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Bromeliad Invertebrate Communities on Saba, Netherlands Antilles

Barbara A. Richardson and
Michael J. Richardson



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Cover Photograph: *Tillandsia utriculata* L. (Bromeliaceae), in dry forest on the Spring Bay Trail, Saba, Netherlands Antilles. Photograph © M.J. Richardson.

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Bromeliad Invertebrate Communities on Saba, Netherlands Antilles

Barbara A. Richardson^{1,*} and Michael J. Richardson¹

Abstract - We sampled tank bromeliads and censused their invertebrate fauna at four elevations on the small Caribbean island of Saba. We expected that invertebrate communities would show a strong response to the elevational gradient, as found on the larger island of Puerto Rico, but there was no difference in overall animal abundance, species richness, or biomass in bromeliads at the different sites. A weak rainfall gradient and relatively recent anthropogenic disturbance may be reasons for the lack of elevational response. The structure of the community in dry forest bromeliads was different from those in the wetter forests, due to the dominance of the larvae of one particular species (*Forcipomyia antiguensis*). The aquatic larvae of some bromeliad-specialist genera (e.g., *Monopelopia*, *Corethrella*, *Wyeomyia*, and *Scirtes*) common in other Caribbean and mainland sites were absent from Saba. Their absence may be due to the target island effect, which reduces the chances of successful immigration and survival on small islands.

Introduction

Saba is a small, tropical, volcanic island at the northern end of the Lesser Antilles archipelago in the Caribbean Sea (17°38'N, 63°14'W), with an area of 13 km² and an elevational maximum of 877 m above sea level (a.s.l.) at the summit of Mount Scenery (Fig. 1). The mountain is capped by a small area of tropical cloud



Figure 1. Saba from the sea (Photograph © Carole Iritz).

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forest rich in epiphytes and vines. Below the cloud forest is secondary moist tropical forest that becomes increasingly drier with descending elevation until it merges into the remnants of dry evergreen forest at about 350 m a.s.l. and then into dry scrub vegetation near the sea. Thus, in a very short linear distance, ≈ 2 km, there is a marked elevational gradient of vegetation types, which is, however, complicated by disturbance, both natural and human. Hurricane Georges in 1998, followed by Hurricane Lenny in 1999, destroyed many of the massive old *Freziera undulata* (Sw.) Willd. (Mountain Mahogany) trees that dominated the cloud forest, and only five now remain standing and alive (T. van t'Hof, Ecolodge Rendez-Vous, Saba, NA, pers. comm.). They have been replaced by a thicket of *Freziera* and other saplings, and a diverse flora of palms, ferns, and other herbaceous plants. In spite of the steep slopes and deep ravines, many parts of the mountain below the wettest part of the cloud forest were extensively cultivated up until the 1970s with root crops, fruit trees, and areas of grass for grazing cattle. Few gardens exist now, as most food is imported, but evidence of cultivation can still be seen in secondary forest, with occasional cocoa, coffee, and citrus trees. Also, feral goats are found in the drier lower habitats, with consequential effects on the vegetation.

Tank bromeliads, essentially self-contained microcosms, were sampled as part of an ongoing study of the diversity and ecology of their invertebrate fauna along elevational gradients on Caribbean islands of different sizes (Hansen and Richardson 1998; Richardson 1999; Richardson et al. 2000a, 2000b, 2002, 2006; Wagner et al. 2008, 2010). Their aquatic and terrestrial invertebrate fauna contributes to the breakdown of litter that collects in the bromeliad rosettes, the nutrients from which are directly absorbed by the leaf bases, where organic matter and water accumulates (phytotelmata). There is no evidence that species making up this litter-based fauna are specific to particular bromeliad species (Benzing 2000), but rather are habitat-related and dependent on factors of the wider forest ecosystem, particularly the habitat structure and plant species heterogeneity (Richardson and Richardson 2013, Richardson et al. 2000a). During the long-term study in the Luquillo Experimental Forest on the windward side of Puerto Rico, it was found that there were marked differences along the elevational gradient, with strong associations between forest type, bromeliad abundance, and invertebrate community parameters (Richardson and Richardson 2013). We sampled the bromeliads on Saba to find whether the same effects would be observed on a much smaller island.

Saba is the only island in which it has been possible to survey dry tropical forest in the same general locality as moist tropical forest, in order to make comparisons of these invertebrate communities that may be influenced by climatic and vegetational differences along an elevational gradient.

Field-Site Description

At the summit of Mount Scenery, the location of the surviving five old *F. undulata* trees, there were large, dead trunks with a huge burden of epiphytic bryophytes, ferns, orchids, and bromeliads. The site also contained *Prestoea montana* (R. Graham) Nichols. (Sierra Palm), *Cecropia peltata* L., *Rapanea*

ferruginea (Ruiz and Pav.) Mez, *Freziera* saplings, and *Cyathea* spp. (tree ferns). Below the summit, the Lower Mount Scenery and Sandy Cruz sites were in secondary moist tropical forest, where *P. montana*, *Cyathea* spp., *Sloanea massoni* Sw., *Psychotria berteriana* DC., *Myrcia citrifolia* (Aubl.) Urban, *C. peltata*, and *Cordia sulcata* DC. were prominent. The lowest site sampled was in dry evergreen forest on the Spring Bay Trail, where *Tabebuia pallida* (Lindl.) Miers, *Pisonia subcordata* Sw., and *Comocladia dodonaea* (L.) Urban are the main tree species (Stoffers 1956). Tank bromeliads were collected at four elevations on the eastern, windward side of the island (Table 1). At the three higher levels, *Werauhia* spp. and *Guzmania* spp. occurred over the elevational range. *Werauhia urbaniana* (Mez) J.R. Grant (= *Vriesea antillana* L.B. Sm. and Pittendr.) and *Guzmania* sp. occurred on the two Mount Scenery sites, and *W. ringens* (Griseb.) J.R. Grant (= *Vriesea ringens* (Griseb.) Harms) and *W. urbaniana* were collected on the Sandy Cruz Trail. *Tillandsia utriculata* L. occurred only in the dry forest. Recent rainfall records for Saba are fragmentary, except for those from Windwardside (F. Hassell, Windwardside, Saba, NA, pers. comm.), 17°37'49"N, 63°13'52"W, 400 m a.s.l., above and approx. 0.5 km from the Spring Bay Trail site, and below and approx. 1 km from the other three sites. Hassell's observations from 2004–2008 are of an annual total rainfall of 1026–1284 mm. These records are consistent with earlier data from 1891–1933 from three stations on the island <400 m a.s.l., which indicate that total annual rainfall during those years ranged from 1055 to 1124 mm (Braak 1935 in Augustinus et al. 1985). There is no particular wet or dry season, but these records show that the second half of the year tends to be the wetter. Westermann and Kiel (1961) state that the mean annual rainfall is about 1000 mm, varies with elevation and aspect, and has been known to be more than 1920 mm on the higher slopes of the mountain, but they give no indication of where on the island the observations were made. Garcia-Martino et al. (1996) provide an elevational relationship between precipitation and elevation from the Luquillo Experimental Forest in Puerto Rico, in the Greater Antilles 275 km distant. Using their data, from a base value of 1155 mm p.a. at Windwardside, an estimate for the summit of Saba at 877 m would be approx. 1500 mm p.a.

Methods

From experience and analysis of the data from previous studies in Puerto Rico (Richardson 1999, Richardson et al. 2001), which were based on 20 plants per location, it was decided that 10 replicate microcosms collected over a wide area at each site were sufficient to allow identification of the major components of the

Table 1. Bromeliad collection localities.

Site	Elevation (m a.s.l.)	Coordinates (N; W)	Bromeliad identity
Mount Scenery	825–844	17°38'06"; 63°14'24"	<i>W. urbaniana</i> , <i>Guzmania</i> sp.
Lower Mount Scenery	585–705	17°37'48"; 63°14'24"	<i>W. urbaniana</i> , <i>Guzmania</i> sp.
Sandy Cruz Trail	530–590	17°38'17"; 63°14'06"	<i>W. ringens</i> , <i>W. urbaniana</i>
Spring Bay Trail	290–333	17°37'58"; 63°13'41"	<i>T. utriculata</i>

fauna. We sampled them using methods described in Richardson (1999), from each of the four elevational sites, between 20 January 2009 and 6 February 2009. Whole plants, including their retained water, were collected and returned to the laboratory. We recorded plant diameters and numbers of leaves (as an indication of the size of the detrital catchment), the volume of water contained, and the maximum amount of water that could be held when full. Plants were then dissected leaf by leaf, and the leaves and axillary organic soil were washed into water. As we dissected the plants, the dry litter retained in the rosette was examined, and all organisms collected into ethanol. We examined in white trays all washings and detritus collected during dissection and all water collected from the plant, and placed animals collected into ethanol. Collembola and ants were occasionally seen, but were not readily collectable by the methods used and so were not included in the study. We collected, dried, and weighed the organic detritus as a measure of the resource amount available for the fauna. Organism dry weight was estimated using allometric equations derived from earlier work on bromeliad and forest floor litter invertebrate studies (Richardson et al. 2000a; additional data to cover adult Diptera, Hemiptera, and lumbricid worms were obtained and archived at <http://luq.lternet.edu/data/luqmetadata134>). We used Margalef's and Simpson's (1/D) indices to estimate diversity and Sørensen's coefficient to compare intersite similarity (Magurran 2003). Data were analyzed by one-way ANOVA, using Tukey's HSD test for significance. Relative abundance data were compared after arcsin transformation, and detransformed back to percentages for graphing. All raw data are archived at <http://luq.lternet.edu/>.

The effectiveness of using ten plants to assess the composition of the bromeliad invertebrate community on Saba was examined by constructing cumulative frequency curves for each of the four sites, from mean values of 10 random sequences of the ten plants.

Results

Physical parameters of the microcosms

There was considerable variation in plant size within collections from all sites; thus we found few overall significant differences in the parameters measured (Table 2). Plants in the cloud forest at the summit (*Werauhia* spp. and *Guzmania* spp.) were the smallest and contained smaller amounts of litter than in other habitats. *Tillandsia utriculata* in the dry forest along Spring Bay Trail had significantly more leaves than the bromeliad species in the other habitats and contained more

Table 2. Mean physical parameters of plants sampled. Values in any column sharing the same superscript letter are not significantly different ($P < 0.05$, $n = 10$ for each locality). \pm SE in parentheses. Detritus given in dry weight per rosette.

	Plant diam. (cm)	No. of live leaves	Water content (ml)	Water capacity (ml)	Water temp. (°C)	Detritus (mg)
Mount Scenery	54 (2.6) ^A	33 (2) ^A	189 (42) ^{AB}	292 (55) ^A	18.6 (0.2) ^A	5.0 (1.4) ^A
Lower Mount Scenery	102 (8.2) ^B	44 (6) ^A	252 (65) ^{AB}	481 (117) ^A	18.3 (0.2) ^A	16.9 (3.4) ^{AB}
Sandy Cruz Trail	80 (5.2) ^{AB}	37 (3) ^A	269 (41) ^B	321 (32) ^A	20.0 (0.1) ^B	14.5 (3.9) ^{AB}
Spring Bay Trail	94 (5.2) ^B	62 (5) ^B	77 (30) ^A	368 (109) ^A	21.5 (0.3) ^C	28.6 (7.8) ^B

detritus than the smaller plants of the cloud forest on Mount Scenery (Table 2). There was no significant difference in water capacity of the plants at the different localities. Although capacities were similar, the dry-forest plants were significantly drier ($P < 0.001$), on average filled only to 20% capacity, compared to 50–80% for the other bromeliad species at higher elevations; sampling was, however, carried out during the drier part of the year. The temperature of water in bromeliad axils decreased significantly with increasing elevation ($P < 0.0001$; Table 2), from 21.5 °C in the dry forest to ≈ 18.5 °C at higher elevations.

Community composition and distribution of species

A total of 10,524 animals were collected from the 40 plants (Table 3), with a species pool from all elevations of 91. Seventeen taxa contributed at least 4% of either total abundance or biomass (dry weight) in at least one of the four habitats (Table 4). These species accounted for >97% of the total community by number and >95% of biomass.

There were no significant differences among plants from the four habitats in total animal abundance, number of species per plant, or in Margalef's diversity index, which measures species richness. Simpson's diversity index, which measures dominance and from which evenness can be derived (Table 3), was significantly lower in the dry-forest bromeliads, demonstrating a different community structure from those in plants at other elevations. This result was attributable to the high abundance of the larvae of *Forcipomyia antiguensis* Saunders (Ceratopogonidae), which accounted for 65% of the total community. The cumulative frequency curves all had R^2 values > 0.984 , and extrapolations to double the sample size indicated that the 10-plant samples yielded 78–84% of the species that might have been found with a sample size of 20 plants.

The most-abundant organisms were aquatic, dipteran larvae and the small naidid worm *Dero (Aulophorus) superterrenus* Michaelsen (Naididae). There was considerable difference in the contribution of individual taxa to relative abundance and relative biomass at the four sites (Table 4). Seven dipteran larval species occurred at all sites; four were widespread, and occurred in more than half the plants at each site (Table 4): *Trentepohlia dominicana* Alexander (Tipulidae), *Tanytarsus bromelicola* Cranston (Chironomidae), *Culex bisulcatus* Coquillett (Culicidae), and

Table 3. Summary of invertebrate community parameters. Values in any column sharing the same superscript letter are not significantly different ($P < 0.05$, $n = 10$ for each locality). DW = dry weight.

	Mean no. animals/plant	Mean biomass (mg DW)/plant	Total no. of species in 10 plants	Diversity*		Evenness*
				Margalef	Simpson	
Mount Scenery	338.2 ^A	108.0 ^A	30 ^A	3.6 ^A	4.3 ^A	0.14
Lower Mount Scenery	186.4 ^A	108.7 ^A	42 ^A	5.4 ^A	5.3 ^A	0.13
Sandy Cruz Trail	186.3 ^A	171.6 ^A	32 ^A	4.1 ^A	5.4 ^A	0.17
Spring Bay Trail	341.5 ^A	178.5 ^A	49 ^A	5.9 ^A	2.2 ^B	0.05

*Diversity and evenness values are calculated from the pooled data from each set of ten plants, and the significance values from the individual plant data.

a *Larsia* sp. (Chironomidae). Predatory larvae of a *Bezzia* sp. (Ceratopogonidae) were found only at high elevations, and *Alepia apexalba* Wagner, Richardson, and Richardson (Psychodidae), recently described and possibly endemic to Saba, was present only in dry-forest bromeliads. The distribution of *Forcipomyia antiguensis* was unusual in that it was highly abundant and occurred in all plants in both the dry forest and the cloud forest, but was low in abundance in the two mid-elevational sites. The Naididae and large lumbricid worms were absent from the dry forest. The aquatic organisms were detritivores (shredders or collector/gatherers), with the exception of the predatory *Bezzia* sp. and *Larsia* sp. larvae and infrequent planarians.

Terrestrial detritivores responsible for the breakdown of incoming litter, e.g., cockroaches, millipedes, beetles, and lumbricid worms, although less abundant, contributed a high proportion of animal biomass. By virtue of their relatively large size, a single such individual would greatly influence the biomass of a sample. They

Table 4. Mean components of the community – relative abundance (%), biomass (% d.w.), and frequency of occurrence (in parentheses). **Major contributors by number or weight. * = immature forms—larvae, pupae or nymphs.

	Spring Bay Trail	Sandy Cruz Trail	Lower Mt. Scenery	Mount Scenery
Abundance				
Ceratopogonidae, <i>Forcipomyia antiguensis</i> *	65.0 (100)**	<1.0 (20)	2.7 (70)	35.0 (100)**
Chironomidae, <i>Polypedilum</i> sp.*	<1.0 (20)	30.0 (90)**	2.9 (50)**	27.0 (100)**
Tipulidae, <i>Trentepohlia dominicana</i> *	5.0 (80)	13.0 (100)**	26.0 (100)**	5.4 (100)
Chironomidae, <i>Tanytarsus bromelicola</i> *	12.0 (70)**	14.0 (80)**	11.0 (90)**	6.1 (70)
Chironomidae, <i>Metricnemus</i> sp.*	<1.0 (20)	4.6 (80)	29.0 (100)**	2.8 (100)
Culicidae, <i>Culex bisulcatus</i> *	1.5 (50)	9.4 (90)	13.0 (80)**	1.0 (80)
Annelida, <i>Dero superterrenus</i>		22.0 (70)**	<1.0 (50)	<1.0 (10)
Ceratopogonidae, <i>Bezzia</i> sp.*			<1.0 (10)	18.0 (100)**
Psychodidae, <i>Alepia apexalba</i> *	10.0 (100)**			
Chironomidae, <i>Larsia</i> sp.*	2.8 (50)	3.1 (90)	4.8 (70)	3.2 (100)
Ceratopogonidae sp.*	<1.0 (20)	<1.0 (10)	4.1 (20)	
Biomass (dry weight)				
Annelida, Lumbricidae		49.0 (30)**	30.0 (30)**	47.0 (20)**
Blattidae, cf. <i>Pelmatosilpha coriacea</i> Rehn	44.0 (70)**	26.0 (60)**	16.0 (10)**	3.8 (10)
Tipulidae, <i>Trentepohlia dominicana</i> *	7.1 (80)	9.9 (100)	35.0 (100)**	11.0 (100)**
Chironomidae, <i>Polypedilum</i> sp.*	<1.0 (20)	5.9 (90)	1.6 (50)	15.0 (100)**
Orthoptera, Eneopterinae sp.*	17.0 (30)**			
Ceratopogonidae, <i>Forcipomyia antiguensis</i> *	3.9 (100)	<1.0 (20)	<1.0 (70)	8.0 (100)
Coleoptera, Tenebrionidae	12.0 (10)			
Diplopoda, <i>Eurymerodesmus</i> sp. 1	<1.0 (10)	5.3 (40)	1.9 (10)	
Ceratopogonidae, <i>Bezzia</i> sp.*			<1.0 (10)	6.6 (100)
Platyhelminthes, sp. 7	5.1 (20)			

were most abundant at low elevations, where cockroaches alone contributed 44% of biomass to the dry forest community and, except for large lumbricid worms, terrestrial species were infrequent in the cloud-forest microcosms. Predatory spiders, of many different species, although low in abundance and biomass, were present at all elevations.

Discussion

Community composition at different elevations, particularly the aquatic component, is influenced by both differences in the physical properties of the bromeliad habitat and the forest types in which the adults have to survive (Richardson 1999, Richardson et al. 2000a). The bromeliad invertebrate communities on the very small island of Saba can be compared with those from two other islands in the same general region and similar in general volcanic character and history but differing greatly in area (Saba, 13 km², Dominica 750 km², Puerto Rico 9104 km²). Saba, although it is large enough to attract orographic precipitation, is a relatively dry island (\approx 1500 mm p.a.), whereas tropical wet forest and cloud forest are supported by rainfall of $<$ 5000 mm p.a. in Puerto Rico and \approx 6350 mm p.a. in Dominica.

In the Luquillo Mountains of Puerto Rico, increasing rainfall, and other climatic and edaphic changes, along an elevational gradient, result in three clearly defined forest types with differences in net primary productivity, number of tree species, and structural diversity (Brown et al. 1983, Weaver and Murphy 1990). Bromeliad animal abundance and nutrient inputs declined significantly with increasing elevation and rainfall, and bromeliads were uniformly smaller in the cloud forest. Animal species richness and biomass, however, peaked at the mid-elevation in the Palo Colorado forest (Richardson et al. 2000a), which was the most heterogeneous, with the highest diversity of vines, epiphytes, and herbaceous ground cover (Weaver and Murphy 1990). It has been suggested that the greater the structural heterogeneity and plant species richness of the overall forest environment, the greater the resource provision to support a higher animal species richness (Lawton 1986, MacArthur and MacArthur 1961, Uetz 1991).

The absence of the anticipated effects of the elevational gradient on animal communities in bromeliads on Saba, compared to those found in Puerto Rico along a similar elevational gradient, may be explained by the drier climate, less pronounced rainfall gradient, and more recent anthropogenic disturbance (up to the 1970s), which have resulted in a more uniform environment with few differences among microcosm habitats. The apparent randomness of the Sørensen coefficients between pairs of sites (Table 5), rather than becoming progressively dissimilar with increasing separation as might be expected, would indicate that factors other than

Table 5. Sørensen's similarity coefficient matrix.

	Mount Scenery	Lower Mount Scenery	Sandy Cruz Trail	Spring Bay Trail
Mount Scenery	1.000	0.283	0.435	0.499
Lower Mount Scenery		1.000	0.470	0.222
Sandy Cruz Trail			1.000	0.218
Spring Bay Trail				1.000

the elevational gradient are operating to influence community composition on Saba. Also, forest areas are small there, which reduces dispersal distance, allowing more even distribution. In Puerto Rico, the forest area is much larger and less recently disturbed; small subsistence farming in the lower forest area more or less ceased at the turn of the last century (1890–1930), and the forest has since been protected by the USDA Forest Service. Thus, secondary forest is well-established on Puerto Rico compared to Saba.

Comparisons of the aquatic fauna of Saban bromeliads with those on Dominica and Puerto Rico

The opportunity was taken to compare the invertebrate community composition of the Saban bromeliads with those from two other, larger, Caribbean islands from where bromeliad invertebrate faunas had been studied by the same authors and methods (Fig. 2). On Saba, as in the Luquillo Mountains of Puerto Rico and

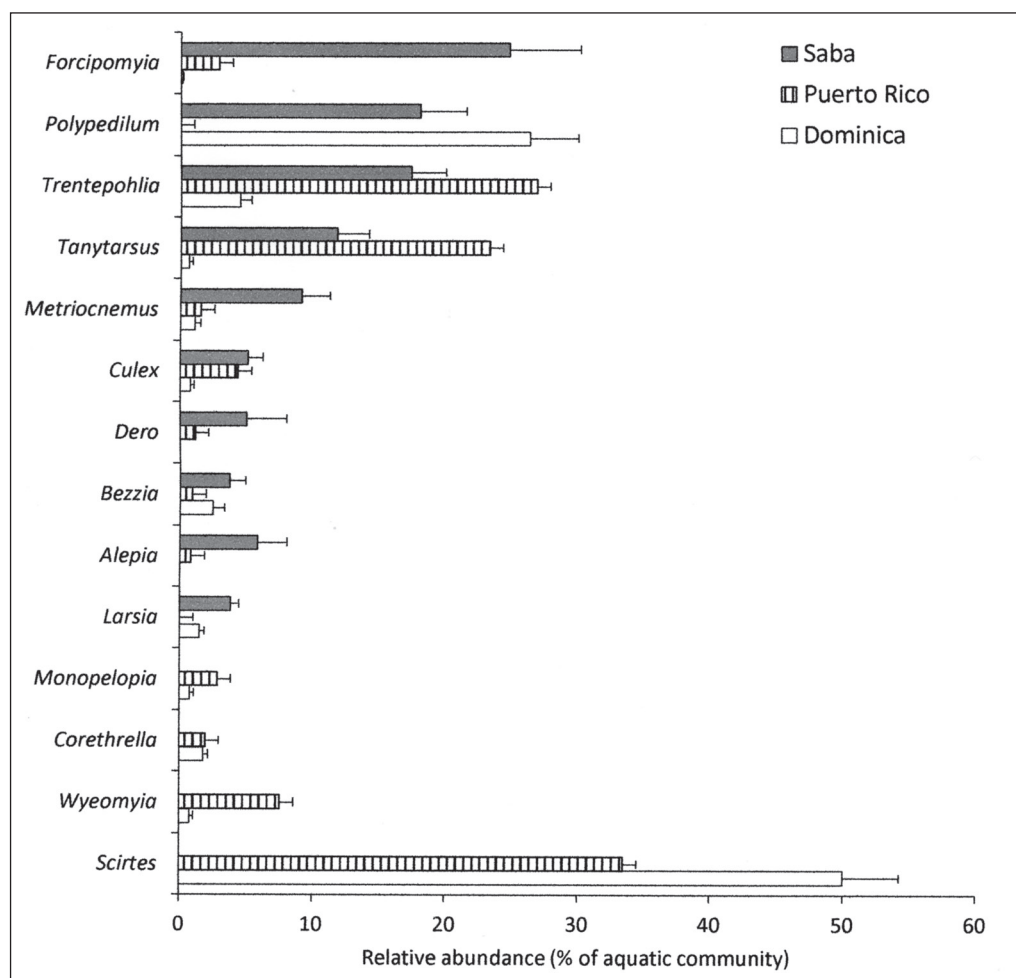


Figure 2. The relative abundance of particular aquatic genera in bromeliads on Saba, compared to Puerto Rico and Dominica. Error bars are the SEs for each taxon, from Saba, Puerto Rico, and Dominica ($n = 40, 370, \text{ and } 30$ plants, respectively).

other mountainous islands, there is no permanent standing water, so phytotelmata are important habitats for insects with aquatic larvae that are known bromeliad specialists. Some species were widespread and abundant on Saba and also found in Puerto Rico and Dominica, such as *Trentepohlia dominicana* and *Tanytarsus bromelicola*; others were closely related species such as *Culex bisulcatus* on Saba and Dominica, which is replaced by *C. antillumagnorum* Dyar in Puerto Rico (Fig. 1). The predatory Tanypodinae were represented on Saba by *Larsia* sp., which also occurred in Dominica, together with *Monopelopia* sp., while *Monopelopia* alone occurred in Puerto Rico (P. Cranston, University of California, Davis, CA, USA, pers. comm.; Richardson 1999).

Forcipomyia antiguensis, the most abundant species in bromeliads on Saba, was described from Antigua, 170 km to the southeast (Saunders 1956), and has not been recorded elsewhere (W. Grogan, Florida State Collection of Arthropods, Gainesville, FL, USA, pers. comm.), except for two larvae found in a single plant from Dominica in 2002 (B.A. Richardson and M.J. Richardson, unpubl. data), and unconfirmed material from bromeliads in French Guiana (R. Cereghino, Université Paul Sabatier, Toulouse, France, pers. comm.). Some psychodids, such as *Alepiea* spp., are mainly found in bromeliads and have a high rate of speciation and endemism, and new species have been described recently from the area (*A. apexalba* from Saba and *A. zavortinki* Wagner, Richardson, and Richardson [Psychodidae] from Puerto Rico [Wagner et al. 2008, 2010], and *A. symmetrica* Wagner and Hribar from Florida [Wagner and Hribar 2005]).

Compared to the bromeliad fauna on neighboring islands, there were notable absences on Saba. *Wyeomyia* mosquitoes were absent, whereas they were a major component of similar habitats in Puerto Rico and Dominica (Richardson 1999; B.A. Richardson, unpubl. data). No *Corethrella* species were found on Saba. These are exclusively frog-biting midges; the females require a blood meal before oviposition. There is evidence that the females are preferentially attracted to certain frog species, which they identify by their calls and chemical cues (Borkent 2008). Their presence on islands is, therefore, dependant on frog diversity. There is only one species of frog on Saba, while there are about 11 tree frog species in the Luquillo Mountains of Puerto Rico where, in the cloud forest at the highest elevation, *Corethrella belkini* Borkent (Corethrellidae) is a major component of the bromeliad fauna. In Dominica where there are three tree frog species, *C. caribbeana* Borkent was recorded at all elevations in a similar study. Larvae of the marsh beetles (Scirtidae), very numerous in both Puerto Rican and Dominican bromeliads (Richardson 1999; B.A. Richardson, unpubl. data), were also absent from Saba.

The islands of the Greater and Lesser Antilles are volcanic in origin and have never been linked to a continental landmass for any significant period of time, even with the controversial possibility of short-lived land-connections between what is now Puerto Rico and Venezuela during the mid-Cenozoic period 33–35 Mya (GAARlandia; Iturralde-Vinent and MacPhee 1999). Colonization of the bromeliad habitat can, therefore, only have been by chance dispersal dependant on wind and marine currents between Florida, Central and South America, and the Antilles. The islands have high levels of endemism and are a Caribbean diversity hotspot (Myers

et al. 2000). Associations with continental land masses are evidenced by *Tanytarsus bromelicola* also occurring in Florida (Cranston 2007) and the Saba *Polypedium* sp. and *Metriocnemus* sp. being very similar to those described and illustrated by Picado (1913) (as *Chirocladius pedipalpus* Picado and *Metriocnemus abdominoflavatus* Picado) from Costa Rica, but adult males would be needed to confirm their identity (P. Cranston, pers. comm.). Picado (1913) also found a *Scirtes* sp. to be very common in Costa Rica. *Dero superterrenus* was originally described from Costa Rica, is abundant in bromeliads in Florida, and is widely distributed in the neotropics, including Brazil (Frank and Fish 2008). This wide distribution may be because it is not a bromeliad specialist but also occurs in other phytotelmata, such as tree holes and *Heliconia* floral bracts (Richardson et al. 2000b).

MacArthur and Wilson's equilibrium theory of island biogeography was developed to explain two very general patterns—the tendency of the number of species to increase with increasing island area and to decrease with isolation, and has since been modified to include the target-island effect (Brown and Lomolino 1998), i.e., “large islands may serve as more effective target areas for potential immigrants”, and its converse, small islands are more likely to be missed by dispersing organisms, and their chances of survival are reduced. The absence from Saba of some common bromeliad specialists such as *Scirtes*, *Wyeomyia*, and *Monopelopia*, may be due to this effect, and for host-dependent species like *Corethrella*, the island effect is compounded. It is important, however, to recognize that disturbance through fragmentation of habitat and individual species characteristics, such as body size and dispersal ability, may also influence survival and hence community composition within ecological networks (Hagen et al. 2012).

On Saba, both cloud forest (Mount Scenery) and the lower dry forest (Spring Bay Trail) were unsuitable for agriculture and thus relatively undisturbed, and both have bromeliads in abundance. At intermediate elevations, distribution of the bromeliad habitat for invertebrates is more patchy (B.A. Richardson and M.J. Richardson, pers. observ.). This patchiness may explain the much-reduced abundance of *Forcipomyia antiguensis* at mid-elevation. It is hoped that this paper will provide a baseline for future work on the bromeliad fauna of Saba as the secondary forest at intermediate elevations recovers from the effects of agriculture.

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