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Height and phytotelm size affect the invertebrate communities of epiphytic bromeliads in the Amazon rainforest

Xaali O'Reilly-Berkeley[1,2,3,4,5] | **Alex Pazmiño-Palomino**[5,6] | **Andrea Hidalgo-Cárdenas**[7] | **Sofía I. Trujillo-Regalado**[7] | **Hannah Mossman**[2,5] | **Jennifer K. Rowntree**[2,8] | **Richard F. Preziosi**[2,4,5,8]

[1]Universitat Autònoma de Barcelona, Departament de Biologia Animal, de Biologia Vegetal i d'Ecologia, Bellaterra (Cerdanyola del Vallès), Spain

[2]Manchester Metropolitan University, Department of Natural Sciences, Manchester, UK

[3]CREAF, Bellaterra (Cerdanyola del Vallès), Spain

[4]Timburi Cocha Research Station, San José de Payamino, Ecuador

[5]Instituto Nacional de Biodiversidad, Quito, Ecuador

[6]Museo de Entomología, Facultad de Recursos Naturales, Escuela Superior Politécnica de Chimborazo, Riobamba, Ecuador

[7]Universidad Central del Ecuador, Quito, Ecuador

[8]University of Plymouth, School of Biological and Marine Sciences, Plymouth, UK

Correspondence
Xaali O'Reilly-Berkeley, Universitat Autònoma de Barcelona, Departament de Biologia Animal, de Biologia Vegetal i d'Ecologia, Campus de la UAB, 08193 Bellaterra (Cerdanyola del Vallès), Barcelona, Spain.
Email: xaali.oreilly@uab.cat

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Abstract

1. Tank bromeliads are found in rainforests across the Neotropics and harbour diverse invertebrate communities between their leaf axes. Various factors influence the invertebrate species richness and differences in composition in bromeliad phytotelmata, most notably, habitat size. However, there has been little work on invertebrate communities in bromeliads in western Amazonia or at different heights in the canopy.
2. We collected 63 epiphytic bromeliads (*Aechmea hoppii* (Harms) L.B.Sm, *A. nidularioides* L.B.Sm) on the eastern edge of the Tropical Andes Biodiversity Hotspot in Ecuador and explored which biological and physical variables explained the differences in invertebrate composition among bromeliads. We extracted a total of 7524 individual aquatic and terrestrial macroinvertebrates and identified 300 morphospecies belonging to 27 orders, within the phyla Arthropoda, Annelida and Platyhelminthes. We recorded information on bromeliad location within the forest (height in canopy, primary or secondary forest), plant size (phytotelmata volume, base circumference, length of longest leaf), phytotelm pH and temperature and counted the number of leaves as a measure of habitat complexity.
3. Overall, our results indicate that height in the canopy and phytotelm size explained statistically significant portions of the variation in different parts of the bromeliad community. Bromeliad size was positively correlated with alpha diversity of both terrestrial and aquatic invertebrates, whereas height in the canopy affected beta diversity. The sampling time of year in which bromeliads were collected affected the aquatic community, suggesting biological seasonality in the absence of climatic seasonality.
4. By extending the height from the ground at which most bromeliad studies have been carried out, our work has highlighted the potential importance of vertical variation of bromeliad invertebrate communities throughout the canopy. Additionally, we fill in a geographic gap in this body of work.

KEYWORDS
Amazon biodiversity, bromeliad, canopy invertebrates, tropical invertebrate community

INTRODUCTION

Bromeliads constitute one of the most diverse families of flowering plants in the neotropics, with over 3500 species, nearly half of which are epiphytic and many possess a tank-like morphology (Zizka et al., 2020). The elongated strap-like leaves of tank bromeliads are arranged in a rosette around a central gap, known as a tank or phytotelm (pl. *phytotelmata*). This provides a space in which rainwater and debris from the canopy accumulate, forming a protected oasis rich in nutrients, courtesy of diverse communities of detritivores, primary producers and nutrient cyclers within them (Figure 1) (Bermudes & Benzing, 1991; Brandt et al., 2017; Brouard et al., 2011; Carrias et al., 2001; Carrias et al., 2014; Louca et al., 2017). Bromeliads have been called "biodiversity amplifiers", due to the concentration and diversity of invertebrate fauna they harbour in their phytotelmata compared to the surrounding habitat (Da Rocha et al., 2000; Hénaut et al., 2014). They house both aquatic and terrestrial invertebrates, serve as nurseries for amphibians (Almendáriz et al., 2000; Mccracken et al., 2007; Sabagh et al., 2017) and provide nutrition and hydration for birds and even Andean bears (DeMay et al., 2014; Goldstein & Goldstein, 2019; Palacios-Mosquera, 2018; Piacentini & Varassin, 2007).

Most members of the aquatic community within bromeliads tend to be less mobile than those in the terrestrial matrix for at least the larval part of their life cycle, remaining in a particular bromeliad. The terrestrial community is usually composed of more mobile

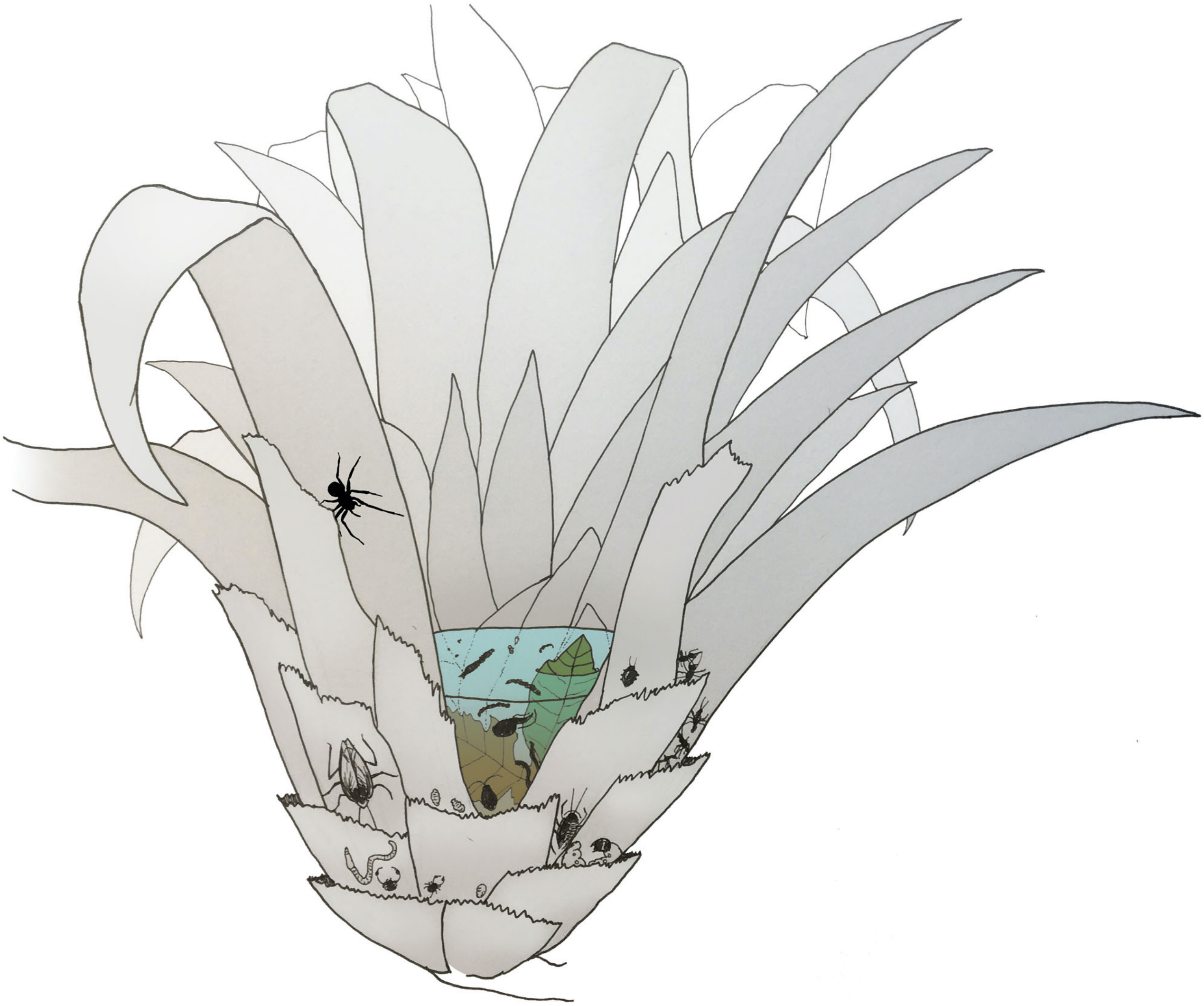

FIGURE 1 Diagram of a bromeliad community. Front leaves have been cut to illustrate that invertebrates inhabit leaf axes as well as the central phytotelm.

foragers or predators that visit bromeliads briefly to feed or breed, or temporary tenants that use the plant for nourishment and shelter but can move on from the bromeliad when they need to (Zillikens et al., 2005). Given the different niches and needs of these broadly distinguishable communities within bromeliads, studies typically analyse them separately and most centre on the aquatic community, revealing that the aquatic community is sensitive to variation among bromeliad microhabitats (Cotgreave et al., 1993; Jocque & Field, 2014; Lopez et al., 2009; Marino et al., 2013). Habitat size and water volume have been shown to be the bromeliad features that best correlate with species richness and abundance of communities within them (Jocque & Field, 2014; Méndez-Castro et al., 2018; Srivastava, 2006; Srivastava et al., 2008a). Detrital content (Armbruster et al., 2002; Dézerald et al., 2017; González et al., 2014), bromeliad species (Jabiol et al., 2009; Marino et al., 2013) and even bromeliad genotype (Zytynska et al., 2012a) have been shown to explain significant portions of the variation among bromeliad aquatic invertebrate communities, depending on the combination of factors examined, the portion of the community included and the location of the study. Fewer studies focus on factors influencing the terrestrial bromeliad community composition in isolation, as they are more transient (Jocque & Field, 2014). Nonetheless, leaf and bromeliad architecture have been shown to affect spider diversity (De Omena & Romero, 2008; Gonçalves-souza et al., 2010; Gusmão et al., 2020). Other studies have examined different aspects of the interactions between terrestrial and aquatic components, revealing functional relationships between bromeliad hosts and their associated communities (Céréghino et al., 2011, 2019). However, there are geographic differences in the factors that influence community composition and trophic interactions within bromeliads (LeCraw & Srivastava, 2019).

Despite the rich literature on bromeliad invertebrate communities across the neotropics, many geographical areas and bromeliad species remain unexplored. Western Amazonia is particularly unmapped in terms of bromeliad invertebrate communities. This is significant because the north-western corner of the Amazon rainforest falls within the eastern edge of the Tropical Andes biodiversity hotspot, by some measures the most biodiverse place on Earth (Myers et al., 2000). This area includes the northern section of the Andes mountain range, as well as its flanking regions as it descends into the Amazon basin. Between the period of 1990 and 2007, Ecuador lost the highest relative amount of forest cover in South America (Peres et al., 2010), and so documenting this region may be crucial to informing its conservation. To the authors' knowledge, the only comprehensive published study of whole bromeliad-associated invertebrate communities in Ecuador was that of Armbruster et al. (2002), nearly two and a half decades ago and not quite within the Tropical Andes hotspot. Although bromeliads generally contain a set of functional groups of invertebrates, the proportion and composition of these, as well as their responses to change, vary across environmental and geographical gradients (Céréghino et al., 2022; Dézerald et al., 2013; LeCraw & Srivastava, 2019; Srivastava et al., 2020a), and so filling in geographic gaps in our knowledge of these systems is relevant.

Additionally, most bromeliad studies focus on plants on or near the ground. However, the forest canopy is an important reservoir of floral and invertebrate diversity in tropical forests (Cascante-Marín & Nivia-Ruíz, 2013; Davidson et al., 2003; Davis & Sutton, 1998; Quaresma et al., 2017; Stork & Grimbacher, 2006). In the Neotropics, forest canopies are laden with layers of epiphytes, including a high diversity of vascular epiphytes such as orchids, aroids and bromeliads (Flores-Palacios & García-Franco, 2006; Freiberg & Freiberg, 2000; Ge & Dodson, 1987; Hayward et al., 2018; Winkler et al., 2009; Quaresma et al., 2017), of which bromeliads in particular are important reservoirs of terrestrial and aquatic arthropods. Studies that have considered the effect of distance from the ground on communities in bromeliads have found a negative relationship (Brouard et al., 2012; Kratina et al., 2017) or no relationship (Antonetti et al., 2021) between microfauna and the height of the bromeliad on the phorophyte. However, the range of heights occupied by bromeliads has a positive effect on spider diversity, with bromeliad species occupying a greater range of heights housing a greater abundance of spiders (Gonçalves-Souza et al., 2011a; Gonçalves-Souza et al., 2011b). The bromeliads in the aforementioned studies were all found within 2.5 m from the ground while average canopy height in the Amazon is around 30 m (Helmer & Lefsky, 2006; Sullivan, 2018, *unpublished data*), although emergent tree heights of up to 88 m have been reported (Gorgens et al., 2019). Zytynska et al. (2012), however, collected bromeliads from up to 17 m above the ground and did not find any relationship of height with species richness or community composition, which suggests the bromeliad phytotelmata could be buffering against microenvironmental changes throughout the canopy, where community composition is known to change (Ashton et al., 2016; Brühl et al., 1998; Stork et al., 2016).

Here, we aim to address the north-western Amazonian gap in the bromeliad invertebrate literature and extend the height in the canopy at which such studies are carried out by examining potential factors that may explain the variation in macroinvertebrate communities within two congeneric and vegetatively indistinguishable epiphytic bromeliad species, *Aechmea hoppii* (Harms) (L.B. Smith, 1953a) and *A. nidularioides* (L.B. Smith, 1953b), in San José de Payamino, Ecuador. This relatively understudied region of north-western Amazonia falls on the eastern edge of the Tropical Andes Biodiversity Hotspot. We thus anticipated we would find a larger overall number of morphospecies among the bromeliads than (Armbruster et al., 2002) and a distinct set of variables explaining differences in community structure among bromeliads. We expected that environmental and plant characteristics in our more geophysically diverse environment would explain community patterns to a lesser degree than in the lower, flat regions of Amazonia, as biomes overlap or transition in this area. We analyse the aquatic and terrestrial communities separately in order to evaluate the differences in factors influencing these distinct components of the bromeliad invertebrate fauna, expecting different factors to affect differences in community composition in each group, due to their distinct relationships with bromeliads. We ask whether the height at which bromeliads are found influences the invertebrate community, given that bromeliads may act as oases with more stable conditions within them and therefore expecting there may be less community turnover than in non-aquatic bromeliad arboreal communities. We analyse whether there are differences between bromeliad communities in continuous primary and secondary forest, hypothesising that bromeliads may offer shelter for diverse assemblages in both habitats, although expecting differences in the starting communities of altered habitats to be reflected in the bromeliads. However, we expect there to be differences in how these variables affect the distinct (aquatic and terrestrial) parts of the community, as these components tend to be fundamentally different in their composition, transiency and in many cases live stages. We thus discuss the complex set of patterns that emerge in the aquatic and terrestrial invertebrate communities in the bromeliads in one of the most biologically rich areas on Earth.

MATERIALS AND METHODS

Study site

Bromeliads were collected in San José de Payamino, Orellana, Ecuador, hereafter referred to as Payamino. Researchers were based at the Timburi Cocha Research Station in Payamino (−00.4827500°, −077.2847500°). Payamino is a 17,000 ha expanse of Amazon rainforest owned and managed by an indigenous Kichwa community on the eastern edge of the Tropical Andes Biodiversity Hotspot. It is in the buffer zone of the core Sumaco Napo Galeras National Park and within the Sumaco UNESCO Biosphere Reserve (Figure 2). The buffer zone is protected by certain laws and regulations, but they are not as stringent as in the core national park. This makes it an ideal area to study primary and secondary forests in unison.

Elevation of the area ranges between 200 and 714 m above sea level (m.a.s.l.). Mean tree height is 18.2 m (Sullivan 2018, *unpublished data*). The area is a patchwork of mature primary and old secondary forest, interspersed with small areas of basic family properties (*fincas*) consisting of small open wooden houses or platforms and cultivated land (*chacras*). Henceforth, we use the term *primary forest* to refer to mature areas of rainforest with minimal or no human disturbance in the collective memory of the local community. *Secondary forest* refers to regenerated or anthropogenically disturbed areas of rainforest (Brown & Lugo, 1990). This includes areas formerly used as farmland that are now fully forested, areas that look mature but may be scarred by frequently used trails and patches of forest that are selectively weeded or logged.

The forest is a humid tropical forest. Average rainfall is 3661 mm y^{-1}. There are no defined seasons in the area, with a mean annual temperature of 24.0°C, varying between 23.4 and 24.4°C between the coldest and warmest quarters of the year. Evapotranspiration does not surpass precipitation at any point throughout the year, so there is no dry season (Sullivan et al., 2020). There are, however, seasonal patterns in fruiting trees (Stafford et al., 2016).

Field sampling

The two focal species of bromeliad were picked in situ following exploratory surveys of the area prior to sampling. *Aechmea hoppii* and *A. nidularioides* were chosen owing to their abundance and apparent ubiquity throughout primary and secondary forest on both sides of the main river. The physical vegetative characteristics of these species make them virtually indistinguishable from each other but distinguishable from the many other epiphytic bromeliads in the area, allowing identification even when no inflorescence is present.

Sampling took place in January–February and July–August 2018. Sixty-three suitable bromeliads (based on the morphospecies and accessibility) were selected from the ground by the same person throughout the study. Host tree species were not recorded. Bromeliads were reached using double-rope canopy access methods or ladders, depending on their position above the ground, which ranged from 1.96 to 20.20 m (97% of which were positioned over 2.5 m from the ground).

When an accessible bromeliad of the correct species was identified, forest type (i.e. primary [$n = 28$] or secondary [$n = 35$]) and GPS coordinates were recorded. The vertical position of the bromeliad in the canopy was measured from the base of the bromeliad to the ground directly beneath it, using a standard 50 m tape measure. Central phytotelm temperature and pH were recorded using a handheld pH meter (PH20, Apera Instruments) prior to removing the bromeliad from its host tree. The bromeliad was then sawn off the tree at the base and lowered to the ground in a large heavy-duty bin bag, to avoid losing the contents or inhabitants of the epiphyte.

Collected bromeliads were returned to the Timburi Cocha Research Station for processing. The entire contents of the collection bag, including the plant and any debris or water that may have been loosened from it, were emptied into a large glass aquarium. We therefore collected phytotelm and leaf fauna, without the root mass. This allowed plant characteristics to be measured without losing invertebrates. Total phytotelm capacity, base circumference and the length of the longest leaf were measured, in addition to counting the total number of leaves on the bromeliad. The total capacity of the phytotelmata was measured by filling the central cavity and leaf axes with known volumes of water until they overflowed. Base circumference was measured around the section of the plant base or stem where the bottom leaves ended and the stem's diameter evened out.

Invertebrate identification

Following measurement, bromeliads were dissected leaf-by-leaf and scoured for macroinvertebrates visible to the naked eye (>2 mm in length) (Table S1). All leaf litter, soil and water from the bromeliads were examined in equal detail. All collected invertebrate specimens were collected whole and preserved in 96% ethanol for later identification. There was occasion for some ants to escape, which cannot be accounted for, but this was generally only a few individuals when it occurred and represented a small proportion of the overall number of

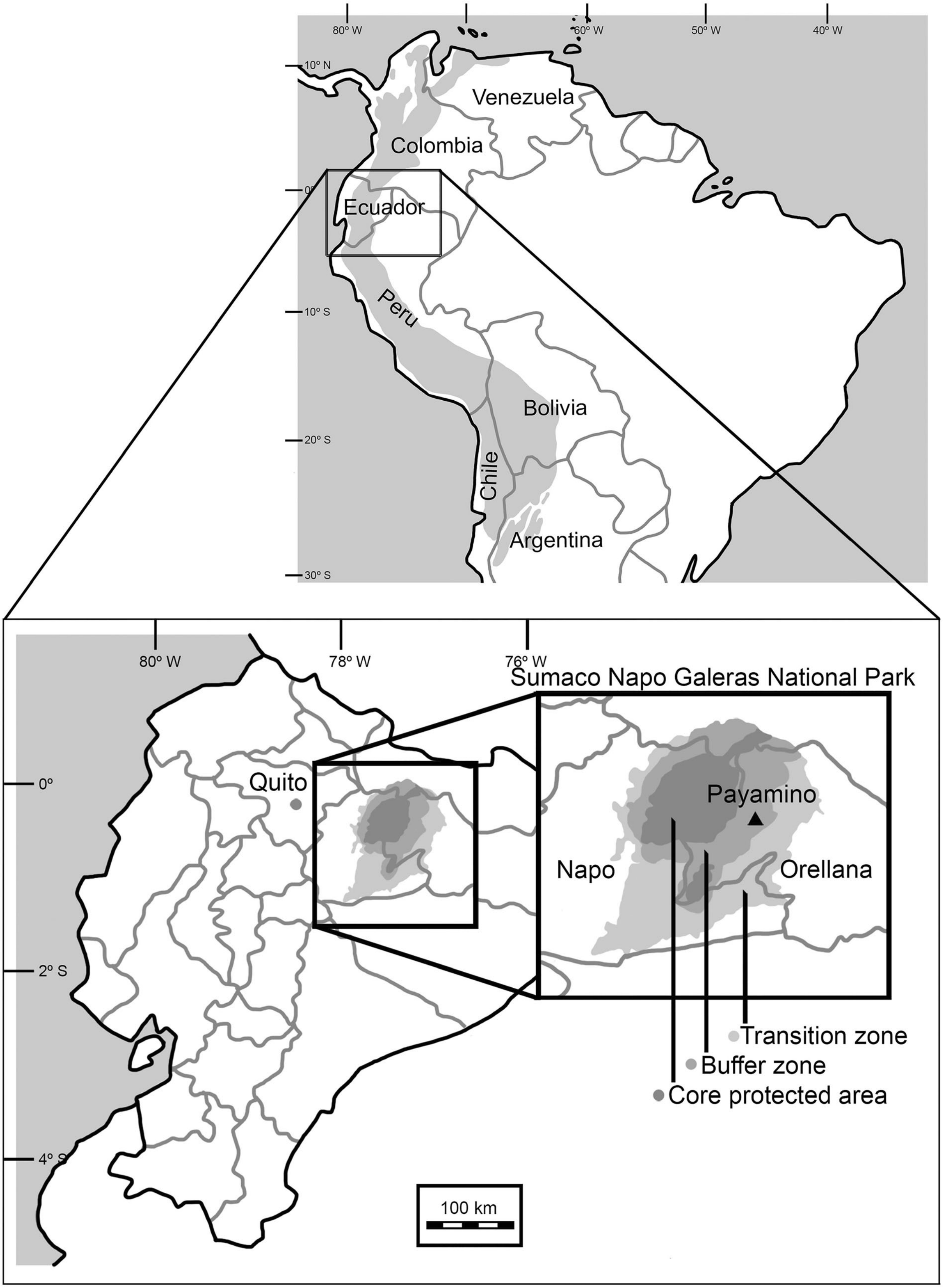

FIGURE 2 Map of South America and Ecuador. Shaded area in the top map represents the Tropical Andes Biodiversity Hotspot. Shaded area in the bottom map represents the Sumaco Napo Galeras National Park, with the darker greys having higher levels of protection.

individuals. Invertebrates were transferred to the entomology laboratory of the National Biodiversity Institute (Instituto Nacional de Biodiversidad del Ecuador, INABIO) in Quito, Ecuador, for processing, where reference samples have been kept and are available upon reasonable request.

Individual invertebrates were defined as either aquatic or terrestrial. Whether an invertebrate was considered aquatic or terrestrial was based on its life stage at the time of collection; for example, aquatic beetle larvae are considered part of the aquatic community, even if the adult instars would not be had they continued to grow. All collected invertebrates were classified at least down to the level of order and classified into morphospecies. Both general (McGavin, 2000; Kočík et al., 2002; Triplehorn & Johnson, 2005) and taxon-specific keys (Andersen, 2010; Brito & Borges, 2015; Domínguez & Fernández, 2009; Fernández et al., 2019; Grismado et al., 2015; Hebard, 1924; Kury, 2002; Merritt et al., 2008; Prat et al., 2010; Vidlicka, 2014) were used to classify the samples and then split into morphospecies.

Data analysis

All statistical analyses were carried out in R (R Core Team, 2020). The relative percentage of aquatic and terrestrial invertebrates in the total sample was calculated in terms of the number of individual invertebrates and morphospecies richness. Likewise, the abundance of different orders across the samples was calculated as a percentage of the number of individuals within each class and each order over the total number of invertebrates, as well as the percentage of the number of morphospecies per class or order over the total number of invertebrates.

Variables influencing alpha diversity

Generalised linear models (GLMs) were used to investigate relationships between the number of morphospecies or the number of individuals in the bromeliads and bromeliad volume (log-transformed), height on host, forest type and the longest leaf. These explanatory variables were chosen by model simplification using stepwise deletion of the original models, which included all the measured variables (Crawley, 2015). The models were fitted with a quasi-Poisson family distribution due to the overdispersed nature of the count data. This analysis was performed for the aquatic and terrestrial community subsets separately, as well as the most common orders (by number of morphospecies) in the dataset; these were Araneae, Blattodea, Coleoptera, Diptera, Hymenoptera, Isopoda, Lepidoptera and Oligochaeta. We corrected for multiple testing using the Holm method (Aickin & Gensler, 1996). We treated Oligochaeta as an order, as we did not possess the taxonomic expertise to classify these samples further and only analysed the number of individuals for this group.

Variables influencing beta diversity

To investigate how plant and environmental factors explained the variation among invertebrate communities, permutational multivariate analyses (PERMANOVA) were run using Bray–Curtis distance matrices with the *adonis2* function of the *vegan* package in R (Oksanen et al., 2020). Separate analyses were conducted on the aquatic invertebrates and terrestrial invertebrates. Nine environmental variables were included in the PERMANOVAs: forest type (primary/secondary), height of the bromeliad on tree, log-transformed bromeliad volume (phytotelmata capacity), longest leaf of the bromeliad, number of leaves, base circumference, phytotelm pH and temperature and the sampling time (January–February or July–August). Although phytotelm capacity, longest leaf and base circumference are all measures of bromeliad size, all were included as they were not highly correlated ($r < 0.4$). This was done for both presence/absence data and using abundance data. However, as 45.6% (137) of invertebrate morphospecies present were only found once in the whole dataset, we repeated the permutational analyses treating the data as binary (presence/absence). Removing singletons from the dataset produced the same results; therefore, we retained them. Of the aquatic morphospecies, 45.4% were singletons and similarly, 46.6% of terrestrial morphospecies were singletons.

RESULTS

Environmental variables and diversity of macroinvertebrates

Sampled bromeliad size was highly variable: phytotelmata capacity ranged from 80 mL to 1400 mL (mean 389.36 ± 245.86 SD); longest leaf, 19–238 cm (mean 141.48 ± 40.22 cm SD); base circumference, 9–25 cm (mean 14.34 ± 3.05 cm SD); number of leaves, 8–29 (mean 17.98 ± 4.20 cm SD). Central phytotelm pH was mostly acidic but with a great deal of variation, from strongly acidic pH 3.4 to few phytotelmata exhibiting neutral or mildly alkaline pH 8.2 (mean 5.83 ± 0.93 SD). Phytotelm temperature varied between 22.2 and 30.0°C (mean 25.71 ± 1.71°C SD). Height at which bromeliads were collected ranged between 1.96 and 20.20 m above the ground (mean 7.77 ± 4.14 m SD), with 97.3% of bromeliads found above 2.5 m from the ground.

A total of 7524 individual terrestrial and aquatic macroinvertebrates (length >1 mm) belonging to 300 different morphospecies were collected from the 63 bromeliads, the vast majority of which were arthropods. The terrestrial community consisted of 78.9% of all individuals and 76.0% of morphospecies, while 18.7% and 15.7% of individuals and morphospecies, respectively, were aquatic. The lifestyle of 8.3% of morphospecies was both terrestrial and aquatic, and that of 2.4% of individuals was indeterminable. Morphospecies with terrestrial and aquatic habitats were included in both categories for analysis, while indeterminable ones were not included in either category.

Insects comprised 89.2% of individuals; crustaceans, 5.0%; arachnids, 2.6%; other arthropod classes made up fewer than 1% each. The predominant non-arthropod classes in terms of numbers of individuals were Clitellata (phylum Annelida) and Rhabditophora (phylum Platyhelminthes), but these only accounted for 2.2% and 0.1% of individuals, respectively. Hymenoptera were the most abundant order, with 66.0% of all individuals; in fact, all Hymenoptera individuals collected, apart from two, were ants (family Formicidae). Beetles (order Coleoptera) were the next most abundant group, comprising 16.3% of individuals, with the remaining 25 orders accounting for fewer than 17.7% of individuals.

In terms of morphospecies richness (rather than abundance), Insecta was still the most prominent class, comprising 202 of the 300 morphospecies of invertebrates (67.3%). Arachnids were the next most speciose class with 65 morphospecies (21.6% of total), including 42 morphospecies of spiders (Araneae) and nine morphospecies of harvestmen (Opiliones). We counted five morphospecies of Pseudoscorpionida, three of Scorpionida and one of Schizomida, but for lack of taxonomic expertise cannot guarantee that the 30, 39 and 10 individuals found of each of these orders do not comprise more or fewer morphospecies. Following arachnids in terms of number of morphospecies per class were myriapods (Diplopoda, 3.1%; Chilopoda, 1.0%) and malacostracans (1.7%), although these classes did not contain the most speciose orders. The orders with the greatest number of morphospecies were Hymenoptera (26% of all morphospecies, all but one of which were ants); Coleoptera (19.2%); Araneae (14.4%); Diptera (9.6%); and Blattodea (6.2%).

Variables influencing alpha diversity

Phytotelm capacity (volume) was the only variable analysed which significantly positively correlated with species richness in the aquatic and terrestrial communities (Table 1; Figure 3). The longest leaf of bromeliads was negatively correlated with the number of morphospecies and the number of individuals in the aquatic community. Other than that, the number of individual aquatic invertebrates within bromeliads correlated with the longest leaf (Table 1).

The abundance and morphospecies richness within orders was not affected by any of the tested variables.

Variables influencing beta diversity

Forest type and sampling time were the only variables that accounted for statistically significant portions of the differences between aquatic communities, whether presence/absence data were used or abundances were included (Table 2). Overall, 23.4% (presence–absence) or 20.0% (with abundances) of the total variation between aquatic communities was explained by the nine environmental and physical variables measured.

Height on host tree and phytotelm capacity explained small but significant portions of the variation among terrestrial bromeliad communities, but sampling time did not (Table 2). The measured variables put together explained 16.9% of the total variation between terrestrial communities using presence/absence data. When abundance data were included, only phytotelm capacity was statistically significant (Table 2), and 15.8% of the variation was explained by the measured variables.

DISCUSSION

Height of bromeliad attachment to the host tree significantly affected community composition in bromeliads in our study. Bromeliad size only influenced alpha diversity. Contrary to our expectations, both the aquatic and terrestrial components of the community were affected in very similar ways by the measured variables. Although results were not identical, they were similar whether presence–absence data were used or abundances were included, despite a large portion of the dataset being represented by singletons, not an unusual phenomenon in tropical forest datasets (Armbruster et al., 2002; Novotný & Basset, 2000; Stork et al., 2016). Whether bromeliads were collected in primary or secondary forest did not have a significant effect on alpha or beta diversity, suggesting that bromeliads may act as a

TABLE 1 Effect of environmental and plant variables on morphospecies richness and abundance.

		Morphospecies richness		Abundance	
Community	**Variable**	**Estimate ± SE**	***p***	**Estimate ± SE**	***p***
Aquatic community	Volume (log)	0.329 ± 0.110	0.004*	0.462 ± 0.245	0.064
	Height	−0.001 ± 0.014	0.924	−0.006 ± 0.033	0.853
	Forest type	0.019 ± 0.131	0.882	−0.062 ± 0.298	0.836
	Longest leaf	−0.003 ± 0.001	0.050*	−0.008 ± 0.003	0.021*
Terrestrial community	Volume (log)	0.346 ± 0.088	<0.001*	0.316 ± 0.389	0.420
	Height	0.009 ± 0.013	0.463	−0.049 ± 0.058	0.408
	Forest type	−0.232 ± 0.108	0.036	0.156 ± 0.468	0.739

Note: Results of the Generalised linear models (GLMs) performed on different factions of the community. Models were simplified sequentially, but volume, height and forest type were retained in all models as they were of interest to us. Significance ($p < 0.050$) indicated by *.

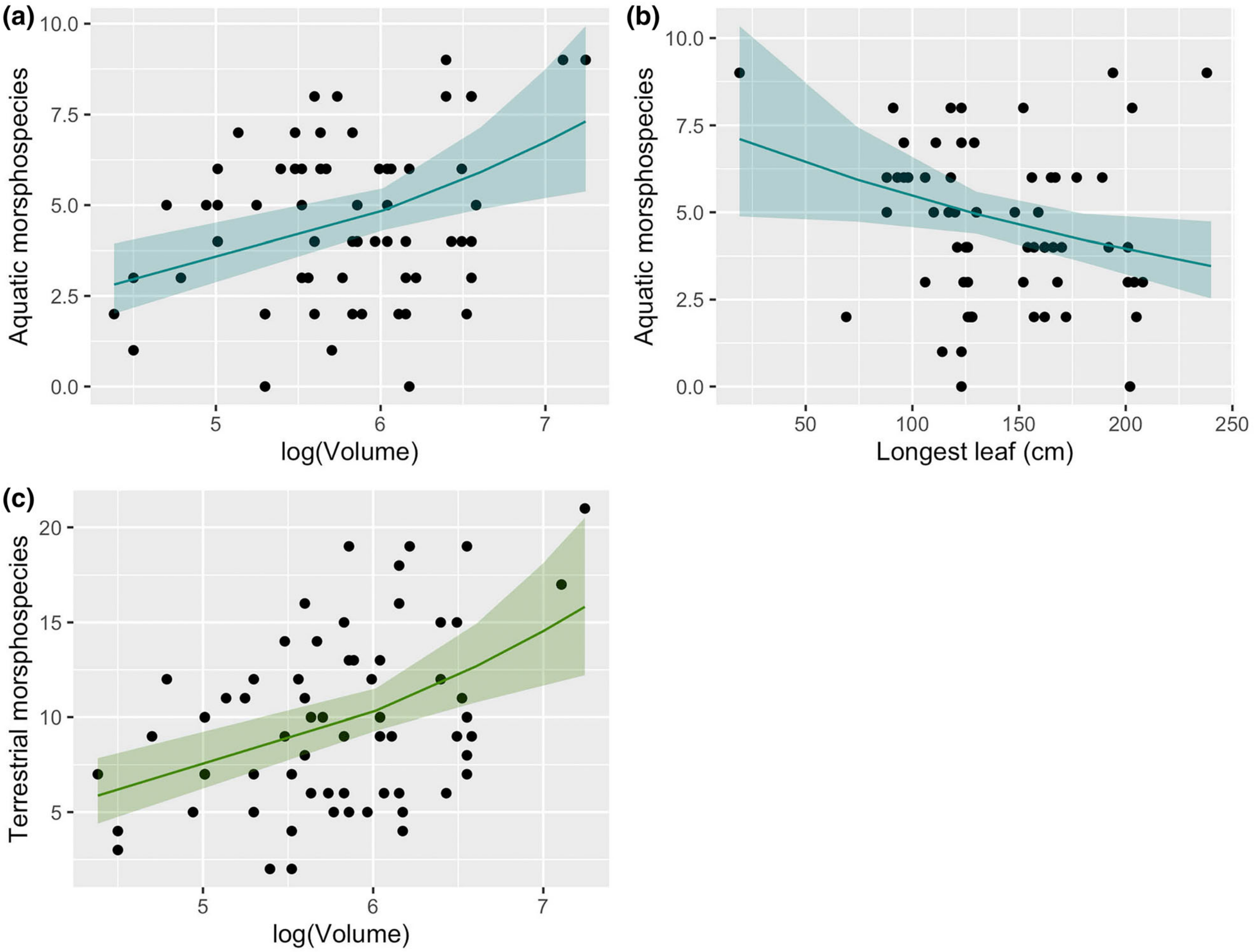

FIGURE 3 Trends in species richness according to different bromeliad traits. The number of morphospecies increased significantly with bromeliad capacity or volume in the aquatic (a) and terrestrial communities (c) and decreased in the aquatic community with increasing length of the longest leaf (b).

TABLE 2 Results from PERMANOVAs of different factions of the community.

		Presence–absence				Abundance			
		F	df	R^2	*p*	F	df	R^2	*p*
Aquatic community	Height	2.276	1, 50	0.035	0.027*	1.961	1, 50	0.031	0.035*
	Sample time	3.265	1, 50	0.050	0.002*	3.856	1, 50	0.061	<0.001*
Terrestrial community	Height	1.618	1, 53	0.025	0.015*	1.329	1, 53	0.021	0.043*
	Sample time	1.369	1, 53	0.021	0.077	1.036	1, 53	0.016	0.383

Note: We have only displayed the statistics for height on the tree and sampling time as they are the only factors that explained significant portions of variation in either of the subsets of data. Sample time was either in the January–February field collection or in July–August. Significance indicated by *.

buffer against anthropogenic disturbance, although it may also reflect the healthy state of Payamino's secondary forested areas.

Effect of height

The height at which bromeliads were found—which ranged from about 2 m to 20 m—had no effect on the species richness or number of individual invertebrates within the bromeliads in our dataset. This mirrors some studies that found no effect of height on phytotelmata communities (Gossner & Petermann, 2022; Jocque & Field, 2014; Zytynska et al., 2012b), although it contrasts with other studies of phytotelmata and canopy invertebrates in general that find a decrease in diversity as one ascends towards the top of the canopy (Chapin & Smith, 2019; DeVries et al., 1997; Yanoviak, 1999). However, bromeliad attachment height did have a significant effect on community composition, despite the amount of variation explained being small. There are a number of reasons why vertical stratification may occur in forests, such as the contrasting environmental variables (e.g., temperature, humidity) between ground, understorey and canopy layers; the uneven availability of resources (such as leaf litter and fresh leaf tissue); and the behavioural traits and dispersal capabilities of different taxa (Basset et al., 2003). Our results suggest that rather than causing stratification in terms of the number of species or abundances, communities may simply be equally rich but structured differently across the vertical canopy gradient.

Of the individual orders analysed, height had no effect on morphospecies richness. Other studies have not found spider abundance or richness to vary vertically (Kitching et al., 1993; Yoshida et al., 2021), but we expected other groups may, as both cockroach and fly abundance were found to increase and decrease (respectively) with height in a tropical forest in Borneo (Dial et al., 2006). The differences caused by height indicated by the multivariate analyses, therefore, are likely due to differences at lower taxonomic levels and species turnover, rather than differences in alpha diversity, and may take the shape of species replacement. Although beyond the scope of our data, it would be interesting to see if species replacement is occurring within functional groups with ascending height, or whether functional diversity itself is changing.

Overall, we find that the height at which the bromeliad is attached to its host tree affects the composition of the invertebrate community, although it explains more variation in the aquatic component. Further investigation is required to understand the nature and drivers of this variation. Particularly, microclimatic variation throughout the understorey and canopy could be measured alongside invertebrate collections, as well as leaf litter quantity and quality, which may differ in accumulation across the vertical gradient and could drive differences in energy inputs into the bromeliad microcosm. It would be interesting to ascertain the extent to which the bromeliad microcosm does or does not buffer against changes in conditions found throughout the canopy.

Effect of bromeliad size and complexity

Bromeliad capacity explained a significant portion of the variation between terrestrial communities. Richness was positively correlated with volume, as has been shown by previous studies on bromeliad invertebrates (Jabiol et al., 2009; Jocque & Field, 2014; Méndez-Castro et al., 2018). Habitat size is known to affect different invertebrate taxa to different extents, with predators generally requiring a larger area (Romero et al., 2016; Srivastava et al., 2008b; Srivastava et al., 2020b). However, the only fully predatory group at the order level that was common enough to analsze separately from the rest of the community was spiders, which seemed unaffected by any of the measured variables. Bromeliad size did not affect patterns within any of the most common orders in the dataset, and so it does not appear that the effect of size on the communities is driven by patterns within individual orders. However, we do not have the data to investigate whether these patterns could be driven by turnover within, for instance, functional groups, which could explain patterns hidden by grouping diverse assemblages of invertebrates taxonomically.

In addition to size, plant architecture and complexity have previously also been shown to affect bromeliad invertebrate communities (Armbruster et al., 2002; Carrias et al., 2014; Gonçalves-Souza et al., 2011a; Gonçalves-Souza et al., 2011b). However, here we found no effect of the number of leaves on the community in terms of richness or composition. Instead, the longest leaf of bromeliads was marginally significantly correlated with the richness and abundance of the aquatic community. The longest leaf did not correlate significantly with any of the other size variables measured, and so the reason for its effect on the aquatic community here is unclear. Leaf length has been shown elsewhere to affect patterns of spider functional composition, but spiders are not part of the aquatic community (Gusmão et al., 2020). Longer leaves imply greater overall surface area of the plant, but how this might affect the aquatic community in the phytotelm is not obvious.

Effect of sampling time

Field collection took place over two different periods within the same year. Although San José de Payamino does not have marked seasons (Irvine, 1987; Sullivan et al., 2020), with sporadic wetter and drier periods throughout the year (*pers. obs*), the time at which we sampled (whether January–February or July–August) did have a significant effect on the aquatic community within bromeliads. However, there are seasonal patterns in fruiting trees (Stafford et al., 2016), and it is expected that biological seasons (defined breeding seasons, for example) likely occur regardless of the otherwise stable annual climate. Many of the representatives of the aquatic community in the bromeliads we collected were in their larval state. Although specimens were not classified according to their larval state, there was a greater relative abundance of Coleoptera during the second sampling season, which were a common component of the larval community in our dataset (*pers. obs*.). It would be interesting to be able to ascertain whether the differences driven by collection time were indeed driven by differences in the larval community since the terrestrial community was not affected in the same way.

Effect of forest type

Whether bromeliads were found in primary or secondary forest did not affect bromeliad communities. This was contrary to our expectations, as we thought the starting invertebrate community may differ between forest types. Certainly, bromeliads act as a buffer against numerous environmental conditions (Fernandez Barrancos et al., 2017; Scheffers et al., 2014), and these results might suggest that human disturbance could be one of them. However, we recorded at least one introduced ant species twice in the bromeliads we sampled in primary forest, *Monomorium* *floricola* (Wetterer, 2009), which could be associated with biological invasion processes, emphasising that these assemblages are not immune to human disturbance, even those we consider to be in a "primary" or near-pristine state. Other studies have found that local environmental conditions (Ngai et al., 2008) or differences in the occurrence and size of bromeliads themselves among forest types (Srivastava et al., 2005) drive differences between primary and secondary forest communities in bromeliads, although this could not be the case in our dataset. Local environmental conditions such as canopy cover or shade have also been found to affect bromeliad invertebrate communities (Busse et al., 2018; Méndez-Castro & Rao, 2014), and it can be expected that different stages of forest succession exhibit different canopy densities and light conditions (Matsuo et al., 2021). Although we did not measure canopy cover or tree densities in this study, the secondary forest areas were well forested. Another study in Payamino measured certain differences between the primary and secondary forest of the area, namely, the difference in NDVI values, which were found to be lower in primary forest than in secondary forest (Oldekop et al., 2012). Despite this, it is possible that the lack of differences in bromeliad communities between forest types is, in fact, due to the level of preservation of the secondary forest areas of Payamino, which are managed by a local Kichwa community. We caution against extrapolating this to mean that conserving secondary forests may suffice to preserve biodiversity, as other groups may be found to be affected by even subtle differences between primary and secondary forest (Parry et al., 2007).

CONCLUSION

In this study, we studied the invertebrate communities in two species of *Aechmea* bromeliads in a part of the Ecuadorian Amazon and Tropical Andes Biodiversity Hotspot, in the context of a range of environmental and plant measurements. The average number of morphospecies per bromeliad (300 morphospecies in 63 bromeliads) was higher than in the last comprehensive study of bromeliad invertebrate communities in Ecuador (354 morphospecies in 209 bromeliads) (Armbruster et al., 2002), reflecting the extremely high biodiversity within the Tropical Andes Biodiversity Hotspot (Myers et al., 2000). We found that community structure in bromeliads at different heights on the host tree and that bromeliad volume was positively correlated with morphospecies richness. Future studies may increase our understanding of these patterns by focusing on functional diversity, which we were unable to analyse because we did not classify the invertebrates into functional groups or measure their traits. However, our study fills in a geographic gap in the study of bromeliad fauna and adds to the limited literature on the communities of bromeliads higher in the canopy, demonstrating the need to explore this realm of the rainforest in order to fully understand community dynamics in these biodiversity amplifiers.

AUTHOR CONTRIBUTIONS

Xaali O'Reilly-Berkeley: Conceptualization; investigation; funding acquisition; writing – original draft; methodology; writing – review and editing; formal analysis; project administration; resources; supervision; data curation. **Alex Pazmiño-Palomino:** Investigation; writing – review and editing; methodology; supervision; data curation; project administration. **Andrea Hidalgo-Cárdenas:** Investigation; writing – review and editing; data curation. **Sofía I. Trujillo-Regalado:** Investigation; writing – review and editing; data curation. **Hannah Mossman:** Conceptualization; formal analysis; supervision; writing – original draft; writing – review and editing. **Jennifer K. Rowntree:** Conceptualization; investigation; supervision; project administration; methodology; writing – review and editing; writing – original draft. **Richard F. Preziosi:** Conceptualization; investigation; funding acquisition; writing – review and editing; methodology; project administration; resources; supervision.

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CONFLICT OF INTEREST STATEMENT

The authors declare there are no conflicts of interest. The first author's current email address reflects their current institutional affiliation, not that under which the present work was undertaken.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in Dryad at: https://doi.org/10.5061/dryad.41ns1rnt9 (O'Reilly-Berkeley et al., 2025).

ETHICS STATEMENT

The field work for this project was carried out with permission from the Ministry of the Environment, Water, and Ecological Transition of Ecuador (Ministerio de Ambiente Agua y Transición Ecológica MAATE) under the access to genetic resources research permits

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ORCID

Xaali O'Reilly-Berkeley https://orcid.org/0000-0002-6508-1230

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1: Supporting Information

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