environmental Associations (NMDS)

NMDS was used to visualize variation in microfaunal community composition across sample tanks, based on Bray-Curtis dissimilarities. Taxa present in fewer than 10% of samples were excluded prior to ordination to reduce distortion from rare taxa. A three-dimensional solution produced a moderate model fit (stress = 0.118) and was used for all subsequent analyses.

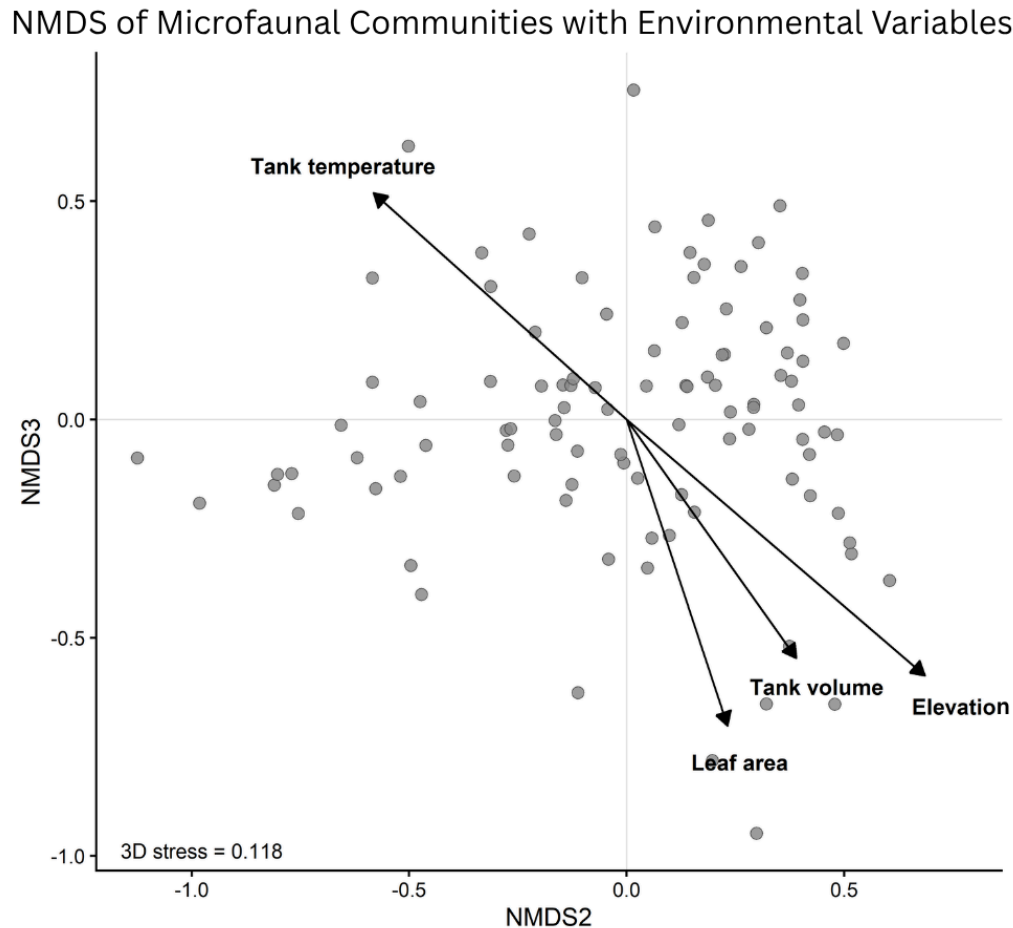


Figure 6. NMDS ordination of bromeliad phytotelm microfaunal community composition (Hellinger-transformed abundances, three-dimensional solution). Points represent individual bromeliad tanks. Arrows indicate environmental vectors significantly correlated with the ordination after Benjamini-Hochberg correction ($q < 0.05$), fitted across all three retained axes using envfit (9999 permutations), with arrow length proportional to r^2 . Axes 2 and 3 are shown because the fitted vectors load only weakly on axis 1.

A PERMANOVA (adonis2, 9999 permutations) was used to test whether the seven measured environmental variables (canopy cover, elevation, largest leaf area, tank temperature, total leaves, total wells, and tank volume) jointly explained variation in community composition. The

full model was statistically significant and explained a small proportion of variance in composition ($R^2 = 0.124$, adjusted $R^2 = 0.058$, $F_{7,92} = 1.86$, $p = 0.003$; Table 3).

Table 3. PERMANOVA (adonis2) results testing the joint effect of all seven environmental variables on community composition (Hellinger-transformed abundances, Bray-Curtis dissimilarity, 9999 permutations) Adjusted $R^2 = 0.058$

Source	Df	Sum of Sqs	R^2	F	p
Environmental variables	7	1.6794	0.1242	1.864	0.0038
Residual	92	11.8400	0.8758		
Total	99	13.5194	1.0000		

To identify which individual environmental variables were most strongly associated with the ordination, vector fitting (envfit, 9999 permutations) was performed for each variable independently. Following Benjamini-Hochberg correction, four of the seven variables were significantly correlated with the ordination ($q < 0.05$; Table 4). Elevation showed the strongest individual association ($r^2 = 0.200$, $q = 0.0014$), followed by tank temperature ($r^2 = 0.174$, $q = 0.0018$), largest leaf area ($r^2 = 0.136$, $q = 0.0070$), and tank volume ($r^2 = 0.113$, $q = 0.0220$). Total wells and total leaves fell just short of significance after correction (both $q = 0.064$), and canopy cover was not associated with composition ($q = 0.881$).

Table 4. Environmental vector fit (envfit) on the NMDS ordination ($k = 3$, stress = 0.118), 9999 permutations. Vectors were fitted independently across all three retained NMDS axes; r^2 values are marginal correlations with the ordination and are not adjusted for covariance among predictors.

Variable	NMDS1	NMDS2	NMDS3	r^2	p	q	Sig.
Elevation	-0.222	0.741	-0.634	0.200	0.0002	0.0014	**
Tank Temperature	0.429	-0.674	0.601	0.174	0.0005	0.0018	**
Largest Leaf Area	-0.256	0.304	-0.918	0.136	0.0030	0.0070	**
Volume	-0.263	0.560	-0.785	0.113	0.0126	0.0220	*
Total Wells	-0.287	0.346	-0.893	0.078	0.0476	0.0644	n.s.
Total Leaves	-0.122	0.467	-0.876	0.076	0.0552	0.0644	n.s.
Canopy Cover	0.737	0.306	0.602	0.007	0.8805	0.8805	n.s.

Taxon-Specific Environmental Associations (Spearman Correlations)

Spearman rank correlations were calculated between counts of each of the 20 taxa and each of the seven environmental variables measured (140 pairwise comparisons total). To account for the large number of comparisons, p-values were adjusted using the Benjamini-Hochberg false discovery rate (FDR) procedure. Of the 140 correlations tested, 34 were significant at the

uncorrected threshold ($p < 0.05$); 13 remained significant following FDR correction ($q < 0.05$; Figure 7).

Ostracod abundance showed the most consistent environmental associations, correlating significantly with five of the seven variables measured: positively with elevation ($\rho = 0.38$), largest leaf area ($\rho = 0.44$), total leaves ($\rho = 0.29$), and tank volume ($\rho = 0.34$), and negatively with tank temperature ($\rho = -0.40$). *Nauplius* larva abundance was negatively correlated with both tank volume ($\rho = -0.38$) and total wells ($\rho = -0.31$). Lecane Rotifer and Copepod abundance were each negatively correlated with tank volume ($\rho = -0.33$ and $\rho = -0.31$, respectively). Bdelloid Rotifer and Flatworm abundance were positively correlated with elevation ($\rho = 0.30$ and $\rho = 0.31$, respectively), while Unknown Larva abundance was negatively correlated with elevation ($\rho = -0.32$). Nematode abundance was positively correlated with largest leaf area ($\rho = 0.30$). Tardigrade abundance showed no significant association with any environmental variable at either threshold.

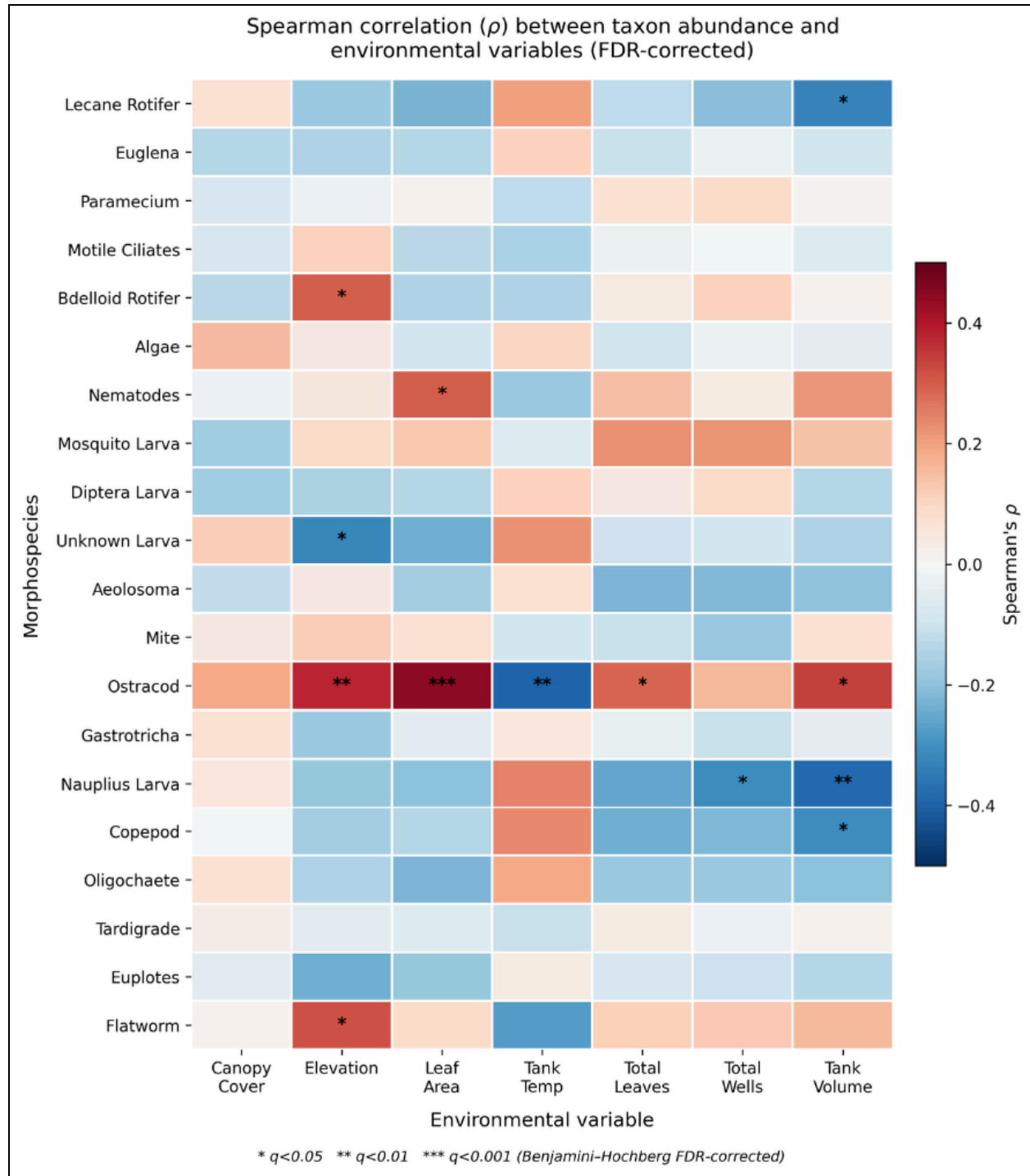


Figure 7. Spearman correlations (ρ) between taxon abundance and environmental variables, with significance adjusted for multiple comparisons using the Benjamini-Hochberg false discovery rate procedure ($q < 0.05$). Asterisks indicate FDR-corrected significance levels (* $q < 0.05$, ** $q < 0.01$, *** $q < 0.001$).

Taxon-Specific Environmental Associations (Negative Binomial GLMs)

Taxon-specific relationships between abundance and the seven environmental variables were re-examined using negative binomial GLMs fitted separately for each taxon, with all seven variables entered simultaneously. Of 133 taxon-environment coefficients tested across 19 taxa, 23 were significant at the uncorrected threshold ($p < 0.05$); following Benjamini-Hochberg correction, three remained significant ($q < 0.05$; Table 5). Motile Ciliate and bdelloid rotifer abundance were both negatively associated with largest leaf area ($q = 0.00088$ and $q = 0.034$ respectively), and Euplotes abundance was negatively associated with elevation ($q = 0.0098$).

Table 5. Negative binomial GLM coefficients significant after Benjamini-Hochberg correction ($q < 0.05$), across 19 taxa and 133 taxon-environment coefficients. Ostracoda was excluded and analysed separately (see Methods). Estimates are given on the standardized scale (per standard deviation of the predictor) alongside original-scale equivalents. Because the four structural predictors are strongly intercorrelated ($\rho = 0.30$ – 0.88), coefficients attributed to individual size variables should be interpreted as partial effects within a collinear predictor set rather than as independent drivers.

Taxon	Predictor	Estimate (scaled)	Estimate	SE	p (raw)	q (BH-adj)	Sig.
Motile Ciliates	Leaf Area	−0.8176	−0.00617 per cm ²	0.1815	6.62e-06	8.81e-04	***
<i>Euplotes</i>	Elevation	−1.4389	−0.00411 per m	0.3791	1.47e-04	9.80e-03	**
Bdelloid Rotifer	Leaf Area	−0.5124	−0.00386 per cm ²	0.1522	7.60e-04	3.37e-02	*

Ostracod Occurrence and Elevation

Ostracods were detected in 12 of 100 sampled bromeliads (258 individuals). All occurrences were recorded at or above 1,951 m; no ostracods were found in the 64 samples below this elevation. When present, abundance was highly variable ranging between 1 and 47 individuals.

Because negative binomial models failed to converge for this taxon and Poisson regression was strongly overdispersed (Pearson dispersion = 13.50), ostracod occurrence was modelled as presence/absence using logistic regression. A model containing elevation alone was highly significant (likelihood-ratio test, deviance = 11.84, $df = 1$, $p = 0.00058$), explaining approximately 16% of the null deviance. The odds of ostracod occurrence increased 1.32-fold per 100 m of elevation (95% CI 1.12–1.55), corresponding to a 4.5-fold increase across the 550 m elevational range of the reserve.

Univariate logistic models fitted separately for each of the seven environmental variables identified three significant predictors following Benjamini-Hochberg correction (Table 6): largest leaf area ($q = 0.0016$), tank temperature ($q = 0.0020$), and elevation ($q = 0.0021$). Ostracod occurrence increased with leaf area (odds ratio 1.13 per 10 cm², 95% CI 1.06–1.20) and

elevation, and decreased with tank temperature (odds ratio 0.51 per °C, 95% CI 0.35–0.75). Tank volume showed a positive association that did not survive correction ($q = 0.073$), and canopy cover, total leaves, and total wells were not significant.

Table 6. Univariate logistic regression of Ostracoda presence/absence on each environmental variable ($n = 100$, 12 presences). Estimates are on the log-odds scale; p -values adjusted across seven comparisons using Benjamini-Hochberg FDR correction.

Predictor	Estimate	SE	z	p	q	Sig.
Largest Leaf area (cm ²)	0.01212	0.00330	3.68	0.00023	0.0016	**
Tank temperature (°C)	−0.67595	0.19659	−3.44	0.00059	0.0020	**
Elevation (m)	0.00275	0.00083	3.32	0.00092	0.0021	**
Tank volume (cm ³)	0.00192	0.00094	2.04	0.042	0.073	n.s.
Canopy cover (%)	0.04126	0.02444	1.69	0.091	0.128	n.s.
Total leaves	0.01883	0.01747	1.08	0.281	0.328	n.s.
Total wells	0.01758	0.03188	0.55	0.581	0.581	n.s.

Discussion

This study established a baseline characterization of aquatic microfaunal communities within bromeliad phytotelmata of a Costa Rican tropical montane cloud forest and evaluated the influence of environmental and habitat variables on community composition. A total of 128,789 individuals and 20 morphospecies were documented across 100 bromeliads. Ciliates and *Euglena* were the most abundant groups, together accounting for 91% of all individuals recorded. The seven measured environmental and structural variables jointly explained a small but statistically significant proportion of compositional variation ($R^2 = 0.124$, adjusted $R^2 = 0.058$), with elevation the strongest individual correlate. Host bromeliad species identity also accounted for a minor share of variation ($R^2 = 0.193$, adjusted $R^2 = 0.116$). At the individual taxon level, Ostracoda were found to be the most environmentally responsive group. Taken together, these results indicate that: habitat variables of the host bromeliad explain a minor but significant amount of variation in whole-community composition, that elevation is the clearest structuring gradient among them, and that large, high-elevation tank bromeliads warrant particular attention in future work.

Microfaunal communities in these phytotelmata were overwhelmingly structured around ciliates. Ciliates occurred in all 100 sampled bromeliads and bdelloid rotifers in 90, making these the two most widely distributed groups documented. This pattern is consistent with the broader phytotelm literature, in which ciliates are repeatedly reported as the dominant microfauna group (Dunthorn et al., 2012). Both ciliates and bdelloid rotifers are bacterivores and detritivores, forming the first consumer level, and their prevalence is consistent with the detritus-based food

webs that characterize these systems (Leroy et al., 2016). Ciliates exhibited considerable internal morphological diversity, with at least 10 distinct morphotypes documented over the course of the project. Because ciliate identification is difficult without specialized taxonomic expertise and molecular tools, all motile forms were pooled into a single "Motile Ciliates" category for statistical analysis, though distinguishing morphological traits were noted in the project database. A small number of identifiable forms were encountered, including a *Litonotus* sp. and a cluster of *Vorticella* sp. living epibiotically on a mosquito larva. This pooling conceals ecologically significant variation, and the group deserves finer-scale study. Regional surveys have repeatedly uncovered undescribed ciliate diversity in this system — Dunthorn et al. (2012) identified 45 undescribed bromeliad-endemic ciliate species across Central American phytotelmata in a single study — raising the possibility that some morphotypes documented at Cloudbridge are locally endemic. Resolving this would require molecular barcoding, and until that work is undertaken it cannot be determined whether any taxa documented here represent undescribed diversity.

Direct comparison of these figures to other bromeliad phytotelm surveys is complicated by differences in taxonomic resolution, sampling volume, and whether samples are drawn from individual phytotelmata or pooled across a plant. The 20 morphospecies documented here fall within the range reported by surveys employing comparable morphological resolution: Antonetti et al. (2021) identified 23 taxa in *Vriesea platynema* phytotelmata in Brazilian Atlantic Forest, with a dominant assemblage — *Philodina*, *Paramecium*, and Diptera larvae — closely mirroring that observed at Cloudbridge. Surveys with dedicated taxonomic support for protistan groups report substantially higher richness. Working in Costa Rican tank bromeliads at Estación Biológica Pitilla, Kratina et al. (2017) recorded 109 microfaunal taxa across 43 bromeliads, with a mean of 13.4 taxa per sample, drawing on specialist identification of amoebae, ciliates, and flagellates. The lower richness reported here is therefore best interpreted as a consequence of morphospecies-level pooling, particularly the aggregation of ciliate morphotypes.

Several morphospecies were encountered only rarely, most notably tardigrades (6 individuals across 6 samples), flatworms (20 individuals), and gastrotrichs (57 individuals). This could be explained by a few reasons: rarity reflects genuinely low abundance in this system; rarity is a detection artifact of the subsampling volume, since taxa at low density are unlikely to appear in a small subsample; these taxa depend on microhabitat conditions poorly represented at this site (warmer temperatures, altered nutrient foundations, lack of dispersers). Their consistent rarity means that abundance-based analyses have very limited power to detect environmental associations for these groups, and the absence of significant correlations for tardigrades in particular should be read as an absence of evidence rather than evidence of absence.

Host species identity was associated with compositional variation and, in adjusted terms, accounted for a somewhat larger share (~12%) than the seven measured environmental variables, a result consistent with work on bromeliad macroinvertebrates showing that community composition is structured by bromeliad species and the morphological traits constrained by

species identity (Marino et al., 2012). Due to the difficulty of bromeliad identification in this system, this comparison is indicative rather than formal. As unidentifiable bromeliads were removed from host-species analysis, two models were fitted to different sample sets ($n = 81$ and $n = 100$ respectively) and the host model contains singleton groups that inflate R^2 by construction. When taken together, the models show that host bromeliad identity tracks composition about twice as closely as the measured habitat variables, yet both models leave most compositional variation unexplained. Host bromeliad species differ in rosette architecture, leaf arrangement, tank number and geometry, and detrital retention, and none of these was measured directly here. Species identity may therefore act as a composite of several of them at once. Most samples came from *T. leiboldiana*, and several host species had too few individuals for reliable group-level estimates. Testing the host species effect properly will take more identifiable bromeliad species, with enough individuals of each.

Contrary to expectation, the smallest host species sampled — *Tillandsia leiboldiana* — contained some of the highest *Euglena* abundances recorded. This is an observational pattern rather than a formally tested result, and it runs counter to Petermann et al. (2015), who reported higher *Euglena* abundance in larger bromeliads; notably, *T. leiboldiana* is not present at their study site. Whether this reflects a species-specific interaction, a size-driven effect such as faster turnover or higher light penetration in small tanks, or the disproportionate representation of *T. leiboldiana* in the sample, cannot be determined with the present data. Regardless, the high abundance of *T. leiboldiana* within the reserve presents an opportunity to test whether this trend is significant and a unique feature to this specific ecosystem.

Elevation was the strongest individual correlate on community composition (envfit $r^2 = 0.200$) and was associated with the counts of bdelloid rotifers, flatworms, *Euplotes*, and Ostracoda. Two of the three predicted variables were found to be influential — tank temperature ($r^2 = 0.174$) and tank volume ($r^2 = 0.113$) — while canopy cover showed no association with composition ($r^2 = 0.007$, $q = 0.881$). Elevation was not predicted to significantly influence composition, but its emergence as the strongest single correlate is consistent with work reporting altitudinal structuring of phytotelm communities (Malfatti et al., 2020). The reserve spans over 550 m of elevation in a short horizontal distance, and the resulting steep gradients in temperature, precipitation, and fog immersion may compress into a small area the kind of environmental variation that would occur over much greater distances in flatter terrain. One important caveat is that elevation is not independent of the other variables measured at this site. Tank temperature was negatively correlated with elevation, and larger bromeliads were found in greater abundance at higher elevations in remaining sections of old-growth forest, as the reserve's lower slopes are almost entirely reforested cattle pasture. Elevation is therefore best understood as a composite that combines thermal, hydrological, and forest-structural changes. These findings imply that the presence of larger, complex phytotelm communities is tied to old-growth forests, which presents a unique conservation case for protecting the remaining stands around the reserve.

Tank volume, largest leaf area, total leaves, and total wells were each individually associated with community composition in the envfit analysis, but these variables are not independent of one another; all are proxies for plant size. Their apparent significance as four separate predictors is actually one underlying size gradient measured four ways. This is visible in the ostracod analysis, where largest leaf area was the only structural variable to survive correction as a predictor of occurrence, despite tank volume and total leaves both showing significant marginal correlations. This shows the importance of using multiple variables as proxies for size and future work in this system would benefit from increasing these measurements by identifying additional composite size variables.

The three taxon-level associations that survived correction were all negative, and two of them were with the largest leaf area. Larger bromeliads therefore supported lower counts of the numerically dominant taxa, a pattern also visible in the Spearman correlations, where *Lecane* rotifers, copepods, and nauplius larvae were each negatively correlated with tank volume—opposing previous findings of abundance positively correlated with tank volume (Marino et al., 2012). One possible explanation is that larger tanks hold more water per unit of detrital input and therefore dilute the density of bacterivorous consumers even if total numbers within the plant are comparable. A second explanation is desiccation-driven habitat filtering. Smaller bromeliads dry more frequently than larger ones (Zotz & Thomas, 1999), and the two taxa driving the leaf-area result are among the most desiccation-tolerant microfauna known: bdelloid rotifers can enter anhydrobiosis at any life stage and resume activity when rehydrated (Ricci, 1998), and many ciliates are capable of forming desiccation-resistant cysts. Notably, bdelloid fitness has been reported to decline under saturated conditions relative to repeated desiccation cycles, suggesting that small, intermittently drying tanks may be favoured by this group (Ricci et al., 2007). Distinguishing these explanations would require density estimates from known sample volumes together with direct measurement of tank hydroperiod, neither of which was recorded here.

Ostracoda were the most environmentally sensitive taxon, with significant Spearman correlations for five of seven variables. Ostracod presence was found to be positively correlated with elevation, largest leaf area, total leaves, and tank volume, and negatively with tank temperature. Logistic modelling of occurrence confirmed leaf area, tank temperature, and elevation as significant predictors after correction for multiple comparisons. Both approaches show ostracods were more likely to occur in larger tanks, at higher elevations, and at lower water temperatures. Ostracods were absent from all 64 sampled bromeliads found below 1,951 m, despite being locally abundant where they did occur and the odds of occurrence were found to increase roughly 4.5-fold across the reserve's elevational range. Tank temperature declines with elevation at this site, so the two effects are not independent. The driver may be either, both, or something not measured here. Separating the two would require sampling across multiple sites and seasons. Ostracods were not the target of this project and were found in only 12 samples, which is too few for multivariate modelling; the associations reported here are therefore univariate and cannot separate the independent contributions of correlated predictors. Ostracods

may be comparatively poor dispersers, and their absence from lower-elevation bromeliads warrants further investigation.

With those caveats, ostracods remain the most promising candidate for future indicator-species work in this area. They are large and easily identifiable under a compound microscope, occupy a restricted but well-defined section of the elevational gradient, and show an apparent response to water temperature — a variable that is likely to shift directly under climate change. A halving of occurrence odds per degree of tank temperature implies that modest warming could measurably contract their distribution even further within the reserve. Targeted sampling designed around this group — stratified by elevation, with greater sample volumes and effort concentrated in old-growth forest at the upper extent of the reserve and extending into Chirripó National Park — would be the logical next step.

The measured environmental variables account for about an eighth of compositional variation, and under 6% once adjusted for the number of predictors. A majority of community variation remains unexplained and could be explained by several non-exclusive mechanisms. Community assembly may be largely stochastic, with composition varying across tanks through dispersal limitations, colonization history, and ecological drift via organisms or wind (Petermann et al., 2015; Maguire, 1971). Alternatively, assembly may be substantially deterministic but driven by variables not measured here, including detrital quantity and quality, water/nutrient chemistry, dissolved oxygen, and predator presence; Céréghino et al. (2020) and Kratina et al. (2017) both report environmental control of phytotelm community structure through such variables. The comparatively larger share of variation associated with host species identity lends some weight to this second possibility, since host identity integrates additional unmeasured habitat properties.

However, it cannot be concluded that assembly in these phytotelmata is predominantly stochastic. A low explained variance demonstrates that the variables measured here have limited predictive power; it does not distinguish stochastic assembly from a predictable one along axes or variables that were not quantified here. The most likely scenario is an interaction between the two, with deterministic filtering operating along strong gradients such as elevation while stochastic processes dominate at finer scales within them.

Limitations

Several limitations were present in this study that tempered interpretation of these results. No organism was identified beyond morphospecies level, owing to limited taxonomic resources and tools available; true diversity is almost certainly higher than the 20 morphospecies reported, particularly within the pooled ciliate category. Larvae that could not be resolved further were grouped as "Unknown Larva," though most were subsequently identified to Scirtidae and Chironomidae.

Bromeliads were sampled opportunistically along the reserve's trail network under fixed criteria (<2 m above ground, <3 m from trail, >10 mL standing water), so the sample is not a true random draw from the reserve's bromeliad population. Canopy-height bromeliads were excluded and trail-adjacent plants may experience edge effects, restricting the range of canopy cover sampled and offering one explanation for the absence of a canopy signal. Host species assignment was a further constraint. Nineteen of the 100 sampled bromeliads could not be resolved to species and were excluded from the host-level analysis, and two of the eight retained groups (*Werauhia* sp., *Aechmea* sp.) are genus-level assignments. Many phytotelm bromeliads are difficult to identify vegetatively, and most individuals encountered were not flowering

Limiting samples to >10 mL threshold excludes the small, frequently drying tanks most relevant to the desiccation hypothesis discussed above. Sampling was restricted to a single rainy season (June–October 2025), and phytotelm communities shift measurably between seasons (Séguigne et al., 2025; Buosi et al., 2014); this is therefore a wet-season baseline and should be compared against future wet-season sampling. Tank temperature was recorded once per plant and reflects conditions at the moment of sampling rather than a tank's thermal regime; time of day was roughly standardized to morning hours (7:00 a.m. - 11:00 a.m.), but long-term monitoring of each individual bromeliad would be required to completely verify these results.

Count data are semi-quantitative: a fixed 10 mL sample was pooled across wells and subsampled onto 15 squares, but volume per square was not standardized, so counts are comparable in relative terms and do not represent densities per unit volume. Individuals were distinguished by morphology and movement rather than by fixation and chamber counting, so counting error likely increases with density.

Future directions and conclusion

This study demonstrates the research potential of bromeliad phytotelm ecology in the Talamanca region. The most immediate priorities are to test whether the patterns observed here hold between seasons and across a wider elevational and geographic range, and to establish periodic resampling so that changes can be detected relative to this baseline. Molecular barcoding of the ciliate assemblage would clarify whether the morphological diversity observed here reflects undescribed and potentially endemic species. A balanced sampling design across host bromeliad species would allow the host identity effect to be tested properly, and direct measurement of detrital and water-chemistry variables would help resolve how much of the unexplained compositional variation is genuinely stochastic. Ostracoda in particular warrants targeted investigation as a candidate indicator taxon. As the first characterization of bromeliad phytotelm microfauna in Costa Rica's Talamanca Mountains, this study provides a foundation for that work.

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