vol. 200, no. 1 the american naturalist july 2022

Special Section

Colonial Legacies Influence Biodiversity Lessons: How Past Trade Routes and Power Dynamics Shape Present-Day Scientific Research and Professional Opportunities for Caribbean Scientists*

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Submitted July 20, 2021; Accepted March 17, 2022; Electronically published May 31, 2022

Dryad data: https://doi.org/10.5061/dryad.02v6wwq5b.

abstract: Scientists recognize the Caribbean archipelago as a biodiversity hotspot and employ it for their research as a natural laboratory. Yet they do not always appreciate that these ecosystems are in fact palimpsests shaped by multiple human cultures over millennia. Although post-European anthropogenic impacts are well documented, human influx into the region began about 5,000 years prior. Thus, inferences of ecological and evolutionary processes within the Caribbean may in fact represent artifacts of an unrecognized human legacy linked to issues influenced by centuries of colonial rule. The threats posed by stochastic natural and anthropogenically influenced disasters demand that we have an understanding of the natural history of endemic species if we are to halt extinctions and maintain access to traditional livelihoods. However, systematic issues have significantly biased our biological knowledge of the Caribbean. We discuss two case studies of the Caribbean's fragmented natural history collections and the effects of differing governance by the region's multiple nation states. We identify knowledge gaps and highlight a dire need for integrated and accessible inventorying of the Caribbean's collections. Research emphasizing local and international collaboration can lead to positive steps forward and will ultimately help us more accurately study Caribbean biodiversity and the ecological and evolutionary processes that generated it.

Keywords: natural laboratories, environmental archeology, heterogeneous histories, national identity, equitable science, collecting practices.

Introduction

Across millennia, islands have served as important places for a wide range of human activities and supported diverse livelihood and cultural practices. Yet over the most recent 500 years, islands have attracted scientists who saw the potential for discovery, extraction, and experimentation in their ostensible remoteness and isolation, fashioning them into natural laboratories. Indeed, the phrase "natural laboratory"

* This article is part of a cross-disciplinary special section titled "Nature, Data, and Power: How Hegemonies Shape Biological Knowledge."

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American Naturalist, volume 200, number 1, July 2022. Published by The University of Chicago Press for The American Society of Naturalists. https://doi.org/10.1086/720154

is ubiquitous in island-focused biological literature, describing a paradoxical place in which to exert control in the wilderness (i.e., environments largely outside of human influence) and thus clarify fundamental biological processes. Not surprisingly, island systems are where the modern scientific fields of evolutionary biology and ecology formed their identities, shaped by the stories of naturalists who ventured into the unknown and returned with specimens (e.g., Charles Darwin and the *Origin of Species*) and those who distilled living communities into powerful equations (e.g., Macarthur and Wilson and *The Theory of Island Biogeography*; Whittaker and Fernandez-Palacios 2007). A brief turn to history shows us that islands have been treated as laboratories where explorers—and later biologists—went to solve complicated scientific problems and subsequently transferred these solutions elsewhere to their own continents, societies, and academic institutions (Quammen 2004).

As islands have been labeled as laboratories, so too have archipelagoes received the experimental designation of replicates, in which each island represents repeated applications of experimental treatments (Ricklefs and Bermingham 2008). These natural replicates have been leveraged to disentangle the geologic and environmental conditions that produce patterns of endemism, community assembly, and extinction, thereby reducing places to comparative data sets from which to extract patterns. But while the biota of archipelagic islands might be replicated, the people and cultures on these islands are not; biogeographically similar islands can differ markedly in their human histories and cultural diversity in ways that shaped and continue to shape biological communities and landscapes through time.

Despite increasing evidence that modern insular biodiversity is imprinted by—and, in some cases, a direct result of—long-term socioecological systems (e.g., Siegel et al. 2018; Kemp et al. 2020), such histories are usually considered at shorter timescales (e.g., decadal deforestation) often overlooking deeper timescales of human presence and influence. In many cases, centennial to millennial human histories on islands have been or continue to be obscured under the assumption that Indigenous peoples, their knowledge, and their biocultural diversity were homogeneous, inconsequential, and obliterated by colonial genocide (Benn Torres 2014), leaving islands as sterile petri dishes awaiting inoculation. Many of the same factors that make island systems attractive to biologists also made them attractive to European colonizers for resource extraction and trade, serving as laboratories for capitalism in which early naturalists played an active role (Moore 2010). Although often unacknowledged in scientific studies, such industries rapidly altered landscapes, species interactions, and evolutionary pressures.

Here, we—a group of Caribbean and non-Caribbean scientists who study natural and human systems in the archipelago—focus on this region as a frequently studied region of exceptional biological and cultural diversity within its historical context as the birthplace of European colonialism in the Americas. We consider how legacies of colonialism overall have had and continue to have an impact on biological scientific practice in the region. This includes how research findings may be biased by past anthropogenic activities and/or how scientific endeavors themselves were or continue to be conducted. We feature two contemporary examples from two historically different Caribbean nations—Trinidad and Tobago and the Bahamas—that highlight different but effective approaches to (1) address how biases of international research agendas have shaped the formation of natural history collections (Trinidad and Tobago) and (2) focus on mechanisms to support and regulate international collaborations in biological and heritage research (the Bahamas). We emphasize that we cannot, nor do we purport to, represent all approaches to science in the Caribbean, but we present this paper as a point of critical reflection, discussion, and action.

Lessons from the Caribbean Laboratory

The diverse sizes, geomorphic forms, and geotectonic histories of the Caribbean's 17,000 islands have captivated naturalists for centuries. Biogeographers group the archipelago into three contrasting systems that otherwise experience similar tropical climatic conditions, forming laboratories within a laboratory: the Bahamian Archipelago, Greater Antilles, and Lesser Antilles.

The Bahamian Archipelago (the Bahamas, Turks and Caicos Islands) consists of marine carbonate sediments situated on shallow banks. The region's sheer quantity of islands (12,000 cays) and their continued exposure to disturbances, such as hurricanes (Winkler et al. 2020), has made them a key arena in which to study ecological processes, particularly in facilitating experimental population translocations (Spiller et al. 1998; Losos and Spiller 1999). Islands of the Greater Antilles consist of old continental crust fragments that have been continuously exposed since at least the Eocene and reached their current position by the Miocene (Pindell and Kennan 2009). Their large size, topographic variation, and changing proximities to other land masses have made them a central focus of deep time diversification and adaptive radiation studies.

Located at the eastern edge of the Caribbean plate, the Lesser Antilles is mostly an active volcanic chain that formed during the Eocene to mid-Oligocene. Research here has primarily focused on addressing biogeographic questions of extinction and colonization (e.g., lineage accumulation; see Ricklefs and Bermingham 2001), given the chain's stepping-stone configuration between South America and the Greater Antilles (Ricklefs and Cox 1972; Ricklefs and Bermingham 2001). Trinidad, Tobago, and the ABC islands (Aruba, Bonaire, Curaçao) are sometimes included with the Lesser Antilles. While they share fauna and flora with continental South America, they possess colonial legacies similar to the rest of the Caribbean and are comparatively understudied (Koopman 1958; Hedges et al. 2019).

Research in the Caribbean has contributed to foundational concepts in ecology, evolution, population biology, and allied biological disciplines both by incorporating specimens (whole and partial organisms, their isolated molecules, and/or associated metadata) collected from the region into phylogenetic and biogeographic analyses and by using the region as a space to conduct observational and experimental field studies. The region's high proportion of endemic species within broadly distributed clades allows for comparative studies within and between the three major archipelagos. Some of these lineages, including *Anolis* lizards and *Poecilia* guppies, have gained model system status both in the field and in captivity (Magurran 2005), whereas other vertebrate (e.g., *Eleutherodactylus* frogs, noctilionoid bats), invertebrate (*Cerion* snails), and plant systems (e.g., Cactaceae; Majure et al. 2021) continue to gain traction as the focus of international research programs.

As an insular system, the Caribbean has corroborated the central tenets of the equilibrium theory of island biogeography and extended its predictions to account for deeper time evolutionary processes. While MacArthur and Wilson (1963) did not initially consider how island area may also influence in situ speciation in reaching dynamic equilibrium, Losos and Schluter (2000) found that for *Anolis*, an island size threshold exists at 3,000 km^2, whereby in situ speciation exceeds immigration as the source for new species. Similarly, Valente et al. (2017) documented the first instance of dynamic equilibrium between immigration, speciation, and extinction in Caribbean bats over million-year timescales.

Decades of productive debate have centered on the relative roles of vicariance and dispersal in generating Antillean lineages, including a potential Oligocene connection spanning the Greater Antilles and Aves Ridge (GAARlandia; Hedges 2006). Addressing this conundrum has spurred innovation in phylogenetics, led to new modeling approaches, and highlighted the need for interdisciplinary collaboration between biologists, paleontologists, and geologists (Marivaux et al. 2020; Cornée et al. 2021). While such debates have incentivized paleontologists to search for fossils representing key divergence points for calibration, the paucity of deep-time records from the region also requires molecular phylogenetic inferences (for reviews, see Crews and Esposito 2020; Roncal et al. 2020; Rodriguez-Silva and Schlupp 2021). The resultant evolutionary relationships have served as the backbone for addressing questions at the ecology-evolution interface, such as adaptive radiations, taxon cycles, phenotypic convergence, and character displacement (Ricklefs and Bermingham 2008).

The Bahamas have played an integral role in research on community ecology (Losos and Spiller 1999) and species interactions (Schoener and Spiller 1987), as these small islands are easy to manipulate for ecological studies in ways not thought possible on continents. Hurricane activity has garnered real-time insights into morphological evolution (Donihue et al. 2018), dispersal (Censky et al. 1998), and population ecology (Spiller et al. 1998). Similarly, the guppies of Trinidad have been foundational for eco-evolutionary research and the study of natural selection in the wild as it is seen in population differentiation, local adaptation, density-dependent regulation, sexual selection, and size-specific predation (Reznick and Travis 2019).

Last, the Caribbean has an exceptionally high postglacial extinction rate (Turvey and Fritz 2011). Because of the presence of ground sloths' fossils, the Greater Antilles has been used as a comparative experiment in Late Quaternary megafauna extinctions in comparison with continental systems (Steadman et al. 2005). Advances in ancient DNA and other technologies have facilitated use of the Caribbean's rich Holocene fossil and archeological record as part of transdisciplinary collaborations among paleontologists, archeologists, and conservation biologists (e.g., Turvey et al. 2007; Cooke et al. 2017; Oswald et al. 2020).

Recognizing Heterogeneous Histories

These Caribbean-based insights into basic ecological and evolutionary biology do not exist in a vacuum. Rather, the data that underlie these findings and the very act of research itself in the region have been shaped by colonial practices, supported by colonial infrastructure, and influenced by colonial mentalities. Recognizing this colonial legacy prompts us to re-examine these contributions to fundamental scientific concepts and identify biases that dually influence the robustness of theories and who has been able to participate in forming those theories. These biases have meant that certain data sets, knowledge, and specimens have been unintentionally unincorporated (e.g., Trinidad's fossil record exported by colonial petroleum scientists [fig. 1]) into research and also that some questions themselves have been left unposed.

Despite the breadth and depth of Caribbean-based research programs, a long-term history of questionable collecting practices precludes our ability to fully understand ecological and evolutionary processes, such as insular diversification and extinction, and also render it difficult for Caribbean-based scientists to build capacity in natural history collections and biodiversity research. Natural history collections from the Caribbean are inextricably linked to the trans-Atlantic slave trade. For example, British collectors like Hans Sloane and James Petiver capitalized on the routes of the slave trade to gain access to regions that were

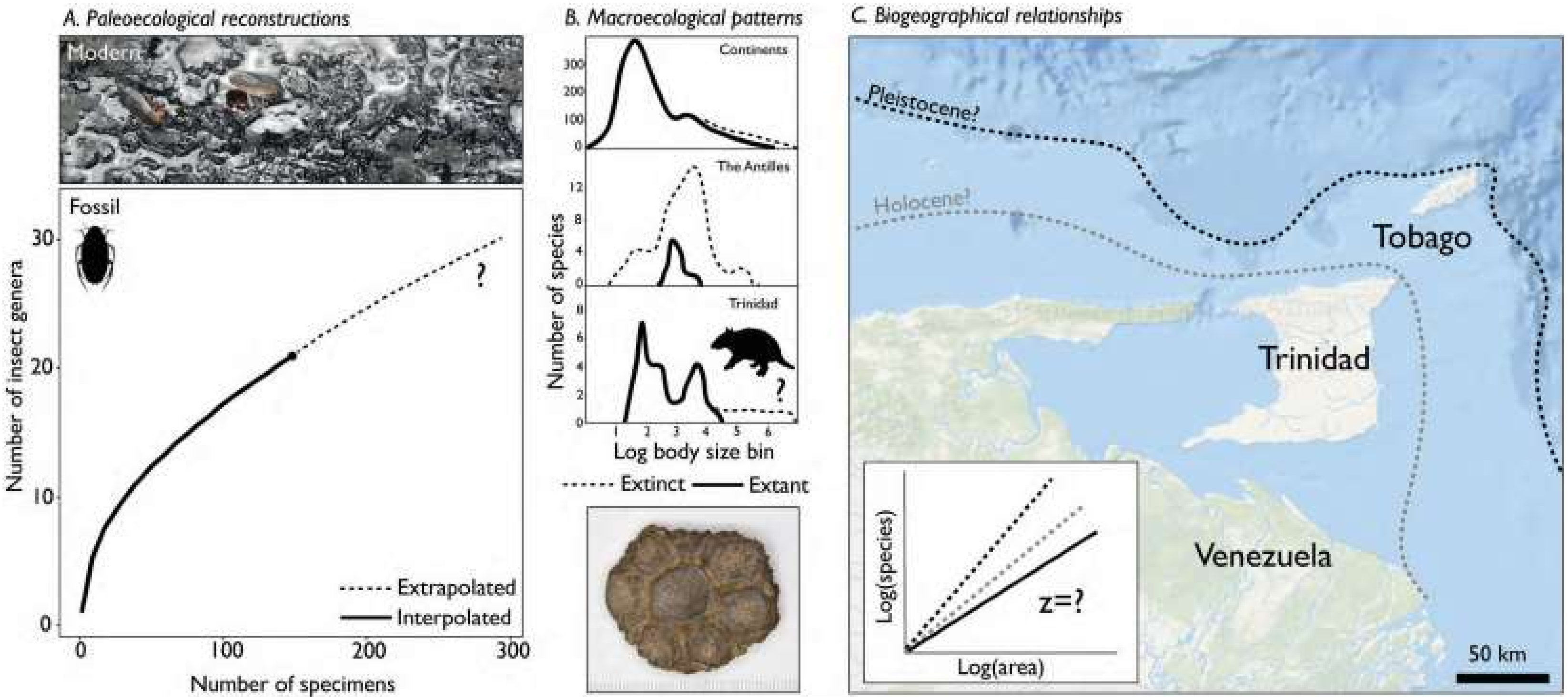

Figure 1: Colonial petroleum exploration and other activities led to the poorly documented export of fossils and loss of site context in Trinidad and Tobago. This undermines our ability to do the following. *A*, Accurately reconstruct the paleoenvironment of Trinidad and compare past and present biological communities. For example, the asphaltic insect fauna of Apex Oilfield has clearly not been sampled to saturation, yet we cannot relocate the original locality, as corporate owners have changed over time (redrawn from Mychajliw et al. 2020). *B*, Accurately reconstruct macroecological patterns of extinction when comparing continents with oceanic and shelf islands. Here, we show that only with the newly retrieved fossils from Trinidad and Tobago do we see that Trinidad likely follows the pattern of continental species losses (redrawn from Cooke et al. 2017; Mychajliw et al. 2020). *Inset*, a glyptodon scute (UWIZM.2019.4.12) recently accessioned in the UWIZM decades after its excavation from hydrocarbon-bearing sediments in southern Trinidad. *C*, Accurately reconstruct community assembly and species-area relationships. Without knowing the species richness of Trinidad and Tobago through time, we cannot calibrate species-area curves as they relate to changes in sea level over the Pleistocene and Holocene. Map and graph represent hypothetical relationships and sea levels. Symbols courtesy of phylopic.

otherwise off-limits and exploited the knowledge that enslaved Africans and Indigenous people possessed about the natural world (Murphy 2013, 2019; see critique by Wynn-Grant 2019). But these non-European people were rarely, if ever, acknowledged for their contributions, and their collecting efforts did not lead to freedom or social mobility the way it did for Petiver, who was born to a working-class family. Instead, their contributions live on in the common names of some endemic species: in Cuba, names for two species of hutia—*Jutia conga* and *Jutia carabali*—pay homage to regions of Africa (Congo and Calabar) from which many enslaved people were taken. Natural history collections became a status symbol of the gentry, and such private collections became the foundation for some of the largest museum collections in the world (Françozo and Strecker 2017).

In much of the Caribbean's biodiversity literature, European activity is centered and equated with human activity. This is harmful not only to the Indigenous populations that still exist in the Caribbean, such as the Kalinago of St. Vincent and Dominica, but also to scientific accuracy. The pre-Columbian Caribbean was culturally heterogeneous, with archeological evidence indicating multiple temporally staggered arrival episodes originating from different areas of South and Central America and persistent interaction between the islands and with the continents (Chanlatte Baik 2013; Fitzpatrick 2015; Keegan and Hofman 2016).

Although Trinidad was settled by 8,000 years ago, humans first arrived in the Antilles at least 5,500 years ago. Most of the Greater Antilles, Barbados, and several islands in the northern Lesser Antilles were colonized by humans during the Archaic Age (~5,500–2,500 years ago; Napolitano et al. 2019). During the subsequent Ceramic Age (~2,500–2,000 years ago), a major population dispersal known as Saladoid led to settlement of most of the Lesser Antilles and Puerto Rico. Around 1,500 years ago, ceramic-making horticulturalists (Ostionoid) entered Jamaica and the Bahamian Archipelago for the first time, with incursions into parts of the other Greater Antilles. A final pulse of Cayo settlers from South America influenced the already occupied southern Lesser Antilles two to three centuries before European arrival.

As Indigenous people encountered one another, intercultural dynamics followed disparate trajectories, with some societies remaining relatively isolated and others blending, giving rise to new syncretic cultures (Hofman and van Duijvenbode 2011). While larger migrations are used to frame cultural historical units, Indigenous peoples within these periods were neither physically nor culturally static (e.g., Hofman et al. 2018). The heterogeneous nature of community histories and interactions, the regional variability in sociopolitical complexity, and the social networks that developed and evolved over the millennia are a testament to the abilities of Caribbean islanders to move across this fluid realm and create a mosaic of cultural behaviors before the arrival of Europeans.

Division of the Caribbean by European nations added an additional level of cultural complexity to the landscape. The most widespread colonial groups were the Spanish and the British, followed by the French and the Dutch, although other countries, such as Denmark, also had short-lived colonies. Europeans forcibly moved enslaved Africans to all parts of the Caribbean (Eltis 2007), and the abolishment of slavery was uneven across the archipelago. After emancipation, Caribbean colonies shifted toward employing indentured servants from India and China. Sizable descendant communities of all these groups exist, and many individuals in the Caribbean today identify as multiracial. Moreover, contemporary Caribbean geography encompasses 28 countries and additional states and territories situated near the Caribbean Sea, Gulf of Mexico, and Atlantic Ocean (United Nations Caribbean Environment Programme, https://www.unep.org/cep/who-we-are/cartagena-convention).

The entry of Europeans into the New World has been considered the salient ecological baseline by many researchers and conservation biologists. Until recently, preserving primitive vignettes has been the guiding principle of the North American model of wildlife management, assuming that the preceding millennia of Indigenous ecological impacts were minimal and prioritizing wilderness as a space with no human history (Leopold et al. 1963). Certainly, the introduction of Eurasian domesticates and the widespread deforestation for monoculture plantations contributed to dramatic ecological transformations and extinctions (Paravisini-Gebert 2014; Cooke et al. 2017). But we must ask ourselves what opportunities to understand the evolution of biological communities have been missed as a result of neglect of the Indigenous socioecological legacies into which European influences became braided? Within the Caribbean—a focal point of the New World—how have Indigenous, Creole, and Afro-Caribbean land management practices continued to shape community composition and ecology through the colonial period to today? While scholars from the social sciences and humanities have challenged this notion that Indigenous land use was inconsequential (the pristine myth; Denevan 1992), the long-term structural influence of those ideas on natural history and collection-based inquiry persists.

Environmental archeology—the analysis of animal, plant, soil, or other environmentally derived specimens from archeological contexts—is a valuable resource for evaluating species responses to anthropogenic change and offers the diachronic data often called for by neontologists on timescales of ecological relevance, providing opportunities to engage the pristine myth head-on (e.g., LeFebvre et al. 2019; Wallman et al. 2018). Local and ecological knowledge perspectives are also important but can be obscured by the narrative that Indigenous Caribbean peoples became extinct

(Castanha 2010)—a narrative that ignores the diverse ways in which Indigenous Caribbean communities and self-liberated Africans reacted to, resisted, and were transformed by European colonization (Fuller and Benn Torres 2018; Hofman 2019). Many islanders carry Indigenous American genetic ancestries and can be connected to precontact genetic lineages (Moreno-Estrada et al. 2013; Fernandes et al. 2020; Nieves-Colón et al. 2020). Rural communities in Jamaica and Puerto Rico continue to use Indigenous techniques, such as *conuco* farming, *aholla'o de mina* composting, and the rearing of guinea pigs for consumption (Picking and Vandebroek 2019; Pagán-Jiménez et al. 2016). Similarly, African traditional knowledge informs subsistence and hillside farming practices, ecological activism, and medicinal plant use among Afro-descendant and Maroon communities in Jamaica (Connell 2020; Picking and Vandebroek 2019). Thus, far from being relics of a vanished past, Indigenous and Afro-descendant communities were active participants in the Caribbean creolization process and continue to have an important legacy for present-day island societies.

How Have These Histories Shaped Scientific Inquiry and Practice?

The acceptance of the scientific practices within the Caribbean has been influenced by the colonial past. For example, our understanding of evolutionary radiation is biased toward survivors. Investigations of the fossil record have shown that the extant radiations are a fraction of what diversified in the Caribbean as a result of Holocene extinctions. These include diverse but extinct flightless rails (*Nesotrochis*), whose closest relatives today are now restricted to Africa and New Guinea, and a widespread and speciose rodent fauna that is represented by only a few disparately distributed modern species (Oswald et al. 2021; Turvey et al. 2021). These extinctions represent lost opportunities to study organisms in their natural environment and question whether present-day radiations are the exception or the rule. Aside from losing species, colonial practices also destroyed irreplaceable data sources. Bird guano, known as white gold, was harvested for fertilizer but could have been used to reconstruct patterns in bird abundance and ocean chemistry (Duda et al. 2020).

Reptile introductions in the Caribbean are a largely modern phenomena (Kemp et al. 2020), but the global economies that drive *Anolis* translocations in the Caribbean have their origins in colonial trade routes. Aspects of the species-isolation relationship could be tested only because of events catalyzed by European colonization (Helmus et al. 2014). For mammals, such introductions have largely been viewed in light of eradications rather than opportunities to study adaptation over microevolutionary timescales. For example, pigs arrived with Columbus's first settlement on Hispaniola (Deagan and Cruxent 1993). These pigs became vital to Haitian farming livelihoods over centuries and came to be known as Creole pigs distinct from other lineages because of this isolated history in Hispaniola. Their eradication by the US Agency for International Development in the 1970s (Moore 2017) devastated rural economies and erased this experiment in local adaptation.

Studies in invasion biology and responses to agriculture and urbanization are also possible only because of the human legacy of land use, such as the recent reforestation of Puerto Rico (e.g., Winchell et al. 2016). Historical events surrounding 1492 CE have served as hypotheses to test with sediment and pollen data from lake cores, such as gold mining and cattle introduction along the Ruta de Colón in Hispaniola (Castilla-Beltrán et al. 2020). Yet the events studied by paleoecologists could be broadened to include additional meaningful cultural events; for instance, did widespread plantation fires on the eve of the Haitian Revolution leave a charcoal spike?

Many field studies have been conducted in what are today protected areas but, in the past, had divergent, complex land use histories tied to colonial and more recent environmental policies. Tobago's Main Ridge Forest Reserve was protected to maintain precipitation regimes for colonial agriculture (UNESCO 2011). In the Dominican Republic, many national parks were created by Trujillo, a dictator in the 1930s–1960s, by forcibly removing people from their farms and homes (Holmes 2010). While we cannot and should not erase the past, it is possible to thoughtfully move forward. The Asa Wright Nature Centre is a key logistical nexus that, within the recent past, supported visiting international researchers and birding ecotourists alike in northern Trinidad. The center (pre-COVID pandemic) focused on supporting local livelihoods by training naturalist guides and collaborations with the University of the West Indies, St. Augustine. The center openly acknowledged its past as the Spring Hill Plantation (https://asawright.org/about-the-centre/a-brief-history/).

Centering the Caribbean

In the colonial period, the Caribbean was "a place on the periphery where one went to explore and take data" (McClellan 2010, p. 117), and this sentiment can still underlie research agendas originating outside of the region and impact our understanding of biological processes. To meaningfully move forward, Caribbean communities can no longer be seen as peripheral to Caribbean science. Non-Caribbean researchers must respect Caribbean scientists, communities, and knowledge by centering and following local policy, understanding priorities, and supporting research directives. This will have to be a concerted effort between Caribbean and foreign researchers, international and regional funders, as well as national policy makers and implementers. Doing so is essential to the collaborative production of both empirically accurate and culturally holistic science. Below we offer two examples of contemporary approaches to guiding and regulating biodiversity research and natural history collections within the Caribbean, one from Trinidad and Tobago and one from the Bahamas.

Trinidad and Tobago: Natural History and National Identity

The twin island nation of Trinidad and Tobago sits on South America's continental shelf and was once connected to the mainland, giving it a largely continental flora and fauna with few endemic species. This history makes it an ideal place to study facets of ecosystem decay, extinction debt, and disequilibrium, but we know very little about the timing and dynamics of this former land bridge (fig. 1). This information has conservation consequences, as little work has been done to delimit the divergences and thus genetic distinctiveness of Trinidad and Tobago populations deriving from continental species.

Such research is just formally beginning on Trinidad and Tobago since the last publication on fossil mammals 60 years ago (Wing 1962). While paleontologists studying other Caribbean islands contend with poor preservation, Trinidad has tar pit fossils preserved in asphalt seeps (Mychajliw et al. 2020). Knowledge of colonial oil prospecting led an international team to begin recontextualizing fossils discovered and exported while drilling in the early to mid-1900s. Piecing these Quaternary mammal fossils together has revealed previously unrecognized biodiversity and natural history heritage meaningful to the islands (fig. 1). They reinforce the narrative that Trinidad and Tobago was part of a Venezuelan grassland and contained megafauna such as ground sloths—providing an even more apt control for continental extinctions (Steadman et al. 2005). Most importantly, many fossils are returning to Trinidad and Tobago. While this nation lacks a formal paleontology community, international researchers have recently worked to form equitable collaborations that align with locally established expertise in related fields, such as microbiology. This marriage of expertise has resulted in entirely new lines of research for tar pit science on a global scale that would not have been considered otherwise (Mychajliw et al. 2020).

Instead of biogeographic research, Trinidad and Tobago's most famous research was conducted on the guppy, *Poecilia reticulata* (Peters 1859), named after Robert John Lechmere Guppy, who sent specimens to the Natural History Museum in London. The choice of scientific focus on this fish species and who has been able to participate in the associated research program has been historically shaped by non–Trinidad and Tobago scientists. A confluence of geographic and biologic factors allows for the study of short-lived populations with different predation intensities across a relatively small area, such that "it is possible to visit Trinidad for the first time and complete a publishable study within a few weeks" (Magurran 2005, p. 13). More than 1,000 publications have been published using Trinidadian guppies. Yet 2002 CE (see Evans et al. 2002) was the first year a Trinidadian author published on this system, and in 2012 CE, the first Trinidadian first-author manuscript was published (see Mohammed et al. 2012), which additionally highlights the limited accessibility to academic resources by local scientists and students. Despite the fact that these fish have now been dispersed in laboratories and wild systems globally, very little information about them is recorded in international databases (e.g., the Global Biodiversity Information Facility [GBIF], an international organization that focuses on making scientific data on biodiversity available via the internet; http://gbif.org), and very few samples are accessioned at any of the natural history museums in Trinidad and Tobago.

Several curated local natural history collections are based within Trinidad. The National Herbarium and the University of the West Indies Zoology Museum (UWIZM) are both located on the University of the West Indies (UWI) campus at St. Augustine (fig. 2). The first Trinidadian museum, the Imperial College of Tropical Agriculture (ICTA), was founded in 1921 and focused on agriculture pests, biasing what taxa are now available to current researchers. Both the National Herbarium and the ICTA agricultural collection were absorbed into UWI in 1960. Because of the ICTA, Trinidad and Tobago does have a fair number of locally curated specimens. While the Angostura Barcant Butterfly Collection (a privately held collection by the House of Angostura rum company, Angostura Holdings Limited) includes over 600 different species of butterflies, the collection of specimens coincided with colonial activity, and thus the geographic occurrences have biased the perceived historical distribution of certain butterflies. Conversely, large knowledge gaps remain with Trinidad and Tobago's archeology, where several publications cannot be accessed digitally (e.g., Reid 2018). The UWI masters program in Biodiversity Conservation and Sustainable Development in the Caribbean within the last decade has produced several graduates specialized in specific taxonomic fields not limited to insular Caribbean territories.

The Bahamas: Progressing toward Equitable Science

For over three decades, the Florida Museum (FM) and the National Museum of the Bahamas (NMB)/Antiquities, Monuments, and Museum Corporation (AMMC) have shared a peer-based, collaborative, and supportive relationship spanning paleontological and archeological natural history research

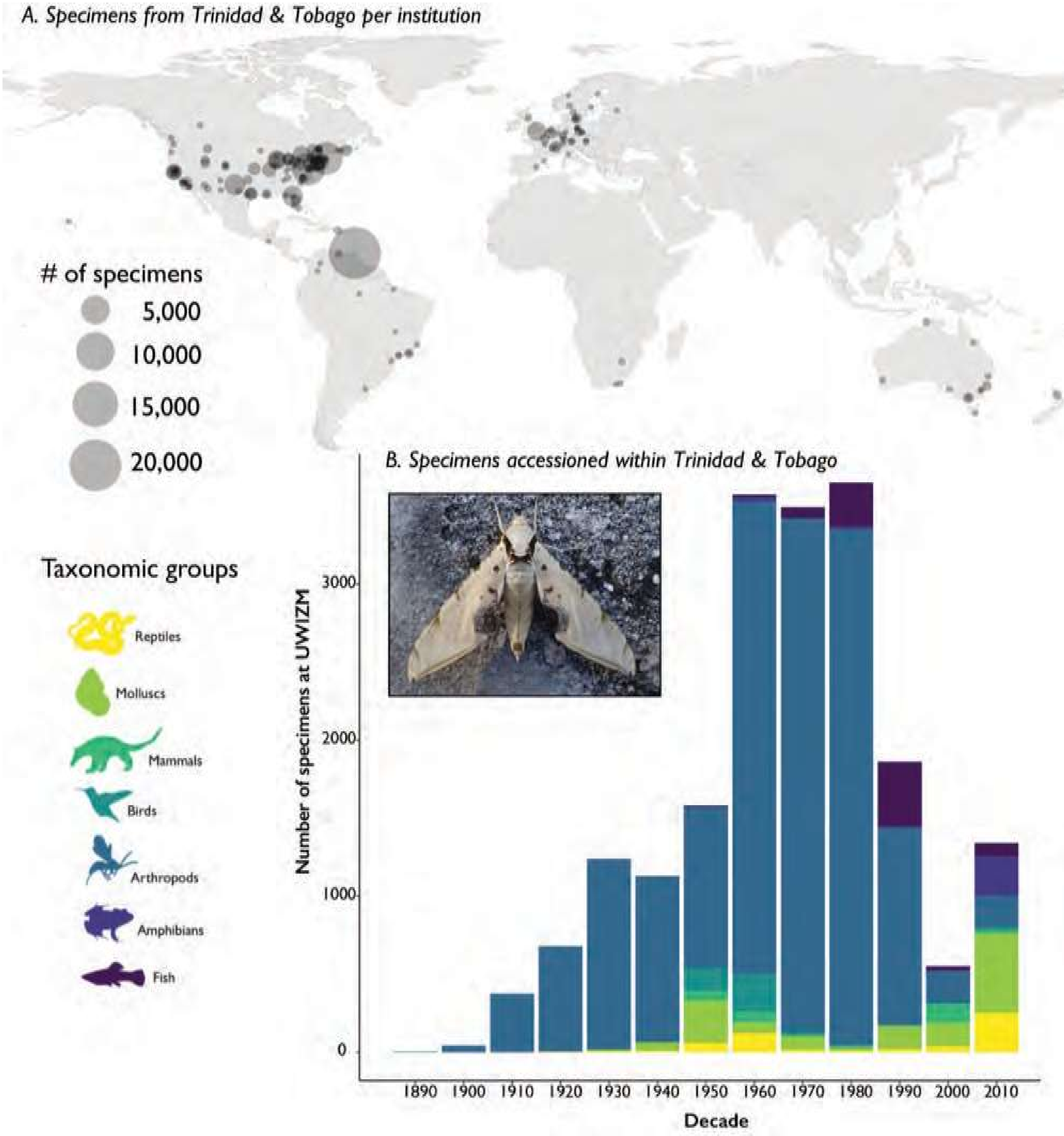

Figure 2: *A*, Number of specimens from Trinidad and Tobago in digital natural history collections worldwide. Each circle represents an institution; circle size represents the number of specimens in each institution's collections. The biggest collections are from the UWIZM (*n* p 20,182), the Harvard Museum of Comparative Zoology (*n* p 6,964), and the Smithsonian National Museum of Natural History (*n* p 6,767; https://www.gbif.org/country/TT/summary). R code used to produce the figures can be found at https://doi.org/10.5061/dryad.02v6wwq5b. *B*, Accessioning patterns within the UWIZM collection located in Trinidad and Tobago across select animal taxa through time. Local collections are dominated by arthropods, with early research focused on agricultural pests. *Inset*, one of the many Lepidopteran specimens (family Sphingidae) at the UWIZM. Photo by Ryan S. Mohammed. Symbols courtesy of phylopic.

and specimen curation (fig. 3). Since 2009, this relationship has been formalized through a living cooperative agreement. It is focused on a shared vision of mutually beneficial support and the leveraging of resources across both the FM and the AMMC for the documentation, curation, and conservation of the Bahamas's natural and cultural history. Primary to this agreement and the success of the relationship are partnerships in interdisciplinary research design, field excursions, and laboratory analyses; explicit acknowledgment that all Bahamian collections are the property

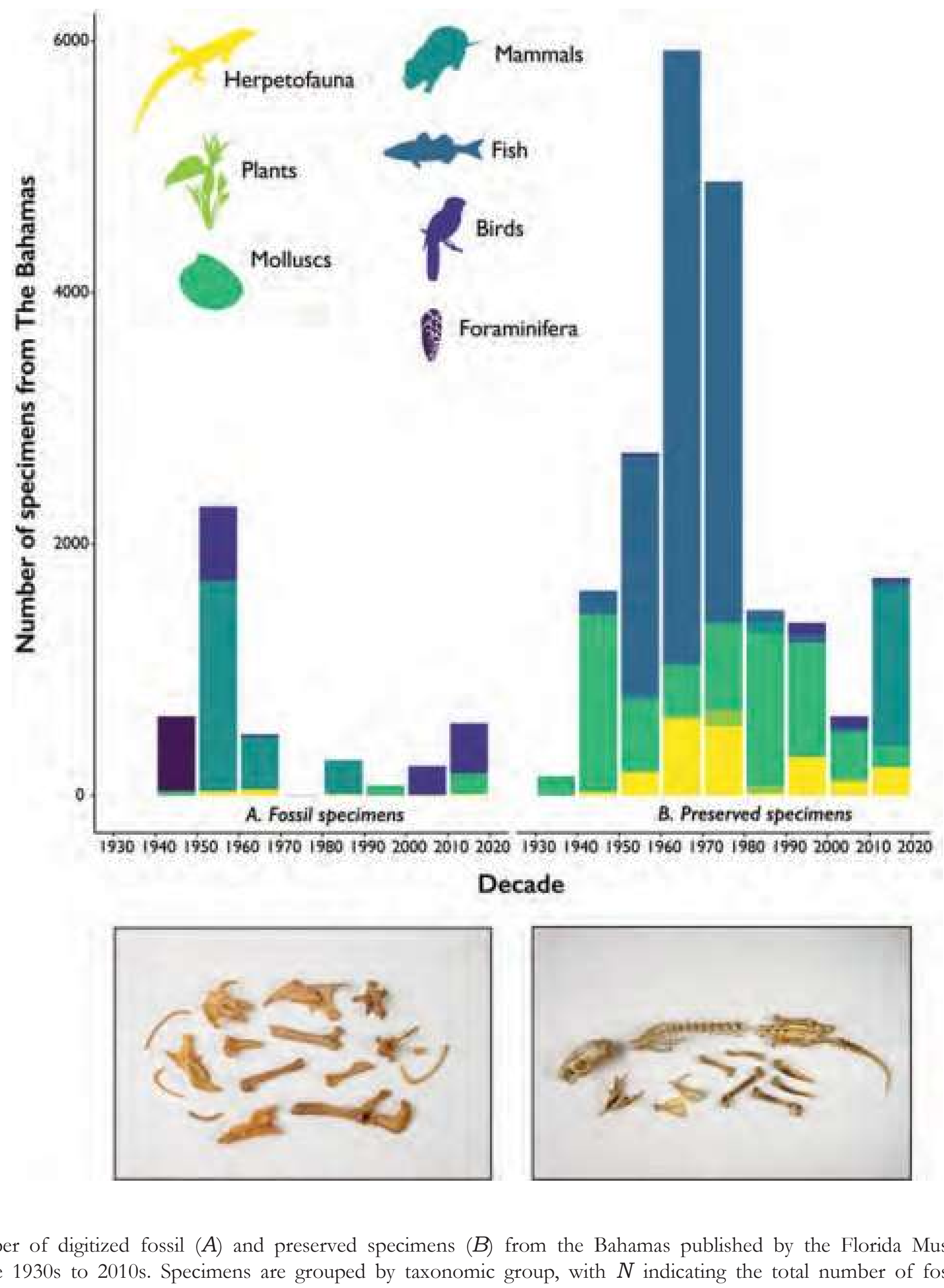

Figure 3: Number of digitized fossil (*A*) and preserved specimens (*B*) from the Bahamas published by the Florida Museum during each decade from the 1930s to 2010s. Specimens are grouped by taxonomic group, with *N* indicating the total number of fossil and preserved specimens from each taxonomic group. Data are accessed through GBIF (https://doi.org/10.15468/dl.n55a8m). R code used to produce the figures can be found at https://doi.org/10.5061/dryad.02v6wwq5b. Symbols courtesy of phylopic. *Bottom*, photos of Bahamian hutia (*Geocapromys ingrahami*) fossil specimens from Garden Cave, Eleuthera (NMB.EL229.002; *left*) and contemporary specimens collected in 1987 from Little Wax Cay (UF 24168, Mammals Collection; *right*). Photos by Kristen Grace/Florida Museum.

and heritage of the Bahamas; shared museum specimen catalogs and implementation of AMMC guidelines for specimen accession and site numbers; local Bahamian museum exhibit designs and implementation; the codevelopment of K–12 educational materials; collaborative consultations for public archeological outreach and site preservation; and securing funds for research, specimen curation, and mentorship and training opportunities for Bahamian and American early career professionals. Thus far, two persons from the AMMC have obtained graduate degrees at the University of Florida during the agreement.

While the AMMC and FM have collaborated across numerous Bahamian natural history sites, a particularly poignant example of the peer relationship between the AMMC and FM has been in research based on Abaco Island. From 2004 to 2019, the AMMC field office in Marsh Harbour, Abaco, curated the largest natural history collection and associated research laboratory in the Bahamas. The collection represented natural and cultural history specimens and artifacts spanning prehuman, Indigenous (e.g., Lucayan), and colonial eras. This collection largely comprises fossil vertebrate specimens obtained through research awards funded by the National Science Foundation to the FM as well as associated FM research endowments in support of collaborative research with AMMC curators, staff, and Bahamian and American graduate students. Leveraging FM catalog numbers and AMMC site numbers, these collections were cross-curated between the institutions, with approximately half of the physical specimens housed for study at the field office on Abaco and the other half at the FM. Up until the summer of 2019, these collections were actively growing, including archeological investigations across a number of highly vulnerable, eroding coastal sites around Abaco and surrounding cays. This work was funded through the National Geographic Society to co–principal investigators from the FM and AMMC and included field training for an AMMC early career archeology professional, FM undergraduate and postbaccalaureate students, as well as in-field workshops for local primary education teachers.

On September 1 and 2, 2019, category 5 Hurricane Dorian made landfall on Abaco and Grand Bahama. The effects of this storm were and, in many ways, remain nothing short of devastating to the people and infrastructure of these islands. Among the devastation was the complete loss of the AMMC museum and laboratory facility in Marsh Harbour as well as many of the sites represented in its collections. With the full support of the NMB/AMMC, the FM mounted a rescue effort 3 weeks after the hurricane. A significant portion of the collection—representing over 40 natural history and heritage sites across 14 different Bahamian islands and some Abaco heritage sites—was recovered in various states of preservation. With funding from the National Science Foundation's Collections in Support of Biological Research program awarded to the FM, the salvaged AMMC collection is currently housed at the FM, where it is being restored and conserved through equitable decision-making and collaboration among personnel from both the FM and the AMMC. This effort includes renewal of the cooperative agreement, FM collection visits by AMMC colleagues, and the first phases of repatriating studied specimens (e.g., assemblages from archeological sites on Abaco).

More broadly, in March 2021, the Bahamas government enacted new legislation to safeguard and regulate the access and use of biological resources and traditional knowledge obtained from the Bahamas. The Biological Resources and Traditional Knowledge Act seeks to prevent the inequitable access and distribution of benefits derived from Bahamian resources, as has frequently occurred in the past and resulted in fragmented Bahamian collections throughout the world. The act requires the approval of research permits by all governmental and nongovernmental stakeholders through a single portal administered by the Department of Environmental Planning and Protection. The act further necessitates the tracking of past, current, and future collections. In so doing, the act seeks to address colonial legacies in research and collections from the Bahamas.

Collecting Practices: Past, Present, and Future

Colonial practices, such as private collecting, impacted where and how natural history resources are stored and who has access to them. Although private collections can play an important role in evolutionary biology and other aspects of the natural sciences, scientists must have access to them first. Only three Dominican amber fossils of *Anolis* had been described prior to the recent description of 17 privately owned amber fossils of *Anolis*, providing evidence of the stability of some *Anolis* ecomorphs since the Miocene (Sherratt et al. 2015). Phylogenetic calibrations for well-studied Caribbean radiations rely on coveted, rare deep-time fossils. While some private collections may be extensive (e.g., the Barcant butterfly collection, Angostura, Trinidad) and open to the public for viewing, not all of them are well curated or digitized. In some cases, the lack of specimen metadata (e.g., locality, collection date) limit their discoverability and research utility.

Extractive sampling and curation practices impact the entire scientific community but particularly the communities from which the samples originated. Today, scientists from outside of the Caribbean make annual research expeditions to run behavioral studies, collect phenotypic and genotypic data, document species ranges, excavate archeological or paleontological sites, or run large-scale manipulative studies using plots of land or even individual islands as replicates. Extractive sampling combined with a history of chronic underfunding for local museum infrastructure indicates that many Caribbean nations lack the museum specimens necessary for comparative research, temporal studies, and systematics. Caribbean scientists must often travel to Europe or continental North America to visit collections, and early-career scientists may need to go abroad to complete their studies. Indeed, the Caribbean has among the highest percentages of tertiary educated emigration in the world (Docquier and Schiff 2008). When scientists leave the Caribbean to pursue professional opportunities unavailable in their home country, this creates local gaps in training and expertise.

Despite these challenges, Caribbean scientists have always played an instrumental role in developing regional collections and existing infrastructure that continue to advance biodiversity science and inspire Caribbean communities today. Caribbean museums and other institutions, such as the Trinidad and Tobago Field Naturalist's Club (TTFNC), remain important venues for the publication of Caribbean-based research, with a particular focus on taxonomy, natural history, and paleontology (e.g., *Novitates Caribea*, *Revista Digital de Arqueología de Cuba y el Caribe*, *Journal of the Barbados Museum and Historical Society*, and *Living World Journal* of the TTFNC). Though Caribbean authors have not always been included in internationally led papers (Tydecks et al. 2018; Maas et al. 2021), they are nonetheless prolific contributors to documenting and analyzing Caribbean biodiversity. By not referencing this regional literature, nonlocal researchers may be missing key revisions, occurrences, or observations that detract from the strength of their studies and, by not citing this literature, may miss opportunities for collaboration and professional development of the Caribbean's academics (Pettorelli et al. 2021).

While biologists may consider natural history specimens as neutral items, these same specimens, when part of museum exhibits, serve as building blocks of identity; natural history exhibits can also be national history exhibits (Cummins 2013). The early histories of museums in the Caribbean are varied, but an aim of many was to curate a homogeneous colonization narrative (e.g., 1930s Survey of Museums in the British Empire; Galla 2013). But as local collections are built and some specimens return to their countries of origin, new exhibits can be created that tell stories of importance to national heritage. For example, the Museo Nacional de Historia Natural of the Dominican Republic has recently developed an evolution exhibit (Sala Historia de Vida) that features endemic mammals such as *Nesophontes* excavated by a Dominican paleontologist.

Natural history collections are increasingly revisited through a new lens of global change threats (Thompson et al. 2021). But the dearth of local collections hinders tracking and responding to biodiversity-based challenges in the region, and existing collections often do not reflect local applications or the priorities of local researchers (Baker et al. 2019; Armenteras 2021). For example, while researchers have focused intently on rare endemic species, there are relatively few physical samples of invasive mammals; rats and mongoose are virtually absent from zoological collections yet remain a costly legacy of colonial practices for local governments. This line of use also underscores the need for US and European institutions that hold Caribbean specimens to actively engage with institutions in the specimen country of origin. International museum collections, particularly ones built by historical collectors, may have unintentionally captured key moments in global change transitions. Coastal erosion or land use change may have erased some of these habitats where the flora and fauna were extracted, making it impossible to build new local collections documenting these same organisms or ecosystems.

Considering these historical asymmetries, a stated goal of GBIF is to "digitize biodiversity data from specimens in developed countries that were originally collected in other parts of the world, so that the data can be easily shared with the countries of origin" (Edwards 2004, p. 32). Yet specialized expertise and necessary technological infrastructure can be required to use these data sets, which can limit their accessibility to researchers in the specimens' countries of origin. While the mission of increasing access to biodiversity data is notably positive, caution should be taken when emphasizing the value of digital data in relation to physical natural history collections, given that not all data and outreach extensions can be drawn from electronic sources.

GBIF contains roughly 1 million records of digitized natural history specimens representing the Caribbean. By comparison, there are now 5 million records from the Caribbean-derived georeferenced photographs uploaded through the citizen science platforms iNaturalist and eBird (Sullivan et al. 2014). This is unsurprising, given the magnitude of tourism in the region, and remote users of these digital data sets should be aware of potential biases associated with tourist-derived data. For example, preserved specimens may have been collected from different time points and locations than tourist sightings (fig. 4), and such biased sampling can lead to improper characterization of a species' ecological niche (Boakes et al. 2010; Torres-Cristiani et al. 2020). However, tourism can be positively harnessed by Caribbean scientific organizations to collect data in line with local research priorities. The Environmental Research Institute Charlotteville of Tobago encourages recreational divers to participate in its Reef Check (https://www.reefcheck.org) program, and locally trained guides lead inventories on forest biodiversity (https://www.eric-tobago.org/forest-check-tobago.html). These data sets have

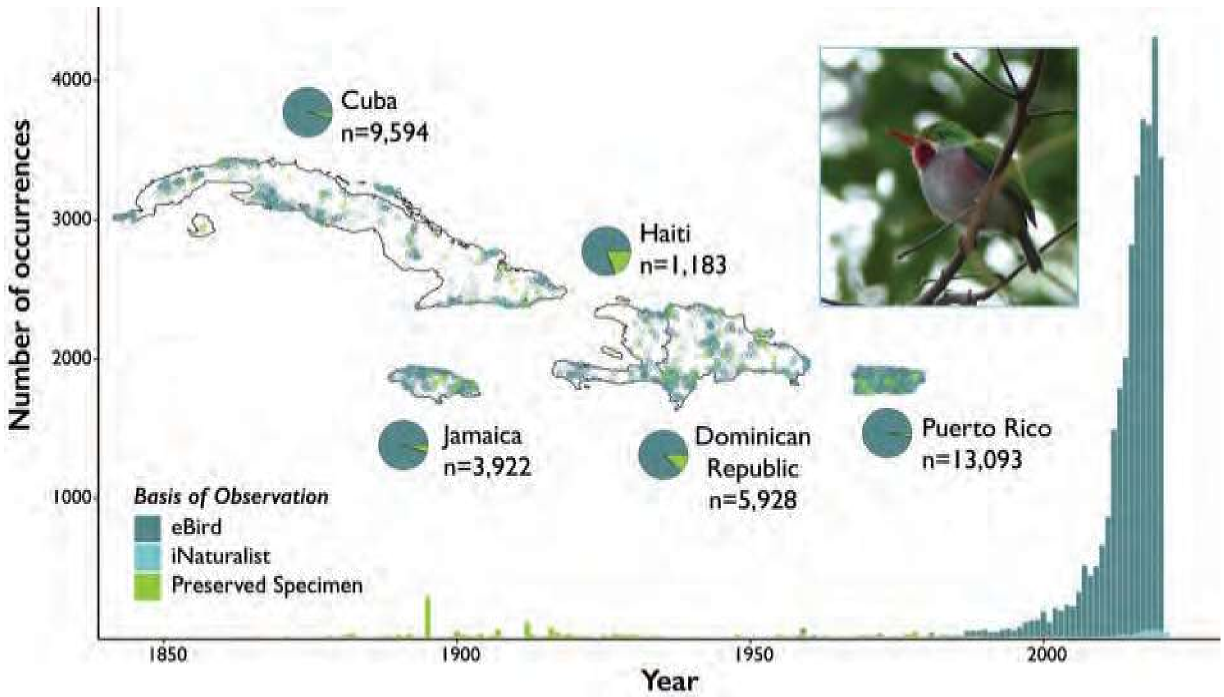

Figure 4: Differing spatial and temporal distributions of citizen science (iNaturalist, eBird) and physical specimen occurrence data from GBIF for an endemic and charismatic radiation of birds, the todies (family Todidae, genus *Todus*), in the Greater Antilles. Photo by iNaturalist user krisskinou (https://www.inaturalist.org/observations/21873982). R code used to produce the figures can be found at https://doi.org/10.5061/dryad.02v6wwq5b.

resulted in publications utilizing citizen science (e.g., Fanovich et al. 2017) and were used in support of the recent UNESCO North-East Tobago Man and the Biosphere Reserve designation (NETMABR).

Conclusion

In 1880, a foundational biogeographic text, *Island Life*, noted that "in islands we have the facts of distribution often presented to us in their simplest forms . . . we are therefore able to proceed step by step in the solution of the problems they present" (Wallace 2013, p. 123). Scientists have proceeded through the Caribbean in this way, distilling ecological and evolutionary observations into foundational theories, turning a diverse ecosystem into a replicated biogeographic laboratory. Laboratories are meant to control variables in the service of experimentation, and Caribbean islands are sometimes construed as untouched until European contact. Against this backdrop, much research has been devoted to how biological communities assemble, tracing the arc of species death and life then replicated across islands to disentangle causative processes. Yet the Caribbean's past reveals that these are humanized spaces, and the persistence of the biodiversity that scientists wish to study is inextricably linked to ongoing interactions with the human communities who inhabit this region now and who have done so for generations.

When rooted within local human communities, research priorities may change and lead to data that are of use and readily accessible to solving local problems of today and the future (e.g., Eelderink et al. 2020; Iwama et al. 2021). However, while not all research programs may lead to direct applications or are situated in an applied context, they should all meet the same ethical responsibilities in acknowledging and averting colonial dynamics. For centuries, islands have been places to address fundamental scientific questions about how the world works, and their explanatory power can be strengthened only through engagement with their complex human pasts; "no human impact" can no longer be the default assumption when designing hypotheses. Placing the burden to exclude humans as an explanatory variable on biologists—rather than assuming human impacts are negligible—not only represents an opportunity for collaboration across disciplines but also strengthens the validity of biological research results. Accurately recognizing humans as part of insular—and therefore ecological and evolutionary—histories requires a reframing of these natural laboratories as socioecological landscapes where people have and continue to live.

Acknowledgments

We are grateful to the many Caribbean institutions, organizations, scientists, communities, colleagues, students, and friends who have pioneered biodiversity research and natural history collections. This author list includesa range of Caribbean and non-Caribbean scholars, and we acknowledge that our views may not represent the whole region; we hope this contribution provokes critical reflection, discussion, and action that advances practice in the region.
L.M.D. was supported in part by the National Science Foundation (NSF; DGE 1633299). M.J.L. was supported in part by the NSF (RAPID CSBR 2010764). This work was supported by the National Socio-Environmental Synthesis Center (SESYNC) under funding received from the NSF (DBI 1639145). A.M.M. and R.S.M. thank the La Brea Tar Pits and Museum and the National Trust of Trinidad and Tobago. David Steadman and William Keegan offered comments on previous versions of the Bahamas text. Angelo Soto-Centeno, Lázaro Vinola, and Joha Orihuela provided helpful guidance on earlier drafts.

Statement of Authorship

R.S.M. conceived and directed the planning, with input from M.K., M.J.L., and A.M.M. A.A.W. and M.S. analyzed the historical data, with assistance from A.M.M. R.S.M., M.K., M.J.L., and A.M.M. wrote the first draft of the manuscript, with all other authors contributing with case study examples and participating in revision of the final manuscript.

Data and Code Availability

We consolidated both of the personal GitHub code archives (https://github.com/ashleywrean/colonialism-biodiversity, https://github.com/mylesstokowski/colonial-sci) into a single Dryad entry (https://doi.org/10.5061/dryad.02v6wwq5b). Note that our code directly pulls from the GBIF and other relevant databases and therefore is responsive to database updates; users can employ our code to make the most up-to-date (and therefore accurate) analyses on the basis of new additions to these databases. Anyone can use this code to remake our figures and see updates if any new specimens have been accessioned/digitized. GBIF and iNaturalist are well-established, open-access databases that we do not foresee being inaccessible in the near future—we see these databases as even more accessible and universally used than Dryad.

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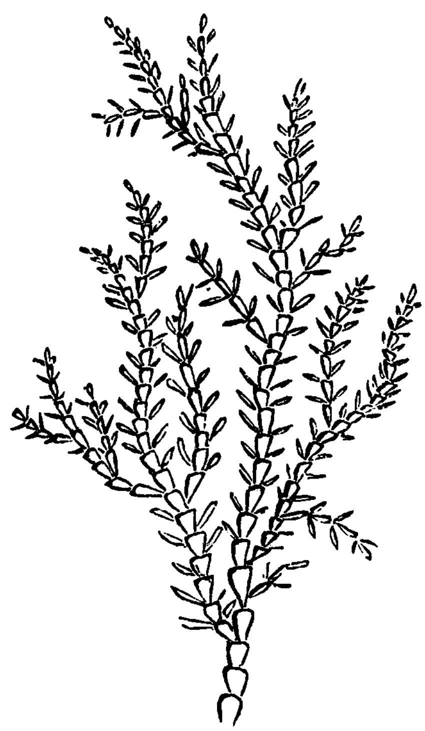

"On every part, encrusted in their lime covering which moulds itself to the joints, swellings, depressions, ridges, or into the flutings and channels of the surface, or surmounts the very tips in the form of seed-vessels, one would scarcely suppose that these elegant marine productions—so abundant in every tide pool, and fringing the deep cool grottos beneath the water-covered rocks, or lining with patches of pleasing and varied colors their sides, or laying down tessellated and mosaic pavements, by encrusted pebbles presenting to the vision variety springing from their secreted cements—were sea-weeds and marine vegetation." Figured: "These lime-bearing algæ . . . the Corallines." From "The Sea-Weeds at Home and Abroad" by John L. Russell (*The American Naturalist*, 1870, 4:274–297).