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An unavoidably short history of inland aquatic animal diversity research in the US Virgin Islands

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Abstract The first freshwater species from the US Virgin Islands (USVI) was described 190 years ago, but research on inland aquatic animals, particularly invertebrates, remains limited. Due to a complex history of European colonization in the Caribbean, natural history writings about inland aquatic diversity for the USVI began almost 250 years later than those from elsewhere. Those early writings were produced primarily by clergy and largely recorded indigenous knowledge from other islands. Proposed in the first natural history by West in 1793, and reinforced later by Ledru in 1810, an assumption emerged that Puerto Rico and USVI faunas were almost identical. This partially explains the paucity of work in almost all aquatic faunal groups but birds. We review the history of inland aquatic faunal observations and studies in the USVI, from pre-Columbian traditions to recent faunal assessments. We discuss the pivotal *Scientific Survey of Porto Rico and the Virgin Islands* and the importance of local and foreign naturalists and taxonomists for our understanding of aquatic biota. Since 1900, 155 articles included observations on USVI inland aquatic animals, without clear trends toward increased or decreased publication output since the 1960s. Taxonomic bias toward studies on insects and birds, and geographic bias toward vertebrate work from St. Croix, are evident. Descriptive articles overwhelmingly outnumber manipulative ones. Despite overlap between USVI and Puerto Rican inland aquatic vertebrate faunas, recent surveys from St. Thomas have documented many new records and undescribed aquatic invertebrates. The historical assumption that the two faunas are equivalent appears to depend on taxonomic context. This hypothesis requires further evaluation.

Keywords Aquatic habitats · Caribbean islands · Freshwater fauna · Inland water · Species diversity surveys

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Introduction

Nested in the northern Leeward Islands of the Caribbean, east to southeast of Puerto Rico, the US Virgin Islands (USVI) territory is comprised of St. Thomas, St. John, and St. Croix, and multiple small inhabited or uninhabited islands. These Lesser Antilles sprawl between latitudes 17° 39′ 33″ and 17° 25′ 26″ North, and longitudes − 065° 05′ 56″ and − 064° 33′ 33″ West. As part of the historical "West Indies," and because of the importance of marine fisheries, the coastal marine biodiversity of the US Virgin Islands is relatively well characterized. From early natural history treatises conducted more than two centuries ago (West 1793; Ledru 1810), through comprehensive assessments of marine fish fauna starting in the 1900s (Nichols 1929, 1930; Fowler 1951; Randall 1963; Ogden et al. 1975; Clavijo et al. 1980; Gladfelter et al. 1980; Smith-Vaniz and Jelks 2014), to more modern assessments of coral reef community structure (Causey et al. 2000; Lang 2003; Rothenberger 2008; Smith et al. 2014; Rogers 2017; Blondeau et al. 2020), nearshore biodiversity studies continue to focus on this region of the Caribbean. The USVI are included in extensive monitoring efforts, such as the National Coral Reef Monitoring Program, managed by the US National Oceanographic and Atmospheric Administration (https://www.coris.noaa.gov/monitoring/). As a result, the biodiversity of key marine groups, such as corals and fishes, is continuously assessed within a long-term monitoring framework.

In stark contrast, very little is known about inland aquatic biodiversity of the US Virgin Islands (Platenberg 2006; Rogers and Cruz-Rivera 2021). Surface water availability in these islands is strongly influenced by seasonality, with a variable rainy season spanning from May through November and precipitation peaks in May, September, October and November (Bonnin et al. 2006; Mayor 2006; McNair et al. 2008; Martinez et al. 2019). Various permanent freshwater and saline ponds, and a handful of streams and springs occur in the USVI, but most of the lotic systems are seasonal storm drainage temporary creeks and streams locally known as ghuts or guts (Cosner and Bogart 1972; Platenberg 2006; Nemeth et al. 2007; Gardner 2008; Gardner et al. 2008; Heartsill-Scalley 2012). Although a few of these aquatic environments contain some water year round, their volume fluctuates dramatically between rainy and dry months; periodically, most dry out completely. Lentic environments range from temporary freshwater shallow depressions that may dry out seasonally, through permanent freshwater ponds or wetlands that contain some water all the time, to brackish, saline, or hypersaline ponds that may or may not completely dry out depending on their interaction with ground water, mangrove channels, or tidal inundation (Platenberg 2006; Gardner et al. 2008; Rogers and Cruz-Rivera 2021). Phytotelmata are abundant, particularly native and introduced "tank bromeliads" that are commonly used in landscaping (Miller 1970, 1971). Alterations of watershed structure and water demands for consumption and agriculture have influenced most of these environments over the past century, and some ghuts and ponds have virtually disappeared (Chase and Hobbs 1969; Johnston 1981; Platenberg 2006; Gardner 2008; Heartsill-Scalley 2012).

Prehistoric use of inland water resources and early names

Access to surface freshwater sources was a central element for the establishment of early tribal American settlements (Jazwa et al. 2016; Prufer et al. 2017; see also Sivapalan et al. 2012). Humans first moved to the Caribbean islands about 6000 B.C. (Wilson 2007). For millennia, the pre-Arawak peoples discovered and colonized the Antilles forming a metapopulation of relatively small, diverse but interconnected groups across islands (Wilson 2007; Rodríguez Ramos 2019; Fernandes et al. 2021). The earliest settlements in the US Virgin Islands have been dated to about 1000 B.C., although similarities between artifacts excavated in Krum Bay, St. Thomas, and those from St. Kitts dated 2090–2210 B.C., suggest a much older colonization period (Bullen and Sleight 1963; Wilson 2007; Keegan and Hofman 2017).

Although there are no cultural artifacts explicitly[1] depicting freshwater or mangrove species in the Virgin Islands from pre-Columbian times (de Booy 1919; Hayward et al. 2009), excavations of local archaeological sites (Wetmore 1937; Righter and

[1] Hayward et al. (2003) refer to a "frog with a human-like face, a grouping of partial faces, and a verbal description of an anthropomorphic figure" as part of the petroglyphs found in the Salt River, St. Croix.

Lundberg 1991; Quitmyer 2003) and cultural representations from other Caribbean islands show a clear awareness and utilization of inland water invertebrate and vertebrate fauna. Wetmore (1937) identified bones of two heron species, two duck species, flamingos, the purple gallinule and a goose, from a kitchen midden in Concordia, St. Croix, presumed to be of pre-Columbian origin. Quitmyer (2003) identified the animal remains in middens dated between 460 and 950 CE from Cinnabon Bay, St. John. Vertebrate animal remains from inland aquatic species included herons (Ardeidae), purple gallinule [*Porphyrio martinica* (Linnaeus, 1766)], and presumably a freshwater turtle (*Trachemys* sp.).[2] Invertebrates found included the freshwater neritid snail *Vitta virginea* (Linnaeus 1758), an unidentified neritid species (possibly *Nereina punctulata* (Lamarck, 1816), which is known from the Virgin Islands [Rogers and Cruz-Rivera, 2021]), swimming crabs (*Callinectes* spp.), the hermit crab *Coenobita clypeatus* (Fabricius, 1787), and semi-aquatic[3] crabs (Gecarcinidae). Gecarcinid crabs have also been found in archaeological sites from St. Thomas (Righter and Lundberg 1991), and their relative use in human maintenance diets has been used as one criterion contrasting Saladoid and Ostionoid periods in Puerto Rico (Carlson and Keegan 2004).

Outside of the US Virgin Islands, amphibians are well represented throughout the prehistoric Caribbean in carved pendants, pottery, and rock art, predating Taino culture and continuing within it (Flaherty Frassetto 1960; Rodríguez Ramos 2007; Waldron 2011; Martínez Palmer 2017). Coquí tree frogs (*Eleutherodactylus coqui* Thomas, 1966 and *E. portoricensis* Schmidt, 1927) and other Caribbean endemic taxa, such as other *Eleutherodactylus* spp. and the widespread Caribbean white-lipped frog, *Leptodactylus albilabris* (Günther, 1859), are explicitly or implicitly represented in the mythology and art of multiple pre-Columbian Caribbean groups (Robiou Lamarche 2006; Atkinson 2008; Oliver 2008; Hayward et al. 2009; Martínez Palmer 2017). For example, the Taino word *tona* is a generic term for frogs and originates from a myth in which children transformed into frogs after a deity tricked their mothers and took them away (Pané 1498, reprinted 2020). The word is a disambiguation of the word for mother, *toa*, and refers to the cries of the children calling for their mothers as they became hungry, cries now represented by the calls of different species of Caribbean eleutherodactylid and leptodactylid frogs. These species, however, are different than the two named by the onomatopoeic Taino word *cokí*. Although now the word is a common name in Spanish (*coquí*) to designate Antillean species of the genus *Eleutherodactylus*, for the Taino it referred to two species with similar vocalizations (Table 1). Oliver (2008) proposes that the Taino people related the egg-laying behavior of Caribbean tree frogs to both weather and fertility. He argues that a phenomenon seen in tropical rain forests, where frogs jump off tree leaves to puddles in a sort of "frog rain" during seasonal rainfalls, promoted the mythology connecting the frogs as crying children, the onset of the rainy season, and symbols of fertility. In fact, petroglyphs and artifacts of humanoid figures with (seemingly) frog limbs have often been interpreted as representations of *Atabey* (= *Atabeira*, *Atabex*), the Taino Goddess of the Earth and Mother of the Waters (Arrom 1989; Saunders 2005; Robiou Lamarche 2006; Oliver 2008). Other freshwater dwelling species may have had ritualistic significance as well. The abundance of claws from the freshwater crab *Epilobocera sinuatifrons* (Milne-Edwards 1866), *buruquena* in Taino, in a funerary cave from Puerto Rico has been interpreted as a sign of consumption of this species as part of funerary ceremonies (Oliver and Narganes Storde 2005).

However intertwined with mythology some inland aquatic animals may be, it is in the surviving knowledge of the Taino language that the attention to Caribbean aquatic species is observed. While it is known that different native Caribbean populations spoke unique languages (Granberry 2012), they also interacted through a complex commercial and cultural network across islands and coastlines (Wilson 2007; Laffoon et al. 2014; Rodríguez Ramos 2019). Granberry (2012) explains that between 1 and 500 A.D., a language of Arawak origin, the "classic" Taino, emerges as *lingua franca* in the Caribbean,

[2] Although there is a native species of this freshwater turtle genus in Puerto Rico, the only species in the USVI is introduced (Platenberg 2007; Turtle Taxonomy Working Group 2021). If correct, his zooarchaeological record suggests the animal was brought from outside of St. John.

[3] Gecarcinid crabs are largely referred to as "land" crabs. However, they depend intimately on inland waters for maintenance and reproduction.

Table 1 Taino words used for naming inland aquatic species and their approximated or known scientific name. An "*X*" on the last column indicates that species is native to the US Virgin Islands (USVI). Sources: Coll y Toste (1972), de las Casas (1967), Miner Solá (2008), Manicato Taíno Cultural Center of Lancaster (2016)

Taino word	Type of animal	Scientific name(s)	Taxon	USVI
Burukena (buruquena)	Freshwater crab	*Epilobocera sinuatifrons* (A. Milne-Edwards, 1866)	Arthropoda: Crustacea	X
Cobo[a]	Land hermit crab	*Coenobita clypeatus* (J. C. Fabricius, 1787)	Arthropoda: Crustacea	X
Guábara[b]	Freshwater shrimp	*Atya* spp.	Arthropoda: Crustacea	X
Jaiba[2]	Swimming crab	*Callinectes* spp.	Arthropoda: Crustacea	X
Juey	Land crab	*Cardisoma guanhumi* Latreille, 1852	Arthropoda: Crustacea	X
Corasí[2]	Mosquito	Culicidae	Arthropoda: Insecta	X
Jején[2]	Biting midge	*Culicoides* spp.	Arthropoda: Insecta	X
Mabiche[c]	Mosquito	Culicidae	Arthropoda: Insecta	
Area	White mullet	*Mugil curema* Valenciennes, 1836	Chordata: Actinopterygii	X
Dajao (dahao)	Mountain mullet	*Agonostomus monticola* (Bancroft, 1834)	Chordata: Actinopterygii	X
Guabina	Bigmouth sleeper	*Gobiomorus dormitor* Lacepède, 1800	Chordata: Actinopterygii	X
Guabina	Guavina	*Guavina guavina* (Valenciennes, 1837)	Chordata: Actinopterygii	X
Mapiro/masaguán	Fat sleeper	*Dormitator maculatus* (Bloch, 1792)	Chordata: Actinopterygii	X
Saga[d]	River goby	*Awaous banana* (Valenciennes, 1837)	Chordata: Actinopterygii	X
Saje (çage)[e]	Unknown	Unknown	Chordata: Actinopterygii	
Setí/camiguana	Sirajo goby (larva)	*Sicydium* spp.	Chordata: Actinopterygii	X
Cokí (coquí)	Coqui tree frogs	*Eleutherodactylus coqui* Thomas, 1966; *E. portoricensis* Schmidt, 1927	Chordata: Amphibia	X
Maco/tona	Frog or toad	Undetermined, could refer to the Caribbean white-lipped frog, *Leptodactylus albilabris* (Günther, 1859), or other *Eleutherodactylus*	Chordata: Amphibia	X
Guanabá	Bitterns	*Botaurus lentiginosus* (Rackett, 1813), *Ixobrychus exilis* (Gmelin, 1789)	Chordata: Aves	X
Guanama/ guanana	Snow goose	*Anser caerulescens* (Linnaeus, 1758)	Chordata: Aves	
Guareao	Limpkin	*Aramus guarauna* (Linnaeus, 1766)	Chordata: Aves	
Guincho	Osprey	*Pandion haliaetus* (Linnaeus, 1758), *P. haliaetus ridgwayi* Maynard, 1887)	Chordata: Aves	X
Tigua	Least grebe	*Tachybaptus dominicus* (Linnaeus, 1766)	Chordata: Aves	X
Tujuy	Caribbean coot	*Fulica americana caribaea* Ridgway (1884)	Chordata: Aves	X
Yaboa	Night herons (Ardeidae)	*Nyctanassa violacea* (Linnaeus, 1758); *Nycticorax nycticorax* (Linnaeus, 1758)	Chordata: Aves	X

Table 1 continued

Taino word	Type of animal	Scientific name(s)	Taxon	USVI
Yaguasa	West Indian whistling duck	*Dendrocygna arborea* (Linnaeus, 1758)	Chordata: Aves	X
Caimán	Spectacled caiman; Cuban crocodile	*Caiman crocodilus* (Linnaeus, 1758); *Crocodylus rhombifer* (Cuvier, 1807)	Chordata: Reptilia	
Jicotea	Central Antillean slider	*Trachemys stejnegeri* (Schmidt 1928)[f]	Chordata: Reptilia	

[a]Miner Solá (2008) defines this word as designating the giant Caribbean hermit crab that uses queen conch shells *P. diogenes* (Linnaeus, 1758) and the queen conch itself, *A. gigas* (Linnaeus, 1758). Both are marine species. However, the word is also the common name for the iconic semiaquatic hermit crab *C. clypeatus* (J. C. Fabricius, 1787) in Puerto Rico. We include it here because its use can be traced to Taino vocabulary

[b]Miner Solá narrows the use of these Taino words to single species. However, that is unjustified because those species are often indistinguishable to the naked eye from other related animals that occupy similar niches sympatrically or allopatrically

[c]Miner Solá (2008) argues that this is a small coastal species distinct from both the corasí and jején

[d]Records of saga for St. Croix, Virgin Islands (Ogden et al. 1975; Clavijo et al. 1980) and Puerto Rico (Martin and Patus 1984) have been historically recorded as *A. tajasica* (Watson 1996), but this is a mistake; that species is from Brazil (Watson 1996; Smith-Vaniz and Jelks 2014)

[e]de las Casas (1551) writes that sajes are small edible freshwater fishes but provides no further description other than "delicious"

[f]There are various subspecies of this freshwater turtle in the Antilles. The name arguably applied to all of them

strengthening common regional themes that many historians use as markers to define these populations as Taino or "Tainized" (Rodríguez Ramos 2019). The Taino language had specific terms for different aquatic habitats, with the word *amá* meaning river, *nitabo* denoting a freshwater pond, *bibagua* a salt pond, and *jagüey* a shallow well (Coll y Toste 1972; Miner Solá 2008; Manicato Taíno Cultural Center of Lancaster 2016). The Taino names of over 130 rivers in Cuba, Dominican Republic, and Puerto Rico are also recorded. There are over 25 known Taino words that refer to either species of nonmarine aquatic animals or complexes of similarly related species (Coll y Toste 1972; Contreras Oyarzún 1998; Miner Solá 2008; Manicato Taíno Cultural Center of Lancaster 2016; Table 1). The names suggest some knowledge beyond general morphological tendencies of a taxon, but this must be contextualized. According to Miner Solá (2008), the Taino used the word *buruquena* (*burukena*) to identify the freshwater crab *Epilobocera sinuatifrons* but the word *jaiba* to identify swimming crabs (Portunidae) in the genus *Callinectes*, which live in more estuarine conditions but venture into rivers; *juey* was the word for the semiaquatic land crab *Cardisoma guanhummi* Latreille, 1852 (and still is in some countries). Similarly, the word *guábara* is still used in some Caribbean islands to refer to freshwater shrimp of the genus *Atya*, and not to the more abundant and larger clawed *Macrobrachium* spp. It is plausible that the Taino word *camarón* (Nin 2020) referred to the latter genus, but this is speculative because the word is broadly used for both marine and freshwater shrimp. Like any dead language, interpretations—especially those based on early explorer notes—must be used with caution. In his 1551 *Apologética Historia Sumaria*, Fray Bartolomé de las Casas (in O'Gorman 1967) refers to *lagostines* (not a Taino word) as a type of river shrimp, but he did not mention *guábara* or *camarón*. This may be a reflection of the local language spoken in the region of Hispaniola he was located (Granberry 2012). Casting some doubt on the interpretation of *jaiba*[4] as *Callinectes*, de las Casas (in O'Gorman 1967) speaks of these animals as found in streams and having burrows underwater, which *Callinectes* crabs do not excavate, and also as occurring in trees, which *Callinectes* do not climb.

[4] Spelled *xayba* in earlier editions.

The historical pairing of the term to a species may be a construct of its modern use. De las Casas admitted to being uncertain if the crabs from streams and trees were the same species and he made these observations in Hispaniola. Thus, he may have been referring to the river species *Epilobocera haytensis* Rathbun, 1893 or *Pseudothelphusa americana* DeSaussure, 1857 and the semiarboreal *Sesarma* species and *Aratus pisonii* (Milne-Edwards 1837). Whether the Taino referred to all these as *jaiba*, or whether *jaiba* and *buruquena* were terms for freshwater crabs in different islands, needs further clarification.

Certain Taino names were specific to particular life stages. *Setí* (*tetí* as spelled by de las Casas, 1551 in O'Gorman 1967) are the juveniles of the amphidromic sirajo goby, a complex of four species in the genus *Sicydium* (Engman et al. 2017), which seasonally swim up rivers in large schools (Erdman 1961; Engman et al. 2017). The name (sometimes also spelled cetí) is still used in some islands, where fishing of the small incoming gobies historically supported an artisanal fishery. In Puerto Rico, a festival was celebrated around these recruitment events, but is no longer. Taino names for wetland and inland aquatic birds also appear to show high specificity (Table 1). Taken together, it can be argued that the first assessments of inland aquatic biodiversity of the Caribbean came from Taino oral traditions. This information was not lost completely thanks to the contributions, albeit controversial at times, of figures such as Pedro Mártir de Anglería, Fray Ramón Pané, Fray Bartolomé de las Casas, and Gonzalo Fernánadez de Oviedo y Valdés, who chronicled the language, life and traditions of the native inhabitants during the Spanish takeover of the Antilles (Salas 1959; Contreras Oyarzún 1998; Asúa and French 2005; Robiou Lamarche 2006; Thompson 2010). Although most of the taxa in Table 1 are also native to the Virgin Islands, this explains why these Taino animal names are not used there, where the current official language is English, and the Spanish never had an extensive presence. Many of these terms are still the common names for several freshwater species in the Spanish speaking Antilles.

Colonization history of the Virgin Islands and early inland aquatic animal descriptions

Columbus' 1493 arrival on St. Croix was defined by conflict and Taino arrows wounding two of his men as they looked for drinking water. He named his landing site on the Salt River *Cabo de Flechas* (Cape of the Arrows) and left for Puerto Rico (Knox 1852). Over the following centuries, the Virgin Islands were recolonized—at times jointly, others sequentially—by Spain, Holland, England, the Knights of Malta, France, and Denmark (Knox 1852; Taylor 1888; Dookhan 1994). Consolidation of the archipelago under the same jurisdiction only happened (technically) twice throughout that period. Although Spain claimed the Virgin Islands following Columbus' landing, it never established more than outposts in St. Croix, which were lost and retaken after conflict or ceded to other expanding colonial powers. After a period of French control, the Danish purchased St. Croix and consolidated the Virgin Islands again under the same flag in 1733. They became the Danish West Indies. Almost two centuries later, annexation of the territory by the USA was officially concluded (1917). Understanding the production of early species descriptions, inventories, and natural history for the archipelago, or lack thereof, must acknowledge its links to this complex history of colonization.

Perhaps the most salient difference between the birth of aquatic natural history for the Virgin Islands compared to that of other Caribbean islands is the discrepant chronology. One of the explicit goals of the second voyage of Columbus was to convert native Americans to Christianity, whom he described as receptive to the Christian faith (Colón 2010; see also Johnson 1993; Black 1995; Prien 2013). Religious figures like Fray Ramón Pané and Fray Bartolomé de las Casas became key observers and chroniclers of the Taino culture, traditions, myths, and the natural world of the Caribbean. In the background of a brutal campaign of conquest and exploitation, Spanish clergy, in fact, were central to the documentation of the natural history, resources, and species diversity of Insular, Central, and South America (Thompson 2010; Prieto 2011). In tandem, the Renaissance established Natural History as a field of university study and an endeavor of royalty during the XVI century (de la Luz Ayala 2005; Eamon 2018). European courts hired naturalists and sponsored their expeditions around the

world. Within this cultural phenomenon, the most extensive early works compiling what was known of Caribbean species diversity focused on lands invaded by Spain and were written by Gonzalo Fernánadez de Oviedo y Valdés, tasked by Holy Roman Emperor Charles V (1516–1556), who named Oviedo the first Chronicler of the West Indies in 1532. Given the limited interest in the Virgin Islands by the Spanish Crown, early historians traveled to the Greater Antilles, where larger settlements had been established. Despite occasional Spanish excursions, the fauna and flora of the Virgin Islands remained ignored for the next 250 years.

Oviedo produced two comprehensive works introducing the culture, fauna and flora of the New World: *Sumario de la natural y general historia de las Indias* (1526) and the better known *Historia general y natural de las Indias, islas y tierra firme del Mar Océano* (1535). His *Sumario* described over 80 types of plants and animals, which were discussed mainly as one per chapter, but the very short chapters themselves were organized sequentially as implicit natural groups (i.e., mammals, birds, insects, reptiles, etc.). As noted above, the works of de las Casas, such as *Apologética Historia Sumaria*, contained many descriptions of plants and animals, but these were intertwined with an organic narrative of place, culture, geography, philosophy, and religion. In contrast, Oviedo's approach was detail-oriented and encyclopedic (Thompson 2010). The *Sumario* discussed a few aquatic and semiaquatic animals. For example, like de las Casas did when discussing the *jején* (biting midge, Table 1), Oviedo noted the relation between mosquito abundances and water bodies, stating "Mosquitos there are many and very annoying and of many forms, especially in some parts of the coast of the sea and of rivers, and also in many parts of the land there are none." (Fernández de Oviedo y Valdés, 1526, in Miranda 1950) (translated by EC-R). He also spoke of the relation between seasonal rains and frogs of various kinds and advised to not allow water to accumulate to be rid of these animals, which he clearly disliked for being ugly and noisy ("These frogs sing in three or four ways and none of them is placid.") (translated by EC-R). Interestingly, he also noted the inverse relation between the presence of frogs and land development for cattle, which he deemed "healthier and more peaceful." (Fernández de Oviedo y Valdés, 1526, in Miranda 1950) (translated by EC-R). Notably, Oviedo provides the first detailed description of the semiaquatic crab *Cardisoma guanhumi* Latreille, 1828 (Fernández de Oviedo y Valdés 1526, in Miranda 1950). His description of the asymmetric claws, rounded body, smooth carapace, number of limbs, whitish to bluish color, and burrowing habit leaves little doubt. Oviedo's following work, *Historia general y natural de las Indias*, was his *magnum opus*, but he only saw the first of three parts published before passing away in 1557. After spending 14 years working on a new version of part 1 (along with the other two parts), the corrected first part was finally published by the Royal Academy of History in Madrid in 1851, over 300 years after the first edition was released (Carrillo, 2002). The monumental collection included five books dedicated to botany and four dedicated to zoology, including book 13, dedicated to aquatic animals. Oviedo's work was controversial in his description of native inhabitants of the Caribbean, which was strongly criticized by de las Casas, who sought to stop the publication of the *Historia general* (de la Luz Ayala 2005). His species descriptions were at times inaccurate as well, by relying solely on memory (for the *Sumario*) and on second-hand accounts, albeit going to great lengths vetting his sources as reliable (Carrillo 2002; Prieto 2009; Thompson 2010). Nevertheless, his writings helped usher a natural history tradition based on firsthand experience and observation, and on highlighting the uniqueness of the American natural world rather than force fitting it to that of European texts and ancient treatises (Prieto 2009; Marroquín Arredondo 2015). Some of his organismal descriptions approached a quasitaxonomic detail, including those of some Caribbean inland aquatic animals (e.g., semiaquatic crabs), described from elsewhere, but present in the Virgin Islands.

Danish control of the Virgin Islands engendered one of the largest slave markets in the hemisphere (Hall 1992; Bendtsen 2016; Jensen and Simonsen 2016). A study by Sichler (2003) showed that plantation slaves (Cinnamon Bay cotton and sugar plantation) and freed slaves (East End) from St. John consumed some of same the inland aquatic species exploited by native Caribbean groups, although to a significantly lesser extent. Animal remains in these archaeological digs are overwhelmingly dominated by coral reef fish. However, in contrast to Taino sites, remains of brackish water fishes were also found.

Brackish water/tidal flat fishes from the Cinnamon Bay site accounted for 0.5% of identified animal specimens. The freshwater snails *Vitta virginea* and *Nereina punctulata* were also present and accounted for 2.4 and 0.5% of animals identified at Cinnamon Bay, respectively. At the East End Preserve, only *Nereina punctulata* was found, but it accounted for $< 0.1\%$ of individuals identified. Mistakenly, all snails found in this zooarchaeological study were classified as marine (Sichler 2003).

It was under Danish ruling that the first efforts to systematically catalogue the natural resources of the Virgin Islands occurred. In some respects, this is ironic, as most of the natural forest of the islands still standing after French occupation (Taylor 1888) was cleared by the Danish to develop agriculture (Hatch 1972; Tyson 1987; Power 2011). Additionally, as thought by Europeans at the time, both the French and Danish believed bouts of tropical diseases, such as malaria, that claimed the lives of some of their men were caused by breathing "poisonous" forest air carrying noxious soil particles (Taylor 1888; Power 2011). Their solution was to burn the forest down. The first comprehensive inventory of species in the Danish West Indies was compiled by botanist and school headmaster Hans West (1793) on St. Croix. His observations included marine, terrestrial, and freshwater taxa. He catalogued two bird species, 11 reptiles, 36 fish, and 37 invertebrates from St. Croix, of which both birds and mosquitos were inland water species. West (1793) only provided a couple plant names for St. Thomas and no taxa for St. John, giving his opinion that the faunas and floras were all similar.

From 1796 to 1798, a French expedition to Tenerife, Puerto Rico, St. Thomas, and St. Croix, captained by Nicolas-Thomas Baudin, culminated with an official multivolume report by André-Pierre Ledru a decade later (Ledru 1810). This was the first European expedition to collect specimens from the Virgin Islands (Jansen and Fuchs 2019). Chapter XIX of the collection was devoted to the natural history of the two Virgin Islands visited. Although notes on geography, freshwater bodies, and water use are scattered among various chapters, only terrestrial and marine species are included in chapter XIX. In it, a list of 18 vertebrates (birds and turtles) and 27 arthropods (insects and arachnids) was provided. While some of these are now understood as morphotypes of the same taxon (e.g., two stages of the green turtle *Chelonia mydas* were treated as separate species), Ledru (1810) included scientific names with authorities for almost all of these records; only eight parasitoid wasps, which he concluded were species in the genus *Sphex*, were added as unidentified. Despite not treating it as such, Ledru (1810) provided the first faunal longitudinal comparison for the Virgin Islands. Reptiles other than turtles, along with many other vertebrate and invertebrate taxa, had been annotated earlier by West (1793) and Ledru built upon that work. Interestingly, he did list aquatic birds, amphibians, and aquatic invertebrates, such as *Culex* mosquitos, in chapter XXVIII—devoted to the natural history of Puerto Rico—but he failed to directly link these records to species found in St. Thomas and St. Croix, despite suggesting he would do so. Ledru's species list for the Virgin Islands was purposely incomplete, and he succinctly justified this by summarizing the consensus at the time:

> "The researches of Doctor West, the historian of the Danish colonies in the West Indies, compared to those that we have made ourselves in Saint-Thomas, Sainte-Croix and Porto-Ricco, prove that lizards, snakes, fish, molluscs, crustaceans, arachnids, radials, and polyps, are nearly the same in these islands very close to each other: thus, to avoid unnecessary repetitions, we will deal with these animals in the chapter on the natural history of Porto-Ricco" (Ledru 1810, ch. XIX, pp. 44, translated by EC-R).

We propose that this viewpoint has dominated more than two centuries of biogeographical studies in the Caribbean and has likely contributed to an overall scarcity of faunal studies devoted to the USVI, especially for freshwater organisms (Platenberg 2006). As a result, nearby Puerto Rico, admittedly a larger and more landscape diverse island, has been a main focus of species diversity studies in the region, while St. Thomas, St. John, and St. Croix faunal diversity has been assumed as "covered" by that research. The historical inertia of Ledru's assessment (Ledru 1810) is particularly curious when one considers that 18% of the species provided by his account were named after their discovery in either St. Thomas or St. Croix.

Complicating the development of a reliable natural history framework for the Virgin Islands, are two

comprehensive books devoted to the history and (to a smaller extent) natural history of the Danish West Indies, and published decades later (Knox 1852; Taylor 1888). These works fail to mention the contributions of West (1793) (limited though they were) and Ledru (1810) to the zoological knowledge of the territory. In 1852, Reverend John P. Knox, Pastor of the Reformed Dutch Church of St. Thomas, published his impressively titled *A Historical Account of St. Thomas, WI: With Its Rise and Progress in Commerce; Missions and Churches; Climate and Its Adaptation to Invalids; Geological Structure; Natural History, and Botany; and Incidental Notices of St. Croix and St. Johns; Slave Insurrections in These Islands; Emancipation and Present Condition of Laboring Classes*. His section on the zoology of St. Thomas begins by stating: "On this subject we can only be general, as no naturalist has yet fully investigated the animated nature of the island and we are not competent to the task." Either the pastor was unaware of the existing species accounts published by the two earlier naturalists, one of whom explicitly documented St. Thomas' fauna, or purposely dismissed them. Knox (1852) described animals largely by using common names (mosquito, sugar ant, scorpion, etc.) but used contemporary scientific names for the jigger (chigoe flea) and several birds. The only inland aquatic species listed are birds, such as the vaguely defined ducks, plovers, and kingfishers, but the green heron is identified by its binomial (*Ardea viridus*; now *Butorides virescens* (L., 1758)). Taylor (1888) expanded upon Knox (1852) in his *Leaflets from the Danish West Indies: Descriptive of the Social, Political, and Commercial Condition of These Islands*. His Chapter XXXI, dedicated to zoology, describes various terrestrial animals covered by Knox (1852) in similar general terms (often plagiarizing); however, he makes a more consistent use of scientific names for these animals. Taylor (1888) also credits and quotes Knox (1852) *verbatim* when discussing birds. However, Taylor's summary also encompasses additional insects and arachnids not covered by Rev. Knox, plus crustaceans, fishes, echinoderms, sea and land turtles, mollusks, and domestic animals. Several species are illustrated as well. In total, Taylor (1888) mentions 68 taxa, of which 22 are identified at least by genera. Inland aquatic species, in addition to those birds quoted from Knox (1852), included mosquitos ("*Culex musca*"), biting midges ("*Simulia pertinax*"), semiaquatic (land) crabs, and eels. Curiously, Taylor was aware of Ledru (1810), but he only mentions that author in reference to a type of dance brought by slaves into the islands (Taylor 1888, p. 62).

The first true taxonomic description of an inland aquatic species from the US Virgin Islands was the shorefly (Hexapoda: Ephydridae) *Paralimna thomae* (Wiedemann 1830) (as *Ephydra*) (Ale-Rocha and Mathis, 2015), named eponymously from its collection in St. Thomas (labelled; 'Isle S. Thomas'), although an exact location was not provided. It will not be until the late 1800s and early 1900s that freshwater invertebrates from the US Virgin Islands are catalogued and taxonomically reviewed as part of biogeographical surveys of the West Indies. Such was the case for freshwater snails (Simpson 1895), ostracods (Brady 1902), mosquitos (Dyar and Knab 1906; Dyar 1920), aquatic beetles (Leng and Mutchler 1914; 1917), and shoreflies (Cresson 1916). The first observations on inland aquatic birds also originate from this period (e.g., Newton and Newton 1859; Ridgway 1884; Cory 1886, 1887, 1888). Similar to the case with inland aquatic fauna, the flora was first assessed under Danish control of the territory in the late 1760s by Gesch Oldendorp, followed by only a handful of collections until the late 19th and early twentieth century (e.g., Knox 1852; Eggers 1879; Millspaugh 1902; Britton 1918). Acevedo-Rodríguez (1996) provides a comprehensive account of these pioneering botanical studies. Although Knox (1852) included several mangroves and algae that can potentially occur in brackish channels of St. Thomas, he only listed the species names without stating locations or habitats. The first exhaustive work providing unequivocal information on aquatic plants was Eggers (1879). His monograph listed 31 plant species obligately or facultatively associated with ghuts (what he called rivulets) and ponds of St. Thomas, St. John, St. Croix, and Water Island. Of relevance to inland aquatic animals also, that work listed eight bromeliads, most capable of developing phytotelmata (see Greeney 2001; Frank and Lounibos 1983, 2009). The inland aquatic flora of the Virgin Islands needs reviewing, especially the freshwater algae, and we encourage botanists, phycologists, and biogeographers to address this knowledge gap.

The first comprehensive biodiversity assessment for the USVI and beyond

The end of the Spanish-American War ceded control of Puerto Rico to the USA in 1898 under the Treaty of Paris. In 1917, the Virgin Islands were officially transferred to the jurisdiction of the USA after their purchase was formalized by Denmark in the Treaty of the Danish West Indies, signed on 1916. The US government, eager to capitalize on the strategic and economic advantages brought by these two events, and driven by a doctrine of "civilizing" a Caribbean archipelago neglected by other imperial powers, initiated a series of comprehensive surveys of the archaeology, geology, paleontology, demography, natural resources, and species diversity of these islands (Baatz 1996; Brock 2014). A series of 19 volumes published between 1919 and 1960 as the *Scientific Survey of Porto Rico and the Virgin Islands*, conceived by president and cofounder of the New York Botanical Garden Nathaniel Lord Britton and produced by the New York Academy of Sciences, became the first comprehensive species diversity assessments for the *now* US Virgin Islands. The influential work covered terrestrial, marine, and freshwater fauna and flora, with animal chapters often organized by orders. Mosquitos, biting flies, and other flies with aquatic larvae were discussed within the Diptera (Curran 1928); dragonflies and damselflies were included together in the chapter on Odonata (Klotz 1932); several aquatic insect families were covered within the Hemiptera and Heteroptera (Barber 1939); and freshwater crabs, hermit crabs, shrimp, and amphipods were covered in chapters devoted to *Brachyura* (Rathbun 1933), Macrura and Anomura (Schmitt 1935), and Amphipoda (Shoemaker 1935). Vertebrate chapters including inland aquatic animals covered birds (Wetmore 1927a, b), amphibians and reptiles (Schmidt 1928) and fishes (Nichols 1929, 1930). In total, these inventories recorded 35 inland aquatic insects, seven crustaceans; four amphibians; and 27 aquatic birds occurring in the USVI, with multiple unconfirmed records among these taxa. Although the Virgin Islands fish fauna was discussed in the introductory sections of Nichols (1929), freshwater fish records besides those from Puerto Rico were treated as "West Indies." Only one freshwater-tolerant marine fish was distinctly recorded from St. Croix.

As seminal as these scientific efforts were, their impact on the two US territories involved was notably different. Brock (2014) documented how the scientists involved in the expeditions from the *Scientific Survey* became allies of the Puerto Rican government and mentors of eventually influential local scientists, contributing to the shaping of social dynamics for the following generation by training a new professional class. A similar phenomenon did not occur in the USVI. Evidently, the lack of an institution of higher education in the US Virgin Islands at the time was a key factor; the College (currently University) of the Virgin Islands was founded in 1962. However, focusing solely on this overlooks that—with the noteworthy exception of avian research—relatively little work on inland aquatic fauna or flora of the USVI occurred during the first half of the twentieth century. This was despite the array of taxonomists and biogeographers from elsewhere, including those from neighboring Puerto Rico, who were actively researching aquatic fauna of the lesser Antilles (e.g., Curran 1928; García-Díaz 1938; Barber 1939; Ferguson and Richards 1963; Fairchild 1966; Flemmings and Walsh 1966), and the burgeoning formalization of aquatic ecology and limnology as *bona fide* fields of study. The influential essay *The Lake as a Microcosm* (Forbes 1887) heralded the establishment of limnology in North America (Egerton 2014) and remains influential still (Hansson et al. 2013). Important textbooks on inland aquatic biology were available by the early 1900s (e.g., *The Life of Inland Waters* [Needham and Lloyd 1916]; *Fresh-Water Biology* [Ward and Whipple 1918]). Yet, between 1900 and 1950, only 12 studies contained *any* information about non-marine aquatic invertebrates of the VI; 20 studies included observations on freshwater and mangrove vertebrates, of which 17 were on birds (Fig. 1).

Egerton (2016) points out that limnological progress in Canada and the USA occurred in parallel because: "both spoke the same language and had been part of the same scientific culture. In contrast, Mexico, Central America, and the West Indies mainly spoke Spanish, and U.S. and Canadian scientific influence did not have much impact until after World War II." In reference to the 1963 comprehensive publication *Limnology in North America* (Frey 1963), which contained a chapter covering the West Indies, Egerton (2016) highlighted a quote from that chapter by Candelas and Candelas underscoring the lack of

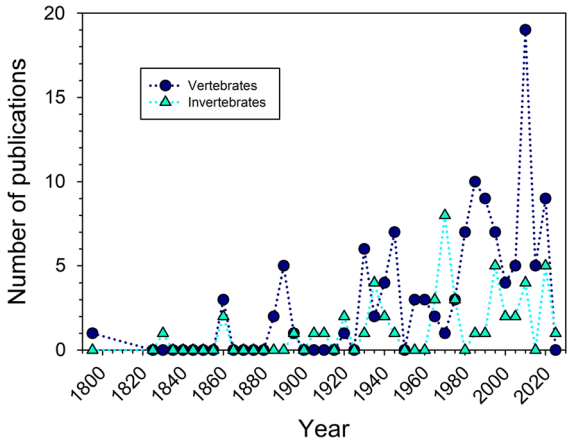

Fig. 1 Publications on inland aquatic fauna of the United States Virgin Islands. Break on the x-axis indicated a period of decades without any publications produced. Sources are listed in tables S1 and S2

Caribbean studies on freshwater habitats at the time. While there is truth to that assessment, there is also an element of artifact because of the type of studies considered by that review. By adhering to the contemporary definition of limnology, those authors dismissed a natural history that was mostly hidden in the primarily taxonomic literature (see previous sections). It also underplayed the role the *Scientific Survey* had as a comprehensive reference for multiple aquatic taxa; a possibility Egerton (2016) recognized in relation to the development of ecology in Puerto Rico.[5] While it would be difficult to argue against the language barrier that has limited the dissemination of Latin American science, the transfer of scientific knowledge in English would have been theoretically easier in the USVI because of the widespread use of English Creole and English even before the transfer from the Danish to the USA. In fact, the use of English was touted as an asset in early twentieth century US texts describing life in the Virgin Islands, such as *The Virgin Islands, Our New Possessions: And the British Islands* (de Booy and Faris 1918). Yet, research on inland aquatic waters of St. Thomas, St. John and St. Croix remained low. When the NY Academy of Sciences published volume 776, issue 1, of its Annals titled *The Scientific Survey of Puerto Rico and the Virgin Islands: An 80-Year Reassessment of the Islands' Natural History* in 1996, only five of 18 articles included discoveries or updated species lists from the USVI (Figueroa Colón 1996).

This is not to say the US Virgin Islands were devoid of naturalists in the twentieth century. Crucian[6] researcher Harry A. Beatty became an important figure in the study of vertebrates and invertebrates in both terrestrial and aquatic habitats of the USVI. Beatty did not taxonomically describe any species, but he developed comprehensive faunal lists for birds (Beatty 1930), insects (Beatty 1944c), and crustaceans (Beatty 1968) of St. Croix, where he was born. These works, and several others of narrower scope (Tables S1, S2), included dozens of aquatic species. He also reviewed mammal, arachnid, and endoparasite faunas of that island (Beatty 1944a, b, d). Beatty's passion was birds, and he contributed notes on the avifaunas of Puerto Rico, Dominican Republic, and Venezuela, as well as conducting important work on animal vectors of malaria and filarial parasites during his employment with the VI Department of Health in St. Croix (Skov 1944). He was an avid collector of animals big and small, obtaining specimens, which he sent to experts around the US for description. The hadziid amphipod *Metaniphargus beattyi* Shoemaker, 1942, was discovered by Beatty in a deep well from Frederiksted, St. Croix. Shoemaker (1942) established the specific epithet of the new species "in honor of Harry A. Beatty, an ardent collector who has given many fine specimens of Crustacea to the United States National Museum."

Another figure who contributed notably to the understanding of freshwater invertebrate fauna of the USVI was Douglas G. Smith. In contrast with Beatty, Smith was a taxonomist and he described various freshwater invertebrates from St. John. These included snails (Smith and Brousseau 1996), and the only freshwater bryozoan and sponge species recorded to date from the US Virgin Islands (Smith 1993, 1994). He also contributed distributional data for inland branchiopod crustaceans, such as brine shrimp and clam shrimp (Smith and Little 2003; Rogers and Cruz-Rivera 2020). The prolific Dutch entomologist Nico Nieser also merits mentioning. While at the *Zoölogisch Laboratorium der Rijks-Universiteit* in Utrecht, Nieser conducted extensive taxonomic descriptions and

[5] When discussing a review of Puerto Rican ecological science by Herminio Lugo Lugo in page 270.

[6] Native of St. Croix.

distributional assessments of freshwater insects from the Antilles, based primarily on specimens collected by Dutch naturalist P. Wagenaar Hummelinck between 1930 and 1967. His works covering the USVI included the orders Notonectidae (Nieser 1967, 1969c), Corixidae (Nieser 1969a), and Pleidae et al. (1969b).

St. Croix has been historically, and continues to be, a focus of bird enthusiasts and researchers, with the first observations on inland aquatic birds dating back to the 1800s (Newton and Newton 1859; Ridgway 1884; Cory 1886, 1887, 1888; Table S2). Here, we find a broader literature and variety of naturalists contributing reports on aquatic animals. The history of ornithology for the Virgin Islands has been reviewed (Wiley 1996; Levy 2008). Hence, we only consider works related to aquatic non-marine species. Besides Beatty, well-known twentieth century naturalists and ornithologists, such as Charles F. Leck, Alexander Wetmore, Stuart T. Danforth, Robert L. Norton, and James Bond contributed publications on mangrove and inland aquatic birds (Table S2). Crucian ornithologist, naturalist, explorer, and writer George A. Seaman was Supervisor of Wildlife for the Virgin Islands between 1949 and 1969 (Johnson 2014; Highfield 2014). His writings about terrestrial and aquatic birds and other taxa, and humans impacts on them, were summarized in three books (Seaman 1973, 1980, 1993). He also published focused accounts on bitterns, ducks, and other inland aquatic birds (Seaman 1954, 1958, 1959). The ornithological tradition of the USVI, particularly St. Croix, has continued through the contemporary works of Douglas MacNair, Lisa D. Yntema, Fred W. Sladen, Carol Cramer-Burke and collaborators (Table S2).

The low diversity of amphibians, reptiles, and fish for the territory coupled with the increasing number of introduced species has resulted in a push for distributional records and conservation plans. There are only 17 species of native amphibians and freshwater/brackish water fishes in the USVI (excluding freshwater-tolerant marine fishes), and 12 introduced species including a freshwater turtle as the only inland aquatic reptile (Philibosian and Yntema 1977; Nemeth et al. 2007; Platenberg 2007; Smith-Vaniz and Jelks 2014). While comprehensive assessments of these groups were part of the *Scientific Survey* (Schmidt 1928; Nichols 1929, 1930), this fauna was revisited in the 1970–1980s, by John A. Yntema, of the Bureau of Fish and Wildlife. He produced comprehensive summaries of the amphibian, reptile, and fish (and mammal) faunas of the USVI with various collaborators, including Richard Philibosian, Ileana E. Clavijo, and noted ecologist and conservationist John C. Ogden. The most recent works on non-avian aquatic vertebrate taxa in the USVI have been produced by Renata J. Platenberg, currently at the University of the Virgin Islands, and her collaborators (e.g., Nemeth et al. 2007; Platenberg 2007; Platenberg and Boulon 2011; Platenberg et al. 2020).

The role of the University of the Virgin Islands in the study of inland water biota has increased over the past four decades. In 1973, the University's Water Resources Research Institute (UVI WRRI) was established through funding from the US Geological Survey. As part of its mission, the Institute has provided grants for research and education related to hydrology, ecology, utilization, and conservation of freshwater, wetlands, and watersheds of the territory. While hydrological and water safety studies have overwhelmingly dominated the supported research, some VI WRRI-funded work has assessed USVI aquatic species diversity since 2000, particularly in relation to watershed health and ecosystem stressors (Nemeth and Platenberg 2007; Nemeth et al. 2007; Gardner et al. 2008; Rogers and Cruz-Rivera 2020, 2021). Additionally, the University's Center for Marine and Environmental Studies was established in 1999. Although research from this unit has primarily focused on marine coastal ecosystems, particularly coral reefs, an increasing number of studies and graduate student theses have begun focusing on estuaries, mangroves, and watersheds (e.g., Colletti 2011; Keller et al. 2017; Durdall 2018; Jerris 2019). Also noteworthy is a recently established interdisciplinary program focused on ridge-to-reef processes aimed at elucidating links and connectivity among land, freshwater, and marine resources at multiple scales. Inland water studies appear poised toward a period of growth in the US Virgin Islands.

What we have learned: were west and Ledru correct?

In total, only 47 works[7] documenting any aspect of aquatic inland invertebrates in the USVI have been

[7] The numbers include all relevant chapters from the Survey, unpublished theses, and grey literature. They exclude works on

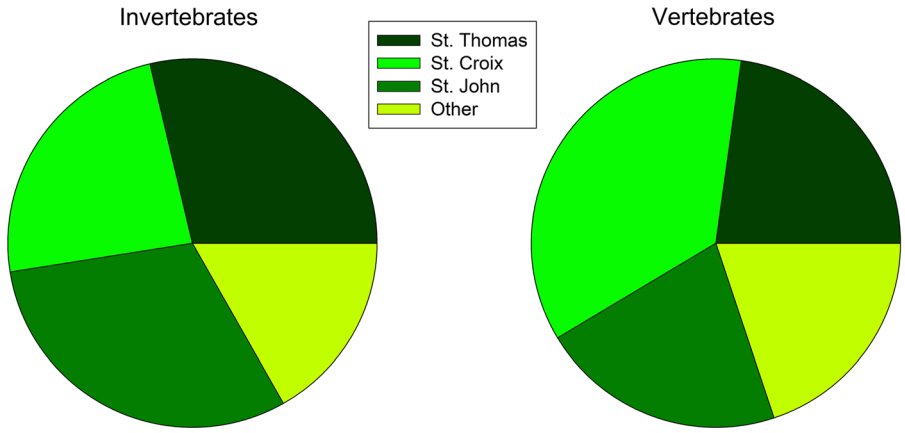

Fig. 2 Geographic focus of studies on US Virgin Islands aquatic fauna since 1900

published since 1900 (Fig. 1; Table S1). Taxonomically, these include two studies on Mollusca, one on Bryozoa, one on Porifera, nine on Crustacea, 26 on Hexapoda, and eight presenting checklists or collections of total invertebrates. Thus, 53% of these articles are on insects and collembolans (springtails). These studies encompass 65 authors, of which only two coauthored > 2 articles. For vertebrates, patterns showed a similar level of taxonomic bias, although based on more than twice as much research productivity: 108 publications since 1900 contain information on at least one inland aquatic vertebrate species from the territory (Fig. 1; Table S2). Of these, 73 articles (67.6%) contained data on birds (primarily distribution records), 18 focused on amphibians or amphibians and freshwater turtles, seven on fish, and 10 reports discussed total vertebrate fauna or both vertebrates and invertebrates. One hundred and eight authors are represented in this vertebrate literature, 12 of whom published four or more articles. Four articles on bird biogeography only included total numbers of reported bird species for the Virgin Islands. It was unclear if those works counted inland aquatic birds and were not considered in the calculations. Thus, some of our numbers could be underestimations. "Gray literature" (non-peer reviewed reports, environmental impact assessments, non-expert identification guides, and unpublished theses) contributed approximately 13% and 23% of invertebrate and vertebrate publications, respectively. Almost all publications were descriptive regardless of taxon (i.e., not based on the outcome of manipulative experiments).

A noticeable difference between inland aquatic vertebrate and invertebrate studies is the geographic focus (Fig. 2). Considering the locations where collections, observations or field experiments occurred, publications on invertebrates were distributed more evenly among islands. The number of papers with inland aquatic invertebrate observations was only slightly lower for St. Croix (ca. 24%); around 29% contained data from St. Thomas and ca. 31% from St. John. Approximately 17% of these works also contained comparative observations from other islands outside the USVI. In contrast, more than a third (ca. 36%) of vertebrate studies have been performed in St. Croix, with $< 23\%$ of the scientific literature containing information from either of the other two main US Virgin Islands and about 20% providing observations from other islands in the Antilles (Fig. 2). This pattern is driven, not surprisingly, by works on St. Croix mangrove and wetland birds.

It should be asked why inland aquatic invertebrate research in the USVI has approximated one article every three years over the past century, while the vertebrate literature is richer. First, the numbers for vertebrates are arguably deceptive. Although publications on vertebrates suggest an average scientific productivity of almost one article per year, nonpeer reviewed literature accounts for almost one quarter of

Footnote 7 continued
zooarchaeology, due to the qualitative nature of many of those (i.e., "freshwater turtle," "land crabs," etc.). Strictly bibliographic lists are also excluded. Studies on biogeographical patterns and regional species checklists are included because they address distribution and species diversity hypotheses, despite using previously published articles.

all these publications. This gray literature includes several popular guides for birds, reptiles, and amphibians that have been updated periodically to add new details but are essentially the same original species list (e.g., Raffaele et al. 2020 and earlier editions; Table S2). More importantly, 37 of all these articles (34%) have been reviews of preexisting information and not contributions of new data. In short, despite a longer history of research, primary works on aquatic vertebrates in the USVI remain low and strongly biased toward avian studies.

These caveats aside, it is not unusual that island vertebrate faunas are better characterized than invertebrate ones. Besides the obvious advantage of size making vertebrates easier to notice and distinguish in the field, identification of invertebrates often requires collection, microscopic observation, dissection of minute parts, and access to a literature that is not readily available to everyone; there are no "field guides" to the mosquitos or earthworms of the Caribbean, and few amateur naturalists take on hobbies along the lines of "shrimp watching." The trend in ecology to divorce natural history from experimental science only exacerbates the biodiversity knowledge crisis and reinforces false assumptions concerning patterns of species distribution and abundance. The conclusions of early naturalists like West and Ledru found easy support from a scientific tradition dominated by ornithologists, ichthyologists and herpetologists (Wetmore 1927a, b; Schmidt 1928; Nichols 1929, 1930; Leopold 1963). The works of these researchers promoted a sort of historical inertia and false comfort in knowing that by studying Puerto Rico, insights into the biodiversity of the Virgin Islands could be obtained. Considering that there has been more than twice as many publications on USVI vertebrates than invertebrates, this assumption appears justified. For example, all 17 species of native inland fishes and amphibians found in the US Virgin Islands are also found in Puerto Rico. In fact, all introduced species in those phyla occurring in the USVI are found there as well (Martin and Patus 1988; Joglar et al. 2007; Platenberg 2007; Kwak et al. 2007; Smith-Vaniz and Jelks 2014; Barker and Rodríguez-Robles 2017; Rodríguez-Barreras et al. 2020). For inland aquatic birds, the basic dispersal ability provided by powered flight and the migratory nature of most species found in USVI wetlands result in a fairly homogeneous bird biota for Puerto Rico and the Virgin Islands (Wetmore 1927a, b; Leopold 1963; Rafaelle et al. 2020).

However, historical consensus from vertebrate work cannot be considered the only explanation for the limited effort on US Virgin Island nonmarine aquatic fauna. Larger invertebrates, such as inland aquatic shrimp and crabs, also appear to be shared by both the USVI and Puerto Rico (and sometimes other Antilles), but the higher species diversity of Puerto Rican freshwater crustaceans (Pérez-Reyes et al. 2013) has attracted more research on these species there. There are also artisanal fisheries for freshwater shrimp, fishes, and semiaquatic crabs in Puerto Rico that have motivated investigations, regulation, and management of these animals (Kwak et al. 2007; Neal et al. 2009; Matos-Caraballo and Agar 2011; Alston and Carro 2013; García-Quijano et al. 2015). These historical elements are absent, limited, or lost in the USVI (e.g., semiaquatic crabs are consumed to some extent in the VI, but not regulated; Platenberg 2006). The earlier establishment and greater number of institutions of higher education in Puerto Rico likely contributed to the observed patterns as well (Brock 2014). As noted before, these neighboring investigators largely overlooked the Virgin Islands, despite the increasing ease of travel through the decades. The paucity of studies assessing inland water animal diversity in the USVI has been underscored by others. Platenberg (2006) noted: "The need for an assessment of these inland water sources was highlighted by Smith (1993), who discovered a new species of ectoproct on St. John, simply because no one had ever looked for them there before." Similarly, in their authoritative monograph on the fishes of St. Croix, Smith-Vaniz and Jelks (2014) stated: "Aside from our limited recent efforts, we are unaware of any comprehensive survey of the freshwater habitats of the island."

The authors' own experiences reflect this reality as well (Rogers and Cruz-Rivera 2021). Reminiscent of Platenberg's observation above, a species of clam shrimp (Crustacea: Limnadiidae) was described very recently from ponds (water hazards) on the golf course of the University of the Virgin Islands in St. Thomas, an institution that has been in place since 1962 (Rogers and Cruz-Rivera 2020). The crustacean was one of three confirmed undescribed arthropods discovered in two weeklong aquatic macroinvertebrate surveys during 2019. Several gastropods, oligochaetes, acari,

collembolans, copepods, and ostracods from these collections may be undescribed species also and await further analysis (Rogers and Cruz-Rivera 2021). Furthermore, outcomes from these and two other additional short samplings showed: (1) that a remarkable 46% of all taxa collected during those surveys were new records for either the islands sampled or the US Virgin Islands as a whole, and (2) samples collected sequentially from the same site had < 50% taxonomic similarity (Rogers and Cruz-Rivera 2021). These results suggest an understudied and underestimated degree of aquatic animal diversity for the USVI. The case for studies on aquatic microhabitats, such as phytotelmata, is also strong. Despite a well described bromeliad flora with comprehensive taxonomic inventories starting in the 1800s (Eggers 1879; Britton 1918; Britton and Wilson 1924), phytotelmata are notably under-sampled, with one unpublished thesis (Miller 1970), three peer reviewed publications discussing phytotelmata invertebrates (Miller 1971; Chadee 1998; Rogers and Cruz-Rivera 2021), and only a passing reference on bromeliad use by amphibians (Philibosian and Yntema 1976). One of the confirmed undescribed species mentioned above, a ceratopogonid fly (biting midge) in the genus *Forcipomyia*, which may be important to public health, was found in bromeliad samples from St. Thomas.

Conclusions

The first observations of inland aquatic animals in the Caribbean began with the discovery of the Antilles by the early native American people. The variety of Taino words for freshwater and mangrove species, many of which are still used, remains as evidence of this. The prominence of Caribbean inland water habitats was not lost on Christopher Columbus. In his 1493 letter to Luis de Santángel, Columbus spoke not only of the beauty and suitability for agriculture of the lands in Hispaniola, but also of its *plenty of rivers and good and large, which is a marvel* (Colón 2010; translation by EC-R). However, the documentation of natural history started by Spanish explorers, clerics, and official chroniclers in the 1400–1500 s was not to include the *Once Mil Vírgenes*—the name given to the Virgin Islands by Columbus—as the colonization of the Americas focused on the Greater Antilles. There would not be *good and large* rivers to document in the Virgin Islands, and the reported reception by the local inhabitants settled any immediate desires of colonization from Columbus' men. The written natural history of the Virgin Islands is unavoidably short, compared to that of other nearby islands, because it began officially in the late eighteenth century, during Danish control and through the writings of Hans West. Later, in 1810, the French chronicler André-Pierre Ledru, one of the four naturalists in the Baudin expedition (Jansen and Fuchs 2019), documented his agreement with West that the Virgin Islands fauna was largely present in Puerto Rico. The first formal scientific accounts of aquatic inland species of the territory occurred in the nineteenth century, with the taxonomic descriptions of a shorefly from St. Thomas and observations on the habits of aquatic birds in St. Croix. Since then, fewer than 150 articles and books have been published on USVI aquatic fauna overall, and while average productivity has modestly improved since the 1960s (Fig. 1), there is no clear trend toward an increased research effort. While the similarity between aquatic faunas of Puerto Rico and the Virgin Islands appears settled for aquatic vertebrates and some of the larger invertebrate groups, recent work suggests inland aquatic invertebrates deserve further attention.

The effects of land development on St. Thomas ghuts have been the focus of prior investigations (Nemeth et al. 2007; Nemeth and Platenberg 2007). Extensive conversion of natural habitats and resources to agricultural use during French and Danish occupation drastically altered the USVI landscape (Taylor 1888; Hatch 1972; Tyson 1987; Power 2011). This, coupled with the extensive introduction by the USVI government of exotic plants during the mid-1900s to attract more tourism (Virgin Islands 1967), have greatly altered the ecology and biodiversity of the islands, probably irreparably. We contend that studying diversity of aquatic invertebrate faunas in the US Virgin Islands will not simply produce new locality records for broadly dispersed species expected to be there. The discovery of undescribed species even from developed areas and during very short surveys point to a poorly understood faunal biodiversity. The lack of this information also hinders the proper management and conservation of water resources. Native species were more abundant, and their diversity was higher, in less developed watershed habitats (Nemeth et al. 2007; Nemeth and Platenberg 2007). As early as 1969, Chase and Hobbs warned that water use and its

concomitant environmental effects on freshwater systems of St. Thomas and St. Croix could lead to—or may have already resulted in—local extinction of some of the species they studied. Understanding the biodiversity of nonmarine aquatic habitats in the USVI will require considering their role in the ecology of other species not intuitively associated with these systems. For example, Bacle et al. (2008) noted the importance of ghuts and freshwater reservoirs for bats in St. Thomas and St. John. Similarly, animals such as "land" crabs (Gecarcinidae) and the hermit crab *Coenobita clypeatus* (Fabricius, 1787) are commonly associated with, and dependent on, inland water habitats of the Virgin Islands (Platenberg 2006; Gardener et al. 2008; Rogers and Cruz-Rivera 2021), although they are classified by many as terrestrial. We are hopeful that newer platforms of public engagement in science, such as iNaturalist (https://www.inaturalist.org/), will stimulate new local interest in this biota and motivate funding agencies to budget needed allocations to the study and conservation of these dynamic environments. Knowing the aquatic biodiversity of the USVI will allow the development of relevant manipulative ecological and environmental studies needed to evaluate the natural services provided by these habitats, their connectivity with ecosystems, and their resilience to multiple stressors in a changing Caribbean.

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Data availability All references used in this review are provided as supplemental material.

Declarations

Conflict of interest The authors declare no direct or indirect conflicts of interest related to this work.

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