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# Environmental determinants of macroinvertebrate diversity in small water bodies: insights from tank-bromeliads

Olivier Dézerald · Stanislas Talaga ·  
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**Abstract** The interlocking leaves of tank-forming bromeliads (Bromeliaceae) collect rainwater and detritus, thus creating a freshwater habitat for specialized organisms. Their abundance and the possibility of quantifying communities with accuracy give us unparalleled insight into how changes in local to regional environments influence community diversity in small water bodies. We sampled 365 bromeliads (365 invertebrate communities) along a southeastern to northwestern range in French Guiana. Geographic locality determined the species pool for bromeliad invertebrates, and local environments determined the

abundance patterns through the selection of traits that are best adapted to the bromeliad habitats. Patterns in community structure mostly emerged from patterns of predator species occurrence and abundance across local–regional environments, while the set of detritivores remained constant. Water volume had a strong positive correlation with invertebrate diversity, making it a biologically relevant measure of the pools' carrying capacity. The significant effects of incoming detritus and incident light show that changes in local environments (e.g., the conversion of forest to cropping systems) strongly influence freshwater communities. Because changes in local environments do not affect detritivores and predators equally, one may expect functional shifts as sets of invertebrates with particular traits are replaced or complemented by other sets with different traits.

**Keywords** Freshwater biodiversity · Linear mixed effect modelling · Microcosms · Phytotelmata · Ponds

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## Introduction

Ponds are subject to anthropogenic pressure (e.g., agriculture, industry, urbanism, deforestation) even though these ecosystems have obvious ecological functions (Hansson et al., 2005) and recognized social and economic uses (Chapman et al., 2001). In light of recent economic development, a major challenge is to understand the turnover of pond communities in relation to changes in local–regional environments and pond habitat characteristics (EPCN, 2008). More specifically, our ability to predict the responses of the biota to changes in landscape and aquatic habitat resources will contribute to the success of future conservation actions. Incoming detritus (e.g., leaf litter, an important food resource at the base of the food webs) and light regime (i.e., energy available for photosynthesis) play key roles in shaping community diversity in ponds through nutrient availability (Ruggiero et al., 2005). The surrounding land-cover (<200 m, Declerck et al., 2006) can therefore explain significant variation in pond community diversity, because the extent and nature of perennial vegetation affects allochthonous and autochthonous contributions to the aquatic food webs through direct (nutrient inputs) and indirect (light) effects, ultimately changing the communities (Céréghino et al., 2008). However, the responses of biological communities to these variables also depend on interactions between environmental changes and intrinsic pond features, such as size (Oertli et al., 2002) or trophic status (Ruggiero et al., 2005).

It is challenging to study the effects of environments on entire pond communities, first because different taxonomic groups with high species diversity do not respond equally to environmental changes (Oertli et al., 2002), and, second, because high population densities and the diversity of pond microhabitats often preclude the accurate quantification of biological diversity (Oertli et al., 2005). To tackle

these issues, we focused on small, spatially discrete pools that are highly frequent and naturally span a broad range of environmental gradients. Bromeliaceae are flowering plants represented by 59 genera and some 3,140 species native mainly to the Neotropics (Givnish et al., 2011). The interlocking leaves of tank-bromeliads form pools that collect rainwater (from a few millilitres to a few litres), leaf litter and other organic detritus. These pools, or phytotelmata (“plant-held waters”), provide a habitat for aquatic organisms, notably bacteria, algae, fungi, protozoa, zooplankton, macroinvertebrates, and amphibians (Kitcing, 2000; Frank & Lounibos, 2009). Because they host simple communities but yet contain multiple trophic levels, bromeliad pools and their aquatic biota have proven to be ideal model systems for studying the rules by which communities are assembled (Armbruster et al., 2002).

While there has been increasing interest in the study of habitat and the spatial distribution of invertebrates in ponds and pools (Boix et al., 2012), most studies have focused on one scale, e.g., a region (Trigal et al., 2007), a network of ponds (Angélibert & Giani, 2003), or the suitable microhabitats within a pond (Van de Meutter et al., 2005). Our study focused on the macroinvertebrate communities inhabiting tank-bromeliads in French Guiana, where the juxtaposition of contrasting environments (i.e., pioneer growths, plantations, savannahs, primary forest) offered us opportunities to analyse patterns of invertebrate diversity at multiple spatial scales. Specifically, we sampled 365 bromeliads (i.e., 365 invertebrate communities) representing a range of food and habitat resources (i.e., amount of detritus and pool size), surrounding vegetation (i.e., open to closed forest environments), and geographic locations (i.e., southeastern to northwestern French Guiana). Assuming that the bromeliads that grow in primary forests consistently receive higher litter inputs and lower incident radiation than bromeliads in more open sites, we predicted that, for a given geographical location (or species pool), local environments and bromeliad habitats shape community composition and, more specifically, the proportions of detritivores and predators. To test these assumptions, multivariate ordination was used to interpret changes in the quantitative and qualitative structure of the macroinvertebrate communities in relation to geography. Then, we used linear mixed effect modelling to further examine the effects of small-scale variables on species richness and abundance and on predator:detritivore

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ratios (both in terms of richness and abundance), while controlling the effects of surrounding vegetation types (“site”) and geography (“locality”). We discuss bromeliad freshwater invertebrate diversity and distribution in the context of pond research and conservation in an attempt to draw the attention of pond ecologists to miniature pools that effectively mirror what can be seen in larger systems.

## Materials and methods

### Study area and bromeliads

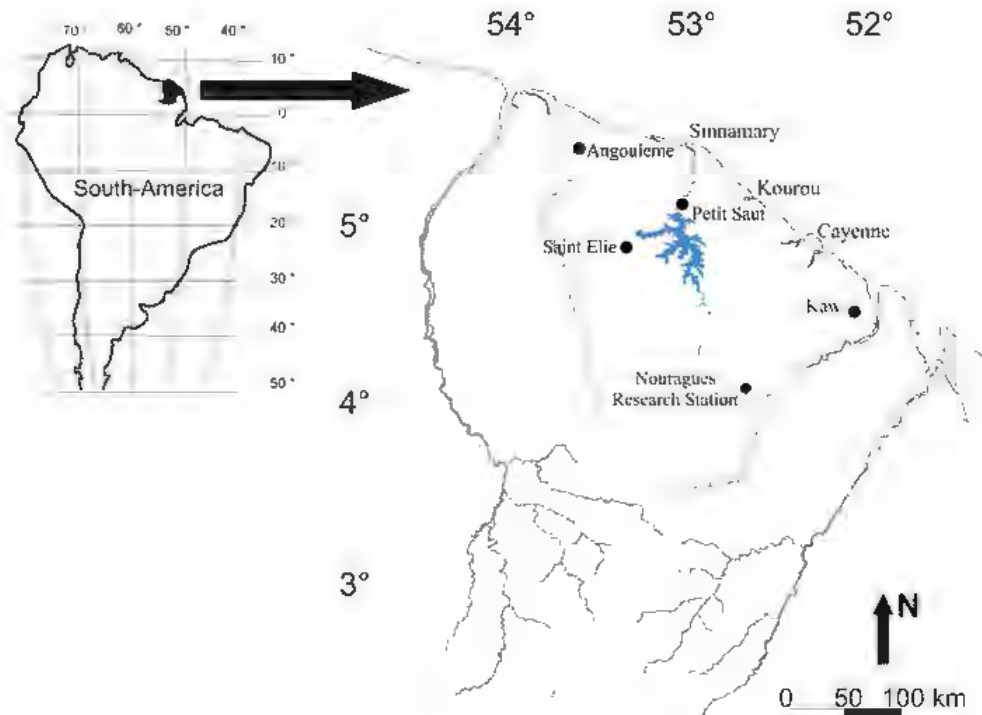
This study was conducted in French Guiana, East Amazonia, from March 2006 to October 2011. The climate is tropical moist with 3,000–3,400 mm of yearly precipitation mainly distributed over 280 days. There is a major drop in rainfall between September and November and another shorter and more irregular dry period in March. The maximum monthly temperature averages 33.5°C (32.1–35.8°C), and the monthly minimum averages 20.3°C (19.7–21°C).

We selected five sampling localities distributed across a south-east to north-west range (Fig. 1) and sampled 365 bromeliad pools in the understorey of primary forests, in pioneer growths, a rock savannah,

and plantations. Full descriptions of the Nouragues, Petit Saut and Kaw localities and their bromeliads can be found in Bongers et al. (2001), Céréghino et al. (2011), and Brouard et al. (2012), respectively. Saint Elie and Angoulême are *Citrus grandis* plantations. The main characteristics of the sampling localities, vegetation types (hereafter “sites”, within localities) and number of sampled bromeliads are provided in Table 1. The seven bromeliad species represented here were either epiphytes (<2 m above ground) or had taken root on the ground.

The percentages of total incident radiation above the bromeliads (IR) were calculated using hemispherical photographs and an image processing software (Gap Light Analyzer 2.0) (Frazer et al., 1999), as described in Leroy et al. (2009). To characterize habitat size, we emptied the wells in each plant by sucking the water out (see invertebrate sampling) and recorded the corresponding volume of water (WV, ml). In order to prevent the influence of seasonality (i.e., dry vs. rainy season) on water volume, we sampled bromeliad tanks that were full of water at the time of sampling. The amount of fine particulate organic matter (FPOM; 1000–0.45 µm in size, the food resources at the base of the food webs) was expressed as preserved volume (ml after decantation into graduated test-tubes; see also Paradise, 2004).

**Fig. 1** Distribution of sampling localities (Nouragues, Kaw, Petit Saut, Angoulême, Saint Elie) across a south-eastern to north-western range in French Guiana



## Aquatic invertebrate communities

For both ethical (extensive sampling could destroy local populations) and legal reasons (the Nouragues Research Station is located in a nature reserve), we used a non-destructive sampling technique. To sample the water retained in the tanks, we used 5- and 10-ml micropipettes with the end trimmed to widen the orifice. Although less efficient than plant dissection, we and other researchers have already successfully used this technique (Céréghino et al., 2010; Jocqué et al., 2010a). It was consistently used for all of the samples. The samples were preserved in the field in 4% formalin (final concentration). The invertebrates were sorted in the laboratory and preserved in 70% ethanol. They were identified to genus, species or morphospecies and enumerated. Species abundance data were expressed as number of individuals per plant. Invertebrate taxa were partitioned into predators (carnivorous species which attack and consume living prey organisms) and detritivores (species which sift fine particulates from the water column and/or gather FPOM from the accumulated debris), and these functional groups were used to calculate predator:detritivore richness ratios (PDRR) and predator:detritivore abundance ratios (PDAR). The distribution of invertebrate taxa (and the corresponding functional groups) among sites is given in the supplementary online material.

## Data analysis

First, a correspondence analysis (CA; Jongman et al., 1995) was used to ordinate the samples (bromeliads) according to macroinvertebrate morphospecies abundances (after  $\log n + 1$  transformation), thus summarizing the variability of the data and providing insights for the elaboration of the subsequent richness and abundance models. The significance of the axes was determined at  $P < 0.05$  by testing the eigenvalues of the inertia matrix. The plots of the first two ordination axes usually capture most of the variance and consequently contain most of the information that is likely to be interpretable (Waite et al., 2000). The bromeliads which were neighbours in the scatterplot were expected to host similar invertebrate communities. Conversely, the bromeliads that were separated from each other by a large distance were expected to be distant in the feature space based on their macroinvertebrate communities.

To further analyze the relationship between species richness, overall invertebrate abundance, PDAR and PDRR (dependent variables) and environmental variables (independent variables), we used linear mixed effect modelling. “Site” (vegetation types) was nested within ‘locality’. In contrast, a given bromeliad species could be sampled in many localities or many sites, therefore the variable “bromeliad species” was not nested within the former or the latter. Since “locality”, “site”, “site nested within locality” or “bromeliad species” (i.e., various spatial components) could be included as random factors, we conducted a model selection based on the Bayesian Information Criterion (BIC) of the full models (models considering all environmental variables) for each dependent variable. This procedure allowed us to identify the spatial scale that best accounted for patterns for each dependent variable. Then, for a selected random factor (lowest BIC), the relationships between dependent and independent variables were explored using a stepwise backwards removal procedure and only the final models containing significant variables were presented. We used the `glmer` function in R software V.2.14.1 (nlme package) to analyse species richness and invertebrate abundance because these dependent variables followed a Poisson distribution. PDAR and PDRR were ranked because they were not normalized by the usual transformations (Aulchenko et al., 2007), and we used the `lme` function (lme4 package) to analyse these variables. Generalized linear mixed models with species richness and abundance were fit using the Laplace approximation while models with predator-to-prey ratios were fit using restricted maximum likelihood (REML). Based on model residuals, the violation of homogeneity and normality was assessed graphically. All statistical analyses were evaluated under a 95% confidence level.

## Results

When a CA was carried out on the invertebrate abundance matrix (Fig. 2), the first two axes contributed 18.6 and 10.4% to the overall variance, respectively. The distribution of invertebrate taxa (Fig. 2b) compared to the grouping of samples by locality (envelopes in Fig. 2a) showed that (i) with the exception of the Nouragues locality, invertebrate taxa found in species-poor localities (e.g., Saint Elie, Kaw)

**Table 1** Main characteristics of the sampling sites and plants sampled (seven bromeliad species)

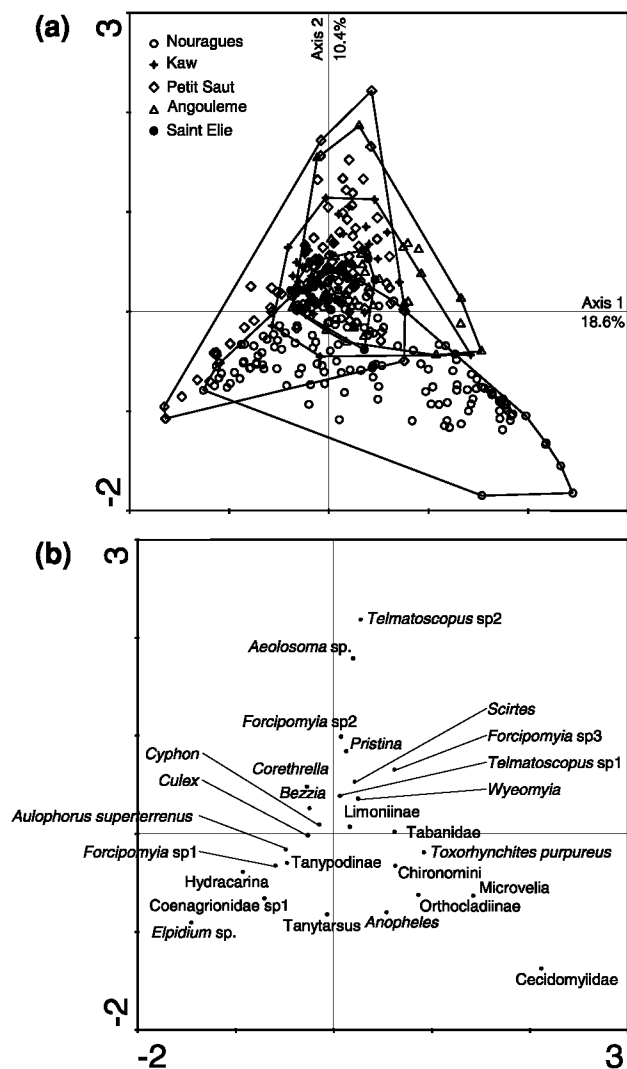
Locality	Site	Bromeliad	N	IR	WV	FPOM	Taxa	Ind
Nouragues	Rock savannah	CB	29	73.3 ± 2.4	40.62 ± 3.75	0.74 ± 0.08	10.55 ± 0.15	32.96 ± 3.83
		AA	31	66.97 ± 2.73	949.23 ± 102.64	10.84 ± 1.26	14.87 ± 0.42	242.25 ± 32.15
	Transition forest	VP	30	25.12 ± 0.29	73.2 ± 9.11	1.7 ± 0.28	10.3 ± 0.35	9.4 ± 1.85
		AB	26	25.69 ± 0.47	137.85 ± 21.1	1.08 ± 0.25	11.23 ± 0.32	16.5 ± 2.76
		VS	26	18.75 ± 0.4	48.54 ± 5.03	4.29 ± 0.42	10.35 ± 0.25	11.11 ± 1.55
Petit Saut	Primary forest	GL	19	15.9 ± 0.6	17.46 ± 2.53	1.04 ± 0.16	10.21 ± 0.29	5.1 ± 1.2
		AM	63	39.33 ± 2.63	84.38 ± 10.1	6.16 ± 1.26	12.49 ± 0.28	76.47 ± 10.63
	Pioneer growth	VS	34	16.64 ± 0.38	26.18 ± 3.84	3.46 ± 0.71	10.68 ± 0.23	25 ± 6.03
		AM	45	35.1 ± 2.98	92.46 ± 11.82	4.3 ± 0.68	11.78 ± 0.28	71.88 ± 11.56
		AM	35	33.03 ± 2.95	31.01 ± 4.54	2.32 ± 0.31	11.8 ± 0.34	75.68 ± 30.71
Saint Elie	Citrus plantation	AM	27	32.07 ± 1.3	56.41 ± 8.29	4.58 ± 0.86	14.22 ± 0.36	37 ± 5.17

CB: *Catopsis berteroniana*; AA: *Aechmea aquilega*; VP: *Vriesea pleiosticha*; AB: *Aechmea bromeliifolia*; VS: *Vriesea splendens*; GL: *Guzmania lingulata*; AM: *Aechmea mertensii*; N number of plants sampled; IR incident radiation (%); WV water volume extracted (ml); FPOM fine particulate organic matter (ml after decantation in test-tubes); Taxa number of taxa per plant. Ind number of individuals per plant. Values are means ± standard errors

were mostly subsets of the taxa found in richer localities (e.g., Angoulême, Petit Saut), (ii) a small set of detritivores (e.g., *Culex* spp., *Wyeomyia* spp., *Cyphon* sp1, *Telmatoscopus* sp1, Limoniinae, *Forcypomyia* sp1, *Aulophorus superterrenus*) remained fairly common across localities and sites, and (iii) localities with larger species pools (i.e., Petit Saut, Nouragues, Saint Elie) had additional detritivores (e.g., *Tanytarsus* sp., *Telmatoscopus* sp2, *Anopheles* sp., Orthocladinae, *Elpidium* sp., *Aeolosoma*), but notably included predators (e.g., *Toxorhynchites purpureus*, *Microvelia* spp., Tabanidae, Coenagrionidae) in the bromeliad communities.

Overall, mean invertebrate abundance was higher in open areas than in the primary forest understory (see Table 1), while mean taxonomic richness showed little variability (10–14 morphospecies) between sites and localities; for instance, abundance was up to 48-times higher in *A. aquilega* bromeliads in a rock savannah (242.25 ± 32.15 individuals per plant) compared to *G. lingulata* in a nearby primary forest (5.1 ± 1.2 ind. plant<sup>-1</sup>). Invertebrate abundance was also higher in pioneer growths and plantations (37 ± 5.17 to 76.47 ± 10.63 ind. plant<sup>-1</sup>) than in the primary forest (up to 25 ± 6.03 ind. plant<sup>-1</sup>).

The lowest BIC values were obtained with “locality” as the random factor for the species richness model (138.92; Table 2), and with “site” a random factor for the abundance, PDRR and PDAR models (14238.47, 1002.05, and 980.64, respectively; Table 2). Whatever the geographical locality, the number of taxa per pool increased with water volume ( $P < 0.0001$ ; Table 3). Other variables were not significantly correlated with taxonomic richness in a given locality. At the scale of “site”, there was a negative correlation between invertebrate abundance and the ratios IR:WV and WV:FPOM ( $P < 0.0001$ ; Table 3). For a fixed water volume, the number of individuals per pool thus decreased with increasing incident radiation and amounts of FPOM. There was also a positive correlation between abundance and the ratio IR:FPOM ( $P < 0.0001$ ), so that, for a given light environment, invertebrate abundance increased with increasing amounts of FPOM. In terms of taxonomic richness, the predator to detritivore ratio (PDRR) had a mean value (±SE) of 0.38 ± 0.01. In terms of abundance, the predator to detritivore ratio (PDAR) had a mean value of 0.27 ± 0.01. Both PDRR and PDAR increased with increasing water volume ( $P = 0.004$  and  $P = 0.002$ , respectively) and decreased with increasing incident



**Fig. 2** Correspondence analysis (CA) of invertebrate taxa and bromeliads (axes 1 and 2). Distribution of: **a** bromeliads according to geographical locations, and **b** taxa on the first two axes of the CA

**Table 2** BICs of the full models with species richness, overall invertebrate abundance, predator:detrivore richness ratio (PDRR), and predator:detrivore abundance ratio (PDAR) as dependent variables and four random effects: site, locality, the site nested within the locality (locality/site), and the bromeliad species

Models	Random effects			
	Site	Locality	Locality/ site	Bromeliad species
Richness	143.57	138.92 <sup>a</sup>	144.82	145.00
Abundance	14238.47 <sup>a</sup>	16810.9	14244.28	15591.84
PDRR	1002.05 <sup>a</sup>	1002.6	1007.04	1005.41
PDAR	980.64 <sup>a</sup>	984.77	984.44	995.35

<sup>a</sup> Lowest BIC values

radiation ( $P = 0.001$  in both cases). Moreover, both models showed a positive and significant interaction between incident radiation and amounts of FPOM ( $P = 0.03$  for the two models; Table 3).

## Discussion

Not surprisingly, in our study there was a trend for invertebrate communities from different localities to exhibit differences in taxonomic composition and species abundance, a common pattern in freshwater invertebrate communities. Nevertheless, it is worth noting that patterns of taxonomic richness and overall invertebrate abundance mostly emerged from patterns of predator species occurrence and abundance across local/regional environments, while a set of generalist species remained relatively constant at lower trophic levels (“detrivores” *sensu lato*). Future research could therefore examine whether the composition of the biological traits of pond detritivores is independent of geography (on a regional scale) despite a spatial turnover in the taxonomic composition. If generalist detritivores share biological traits that determine sensitivity to disturbance (e.g., resistance to desiccation, dispersal ability), then larger changes in community diversity could be expected under future regional development scenarios.

The model selection based on BICs for taxonomic richness and invertebrate abundance suggested that geographical locality determined the potential species richness for bromeliad pools, then local conditions (sites) determined species abundance patterns through the selection of traits that are best adapted to the bromeliad habitats. In general, ponds and pools tend to show positive species–area relationships (e.g., Ruggiero et al., 2008) with larger habitats being more easily colonized by immigrants (Drakare et al., 2006). We also noted that, regardless of locality or site, water volume (habitat size) had a strong correlation with both invertebrate richness and abundance, making it a biologically relevant measure of the pools’ carrying capacity. There was, however, a trend for pools with higher radiation incidence to accumulate more water (WV to IR ratio,  $r = 0.32$ ,  $P < 0.05$ , log-transformed data) certainly because in open areas there are fewer overhanging trees to keep most or all of the rain from reaching the bromeliads. Hence, even for a given bromeliad species and/or bromeliad size, the containers



**Table 3** Models assessing the influence of environmental variables and their interactions on the overall species richness, overall invertebrate abundance, predator:detritivore richness ratio (PDRR), and predator:detritivore abundance ratio (PDAR)

Fixed effect	Estimate $\pm$ SE	DF	<i>z</i>	<i>P</i>	Random effect
<b>Richness</b>					Locality
Intercept	2.043 $\pm$ 0.067	359	30.334	<0.0001	
<b>Slope</b>					
WV	0.116 $\pm$ 0.013	359	9.117	<0.0001	
<b>Abundance</b>					Site
Intercept	1.119 $\pm$ 0.35	350	3.198	0.0014	
<b>Slope</b>					
IR	-0.243 $\pm$ 0.05	350	-4.817	<0.0001	
WV	0.859 $\pm$ 0.04	350	17.18	<0.0001	
FPOM	0.522 $\pm$ 0.066	350	7.957	<0.0001	
IR:WV	-0.061 $\pm$ 0.012	350	-4.961	<0.0001	
IR:FPOM	0.142 $\pm$ 0.018	350	7.700	<0.0001	
WV:FPOM	-0.141 $\pm$ 0.007	350	-19.412	<0.0001	
<b>PDRR</b>					Site
Intercept	1.067 $\pm$ 0.644	352	1.655	0.099	
<b>Slope</b>					
IR	-0.495 $\pm$ 0.168	352	-2.947	0.003	
WV	0.161 $\pm$ 0.055	352	2.908	0.004	
FPOM	-0.835 $\pm$ 0.386	352	-2.163	0.031	
IR:FPOM	0.242 $\pm$ 0.108	352	2.231	0.026	
<b>PDAR</b>					Site
Intercept	1.233 $\pm$ 0.656	352	1.879	0.061	
<b>Slope</b>					
IR	-0.542 $\pm$ 0.167	352	-3.239	0.001	
WV	0.173 $\pm$ 0.054	352	3.174	0.002	
FPOM	-0.831 $\pm$ 0.375	352	-2.215	0.027	
IR:FPOM	0.231 $\pm$ 0.105	352	2.201	0.028	

Only significant variables are presented in the table (SE = standard error)

IR incident radiation, WV water volume, FPOM fine particulate organic matter

hold more water at sun-exposed sites. In any case, larger pools hosted more species, and richer pools contained higher proportions of large-bodied predators (e.g., Coenagrionidae damselflies, Tabanidae and *Toxorhynchites* dipterans). In addition to their intrinsic value for biodiversity (e.g., damselflies), predators satisfy the criterion of “more easily surveyed taxa” because they are mostly represented by large organisms. They are easier to observe and, thus, more difficult to overlook. Surrogacy, or how easily surveyed taxa do well at representing other taxa, is a critical question in pond conservation planning (Oertli et al., 2005). However, Heino et al. (2005) demonstrated that congruence in species richness among freshwater taxa is generally

low, mainly because of their differing responses to major environmental gradients. Our results therefore suggest a functional (rather than taxonomic) approach to surrogacy for small water bodies where the diversity of predators could be an efficient surrogate for the assessment of the broadest communities they belong to. Our models did show that the predator to detritivore ratio (both in terms of richness and abundance) is positively correlated with water volume, thus suggesting that predators largely account for patterns in overall diversity. As a first approximation, the number of predator taxa indeed shows linear relationships with the overall number of taxa (Pearson’s  $r = 0.75$ ). Hence, further analyses could test the relationship between the

species richness of predators and the overall invertebrate species richness in ponds and pools.

Detritus in the form of leaf litter is a main source of energy in tank-bromeliad ecosystems (Benzing, 2000). Debris-chewing invertebrates process incoming litter. Small particles of organic matter, including faeces, then collect in the plant pools and are further processed in the gut of invertebrate collectors and filterers (Kitching, 2000). In a review of leaf traits and decomposition, Hättenschwiler et al. (2011) reported that tree species native to French Guiana share traits that provide an exceptionally poor decomposer substrate. *Citrus grandis* (Saint Elie and Angoulême plantations) has an Asiatic origin, but the waxy coating of its leaves, and not its origin, probably accounts for its poor quality as a decomposer substrate. Therefore, leaf species origin probably has little or marginal effect on invertebrate community patterns. However, while the bromeliads in plantations and in the rock savannah had only one leaf species (*Citrus grandis* trees and *Clusia minor* shrubs, respectively), overhanging trees in pioneer growths (*Vismia* spp. Clusiaceae; *Miconia* sp. and *Bellucia* sp. Melastomataceae) and primary forests (mostly species from the Caesalpiniaceae family, namely *Eperua* spp., *Vouacapoua americana*, *Dicorynia guianensis*, and *Hymenaea* sp. and also species from the Burseraceae, Meliaceae, and Sapotaceae families) contributed a higher number of leaf species to individual bromeliads. Although this aspect should be tested in bromeliads pools, it has been demonstrated that leaf species mixtures decompose slightly faster than single leaf species in freshwater, a pattern determined by the responses of detritivores to resource heterogeneity (Sanpera-Calbet et al., 2009). Nevertheless, whilst bromeliads in primary forests consistently had more diverse leaf species and higher litter inputs than bromeliads in other sites, the amount of FPOM inside bromeliad pools from primary forests was not necessarily higher than those from more open areas (see, e.g., *Aechmea aquilega* and *A. mertensii* in a rock savannah and a plantation, respectively; Table 1). However, FPOM concentrations (the FPOM to WV ratios) show that bromeliads in primary forests had higher concentrations (0.011–0.018 ml FPOM/ml WV) than bromeliads in open areas (0.047–0.088 ml FPOM/ml WV). This indicates that particle concentration rather than amount *sensu stricto* affects species abundance. Hence, the ratio WV:FPOM negatively

correlated with invertebrate abundance at a given site (fewer individuals at a higher particulate concentration for a fixed water volume), and invertebrate abundance was the lowest at forested sites (higher FPOM concentrations). FPOM concentration is related to the extent of open water in small pools. Higher FPOM concentration could therefore decrease the amount of available space in tank-bromeliads to the detriment of open-water swimmers (culicid larvae are typically less abundant in FPOM-rich pools). The amount of FPOM is seen as a relevant indicator of available resources at the lower end of the food chain in plant-held waters (Frank, 1983; Céréghino et al., 2010), and nutrient rich habitats are expected to sustain more species than nutrient-poor habitats (Paradise, 2004). Hence, our results suggest that the relationship between FPOM and community diversity in small pools is not exclusively generated through trophic effects, but also through the physical quality of the habitats.

Throughout the world, ponds and pools come in all shapes and sizes. Ecologists have a long history of documenting freshwater organisms from even the smallest pools like bromeliads (Picado, 1911), tree holes (Kitching, 1987) and rockpools (Jocqué et al., 2010b) to the largest shallow lakes (Batzer & Wissinger, 1996). However, natural microcosms have only recently been exploited as “shortcuts” to highlighting ecological patterns in nature (Srivastava et al., 2004; Brendonck et al., 2010). The success of current and forthcoming pond action plans will be measured in terms of biodiversity and/or the status of target species of conservation interest. A related problem is the lack of understanding of the potential colonisation of rehabilitated systems by “desired” species and/or assemblages. Previous studies suggested that insect predators play an important role in small water bodies with rapid community development and strong abiotic constraints (Magnusson & Williams, 2009). The significant effects of water volume, fine detritus (amount and concentration), light environment, and certainly predation (this study) show that local-scale factors play a crucial role in shaping community structure, and, more importantly, that changes in local environments (e.g., the conversion of forest to cropping systems, pioneer growths along forest roads) strongly influence freshwater communities. Moreover, because local environments do not equally impact the abundance and richness patterns of detritivores and

predators, one may expect functional shifts (e.g., nutrient dynamics in bottom-up vs. top-down controls) as sets of invertebrate species with particular traits are either replaced or complemented by other sets with different traits when shifting from forest under stories to anthropogenically-disturbed, open areas.

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