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Sites and species contribution to the β -diversity of Odonata assemblages in Haiti: implications for conservation.

PIERRE MICHARD BEAUJOUR^{a,b*}, GLADYS LORANGER-MERCIRIS^a AND FRANK CEZILLY^{b,c}

^a*UMR ISYEB-MNHN-CNRS-Sorbonne Université-EPHE, Université des Antilles, Campus de Fouillole, 97157 Pointe-à-Pitre Cedex (Guadeloupe), France*

^b*Caribaea Initiative, Le Raizet, Les Abymes, Guadeloupe, French West Indies*

^c*UMR CNRS 6282 Biogéosciences, Université de Bourgogne, Dijon, France*

*Corresponding author:

Pierre Michard Beaujour, pmichardb@gmail.com

Abstract

Understanding the ecological determinants of assemblage diversity in freshwater insects is of crucial importance for conservation biology and environmental management. This is particularly true in Haiti, where severe and ongoing environmental degradation of aquatic ecosystems is a major threat to the local invertebrate fauna. Here, using Odonates assemblages sampled from 67 waterbodies belonging to 14 different Haitian watersheds, we assessed species uniqueness (U) from both rarity based on spatial occupancy and taxonomic species distinctness (TSD), and species contribution to total β diversity (SCBD). We assessed between-site variation in species richness (SR), relative taxonomic distinctness (RTD), mean species uniqueness per site (Mean U), and the contribution of individual sites to total β diversity (LCBD), based on presence-absence data. We then examined the relationships between these variables and the physico-chemical characteristics of the sites. In total, we recorded 49 different odonate species (including two endemic species of conservation interest), belonging to 40 genera and 7 families, with a relatively high percentage (69.4%) of rare species (i.e. occurring in 10% or less of sampled water bodies). TSD was negatively correlated with spatial occupancy, while U was significantly higher in Zygopeteran species compared to Anisopteran species. SR varied among the 67 sites, ranging from 2 to 17 species, while SCBD was positively correlated with site occupancy. Differences in assemblage composition between sites were mainly due to species replacement, while only a few sites had assemblages consisting of a subset of larger assemblages found at other sites. The observed positive correlation between dissimilarity and geographic distance between sites further suggests that the turnover of species may take place over some ecological gradient and/or might be explained by species ecological requirements and limited ability to disperse. LCBD and Mean U

increased with increasing altitude and decreasing temperature and conductivity, whereas SR and RTD did not. All variables were independent of pH. Overall, SR and RTD were higher in lotic than in lentic sites, and in sites with natural riparian vegetation compared to sites with anthropogenic or mixed riparian vegetation. Mean U provided a relevant index for site selection for odonates conservation in Haiti, whereas β diversity appeared to be of limited interest for this purpose. Globally, our results advocate the importance of conserving a wide diversity of waterbodies to protect Odonate diversity in Haïti, and particularly in forested areas at > 1000m altitude.

Keywords: Odonata, conservation, Hispaniola, β diversity, species uniqueness, taxonomic distinctness.

Introduction

Few data are available on insect populations in the tropics, where more than fifty percent of the world's insect species occur (Stork 2018, Garcia-Robledo et al. 2020). This is particularly true for Haïti, located in the western third of Hispaniola, the second largest island and biodiversity hotspot within the larger insular Caribbean (Nieto-Blázquez et al. 2022). Although Haiti has a rich and diverse fauna (Posner et al. 2010), there is an important knowledge gap regarding the conservation status of many species, especially invertebrates (Posner et al. 2010, Beaujour and Cezilly 2022). This is mainly due to lack of scientific expertise, limited research facilities, and logistical difficulties (Saint-Louis et al. 2021, Vallès et al. 2021, Exantus et al. 2021). In addition, the increase in violence problems (Kovats-Bernat 2002), with armed groups often blocking roads and ransoming or killing people, can make fieldwork in natural areas particularly difficult and quite dangerous. Nevertheless, the extreme level of environmental degradation in Haiti requires special attention to its impact on vulnerable species such as insects, especially in aquatic ecosystems. Indeed, several factors contribute to the poor health of aquatic ecosystems in Haïti (Posner et al. 2010), including deforestation (Hedges et al. 2018), increasing urbanization (Capps et al. 2016), inadequate waste management practices and widespread pollution (Emmanuel et al. 2008), and the introduction of non-native species (Rodriguez-Silva et al. 2020). However, so far, little effort has been made to document the diversity and distribution of aquatic invertebrates in running and still waters of Haiti (see however Cineas 2022).

In this context, we conducted a survey of odonates in Haiti, in an attempt to document spatial variation in assemblage composition and relate it to environmental factors. Odonates are a particularly interesting group of aquatic invertebrates (Clausnitzer et al. 2009) due to their significant contributions to the functioning of freshwater ecosystems (Contreras-Ramos, 2010; Vincy et al. 2016). They play a multifaceted role in ecosystems, serving as prey for both vertebrates and larger insects, while also acting as top predators preying on smaller aquatic insects, particularly in environments without vertebrates (Corbet 1999). In addition, the particular dependence of both larvae and adults odonates on specific water conditions for their survival (Dolný et al. 2012), coupled with their high sensitivity to habitat disturbance, has made them reliable indicators of water quality (Clausnitzer 2003, Harabiš and Dolný 2012, Golfieri et al. 2016). Understanding the distribution of both rare and common species within a given community can provide crucial information for the management, restoration, and conservation of freshwater ecosystems, benefiting entire wetland biotic assemblages (Bried et al. 2007).

Although data from long-term and regular monitoring may be necessary to assess the potential decline of insect species, including odonates (Dolný et al. 2012), their interpretation can be difficult, if not controversial (Blüthgen et al. 2022, 2023). In addition, they are usually restricted to a limited number of sites, which calls into question the general validity of the results. Recently, it has been proposed to pay more attention to spatial evidence when investigating the causes of insect decline (Blüthgen et al. 2022). In particular, quantifying spatial variation in species composition is of prime importance to identify the factors that generate patterns of β diversity (Carvalho et al. 2012, Legendre and De Cáceres 2013) and document species rarity and commonness (Renner et al. 2020). Accordingly, we relied on intermittent sampling of odonate species over a 26-month period to include multiple sites reflecting the diversity of aquatic habitats in Haiti. Specifically, we examined spatial variation in species richness and taxonomic distinctiveness, and assessed to what extent the relative contribution of different species and sites contribute to overall β diversity across our study area (Legendre and Gauthier 2014).

Materials and methods

According to the literature, there are potentially 58 species of odonates in Haiti (Meurgey 2013), of which three are endemic to Hispaniola (Torres-Cambas et al. 2015a, 2015b, 2016; Perez-Gelabert 2020). Although occasional photographic documentation and historical surveys have

been conducted throughout the country (Christiansen 1947, Westfall 1976), knowledge about the distribution and relative abundance of odonates in Haiti is very limited (Perez-Gelabert 2020). This is partly due to the difficulty in discerning observations specific to Haiti in the literature, given the widespread practice of referring to the entire island as “Hispaniola”. A lack of trained conservation scientists and entomologists in Haiti also contributes to this information gap (Vallès et al. 2021).

Study area

We surveyed the distribution of odonate species between January 2019 and May 2021 in Haiti, (figure 1), a Caribbean country, located (18.9712° N, 72.2852° W) in the mountainous western third of the island of Hispaniola. Haiti has a complex topography, with altitude ranging from sea level to 2680 m at Pic La Selle. Altitudinal variation results in a temperature and rainfall gradient which becomes subtropical and temperate over 1.200-1.500 m (Carmona et al. 2010). Mean monthly temperature vary between 19 and 33°C at low elevations (Taylor et al. 2015), but can be close to 0°C at the highest elevations during the coolest months of the year.

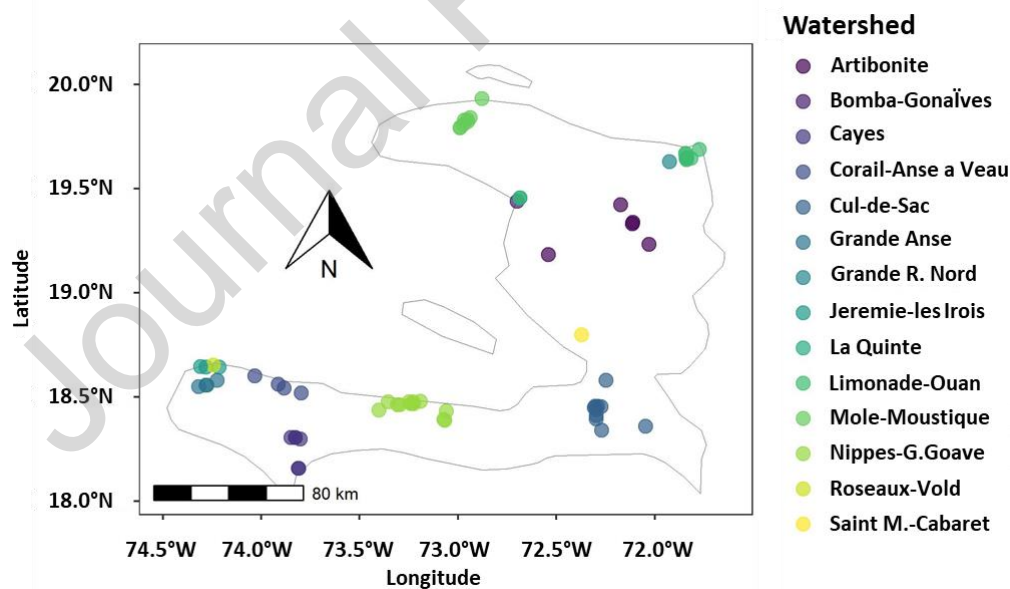


Figure 1. Geographic distribution of sampling sites across Haiti, differentiated by fourteen watersheds (color-coded dots). Map generated using the R v4.3.0 software.

Our survey took place at 67 different sites, and included a whole range of different waterbodies, such as rivers, lakes, ponds, rice fields, temporary and permanent ponds, based on their accessibility and safety issues. Overall, the 67 sampled sites were distributed in 14 of the 30 major watersheds identified in Haiti (Bannister et al. 2006). Nine of them were situated at elevations above 1000 m asl, while 58 were situated at elevations below 500 m asl, reflecting the difficulty of accessing some mountainous areas. Although we were not able to survey all sites of potential interest, our sample covers a wide range of sites with contrasting ecological characteristics (see Annexe A for details).

Data collection

We originally planned to conduct three replicates per site. However, road blockages and security concerns, as well as the global health crisis from COVID-19 during our study period, prevented us from doing so. In addition, temporary pools could not be sampled at any time of the year. As a result, the majority of sites (57) were sampled only once, while six sites were sampled twice and four sites were sampled on three occasions.

We sampled 24 river sites, where the transect length varied due to natural obstacles such as ravines, cliffs, or hazardous slopes. Specifically, most river sites (20 out of 24) were sampled using a 1 km transect. Two river sites were sampled along 500-meter transects, and the remaining two river sites had unique transect lengths of 780 meters and 800 meters, respectively. For lakes ($n = 4$), permanent pools ($n = 13$), and temporary pools ($n = 21$), sampling was conducted by walking along the edges and margins of the waterbodies. These are areas where aquatic vegetation is most abundant, providing perches for Odonata species (Briggs et al. 2019). Finally, we walked along a continuous 1-km transect to adequately sample five larger ponds. At each site, we relied on observations of adult Odonata present along the transect to document assemblage composition and taxonomic diversity. We conducted sampling between 09:00 and 15:00 at each site. Sampling lasted for six hours along 1 km transects sites, whereas at sites ($n=4$) with transects between 500 meters and 800 meters long, the duration of sampling ranged between four and five hours.

Taxonomic identification

Most Odonata individuals were identified without being captured, based on morphological characteristics. In most cases, species could be identified by direct visual observation or using

binoculars (Kite Optics Petrel KT 10×42). Whenever individuals were difficult to approach, we used a digital single-lens reflex camera (Pentax K-50) equipped with a 100mm macro telephoto lens (smc Pentax-D FA MACRO 100mm F2.8 WR) to assist in identification. However, in cases where immediate identification in the field was not possible, we captured specimens using a butterfly net consisting of a 90 cm Khaki polyester pocket with an 8mm mesh size, attached to a 40-cm diameter aluminum folding frame attached to an aluminum adjustable telescopic handle (3x60 - 129cm). Collected specimens were preserved in 70% ethanol and subsequently identified using several keys (Esquivel 1990, Meurgey and Picard 2011, Torres-Cambas et al. 2016, Tennessen 2019).

Environmental characterization

We categorized the different study sites according to two classifications. First, we characterized sites according to water dynamics (Seidu et al. 2019) and flooding duration (Schindler et al. 2003), with three categories: permanent stagnant water (PSW; 22 sites), temporary stagnant water (TSW; 21 sites), and running water (RW; 24 sites). Second, we classified sites according to the type of riparian vegetation within approximately a 100-meter radius (Naiman et al. 1993), with three categories. Natural vegetation (NV; 22 sites) was much diversified and dominated by *Pinus occidentalis*, *Artocarpus incisa*, *Catalpa longissima*, *Zuelania guidonia*, *Agave* spp, *Bambusa vulgaris*, *Datura* spp., *Eucalyptus* spp., *Annona* spp., *Heliconia* spp., *Pteridium* spp., *Strelitzia regina* spp., and *Pisonia aculeata*. Anthropogenic vegetation in agricultural areas (AV; 20 sites), was mainly dominated by plants produced for human consumption, such as *Zea mays* L., *Oryza sativa* L., *Cajanus cajan*, *Musa* spp., *Phaseolus* spp. and *Lepidium* spp, *Solanum melongena*, *Allium porrum* L. Mixed vegetation (MV; 25 sites), was characterized by substantial amount of AV associated to small amounts of NV, including in some sites small orchards of *Moringa oleifera* Lam., *Passiflora* spp. and *Citrus* spp.

We evaluated the physicochemical characteristics of water's surface at each sampling location, focusing on temperature (°C), electrical conductivity (µs/cm), and pH. Measurements were taken using a Combo pH/EC/TDS/Temperature Meter - HI98129, with three readings averaged for each parameter at each site. Site altitudes and geographical coordinates were obtained using a portable, waterproof IPX7 Garmin Montana 680 GPS.

Data analysis

Although we recorded the number of individuals of each species encountered during each transect we did not use this information in our analyses because our sampling effort differed between sites, and, more importantly, because the abundance of odonate species can vary seasonally in relation to their life cycle (Pires et al. 2014). Therefore, we limited our analyses of the presence-absence of the different species at the different sampled sites.

We used a Wilcoxon-Mann-Whitney test to assess to what extent the median number of sites where each species was observed differed between Anisopterans and Zygopterans. Defining “rare species” is complex (Hartley and Kunin 2003) and becomes even more challenging for species with insufficient ecological and phylogenetic data (Renner et al. 2022), such as those found in Haiti. Following Renner et al. (2022), we therefore considered a species to be “rare” if it occurred in 10% or less of all sampled sites. We then defined the “uniqueness” of a species, U , as the ratio between its taxonomic distinctiveness score (TDS) and the number of sites where it was recorded (rarity), with TDS calculated for each species using the equation:

$$TDS = \frac{1}{\sqrt{(f \times g \times s)}}$$

where f is the number of represented families in the suborder to which the species belongs, g is the number of different represented genera in the family, and s is the number of represented species of the same genus (Freitag and Van Jaarsveld 1997). Taxonomically more distinct species therefore receive higher scores than species from more speciose taxa and can be considered to contribute more to β diversity. High values of U are indicative of taxonomically distinct species occurring at a limited number of sites. We considered a species to be “unique” (whose presence is unusual and of special interest due to its taxonomic distinctiveness) if it belonged to the fourth quartile of the distribution, and “banal” (species of low taxonomic interest occurring in a large number of sites) if they belonged to the first quartile of the distribution. All other species were considered as “average”.

We calculated species richness (SR) as the number of species observed at each site, pooling data from the different surveys when a site was sampled on more than once. Because sampling effort varied between sites, we used a Wilcoxon-Mann-Whitney test, using the `wilcox.test()` function from the `stats` (R Core Team, 2023) package in R, to compare SR at sites that were surveyed on only once ($n = 57$) with cumulated SR at sites that were surveyed on more than once

($n = 10$). We repeated the test using this time the lowest SR value on any sampling occasion for sites surveyed on more than once. In addition, we calculated, for each site, Chao 1 index, with $Chao1 = S_{obs} + N_1(N_1-1)/(2(N_2+1))$, where N_1 and N_2 are counts of singletons (i.e. species represented by a single individual in the sample) and doubletons (i.e. species represented by only two individuals in the sample), respectively (Gotelli and Colwell 2011). We then examined the ratio between the total number of observed species and Chao 1 as an index of overall sampling coverage (Chao et al. 2020).

To further assess diversity among the different sampled sites, we also calculated relative taxonomic distinctness (RTD) which evaluates to what extent an assemblage consists of closely related species or distantly related ones, based on presence-absence (Ellingsen et al. 2005). We calculated the index according to the following equation:

$$RTD = \frac{1}{\sqrt{(N_{family} \times N_{genus} \times N_{species})}}$$

where N is the number of different units within a given taxon. RTD decreases with increasing taxonomic distance between species composing the assemblage. In addition, we calculated the mean species uniqueness per site, Mean U , with:

$$Mean U = \frac{\sum_{i=1}^n U_i}{n}$$

Where n is the number of species recorded at each site.

Following the methodology outlined by Legendre and De Cáceres (2013), we calculated total β diversity (BD_{total}) as the sums of squares in the variation of taxon presence across sampled sites. We then decomposed β diversity into two different components (Legendre et De Cáceres 2013, Buckley et al. 2021), ‘species contribution to beta diversity’ (SCBD) and ‘local contribution to beta diversity’ (LCBD), which describe, respectively, the relative contributions of different taxa and sampling units to overall beta diversity. To that end, we initially Hellinger-transformed site-by-species presence-absence community matrix Y (Legendre et al. 2005). Y is a binary matrix with sampling sites as rows, and species on which to measure the dissimilarity in columns, such that the value at row l and column i of matrix Y , is 1 if species i is found at location l , and 0 otherwise. The row sums give the richness at the locations, and the column sums give the number

of occurrences of the species. Using the function ‘beta.div’ in R, we then estimated BD_{total} as the unbiased total sum of squares (SS_{total}), derived from the presence-absence community matrix. SCBD was computed by dividing SS attributed to each species by SS_{total} across all sites. Likewise, LCBD was computed by dividing SS attributed to each site by SS_{total} across all sites. As neither SCBD or LCBD was normally distributed, we calculated, for both variables, the median value, interquartile range, and quartile coefficient of dispersion (Botta-Dukát 2023). The quartile coefficient of variation depends only on the central part of variable distribution, and is therefore insensitive to outlier values. It is particularly suited as an index of dispersion for variables calculated as a ratio (Botta-Dukát 2023).

Following (Legendre and De Cáceres 2013), we used permutations to redistribute species across locations and test for statistical significance of LCBD values. This procedure identifies which LCBD values are larger than expected from random variation in species composition, thus indicating which sampled sites are unique in terms of the species found within them. We used the default threshold of 0.05 (after Holm-Bonferroni correction), with 9999 random permutations of each column of the community data matrix. We relied on a Spearman rank-order correlation coefficient to test for a correlation between LCBD and both RTD and Mean U. Relying on “prcomp” in the ‘vegan’ R package, we ordinated sites according to SR, RTD, Mean U, and LCBD, along two major axes (PC1 and PC2), using a Principal Component Analysis (PCA).

Finally, we used the ‘beta.div.comp’ function from the *adespatial* package in R (Dray et al., 2018) to calculate total dissimilarity (BD_{total}) and its individual components: total richness difference diversity, $RichDiff_{total}$ (nestedness) and total species replacement diversity, $Repl_{total}$, among sites (Legendre 2014). For this analysis, we applied Jaccard-based indices from the Podani family as defined by Legendre (2014), using the presence-absence community matrix. We assessed to what extent dissimilarity in the composition of odonate assemblages was explained by geographic distance between sites. To do so, we relied on the *vegan* package in R (Oksanen et al. 2022) to compute the pairwise matrix of similarity in assemblage composition between sites based on the Jaccard occurrence index, and on to the ‘*geosphere*’ package in R (Hijmans et al. 2017) to compute the pairwise matrix of geographical distances between each pair of sites. We then performed a Mantel test with 999 permutations to assess the correlation (Spearman’s method) between the two matrices, using the “mantel” function from the ‘vegan’ package in R.

Since all physicochemical variables describing sites, except pH, were highly correlated between themselves (see results), we conducted a second PCA to reduce the variables to two principal axes (PC1 and PC2). We then used Spearman rank-correlation tests to analyze the association between the two principal axes (PC1 and PC2) and SR, RTD, Mean U, LCBD. We used the non-parametric Kruskal-Wallis test (R function 'kruskal.test') to compare the median values of SR, RTD, Mean U, and LCBD between the three vegetation types and between the three categories of water dynamics. We relied on Dunn's post hoc test, using the “dunnTest” function from the “FSA” package, to identify pairs of vegetation and pairs of water dynamics categories that differed significantly, with p -values adjusted using the Bonferroni method.

All analyses were performed using the R v4.3.0 (R Core Team 2023) and Rstudio v2023.3.1.446 (Posit Team 2023) softwares. Graphs were generated in the R software, using the ggplot2 (Wickham 2016) and GGally (Schloerke et al. 2021) libraries. All statistical tests were considered significant at $p < 0.05$.

Ethical note

Consent and approval was obtained from the Ministry of Environment of Haiti in the framework of an MOU with the NGO Caribaea Initiative. The study complies with general guidelines for insect studies in the wild and commonly accepted norms of animal research.

Results

Overall, we recorded 49 different odonate species, belonging to 40 genera, 7 families, and 2 suborders (see Table 1).

Table 1: List of observed species according to taxonomic divisions, number of watersheds (nW) and sampling sites (nS) where observed, taxonomic distinctiveness score (TDS), and uniqueness (U, with A = unique, B = average, C = banal). The IUCN conservation status for each species is indicated as LC (Least Concern), NT (Near Threatened), or EN (Endangered).

Suborder	Family	Species	IUCN status	nW	nS	TDS	U
Anisoptera	Aeshnidae	<i>Anax amazili</i>	LC	1	1	0.204	A

Anisoptera	Aeshnidae	<i>Anax concolor</i>	LC	2	2	0.204	A
Anisoptera	Aeshnidae	<i>Coryphaeschna adnexa</i>	LC	1	1	0.204	B
Anisoptera	Aeshnidae	<i>Coryphaeschna viriditas</i>	LC	3	3	0.204	B
Anisoptera	Aeshnidae	<i>Gynacantha nervosa</i>	LC	1	1	0.288	A
Anisoptera	Aeshnidae	<i>Rhionaeschna psilus</i>	LC	1	1	0.288	A
Anisoptera	Gomphidae	<i>Aphylla caraiba</i>	LC	3	6	0.577	B
Anisoptera	Libellulidae	<i>Brachymesia furcata</i>	LC	3	17	0.096	C
Anisoptera	Libellulidae	<i>Brachymesia herbida</i>	LC	7	21	0.096	B
Anisoptera	Libellulidae	<i>Cannaphila insularis</i>	LC	3	10	0.136	B
Anisoptera	Libellulidae	<i>Dythemis rufinervis</i>	LC	1	1	0.136	A
Anisoptera	Libellulidae	<i>Erythemis attala</i>	LC	3	4	0.079	B
Anisoptera	Libellulidae	<i>Erythemis plebeja</i>	LC	7	19	0.079	A
Anisoptera	Libellulidae	<i>Erythemis vesiculosa</i>	LC	8	16	0.079	A
Anisoptera	Libellulidae	<i>Erythrodiplax berenice</i>	LC	2	3	0.068	B
Anisoptera	Libellulidae	<i>Erythrodiplax fervida</i>	LC	3	4	0.068	B
Anisoptera	Libellulidae	<i>Erythrodiplax justiniana</i>	LC	3	5	0.068	B
Anisoptera	Libellulidae	<i>Erythrodiplax umbrata</i>	LC	9	22	0.068	C
Anisoptera	Libellulidae	<i>Idiataphe cubensis</i>	LC	2	2	0.136	B
Anisoptera	Libellulidae	<i>Macrodiplax balteata</i>	LC	1	3	0.136	B
Anisoptera	Libellulidae	<i>Macrothemis celeno</i>	LC	7	24	0.136	C
Anisoptera	Libellulidae	<i>Miathyria marcella</i>	LC	2	3	0.136	B
Anisoptera	Libellulidae	<i>Micrathyria aequalis</i>	LC	4	6	0.068	B
Anisoptera	Libellulidae	<i>Micrathyria didyma</i>	LC	8	18	0.068	C
Anisoptera	Libellulidae	<i>Micrathyria dissocians</i>	LC	1	1	0.068	B
Anisoptera	Libellulidae	<i>Micrathyria hagenii</i>	LC	3	5	0.068	B
Anisoptera	Libellulidae	<i>Orthemis discolor</i>	LC	8	13	0.079	B
Anisoptera	Libellulidae	<i>Orthemis feruginea</i>	LC	6	14	0.079	C
Anisoptera	Libellulidae	<i>Orthemis macrostigma</i>	LC	12	36	0.079	C
Anisoptera	Libellulidae	<i>Pantala flavescens</i>	LC	2	4	0.096	B
Anisoptera	Libellulidae	<i>Pantala hymenaea</i>	LC	1	1	0.096	B
Anisoptera	Libellulidae	<i>Perithemis domitia</i>	LC	1	1	0.136	A

Anisoptera	Libellulidae	<i>Scapanea frontalis</i>	LC	1	8	0.136	B
Anisoptera	Libellulidae	<i>Sympetrum gilvum</i>	LC	1	2	0.136	B
Anisoptera	Libellulidae	<i>Tauriphila australis</i>	LC	3	4	0.136	B
Anisoptera	Libellulidae	<i>Tholymis citrina</i>	LC	1	4	0.136	B
Anisoptera	Libellulidae	<i>Tramea abdominalis</i>	LC	11	19	0.068	C
Anisoptera	Libellulidae	<i>Tramea binotata</i>	LC	1	2	0.068	B
Anisoptera	Libellulidae	<i>Tramea calverti</i>	LC	3	6	0.068	B
Anisoptera	Libellulidae	<i>Tramea insularis</i>	LC	7	14	0.068	C
Zygoptera	Coenagrionidae	<i>Enallagma civile</i>	LC	1	4	0.204	B
Zygoptera	Coenagrionidae	<i>Enallagma coecum</i>	LC	3	4	0.204	B
Zygoptera	Coenagrionidae	<i>Ischnura capreolus</i>	LC	2	5	0.204	B
Zygoptera	Coenagrionidae	<i>Ischnura ramburii</i>	LC	14	39	0.204	C
Zygoptera	Coenagrionidae	<i>Telebasis dominicana</i>	LC	1	3	0.204	B
Zygoptera	Coenagrionidae	<i>Telebasis vulnerata</i>	LC	2	5	0.204	B
Zygoptera	Lestidae	<i>Lestes forficula</i>	LC	2	4	0.5	A
Zygoptera	Hypolestidae	<i>Hypolestes hatuey</i>	NT	1	1	0.5	A
Zygoptera	Synlestidae	<i>Phylolestes ethelae</i>	EN	1	2	0.5	A

The majority of recorded species (81.6%) belonged to the suborder Anisoptera. However, there was no significant difference between the number of sites at which Anisoptera species ($n = 40$, median = 4) and Zygoptera species ($n = 9$, median = 4) were observed (Mann-Whitney-Wilcoxon test: $W = 192.5$, $P = 0.7551$). Among families, Libellulidae were predominant, accounting for 67.3% (33) of all recorded species, followed by Aeshnidae with 12.2% (6), Coenagrionidae with 12.2% (6), and Gomphidae, Hypolestidae, Lestidae, and Synlestidae, each representing 2.0% (1) of the total number of recorded species. Overall, 32 species were exclusively found at elevations < 500m, four were found only at elevations > 1000 m, whereas 13 were found at both low and high elevations. All observed species were of “Least Concern” according to IUCN (2023), except for two Hispaniolan-endemic species that were found only at high-altitude sites, at 1701 m and 1223 m for the “Endangered” Hispaniolan Malachite, *Phylolestes ethelae* (Christiansen 1947), and at 1342 m for the “Near Threatened” *Hypolestes hatuey* (Torres-Cambas 2015, figure 2).



Figure 2. Two Hispaniolan-endemic species of conservation concern: the “Endangered” Hispaniolan Malachite, *Phyllestes ethelae* (A), and the “Near Threatened” *Hypolestes hatuey* (B) (Copyright: Pierre Michard Beaujour).

Overall, 34 species (69.4%) were classified as rare, having been observed in 10% of sites or less. At the sub-order level, the proportion of species classified as rare did not differ significantly between Anisopterans (0.650) and Zygopterans (0.889; Fisher's exact test, $P = 0.2423$). TDS varied between 0.014 and 0.577, and was negatively correlated with the number of sites in which a species was recorded (Spearman rank-order correlation coefficient, $r_s = -0.35$, $P = 0.0147$). Species uniqueness, U , ranged from 0.002 to 0.045 (Table 1), and was significantly higher in Zygopteran species compared to Anisopteran species (Mann-Whitney test, $W=102.5$, $P = 0.0466$).

SR varied among the 67 sites, ranging from 2 to 17 species (Figure 3). There was a significant difference in SR between sites surveyed only once ($n = 57$, median = 5) and those surveyed multiple times ($n = 10$, median = 6.5; Mann-Whitney-Wilcoxon test: $W=167.5$, $P = 0.0373$). However, the difference was still significant when considering the lowest value recorded on any occasion (first, second, or third) at sites surveyed on several occasions ($n = 10$, median = 6.5; Mann-Whitney-Wilcoxon test: $W=169$, $P = 0.0398$), suggesting that the difference in SR was not due to differences in sampling effort. This was confirmed by calculations of the Chao 1 index that revealed a 100% sampling coverage for all sites, but a single one for which we had 88.9% sampling coverage. Consequently, we considered the cumulated SR recorded at each site to be a reliable index of diversity. When including taxonomic information in the assessment of assemblage diversity, RTD ranged from 0.035 to 0.5 among sites and was negatively correlated to SR ($r_s = -$

0.92, $P < 0.001$), whereas mean uniqueness, Mean U, varied between 0.003 and 0.102, and was independent of SR ($r_s = -0.17$, $P = 0.1641$).

Based on the matrix of presence-absence of species among sites, BD_{total} was 0.74. SCBD ranged from 0.001 to 0.068, with a median value of 0.012 (interquartile range [0.005-0.033], quartile coefficient of dispersion = 0.737), was negatively correlated with species uniqueness (Spearman's rank correlation; $r_s = -0.35$, $P = 0.0147$), and was positively correlated with species occupancy (number of sites where each odonate species was found; $r_s = 0.95$, $P < 0.0001$). The latter correlation was significant for both Anisoptera ($r_s = 0.95$, $P < 0.0001$) and Zygoptera ($r_s = 0.94$, $P = 0.0009$) considered separately.

LCBD ranged from 0.010 to 0.022 (Figure 3), with a median value of 0.015 (interquartile-range: [0.012-0.017]; quartile coefficient of dispersion = 0.172). However, none of the LCBD values was significant after Bonferroni-Holm correction ($0.268 \leq P_{adjusted} \leq 1$). Still, LCBD was negatively correlated with SR ($r_s = -0.43$, $P = 0.0002$), and positively correlated with both RTD ($r_s = 0.33$, $P = 0.0062$) and Mean U ($r_s = 0.61$, $P < 0.0001$).

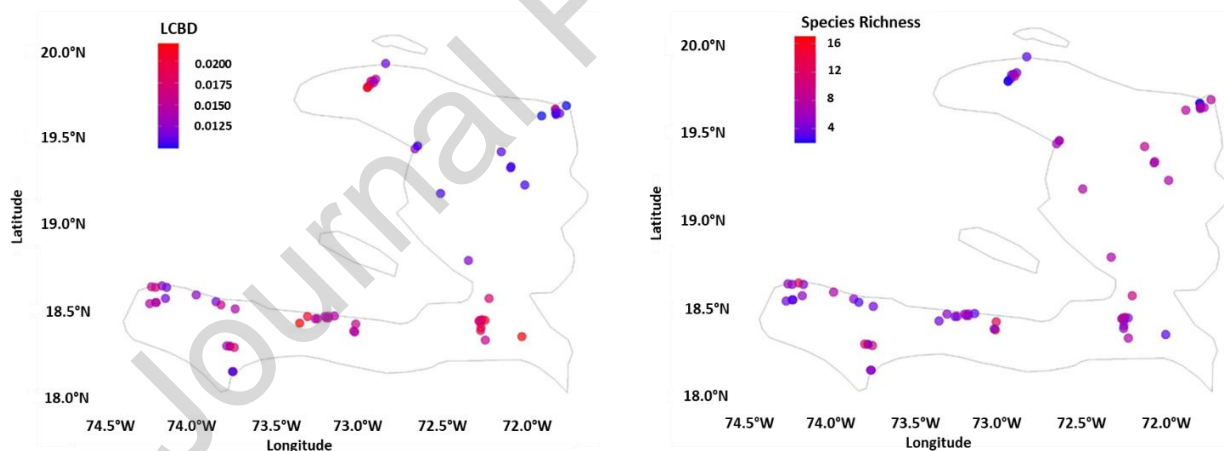


Figure 3. Distribution of the local contribution to beta diversity (LCBD) (on the left) and species richness of odonates (on the right) across 67 sites, each represented by a colored circle. The grey lines delineate the borders of Haiti.

This was reflected in the PCA ordination of sites according to SR, RTD, Mean U, and LCBD (Figure 4, Table 2). The first principal component (PC1), to which SR and RTD mainly contributed, explained 50.4% of the variance, while the second principal axis (PC2) to which Mean

U essentially contributed, explained 35.8%. LCBD had moderate contributions to both PC1 and PC2.

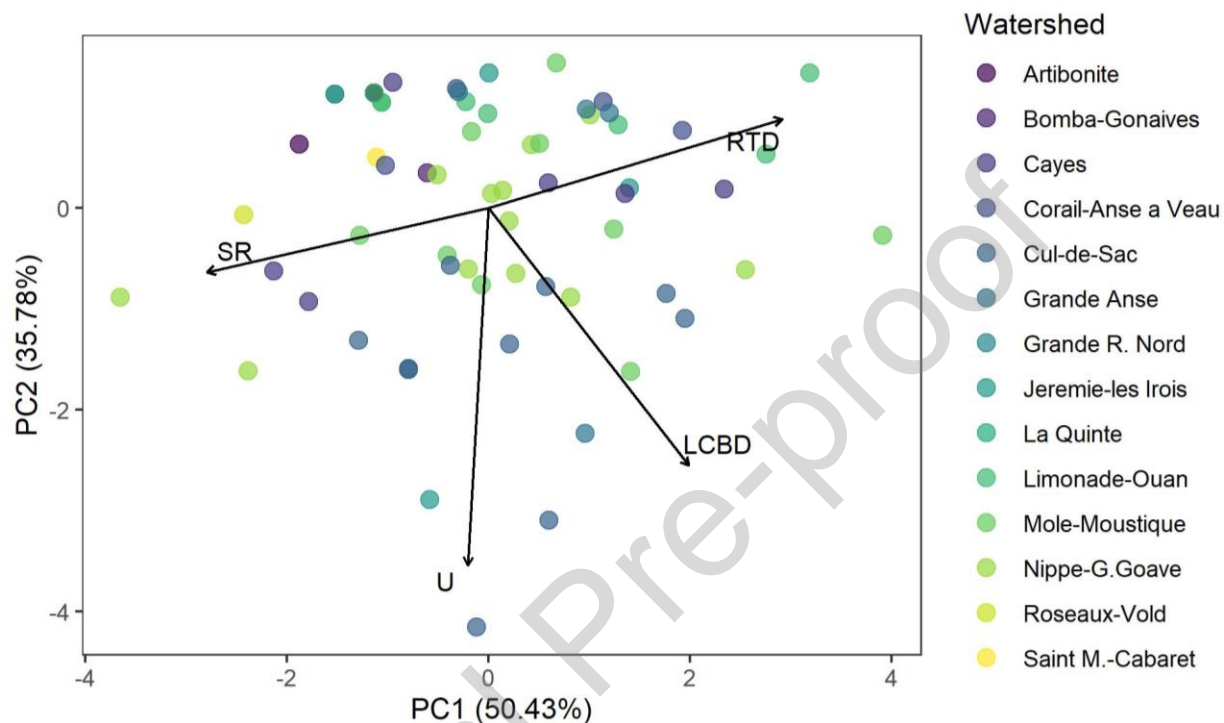


Figure 4. Principal component analysis showing site ordination according to species richness, relative taxonomic distinctness, mean uniqueness per site, and local contribution to β diversity. PC1 and PC2 account for 86.2% of the variance.

Table 2. Factor loadings of species richness (SR), relative taxonomic distinctness (RTD), mean uniqueness per site (Mean U), and local contribution to β diversity (LCBD) to PC1 and PC2.

	PC1	PC2
SR	-0.8812	0.1692
RTD	0.9190	-0.2338
Mean U	-0.0650	0.9416
LCBD	0.6258	0.6794

Total dissimilarity (D_{total}) was 0.41, of which 31.4% and 68.6% were accounted for by $RichDiff_{total}$ and $Repl_{total}$, respectively. There was a positive and statistically significant correlation

between geographical distances among sites and species assemblage dissimilarity measured by Jaccard distance (Mantel tests; $r = 0.17$, $P = 0.001$).

The distributions of physicochemical variables measured at each site (Table 3) tended to deviate from a normal distribution (Shapiro-Wilk test ($0.595 \leq W \leq 0.966$; $0.0001 \geq P \geq 0.0672$)). Temperature and conductivity were positively correlated between themselves (Spearman rank-correlation test, $r_s = 0.62$, $P \leq 0.0001$) and negatively correlated with altitude ($r_s = -0.59$ and -0.97 , respectively, $P \leq 0.0001$). All three variables were independent of pH ($0.4671 \leq P \leq 0.7470$). Principal Component Analysis based on physicochemical variables retained two components that accounted for 84.3% of the total variance (PC1: 59.3%, PC2: 25.0%). Variable loadings indicated that the PC1 was primarily influenced by altitude (0.577), conductivity (-0.581), and temperature (-0.571), whereas PC2 was essentially influenced by pH (-0.996). LCBD ($r_s = -0.27$, $P = 0.0250$) and Mean U ($r_s = -0.32$, $P = 0.0079$) were correlated with PC1, meaning that they decreased with increasing temperature and conductivity and increased with increasing altitude, whereas there was no correlation between PC1 and either SR ($r_s = -0.06$, $P = 0.6449$) or RTD ($r_s = 0.10$, $P = 0.4143$). All four indices were independent of PC2 ($0.2012 \leq P \leq 0.7354$), indicating that they were not affected by variation in pH.

Table 3. Median values, interquartile ranges, and minimum and maximum values of physicochemical parameters measured at the 67 study sites.

	Median value	Interquartile range	Minimum	Maximum
Temperature (°C)	21.0	19.9-22.3	17.0	27.1
Conductivity (µs/cm)	28.0	27.0-29.9	25.5	33.3
pH	7.1	6.9-7.4	6.3	7.7
Altitude (m)	90	18-238	0	1971

Median values of SR, RTD, and Mean U, but not LBCD, differed significantly between hydrological types (Figure 5, Table 4), while median values of all four indices differed significantly between riparian vegetation types (Figure 5, Table 5).

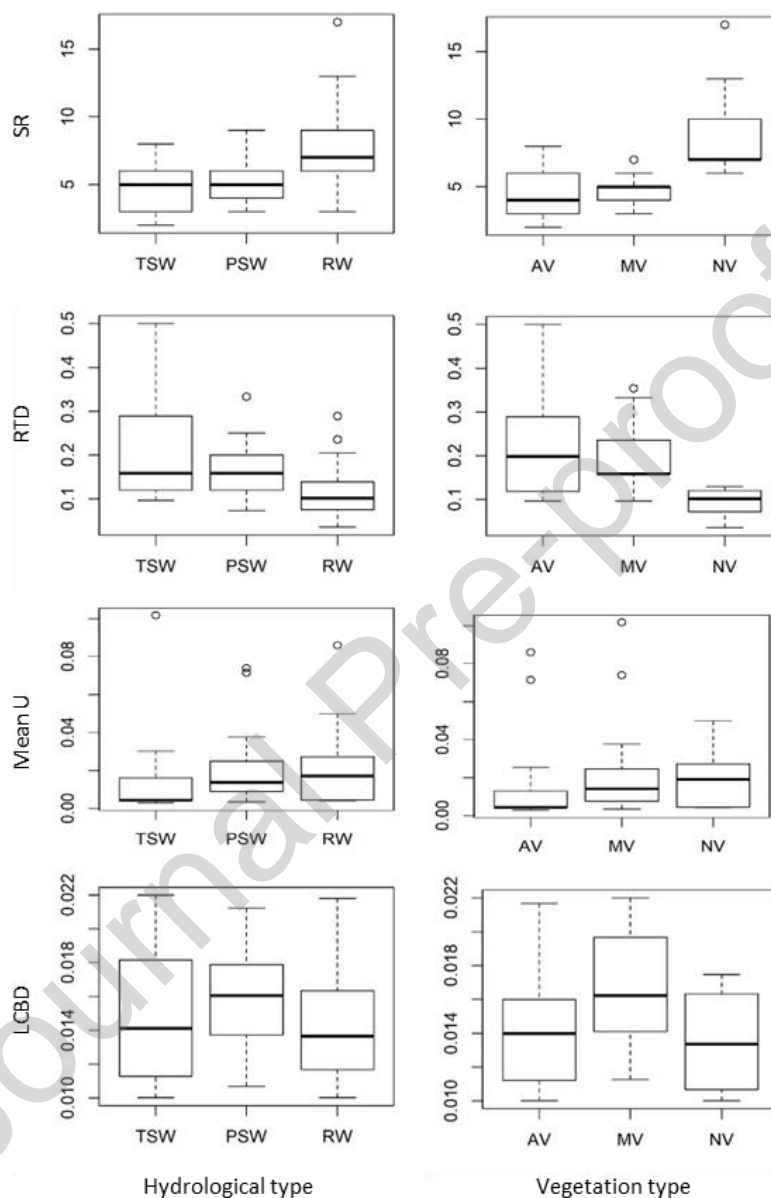


Figure 5. Boxplots illustrating comparative analysis of SR, RTD, and LCBD values (median, interquartile range, maximum, and minimum) across different categories of hydrological type (left; TSW: temporary stagnant waters, PSW: permanent stagnant waters, RW: running waters) and riparian vegetation type (right; AV: anthropogenic vegetation (agricultural), MV: mixed vegetation, NV: natural vegetation). The dark horizontal lines within the boxes represent the

median values, while the edges of the boxes indicate the 25th and 75th quartiles. The “whiskers” extend to the minimum and maximum values within the data range.

Table 4. Statistical comparison of median values of species richness (SR), relative taxonomic diversity (RTD), mean species uniqueness per site (Mean U), and local contribution to β diversity (LCBD) according to hydrological type (TSW: temporary stagnant waters, PSW: permanent stagnant waters, RW: running waters).

	Kruskal-Wallis test		Dunn's post-hoc tests					
	X^2	P	TSW-PSW		TSW-RW		PSW-RW	
			z	P_{adjusted}	z	P_{adjusted}	z	P_{adjusted}
SR	35.81	<0.0001	0.35	1	-4.83	<0.0001	-5.47	<0.0001
RTD	13.57	0.0011	-0.94	1	3.53	0.0012	2.59	0.0284
\bar{U}	8.74	0.0125	2.66	0.0228	2.48	0.0392	0.24	1
LCBD	3.24	0.1978	-	-	-	-	-	-

Table 5. Statistical comparison of median values of species richness (SR), relative taxonomic diversity (RTD), mean species unicity (\bar{U}), and local contribution to β diversity (LCBD) according to vegetation type (AV: anthropogenic vegetation, MV: mixed vegetation, NV: natural vegetation).

	Kruskal-Wallis test		Dunn's post-hoc tests					
	X^2	P	AV-MV		AV-NV		MV-NV	
			z	P_{adjusted}	z	P_{adjusted}	z	P_{adjusted}
SR	35.81	<0.0001	0.35	1	-4.83	<0.0001	-5.47	<0.0001
RTD	28.82	<0.0001	0.07	1	-4.56	<0.0001	-4.74	<0.0001
\bar{U}	9.51	0.0085	-2.63	0.0248	-2.76	0.0169	-0.21	1
LCBD	8.69	0.0129	-2.22	0.0774	0.42	1	2.73	0.0187

Overall, lotic sites had significantly higher species richness and taxonomic distinctness compared to lentic sites, whereas the same two variables did not differ between temporary and permanent stagnant waters. On the other hand, mean species uniqueness was lower in temporary stagnant waters compared to the two other categories, whereas it did not differ significantly between

temporary stagnant waters and running waters. Sites with natural riparian vegetation had significantly higher species richness and taxonomic distinctness compared to sites with anthropogenic or mixed riparian vegetation. In contrast, mean species uniqueness was significantly lower in sites with anthropogenic riparian vegetation compared to sites with other riparian vegetation types, but did not differ between sites with mixed riparian vegetation and sites with natural riparian vegetation. LBCD was significantly higher in sites with riparian mixed vegetation compared to sites with other vegetation types, but did not differ significantly between sites with anthropogenic riparian vegetation and sites with natural riparian vegetation.

Discussion

Our large-scale study is the first one to document spatial variation in the species richness of odonate assemblages in Haiti. It allowed us to confirm the presence-absence of 84.5% of all previously reported species for the country (Meurgey 2013) at 67 sites covering approximately 50% of the country's watersheds. Although our sampling effort varied between sites, due to local circumstances, sampling coverage was reasonably high at each site, allowing statistical comparison of species richness and contributions to β diversity. Overall, our results show that species replacement and geographic distances jointly explain the geographic pattern of β -diversity of odonates in Haiti.

The observed relative proportions of the different odonate families were consistent with their known levels of speciation on Hispaniola, with a large predominance of Libellulidae (Perez-Gelabert 2008). Interestingly, we found a relatively high percentage (69.4%) of rare species, i.e. occurring in 10% or less of sampled water bodies. In the absence of similar surveys of odonates in Haiti in the past, it is difficult to determine whether this indicates a recent decline in the abundance and spatial distribution of some species, reflects natural interspecific differences in habitat requirements, or results from incomplete sampling of watersheds. However, this value actually compares very well with recent data reported for the Pampa biome in southern Brazil, where, similarly, about 70% of Odonate species occurred in <10% of the water bodies (Renner et al. 2020; see also Maltchik et al. 2010). Increasing the number of sampled watersheds in the future may provide a better assessment of the proportions of “rare” odonate species in Haiti. The five most unique species were *Hypolestes hatuey*, *Gynacantha nervosa*, *Rhionaeschna psilus*, *Phylolestes ethelae*, and *Anax amazili*, all occurring at only one or two sites.

SCBD, the relative importance of each species in affecting β diversity (Legendre and De Cáceres 2013), showed a relatively large variation between species, as assessed by the quartile coefficient of dispersion (Botta-Dukát 2023). SCBD was positively and tightly correlated with site occupancy, with the first 10 species contributing to 50% of total β diversity being recorded in at least 14 different sites. In contrast, De et al. (2023) reported that odonate species with highest SCBD values had only intermediate levels of spatial occupancy in a survey of 27 sites along the banks of the Ganga River in India. The most ubiquitous species in our survey was the damselfly *Ischnura ramburii* (Rambur's Forktail), found at 39 sites, predominantly in lotic sites (58.2%). This species is particularly widespread throughout the New World up to northern Chile, and on all of the Caribbean islands (Flint et al. 2006, McTavish et al. 2012). Its presence in the Dominican Republic has been reported from river banks, ponds, and ditches, including in poor-quality waters (Flint et al. 2006). The second most ubiquitous species, the dragonfly *Orthemis macrostigma* (Antillean Skimmer), was found at 36 sites, predominantly in lentic ones (61.1%). This is consistent with observations in the French Antilles where the species is mainly found and reproduces in lentic habitats, including natural and artificial ponds, as well as brackish and polluted waters, but can also exploit lotic ones (Meurgey and Daigle 2007). Almost all ubiquitous species with high SCBD values belonged to the Coenagrionidae and Libellulidae families, which are known to have large dispersal abilities and wide distributions (Kalkman and Orr 2012, Sánchez-Herrera and Ware 2012, Rangel-Sánchez et al. 2018). In contrast, the only two species of conservation interest, *P. ethelae* and *H. hatuey*, contributed little to β diversity, with SCBD values in the lowest quartile of the distribution, and had very restricted distributions.

LCBD provides a measure of the originality of the sampled sites, with a large contribution to β indicating that the site contains a set of species that is markedly different from the overall species pool (Legendre and De Cáceres 2013). In fact, LCBD showed little variation among sites as indicated by the value of the quartile coefficient of dispersion. Furthermore, permutation tests showed that no site contributed significantly to β diversity, after correction for multiple testing. This suggests that no site was particularly original in terms of assemblage composition and that all sites contributed approximately equally to global diversity. However, multiple comparison procedures tend to be highly conservative and increase the number of false rejections of true hypotheses as the number of hypotheses tested increases (Pike 2011). In our case, with 67 different sites in our sample, the lowest observed probability value for LCBD (0.004) was well above the

adjusted rejection threshold (0.0007). Nevertheless, we observed a significant negative relationship between LCBD and species richness, suggesting that the relative uniqueness of species composition is most often associated to a small number of species (Legendre and De Cáceres 2013), confirming previous results for aquatic insect assemblages (Heino and Grönroos 2017), including odonates (De et al. 2023). In addition, LCBD decreased with increasing taxonomic diversity of assemblages, whereas it increased with increasing mean species uniqueness (as indicated by positive associations with and both RTD and Mean U), suggesting that site contribution to β diversity is somewhat sensitive to the most taxonomically distinctive species located in species-poor sites. This was largely reflected in the PCA ordination of sites, with LCBD having moderate contributions to both PC1 and PC2. The information gained from considering SR, RTD, Mean U and LCBD was largely corroborated by the partitioning of total dissimilarity (BD_{total}) into nestedness and species replacement, with the latter accounting for about two-thirds of BD_{total} . This suggests that differences in assemblage composition between sites are mainly due to species replacement, while only a few sites had assemblages consisting in a subset of larger assemblages found at other sites. The observed positive correlation between dissimilarity and geographic distance between sites further suggests that the species turnover may occur over some ecological gradient and/or may be explained by species ecological requirements and limited ability to disperse.

Environmental factors had significant but contrasted effects on SR, RTD, Mean U, and LCBD. Both LCBD and Mean U increased with PC1 representing increasing altitude and decreasing temperature and conductivity, whereas SR and RTD did not. Recorded temperatures varied between 17 and 27°C during our study, and decreased with increasing altitude, as did conductivity, known to vary linearly with altitude in the range of environmental temperatures such as recorded in the present study (Hayashi 2004). The significant association between LCBD and PC1 is likely due to the fact that 100% of the nine sites > 1000 m had LCBD values above the median, compared to only 43.1% of the 58 sites < 500m. In addition, five species (10.2%), including the only representatives of two families (28.6%), Hypolestidae and Synlestidae, were found only above 1000m. Most sites above 1000m were located in forested areas, where the assemblage composition of tropical odonate species has been reported to differ markedly from that observed in open habitats (Bota-Sierra et al. 2021), thus explaining the correlation between Mean U and PC1. On the other hand, RTD was not correlated to PC1, indicating that taxonomic diversity

was not influenced by altitude, contrary to what has been observed along a more regular altitudinal gradient in the Sierra de Coalcomán Mountains in Michoacán State, Mexico (Campbell et al. 2010). Similarly, SR was not correlated with PC1, and hence altitude, conductivity and temperature, as found for odonate assemblages in both subtropical (Maltchik et al. 2010) and temperate areas (Ceia-Hasse et al. 2023). The absence of significant correlations between all indices with pH may be due to the fact that it tended to be neutral and varied little between sites, ranging from 6.3 to 7.7, compared to studies reporting an effect of acidification on odonate community structure (Frolich Strong and Robinson 2004, see however Arrowmith et al. 2018).

Overall, species richness and taxonomic diversity of odonates were higher in lotic environments compared to lentic ones. This contrasts with what has been reported from temperate areas, where odonate species diversity tends to be higher in lentic habitats compared to lotic ones (Pires et al. 2013, Worthen and Chamlee 2020), possibly as the result of higher colonization rates at lentic sites (Hof et al. 2006). On the other hand, it is comparable to what has been reported from another tropical area (Koneri et al. 2022). However, comparisons with previous studies are difficult, because both the number of lotic and lentic sites surveyed and the number of genera and species recorded can vary considerably. For instance, Vilela et al. (2016) reported higher diversity of odonates in lentic sites compared to lotic ones, based on the distribution of 31 species and 21 genera at only four ponds and one stream located in the Cerrado Neotropical Savanna, southern Brazil. Therefore, a greater coverage of both lotic and lentic sites in Haiti, particularly over a larger and more continuous range of elevations, would help to better assess variation in taxonomic diversity between running and stagnant waters.

Vegetation type had a strong and relatively consistent effect on odonate assemblage composition in our study, with higher median values of richness and distinctiveness in sites with natural riparian vegetation and lowest ones in sites anthropogenic riparian vegetation, confirming previous findings (Harabiš 2016, Huikkonen et al. 2020, Worthen and Chamlee 2020, Worthen et al. 2021). This might be explained by the fact that, not surprisingly, natural vegetation was more diversified than mixed and anthropogenic vegetation, thus offering opportunities for perching (May and Baird 2002), oviposition for a wider range of species, including both enophytic (Zygoptera and Aeshnidae) or epiphytic (some Libellulidae) species. In addition, the generally high diversity of natural plant species in tropical regions (Covich 1988) directly contributes to the

abundance and diversity of associated macroinvertebrate species (Motomori et al. 2001, Leroy and Marks 2006), on which the different developmental stages of odonate larvae can feed (Jara 2014).

Although taxonomic diversity may be less informative about aquatic ecosystem processes than functional diversity (Modiba et al. 2017), it is an essential indicator of the quality and conservation value of aquatic ecosystems (Vianna and De Marco 2012, Miguel et al. 2017, Vilenica et al. 2022). From this point of view, our results confirm the importance of mountainous areas of Hispaniola for the conservation of endemic odonate species (Paulson 2004). In particular, the endemic and endangered Hispaniolan Malachite was only found at two forested sites, above 1000m. This species is the unique representative of the monotypic genus *Phylolestes*. According to the IUCN Red List, it has a very limited and fragmented distribution, with fluctuations in its areas of occurrence and occupancy, along with a decline in the quality of its habitat. Indeed, although a large part of the La Selle Ridge, where we observed the species, is officially protected, the area is suffering from severe deforestation due to logging, slash and burn agriculture, and livestock (Exantus and Cézilly 2023). Preserving streams and ponds in this area therefore appears to be a priority for conservation. More broadly, our results indicate that preserving natural riparian vegetation along streams is of high importance for the maintaining the diversity of odonate assemblages in Haiti. They also indicate that β diversity is of limited interest in conservation site selection (see also Rocha et al. 2023), at least for odonates in Haiti, as species of highest conservation interest had low SCBD values and were not found at sites with high LCBD values. In that respect, mean species uniqueness per site may provide a more relevant index of conservation value, taking into account both taxonomic distinctness and species ubiquity.

This first detailed study of odonate assemblages in Haiti has, however, some limitations. First, we covered only about 50% of all Haitian watersheds, so a more complete survey may provide additional and useful information, particularly on the distribution of species known for Haiti but that we did not observe at our sampled sites. Second, our assessment of spatial occupancy and taxonomic diversity was exclusively based on adult stages, whereas consideration of other developmental stages may provide a more balanced view of the conservation value of different sites (Giulagnio et al. 2012, Khelifa 2019). In particular, the focus on adults may explain the underrepresentation of certain Gomphidae, particularly riverine species like *Progomphus* spp. for which sampling exuviae is more efficient (Sánchez-Rosario and Bastardo 2021). However, sampling exuviae is difficult because the emergence of odonate is not necessarily synchronous

under tropical climate conditions prevailing in the Greater Antilles (Trapero-Quintana and Reyes-Tur 2017). More to the point, searching for exuviae and larvae, and identifying them at the species level, can be particularly time-consuming and is not necessarily a better alternative to sampling adults (Bried et al. 2012), especially in the harsh conditions we experienced during our survey. Third, because data collection was restricted to morning and early afternoon, some species might have been under-sampled in the present study, such as *Gynathanca nervosa* that is supposedly mainly active at dawn and dusk (Williams 1937). However, all our observations of the species were made between 10:55 and 14:10. Fourth, most sites were sampled on only once, whereas a long-term survey may be more relevant (Dolný et al. 2021). Nevertheless, given the very limited information on the spatial distribution of odonates in Haiti, we consider the present study as a first and important step towards the implementation of a larger and conservation-oriented monitoring program of odonates in Haiti. Such a program is particularly important for Haiti where information on the health and conservation value of freshwater ecosystems is particularly scarce. Indeed, odonates are particularly suitable indicators of aquatic ecosystems (de Oliveira-Junior et al. 2017, Kemabonta et al. 2017). In addition, their role as predators can be particularly important to regulate vectors like mosquitoes (Faithpraise et al. 2014), such as *Anopheles albimanus*, the main vector of *Plasmodium falciparum* responsible for more than 99% of human malaria cases in Haiti (Jules et al. 2022). However, the feasibility of such a monitoring program critically depends on the ability of the Haitian state and international organizations to develop and support research in entomology and conservation biology based on local expertise, which implies substantial investment in academic training and the development of relevant facilities (Vallès et al. 2021).

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Credit authorship contribution statement

Pierre Michard Beaujour: was involved in study design and methodology, data collection, part of statistical analysis, and writing up of the article.

Gladys Loranger-Merciris: was involved in supervision, project administration, and revision of the article.

Frank Cézilly: was involved in study design, supervision, project administration, statistical analysis and writing up of the article.

Declaration of Interest

The authors report no competing interest.

Data Availability

Data will be made available on request.

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Annexe A

List of the 67 study sites with their main characteristics (Type: P = permanent pond, R = river, T = Temporary pond; Flow: RW = running water, SW = stagnant water; Veg = Vegetation Types).

N	Site	Type	Watershed	Latitude	Longitude	Altitude (m)	Flow	Vegetation
		R		18,64	74,306		R	A
1	La Passe, Abricot		Jérémie/Les Irois	661	82	12	W	V

		T		-			
	Sancle, Anse du Clerc,		18,64	74,280			M
2	Jérémie	Jérémie/Les Irois	315	89	54	SW	V
		R		-			
			18,65	74,243			R N
3	Rivye Bonbon	Roseaux/Voldroque	25	36	30	W	V
		P		-			
			18,64	74,214			A
4	Grand site	Jérémie/Les Irois	41	53	236	SW	V
		T		-			
			18,58	74,222			A
5	Mare Mafran	Grande Anse	085	09	34	SW	V
		P		-			
			18,55	74,276			A
6	Abricot, Moron	Grande Anse	688	48	64	SW	V
		P		-			
			18,55	74,281			A
7	Sal mahotièrè, Moron	Grande Anse	717	29	61	SW	V
		R		-			
			18,55	74,317			R A
8	Chambellan	Grande Anse	068	02	66	W	V
		R		-			
			18,60	74,032			R A
9	Rivière Roseaux	Corail/Anse à Veau	114	71	10	W	V
		T		-			
1			18,56	73,913			M
0	Riziere Corail	Corail/Anse à Veau	15	02	302	SW	V
		P		-			
1			18,54	73,882			M
1	Sireyon Pestel	Corail/Anse à Veau	378	22	336	SW	V
		T		-			
1			18,52	73,795			A
2	Mare Pestel	Corail/Anse à Veau	029	09	254	SW	V

		P		-			
1				18,30	73,827		M
3	Etang La droite		Cayes	517	32	126	SW V
		P			-		
1				18,30	73,827		M
4	Etang Lapointe		Cayes	502	24	126	SW V
		R			-		
1				18,30	73,847		R N
5	Courant Lasho		Cayes	65	99	171	W V
		R			-		
1				18,29	73,800		R N
6	Rivière Labaud		Cayes	818	49	97	W V
		P			-		
1				18,15	73,808		A
7	Etang Bamboula Cayes		Cayes	93	52	5	SW V
		T			-		
1				18,15	73,811		A
8	Rizière Torbeck		Cayes	888	61	4	SW V
		T			-		
1			Pte. Riv. de	18,43	73,402		M
9	Arnaud		Nippes/Grd. Goâve	781	75	133	SW V
		P			-		
2			Pte. Riv. de	18,47	73,354		M
0	Blanche		Nippes/Grd. Goâve	705	13	29	SW V
		P			-		
2			Pte. Riv. de	18,46	73,306		M
1	Gras étang		Nippes/Grd. Goâve	378	97	9	SW V
		P			-		
2			Pte. Riv. de	18,46	73,294		M
2	Lac Froide		Nippes/Grd. Goâve	221	22	22	SW V
		P			-		
2			Pte. Riv. de	18,47	73,247		A
3	Turin		Nippes/Grd. Goâve	702	82	18	SW V

		P		-			
2			Pte. Riv. de	18,46	73,238		N
4	Tintriye		Nippes/Grd. Goâve	849	94	0	SW V
		T			-		
2			Pte. Riv. de	18,46	73,226		M
5	Dupa		Nippes/Grd. Goâve	864	49	16	SW V
		R			-		
2			Pte. Riv. de	18,47	73,227		R M
6	Rivière St Sauveur		Nippes/Grd. Goâve	828	2	16	W V
		T			-		
2			Pte. Riv. de	18,47	73,190		M
7	Chalier		Nippes/Grd. Goâve	997	09	16	SW V
		R			-		
2			Pte. Riv. de	18,43	73,059		R N
8	Nan gode		Nippes/Grd. Goâve	316	3	18	W V
		P			-		
2	Dufou, Etang de		Pte. Riv. de	18,39	73,072		M
9	Miragoane		Nippes/Grd. Goâve	24	46	24	SW V
		R			-		
3			Pte. Riv. de	18,38	73,065		R N
0	Rive de Miragoane		Nippes/Grd. Goâve	74	64	52	W V
		R			-		
3				18,44	72,307		R N
1	Momance		Cul-de-Sac	934	8	1425	W V
		R			-		
3				18,45	72,302		R N
2	Kens Viard		Cul-de-Sac	535	79	1223	W V
		T			-		
3				18,45	72,289		M
3	Riv Froide		Cul-de-Sac	731	08	1263	SW V
		P			-		
3				18,45	72,271		M
4	Grise amont 1		Cul-de-Sac	406	56	1274	SW V

		R		-			
3				18,43	72,297		R M
5	Froide Pagnol		Cul-de-Sac	894	36	1501	W V
		T			-		
3				18,41	72,296		M
6	Grise aval 2		Cul-de-Sac	139	19	1398	SW V
		P			-		
3				18,39	72,296		M
7	Pierre Paul, Furcy		Cul-de-Sac	532	85	1515	SW V
		R			-		
3				18,34	72,269		R N
8	Parc la Visite Seguin		Cul-de-Sac	064	66	1923	W V
		R			-		
3				18,36	72,045		R M
9	Unite 2 Foret des Pins		Cul-de-Sac	058	24	1971	W V
		R			-		
4				18,57	72,246		R N
0	Grise Pl		Cul-de-Sac	986	37	61	W V
		P			-		
4				18,79	72,371		M
1	Mare Cabaret		Saint Marc/Cabaret	801	27	126	SW V
		T			-		
4				19,18	72,541		N
2	Artibonite		Artibonite	282	35	223	SW V
		P			-		
4			Bombardopolis/Gonai	19,44	72,698		N
3	Gonaives		ves	012	36	158	SW V
		P			-		
4			Môle St	19,45	72,683		PS M
4	Port-de-Paix		Nicolas/Moustique	605	02	98	W V
		T			-		
4				19,45	72,683		TS A
5	Rizière		La Quinte	605	02	167	W V

		T		-			
4			Môle St	19,79	72,988		TS A
6	Mon Bete, Port-de-Paix		Nicolas/Moustique	197	94	220	W V
		P			-		
4			Môle St	19,79	72,987		PS N
7	Lac Aines, Port-de-Paix		Nicolas/Moustique	668	83	229	W V
		P			-		
4	Lac bois Jean Louis,		Môle St	19,80	72,972		PS M
8	Port-de-Paix		Nicolas/Moustique	725	8	238	W V
		T			-		
4			Môle St	19,82	72,968		TS A
9	T2, Port-de-Paix		Nicolas/Moustique	813	22	182	W V
		P			-		
5	Lac Dupins, Port-de-		Môle St	19,83	72,953		PS N
0	Paix		Nicolas/Moustique	141	17	159	W V
		R			-		
5			Môle St	19,82	72,949		R N
1	Rivière, Port-de-Paix		Nicolas/Moustique	117	43	143	W V
		R			-		
5			Môle St	19,84	72,937		R M
2	Moue, Port-de-Paix		Nicolas/Moustique	019	24	90	W V
		T			-		
5			Môle St	19,93	72,876		TS M
3	T3, Port-de-Paix		Nicolas/Moustique	115	79	20	W V
		P			-		
5				19,42	72,171		PS N
4	Mare Hinche		Artibonite	253	8	389	W V
		R			-		
5				19,33	72,111		R N
5	Pignon amont		Artibonite	758	36	339	W V
		R			-		
5				19,33	72,114		R N
6	Pignon Aval		Artibonite	178	2	327	W V

		R		-			
5				19,23	72,027		R N
7	Rivière Hinquite		Artibonite	294	85	363	W V
		T			-		
5			Grande Rivière du	19,62	71,924		TS A
8	Mare Cap Haitien		Nord	901	49	46	W V
		R			-		
5			Limonade/Ouanamint	19,64	71,840		R N
9	Rivière Fort Liberte		he	639	04	10	W V
		T			-		
6	Mare Louisianne, Fort		Limonade/Ouanamint	19,64	71,838		TS A
0	Liberté		he	586	98	11	W V
		T			-		
6	Mare Collette, Fort		Limonade/Ouanamint	19,64	71,837		TS A
1	Liberté		he	353	13	9	W V
		T			-		
6	Mare Coicoux, Fort		Limonade/Ouanamint	19,64	71,835		TS M
2	Liberte		he	819	04	10	W V
		T			-		
6			Limonade/Ouanamint	19,63	71,838		TS A
3	Pont Collette		he	81	18	14	W V
		R			-		
6	Mission Derak, Fort		Limonade/Ouanamint	19,64	71,814		R N
4	Liberte		he	479	38	66	W V
		R			-		
6	Rivière Cite, Fort		Limonade/Ouanamint	19,66	71,841		R A
5	Liberte		he	746	44	88	W V
		T			-		
6			Limonade/Ouanamint	19,66	71,842		TS A
6	Mare Cite, Fort Liberte		he	817	33	12	W V
		R			-		
6	Rivière Labri, Fort		Limonade/Ouanamint	19,68	71,773		R N
7	Liberte		he	864	75	7	W V

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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