1 **Aquatic invertebrate communities in tank bromeliads: how well do classic ecological**
2 **patterns apply?**
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19 **Summary**
20 Tank bromeliads (Bromeliaceae) often occur in high densities in the Neotropics and represent a
21 key freshwater habitat in montane forests, housing quite complex invertebrate communities. We
22 tested the extent to which there are species richness–altitude, richness–environment, richness–
23 size, richness–habitat complexity and richness–isolation relationships for the aquatic invertebrate
24 communities from 157 bromeliads in Cusuco National Park, Honduras.

25 We found that invertebrate species richness and abundance correlated most strongly, and
26 positively, with habitat size, which accounted for about a third of the variance in both. Apart from
27 bromeliad size (equivalent of the species–area relationship), we found remarkably little evidence
28 of classic biogeographic and ecological relationships with species richness in this system.
29 Community composition correlated with altitude, bromeliad size and position, though less than
30 20% of the variation was accounted for by the tested variables. The turnover component of
31 dissimilarity between the communities correlated with altitude, while the nestedness-resultant
32 component was related to bromeliad size. The unexplained variance could reflect a large
33 stochastic component in the system, associated with the ephemerality of the habitat patches (both
34 the plants themselves and the fluctuations in their water content) and stochasticity due to the
35 dispersal dynamics in the system.

36 We conclude that there is a small contribution of classic biogeographic factors to the
37 diversity and community composition of aquatic invertebrates communities in bromeliads. This
38 may be due to the highly dynamic nature of this system, with small patch sizes and high
39 emigration rates. The patterns may mostly be driven by factors affecting colonization success.
40
41 **Introduction**
42 Bromeliads (Bromeliaceae) are a characteristic component of Neotropical forests. Found from
43 ground level to high in the canopy, they contribute significantly to the habitat complexity
44 (Benzing, 2000), in particular for invertebrates. Bromeliads in a large subset of the family, called
45 tank bromeliads, are capable of holding considerable quantities of water in their leaf axils,
46 creating aquatic habitats that are inhabited by aquatic invertebrate communities (Fish, 1976;
47 Greeney, 2001; Frank and Lounibos, 2009). Tank bromeliads can occur in high densities, and,
48 based on their three-dimensional distribution in forests, may be the phytotelm (plant-held water
49 body) habitat occurring in the highest densities anywhere. For example, Sugden and Robins
50 (1979) recorded a mean density of 17.5 plants per square metre of ground area in a cloud forest in
51 Colombia. If the volume of water retained per plant is on average of the order of 100 cm³ (the
52 average for the bromeliads in our data), then such densities translate into tens of thousands of

litres of water available for colonization by aquatic animals, per hectare. In the absence of other lentic water bodies, as is often the case in mountainous tropical forest areas, phytotelm habitats provide an important freshwater habitat. The profusion of bromeliads, and their use as breeding habitats by vectors for human diseases such as malaria and dengue, render bromeliads important from a range of perspectives. In addition, bromeliads represent self-contained aquatic communities for the aquatic stages of invertebrates, present naturally and at high replication, making them potentially valuable as a study system for tackling prominent ecological and evolutionary questions (Srivastava et al., 2004). Well-defined aquatic communities occurring in clusters are highly suitable for studying metacommunity dynamics (Leibold et al., 2004). Further, bromeliads can be effectively imitated by artificial containers (Srivastava, 2006). These features allow easy manipulation and great flexibility in research design.

Despite the great advantages conferred by tank bromeliads, knowledge of their aquatic invertebrate communities, and what structures them, remains limited—even though research on aquatic invertebrates in phytotelmata dates back at least to 1915 (Picado, 1915; see also Laessle, 1961; Maguire, 1971; Frank and Lounibos, 1983; Kitching, 2000). Most studies on aquatic invertebrates in bromeliads to date have focused on cataloguing species not previously known in phytotelmata (e.g. Mendes et al., 2011). Recently, however, ecological studies have started to contribute to the understanding of this habitat (e.g., Armbruster et al., 2002, Jabiol et al., 2009; Brouard et al., 2011).

The highly dynamic nature of the system (the plants have limited life spans and there can be considerable drying and wetting), and the wide environmental range in which bromeliads are found, mean a lot of variability. This variability offers considerable opportunities but also complicates the study of (invertebrate) community-structuring mechanisms. Additionally, the mixing of terrestrial and (semi-)aquatic components of invertebrate communities hampers straightforward interpretation of results. Earlier ecological bromeliad invertebrate studies included both terrestrial and aquatic species, analyzing them as single communities (e.g., Cotgreave et al., 1993). Although terrestrial–aquatic links are present (Cereghino et al., 2011), the two components are structured differently and should ideally be analysed separately if both groups are included in the study. Tank bromeliads represent discrete habitat units for aquatic invertebrates, but less so for most terrestrial invertebrates. A large proportion of the terrestrial invertebrates found in bromeliads comprises occasional vagrants, increasing noise in analyses. Also, the very high diversity of terrestrial invertebrates in tropical forests presents formidable challenges in terms of identification, typically pushing the taxonomic resolution to ecologically less interesting levels such as that of the family. Ecological studies aiming to unravel community structuring should take these differences into consideration, and for all of these reasons, we restrict our analyses herein to aquatic invertebrates.

Bromeliads can be seen as islands of aquatic habitat in a forest matrix and results from recent studies indicate that these communities fit with at least one well-established biogeographic pattern for islands: the species (richness)–area relationship. Jabiol et al. (2009) found that aquatic insect richness and abundance were positively associated with water volume, a proxy for island/habitat size. In studies considering both terrestrial and aquatic invertebrate communities, positive correlations between invertebrate species richness and bromeliad size have been observed (Armbruster et al., 2002; Montero et al., 2010). Apart from this, little is known about the extent to which aquatic invertebrates in bromeliads follow classic island biogeographic patterns, such as the species–isolation and species–altitude relationships. Altitude, for example, is known to affect species richness in a wide range of taxa and habitats globally (Rahbek, 1995; McCain, 2007). Further, the extent to which these aquatic bromeliad communities are structured according to classic ecological and biogeographic rules remains fragmentarily evaluated: environment (often measured as productivity; Field et al., 2009) and habitat complexity (Hortal et al., 2009) are also

factors affecting species richness in many taxa around the world. For bromeliad invertebrate communities, some studies point towards the importance of light and organic material (a proxy for productivity; Srivastava et al., 2008) in influencing community assembly (e.g. Dezerald et al., 2013). Habitat complexity, measured as the number of leaves, may affect the invertebrate system, as judged by results combining terrestrial and aquatic components (Armbruster et al., 2002).

Much island biogeography theory, including the classic 'equilibrium theory of island biogeography' (ETIB, MacArthur and Wilson, 1967), is based on the idea that species richness on an island (whether a true island or a habitat island) is the result of a dynamic equilibrium between influx and local loss of organisms. Influx includes both colonization from an external source pool and local addition through speciation. Loss of species may result from both emigration of individuals and the deaths of individuals culminating in local extinction. The ETIB focuses on immigration and local extinction, and not speciation (which we do not consider relevant for our dataset, and do not consider further) or emigration. It also assumes some dispersal limitation from the source pool to the island. Bromeliads, although easily recognised as insular habitat patches, may have a differing relative importance of processes to those that underlie the ETIB and related theories. During the aquatic phase of the invertebrates' life-cycles, dispersal limitation is likely to be very strong, especially for the active dispersers, many of which actively avoid leaving the bromeliads at this stage. However, once they have emerged as flying insects, the distances between bromeliads may present almost no barrier to dispersal; instead, limitation may be mainly due to their ability to locate suitable habitat, and this may favour colonization of large bromeliads and those in clusters. In terms of species loss, although competition may play a role, we consider predation (particularly for passive dispersers) and emigration (particularly for active dispersers) to be far more important. It is of interest to ask whether both the different colonization dynamics and the substitution of emigration and predation for demographic extinction are associated with similar biogeographic patterns to those associated with islands more closely matching the assumptions of the ETIB.

A long-term, time-series dataset would be ideal for analysing the processes associated with influx and loss of species in bromeliads. However, investigating patterns of community composition should yield interesting results that are informative about community assembly. For example, the separation of species replacement (turnover) and species loss without replacement (nestedness) when comparing communities, gives insight into community structuring factors (Baselga, 2010). Nestedness of species assemblages—when the lists of species in species-poor communities are subsets of those in species-rich communities—reflects a non-random limitation of species in a community, which could be driven by habitat size or colonization limitation. Spatial turnover— the replacement of some species by others through space—could result from environmental sorting or dispersal constraints. More generally, examining altitudinal and environmental relationships addresses key aspects of biodiversity patterning (Rohde, 1992), reflecting the fact that bromeliads represent independent replicates of aquatic invertebrate communities.

We investigate classic ecological and biogeographic relationships for a large sample of naturally occurring bromeliad aquatic invertebrate communities in montane tropical forest, including cloud forest, in Honduras. . We test the following specific predictions. (1) Larger bromeliads are occupied by more species (equivalent to the species–area relationship). (2) More isolated bromeliads (from other bromeliads) contain fewer species (species–isolation relationship). (3) Bromeliads with more leaves contain more species (habitat heterogeneity hypothesis). (4) There is a positive relationship between detritus content (productivity hypothesis) and species richness. (5) There is a negative relationship between altitude and species richness. In addition, we analyze ecological community structuring parameters in a metacommunity setting, again in relation to size, isolation, altitude, habitat complexity and environmental variables. To gain a better insight into the processes underlying tank bromeliad meta-community patterns and test how well these

157　communities follow island biogeographic patterns, we include an analysis of the dissimilarity
158　between the component communities (beta diversity), partitioning it into turnover and nestedness-
159　resultant components (Baselga, 2010).
160
161　**Material and Methods**
162　*Field site*
163　The bromeliad sampling took place from June to August 2006 and 2007 in Cusuco National Park
164　(CNP), situated in the Merendon Mountain range in north-western Honduras. The core zone of the
165　park consists of lower montane tropical rain forest (a mix of primary and secondary), with patches
166　of primary cloud forest and upper montane rain forest characterized by high densities of
167　bromeliads. We collected 157 bromeliads from five main sampling areas (centred on the field
168　camps 'Base Camp', 'El Cortecito', 'Guanales', 'El Danto' and 'Cantiles'). For a detailed
169　description of the area and permanent sampling lines, see Field and Long (2007).
170
171　*Sampling protocol*
172　In order to minimize the influences of physical structure and possible biochemical differences
173　between species, we only sampled individuals of *Tillandsia guatemalensis* Smith. This is one of
174　the more abundant bromeliad species in CNP, with enough water to accommodate aquatic
175　invertebrate communities. We sampled invertebrate communities completely, by dismantling each
176　bromeliad, leaf by leaf. For a fuller description of the sampling protocol, including the
177　randomization procedure, see Jocque et al. (2010a). We only sampled bromeliads large enough to
178　contain water, which translated into minimum leaf spread of 18 cm, all but four being 20 cm or
179　larger.
180
181　Before sampling each bromeliad, we recorded a range of environmental variables: altitude
182　("altitude", in metres above sea level), attachment height on the tree ("attach"), the width
183　("width") and height ("height") of the bromeliad, the number of other bromeliads within a two-
184　metre radius ("R-Brom"), the amount of light ("light", openness of the canopy, ten-point scale)
185　and the openness to receive water from precipitation ("rain", effectively an inverse shelter
186　measure, ten-point scale). The attachment height on the tree was measured as the shortest distance
187　in cm between the forest floor and the underside of the bromeliad core. The bromeliad core is the
188　central axis where all leaf bases join, and is also the origin of the roots (or 'holdfasts' because
189　they are only used for attachment). For plant width and height we measured from the point of
190　water catchment on the leaves: leaves are angled upwards from the core of the plant until they
191　(particularly outer leaves) bend downwards from the weight of the leaf. Up to this point of
192　bending downwards, the water intercepted by the leaves runs into the leaf axils; beyond that point
193　most water does not run into the tank of the bromeliad. We measured the width of the plant as the
194　largest horizontal distance between the water catchments points of two opposing leaves (cm). We
195　measured the height of the plant from the base of the bromeliad core to the highest water
196　catchment point (cm). We counted the number of other bromeliads on the same tree as the
197　sampled bromeliad, and also on the trees within a two-metre radius. In 2007 we additionally
198　stratified sampling of bromeliads, into two types: individuals that were the only bromeliad
199　attached to the tree (SOLO) and individuals that were one of at least two bromeliads attached to
200　the same tree (MULTI). In MULTI, we targeted bromeliads that were underneath others on the
201　tree, thus allowing dispersal into them via water flow from other bromeliads. This was mostly
202　geared towards the dispersal of the passive dispersers (Ostracoda and Anomopoda).
203
204　After the measurement of these variables in the field, we placed each sampled bromeliad in a
205　bucket and transported it to the nearest camp for immediate processing. We collected the water
206　contained and then took the plant apart, leaf by leaf, rinsing every leaf with 64 µm-filtered river
207　water. During this process, we measured additional variables: amount of water held by the plant
208　(ml), the total number of leaves, fresh weight of the cleaned plant (g) and circumference of the

209 core (mm). The total number of leaves comprised all the green leaves and the leaves with at least
210 the base still green. All washed parts of the plant were weighed with a 500 g Pesola spring meter,
211 once excess water had been removed. We measured the circumference (mm) of the bromeliad
212 core after removing the leaves. Animals were picked out alive from the rinsing water, and fixated
213 in 70% ethanol. After removing all the invertebrates, we manually removed the larger organic
214 debris and then filtered the rest using a 22 µm sieve, to determine detritus content (g). We
215 processed the invertebrates in a laboratory using an OLYMPUS SZX-12 stereomicroscope and
216 identified all to morphospecies; full species identification (and description, in some cases, e.g.
217 Mendes et al., 2011) is ongoing and gives us confidence in the matching of our morphospecies to
218 known species.
219
220 *Statistical analyses*
221 To test predictions 1–5 we first examined linear correlations between all variables. When needed
222 to remove skew and normalize the errors associated with best-fit lines, we either square-root or
223 log transformed variables for further analysis. We used regression to determine the individual
224 contributions of the recorded variables relevant to predictions 1–5, in accounting for the variation
225 in both richness and total abundance. To assess whether any improvement could be made on the
226 simple model for species richness resulting from this exploratory analysis, we used multi-model
227 inference. This ran 16,383 regression models, comparing all against each other using Akaike's
228 Information Criterion (AICc). Many of the potential explanatory variables were highly collinear,
229 particularly measures of bromeliad size and measures of bromeliad position. We therefore ran
230 principal components analyses (correlation method) of these two groups of variables, to create
231 two orthogonal principal components of each phenomenon; in doing so, we square root-
232 transformed most of the variables, to reduce or remove skew.
233
234 Complementary to the correlations with richness and abundance to test predictions 1-5 we
235 analysed community composition using both ordination and analysis of beta diversity. In
236 ordination, the choice of linear or unimodal analysis methods is traditionally based on the amount
237 of variation present in the dataset, reflected as the length of the environmental gradient. Because
238 the environmental gradient in our dataset was less than four, we opted for the linear response (ter
239 Braak and Smilauer, 2002). We used the linear direct analysis (RDA) with forward selection
240 based on 999 Monte Carlo permutations to build a model. We square root-transformed the
241 abundance data to reduce the impact of high abundances. We standardized species abundances
242 (dividing them by the standard deviation of values) to focus on community composition. We also
243 removed rare species (defined as only 1 or 2 individuals in the total dataset) from the analysis;
244 these were three beetle species, a chironomid, a culicid, two Diptera and a copepod species. We
245 included all the measured variables in the initial analyses and, using a forward selection
246 procedure, isolated the factors accounting for the most variance in the dataset.
247
248 When examining for possible effects of altitude (prediction 5), as well as correlating diversity
249 with the continuous altitude data, we looked for patterns in diversity in altitude categories. The
250 altitudinal range was from 1347 m to 2084 m, but samples were not equally spread over all
251 altitudes. We used four categories: <1500; 1500-1600; 1600-1900; >1900. Based on the lowest
252 number of bromeliads sampled in a category (18 below 1500 m), we reduced all the other groups
253 to 20 bromeliads, selecting bromeliads randomly. We then used Kruskal–Wallis tests to test for
254 any differences between the altitudinal categories, for Shannon, Simpson and Margalef diversity,
255 average species richness, dominance Index, evenness and total richness.
256
257 To gain insight into the underlying metacommunity structuring processes, we partitioned beta
258 diversity following the method of Baselga (2010). Splitting overall beta diversity into its (spatial)
259 turnover and nestedness components allows the identification of species replacement or species
260 loss, respectively, as driving factors in community assembly (Baselga, 2010). We used the

261 'betapart' package in R. This calculates the pair-wise Sorensen dissimilarities between all the
262 bromeliad communities (overall dissimilarity or 'beta diversity'), and partitions that into its
263 turnover (Simpson dissimilarity) and nestedness-resultant components. The part of the Sorensen
264 dissimilarity that is due to nestedness rather than turnover is simply the difference between the
265 Sorensen and Simpson dissimilarity measures. We repeated this analysis using Jaccard
266 dissimilarity measures, but because both gave qualitatively identical results in all cases, we focus
267 mainly on the Sorensen–Simpson method. We thus obtained a series of six distance matrices (of
268 pairwise dissimilarities: Sorensen, Simpson, nestedness (Sorensen minus Simpson), Jaccard,
269 Jaccard turnover, Jaccard nestedness), each of which we then correlated with a matrix of
270 geographic distances between the bromeliads, using Mantel tests in the R package 'vegan', with
271 999 permutations to determine significance. We repeated this for other types of environmental
272 distance, focusing on correlating the six sets of community dissimilarities with pairwise
273 differences in altitude, bromeliad size and bromeliad position.
274
275 For statistical analyses we used R (Rstudio, Inc. 2012), STATISTICA (StatSoft, Inc. 2012) and
276 SAM (Spatial Analysis in Macroecology, Rangel et al., 2006).
277
278 **Results**
279 For this study we recognized 42 (morpho)species (Table 1). Ongoing determinations have resulted
280 in a more conservative identification of the recognized morphospecies, with reductions of the
281 numbers of species in the Chironomidae (2), Tipulidae (2), Culicidae (5), Syrphidae (4) and the
282 additions of a Psychodidae species and a copepod, compared to a previous study on the same
283 bromeliads (Jocque et al., 2010a).
284
285 The correlation matrix of the measured variables (Table 2) suggests no correlation between
286 species richness or total invertebrate abundance and detritus content (refuting prediction 4),
287 altitude (refuting prediction 5), attachment height or the number of nearby bromeliads
288 (inconsistent with prediction 2). It also indicates two blocks of correlated explanatory variables.
289 The first is all factors associated with phytotelm size and complexity: weight, width, height, core
290 diameter, water content, detritus content and number of leaves. Weight was by far the strongest
291 correlate ($r = 0.95$) of the first axis of the principal components analysis of these variables, this
292 axis accounting for 62% of the variation in the data. The second block of correlated variables
293 includes factors associated with the positioning of the bromeliad in the environment: the openness
294 to light and rainfall and the number of other bromeliads nearby (Table 2). From the positional
295 variables in the second group, the estimated exposure to light and rainfall were the only variables
296 correlating significantly with species richness, but each only accounted for 4% of the variance in
297 species richness.
298
299 Of all the putative explanatory variables, the total fresh weight of the leaves ('weight') correlated
300 most strongly with both species richness and the total number of individuals (abundance) in the
301 bromeliads (Table 2). This supports prediction 1. Log-transformed weight accounted for slightly
302 more of the variation in richness ($r = 0.58$, $r^2 = 0.33$) than the untransformed (Figure 1). In a
303 partial regression using log(weight) and the number of leaves as explanatory variables, while 11%
304 of the variation in species richness was accounted for uniquely by bromeliad weight, only 0.4%
305 was uniquely accounted for by the number of leaves and this contribution was not significant;
306 shared explained variance was 22%. Very similar results were obtained when analysing total
307 abundance of invertebrates, rather than species richness. This is inconsistent with prediction 3.
308 The correlation between species richness and log(weight) was also stronger than that between
309 species richness and the first axis from the principal components analysis on all the size variables.
310 Further, no combination of explanatory variables improved on log(weight) alone, in accounting
311 for variation in species richness, as judged by Akaike's Information Criterion (AICc) in multi-
312 model inference. This supports prediction 1 and is inconsistent with predictions 2–5.

313
314 A large number of recorded environmental variables together accounted for a relatively small
315 proportion of the community composition in our dataset. The forward selection of the linear
316 redundancy analyses (RDA) isolated altitude, water, number of leaves, total weight of the
317 bromeliad, exposure to precipitation, the total number of bromeliads, detritus content and
318 attachment height of the bromeliads as the strongest explanatory variables (Figure 2), in total
319 accounting for 20% variation of the dataset (sum of all canonical eigenvalues = 0.200, F = 4.563,
320 *p-value* =0.001). In the biplot of species and environmental variables, three groups of variables
321 can be distinguished, with particular species associated with them (Figure 2). One comprises
322 variables measuring the size and complexity of the bromeliad habitat (number of leaves, detritus
323 content, plant weight and the water content). Most of the species associated with variation in these
324 variables are Diptera. The second group contains two position variables: attachment height of the
325 bromeliad on the tree and the exposure to rainfall. Most strongly associated with these variables
326 are passive dispersers (the two ostracod species and the two water fleas). The final group is only
327 altitude, which is most associated with several species of Diptera.

328
329 The results of the beta diversity partitioning are shown in Table 3 and nicely complement the
330 ordinations. The dissimilarity in species composition between bromeliads was positively
331 correlated with both the difference in altitude and the difference in size between bromeliads. It
332 was the turnover component that correlated with altitude and the nestedness-resultant component
333 that correlated with bromeliad size. Thus, invertebrate species tended to replace each other along
334 the altitudinal gradient, while dissimilarity related to bromeliad size was due to smaller
335 bromeliads tending to contain a subset of the invertebrate species found in larger ones. These
336 relationships were quite weak, but strongly significant (Table 3). The correlations with geographic
337 distance were qualitatively identical to those with altitudinal distance, but were quantitatively
338 much weaker and less significant, suggesting that the trend with geographic distance was an
339 indirect result of the altitudinal relationship. Indeed, using partial Mantel tests, when controlling
340 for altitudinal differences no significant correlations between dissimilarity and geographic
341 distance remained, while the correlations with altitude remained almost unchanged when
342 controlling for geographic distance. This suggests no effect of geographic distance in our study
343 system.

344
345 Based on the selection of altitude in the multivariate analysis, its importance in the beta diversity
346 analysis, but its lack of significance in the species richness analysis, we examined possible
347 altitudinal patterns in various measures of species diversity, using our four altitude categories (see
348 Methods). Again refuting prediction 5, we found no significant differences between the categories
349 in any of species richness (H = 1.345, *P* = 0.718), total abundance (H = 0.273, *P* = 0.435),
350 Shannon–Weiner (H = 2.85, *P* = 0.415), Margalef (H = 1.13, *P* = 0.770) or evenness (H = 4.76, *P*
351 = 0.190).

352
353 Finally, species richness did not differ (F = 0.005, p = 0.941) between isolated phytotelmata
354 (SOLO) and phytotelmata occurring in clusters (MULTI) (prediction 2). Nor did community
355 composition differ between the two, as judged by RDA analysis, either with SOLO versus
356 MULTI as the single explaining variable (total sum of the eigenvalues = 0.015, F = 0.774, *P* =
357 0.687) or additionally with the different sampling locations as a covariable (total sum of the
358 eigenvalues = 0.015, F = 0.888, *P* = 0.554).

359
360 **Discussion**
361 With the exception of the influence of habitat patch size, there is remarkably little evidence of
362 classic biogeographic and environmental relationships affecting the diversity in the aquatic
363 invertebrate bromeliad system. These observations support the notion that bromeliads, although
364 easily recognised as an insular habitat system (eg Richardson 1999), do not follow the classic

island biogeography theory in a strict sense. After the publication of the ETIB in 1967, the concept was applied to a wide diversity of habitats with insular characteristics. This was further reinforced by application of the metacommunity concept (see Leibold et al. 2004), a conceptual framework based on well delineated communities. The small community size, temporal instability and highly dynamic colonisation and emigration of most of its inhabitants position the bromeliad phytotelm rather near one extreme of a habitat continuum to which the theory could be applied. In particular the high emigration rate (associated with the emergence of the insect larvae) sets this habitat apart from most other island habitats to which island biogeographic theories (generally) are applied. The dynamics of the insect-dominated invertebrate communities leave little room for extinction or speciation to play significant roles in individual bromeliad communities, and their richness is probably due largely to factors determining the colonisation of bromeliads. The dynamics of the passively dispersing members in these communities are expected to be quite different. Previous research on Ostracoda in Jamaican bromeliads (Little and Hebert 1996) recorded a high diversification rate in bromeliads, most probably due to the limited dispersal between bromeliad clusters of these organisms. This subset of the bromeliad invertebrate communities could lean more towards the classic ETIB. In our system this was difficult to test because of the limited occurrence of microcrustaceans in the sampled bromeliads.

The species–area relationship is the most pervasive of the classic relationships assessed in this study, and it was by far the strongest physical or geographic determinant of either species richness or abundance in the invertebrate communities we analyzed. The size of the bromeliad (600 g range in fresh weight) was positively related to the number of species in the community (Figure 1), a semi-log relationship typical of a species–area curve. Size accounted for about one third of the variance in species richness. This is consistent with prediction 1 from the biogeographic theory. The strong inter-correlation of the variables measuring bromeliad size suggests that most of those could be used reliably to quantify habitat size. About a quarter of the invertebrate species in our data tended to be found more in larger bromeliads; in most cases this remained true after accounting for the number of species in the community (by regressing abundance on bromeliad size with species richness as a covariate, on a species-by-species basis). This is also reflected in the relationship between bromeliad size and the nestedness component of community dissimilarity: smaller bromeliads tend to lack some species found in larger ones.

The positive relationship between phytotelm size and community size or structure supports previous findings, both for bromeliad communities specifically (Richardson 1999) and for aquatic communities more generally (e.g. Srivastava and Lawton, 1998; Kitching, 2000; Armbruster et al., 2002; Frank et al., 2004). Mechanistic interpretation of this association, however, is not straightforward because habitat size is strongly collinear with various likely influences, as is usually the case. Mechanistic elements associated with habitat size that are often thought to affect community size and structure include a larger target for dispersing individuals or any component of size that positively influences colonisation, larger populations and thus smaller extinction probability, and greater habitat complexity or diversity (e.g. Hortal et al., 2009).

For invertebrate communities inhabiting bromeliads, the number of leaves is often used as an indicator for the complexity or diversity of the bromeliad habitat (Srivastava et al., 2006). The aquatic habitat in the phytotelm is composed of many small compartments, associated with the individual leaves, arranged in a spiral, and one relatively large central compartment at the centre. These compartments are isolated in the sense that they collect their own water and organic debris but are all connected in that most aquatic organisms can move from one leaf-axil compartment to the next. Aquatic invertebrate species in bromeliads such as mosquito larvae partition space in bromeliads to co-exist (Gilbert et al. 2008) and a more complex habitat is expected to be able to house more diverse communities. In our data, while the number of leaves did correlate positively with species richness (Table 2), in partial regression this variable did not significantly add to the

variation accounted for by weight, while weight added a lot to the variation accounted for by the number of leaves. Very similar results were obtained when analyzing total abundance of invertebrates, rather than species richness. These results suggest that habitat size, rather than habitat complexity, is what matters for the size and structure of the aquatic invertebrates living in the bromeliads—consistent with prediction 1 but not prediction 3.

While the diversity in larger habitats can be a direct result of better survival of populations, with the larger habitat size allowing larger populations, which tend to persist longer, it is more plausible that the driving factors behind community structure in bromeliads is associated with the factors affecting the colonisation of the habitat patch. Larger aquatic habitats may have higher immigration because they represent a larger target (Dodson, 1992) or there might be active selection, whereby individuals select the larger habitat patches because this increases survival chances—a behaviour observed in other aquatic invertebrates (Binckley and Resetarits, 2005) and also for Odonata in bromeliads (Srivastava et al. 2008). Also the exposure time to colonisation could play a role. Larger bromeliads are typically older ones, available for colonisation longer. However, the highly dynamic nature of aquatic invertebrate communities in bromeliads, with most larval stages emerging and emigrating, and thus communities being reassembled frequently, may decrease the effect of longer exposure to colonisation. Older bromeliads are also usually the ones with more leaves, and this did not add to size in accounting for species richness or abundance.

The strong colonization–emigration dynamics also suggest a strong rescue effect (Brown and Kodric-Brown, 1977). However, the strongest correlate of species richness in our dataset was total abundance ($r = 0.71$ using log(abundance)), which was related primarily to bromeliad size. The population size mechanism may operate partly through a sampling effect, with more colonizing individuals representing more species by neutral or random assembly. We suggest that this might operate in combination with a preference for larger bromeliads, disproportionally decreasing the immigration to smaller bromeliads.

Inconsistent with prediction 2 (species richness–isolation relationship), we found no significant spatial structure in our species richness data. On a very local scale, positioning of the phytotelm (relative to water and resource inputs and other bromeliads) had little or no relationship with the overall invertebrate community, but was relevant for the passive dispersers (Crustacea). The number of bromeliads in the cluster (within 2 m) affected the community composition but there was no effect of presence/absence of other bromeliads on the same tree. On a larger spatial scale, geographic distance (9 km range) appeared to have no effect on species richness or community composition.

Altitude was not correlated with species richness or abundance, inconsistent with prediction 5. This was despite the 800-m altitudinal range sampled, which in ecological terms is very significant: from the lowest occurrences of bromeliads (in numbers greater than the odd scattered individual) to the upper montane dwarf forest at the highest altitude in the study area. Other overall diversity-related parameters (species diversity, evenness) did not vary significantly with altitude, nor could we detect the mid-altitude diversity bulge that occurs commonly in altitudinal studies (Rahbek, 1995, 2005). Currently, consensus on the mechanisms driving this pattern remains elusive, but climatic variables and an area effect are dominant elements in the discussion (Grytnes & McCain, 2007; McCain, 2007; Karger et al., 2011). In our study area, both climate and area change markedly with altitude—area because the mountains are approximately conical in shape. Temperature and evaporation decrease with altitude, while humidity increases; the tops of the mountains in Cusuco National Park are typically in cloud. The north-west side of the mountain range, facing the Altantic Ocean, receives a particularly large amount of rainfall and has higher air humidity. Yet we found no significant relationship between altitude and species richness.

469 Altitude was, however, associated with beta diversity and community composition, with the
470 turnover component of community dissimilarity tending to increase with greater differences in
471 altitude between host bromeliads. This corresponded with a tendency (usually weak) for some of
472 the invertebrate species to occur primarily at either relatively low (some Dipteran larvae and a
473 Coleopteran) or relatively high altitudes (some Chironomid and Culicid larvae). Thus, although
474 the assemblage-level patterns seem invariant to altitude, some species replacement is evident.

476 Some studies on aquatic invertebrates suggest that bromeliad-specific local environment affects
477 insect communities (Ngai et al. 2008), in particular the availability of resources (Srivastava et al.
478 2008) (prediction 4). Bromeliads obtain their nutrients from the decomposition of organic material
479 that falls in the bromeliad (Richardson, 1999). The decomposing detritus is the main source of
480 nitrogen for epiphytic bromeliads (Reich et al., 2003), at least for shaded ones. Recent studies
481 show that food webs in exposed phytotelmata are driven by primary production; Srivastava et al.
482 (2008) found detrital mass to be a strong predictor of species richness in bromeliads. In our data,
483 although detritus content correlated strongly with bromeliad size ($r = 0.87$), its correlation with
484 total invertebrate abundance was much weaker ($r = 0.44$). Indeed, detritus content added nothing
485 to bromeliad size in accounting for variation in total abundance in a partial regression, and the
486 same was true when modelling species richness. The same was also true when adding any variable
487 related to bromeliad position (e.g. openness to light or rainfall input) to bromeliad size, in
488 regressions to account for variation in total abundance or species richness. We thus found no
489 evidence to support the idea that resource input is causing variation in community size or
490 structure, though other measures of resource input might provide such evidence.

492 Overall, surprisingly few variables had significant explanatory power and the overall variance in
493 community composition accounted for, using the measured physical and geographic variables in
494 this study, was relatively low (around 20%). This may be partly due to environmental factors not
495 recorded in this study. Possible candidates include primary production by bacteria and algae
496 within the bromeliads, though we would expect such an influence to be reflected in our detritus
497 variable. More meaningful representation of the positioning of the bromeliad plants in relation to
498 the forest canopy may provide some explanatory power. Even so, there is probably a large
499 stochastic component present in the system. Bromeliad-held aquatic communities may be highly
500 dynamic because of the ephemerality of the habitat patches, both the plants themselves and their
501 water content (which fluctuates, including a seasonal component). Most of the invertebrates
502 remain for a relatively short time, after which they emerge and emigrate from the phytotelm.
503 When dispersing, most inhabitants are therefore highly mobile, either flying or using dispersal
504 vectors that are highly mobile (Lopez et al., 2002). The importance of stochastic elements and the
505 absence of strong short-distance dispersal limitation are in keeping the lack of any differences in
506 diversity or community composition between bromeliads on trees host to no other bromeliads, and
507 those that are found in clusters—even for the passively dispersing species. Chance and stochastic
508 effects may therefore play a large role in these systems.

510 The low explanatory power of altitude and other measured environmental variables may also reflect
511 a lack of meaningful differences in habitat within the bromeliads, for the invertebrates inhabiting
512 them. Water temperature in bromeliads does vary with altitude, but also fluctuates considerably
513 both seasonally and on a daily basis (Jocque and Kolby, 2012). Such an environmental regime may
514 favour generalist species (Jocque et al., 2010b), rendering the environmental differences observed
515 in the study rather small for the study organisms. These considerations are important because the
516 system of bromeliad-held aquatic invertebrate communities appears to be an exception to the
517 dominant pattern of strong diversity and community-composition changes with altitude (prediction
518 5). Further, given the strongly increasing density of tank bromeliads with altitude (in the study area,
519 at least; Jocque et al., 2010a), the usual negative relationship between altitude and habitat area is
520 broken. That is, while mountains are typically conical, giving lower area of higher altitudinal bands,

521   the counteracting effect of increasing bromeliad density with altitude may cancel out, or perhaps
522   even reverse, the usual trend.
523
524   In conclusion, most classic biogeographic and ecological relationships appear not to apply to
525   aquatic invertebrate communities inhabiting bromeliads, perhaps because they are such a highly
526   dynamic habitat system characterized by small patch sizes. Only the species–area relationship was
527   strongly supported, and even this may have been mostly driven by factors affecting colonization.
528   Aquatic metacommunities in bromeliads (and other phytotelmata) may be highly suited to
529   research on the effects of colonization sequence and immigration rate on the stability of
530   community composition. Particularly interesting here would be to investigate priority effects (De
531   Meester et al., 2002), habitat selection and fixed colonization sequences.
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647 **Table 1.** Number of unidentified morphospecies recorded in the sampled bromeliads.

Class	Family	Genus	Species	No. of spp.
Diptera				6
	Chironomidae			5
	Ceratopogonidae	*Bezzia*		3
	Tipulidae	*Trentepohlia*		1
	Culicidae	*Culex*		1
	Culicidae	*Aedes*		2
	Culicidae	*Toxorhychites*		1
	Culicidae	*Wyeomia*		1
	Syrphidae	*Ocyptamus*		1
	Syrphidae	*Copestylum*		4
	Syrphidae	*Meromacrus*		1
	Psychodidae	*Telmatoscopus*		2
Coleoptera				5
	Scirtidae	*Scirtes*		1
Hemiptera	Mesoveliidae			1
Ostracoda	Limnocytheridae	*Elpidium*		1
	Candonidae			1
Branchiopoda	Daphniidae	*Ceriodaphnia*	*laticaudata*	1
	Chydoridae	*Alona*	*bromelicola*	1
Copepoda				1
Oligochaeta	Enchytraeidae	*Hemienchytraeus*		1
Turbellaria				1
Total				42

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Table 2. Correlation matrix of the explanatory variables, the species richness (S) and total Abundance (Abund) of invertebrates recorded in the sampled bromeliads. Values shown are Pearson's *r* for untransformed variables. Significance is indicated as * $0.05 > P > 0.01$, ** $0.01 > P > 0.001$, *** $P < 0.001$. Width, height and core (diameter of) all measure physical bromeliad size. Water content, weight (fresh weight of leaves), number of leaves and detritus content are also related to bromeliad size. Attachment height, access to light and rainfall, and the total number of bromeliads within a radius of 2 m (R-Brom) all quantify position in the forest canopy. The number of invertebrate species (S) and the total number of invertebrates (Abund) per bromeliad are response variables. Mean values with standard deviation (Stdev) and the maximum and minimum recorded values of each variable are presented at the lower part of the table.

	Width	Height	Core	Water	Weight	#leaves	Detritus	Attach	Light	Rain	R-Brom	S	Abund
Altitude	-0.26**	-0.26**	0.15	0.11	-0.11	-0.14	-0.07	-0.02	-0.26**	-0.15	-0.07	-0.1	-0.13
Width		0.55***	0.55***	0.45***	0.80***	0.63***	0.70***	0.11	0.18*	0.20*	0.15	0.48***	0.45***
Height			0.31***	0.18*	0.40***	0.30***	0.46***	0.01	0.37***	0.42***	0.28***	0.26**	0.33***
Core				0.39***	0.69***	0.47***	0.52***	0.16*	0.1	0.18*	0.11	0.42***	0.47***
Water					0.61***	0.52***	0.25**	0.05	-0.04	0.05	0.03	0.35***	0.32***
Weight						0.74***	0.74***	0.15	0.14	0.15	0.09	0.54***	0.49***
#leaves							0.54***	0.11	0.14	0.13	0.08	0.47***	0.32***
Detritus								0.09	0.08	0.14	0.11	0.45***	0.34***
Attach									-0.01	-0.07	-0.07	-0.01	-0.02
Light										0.83***	0.51***	0.19*	0.25**
Rain											0.62***	0.20*	0.31***
R-Brom												0.06	0.08
S													0.62***

	Width (cm)	Height (cm)	Core (mm)	Water (ml)	Weight (g)	#leaves	Detritus (g)	Attach (mm)	Light	Rain	R-Brom	S	Abund
Mean	37.3	12.8	8.8	83.3	174.0	26	28.2	140.1	4.1	3.2	13.0	8.0	55.8
Stdev	12.8	8.3	3.0	85.1	132.5	8	24.5	60.0	2.0	2.7	18.0	3.2	46.6
Max	84	52	27.5	410	613	49	130	369	8	9	114	17	227
Min	17	0	3.5	1	9	11	1	30	1	0	0	1	4

Table 3. Beta diversity partitioning: results of Mantel tests correlating pairwise dissimilarity of aquatic invertebrate communities inhabiting bromeliads with pairwise distance or differences in environmental variables. Size was measured as the first principal component of the size variables. Values given are Mantel's *r*, with significance indicated as * $0.05 > P > 0.01$, ** $0.01 > P > 0.001$, *** $P = 0.001$. P-values were derived from 999 permutations using the 'vegan' package in R, which returns the number of permutations in which the observed *r* is exceeded plus one, then divided by 1000; thus *** represents cases where none of the permutations exceeded the observed correlation. Because the 'P'-value returned is one-tailed, we have doubled it before binning into significance categories, to approximate two-tailed testing (note: this assumes a symmetric distribution of *r* in permutations; no cases were marginal). For negative correlations, we first subtracted the returned '*P*' from 1.

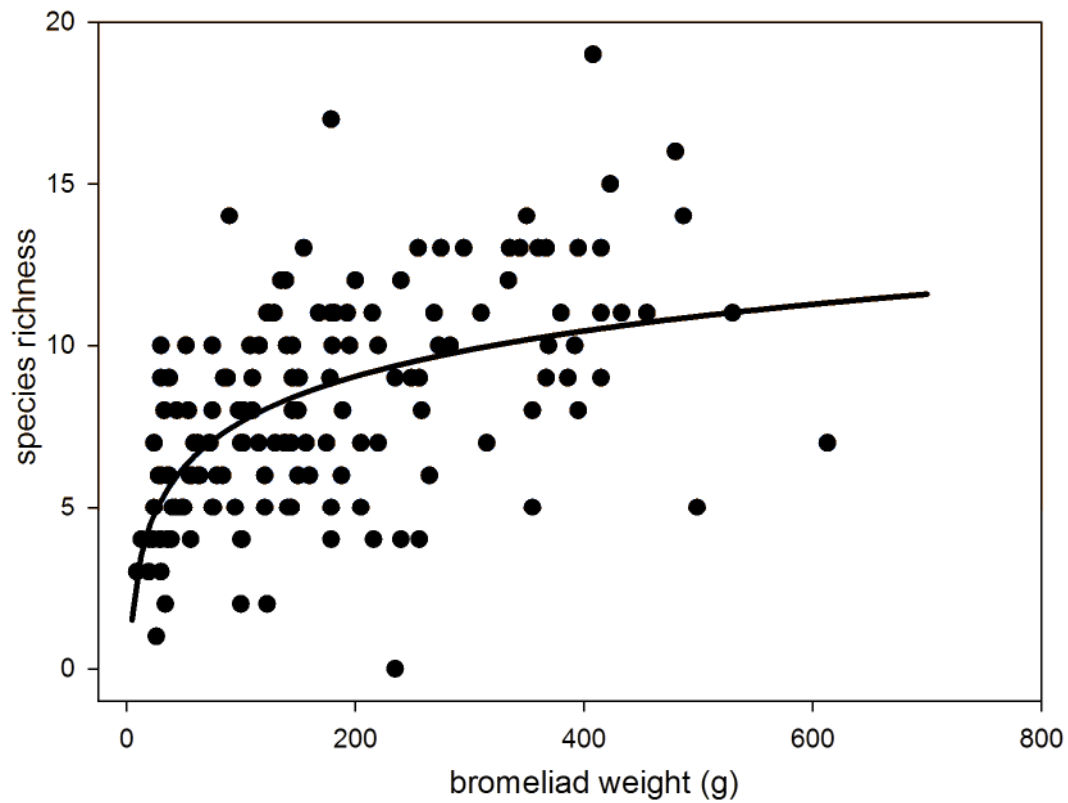| Dissimilarity measure	Geographic distance	Altitudinal distance	Size difference
Sorensen	0.05**	0.19***	0.16***
Simpson (turnover)	0.05*	0.16***	0.02
Nestedness-resultant	-0.01	-0.02	0.17***
Jaccard	0.06**	0.19***	0.16***
Turnover (Jaccard)	0.05*	0.14***	0.01
Nestedness-resultant (Jaccard)	-0.02	-0.03	0.12***

FIGURE 1. Scatter plot of species richness and total wet weight of the washed bromeliad leaves in grams. The correlation is significant and a semi-logarithmic fit is displayed (species richness = −1.66 + 4.65*log(weight)), which accounts for 33% of the variance in species richness.
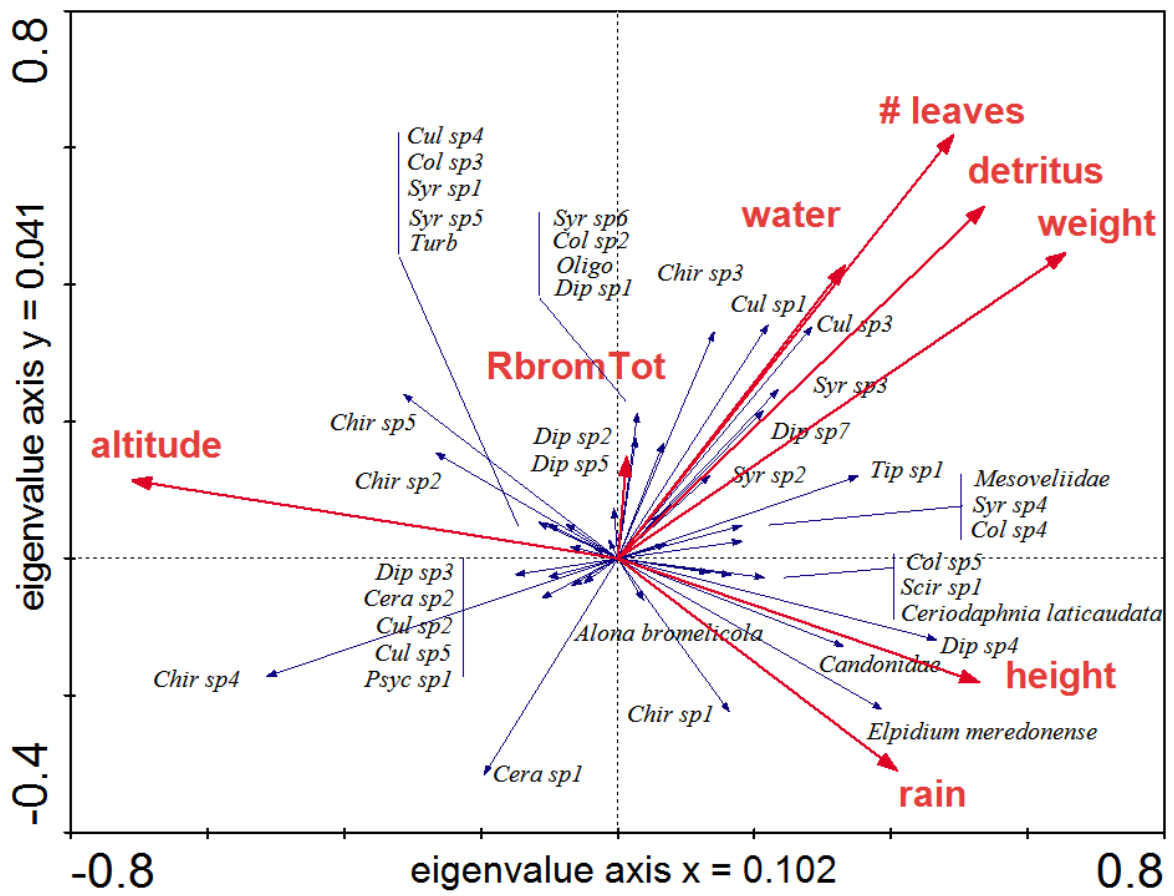
FIGURE 2. RDA biplot of the species and environmental variables. See Table 1 for a list of the species and Table 2 for explanation of the variable names.