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Urbanization impacts the taxonomic and functional structure of aquatic macroinvertebrate communities in a small Neotropical city

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Abstract Due to habitat fragmentation, resource disruption and pollution, urbanization is one of the most destructive forms of anthropization affecting ecosystems worldwide. Generally, human-mediated perturbations dramatically alter species diversity in urban sites compared to the surroundings, thus influencing the functioning of the entire ecosystem. We investigated the taxonomic and functional diversity patterns of the aquatic macroinvertebrate communities in tank bromeliads by comparing those found in a small Neotropical city with those from an adjacent rural site. Changes in the quality of detrital inputs in relation to lower tree diversity and the presence of synanthropic species are likely important driving forces behind the observed structural changes in the urban site. Leaf-litter processors (i.e., shredders, scrapers) were positively affected in the urban site, while filter-feeders that process smaller particles produced by the activity of the shredders were negatively affected. Because we cannot ascertain whether the decline in filter-feeders is related to food web-mediated effects or to competitive exclusion (*Aedes aegypti* mosquitoes were present in urban bromeliads only), further studies are necessary to account for the effects of intra-guild competition or inter-guild facilitation.

Keywords *Aedes aegypti* · Bioindicator · Diversity · Functional traits · Tank bromeliads · Urban ecology

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Introduction

Urbanization is one of the most destructive forms of anthropogenic disturbance experienced by ecosystems worldwide. Generally, species diversity is altered dramatically in urban sites compared to the surroundings. The loss of natural habitat, habitat fragmentation, resource disruption and pollution are among the main causes; moreover, urban areas are hotter and drier than rural ones ('urban heat island effect') because the vegetation is supplanted by impervious surfaces, reducing evaporation and evapotranspiration (McKinney 2002, 2008). Also, the greater density of artificial, man-made habitats (e.g., ponds, domestic gardens) fosters colonization by either native or synanthropic species (Santoul et al. 2009; Talaga et al. 2015).

Even if the presence and abundance of most species are influenced by urbanization, community-level responses cannot only be interpreted as a simplification equivalent to a decrease in α diversity (McIntyre 2000). Indeed, the negative or positive effects of urbanization upon community diversity differ markedly between taxonomic groups, and explanations for the contrasting patterns lie in the nature of the processes acting on the focal taxa studied (Henle et al. 2004). For example, the habitat fragmentation inherent to urban areas

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adversely affects vertebrates due to gene flow disruption between populations (Delaney et al. 2010), whereas invertebrates are less affected given the small habitat size needed to sustain a population (Jones and Leather 2013). Moreover, a higher β diversity can be detected within urban areas where habitat fragmentation increases habitat heterogeneity, promotes edge species, and/or creates specific niches for invertebrates (Jones and Leather 2013).

In the Neotropics, tank bromeliads form a highly discontinuous aquatic meta-habitat embedded within a terrestrial matrix. These phytotelmata ('plant-held waters') provide a habitat to aquatic organisms ranging from bacteria to small vertebrates (Kitching 2000; Brouard et al. 2012). Interestingly, this spatially discrete microecosystem can be sampled exhaustively, providing unbiased records of community-level diversity and a relevant model system to bring out environmental effects on community assembly (Srivastava et al. 2004). The key environmental determinants structuring aquatic macroinvertebrate communities in tank bromeliads are related to the characteristics of the aquatic compartment (i.e., habitat size and complexity, food resources, presence of a top predator) and to the characteristics of the terrestrial matrix most often evaluated as open versus closed environments (Brouard et al. 2012; Dézerald et al. 2013, 2014, 2017; Hammill et al. 2015; Trzcinski et al. 2016). Tank bromeliads are common epiphytes in Neotropical cities where the structure of their aquatic communities can be directly or indirectly influenced by human-mediated pressures (Talaga et al. 2015). The fragmentation of the terrestrial matrix caused by urbanization clearly increases the patchy distribution of trees and, so, that of the epiphytes they host. Consequently, their aquatic compartment might be directly affected by less tree canopy cover that leads to a reduction in incoming detritus (e.g., leaf litter) and to an increase in incident radiation, whereas the characteristics of the terrestrial matrix negatively impact their colonization. Indeed, most macroinvertebrates developing in the tanks of bromeliads are larvae with winged, terrestrial adults that are active dispersers whose range of activity can be limited in the hotter and drier conditions of urban areas (passive dispersers like worms and crustaceans colonize new aquatic habitats through phoresy).

Most studies on urban ecosystems have been conducted in temperate regions in Europe and North America. Those conducted in the Tropics were mostly confined to megacities that are not very different from their temperate counterparts in terms of landscape features. Yet, most tropical urban areas are represented by medium to small urban settlements displaying comparatively low levels of urbanization and are often adjacent to natural habitats (Savard et al. 2000; Grau et al. 2008). Consequently, a reduction in the range of the natural-to-urban gradient is likely to favor exchanges between the two environments and thus limit the influence of urbanization on communities. To test this hypothesis, we investigated the influence of urbanization on the macroinvertebrate communities living in the tanks of an abundant bromeliad species by comparing their biodiversity, and taxonomic and functional structure between an urban and a rural site using a small Neotropical city as a model. We also verified if urbanization favors the presence of synanthropic and/or exotic species.

Materials and methods

Study area

This study was conducted in the coastal region of French Guiana, in and around the city of Sinnamary (05°22′39″N 52°57′35″W) during the 2011 dry season. The area has an equatorial monsoon climate corresponding to an average of 2800 mm of yearly rainfall distributed over 251 days (Peel et al. 2007). There is a major drop in rainfall from mid-July to mid-November (dry season) and a shorter and more irregular dry period in March. Minimum and maximum monthly mean temperatures, relatively stable, vary between 23.6 °C and 31.6 °C.

The residential urban area of Sinnamary, which is home to most of the 3165 inhabitants recorded within the municipality (INSEE 2012), displays a moderate level of urbanization representative of a common form of urbanization in the Neotropics. In an attempt to control the proliferation of adult *Aedes aegypti* (Linnaeus 1762), a well-known mosquito vector of chikungunya, dengue and zika (Christophers 1960), the city of Sinnamary is ULV-sprayed during selected periods with different insecticide. This was the case throughout the sampling period during which each street of the city were sprayed weekly with a solution of 1 g of deltamethrin (Aqua K-Othrine®, Bayer, Leverkusen, Germany) per hectare (*Centre de démoustication de Sinnamary*, personal communication).

Impervious surface areas were calculated within the convex hulls formed by the *A. aquilega* sampled at each site using QGIS software (QGIS Development Team 2015). The percentages of impervious surface areas were 14.23% and 47.59% in the rural and urban sites, respectively, falling into the low (< 20% impervious surface area) and moderate (20–50% impervious surface area) categories proposed by McKinney (2002).

The focal plant taxa and sampling methods

In this region, the tank bromeliad *Aechmea aquilega* (Salisb.) Griseb. naturally occurs along a gradient of anthropogenic disturbance from rural to urban areas. This bromeliad abounds on medium to large trees, either native or exotic species, and mainly comprised of mango trees in the city of Sinnamary

(Talaga et al. 2015). We sampled 26 mature *A. aquilega* on trees at two sites (13 individuals of very similar size per site): the city of Sinnamary and a rural site situated along a dead-end dirt road (*Route de l'Anse*) ca. 2 km away (hereafter, 'urban site' and 'rural site'). The city of Sinnamary was built according to a grid street plan, most of the blocks being squares or rectangles with 60 to 120 m-long sides (Géoportail 2016). We randomly selected one tree per block, none of them situated along the city limits; the sum of the surface areas formed by the selected *A. aquilega* was 10.09 ha. The rural site along the *Route de l'Anse* was characterized by very few dwellings among large fragments of an old secondary forest; the sum of the surface areas formed by the selected *A. aquilega* was 9.75 ha (a surface area close to that of the urban site).

Before being collected, each *A. aquilega* was geolocated with a GPS, its elevation above ground (EG) was measured (in meters), and the percentage of incident radiation (IR) was quantified using the hemispherical photography technique (see Leroy et al. 2009). Each plant was then removed from its supporting tree or building and placed into an individual, sealed plastic bag to prevent spillage and contamination. In the laboratory, the number of leaves forming wells (NW) was recorded, plant height (PH) was measured as the distance from the insertion of the outer leaves to the top of the crown, and plant width (PW) as the maximum distance between the tips of the leaves (both in centimeters). Subsequently, aquatic and semi-aquatic macroinvertebrates were extracted using the following method. First, the bromeliads were turned upside down in a bucket, and the water filtered through a 150 μm mesh. The water filtered from the wells was measured as the total volume of water (in milliliters) held by the plant (WV). The macroinvertebrates retained by the 150 μm net were sorted and kept for identification (see below). The organic matter contained by the plant was separated into two classes: fine particulate organic matter (FPOM; 1000–0.45 μm in size) and coarse particulate organic matter (CPOM; small pieces of fragmented material). Both were expressed in dry mass (in grams) after being placed in an oven until a constant weight was reached.

Diversity assessments

The plants were totally dismantled and each leaf was separated from the base and cleaned with a jet of water directed into a bucket. This technique allowed us to exhaustively collect the remaining aquatic macroinvertebrates, especially benthic organisms living deep in the wells (see Jocqué et al. 2010). All aquatic and semi-aquatic macroinvertebrate organisms were separated from the organic material under a stereomicroscope at 10X constant magnification. The individuals collected were separated into morphospecies or species, enumerated and preserved in 70% alcohol. Mosquitoes were identified to species level using Lane's (1953) keys and individuals belonging to other families were identified using Merritt and Cummins' larval keys (2008). For convenience, both morphospecies and species are regrouped under the term taxa in the rest of the text.

Because functional diversity, or the diversity of species traits in ecosystems, encompases the complementarity and redundancy of co-occurring species, it is accepted as a good predictor of ecosystem productivity and vulnerability. Among the metrics of functional diversity available, we used three indices based mostly on quantitative traits: functional richness (FRic) or the amount of niche space occupied by species in the community; functional evenness (FEve) or the evenness of the abundance distribution in the occupied niche space; and functional divergence (FDiv) or the degree to which the abundance distribution in the niche space maximizes the divergence in functional characters within the community (Villéger et al. 2008). We also used functional dispersion (FDis), an index that takes into account the species' relative abundances that is independent of species richness and represents the average distance of species to the abundance-weighted centroid of all species in the community in the trait space (Laliberté and Legendre 2010). All diversity indices were calculated from species scores in a trait space defined by a Fuzzy Correspondence Analysis of the abundance-weighted species traits (see Dézerald et al. 2015). The biological traits examined were: maximum body size (BS), aquatic developmental stage (AS), reproduction mode (RE), dispersal mode (DM), resistance forms (RF), food (FD), respiration mode (RM), locomotion (LO), and feeding group (FG). The latter comprises predators (Pr) and detritivores composed of: shredders (Sh) that feed on intact leaves which fall into the phytotelmata and produce fine organic matter; scrapers (Sc) that feed on layers of algae, bacteria and organic matter attached to the substrate; filtering-collectors (FC) that feed by filtering small particles of organic matter and microorganisms from the water column; and gathering-collectors (GC) that feed on the organic matter that accumulates at the bottom of the phytotelmata (see details on the biological traits of each taxon in Merritt and Cummins 2008; Céréghino et al. 2011, Dézerald et al. 2013). The categories for each trait were either ordinal or nominal. The information on the biological traits was then structured using a fuzzy-coding technique (Chevenet et al. 1994): scores ranged from 0, indicating 'no affinity', to 3, indicating 'high affinity' for a given species traits category (Appendix S1). This species-traits matrix was analyzed with a Fuzzy Correspondence Analysis (FCA) in order to obtain multivariate scores for the full set of species.

Statistical analyses

Differences in bromeliad descriptors between sites (i.e., EG, IR, PH, PW, WV, NW, FPOM, CPOM) were first tested using Wilcoxon Rank Sum tests. A Non-metric MultiDimensional Scaling (NMDS) ordination was then run on raw abundance data using the Bray-Curtis (abundance-based) and the Jaccard

(incidence-based) indices to determine the taxonomic structure among aquatic macroinvertebrate communities between the rural and the urban sites. In order to test for statistical differences in the structure of the communities between the two sites, a Permutational Multivariate Analysis of Variance (PERMANOVA) was run on raw abundance data using the same two indices. Diversity (D) was calculated and partitioned within each site into α, β and γ diversity by generalizing the Shannon entropy (Marcon et al. 2014). The α diversity is defined as the average local community diversity, γ diversity

Table 1 List of the aquatic macroinvertebrate morphospecies or species occurring in *Aechmea aquilega* in Sinnamary, French Guiana (13 plants in each of the rural and urban areas)

Class	Order	Family	Sub-family	Morpho-species/species	Rank No. of taxa		FFG	Taxa ID*
					Rural	Urban		
Insecta	Coleoptera	Elatheridae		**Elatheridae sp.**	21	27	Sh	1
		Elmidae		**Elmidae sp.**	24	22	Sc	2
		Hydrophilidae		**Hydrophilidae sp.1**	-	23	Pr	3
				Hydrophilidae sp.2	-	24	Pr	4
	Diptera			**Brachycera sp.1**	-	20	GC	5
				Brachycera sp.4	14	9	GC	6
				Brachycera sp.5	20	15	GC	7
				Brachycera sp.6	16	25	GC	8
				Brachycera sp.7	23	-	GC	9
				Brachycera sp.8	-	28	GC	10
				Brachycera sp.9	12	-	GC	11
				Brachycera sp.10	25	14	GC	12
				Brachycera sp.12	-	29	GC	13
				Brachycera sp.15	26	17	GC	14
		Ceratopogonidae	Ceratopogoninae	***Bezzia* sp.1**	7	3	Sc	15
				***Bezzia* sp.2**	9	5	Sh	16
				Ceratopogoninae sp.2	18	7	Sh	17
				Ceratopogoninae sp.3	22	30	GC	18
				***Dasyhelea* sp.**	-	16	Sc	19
			Forcipomyiinae	**Forcipomyiinae sp.2**	6	2	Sc	20
				Forcipomyiinae sp.5	-	18	Sc	21
		Chironomidae	Chironominae	**Chironominae sp.**	2	-	GC	22
			Tanypodinae	**Tanypodinae sp.**	27	-	Pr	23
		Culicidae	Culicinae	***Aedes aegypti***	-	12	FC	24
				Culex pleuristriatus	8	10	FC	25
				Culex imitator	11	-	FC	26
				Wyeomyia pertinans	5	11	FC	27
				Toxorhynchites haemorrhoidalis	10	13	Pr	28
		Tipulidae	Limoniinae	***Trentepohlia* sp.**	3	-	Sh	29
		Psychodidae	Psychodinae	**Psychodinae sp.**	-	21	Sh	30
				***Telmatoscopus* sp.**	4	1	Sh	31
		Tabanidae		**Tabanidae sp.**	19	19	Pr	32
Oligochaeta				**Oligochaeta sp.1**	17	26	GC	33
				Oligochaeta sp.2	13	8	GC	34
	Haplotaxida			***Aulophorus superterrenus***	1	6	GC	35
				***Pristina* sp.**	15	4	GC	36

Taxa are listed alphabetically according to a classical system and highlighted in bold. The rank number of a taxon's relative abundance is indicated for the rural and the rural meta-communities. Functional Feeding Group (*FFG*) for each taxa is abbreviated as follows: Scraper (*Sc*), Shredder (Sh), Gathering-collector (*GC*), Filtering-collector (*FC*) and Predator (*Pr*)

*Taxa ID as in Appendix S1.

corresponds to the diversity of the meta-community composed of all the communities within each site, and β diversity is understood as the diversity between local communities (or the divergence between each community and the meta-community). Diversity profiles were used to compare α, β and γ diversity between the two sites rather than comparing single diversity indices. Entropy is converted into diversity and plotted against different orders of diversity. The importance given to rare species decreases with the order of diversity, and a community is considered more diverse when its profile is higher than the one being compared (Marcon et al. 2014). Finally, evenness was calculated as the ratio of diversity (D) on richness (S) (Tuomisto 2012).

Statistical analyses were conducted in R software (R Development Core Team 2013) using entropart, FD and vegan packages.

Results

Although the water volumes were similar, the number of wells containing the total amount of water in a bromeliad (NW) was significantly higher in the urban site compared to the rural site (Wilcoxon Rank Sum test: W = 20.5, $P < 0.05$). None of the other variables characterizing bromeliads (i.e., EG, IR, PH, PW, WV, FPOM, CPOM) were significantly different between the two sites.

A total of 11,099 aquatic macroinvertebrate individuals belonging to 36 taxa were extracted from the 26 *A. aquilega* bromeliads sampled (Table 1). Nine taxa out of the 36 were exclusively found in the urban site (Table 1). Most of the taxa belonged to the order Diptera, but some Coleoptera were also found. Species richness was slightly lower in the rural meta-community (27 taxa) than in the urban meta-community (30 taxa), with one and three singletons, respectively, and a species turnover of 41.67% (15/36) between the two sites. In addition, two taxa, namely Chironominae sp. and *Trentepholia* sp., were not noted in the urban site, while they were ranked second and third in terms of relative abundance in the rural site (Fig. 1; Table 1). It is worth noting that the culicid species *Aedes aegypti* was found in seven *A. aquilega* in the urban site (63 larvae in total), but was absent from the rural site (Table 1).

The dissimilarity in the taxonomic structure of the aquatic macroinvertebrate communities is represented in Fig. 1. A significant difference between the two sites is shown using both the Bray-Curtis (PERMANOVA; $N = 26$; $F = 8.23$; $P < 0.001$; Fig. 1) and the Jaccard indices (PERMANOVA; $N = 26$; $F = 5.49$; $P < 0.001$).

The local α diversities of the aquatic macroinvertebrate communities tended to be higher in the rural site compared to the urban one for each order of diversity, but the difference was not significant (Fig. 2; Table 2). The analyses of β and γ diversity profiles were less straightforward. While the β diversity in the rural meta-community was higher for orders of diversity between 0.5 and 1, mean values were higher in the urban meta-community for orders of diversity of 0 and 2 (Fig. 2; Table 2). Because diversity measures give more

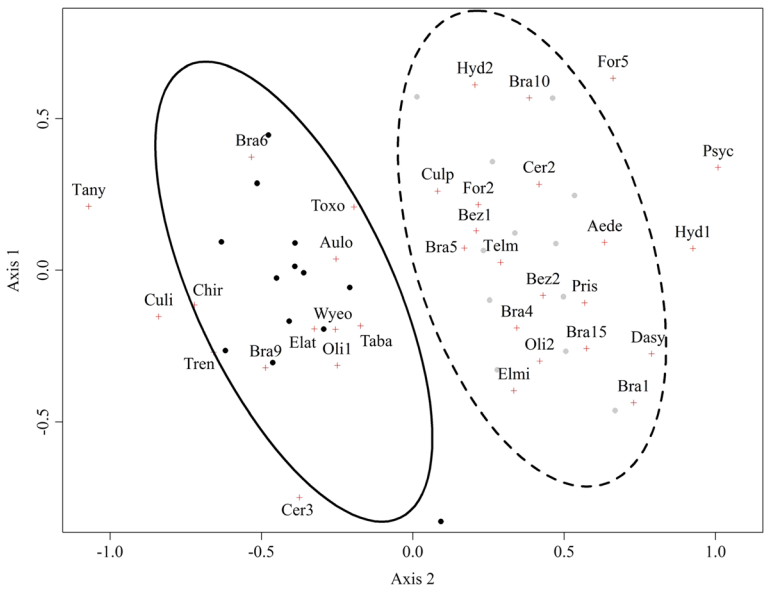


Fig. 1 Non-metric MultiDimensional Scaling (NMDS) ordination based on the Bray-Curtis distance showing the degree of dissimilarity of aquatic macroinvertebrate communities between the rural (*black dots*) and the urban (*gray dots*) sites. Ellipses are drawn around rural (*solid line*) and urban (*dashed line*) communities with a level of confidence of 95%. Taxa are projected in the same ordination space (*red crosses*) and abbreviated with the first four letters of the species' names or with the first three letters followed by the number of morphospecies' names as in Table 1. Note that a similar ordination was obtained with the Jaccard distance

importance to the contribution of abundant relative to rare species with an increasing order of diversity, the higher β diversity in the urban site is due to rare species (for which q = 0) and the heterogeneous distribution of abundant species (for which q = 2). Also, rural β diversity is always included within the range of variation of urban β diversity (Fig. 2). Indeed, higher β diversity reflects larger variations among local communities, a result which is consistent with the hypothesis that habitat fragmentation increases environmental heterogeneity in the urban site. The γ diversity was greater in the urban meta-community than in the rural one for an order of diversity of 0, the contrary being true for orders of diversity of 1 and 2 (Fig. 2; Table 2). A comparison of evenness (E) was unequivocal and showed higher or equal values in the rural site compared to the urban site for all α, β and γ diversities and for each order of diversity (Table 2).

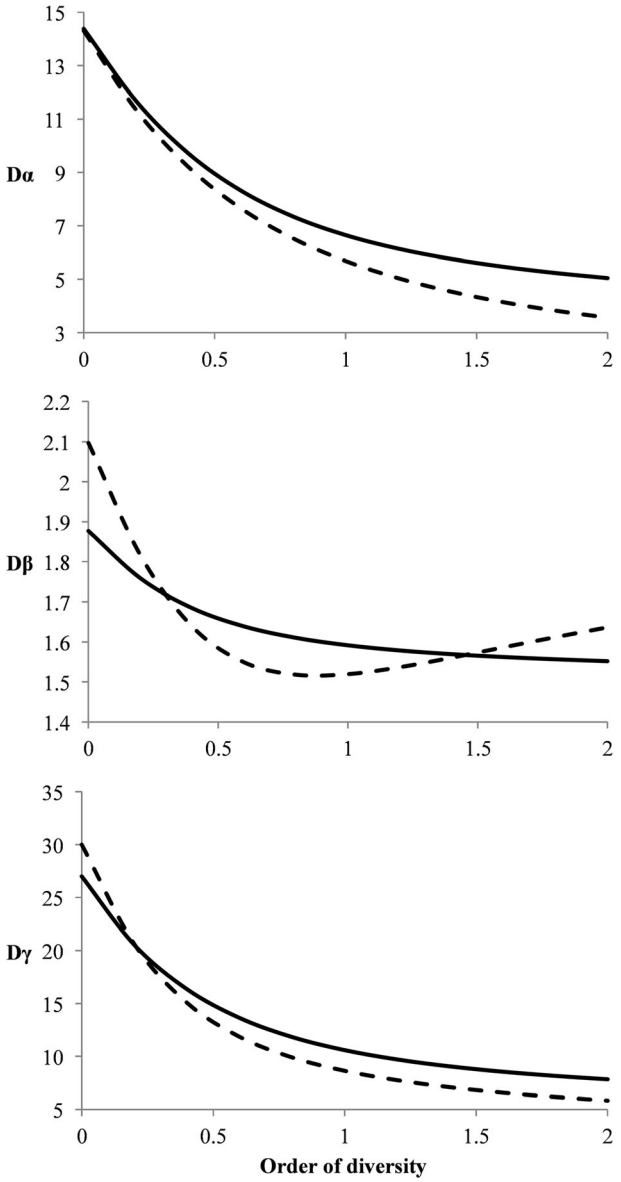


Fig. 2 Profiles of the α, β and γ diversity (D) of the order q computed for the aquatic macroinvertebrate meta-communities in the rural (*solid lines*) and urban areas (dashed lines). The importance given to rare species decreases with order of diversity and a community is considered more diverse when its profile is higher than the one being compared

In terms of functional feeding groups, filtering-collectors and gathering-collectors were significantly more abundant in the rural communities than in the urban ones (Wilcoxon Rank Sum test: W = 125, $P = 0.04$ and W = 124, $P = 0.045$, respectively; Fig. 3), the contrary being true for shredders and scrapers (Wilcoxon Rank Sum test: W = 22, $P < 0.001$ and W = 40, $P = 0.024$, respectively; Fig. 3). Predators tended to be more abundant in the rural site, but the difference was not significant (Wilcoxon Rank Sum test: W = 113.5, $P = 0.140$; Fig. 3).

Concerning functional diversity, FDis was significantly lower in urban bromeliads (Welch two sample t-test: $t = -13.64$, df = 12.38, $P < 0.001$). The three other indices tested did not reveal significant differences between the two sites (Welch two sample t-test: FRic; $t = 0.51$, df = 20.84, $P = 0.619$; FEve; $t = -1.20$, df = 20.89, $P = 0.242$; FDiv; $t = 1.99$, df = 20.54, $P = 0.060$).

Discussion

Bromeliads represent small and discrete habitats that can be abundant in urban and natural sites. They are, therefore, deemed suitable model systems to bring out the environmental effects of human-impacted landscapes on the taxonomic and functional structures of biological communities in the Neotropics. Shifts in this community structure can be explained in at least five ways: (1) the characteristics of the bromeliad habitat are different, (2) the terrestrial characteristics that filter the adult life stage, (3) top-down processes, (4) bottom-up processes, and (5) the presence of synanthropic species. In this context, our study shows that urbanization can have significant impacts on both the taxonomic and functional structure of aquatic macroinvertebrate communities. Yet, despite these important structural shifts, we did not detect significant patterns of α, β and γ diversity between the two sites.

The characteristics of the bromeliads habitat were mostly not affected by the urban environment although we noted significantly more wells per plant in the urban site. This was due to the fact that, although the selected plants were of a similar size, external leaves contained little water in the urban area while their counterparts in the rural area no longer retained water, and so were not counted as 'wells'. Note that the difference noted had no influence on the total water volume of the plants which was similar between the two sites. Also, contrary to our predictions, the bromeliads held comparable amounts of detritus (CPOM and FPOM) and received similar incident radiation in the urban and the rural sites.

Table 2 Values of diversity (D) and evenness (E) for each order of diversity q partitioned into α, β and γ levels for the rural and urban meta-communities

	q = 0			P	q = 1			P	q = 2			P
Index	Rural	Urban	Sign R-:U		Rural	Urban	Sign R-:U		Rural	Urban	Sign R-:U	
Dα	14.65	14.22	>	NS	6.73	5.80	>	NS	5.11	3.69	>	NS
Dβ	1.84	2.11	<	-	1.55	1.51	>	-	1.51	1.63	<	-
Dγ	**27**	**30**	<	-	10.40	8.77	>	-	7.71	6.01	>	-
Eα	0.542	0.474	>	NS	0.249	0.193	>	NS	0.189	0.123	>	NS
Eβ	0.068	0.070	≈	-	0.057	0.050	>	-	0.056	0.054	>	-
Eγ	1	1	=	-	0.385	0.292	>	-	0.285	0.200	>	-

Values for γ diversity of the order q = 0, equivalent to richness (S), are highlighted in bold for each meta-community. Evenness is calculated as the D:S ratio. Welch's two sample t-tests: no differences were significant; '-': the test was not applicable

Because bromeliads characteristics are similar between the two sites, we can assume that terrestrial factors associated with the urban environment itself are the primary drivers of community assembly through trait filtering at the adult life stage. This includes insecticide spraying during the rainy season, something that likely affects the survival and behavior of some terrestrial insects whose larvae develop in *A. aquilega* wells. The impact on untargeted organisms is unknown, but Chironomidae have proven to be sensitive to the insecticide used (Morrill and Neal 1990). This might explain the complete absence of Chironominae sp. and *Trentepohlia* sp. in the city while they abounded in the untreated rural site, though other factors linked to urbanization can also affect them. In fact, we can assume that microclimatic conditions associated with the urban environment (i.e., it is hotter and drier) might select edge species relative to sylvan ones, resulting in the disappearance and/or density reduction of some species.

Though the α, β and γ diversity were not affected, it is worth noting that shredders (Sh) and scrapers (Sc), both detritivorous leaf-litter processors, were positively affected in the urban site, while filtering-collectors (FC) and gathering-collectors (GC) that process much smaller particles produced by the activity of the shredders were negatively affected. However, nothing indicates that predators (Pr), here mainly represented by the top predator species *Toxorhynchites haemorrhoidalis* (Fabricius 1787), are influenced by urbanization (Fig. 3; Table 1). Consequently, the major restructuration observed for detritivores, associated with the absence of significant variation among predators, strongly suggests an alteration in urban communities through bottom-up processes. Dry mass only provides an indication of the quantity of the food resource, not its quality

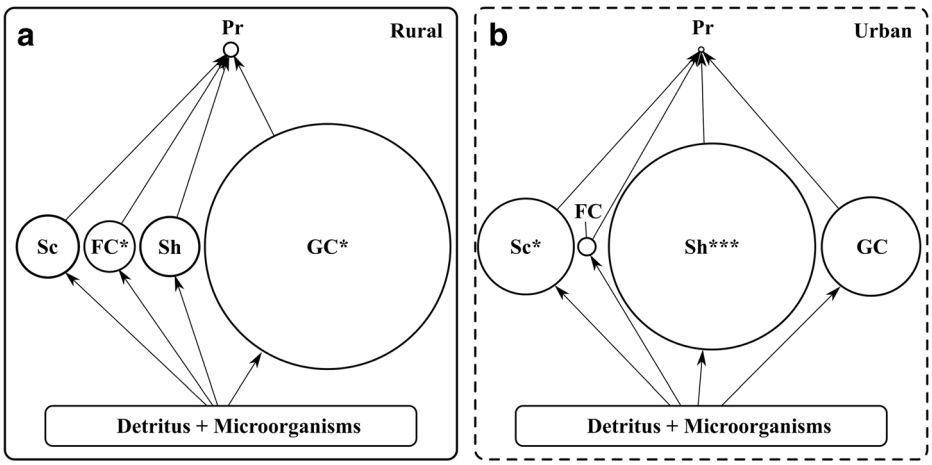


Fig. 3 Composite food web diagrams showing trophic interactions involving the aquatic macroinvertebrate Functional Feeding Groups (FFGs) in the rural (solid line) and urban (dashed line) meta-communities. FFGs are abbreviated as follows: Scraper (Sc), Shredder (Sh), Gathering-collector (GC), Filtering-collector (FC) and Predator (Pr). Circle diameter represents the relative abundance of each FFG standardized by doubling the relative abundance of the least abundant FFG. Predator and detritivore trophic levels are weighted by two and one, respectively, with respect to prior functional analyses. Arrows illustrate interactions pointing to the consumer. Asterisks indicate the FFGs with a significantly higher mean abundance after a pairwise, non-parametric comparison between the two sites (* = $P < 0.05$; *** = $P < 0.001$)

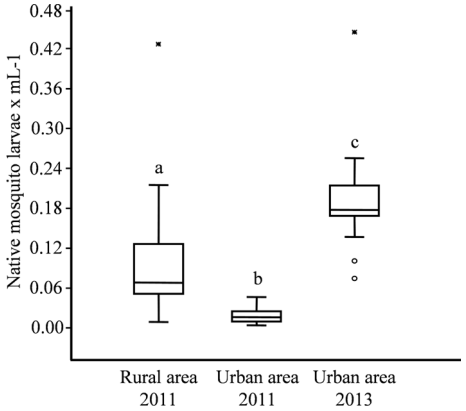


Fig. 4 Comparison of the mean density of native mosquito larvae in the wells of *Aechmea aquilega*. Data from the 2011 dry season correspond to this study (13 *A. aquilega* in each case), those from the 2013 rainy season were taken from Talaga (2016) (32 *A. aquilega*), the sampling method used being strictly the same. Kruskal–Wallis test (χ^2 = 26.05; df = 2; $P < 0.001$) followed by a Nemenyi's *post-hoc* test, different letters indicate significant differences at $P < 0.05$

which can be important to aquatic macroinvertebrates (Yanoviak 1999; Yee and Juliano 2006). Because native tree species occurred in the rural site whereas mango trees greatly dominated in the city, it is likely that the quality and diversity of the leaf litter – that is directly related to urbanization in the study area – accounts for the observed impacts on detritivores.

Despite the change in the relative abundance among functional feeding groups, it should be noted that all of them are present in the two sites, showing that aquatic macroinvertebrates are relatively tolerant of urbanization. At the species level, we noted a turnover of 41.67% between the two sites which reflects changes in the composition of the meta-communities. Yet, the remaining 58.33% corresponds to an overlap of taxa between the two habitats, showing that many species can live in both sites. Concerning functional diversity, the fact that functional dispersion (FDis) is significantly lower in the city compared to the rural site is in line with previous studies showing a reduction in FDis with a higher disturbance intensity (Gerisch et al. 2012; Mouillot et al. 2013).

Not surprisingly, we detected the presence of synanthropic species in urban communities. The presence of these species is both the direct consequence of urbanization but can also be viewed as a biotic factor responsible for the alteration of native communities. Here we show for the first time that *Ae. aegypti* uses tank bromeliads as an oviposition site in French Guiana. The use of phytotelmata as breeding sites has long been known (Belkin and Heinemann 1976) and was specifically reported for urban tank bromeliads in Argentina (Stein et al. 2013), Brazil (Varejão et al. 2005) and Trinidad (Chadee et al. 1998). The percentage of *Ae. aegypti* larvae noted in this study, superior to those reported from other Neotropical areas, is likely seasonal as a control of their presence in Sinnamary during the 2013 rainy season resulted in only three larvae gathered from two *A. aquilega* out of the 32 sampled (Talaga 2016). Furthermore, during the dry season, both the anthropophily of *Ae. aegypti* and the variation in the density of 'natural enemies' (e.g., competing native mosquito larvae) in the wells of *A. aquilega* likely influenced the distribution of *Ae. aegypti* larvae in the urban site (urban environment plus low density of competing larvae) and their absence from the rural site (non-urban environment plus a high density of competing larvae) (Fig. 4). Indeed, during the rainy season, *Ae. aegypti* larvae were rare in the urban site although adequate, but the density of competing mosquito larvae was very high (Fig. 4). Lastly, the presence of *Ae. aegypti* larvae in the wells of urban bromeliads is not necessarily a concern as they rather develop in abundance in artificial containers, so that the role of native tank bromeliads in the production of this vector can be considered marginal (Maciel-de-Freitas et al. 2007).

We have therefore shown that if urbanization influences the macroinvertebrate communities living in the *A. aquilega* tanks in terms of taxonomic and functional structure, this was not the case for biodiversity. Also, at least during the period of this study, urbanization favored the presence of synanthropic and exotic species.

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