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River classification as the basis for freshwater biological assessment in overseas Europe: Issues raised from Guadeloupe (French Lesser Antilles)

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Over the past decade, Europe's Water Framework Directive (WFD) has prompted a large amount of ecological research aiming at establishing river typologies and ecological indicators in member States. Yet, the lack of robust bioindicators in Europe's overseas regions arguably reflects minimal knowledge of the distribution patterns of aquatic species in the Community's outermost areas. Specifically, there has been no published classification of rivers for any European overseas region. Fifty-one sites were sampled for benthic invertebrates and environmental variables (land-cover, physical habitat, and water chemistry) in Guadeloupe, French Lesser Antilles. Redundancy analysis and *k*-means clustering were used to bring out spatial patterns in species composition in relation to environmental conditions. Our results highlighted the importance of land cover and geomorphology in delineating three ecological sub-regions (clusters) for freshwater invertebrates. Deviation from predictable community structure only occurred when river sites were subjected to harsh water chemistry alterations (urban runoff, wastewaters). Changes in species richness did not detect environmental stress efficiently within a given sub-region, probably because most sites are naturally species-poor due to the insular context and/or because disturbance is often weak. However, differences existed between clusters in terms of species identity and numerical dominance. Our a posteriori typology of sites was compared to local a priori expert opinion of river health, in an attempt to better characterize the network of survey sites, and to target sites for reference conditions.

Keywords:

Biological indicators / Overseas regions / Reference conditions / River classification / Tropical river / Water Framework Directive

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Abbreviations: RDA, redundancy analysis; WFD, Water Framework Directive

1 Introduction

During the past decade, much research has been undertaken in the European Union toward developing robust methodologies for the implementation of Europe's most powerful piece of water legislation, the Water Framework Directive (WFD, 2000/60/EC). One of the newer approaches to assessing the ecological quality of rivers within the Framework is the Reference Condition Approach (RCA [1]), where *ecological health* is defined in

terms of similarity to an undisturbed (“reference”) state. RCAs basically rely on classifications of reference sites from rivers of high biological quality, to provide system-specific predictions of the fauna to be expected under undisturbed conditions. By knowing what biota should be present in a given geographic zone, one can estimate the degree to which human activity has altered it [2] because any site can be assessed by comparing its biota to the reference sites, and any change in expected assemblages can indicate environmental changes in the area. Throughout continental Europe, environmental policies aimed at monitoring, improving or preserving the biological quality of surface waters now rely on RCA-derived metrics [3].

Europe’s political boundaries extend far beyond its continental limits. Although some member states (e.g., France, UK, The Netherlands) have overseas regions in various biogeographic areas of the World (Atlantic, Caribbean, Pacific, Indian Oceans), these regions were overlooked during the development phase of methods that fulfil WFD’s requirements. Only recently have ecologists started to collect high-quality biological and environmental data in a standardized manner, so that they can be analyzed according to EU guidelines (e.g., [4]). Examples are recent and ongoing R&D projects supported by French National funds in the Lesser Antilles (this study), French Guiana (South-America), and the Reunion (Indian Ocean), where several biological quality indicators (fish, invertebrates, and diatoms) are taken into account.

Macroinvertebrates constitute relevant biological indicators of ecosystem health, because they form an important part of animal production within freshwater ecosystems, and are tightly integrated into the structure and function of their habitats [5]. Inevitably however, recent macroinvertebrate-based tools cannot be transposed to EU’s outermost regions, at least for three reasons related to differences in invertebrate biogeography and anthropogenic pressure. First, entire indicator taxa are missing from some areas (e.g., stoneflies are absent from the Lesser Antilles in the Caribbean). Second, at coarse taxonomic level, biological traits (e.g., body size, feeding habits), richness, and/or numerical dominance do not compare among biogeographic regions (especially in depauperate insular contexts). For instance, while most crustaceans are not recognized as sensitive bioindicators in rivers of continental Europe [6], their higher diversity and biomass and much larger body size in tropical islands (e.g., *Macrobrachium heterochirus*, *Xiphocaris elongata*, *Micratoryx poeyi*, *Guiniota dentata*) could confer them higher functional importance within invertebrate communities [7–9]. Third, and perhaps more importantly, the mismatch between freshwater biodiversity recognition on the one hand, and lack of robust bioassessment tools in Europe’s overseas regions on the other, arguably reflects minimal knowledge of the distribution patterns of the aquatic

species. In addition to these issues, the development of bioassessment methods may suffer from a lack of taxonomic knowledge in some overseas regions. Little is known for instance about macroinvertebrate taxonomy (at the species level) in the East-Amazonian streams of French Guiana. Hence, if both ecologists and end-users need explicit geographic models (i.e., maps) to design river management actions, numerical patterning is urgently needed to provide theoretical backgrounds. This study takes a step toward analyzing large numbers of site-specific data in European overseas regions to explore spatial patterns of biological communities in relation to environmental conditions.

With the exception of few densely populated areas (capital cities or agricultural lands), anthropogenic disturbance in Europe’s overseas region is often weak or limited to diffuse runoff from small cultivations and/or sparse habitations. Paradoxically, the lack of replication for various disturbance types poses methodological issues as to how to characterize typical species assemblages, or how to calibrate biological indices when uncertainties exist as regards networks of reference sites. Only Wasson et al. [10] proposed a typology of European overseas watersheds, by defining hydro-ecoregions based on geomorphological, hydrological, and climate data. To the best of our knowledge however, there has been no published biological classification (typology) of rivers for any European overseas region. In this study, we focussed on Guadeloupe, a Caribbean archipelago in the Lesser Antilles, and one of France’s 11 inhabited overseas regions. Although routine surveys carried out by local administrations suggest changes in species composition in relation to physical–chemical conditions at local (site) scales [11], we still do not know whether anthropogenic alteration of stream generates spatial discontinuities in predictable gradients, or even overrides geomorphological controls on the distribution patterns of macroinvertebrates at the regional (island) scale. Guadeloupe therefore provides a relevant framework to bring out spatial patterns of macroinvertebrate communities in relation to physical, chemical, and land-use variables in a EU water policy perspective. Our study tested the following hypotheses: (i) geomorphology determines ecological sub-regions that have typical macroinvertebrate assemblages, and, subsequently (ii) reference conditions (species assemblages, richness, evenness, etc) vary across sub-regions, (iii) invertebrate diversity broadly declines as anthropogenic pressures increase. Specifically, we expected that current a priori classification of river sites used by local administrations (“expert knowledge”) do not match the a posteriori classification of rivers sites based on statistical analyses of macroinvertebrate communities, calling for a re-thinking of the network of survey sites and reference conditions. We discuss freshwater invertebrate diversity

and distribution in the context of EU's water policy and make suggestions for future directions.

2 Methods

2.1 Study area and sampling sites

The Guadeloupean archipelago is part of the French Lesser Antilles. It consists of two main islands separated by a narrow salty channel. The northern island, Grande-Terre (848 km²) is a low limestone plateau. Because it only has a single perennial river, this island was omitted in our study. The southern island, Basse-Terre (590 km²), is composed of a North–South volcanic range. The Grande Soufrière Volcano (1467 m a.s.l.) forms the tallest mountain in the Lesser Antilles. The Basse-Terre piedmont is close to the seashore, so that the coastal plain is very narrow. Running waters consist in 55 fast-flowing streams (Fig. 2). The climate is tropical moist and the annual rainfall ranges from <1000 mm on the littoral coast to >10 000 mm on the volcano slopes. There is a major reduction in rainfall between December and April (the dry season, or “Carême”). The mean annual air temperature is 27°C, and ranges from 24–31°C in summer to 20–29°C in winter. In mountain ranges however (500–1400 m a.s.l.), the mean annual temperature is around in 21–23°C.

2.2 Environmental variables

Sampling sites were classified into five a priori groups, based on field observations of potential sources of disturbance: unimpacted, reference sites (REF), sites located below wastewater treatment plants (WTP, usually undersized to handle reuse demands), domestic or industrial runoff (URB, essentially consisting in organic pollution), agricultural runoff (AGRI, organic pollution, organochlorine pesticides), and undetermined impact due to a lack of information for the site (UNDET, neither strong impacts WRP, URB, and AGRI nor reference conditions could be ascertained). UNDET sites were thus subjected to moderate impact(s) due to local human settlements, but we could not assign them to any of the above, more exclusive categories. Unimpacted sites (REF) were defined as sites not subjected to anthropogenic impacts such as chemical pollution, agricultural, or urban runoff, etc.

Fifty-one sampling sites were then characterized using three land-cover variables, 9 physical variables, and 14 chemical variables. For each site, a Geographic Information System (GIS, ESRI ArcGis 10) was used to delineate a geographical buffer zone including the sampling site, and a 1000 m-long × 100 m-large riparian corridor located immediately upstream from the site. This size is well suited to

assign a land-cover influence to each site (see also [5]) and falls within that of the “Reach Buffer” sensu Allan [12], i.e., a buffer of 100 m to several hundred meters in width on each bank and some hundreds of meters to a kilometer in length. The three land-cover variables were percent area within a buffer zone covered by forest (areas occupied by broad-leaved forest, shrubs, and herbaceous vegetation associations), urban development (industrial, commercial, and transport units; artificial and non-agricultural vegetated areas), and agricultural (arable lands, permanent crops, and pasture). Digital land-cover information was obtained from the CORINE land-cover database for Guadeloupe (CLC 2006, French Ministry of Ecology, <http://www.statistiques.developpement-durable.gouv.fr/donnees-ligne/t/telechargement-donnees-sig-corine-land-cover-dom.html>; see also [13]). This database was generated from orthorectified satellite images and provides thematic GIS map layers including up to 44 land-cover classes with a mapping scale of 1:100 000.

Physical variables were elevation above sea level (m), and the percentage composition of substrate types at each site: %litter, %submerged roots, %submerged vegetation, %sand (particle size <2 mm), %gravels (2–25 mm), %pebbles (25–250 mm), %boulders (>250 mm), and % rocky outcrops. These variables were chosen because they characterise the location of sampling sites within the upstream–downstream river continuum.

Water samples for chemical analyses were taken at each site and immediately frozen. Chemical analyses were carried out by the Laboratoire Départemental de la Drôme, France. The chemical variables measured in the laboratory were: turbidity (NTU), suspended solids, total Kjeldahl nitrogen, bicarbonate, chloride, sulfate, nitrate, silica, total phosphorus and potassium, and biological oxygen demand (mg L⁻¹). Three variables (pH, conductivity (μS cm⁻¹), and dissolved oxygen (mg L⁻¹)) were directly measured in the field using a WTW multi-340i probe.

All land cover, physical and chemical data are available in Appendices 1 and 2 (Supplementary Online Material).

2.3 Invertebrate sampling

Macroinvertebrate communities were sampled at 51 sites using a normalized protocol (Multi-Habitat Sampling, norm XP T 90-333 in [14]). During low flow conditions (dry season, March 2011), we took 12 sample units per site on pre-defined habitat types, using a surber sampler (sampling area 0.05 m², mesh size 500 μm). Four sample units were taken from marginal habitats, i.e., from habitats with an individual share of <5% coverage (group A). Eight sample units were taken from major habitats (i.e., with an individual share of at least 5% coverage). Four of these samples were selected according to their hosting capacity (high biogenic potential, based on expert knowledge of

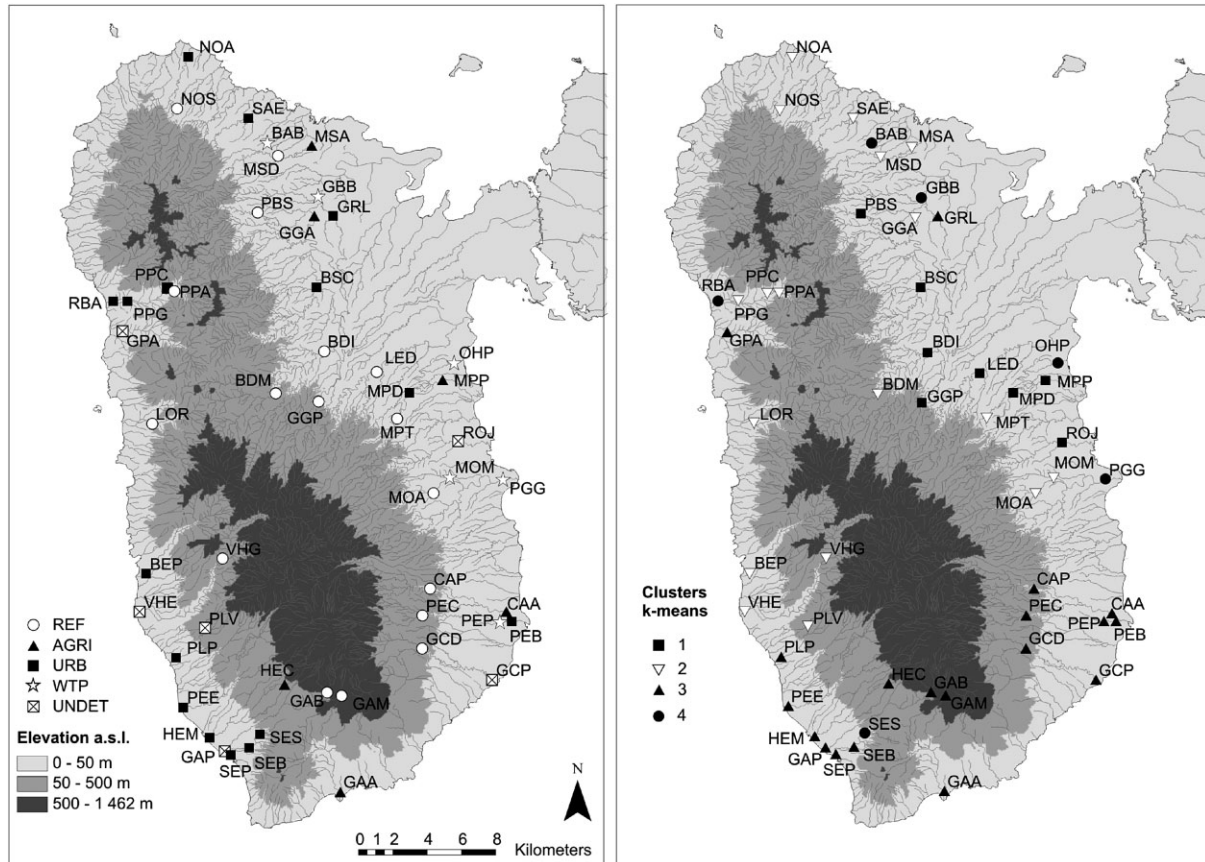


Figure 2. Distribution of sampling sites in the Basse-Terre Rivers. (a) Correspondence with a priori groups (REF, reference sites; AGRI, agricultural runoff; URB, domestic or industrial runoff; WTP, wastewater treatment plants; UNDET, undetermined). (b) correspondence with their location (clusters 1–4) on the RDA ordination space (see also Fig. 1).

($p = 0.01$), Sulfates and Phosphorus ($p = 0.03$), and Chlorures ($p = 0.032$). The land cover variable “%forest” accounted for the greatest proportion of the total canonical eigenvalues (8%, $F = 4.34$, $p = 0.002$).

The k -means algorithm allowed us to identify four clusters of sites (Fig. 1a). Clusters were plotted on a geographical map of Basse-Terre, in order to ease interpretations (Fig. 2). k -Means clusters were not congruent with the a priori classification of sites into disturbance types (Fig. 2a and b), and, overall, anthropogenic disturbance did not overcome geomorphological controls of invertebrate community structure. Indeed, sites in clusters 1, 2, and 3 corresponded to three major biogeographic regions of the island, i.e., north-eastern area, central-northern range, and southern area, respectively. Sites in cluster 1 were mostly characterized by coarse rocky substrates. Sites in cluster 2 belonged to forested areas. Sites in cluster 3 were at higher elevation, close to the Soufrière volcano. Consequently, they were characterized by higher sulfate concentrations. Sites in cluster 4 (mostly pre-identified as WTP and URB) were

characteristic of spatial discontinuities in community diversity generated by severe anthropogenic disturbance. On average, concentrations of nitrogen were 7.5–15 times higher at sites from cluster 4 compared to other sites, and concentrations of phosphorus were 1.6–11 times higher in cluster 4 than in other clusters (Supplementary Appendix 2).

3.2 Macroinvertebrate diversity

Ninety-one taxa were identified from 51 stations. The gradient analysis conducted through the RDA basically portrayed geographic changes in the compositional structure of invertebrate communities, and to a much lesser extent, the impact of anthropogenic disturbance (Cluster 4; Fig 1b, Fig. 2). Sites in cluster 1 showed higher diversity (taxonomic richness and abundance) for insects, especially Ephemeroptera (mostly Baetidae and Leptohyphidae species, see Table 1), Trichoptera (Hydroptilidae, Polycentropodidae, Xiphocentronidae), and Coleoptera (Elmidae). Sites in cluster 2 showed high diversity for

Table 1. Distribution of the various invertebrate taxa among clusters 1–4. Numbers indicate density (individuals per m²) ± SE. Taxa ID as in Fig. 1

Phylum	Class/order	Family/subfamily	Species	ID	Cluster 1	Cluster 2	Cluster 3	Cluster 4		
Nemertea			Unidentified	1	4 ± 1	5 ± 1	5 ± 1	8 ± 3.72		
Plathelminthes	Turbellaria	Dugesidae	Unidentified	3	29 ± 7.57	4 ± 0.63	1 ± 0.31	591 ± 349.11		
Annelida	Hirudinea	Erpobdellidae	Unidentified	4	–	8 ± 8	1 ± 1	5 ± 2.31		
		Glossiphoniidae	Unidentified	5	–	9 ± 9	1 ± 1	8 ± 3.95		
	Oligochaeta		Unidentified	6	22 ± 6.08	32 ± 14.8	42 ± 10.98	109 ± 57.41		
	Polychaeta		Unidentified	7	–	–	3 ± 1	17 ± 4.62		
Mollusca/Gasteropoda		Ancylidae	Unidentified	8	8 ± 4.89	17 ± 6.8	1 ± 1	10 ± 3.57		
		Ampullariidae	<i>Pomacea glauca</i>	9	3 ± 3	–	–	3 ± 1.15		
		Hydrobiidae	Unidentified	10	–	2 ± 0.41	35 ± 3.17	51 ± 33.84		
		Neritidae	Unidentified	11	–	30 ± 8.33	1 ± 0.34	–		
			<i>Neritina</i> sp.	12	–	11 ± 2.55	19 ± 3.6	66 ± 34.93		
			Unidentified	13	–	40 ± 16.5	60 ± 27.11	4 ± 0.87		
			Physidae	<i>Physa</i> sp.	14	56 ± 19.43	18 ± 8.36	8 ± 2.72	302 ± 132.61	
			Planorbidae	Unidentified	15	–	–	4 ± 0.97	1 ± 0.15	
			Thiaridae	Unidentified	16	85 ± 26.7	41 ± 12.27	15 ± 4.39	1336 ± 480.27	
		Mollusca/Bivalvia		Sphaeriidae	<i>Pisidium</i> sp.	17	–	2 ± 0.49	–	2 ± 0.61
					Unidentified	2	2 ± 0.82	5 ± 1.54	1 ± 0.18	2 ± 0.62
		Hydracarina	Ostracoda		Unidentified	18	42 ± 12.77	27 ± 11.98	19 ± 7.59	418 ± 351.7
		Crustacea	Amphipoda	Gammaridae	Unidentified	19	8 ± 4.19	14 ± 4.58	1 ± 0.23	1 ± 1
			Caridea	Atyidae	<i>Atya</i> sp.	20	–	6 ± 1.83	9 ± 4.74	1 ± 1
					<i>Micratya poeyi</i>	21	6 ± 1.6	5 ± 1.25	32 ± 13.61	89 ± 50.23
			<i>Potimirim</i> sp.	22	9 ± 4.38	10 ± 2.07	–	–		
		Xiphocaridae	<i>Xiphocaris elongata</i>	23	1 ± 1	2 ± 0.59	9 ± 3.76	–		
		Palaemonidae	<i>Macrobrachium</i> sp.	24	1 ± 0.16	3 ± 0.92	15 ± 3.98	3 ± 1.26		
	Brachyura	Pseudothelphusidae	<i>Guinotia</i> sp.	25	–	–	3 ± 0.49	–		
Insecta	Trichoptera	Calamoceratidae	<i>Phylloicus</i> sp.	26	7 ± 3.11	5 ± 2.06	2 ± 0.48	–		
		Glossosomatidae	<i>Protophila</i> sp.	27	1 ± 0.2	103 ± 39.77	19 ± 2.75	–		
		Helicopsychidae	<i>Helicopsyche</i> sp.	28	12 ± 3.61	8 ± 2.2	3 ± 0.63	–		
		Hydropsychidae		29	52 ± 17.81	12 ± 3.41	7 ± 2.7	1 ± 0.29		
			Hydroptilidae	Unidentified	30	–	–	1 ± 1	–	
			<i>Alisorichia</i> sp.	31	10 ± 3.98	5 ± 1.04	6 ± 0.49	–		
			<i>Hydroptila</i> sp.	32	9 ± 5.92	28 ± 18.48	2 ± 0.35	5 ± 2.31		
			<i>Neotrichia</i> sp.	33	47 ± 22.58	29 ± 11.19	8 ± 2.3	3 ± 0.85		
			<i>Ochrotrichia</i> sp.	34	–	1 ± 0.17	–	–		
			<i>Oxyethira</i> sp.	35	13 ± 4.56	16 ± 6.26	3 ± 0.77	116 ± 103.84		
	<i>Zumatrichia</i> sp.	36	7 ± 2.47	2 ± 0.17	1 ± 0.13	–				
	Leptoceridae	<i>Oecetis</i> sp.	37	2 ± 0.82	3 ± 1.09	–	–			
	Philopotamidae	<i>Chimarra</i> sp.	38	16 ± 6.33	9 ± 2.8	3 ± 0.49	–			
	Polycentropodidae	Polycentropodidae sp1	39	1 ± 1	3 ± 1	–	–			
		<i>Cernotina</i> sp.	40	10 ± 4.05	7 ± 2.07	–	–			
		<i>Polyplectropus</i> sp.	41	2 ± 0.61	1 ± 1	–	–			
	Xiphocentronidae	<i>Xiphocentron fuscum</i>	42	19 ± 8.33	8 ± 2.39	1.77	–			
Ephemeroptera	Baetidae	Baetidae sp1	43	4 ± 1	1 ± 0.17	–	–			
		<i>Americabaetis</i> sp.	44	79 ± 32.81	47 ± 13.75	31 ± 12.34	5 ± 2.02			
		<i>Cloedes caraibensis</i>	45	24 ± 3.86	14 ± 4.05	6 ± 1.38	–			
		<i>Falceon ater</i>	46	12 ± 4.57	12 ± 3.35	10 ± 2.92	–			
		<i>Caenis</i> sp.	47	2 ± 0.61	7 ± 3.35	15 ± 6.88	4 ± 0.58			
		<i>Caenis femina</i>	48	7 ± 2.6	19 ± 5.96	11 ± 5.41	–			
		<i>Caenis catherinae</i>	49	3 ± 0.94	11 ± 6.18	3 ± 0.57	–			
			Leptohyphidae	Unidentified	50	–	–	1 ± 0.16	–	
			<i>Leptohyphes</i> sp.	51	51 ± 16.08	62 ± 14.53	17 ± 3.89	14 ± 9.43		
			<i>Tricorythodes griseus</i>	52	49 ± 22.51	64 ± 43.46	37 ± 9.92	133 ± 62.07		
	Leptophlebiidae	<i>Hagenulopsis gadeloupensis</i>	53	2 ± 0.29	3 ± 0.90	1 ± 0.26	–			
Heteroptera	Mesoveliidae	<i>Mesovelia</i> sp.	54	7 ± 7	–	1 ± 1	–			
	Veliidae	<i>Rhagovelia</i> sp.	55	3 ± 0.28	2 ± 0.3	2 ± 0.28	–			
		<i>Microvelia</i> sp.	56	–	–	–	5 ± 1.44			
Coleoptera	Dystiscidae	<i>Laccophilus</i> sp.	57	–	–	4 ± 0.97	–			
		Elmidae	<i>Elsianus</i> sp.	58	11 ± 2.87	6 ± 0.95	3 ± 0.56	–		
		<i>Neelmis</i> sp.	59	58 ± 9.71	16 ± 4.09	2 ± 0.23	18 ± 8.76			
		<i>Hexanchorus</i> sp.	60	7 ± 3.44	3 ± 0.64	2 ± 0.18	–			
		Gyrinidae	<i>Gyretes</i> sp.	61	4 ± 1.5	–	2 ± 0.26	–		
		Hydraenidae	<i>Hydraena</i> sp.	62	5 ± 5	1 ± 0.17	1 ± 1	6 ± 2.89		
		Psephenidae	<i>Psephenops</i> sp.	63	11 ± 3.64	6 ± 1.82	6 ± 0.68	–		
		Staphylinidae	Unidentified	64	1 ± 0.25	–	6 ± 1.99	–		
	Diptera	Blephariceridae	Unidentified	65	–	12 ± 2.63	2 ± 0.49	–		
		Cecidomyiidae	Unidentified	66	–	–	1 ± 0.31	–		

(Continued)

Table 1. (Continued)

Phylum	Class/order	Family/subfamily	Species	ID	Cluster 1	Cluster 2	Cluster 3	Cluster 4
		Ceratopogonidae	Unidentified	67	–	–	19 ± 4.69	–
		sF/Ceratopogoninae	Unidentified	68	3 ± 0.71	5 ± 1.3	9 ± 4.36	1 ± 0.24
		sF/Forcypomyinae	<i>Atrigopogon</i> sp.	69	2 ± 0.88	1 ± 0.5	1 ± 0.36	3 ± 0.62
		sF/Dasyheleneinae	Unidentified	70	1 ± 0.2	–	2 ± 0.32	–
		Chironomidae						
		sF/Chironominae	Chironomini	71	66 ± 21.38	51 ± 20.53	18 ± 6.14	4807 ± 4472.2
			Tanytarsini	72	130 ± 43.87	31 ± 10.89	39 ± 28.12	118 ± 66.78
		sF/Orthocladinae	Unidentified	73	101 ± 36.03	26 ± 7.29	90 ± 22.64	117 ± 87.46
		sF/Tanypodinae	Unidentified	74	27 ± 8.7	19 ± 6.20	14 ± 2.86	55 ± 28.99
			<i>Harrisius</i> sp.	75	48 ± 17.47	12 ± 2.68	6 ± 1.08	2 ± 0.58
		Empididae	<i>Hemerodromia</i> sp.	76	13 ± 4.45	7 ± 3.11	2 ± 0.53	43 ± 22.23
		Ephydriidae	Unidentified	77	3 ± 1	–	2 ± 0.32	3 ± 1.44
		Limoniidae	Unidentified	78	1 ± 1	3 ± 0.83	1 ± 0.26	–
		Psychodidae	Unidentified	79	5 ± 1.75	–	2 ± 0.47	–
			<i>Maruina</i> sp.	80	7 ± 0.18	5 ± 2.58	2 ± 0.36	–
		Rhagionidae	<i>Chrysopilus</i> sp.	81	1 ± 0.18	1 ± 0.12	–	–
		Simuliidae	Unidentified	82	9 ± 5.08	43 ± 14.38	32 ± 12.13	–
		Syrphidae	Unidentified	83	–	–	1 ± 1	–
Odonata		Unidentified	Unidentified	84	5 ± 0.71	1 ± 0.14	1 ± 1	–
		Coenagrionidae	<i>Argia concinna</i>	85	21 ± 6.11	11 ± 2.63	7 ± 2.03	–
			<i>Enallagma coecum</i>	86	4 ± 1.06	7 ± 0.5	12 ± 2.89	21 ± 13.91
			<i>Ischnura ramburii</i>	87	–	2 ± 0.33	–	–
		Libellulidae	<i>Brechmorhoga praecox</i>	88	1 ± 1	1 ± 1	–	–
			<i>Macrothemys celleno</i>	89	–	1 ± 1	–	–
			Unidentified	90	5 ± 1.89	2 ± 0.9	1 ± 0.27	4 ± 1.44
Lepidoptera		Pyralidae	Unidentified	91	49 ± 16.73	15 ± 8.07	–	–

above-mentioned insect orders, but also had higher diversity for Odonata (Coenagrionidae, Libellulidae), Diptera (Chironomidae), Crustacea (Atyidae) and Mollusca (Hydrobiidae, Neritidae, Planorbidae). Sites in cluster 3 had high diversity for Mollusca and Crustacea, and for Diptera (Psychodidae, Limoniidae, Empididae, Simuliidae) and Coenagrionidae Odonata (but low diversity for other insect orders). Sites in cluster 4, which were located downstream from wastewater plants and urban outlets, were characterized by higher abundances for Mollusca (Thiaridae and Sphaeriidae), Annelida (Hirudinea and Oligochaetes), and Diptera (Chironomidae, Ephydriidae, Limoniidae).

Box-plots suggested a trend for increasing within-cluster variability in diversity indices from cluster 1 to cluster 4. Taxonomic richness, community evenness (Simpson index) and entropy (Shannon index) differed significantly among clusters (Kruskal–Wallis tests, $p < 0.05$, Fig. 3), and showed a decreasing trend from north-eastern (cluster 1) to south areas (cluster 3). However, taxonomic richness and evenness did not differ significantly between clusters 3 and 4. No clear patterns in community diversity were apparent when sites were divided into a priori groups based on local observations of potential disturbance (Figs. 2a,b and 3).

4 Discussion

This study provides new, quantitative information on the distribution and environmental preferences of freshwater

invertebrates in the French Lesser Antilles. To date, data were insufficient to carry out statistical analysis and validate models, so that expert knowledge was the only option to define networks of survey sites. Therefore, this is the first attempt to use an a posteriori inductive approach to community patterns, where a large volume of site specific data are subjected to ordination and cluster analyses in order (i) to derive spatial schemes and (ii) to classify sites in an objective way. Discussion herein evaluates issues arising from our analysis of freshwater diversity and distribution in Guadeloupe, and considers implications of this knowledge for the development of bio-assessment tools.

Ordination and cluster analyses are frequently used in the exploratory phase of typologies. All site groups were included in our multivariate analysis, regardless of a priori consideration of disturbance. By doing so, we expected that geographically adjacent sites appearing distant in modelling space (according to macroinvertebrate communities) would represent differences among sites in biological quality. Wasson et al. [10] identified two hydroecoregions in Basse-Terre: “wet plains” (cluster 1 in our biological typology) in the north-east, and “wet volcano” in the remaining area (clusters 2 and 3 according to invertebrate communities). Our results thus highlight the importance of land cover (e.g., forest vs. open areas) and geomorphology (particle size, river competence, and erosive forces in relation to elevation, specific water chemistry nearby the volcano) in refining ecological sub-regions for the freshwater biota. Deviation from predictable community structure within a given sub-region primarily occurred when river sites were subjected to harsh

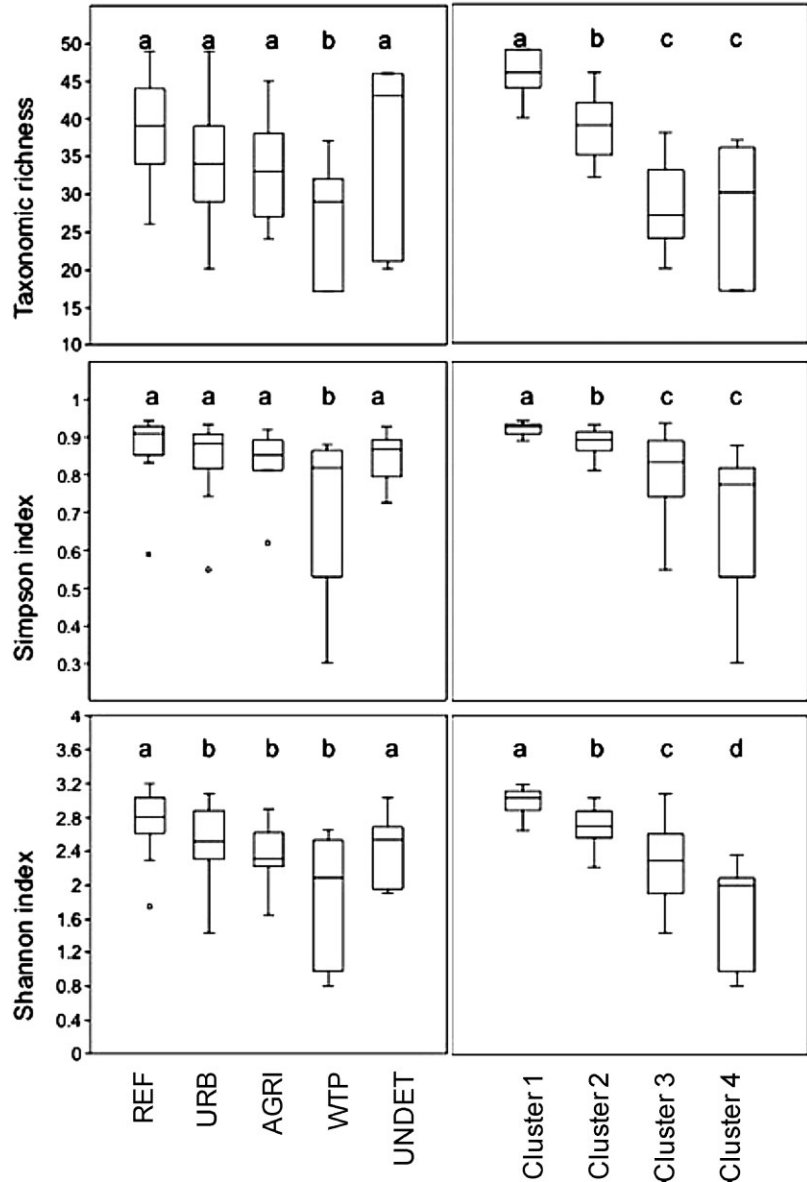


Figure 3. Boxplots of diversity metrics distributions (taxonomic richness, Simpson's evenness, Shannon's Entropy) in the five a priori site groups (left) and in the four clusters derived from the RDA and k -means analyses (right), with comparison of pairs of clusters. Significant differences between groups or clusters were tested with Kruskal–Wallis tests; lowercase letters above boxes indicate significant differences at $p < 0.05$.

anthropogenic disturbance (sites assigned to cluster 4), notably urban runoff and wastewater inputs. In this case, disturbance mostly overrode geomorphological controls on the distribution of macroinvertebrate diversity through water chemistry alterations (phosphorus, nitrogen).

Most bio-assessment systems use common species to assess the ecological quality of surface waters [25], while rare species are rather used in assessing the conservation value of freshwaters [26]. Common taxa are expected to give a closer approximation to spatial patterns of community structure and evenness than do rare ones [27, 28]. Fifty taxa out of 91 occurred in more than 25% of the sampling sites and 30 taxa were found at more than 50% of the sites. Most taxa (84.6%) were therefore widespread and occurred in three or four clusters. Although most invertebrates were keyed to genus or

species, we acknowledge that commonness may drop to lower percentages if some numerically important taxonomic groups such as the Diptera were identified to species. Only 3 and 11 taxa occurred in 1 and 2 clusters, respectively, and in low abundances (< 1 individual per m^2). *Macrothemys celleno* (Odonata) was only found in cluster 1, while *Guinotia* sp. (Crustacea) and *Laccophilus* sp. (Trichoptera) only occurred in cluster 3. However, despite the ubiquity of most invertebrates, individual sites only contained 17–49 taxa. This situation raises concerns as to how to define water quality classes and how to identify sensitive indicator species when (i) the regional species pool is poor (insular context, most genera contained only one or two species), (ii) values for mean or median species richness do not differ greatly between unstressed (torrential streams along volcano slopes,

forest, and plain streams elsewhere) and stressed sites (here mostly urban pollution and inefficient water treatment plants in plain areas). It is worth noting that species richness and community evenness were not significantly different between cluster 3 (influence of the volcano) and cluster 4 (human-impacted sites, urban – domestic pollution). However, species composition differed greatly between clusters 3 (insects) and 4 (molluscs, annelids). Important differences also existed between clusters in terms of numerical dominance. For instance, a small number of pollution resistant-taxa (Glossiphoniidae, Neriitidae, Dugesiiidae, Thyaridae, Oligochaetes, and Tanytarsini) represented 75% of the mean invertebrate density in cluster 4 (impaired sites), but only 15–25% of the mean density in other clusters (see Appendix 2). Conversely, several Trichoptera (e.g., *Xiphocentron fuscum*, *Chimarra* sp.), Ephemeroptera (*Cloedes caraibensis*, *Leptoxyphes* sp., *Americabaetis* sp., *Tricorythodes griseus*), and Coleoptera (*Neoelmis* sp.) made up to 50% of the mean density in clusters 1–3. We therefore anticipate that changes in species richness (either via a loss or a gain of species) would not detect any stress efficiently within a given sub-region (cluster), and recommend to rather consider metrics that quantify changes affecting the density of species and/or functional groups [29].

The ratios between observed biological parameters and the expected values under reference conditions (Ecological Quality Ratios) for these parameters are at the heart of WFD compliant methods to evaluate biological quality in freshwaters [3]. This framework implies that both typology and reference conditions need to be agreed upon before considering further developments. If a priori definitions of reference sites (expert opinion) are not always biologically meaningful [30], congruence between a priori and a posteriori classification of sites should provide robust schemes because they would be based both on knowledge and statistical power. Based on this idea, we can still identify reference sites that are specifically relevant for our ecological sub-regions (clusters 1–3). In cluster 1 (north-eastern Basse-Terre), where variability in diversity indices was the lowest (see Fig. 3), three sites (BDI, LED, PBS) were formerly classified as REF. LED and PBS had the highest taxonomic richness are thus likely sites of high biological quality. In cluster 2 (central-north range), 8 sites out of 18 were a priori considered as reference sites (see Fig. 2). Among these, VHG and MPT hosted the most taxa. Within cluster 3, five sites were a priori classified as REF, but only two sites (GAM and PEC) belonged to the first quartile in terms of taxonomic richness (38 and 34 taxa, respectively). It should be noted however that some sites a priori considered as impacted (URB and AGRI groups) showed high values for community diversity metrics too. This could be due either to weak impacts and/or to the ubiquity (or tolerance) of many species.

The WFD emphasizes the importance of geographic differences in biotic and abiotic characteristics of freshwater ecosystems [31], so that classification has become an integral part of efforts to study, monitor, and manage ecosystems at a regional scale [32]. The published literature unambiguously shows that limited scientific effort has been directed at characterizing how rivers in overseas Europe differ in terms of biological community structure, and how communities respond to changes in abiotic conditions. Our settings (biogeographic history, naturally depauperate fauna, geomorphological influence of volcanoes, concentrated anthropogenic disturbance) certainly apply to most European territories in the Caribbean (French, British, and Netherland Antilles). Based on our study, it is apparent that future work in Guadeloupe and elsewhere should focus on relevant indicator taxa (or combinations of those) in order to eliminate noise from complete datasets. At the same time, further analyses of physical–chemical environments are needed to identify tipping points between natural and disturbed states.

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