

Are small water bodies inside epiphytic bromeliads breeding habitats for cacao pollinators?

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Abstract

Bromeliad plants are a common sight in the Neotropics. Within their leaf axils small water bodies form habitats for a diverse group of organisms. While the aquatic communities inside bromeliads are increasingly studied, relatively little is known about their composition in agricultural settings. In this survey, we studied bromeliad infauna in cacao agroforestry systems in Central Nicaragua. We analysed effects of morphometric and environmental variables on the community composition in different bromeliad morphotypes. Within these communities we focussed specifically on midges which have been reported as potential cacao pollinators. Thus far it is unclear how frequently and abundantly they occur in bromeliads in cacao plantations. Diversity patterns were mainly influenced by bromeliad volume and height above the forest floor. Species richness increased with volume and decreased with height, the latter particularly for passive dispersers. Potential cacao pollinators occurred in over 65 % of the bromeliads and were most abundant in bromeliads with big tanks that were located in the canopy rather than on the forest floor. Due to the high number of bromeliads that cacao plantations can support, they could potentially contribute to a substantial increase in pollinator densities.

Key words: Bromeliads; Cacao plantations; Invertebrates; Nicaragua; Phytotelmata; Pollinators

Highlights

- Potential cacao pollinators occurred in over 65% of sampled bromeliads

- 28 • Pollinator abundance highest in larger bromeliads in the cacao canopy
- 29 • Overall invertebrate richness higher in larger bromeliads closer to forest floor

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31 **Declarations of interest:** none.

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1. Introduction

Bromeliads (Bromeliaceae) are perennial plants that typically grow as stemless rosettes. Apart from one species that has reached Africa, bromeliads are constrained to the Neotropics, where they occur in a wide range of habitats in both urban and agricultural settings (Givnish et al., 2014). Most grow as epiphytes and many have a central tank and lateral leaf axils that can contain bodies of freshwater (*i.e.* phytotelmata) that can act as a habitat for diverse communities of invertebrates and amphibians (Frank & Lounibos 2009, Givnish *et al.* 2014). Some zooplankton taxa such as crustaceans and rotifers complete their entire life cycle inside bromeliads and rely on passive dispersal through phoretic hosts, water films on the host trees or wind dispersal to colonize new bromeliads (Jocque et al., 2013; Lopez et al., 2005). Others, such as amphibians and a wide range of insects, disperse actively and lay their eggs inside bromeliads where their larvae develop until metamorphosis (Frank and Lounibos, 2009).

Earlier work on bromeliads generally reported positive effects of the total water volume on diversity, abundances and biomass of aquatic invertebrates that live inside the central tank and leaf axils (Brouard et al., 2012; Dézerald et al., 2014, 2013). Presumably this is because a larger volume allows for more space and habitat complexity and reduces the risk of drying and might therefore be more attractive for oviposition (Jocque and Field, 2014). However, larger volumes also increase the likelihood that top predators such as damselflies or *Toxorhynchites* mosquitoes colonize, which could limit the abundances of some prey species (Hammill et al., 2015; Petermann et al., 2015). Other variables known to affect bromeliad infauna are the bromeliad species, morphometry of the phytotelm, the amount of detritus, exposure to sunlight and the geographic and altitudinal position of bromeliads (Brouard et al., 2012; Jabiol et al., 2009; Jocque and Field, 2014; Marino et al., 2013). However, none of these studies were performed in agroforestry systems or specifically focused on species that could act as pollinators of commercial crops such as cacao. Early work on cacao

pollination identified a variety of possible pollinators (Glendinning, 1972; Young, 2007), but the consensus nowadays is that the most important cacao pollinators are Ceratopogonidae biting midges of the genus *Forcipomyia* and Cecidomyiidae gall midges (Toledo-Hernández et al., 2017). Both taxa have been reported in bromeliads (Fish and Soria, 1978; Privat, 1979), among other types of larval habitats but it is unclear to what extent they are present or abundant in cacao agroforestry systems. In addition, these reports do not touch upon the ecological preferences of these taxa.

Cacao is one of the most important tropical cash crops and, besides from disease and nutrients, pollination is considered the main factor that limits production (Forbes and Northfield, 2017; Groeneveld et al., 2010). The trees are sciophilous, particularly when young, and are therefore typically grown under a canopy of shade trees (Carr and Lockwood, 2011). Such an environment is also beneficial for the growth of epiphytic plants including mosses, ferns, orchids and bromeliads. Cacao farmers often incorrectly assume that bromeliads are parasitic and remove them from their plantations. In doing so, the biodiversity associated with bromeliads is lost, together with other ecosystem services they provide. For example, preserving ant colonies associated with bromeliads promoted control of pest species in citrus plantations (Hammill et al., 2014). Despite indications that bromeliads might have positive effects on pollination, this remains to be demonstrated. A first step towards this goal would be to quantify how abundant larvae of cacao pollinators are in bromeliad phytotelmata and to test which types of bromeliads would be better sources of pollinators than others.

In this paper, we performed a field survey to investigate bromeliad phytotelm communities in four cacao plantations in central Nicaragua, with a specific focus on the larvae of potential cacao pollinators. We assessed diversity and abundance of the entire aquatic community – and more specifically the larvae of potential pollinators – and discussed the potential relevance of bromeliads as sources of these animals. In addition, we analysed which types of bromeliads may be more likely

to provide sources of pollinators than others. We studied communities in bromeliads with different tank volumes and from different bromeliad morphotypes because these may provide conditions suitable for different species or attract different sets of colonists. Since the height above the ground may be limiting for the dispersal of certain taxa we included bromeliads at different heights in the trees in our survey.

Consistent with earlier work, we expected invertebrate diversity to increase with higher volumes and this especially for some predatory taxa that appear to be positive size selective (Petermann et al., 2015). We also hypothesised that species richness would decrease with height above the forest floor as floor-level bromeliads might be colonised more easily than canopy bromeliads, especially by passively dispersing taxa. Since the ecology of the cacao pollinators' larvae is poorly known (Toledo-Hernández et al., 2017), we had no *a priori* expectations about their potential environmental or trophic requirements.

2. Material and Methods

In July 2016, we sampled the phytotelm communities of 35 bromeliads from four cacao plantations (13°17'35.51" N, 85°23'30.61" W; 13°17'39.99" N, 85°23'26.30" W; 13°21'49.12" N, 85°20'45.95" W; 13°18'03.95" N, 85°23'34.21" W) in the proximity of Waslala , one of the main cacao producing regions of Nicaragua (Trognitz et al., 2011). The area was deforested in the late 1990s, early 2000s and now consists of pastures and plantations with virtually no remaining forest. Of over 60 plantations visited in this region, only four had tank bromeliads on shade and cacao trees. In these plantations, we sampled bromeliads of two different morphotypes that differed in leaf structure, amount of leaf axils and the maximum water volume they could hold. Bromeliads of the first morphotype (A) have a large amount of narrow leaves that form small leaf axils and a small central tank, whereas those of the second morphotype (B) have a smaller amount of broad leaves that form

larger leaf axils and a large central tank (see Fig. 1). We acknowledge that despite the similar structure each morphotype may still comprise different bromeliad species; without flowers, species level and even genus level identifications is often not possible.



Figure 1 Bromeliad morphotypes used in this study: morphotype A on the left and morphotype B on the right.

Within each plantation, we sampled bromeliads of both morphotypes with a wide range of volumes and located both on the plantation floor and in the cacao trees. Maximum water volume of the sampled bromeliads ranged between 7 and 720 ml, 14 of the bromeliads occurred on the forest floor while 21 occurred in the trees at heights between 1 and 3.5 m above the forest floor. 21 and 14 bromeliads were of morphotype A and B, respectively. All sampled bromeliads were of epiphytic habit, with individuals on the forest floor growing on fallen branches. Bromeliads were sampled in a non-destructive way. We used tubes attached to syringes, both with orifice diameters of 4 mm, to suck out the water from the bromeliads, emptying their phytotelm as much as possible. Afterwards, bromeliads were slowly refilled to assess the maximum volume they could hold (hereinafter “volume”) and then emptied again to collect any remaining invertebrates. Samples (the initial content and the rinsing water) were filtered over a 45 μ m mesh and stored on 90% ethanol. Apart from the bromeliads’ volume, their morphotype, diameter, number of leaves and height above the forest floor (hereinafter “height”) were recorded. In the laboratory, all invertebrates (excluding

protists, rotifers and terrestrial taxa) were counted and identified under a stereomicroscope. Identifications were done based on Borkent and Spinelli (2007), Brown et al. (2009), Merritt et al. (2008). We also assessed the amount of fine particulate organic matter (POM) in the samples via sedimentation in cylinders (wet volume). The dataset was partitioned in groups representing passively (Copepoda, Ostracoda, Tardigrada, Oligochaeta, Nematoda, Acari and Turbellaria) and actively dispersing organisms (Diptera, Coleoptera, Lepidoptera). Predator taxa found were *Alluaudomyia* and *Bezzia* (Ceratopogonidae), Tanypodinae (Chironomidae), *Toxorhynchites* (Culicidae), Carabidae (Coleoptera), and Turbellaria. Based on literature and personal observations of taxa frequently visiting cacao flowers (Vandromme unpubl. data), we conservatively considered all ceratopogonids of the taxa *Forcipomyia* and *Alluaudomyia* and Cecidomyiidae as pollinators. Besides this “conservative list”, we also made a more liberal list of potential pollinators that additionally included orthocladid Chironomidae and Sciaridae. Although they are not typically considered as cacao pollinators, we observed these taxa on the staminodes of cacao flowers, suggesting they might be pollinators as well. We also included all other ceratopogonids in this liberal dataset, as these are often mentioned as pollinators (Toledo-Hernández et al., 2017) but were not observed in cacao flowers in our study system. Analyses were run both for the conservative and more liberal pollinator dataset.

2.1 Statistical analyses

Links between environmental variables and richness and abundance patterns of all taxa and of active and passive dispersers were inferred by building mixed models. In the case of the richness of all taxa and of passively dispersing taxa, which had normal error distributions, this was done with general linear mixed models. For the richness of active dispersers and the abundance of all taxa and actively and passively dispersing taxa, which were not normally distributed, this was done using generalised mixed models fit with Poisson error distributions as is appropriate for left skewed error distributions.

156 Similar generalised mixed models with Poisson distribution were run to link environmental variables
157 and the richness and abundance of potential cacao pollinators, for both the liberal and the
158 conservative datasets, as well as for a model predicting the richness and abundance of predators. In
159 both general linear mixed models and generalised mixed models, plantation identity was included as
160 a random factor to take into account that bromeliads in the same plantation may not be fully
161 independent. The main environmental variables corresponding to our hypotheses (volume, height)
162 were always included in the model as fixed factors. We explored a volume x height interaction to test
163 whether any effects of habitat size on both richness and abundance would become less important
164 when bromeliads are positioned higher in the trees. This might be the case when there are less
165 potential colonists there. Additionally, we explored potential influence of other environmental
166 variables by trying to add them step by step to the model. For all models, the environmental
167 variables tested were: volume, height, morphotype, diameter, number of leaves, and POM. Volume
168 was log-transformed to improve the assumption of homoscedasticity.

169
170 Redundancy analysis models (RDA; a multivariate extension of multiple regression) were constructed
171 to test for statistical effects of environmental variables on the community composition. For this
172 purpose, separate response matrices were assembled that contained Hellinger transformed species
173 abundances. This transformation improves reliability of ordination (Legendre and Gallagher, 2001).
174 Separate response matrices were made for all species, only active dispersers, and only passive
175 dispersers. Taxa occurring in three or less bromeliads were removed because interpreting
176 regressions based on less than four points is not robust. These taxa would increase the noise in the
177 model and may confound pattern detection. No RDA models were constructed for the potential
178 pollinators as the vast majority of the taxa occurred in only few bromeliads. Predictor variables
179 included volume and height, the main environmental variables corresponding to our hypotheses.
180 Plantation identity was specified as strata within the RDA to constrain permutations within

plantations and the significance of the models was tested using an F-test based on 999 Monte Carlo permutations.

All analyses were performed in RStudio version 1.0.153 (RStudio Team 2016) using the lme function (*nlme* package) for general linear mixed models, the glmer function (*lme4* package) for generalised mixed models and the rda function (*vegan* package) for RDAs. Graphs were produced using the ggplot (*ggplot2* package) and the ggarrange functions (*ggpubr* package).

3. Results

Overall, 63 taxa were found of which 31 occurred in four or more bromeliads. Diptera were by far the most diverse taxonomic group (45 taxa), followed by the Acari (7 taxa). 14 and 49 taxa were considered passive and active dispersers, respectively. Among the active dispersers, taxa considered as potential pollinators were found in 83% of bromeliads (17 taxa) and in 66% of the bromeliads (14 taxa) when they were more conservatively defined. A complete list of the invertebrate taxa found can be found in Supplementary Table 1.

Species richness in the sampled bromeliad communities was 11.34 ± 5.93 SD and ranged from 0 to 23. Mixed models show that total richness increased with bromeliad tank volume and decreased with height above the forest floor (see Table 1 for the results of all models; Fig. 2a). Similar positive effects of volume were found for richness of passive and active dispersers (Fig. 2c, 2d). The same decrease in richness with height above the forest floor was found in passive dispersers but absent in active dispersers. Species richness of potential cacao pollinators increased with volume regardless of whether they were liberally or conservatively assigned as pollinators (Fig. 4). When pollinators were conservatively defined there was a marginally non-significant trend of more pollinators in bromeliads that were located at greater height. A similar trend was observed when pollinators were more

liberally defined although this was not significant. The richness of predatory taxa was positively influenced by volume, but not by height (Fig. 2b).

The total abundance of all taxa and of active and passive dispersers was positively influenced by bromeliad volume and decreased with height above the forest floor. The interaction effect of volume x height was also found to be significant in all three cases. The positive effect of volume on abundance appears to be more pronounced for bromeliads in the trees as compared to those on the forest floor in the case of all taxa and the active dispersers (see Fig. 3a, c). For the passive dispersers, on the other hand, the positive effect of volume appears to be stronger in floor-level bromeliads, however this relationship was not very clear due to presence of a lot of scatter around the regression line (Fig. 4d). The abundance of potential pollinators also increased with volume regardless of whether they were defined in a conservative or liberal way. Height was positively associated with pollinator abundance in the liberal pollinator dataset, while for the conservative dataset, there was a significant main effect of height and also a significant volume and height interaction term. The latter suggests that large bromeliads found on the forest floor have lower potential pollinator abundances than their counterparts in the canopy with similar volumes, while for small bromeliads such differences were less evident (Fig 4).

Comparing the abundances of the two families included in the conservative list of pollinators, we found 8 individuals in floor-level and 5 in elevated bromeliads for cecidomyiid midges whereas for ceratopogonids we found 5 individuals in floor-level and 119 individuals in elevated bromeliads. In the liberal list we found an additional 6 Ceratopogonidae in the elevated bromeliads. The chironomids in this list were less abundant at floor-level (136 individuals) as compared to in elevated bromeliads (329 individuals) and Sciaridae were only found in elevated bromeliads (2 individuals).

The abundance of predatory taxa was higher in larger bromeliads and decreased with height. A significant volume x height interaction term indicated that the positive effect of volume on predator abundance was less pronounced for bromeliads on the forest floor compared to those in the canopy (Fig. 3c).

Redundancy analysis showed that the total community composition was significantly explained by both volume ($F = 4.916$, $p = 0.001$) and height ($F = 4.916$, $p = 0.001$) (overall model: $F = 2.312$, $p = 0.006$, $r^2_{\text{adj}} = 0.07$). The same was true for the passive dispersers (volume: $F = 2.741$, $p = 0.018$; height: $F = 5.423$, $p = 0.001$; overall model: $F = 4.008$, $p = 0.001$, $r^2_{\text{adj}} = 0.15$). In the case of the active dispersers, only volume was found to be significant ($F = 2.837$, $p = 0.006$), not height ($F = 1.787$, $p = 0.076$), although the overall model remained significant even with this variable included ($F = 2.312$, $p = 0.006$, $r^2_{\text{adj}} = 0.07$).

4. Discussion

In this paper, we investigated diversity and abundances of bromeliad infaunal communities within Nicaraguan cacao plantations with particular attention for potential cacao pollinators.

Overall, we found a remarkable heterogeneity in the composition of bromeliad infaunal communities. As expected, large bromeliads with large potential water volumes held higher abundances and more species, both in terms of active dispersers, passive dispersers and pollinators. Several processes can explain why, next to abundance, also richness is higher in larger bromeliads. Such positive effects of volume are commonly reported in bromeliad infauna studies (Dézerald et al., 2013; Jabiol et al., 2009; Jocque and Field, 2014; Marino et al., 2013). However, few studies try to explain these patterns. Jocqué and Field (2014) discuss multiple possibilities through which larger habitats can house more individuals representing more species. The authors argue that larger

bromeliads generally have more leaves and thus more water filled compartments in which invertebrates can potentially escape predators, reducing the risk of dying. They also argue that larger volumes could sustain larger populations, which are naturally less prone to extinction. However, because many bromeliad inhabitants spend only part of their life cycle inside bromeliads, emerging when reaching the adult life stage, Jocqué and Field argue that the main factor determining the increased richness with increasing volume may be a higher positive habitat selection for larger bromeliads. In the example of predators, previous studies have shown that exceeding a tank volume of about 140 - 200 ml, predators such as damselflies are more likely to establish. Proposedly this may be because the risk of droughts during their larval stage that lasts several months is lower in these bromeliads (Srivastava et al., 2008; Petermann et al., 2015). While damselflies were absent in our study, we observed the same pattern of increased predator richness and abundance in bromeliads with larger water volumes. This indicates that other predators than damselflies, with shorter larval stages, may show the same trend. Indeed, *Toxorhynchites* larvae, the top predator of bromeliad communities in our study region (personal observation), were only present in bromeliads with water volumes of 250 ml and up.

Richness and abundance also responded to height above the forest floor. In general, richness was lower in elevated bromeliads compared to bromeliads at ground level. For this at least two potential explanations can be formulated. First of all, it is possible that ground level bromeliads collected more detritus providing more food for detritivores at the basis of the food web. However, our estimates of fine particulate organic matter in the bromeliads do not support this. A second, more likely explanation is that elevated bromeliads are less easily colonized. This is supported by the fact that less passively dispersing taxa were found in canopy bromeliads as compared to in floor-level bromeliads. For actively dispersing taxa, this was not the case. Amphibians and reptiles are confirmed as dispersal vectors for ostracods and oligochaetes among bromeliads (Lopez et al., 2005) and possibly could also transport eggs or adults of other passive dispersers such as copepods

(Vanschoenwinkel et al., 2008). It is therefore likely that higher bromeliads are less likely to receive passive dispersers than bromeliads located closer to the forest floor, which may be more frequently visited by dispersal vectors. Some researchers mention wind as a potential vector (Jocque et al., 2013). However, wind dispersal of macrozooplankton has only been confirmed for temporary ponds in open areas with a lot of wind (Horváth et al., 2016; Vanschoenwinkel et al., 2008). These conditions do not apply to forested areas where wind speeds are dampened. Finally, rainfall can result in splashing water and overflowing bromeliads which might facilitate downward dispersal of invertebrates.

The group of predators contained both active and passive dispersers and their overall increase in abundance with bromeliad volume was more pronounced in the canopy than in bromeliads at floor-level. In bromeliads on the forest floor, the passively dispersing turbellarian predator was the most abundant predator (81% of all predators present) and it was found exclusively in bromeliads with volumes smaller than 200 ml. By contrast, in the canopy it occurred mainly in bromeliads larger than 200 ml (91%). The presence of the passively dispersing predator in small bromeliads on the forest floor and in large ones in the canopy supports our hypotheses that elevated bromeliads may be less easily colonized by passive dispersers because phoretic hosts may be less frequent there. Bromeliads and their phytotelm grow in size with age (Givnish et al., 2014) so the big canopy bromeliads have had a longer exposure time for colonization through those incoming phoretic hosts. The floor-level bromeliads, on the other hand, are younger but potentially visited more often.

In general, effects of volume and height were also confirmed by redundancy models that show that these variables explain a proportion of variation in community composition in the same way as the mixed models.

We observed potential cacao pollinators in over 65% of the bromeliads we sampled, so we can argue that bromeliads are indeed commonly used as oviposition habitats for these taxa in the study region.

Overall, both species richness and abundance of potential pollinators increased with bromeliad volume. However, the abundances of these cecidomyiid and ceratopogonid midges in bromeliads on the forest floor were unaffected by volume, while in canopy bromeliads their abundances increased with volume. This pattern seems to be mainly accountable for by the distribution patterns of the Ceratopogonidae, including *Forcipomyia*. The cecidomyiid midges were not very abundantly present and occurred about as frequently in canopy and ground-level bromeliads, while ceratopogonid midges were almost exclusively found in canopy bromeliads. As suggested by Kitching (2000), a radiation of *Forcipomyia* species may have occurred in bromeliads. Assuming this is indeed the case, these species could be expected to search for oviposition habitats in the canopy rather than on the forest floor, where epiphytic bromeliads – unless on fallen branches – do not occur. However, it might also be that on the forest floor, ceratopogonids prefer other oviposition habitats over bromeliad phytotelmata such as decaying organic matter of for example soil litter and old cacao husks (Forbes and Northfield, 2017), which are not present in the canopy. However, this hypothesis was not investigated in this study and therefore, this explanation remains speculative.

By contrast, members of the second main group of pollinators, the Cecidomyiidae family, were found in low frequencies both at ground level and higher in the canopy. Hence, we have no indications of their breeding habitat preference with respect to height. Contrary to ceratopogonids, a potential preference of Cecidomyiidae for bromeliads as breeding habitats remains unclear although cecidomyiid larvae have occasionally been found in phytotelmata (Clarke and Kitching, 1993; Jabiol et al., 2009). The relatively abundant presence of Cecidomyiidae in this study confirms that the widely held misconception that members of these groups only have terrestrial larvae must be reconsidered. They are, for instance, left out of widely used identification literature such as Merritt and colleagues' book on the aquatic insects of North America (2008). We found that the larvae of at least some species are aquatic and, given that Cecidomyiidae also pollinate cacao, this provides additional support for maintaining aquatic habitat like bromeliads in cacao plantations.

5. Conclusions

Our study confirms that the maximum volume of water a bromeliad can hold is a main driver of the richness and abundance of its invertebrate communities. Apart from volume, our study points out that even modest differences in a bromeliad's height above the forest floor can also play an important role. Especially for passively dispersing taxa, in future studies the inclusion of bromeliads at the floor level could ensure a more complete coverage of their distributions, as we found them to be more diverse than in the cacao trees. Suspected cacao pollinating taxa based on literature were widespread in the bromeliads within the sampled cacao plantations. This suggests that maintaining bromeliads in the plantations could improve pollinator densities. However, given the poor knowledge of the ecology of these pollinators, it would be necessary to validate the actual pollination activity of these taxa directly to provide more solid evidence. In addition, many of these taxa are morphologically cryptic so there are opportunities for barcoding studies to investigate in more detail how specific the relationship is between midge species that reproduce in bromeliads and cacao flower pollination.

Overall, if the presence of bromeliads would indeed promote pollination efficiency, maintaining bromeliad densities in plantations could be a very cost-effective management practice for smallholder cacao farmers in Latin-America. In addition, not removing bromeliads is also likely to have additional positive side effects as this can promote diversity of other biota that use bromeliads as habitats such as many invertebrates, amphibians and reptiles.

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Table 1 Results of mixed models for species richness and abundance. Included are results of both general linear mixed models (in italics) and generalised mixed models, both specifying plantation identity as a random factor.

	Species richness			Abundance		
	β	χ^2	p	β	χ^2	p
All taxa						
Volume	8.202	41.69	< 0.001	0.798	1560.87	< 0.001
Height	-1.366	6.51	0.011	-1.390	44.18	< 0.001
Volume x Height				0.570	389.57	< 0.001
Passive dispersers						
Volume	1.925	6.54	0.011	0.764	390.72	< 0.001
Height	-1.383	19.01	< 0.001	-1.227	549.27	< 0.001
Volume x Height				0.326	51.87	< 0.001
Active dispersers						
Volume	1.022	59.05	< 0.001	1.493	1210.53	< 0.001
Height	-0.005	0.01	0.920	-0.468	126.05	< 0.001
Volume x Height				0.302	47.892	< 0.001
Potential cacao pollinators, liberal dataset						
Volume	0.681	8.85	0.003	0.606	53.30	< 0.001
Height	0.183	2.78	0.095	0.177	20.82	< 0.001
Potential cacao pollinators, conservative dataset						
Volume	0.770	7.52	0.006	1.666	234.75	< 0.001
Height	0.250	3.81	0.051	-0.749	18.07	< 0.001
Volume x Height				0.583	6.94	0.008
Predators						
Volume	1.438	18.49	< 0.001	0.358	163.47	< 0.001
Height	0.162	1.41	0.235	-3.295	61.75	< 0.001
Volume x Height				1.653	80.54	< 0.001

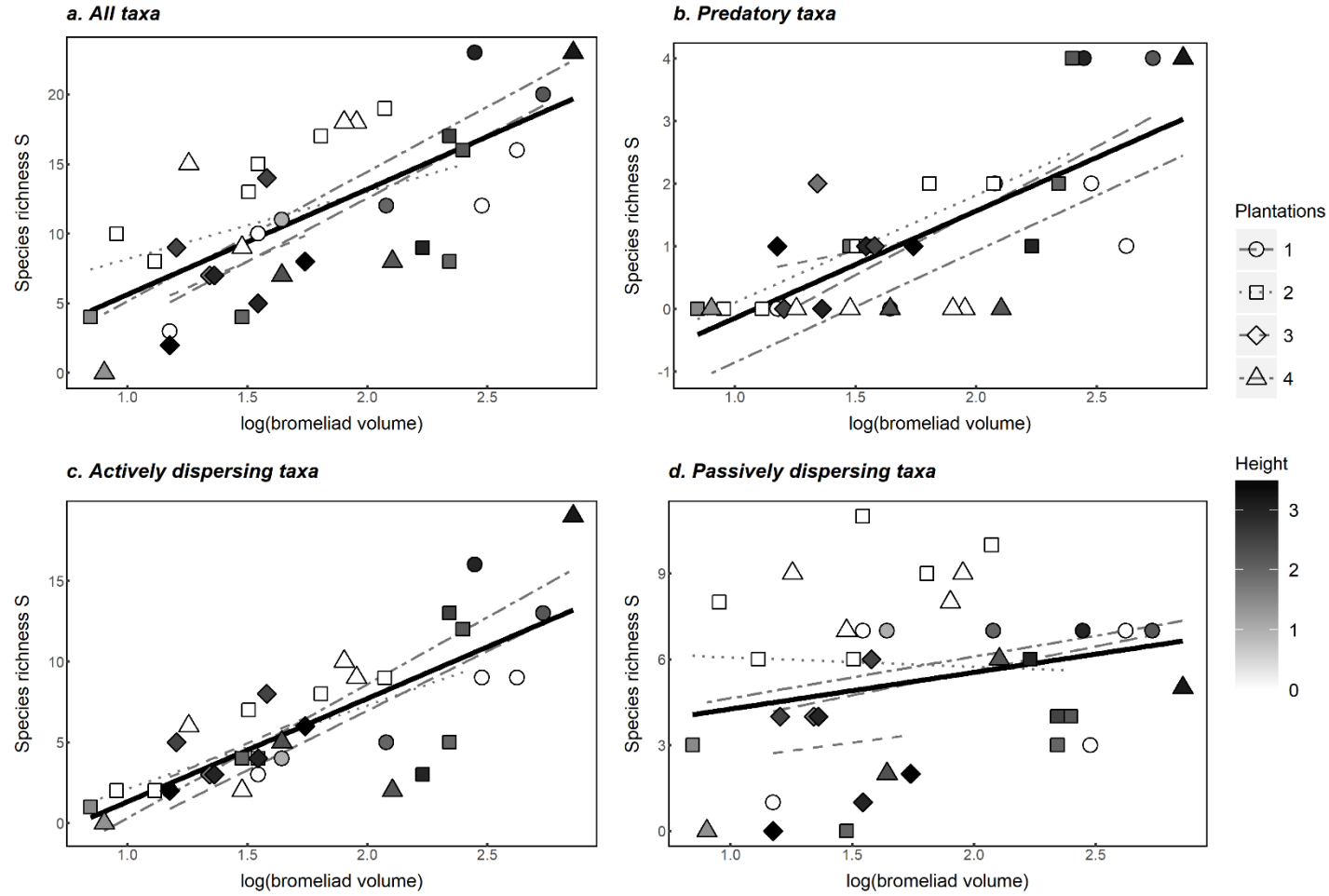


Figure 2 Patterns of species richness with maximum bromeliad water volume for: **a** all taxa; **b** predatory taxa; **c** actively dispersing taxa; and **d** passively dispersing taxa. Each data point depicts one bromeliad, their shape indicates plantation identity and their fill the height above the forest floor at which they were sampled. The total linear regression is shown in the solid black line while regressions for each plantation individually are shown in grey.

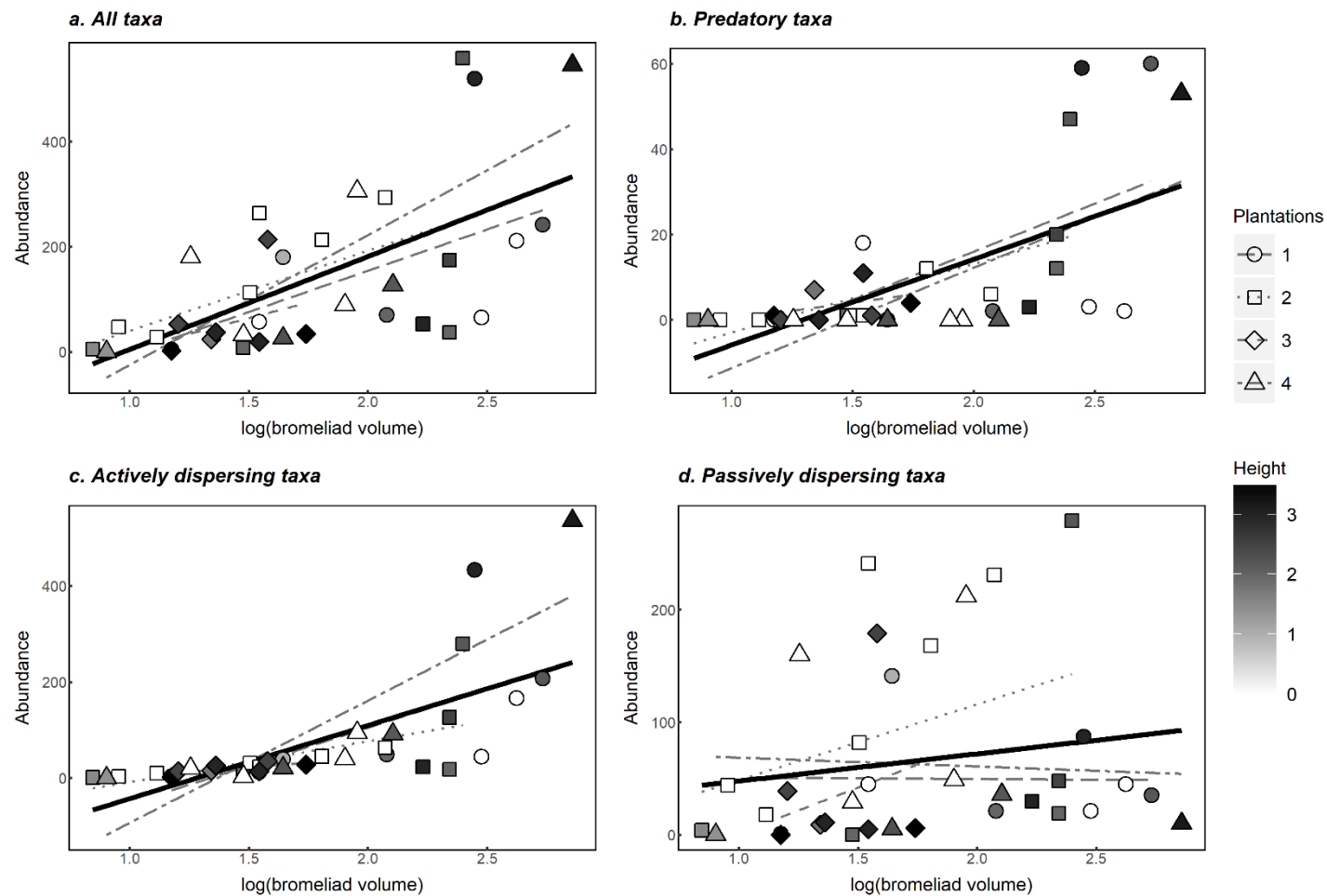


Figure 3 Patterns of total abundance with maximum bromeliad water volume for: **a** all taxa; **b** predatory taxa; **c** actively dispersing taxa; and **d** passively dispersing taxa. Each data point depicts one bromeliad, their shape indicates plantation identity and their fill the height above the forest floor at which they were sampled. The total linear regression is shown in the solid black line while regressions for each plantation individually are shown in grey.

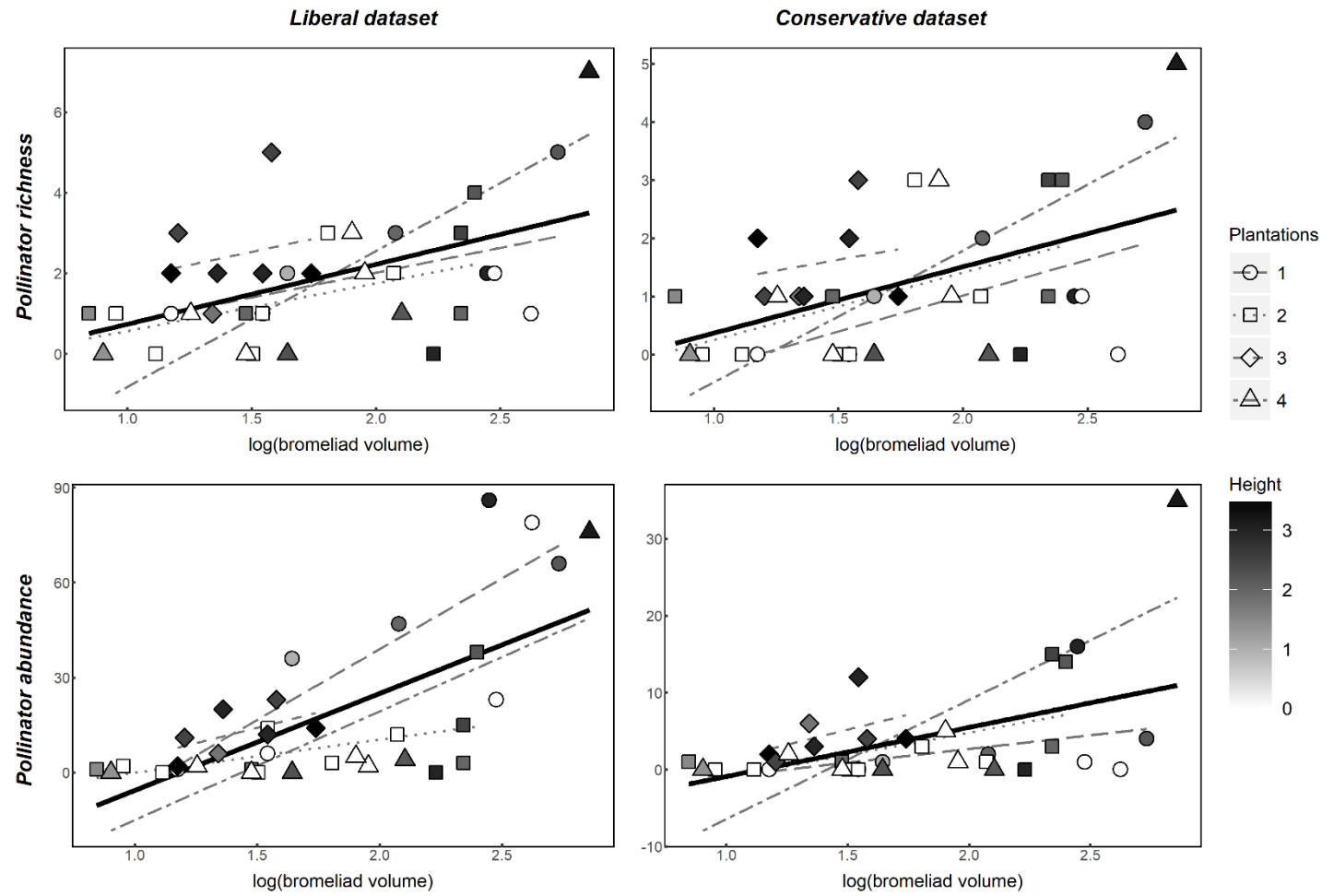


Figure 4 Patterns of pollinator richness (top) and pollinator abundance (bottom) with maximum bromeliad water volume for both the liberally defined (left) and conservatively defined (right) datasets. Each data point depicts one bromeliad, their shape indicates plantation identity and their fill the height above the forest floor at which they were sampled. The total linear regression is shown in the solid black line while regressions for each plantation individually are shown in grey.

Appendix

Table A.1 List of the number of invertebrate taxa found and their abundance. Asterisks indicate taxa considered as potential pollinators.

	Family	Subfamily	Genus	#Taxa	Abundance
Acari				7	663
Coleoptera	Carabidae			1	1
	Sciaridae			1	87
	-			1	1
Copepoda	Cyclopoida			1	381
	Harpacticoida			1	585
Diptera	Cecidomyiidae*			7	15
	Ceratopogonidae		<i>Alluaudomyia</i> *	1	61
			<i>Bezzia</i> *	1	4
			<i>Forcipomyia</i> *	6	63
			_*	1	2
	Chironomidae	Chironominae		2	603
		Orthocladiinae*		2	465
		Podonominae		2	138
		Tanypodinae		2	127
	Culicidae		<i>Aedes</i>	1	8
			<i>Anopheles</i>	1	12
			<i>Culex</i>	1	351
			<i>Toxorhynchites</i>	1	13
			<i>Wyeomyia</i>	2	358
	Ephidridae			2	28
	Psychodidae		<i>Psychoda</i>	3	49
			-	2	37
	Sciaridae*			1	2
	Syrphidae			1	1
	Tipulidae			1	57
	-			5	39
Lepidoptera	-			1	3
Nematoda	-			1	12
Oligochaeta	-			1	538
Ostracoda	-			1	9
Tardigrada	-			1	4
Turbellaria	-			1	118