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Historical ecology of the Swan Islands (Islas del Cisne) chronicles long-term anthropogenic changes in the Western Caribbean

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Abstract

The Swan Islands in the western Caribbean Sea are two of the most remote islands in the region given their diminutive size, distance from land masses, relative isolation from larger human settlements, and lack of accessibility historically. Despite these features, they have been highly sought out by a succession of explorers, naturalists, and biologists since the late 1800s under the guise of studying "pristine" natural places seemingly unspoiled by humans. Here we draw on a rich compendium of historical resources to provide the first synthesis of these early observations which have left a credible record of ecological changes from the pre-contact period to the present. Our detailed analysis shows that, despite their remoteness, these islands have succumbed to a host of deleterious human activities coupled with a series of catastrophic natural events. We find that these effects were minimal or non-existent during the early stages of Indigenous settlement and first European incursion, with only a brief period of localized human impacts in the mid-to late-1600s. However, centuries later in the 1850s, anthropogenic change dramatically accelerated, resulting in widespread deforestation; the introduction of invasive plants and animals; loss of seabirds and turtle nesting beaches; and the extinction of endemic species of reptiles, land snails, and a rodent. These changes contributed to a degradation of the surrounding marine environment which, coupled with severe overfishing and catastrophic natural events, culminated in a rapid collapse of coral reefs after 2007. Our findings show that an understanding of the long-term historical ecology of these unique and vulnerable islands offers valuable insights for the development of a practical and suitably ambitious strategy for their future management and restoration.

1 Introduction

In February 1887, Charles Haskins Townsend, naturalist on the United States research vessel *USFC Albatross*, set foot on the Swan Islands (Fig. 1). He was likely the first biologist to visit these remote coral outcrops in the western Caribbean Sea and spent time collecting birds, reptiles, and specimens of a small mammal unique to the islands, the Little Swan Island hutia, *Geocapromys thoracatus*, now extinct [111, 133, 162].

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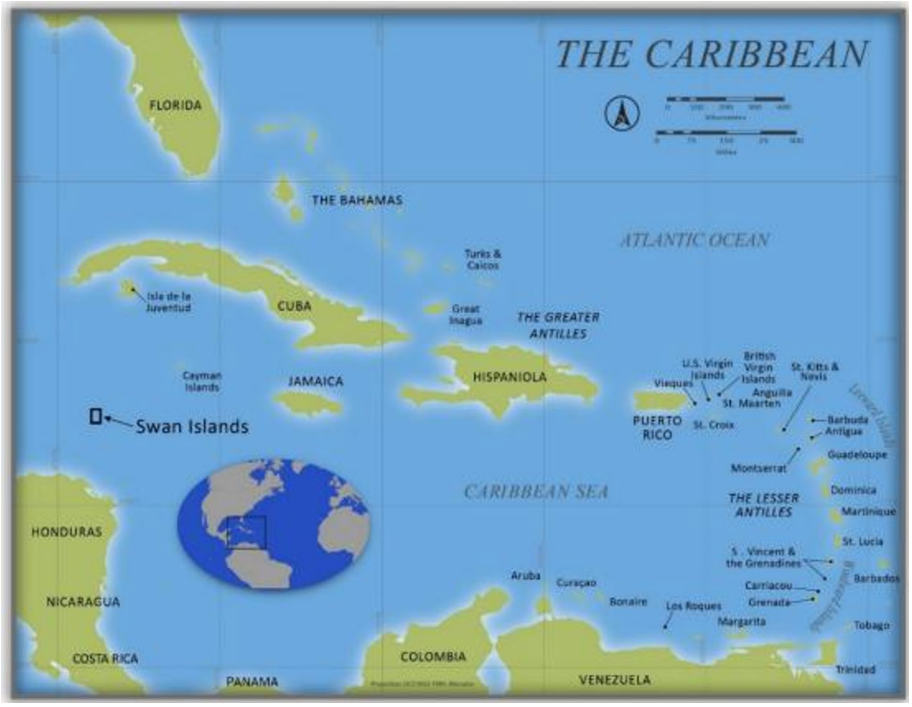


Fig. 1 Regional map of the Caribbean showing the location of the Swan Islands in the western Caribbean Sea (black box). Base map adapted from Wikimedia Commons [171]

Almost 21 years later, on 18 January 1908, the private steam yacht *Zenaida* dropped anchor in what is now known as Harbor Bay on the western end of Great Swan Island [95]. On board was an English surgeon, naturalist, and ornithologist, Percy Roycroft Lowe, private physician to the British aristocrat Sir Frederic John William Johnstone, the owner of the *Zenaida* [82]. For the next three weeks Lowe, with the assistance of the *Zenaida*'s crew, explored Great Swan Island and its sister island, Little Swan Island, boated and waded across the islands' coral reefs with a "fish glass" and boat hook, and fished the waters around the islands with Sir Johnstone and his wife Laura, Countess of Wilton, both avid sport fishers. Lowe collected specimens, took photographs, and made detailed notes of the vegetation, invertebrates, birds, reptiles, mammals, coral reefs, and fish, and published his observations in *A Naturalist on Desert Islands* [95]. In so doing, he created the first comprehensive record—an invaluable 1908 baseline—of the biodiversity and bioabundance of the terrestrial and marine ecosystems of the Swan Islands. He provided descriptive and photographic evidence of thickly wooded islands with large colonies of nesting seabirds, swarms of tame green iguanas, and a tropical ocean filled with massive and plentiful fish "… which ought to satisfy the most blasé and travelled angler in search of fresh ground and fresh conquests for his rod and line." ([95], p. 69)

Following Townsend and Lowe, a succession of explorers, adventurers, naturalists, and biologists have visited the Swan Islands for a multitude of reasons, including the expectation that, by virtue of their remoteness, they harbored unusual species and escaped the worst of the myriad anthropogenic impacts that have affected many other Caribbean islands commencing from when they were first colonized by Indigenous groups. These impacts include deforestation, introduction of non-native species, overfishing, overhunting, pollution, disease, over-population, and coral bleaching associated with a changing climate, culminating in loss of biodiversity and bioabundance [4, 10, 28, 42,

51, 55, 77, 78, 100, 101, 103, 173]. The list of visitors includes some of the most prominent natural historians, conservationists and explorers of their time. Their collections, observations and scientific surveys leave a credible record of change in the terrestrial and marine environments of the Swan Islands up to 2024, the year of the latest surveys of the islands.

In this paper, we compile this rich archival record and integrate it with other historical information on human activities in the Swan Islands to create the first synthesis of the ecological changes that have occurred on these islands from pre-European contact to the present. We take a holistic "ridge to reef" approach that examines the human activities and ecological changes that have occurred both on land and in the adjacent marine environment and their potential linkages [120, 164]. This provides a more integrated understanding of the historical ecology of these islands and has allowed us to consider the role of biotic interconnections when assessing the effects of human activities shaping their land- and seascapes [50, 139].

From an applied perspective, the value of historical ecological data for the management and restoration of ecosystems lies in its ability to comprehend intergenerational loss of information on species biodiversity and abundance and provide insights on the long-term magnitude of ecological changes [35, 102, 153, 172]. We believe that the detailed information on the historical ecology of the Swan Islands provided in this study is vital for illuminating the range of possibilities for the future of these islands.

The goals of our historical ecological analysis are to:

- reconstruct the nature and timing of the ecological changes that have occurred in the Swan Islands from the pre-European contact period to the present and consider the role of human activities and natural events in driving these changes;
- examine potential connections between ecological changes on land and in the adjacent marine environment;
- consider the role of remoteness in affecting the trajectory of ecological change compared to the wider insular Caribbean, and;
- harness this historical knowledge as a reference for the development of a realistically ambitious strategy for the protection and restoration of the Swan Islands.

We have organized the historical information on the Swan Islands into four sections. In Sect. 4 we present an overview of the history of discovery, settlement, and resource use to reveal the timing and extent of human impacts. In Sect. 5 we provide an overview of scientific surveys that have taken place at the islands and in a supplement accompanying this section (Supplement 2: Biological Surveys of the Swan Islands [1887–2024]) we present the detailed observations made during these surveys. In Sect. 6 we provide a historical compilation of major hurricanes impacting the islands. In Sect. 7 we synthesize these three sources of archival information to provide a reconstruction of the historical ecology of the Swan Islands segmented into specific time periods.

Overall, we demonstrate that the relative remoteness of these islands provided considerable protection from major human impacts until the 1850s when anthropogenic change accelerated significantly, resulting in serious degradation of the terrestrial ecosystem and ultimately the collapse of the surrounding coral reefs. We argue that these unique but now degraded islands require the development of a holistic protection and

restoration strategy underpinned by an understanding of their long-term historical ecology.

2 Materials and methods

We undertook an extensive search for historical information on the human and natural history of the Swan Islands. Information sources included books and published papers dating back to 1816, historical maps and drawings, government documents, magazine articles, unpublished reports, newspaper clippings, company records, websites, personal blogs, YouTube videos, photographs, and personal communications. We compiled information from 19 biological surveys of the Swan Islands dating back to 1887 up to the most recent in 2024.

We extracted information from quantitative surveys of coral reef health carried out around the Swan Islands in 2011 and 2013 from the AGGRA Data Explorer (Atlantic and Gulf Rapid Reef Assessment (AGRRA), [5]). Hurricanes are potentially catastrophic events that have occurred naturally in the Caribbean for thousands of years [17, 104, 141] and can cause severe damage to terrestrial and nearshore ecosystems of Caribbean islands, including forests and coral reefs [135, 136, 155, 174]. To assess the historical influence of hurricanes in shaping the ecology of the Swan Islands, we extracted historical data on hurricanes passing within 60 nautical miles of the Swan Islands with wind speeds of Category 1–5 using NOAA's Historical Hurricane Tracks, an online tool that allows users to search for and track the paths and changing intensities of historic hurricanes (National Oceanic and Atmospheric Administration (NOAA), [116]). This site contains global hurricane data going back as far as 1851. The specific location term used in the search was: Great Swan Island, Islas del Cisne, Bay Islands, Honduras. We searched for historical maps referencing the Swan Islands or their historical toponyms using Caribmap, a Web resource (http://www.caribmap.org) of high-resolution map images of Caribbean Islands printed since the early sixteenth century [70].

3 Geographical setting

The Swan Islands (Islas del Cisne) (17° 24′ 60″ N, 83° 54′ 59″ W), which are administered by Honduras, consist of two small, raised coralline islands on the southern flank of the Cayman Trough in the western Caribbean Sea near the southern boundary of the Mesoamerican Reef, the Atlantic Ocean's largest interconnected coral reef system (Figs. 1 and 2 and Supplement 1).

Great Swan (= *Isla Grande/Cisne Grande*), the largest island (about 1 × 3 km)[1] is mostly low-lying with a maximum elevation of about 19 m. It is separated from smaller Little Swan Island (= *Isla Pequeño/Cisne Pequeño*) (about 0.8 × 2.4 km) by a channel about 200 m wide. Little Swan Island is topographically more rugged, surrounded by near vertical cliffs of reef limestone more than 10 m high, and has a maximum elevation of about 26 m. There is a tiny islet, Booby Cay (*Cayo del Pájaro Bobo*) (about 160 m long) off the southwest corner of Great Swan Island that is accessible by wading at low tide. The two main islands have a combined area of about 3.6 km^2 (360 hectares).

Temperatures in the Swan Islands typically vary from 25 to 32 °C (77–90 °F) and the islands experience extreme seasonal variation in monthly rainfall [167, 168]. The dry

[1] Distances, areas and elevations estimated using Google Earth Pro.

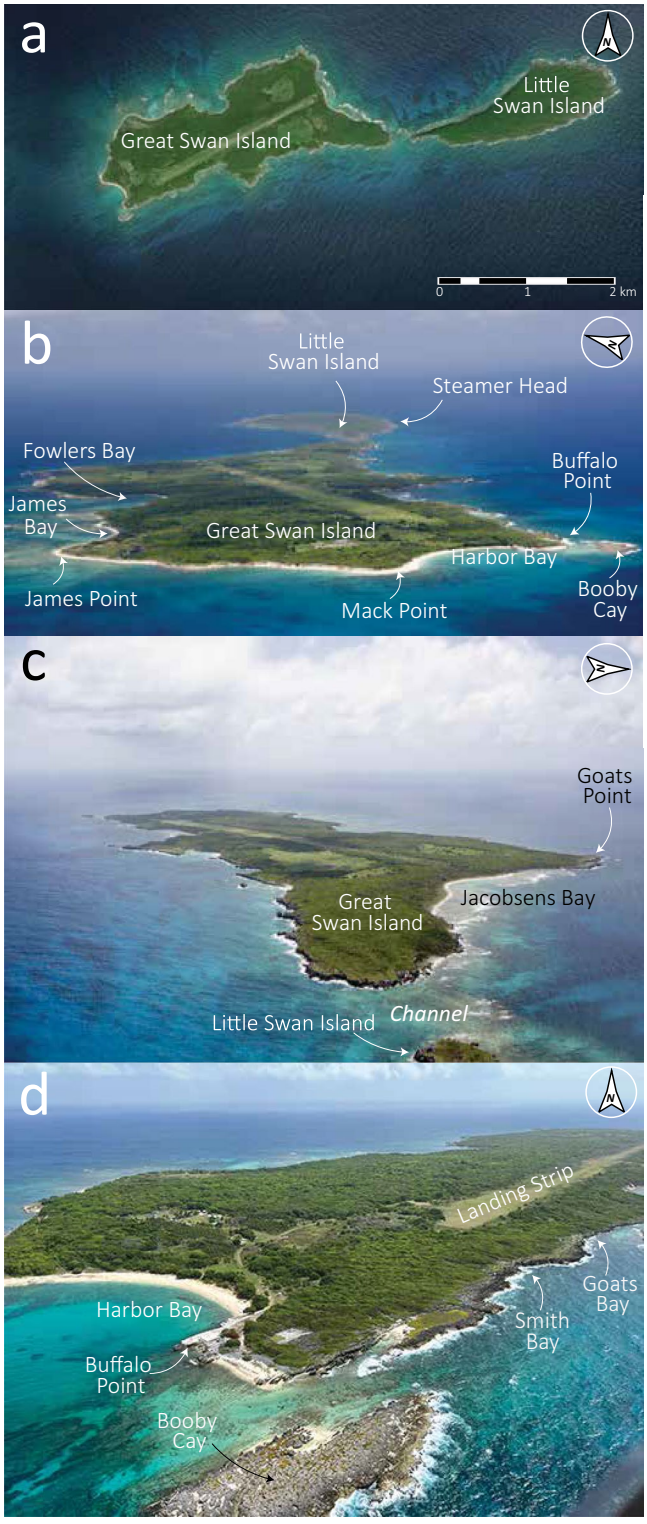


Fig. 2 Satellite and aerial views of the Swan Islands. a. Satellite image taken on 29 June 2023. Source: Google Earth. b, c, and d. Aerial views showing some English location names.

season extends from about December to May and the wet season from about June to November. Annual rainfall is greater than 1000 mm, with about 80% of this falling during the wet season. There are no permanent sources of freshwater on the islands except for an ephemeral brackish-water pond near the southeast corner of Great Swan Island. McCranie ([105], pp. 26-27) classified the forests on the Swan Islands as Lowland Dry Forest, West Indian Subregion.

The Swan Islands are two of the most remote islands in the region given their diminutive size, distance from other land masses, relative isolation from larger human settlements, and lack of accessibility historically. The closest large land masses to the Swan Islands are mainland Honduras, about 170 km to the south, and mainland Belize, about 460 km to the west. The Swan Islands are therefore more insulated from anthropogenic nutrient and sediment pollution originating from mainland regions. The closest islands are the Bay Islands (*Islas de la Bahia)* (about 225 km away), Grand Cayman (335 km), Cuba (500 km), and Jamaica (595 km). There is a grass airstrip on Great Swan Island suitable for rugged aircraft, but there are no regularly scheduled flights. The islands currently have no permanent residents, but Great Swan Island is occupied by a small Honduran naval garrison of less than a dozen personnel who rotate about every four to six weeks ([106]; Germer, personal communication).

4 History of human discovery, settlement, and resource use in the Swan Islands

Refer to Fig. 3 for a summary timeline of human history in the Swan Islands.

4.1 Pre-contact period (5000 BCE – CE 1492)

It is possible that the Swan Islands never experienced any pre-contact settlement because of their small size and remoteness and the presence of the swift Caribbean and Yucatán Currents which flow westward through the Lesser Antilles and from northern Honduras through the Yucatán Channel, respectively, and which would have presented a formidable barrier for voyagers travelling eastward in paddle-propelled canoes [48]. This is the position that Lowe [95] took:

> *… for there does not seem any reason to suppose that the Mosquito Indians, who lived along the shores of the [Central American] mainland, ever had a settlement on the island [Great Swan] or were even likely to have visited it. These Indians were, as we know from Dampier, notoriously skilful with their canoes, and were past-masters*

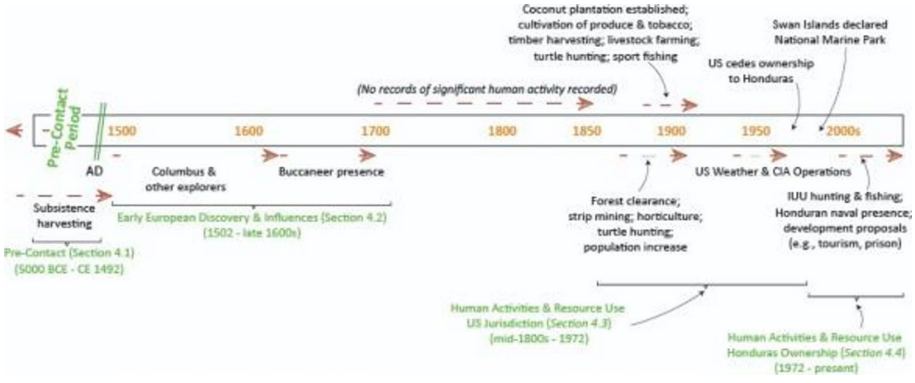


Fig. 3 Timeline of human discovery, settlement, and resource use in the Swan Islands

> *in the art of harpooning turtle and big fish; but ninety-eight miles of open ocean would have been a very formidable voyage to undertake in their cockle-boats, even if there had been any good object in going so far, or even if there had been any likelihood of their hitting off such low-lying islands. Moreover, as the shores of Honduras swarmed with turtle and fish of every kind and description, even the quantities present around Swan Island would have presented no attractions. (Lowe, [95], p. 27)*

However, as Lowe acknowledged, the Indigenous people of the Eastern Caribbean islands were adept seafarers [8, 48]. We also know that, starting some 7000 years ago, Archaic and Ceramic Age peoples who settled the Caribbean undertook extended open-ocean voyages of hundreds, even thousands, of kilometers in their canoes from various jumping off points along the South American littoral and possibly elsewhere [15, 43, 49, 115]. They eventually discovered and settled almost all the islands of the Caribbean and established an active maritime highway stretching some 2500 km from Cuba to Trinidad and the South American mainland before the arrival of Columbus. It is thus possible that pre-contact people were aware of the Swan Islands and visited them, at least occasionally, though there are instances in the Caribbean where islands never appear to have been settled before Europeans (as is the case with the Cayman Islands, for example); [152]. In this regard, Lord Moyne, who visited the Swan Islands in his yacht *Rosaura* for two days in 1937 reported ([113], pp. 81 and 82):

> *Mr. Cardinall [Commissioner of the Cayman Islands] told us [while Lord Moyne was visiting Grand Cayman] that the Grand Cayman labourers who go to Swan Island [Great Swan Island] to cultivate coconuts reported the existence of a mound of shells which resemble the kitchen middens left elsewhere by long-extinct Carib Indian migrants.*
>
> *We arranged to hire some sturdy islanders [while Lord Moyne was on Great Swan Island] to turn over the mound of trochid shells of which Mr. Cardinall had told us, while we sifted from it a pile of thick broken pottery which when reconstructed proved to be of calabash shape. This confirmed Mr Cardinall's opinion that the shell mound was probably left by the Carib Indians who came up centuries ago from the coast of Venezuela and spread over the islands of the Caribbean.*

John Colman, who was the marine biologist on board Lord Moyne's yacht, also recorded that:

> *There is a large kitchen-midden on the western island [Great Swan Island] containing crude pottery and burnt shells, which shows that Indians once lived there ([25], p. 123).*

A midden filled with burned shells, including top shells (likely *Cittarium pica*), suggests that marine mollusks were abundant historically on the Swan Islands and potentially used as a food resource by pre-contact people.

4.2 Early european discovery and influences (1502 – late 1600s)

Columbus and his crew appear to have been the first Europeans to encounter the Swan Islands on their way to Cape Gracias a Dios in Central America in July 1502 during his fourth voyage [24], p. 296; [45], p. 180; [81], Chapter I, Section XIII; [170], p. 57). Records suggest that the crew had to dig pits in the sand to find freshwater, hence Columbus

naming the islands *Islas de los Poros* (Pore Islands) or *Islas de las Pozas* (Islands of the Pools) ([24], p. 296; [81], Chapter I, Section XIII). Unknown Spaniards subsequently attributed various names to the islands, including *Santanilla* and *San Millán* in the 1500s ([45]; [170], p. 57) and the Santanilla Islands appear on published historical maps of the Caribbean islands in the 1600s ([45]) (Fig. 4), implying that explorers were aware of the islands and perhaps made occasional visits following Columbus' initial encounter.

There appear to be no records of further European contact with the Swan Islands until the latter half of the 1600s when buccaneers, including Henry Morgan and Captain

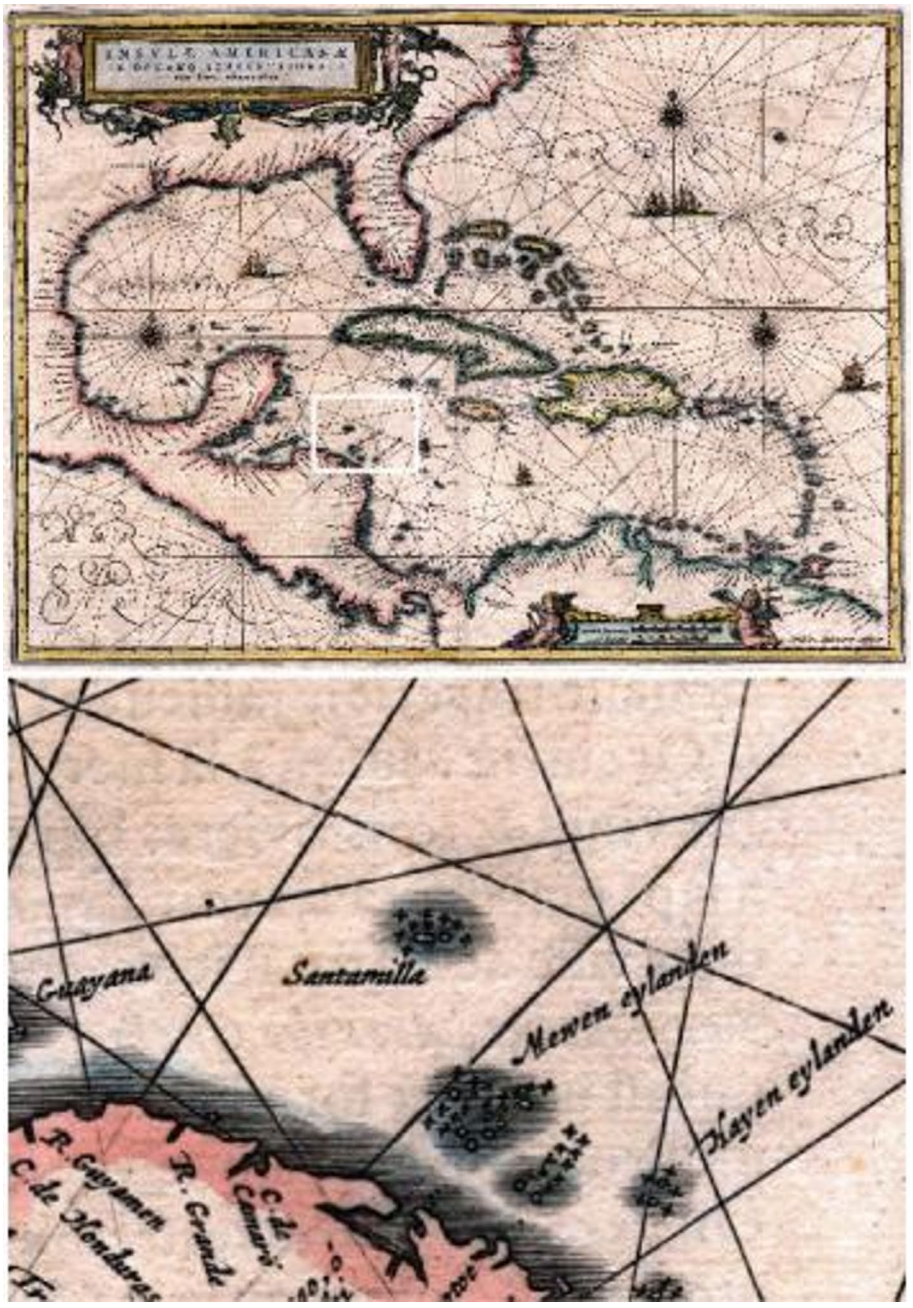


Fig. 4 Historical map from 1644 making reference to the Swan Islands using their historical toponym Santanilla (inset white square). Title: Insulae Americanae in Oceano Septentrionali. Maker: Jansson, Joannes. Language: Latin. Medium: Copperplate. Size (H × W): 37.4 × 51.4 cm. Publication: Jansson, J. 1644. Nouvel atlas, ou Theatre du Monde. (French text). Amsterdam: Johannes Janssonius. Credit: S. Blair Hedges

Charles Swan, from which the islands derived their English name, used Great Swan Island as a temporary redoubt and staging area to attack passing Spanish ships ([13]; [45], p. 197; [95], p. 25; [170]). Lowe ([95], pp. 25–27) referred to the remains of buccaneer breastworks at the northeastern end of the island on the shores of what he called Buccaneer's Bay, now Jacobsens Bay (Fig. 2 and nautical chart in Supplement 1). Fisher ([45], p. 183) also mentions the remains of breastworks on Great Swan Island and Weigel ([168], p. 27) stated that the U.S. Navy Hydrographic Office noted the existence of pirate breastworks on the western part of Great Swan Island in a 1939 report.

4.3 Human activities and resource use under United States jurisdiction (mid 1800s – 1972)

Human activities on the Swan Islands were significant by the mid-1800s. Goats had been introduced from Grand Cayman ([95], p. 19) and in 1857 the discovery of phosphate-rich guano on the Swan Islands (Fig. 5 inset) was reported ([45, 169, 170], p. 59). It was estimated that there were more than three million tons of guano on the islands yielding 40 to 80% bone phosphate of lime (tricalcium phosphate) ([158, 169, 170], p. 60). These guano reserves represented a multi-million-dollar enterprise at that time and the Atlantic and Pacific Guano Company was formed under the United States Guano Islands Act of 1856 which authorized the United States to take possession of the islands to protect United States citizens extracting the resource [169]. The company began clearing native forest to access the guano deposits on Great Swan Island in 1858 to export to Woods Hole, Massachusetts where the guano was mixed with nitrogenous organic waste obtained from the local menhaden fishery to create a more nutrient complete fertilizer ([53, 151], pp. 127, 130; [169, 170], p. 59). The mining operation involved the construction of a settlement (Fig. 5) [87] on Great Swan Island with houses for laborers, extensive sheds for protecting and drying the guano while awaiting shipment, a railroad track from the guano diggings in the northeast part of the island to a pier at the western end from which the product was shipped, and some trails ([169, 170], p. 61). It was reported that 300 men worked on the island in 1887 [169]. Mining operations continued until 1904 under various private companies [169] and the remnants of mining pits are still visible on the eastern part of the island, now transformed into ephemeral fresh or brackish



Fig. 5 A pencil sketch drawn by a member of the guano mining colony on Great Swan Island and reproduced as a wood engraving in an article in the 7 January 1860 New York Illustrated News providing a panoramic view of settlement structures associated with the guano mining operation. Credit: Ken Lawrence [87]. Inset shows chunk of raw guano from Great Swan Island. Source: Johnston [79]

water ponds. The remains of a guano cart were observed in one of these ponds in 2022 (Germer, personal observation).

Mining was not the only extraction activity taking place at this time. An article in the 26 April 1884 edition of the Baltimore Sun reported:

> *The superintendent of the island told Capt. Davis that last year he had to free over three hundred turtles, weighing from 200 to 300 pounds apiece, from his "crawls" because no vessels called at the island.*

Clearly, commercial scale hunting of turtles was underway by this time. In the same article it was reported:

> *The top of the cabin of the Florence Rogers [Capt. Davis' schooner] is honeycombed with coral branches, some of which are two feet in length. Specimens of cocoanuts (sic.), bananas, checkwood, pigeon plumwood, manchinilla, princewood, fustia, sandalwood, ebony and ligum (sic.) vitae, sea mosses, sea coral, sea fans, sea eggs, sea porcupines, turquoise shells, whips made of sea trees, sea shells, sea beans, conchs and brooms of cocoa, all the products of the island, are scattered over the vessel in endless profusion. Lillies, with beautiful variegated leaves, and cacti, all of which grow wild in this veritable paradise, are also among the valuable collection of Capt. Davis.*

It was also reported in this article:

> *Captain Davis brought home with him from Swan Island (sic.) two strange animals for which he can find no name. They are dark gray in color, and about the size of cats, but with heads, teeth and eyes like rats. Their tails are very short. There are but few of them on the island, and they cannot be found on the other islands. A peculiarity of the animals is the strong affection which exists between them. If the male is caught the female becomes a willing prisoner, and vice versa. They were shipped to Boston on Thursday.*

This appears to be the first record of the unique Swan Island hutia (*Geocapromys thoracatus).*

Alonzo Adams, the manager of the last guano mining company on Great Swan Island, remained on the island with his family and a few workers after the mines closed until 1916 ([170], p. 62). Starting in 1904, he cleared more of the native forest of Great Swan Island for the cultivation of fruit trees, vegetables, and tobacco ([170], p. 62) and kept turkeys, chickens, donkeys, and dairy cows ([95], p. 24). In 1908, Adams leased part of Great Swan Island to the American multinational United Fruit Company which cleared more forest along the northern and western parts of the island to establish a coconut plantation consisting of 7,500 trees at the time ([95], p. 16), and export satinwood (*Zanthoxylum flavum*) [169]. The Tropical Wireless Company, a subsidiary of the United Fruit Company, erected a wireless telegraph station on Great Swan Island in 1908 which operated until 1927 [169]. Vessels from the United Fruit Company called at Great Swan Island every three weeks with provisions for their personnel [169]. The inhabitants of Great Swan Island at this time engaged in fishing ([95], p. 10) and commercial turtle hunting, including green turtles (*Chelonia mydas*) for their meat and hawksbill turtles

(*Eretmochelys imbricata*) for their carapace ([95], pp. 36–37). Lowe was told that hawksbill tortoiseshell was worth eight dollars a pound at that time.

Lowe recorded that during his visit to the Swan Islands in 1908:

> *… we found a rough, deserted hut [on Great Swan Island], built of a framework of poles, which was covered with palm fronds. It had been made we afterward found out, by a solitary, self-invited guest from the Cayman Islands, who has sailed over here to catch turtles … Our poaching friend who had occupied this deserted hut must have had a lonely time of it … watching the beach from the door of his hut for the turtle as they came ashore at night. (Lowe, [95], pp. 28–29)*

This suggests that Cayman islanders visited the Swan Islands during this period, and likely earlier, to hunt turtles which regularly nested on the beaches.

In 1914 the Weather Bureau of the United States Department of Agriculture established a weather station on Great Swan Island which was operated on a part-time basis until the 1940s when it became an all-year operation for hurricane monitoring [168, 169]. After World War II, the United States used Great Swan Island as an experimental quarantine station for cattle from Latin America destined for the United States [168]. This project was abandoned in 1949, although Weigel [168] recorded that some cattle and a few horses were still on the island in 1972. In the early 1960s, the CIA established radio stations on Great Swan Island which were removed sometime later in that decade [20]. During his visit in 1971, Weigel [168] noted that the weather station personnel enjoyed catching fish and lobster on a recreational basis.

4.4 Human activities and resource use under Honduras ownership (1972 – present)

The United States formally ceded ownership of the Swan Islands to Honduras in 1972 [165, 168] and they now lie within the Honduran exclusive economic zone. The United States was allowed to continue operating the weather station until it was decommissioned sometime in the early 1980s. In the 1980s, Great Swan Island was also used as a depot for a CIA operation to train and supply contra-revolutionaries fighting in Nicaragua [108]. The impacts on the island's environment of this operation are unknown, although the U.S. Department of Defense carried out environmental clean-up measures after the operation ended ([83], p. 128); bullet casings can still be found scattered throughout the island (Germer, personal observation). In 1991, the Swan Islands were declared a National Marine Park by presidential decree [83, 132, 148].

The only inhabitants on the Swan Islands now consist of a small contingent of Honduran Navy personnel based on Great Swan Island and supplied with food and water by ship from the mainland ([83], p. 128; [106], p. 279). When their normal food supplies run short, they have been reported to be "… living off the land, hunting iguana and eating the bananas" [31]. Refugees from Cuba heading to the mainland have been known to sometimes be sent off course by winds and currents and wash up on Great Swan Island [31] (Germer, personal communication).

In 2012, biologists visiting the islands observed commercial lobster fishers from Honduras harvesting spiny lobster using SCUBA and hunting iguanas (*Iguana iguana*) for food ([106], pp. 274, 278, 283). Honduran Navy personnel allowed the crew of Honduran flagged fishing boats to land on Great Swan Island and hunt iguanas in exchange for

fish, lobster, and queen conch (*Aliger gigas*; formerly *Strombus gigas* and *Lobatus gigas*) (Germer, personal observation). The Navy personnel also sometimes traded iguanas for freshwater from these boats.

Charter boat operators based in Roatán and Grand Cayman currently advertise expeditions to the Swan Islands for game fishing, fly and spin fishing, snorkelling, and exploring [16, 134]. The islands are promoted as a "deserted island paradise", and a "wildlife refuge" with "pristine, isolated coral reefs" and fishing that is "out of this world". However Honduran Navy personnel do not currently allow tourists or other visitors to land on the islands (Germer, personal commination).

The future of the Swan Islands in terms of human use and management of its environment is now at a critical juncture. Honduran Tourism authorities have proposed various developments on the islands, including casinos ([83], p. 128) and visits by cruise ships [144]. In 2023, the Honduran President, Xiomara Castro, proposed construction of a maximum-security prison on Great Swan Island [157]. Regional biologists and professional associations voiced concern that such projects would further damage the islands' ecosystems and they encouraged the government of Honduras to review the feasibility and environmental consequences of such proposals [19, 67]. The prison development was eventually cancelled due, in part, to its being financially unfeasible (Germer, personal communication), but other options for development are still being considered (McField, personal communication).

5 Historical observations of ecological change in the Swan Islands

We documented a total of 19 biological surveys that took place between 1887 and 2024 that provided historical information on ecological change in the Swan Islands (Fig. 6). The observations made during these surveys are comprehensively summarized in Supplement 2 (Biological Surveys of the Swan Islands (1887–2024)) and provide additional information in support of our historical ecological reconstructions in Sect. 7, below.

6 Historical hurricanes impacting the Swan Islands

Between 31 August 1864 and 6 June 2025 (the latest date on NOAA's Historical Hurricane Tracks website at the time of writing), 25 hurricanes passed within 60 nautical miles of the Swan Islands with wind speeds of Category 1 to 5 (64 to > 136 knots) (118 to > 250 km per hour) (Fig. 7 and Supplement 3), an average of one hurricane about every

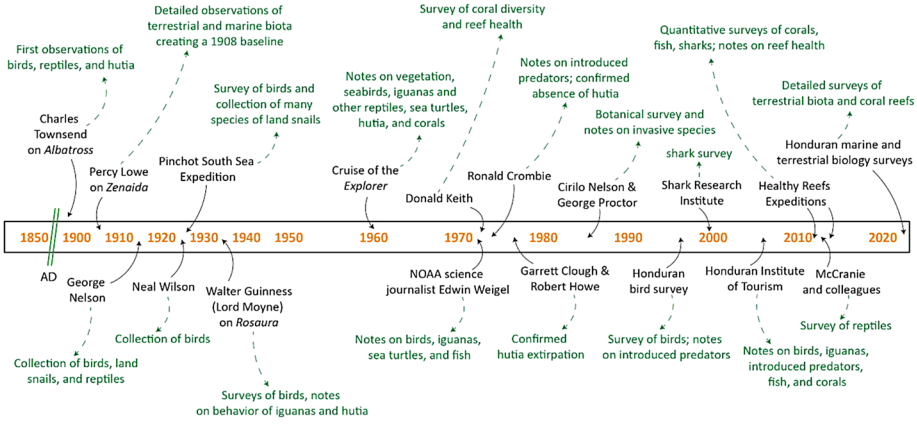


Fig. 6 Timeline of biological surveys of the Swan Islands

6.4 years. The intensity of the hurricanes falls into three clusters. During the 90-year period between 1864 and 1954 there were 12 hurricanes, averaging 1 hurricane every 7.5 years. All of the hurricanes during this period were Category 1 or 2. During the 57-year period between 1955 and 2012, there were 13 hurricanes, averaging 1 hurricane every 4.4 years. Four of the hurricanes during this period were Category 3 and 4, and three were Category 5. Of note, is the short return times between four intense Category 4 and 5 hurricanes from 1998 and 2007 (Fig. 7). During this 9-year period, the interval between Category 5 Hurricane Mitch (7 October 1998) and Category 4 Hurricane Iris (8 October 2001) was three years, the interval between Iris and Category 5 Hurricane Wilma (19 October 2005) was four years, and the interval between Wilma and Category 4 Dean (20 August 2007) was less than 2 years. There have been no Category 1 to 5 Hurricanes passing within 60 nautical miles of the Swan Islands during the roughly 13-year period between 7 August 2012 and June 2025. The "quieter" hurricane period between 1864 and 1954 is corroborated by some of Lowe's observations when he was there in 1908 [95]. Lowe was impressed by the absence of any evidence of hurricane damage to the trees on Great Swan Island and also recorded that "… the "laird" [a settler on the island] had come to the conclusion, from a twenty years' knowledge of the island, that it lay in a zone which was just missed by these terrifying vortices." ([95], p. 91).

7 Reconstructing a historical ecology of the Swan Islands

Below, we provide a reconstruction of the Swan Islands' historical ecology broken down into specific time periods based on a synthesis of the archival record as detailed in Sects. 3, 4, and 5 above and in Supplement 2 (Biological Surveys of the Swan Islands [1887–2024]) and Supplemental Tables 1–4 within Supplement 2).

7.1 Pre-contact period to the mid- CE 1600s—a natural state

Historical reports of the presence of a midden filled with burned top shells on Great Swan Island ([25], p.123; [113], p. 82) suggest that people may have been present on the island in the pre-contact period. A proper archaeological study of this midden, if it still exists, could well help settle the question of if and when the Swan Islands were first

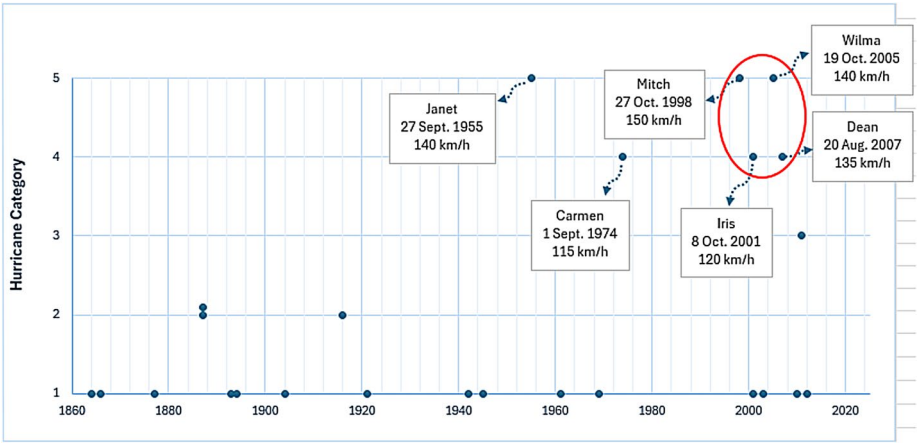


Fig. 7 Occurrence of Category 1–5 hurricanes passing within 60 nautical miles of the Swan Islands between 31 August 1864 and 6 June 2025 (National Oceanic and Atmospheric Administration (NOAA), [116]). Four intense (Category 4 and 5) hurricanes struck the islands between 1998 and 2007 (red circle). See Supplement 3 for further details on all hurricanes

discovered and their resources used by humans. Despite this uncertainty, it is reasonable to assume that in the pre-contact period, any human-presence on the Swan Islands was minimal due to their small size, isolation from the mainland and other islands, and their lack of a permanent source of fresh water, though technologies such as pot stack wells were used in the Antilles for tapping the Ghyben-Herzberg (freshwater) lens [40, 143]. Furthermore, any human activity during this period would have been mostly limited to Great Swan Island because of the difficulty of accessing Little Swan Island given its cliffs and rugged interior which lacks any arable land. There is also little evidence of a sustained human presence on the Swan Islands during the early period of European incursion up until the arrival of buccaneers in the mid-1600s.

It is thus reasonable to assume that throughout the pre-contact period, and up until the mid-1600s, the Swan Islands remained largely undisturbed by direct or intense human impacts and that the terrestrial and marine environments of these islands were in a natural or near natural state. As such, natural ecological processes were the primary drivers of species composition and abundance. This does not mean that the Swan Islands did not experience significant natural disturbances during this period. Over the past 160 years or so, the Swan Islands have been impacted by 25 major Category 1–5 hurricanes (Fig. 7 and Supplement 3). While no paleoenvironmental studies of hurricanes have been carried out specifically in the Swan Islands, studies based on geochemical analyses of lake sediments at other sites in the Caribbean and the eastern seaboard of the USA (see for instance [12, 37, 96]) show that the regional Caribbean has experienced hurricanes for millennia. The circum-Caribbean has also experienced extended periods of drought for many thousands of years based on analyses of sedimentary records at other islands in the Caribbean [14, 63, 96]. It is thus reasonable to infer that the Swan Islands have been exposed to the effects of hurricanes and droughts for many thousands of years which would have periodically impacted the natural forests and coral reefs of the islands. However, the resilience of their intact, biodiverse natural ecosystems would have favored their recovery and re-establishment to approximate pre-disturbance levels, as would have been the case on islands throughout the Caribbean prior to sustained human settlement [89, 124].

It is a useful exercise to reconstruct in a general sense what the terrestrial and marine ecosystems of the Swan Islands might have been like in their natural pre-human state with the view to establishing a conceptual baseline against which to appreciate the scale of the changes that have occurred since sustained human occupation. Such hindcasting is, of course, fraught with uncertainty, but there is sufficient information available to make some reasonable inferences.

When Percy Lowe surveyed the island in 1908, he recorded that "…trees came right down to the sea [on Great Swan Island]…In five yards one could step from the painful eye-aching glare of the beach into the dull gloom of the woods." ([95], pp 91–92). He concluded that in its original state Great Swan Island was completely covered by "uniform forest growth (see also Supplementary Table 1 in Supplement 2). It is thus likely that in their natural state, the Swan Islands were completely covered by forest which could well have been typical of the vegetation macrogroup Caribbean Coastal Lowland Dry Forest on account of their low-lying topography, limestone substrate, and pronounced dry season [117]. Such forests are characterized by a high density of small and medium-sized tropical hardwood tree species with a canopy height of less than about 10

meters. Human-introduced non-native plant and animal species were likely non-existent or rare in this forest.

There must have been enormous colonies of seabirds nesting on both islands throughout the Pleistocene and Holocene to produce the large deposits of phosphate guano present on Great Swan Island ([169, 170], pp. 59, 60). The main producers of guano on Caribbean islands are boobies, frigatebirds, and terns [142]. The Swan Islands were thus almost certainly "seabird islands", densely populated with species such as boobies and frigatebirds prior to sustained human contact. These large seabird populations, by acting as connector species, would have created strong nutrient interconnections between the sea and the land [7, 41, 52, 60, 139].

Reptiles are widely distributed on Caribbean islands today, characterized by old and diverse lineages and considerable endemism [69, 71, 163]. The presence of reptiles, namely geckos, various other lizards, and snakes, including five endemic species, have been recorded from the Swan Islands since the late 1800s [26, 57, 106] and were likely isolated on these islands for millennia prior to sustained human presence. The existence of high numbers of the large green iguana, *Iguana iguana*, on the Swan Islands has been much remarked upon by naturalists since the early 1900s [57, 95, 106, 113]. The native range of this species extends from southern Mexico to central Brazil and Bolivia and includes islands in the Lesser Antilles and the Gulf of Honduras, including possibly the Swan Islands [72, 84, 88, 127], although this species has subsequently been introduced into many other Caribbean islands [127]. It is thus likely that iguana were present on the Swan Islands in their natural state, feeding on a great variety of plant and animal matter and also seabird eggs [88].

Amphibians have never been recorded from the Swan Islands since naturalists first arrived in the late 1800s. Given that they are widely distributed throughout the insular Caribbean today, even on arid islands [71], they may have been present there at some stage before the arrival of naturalists, surviving in wetter micro-habitats. However, it is possible that amphibians never colonized these small remote coral outcrops.

Old and diverse lineages of land snails are present on many islands globally, including the Caribbean [130] and land snails were abundant on the Swan Islands when the early naturalists arrived and comprised several unique species [21, 125]. Land snails thus likely thrived in the forests of the Swan Islands in their natural state. Bats have never been recorded from the Swan Islands, but the insular Caribbean is home to a diverse indigenous bat fauna [85, 128], so it is also possible that bats were present on the Swan Islands before sustained human occupation.

Hutia are adapted for living in natural crevices on Caribbean islands that possess extensive limestone outcroppings with little soil [110, 111], such as that found on Little Swan Island, but not so much on Great Swan Island. Hutia browse on leaves, small twigs, bark, and fruit [22]. The endemic Swan Island hutia, *Geocapromys thoracatus*, may have been present on Little Swan Island since the late Pleistocene or earlier until its abrupt extinction around the mid-1950s, based on its morphological distinctiveness from other species of *Geocapromys*, three living and three extinct [110]. However, it has been suggested that it could have been carried there by early pre-contact visitors to the islands [22].

There are no systematic quantitative estimates of live coral cover from the Caribbean prior to the 1970s, but we know that average coral cover in the 1970s was about 35%

and at some sites was close to 75% [74, 76, 78]. This was at a time when the coral reefs of the Caribbean could no longer be considered natural [77]. These numbers probably thus represent the lower bounds of live coral cover on Caribbean islands in their natural state, including around the Swan Islands. The branching corals, *Acropora palmata* and *Acropora cervicornis*, both major framework building corals, were likely the dominant or co-dominant coral species present in the Swan Islands based on palaeoecological data from many other sites in the Caribbean [28]. There is historical and palaeontological evidence that *Diadema antillarum* was, until recently, abundant on Caribbean reefs for more than 125,000 years [77]. It is thus reasonable to infer that this herbivorous sea urchin was a common occurrence on coral reefs of the Swan Islands in their natural state, although *D. antillarum* may not always have been the dominant component of the sea urchin fauna everywhere in the Caribbean over the past 3000 years [29].

Queen conch (*A. gigas*), which is found in shallow seagrass and sandplains throughout the greater Caribbean today [114], and which was used for millennia for food and secondary resources such as adzes, other tools, and ornaments by Indigenous populations in the Caribbean [51, 118], was probably abundant around the Swan Islands. Similarly, the West Indian top shell (*Cittarium pica*), which was also used extensively for food by Indigenous populations [51, 118], likely thrived in rocky intertidal and shallow subtidal habitats in the Swan Islands in their natural state. Large apex predators such as groupers, sharks, snappers, and jacks are extremely abundant around healthy coral reefs surrounding isolated, uninhabited islands in the Pacific today [11, 140, 150]. We lack comparable studies for the Caribbean because isolated, uninhabited islands with healthy coral reefs no longer exist in the Caribbean. However, O'Dea et al., [119] used fish remains preserved in fossil and archaeological midden deposits from Panama and the Dominican Republic to show significant declines in both the abundance and size of higher trophic level fishes (sharks, snappers, and grunts) in the middle to late Holocene compared to the present. We also know that large predatory fish were still abundant around the Swan Islands in the early 1900s, including goliath groupers, sharks, jacks, snappers, and tarpon [95]. We can thus assume that in the Swan Islands before sustained human presence, predatory fish were at least as large and abundant as in the early 1900s and likely even more so.

In the pre-contact period, green (*Chelonia mydas*) and hawksbill (*Eretmochelys imbricata*) turtles were many times more abundant throughout the Caribbean than in the modern day [77, 103]. It is thus likely that these turtles were an important component of the marine ecosystem of the Swan Islands in their natural state, playing the role of ecosystem engineers—the green turtles grazing the seagrass beds and the hawksbills eating reef sponges [77, 103]. Green, hawksbill, and loggerhead (*Caretta caretta*) turtles were reported nesting on the beaches of Great Swan Island up until the early 1970s [168] and a few turtle tracks on a beach were reported as late as 2007 [144]). It is thus very likely that turtles nested on the beaches of the Swan Islands historically. There is evidence in the archival record that magnificent frigatebirds (*Fregata magnificens*) in the Swan Islands fed on turtle hatchlings in the late 1800s and early 1900s [95] and this behavior has been observed in the Galapagos Islands [137]. It is thus likely that frigatebirds historically feasted on turtle hatchlings at the Swan Islands and perhaps timed their breeding periods to coincide with hatching events.

The Caribbean monk seal (*Neomonachus tropicalis*), the region's only native pinniped, was last seen in 1952 as part of a small colony off the Seranilla Banks [6] which lie between Jamaica and the Yucatán peninsula. This species was officially declared extinct in 2008, the only known seal to have succumbed to this fate. But in the pre-contact period, large colonies existed throughout much of the Caribbean on mainland coasts and offshore islands and atolls, particularly in the Gulf of Mexico and Western Caribbean Sea [6, 101]. It is thus possible that a monk seal population once existed in the Swan Islands which may have been among the last hold outs for this species. In this respect, there are anecdotal reports that monk seals were present on the Swan Islands in the 1950s (Germer, personal communication).

7.2 Mid to late 1600s—buccaneer presence

The temporary occupation of Great Swan Island in the latter half of the 1600s by buccaneers probably resulted in some initial deforestation of the island and the introduction of an early wave of ship-dwelling invasive species such as rats, mice, and cats. Rats and feral cats are particularly harmful to native species on remote islands, preying on a broad range of animals, including seabirds, land birds, bats, insects, land crabs, worms, land mollusks, reptiles and amphibians, as well as vegetation [38, 39, 154]. The buccaneers would also have likely fished the coral reefs and near-shore pelagic waters and hunted sea turtles and iguana. Monk seals may have been hunted as well, if present. However, given the transitory nature of their time on Great Swan Island, the overall impacts of the buccaneers on the terrestrial and marine ecosystems of the islands were comparatively brief and likely minor, although the invasive non-native mammal species they probably brought with them likely began a chain of deleterious direct and indirect effects that persist to the present day, not unlike what occurred in other island regions such as the Pacific [39, 90, 107, 149, 154] .

7.3 1700 to mid-1800s

We discovered no records of human activities in the Swan Islands over the 150-year period following the departure of the buccaneers. This large gap in the historical record is not necessarily evidence of a hiatus of anthropogenic impacts, but it does suggest that human activities on the islands during this period may have been absent or of a minor nature to leave no or few written accounts. A comprehensive field survey that includes archaeological investigation may help to identify human presence during this time interval.

7.4 Mid-1800s to 1940s—onset of significant anthropogenic change

The mid-1800s marked the start of a significant acceleration of human pressures on the islands, particularly Great Swan Island. Deforestation on this island became pervasive to uncover the dense guano deposits and make way for housing, trails, a railroad, and cropping [95, 169]. This likely resulted in increased runoff and soil erosion that would have started to impact the nearshore marine environment, particularly coral reefs that are highly sensitive to changes in temperature, water clarity, and salinity [50, 78, 147]. Ships regularly arriving at the newly built wharf to load raw guano [169, 170] would have provided a constant source of rats, mice, and cats. Goats were present for food ([95], p. 19) and probably horses for labor. The goats would have begun to further alter the natural

landscape by grazing down native plants and damaging sensitive habitat, resulting in further runoff and soil erosion (e.g., [58]. Habitat destruction and the invasive mammal predators must have put great pressure on the seabird populations on Great Swan Island as well as a broad range of other native animal and plant species on the island [38, 39, 107, 149, 154]. Commercial turtle hunting was well underway and the mining workforce of around 300 in 1887 [169] likely fished to supplement their diet, all of which likely began placing pressure on pressure on the turtle and fish populations around the islands. Thus, by the time the first naturalists took an interest in the Swan Islands in the late 1800s and early 1900s, the terrestrial and marine environments of these islands, particularly Great Swan Island, had been significantly altered by humans and were certainly not natural.

By the early 1900s, invasive plants were infiltrating the native forest and colonizing clearings in the forest, including "wild figs" [95], potentially the invasive Asian creeping fig, *Ficus pumila* [32]. Three species of seabirds were present at this time—the red-footed booby (*Sula sula*), brown booby (*Sula leucogaster*), and magnificent frigatebird (*Fregata magnificens*)—but only on Little Swan Island [95, 123, 133]. Introduced predators and habitat destruction during the latter half of the 1800s [95, 169, 170] had probably resulted in the extirpation of all seabird rookeries on Great Swan Island by the 1880s. This significant reduction in the number of seabirds on the islands may have started to disrupt the cycling of nutrients across the land-sea boundary, impacting the health of both the terrestrial and marine environments [7, 41, 60, 139].

The people who replaced the miners in the early 1900s continued to shape the land and seascapes of the Swan Islands [95]. They deforested more of Great Swan Island for cropping and a large coconut plantation (Fig. 8 and Supplementary Fig. 2 in Supplement 2). This, together with previous deforestation associated with the guano mining operation, resulted in a total loss of more than a third of the native forest cover (Fig. 8). Some further forest was then cleared for a weather station, radio facilities, and a quarantine station [168, 169]. Commercial scale hunting of turtles for meat and carapace by locals and transient Cayman Islanders continued [30, 66, 95] and the frigatebirds on Little Swan Island were being culled because they preyed on turtle hatchlings [95]. The extraction of marine resources was accelerating, both for local consumption and by trophy fishers from the United States and further afield who had discovered the rich fishing grounds around the islands [95].

Hutia were abundant on Little Swan Island throughout this period [95, 111, 113, 162] and iguana were present on both islands but apparently more abundant on Little Swan Island [95, 113] (Supplementary Fig. 3 in Supplement 2). An abundant and diverse reptile fauna was present on the islands that included geckos, lizards, anoles, and snakes, six of which were endemic species [25, 26, 113]. However, one lizard, *Ameiva fuliginosa*, which was present in 1887, had disappeared by 1912, apparently an early casualty of cat predation (, pp. 213, 214, 314, 315). Large colonies of brown and red-footed boobies at different stages of development, as well as breeding frigatebirds, were present, but only on Little Swan Island [44], p. 3) [34] cited in [123]) (Supplementary Fig. 3 in Supplement 2).

Land snails were abundant on both islands in 1912 [21] and in 1929 [125], and Colman [25] noted their presence in 1937 on Little Swan Island (See Supplement 2 for details). Twenty-three species were described, nine apparently unique to the islands [125]. Most

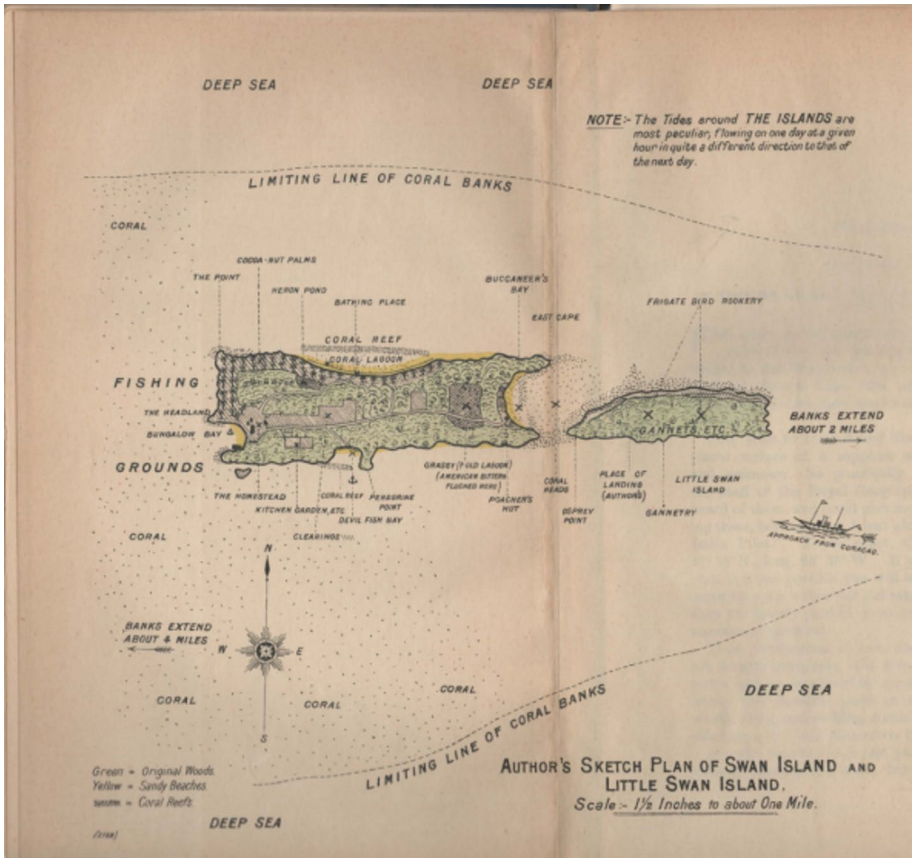


Fig. 8 Lowe's sketch plan of the Swan Islands in 1908 showing the location and extent of forest, beaches, seabird rookeries, coral reefs, fishing grounds, human constructions, and a coconut plantation. The grassy lagoon at the east end of Great Swan Island was probably the site of guano mining

of these species were small in size, less than about 10 mm in diameter, and lived in a variety of habitats, including leaf litter, among stones and rocks, on trees, and on dead wood and other debris [125]. There appears to be no other records of the presence of land snails on the Swan Islands in any other survey after 1937. It is conceivable that subsequent visitors to the islands simply overlooked these mostly small invertebrates, but this seems unlikely given that Pilsbry noted that many of the species were widespread and abundant on the islands, and he was able to make a respectable collection of these animals over the course of a two-day visit, noting that this "… did not permit of anything approaching a full examination of the fauna of these small islands…" [125]. This suggests that there was a rapid and potentially complete collapse of this poorly understood land snail fauna sometime after 1937 and before the cruise of the *Explorer* in 1960 [151], likely related to predation by introduced predators, particularly rats, as has been documented on islands in the Pacific region [18, 65, 149]. It is possible that the land snails were first decimated on Great Swan Island and then on Little Swan Island soon after Colman observed them there when sufficient numbers of invasive predators became established on that island.

Historical records show that the marine ecosystem surrounding the Swan Islands in the early 1900s was still in a well-functioning, intact state [95], particularly in comparison to contemporary benchmarks in the Caribbean [68, 78]). Extensive areas of coral, including stands of staghorn and elkhorn coral, were present (Fig. 8) and coral reef fish,

large spiny lobsters (*Panulirus argus*), sea fans, and black sea urchins (*Diadema antillarum*) were abundant. Seagrass beds were present along the north side of Great Swan Island [95]. Large predatory fish and sharks were spectacularly abundant, including goliath groupers (*Epinephelus itajara*) (Fig. 9). Green, hawksbill, and loggerhead turtles nested on the beaches of Great Swan Island. Nonetheless, the marine environment was under pressure. Fishing by the local population and visiting trophy hunters including, ironically, the naturalists themselves, was beginning to remove large fish from the reefs and commercial turtle hunting was impacting the local turtle populations.

7.5 1950s – 2000—ecological transition

Our detailed synthesis of historical records shows that by the 1960s, some further forest on Great Swan Island had been cleared for the expansion of the coconut plantation, cultivation of yams, bananas, and papayas, and the construction of a grass air strip [80, 151]. However, the 1955 Category 5 Hurricane Janet had destroyed almost all the coconut palms, so few plantation workers were needed on the island [151]. Invasive plants such as *Alysicarpus* spp. (moneyworts) and *Antirhea* spp. had permeated the natural vegetation [129].

Cattle were present on Big Swan Island along with horses, feral cats, rats, and mice [80, 168], and feral cats were present on Little Swan Island in 1960 [151] and rats in the 1970s [23]. Another introduced mammal, the agouti, a rodent native to Central and South America that feeds on mostly fruits and nuts [138], and that was introduced to numerous Caribbean islands by Indigenous groups pre-contact, was present on Great Swan Island by the 1980s [99].

Iguanas were living on both islands but were considered to be most abundant on Little Swan Island [151] and some showed evidence of attacks by feral cats in the early 1970s [80]. Frigatebirds and brown boobies were present on Little Swan Island, but red-footed boobies were not reported during much of this period and may have been rare or locally extirpated by introduced predators [151, 168]. By 1997, however, all three seabird species were present on both islands [1], suggesting that Great Swan Island was being recolonized by seabirds. Overall, though, seabird numbers were very low, probably in the hundreds, judging by the small number of nests recorded (113 brown booby, 12 red-footed booby, and 11 frigatebird nests [1].

The Swan Island hutia was last seen alive on Little Swan Island in the early to mid-1950s and was extinct by 1960 [151]. The cause of the sudden demise of this species is an ongoing point of discussion. Clough [23], Morgan [110], [111], and St Clair [149] concluded that the most likely cause was predation by introduced cats in combination with the effects of Category 5 Hurricane Janet in 1955. Clough [23] suggested the heavy rainfall accompanying the hurricane may have reduced the hutia population by drowning many animals sheltering in natural cavities, with cats preying upon those that remained, further reducing the population below a size from which it could recover. Rats and mice on Little Swan Island may also have outcompeted the dwindling hutia numbers for food in the years after the hurricane [166].

Green, hawksbill, and loggerhead turtles were still nesting on the beaches of Great Swan Island during the 1960s and 1970s [151, 168]. Coral diversity and cover were still regarded as good on the basis of qualitative observations made at many sites around the islands in the early 1970s, especially off the north coast of Little Swan Island. Large

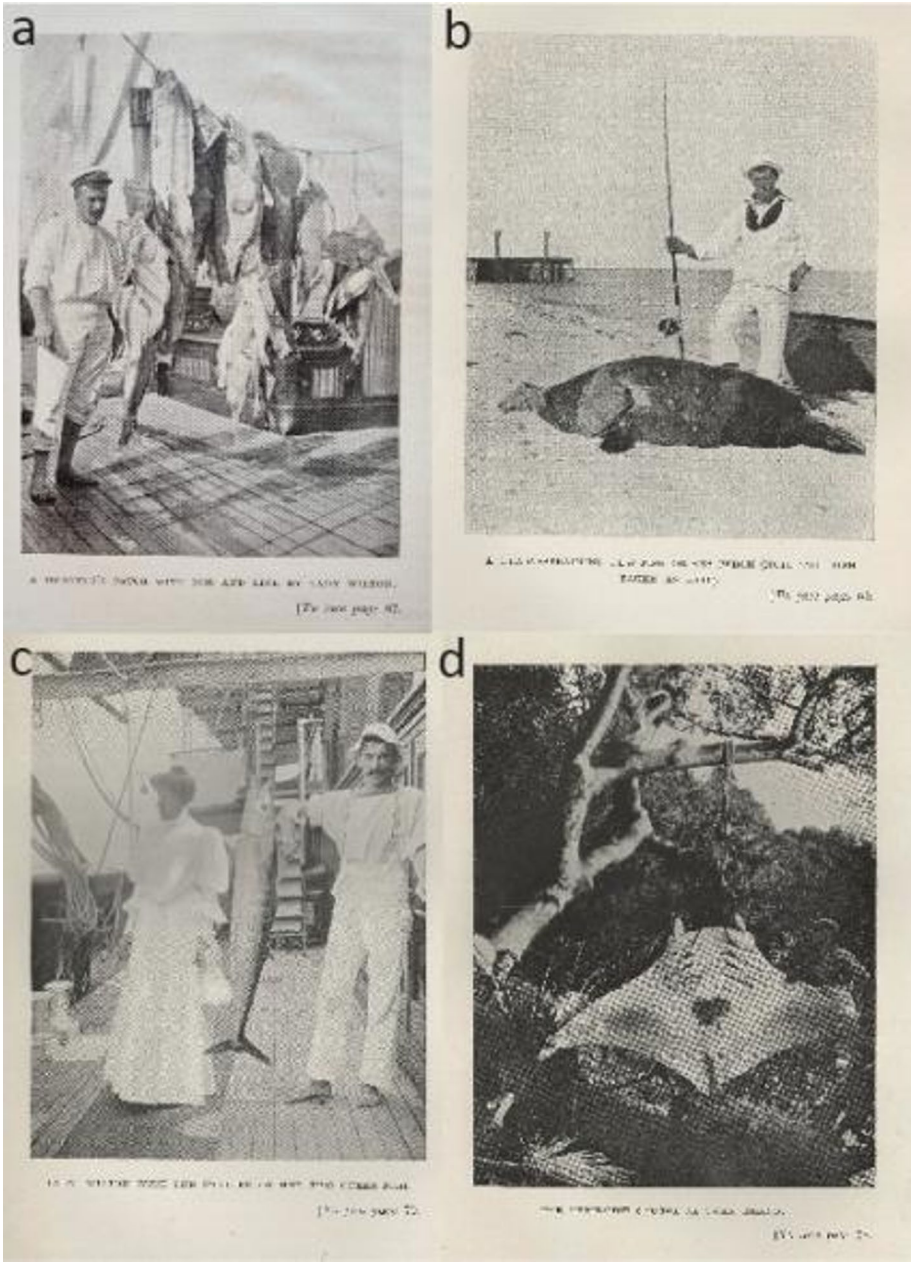


Fig. 9 Sport fishing in the Swan Islands in 1908. (**a**) A morning's catch of goliath groupers (*Epinephelus itajara*) with rod and reel by Lady Wilton ([95], photograph facing p. 67). (**b**) Goliath grouper caught with rod and reel; note the fish taken as bait ([95], photograph facing p.69). (**c**) Lady Wilton with the smaller of two wahoo (*Acanthocybium solandri*) caught in the Swan Islands; this fish weighed 22 kg while the larger fish caught weighed 31 kg ([95], p. 70 and photograph facing p. 70). (**d**) A devil ray (*Mobula mobular*) caught in the Swan Islands ([95], photograph facing p. 78)

stands of staghorn and elkhorn coral were present at several locations, and soft corals were considered abundant [160, 161] (Fig. 10). However, Keith reported that in 1972, much of the coral was broken up, which he attributed to hurricane damage. This is possible given that Category 5 Hurricane Janet struck the Swan Islands in 1955 followed by two Category 1 hurricanes, Carla and Francella, in 1961 and 1969, respectively (Fig. 7) and that a large-scale analysis of the impact of hurricanes on coral cover in the Caribbean revealed no evidence of recovery of reefs to a pre-storm state eight years after a

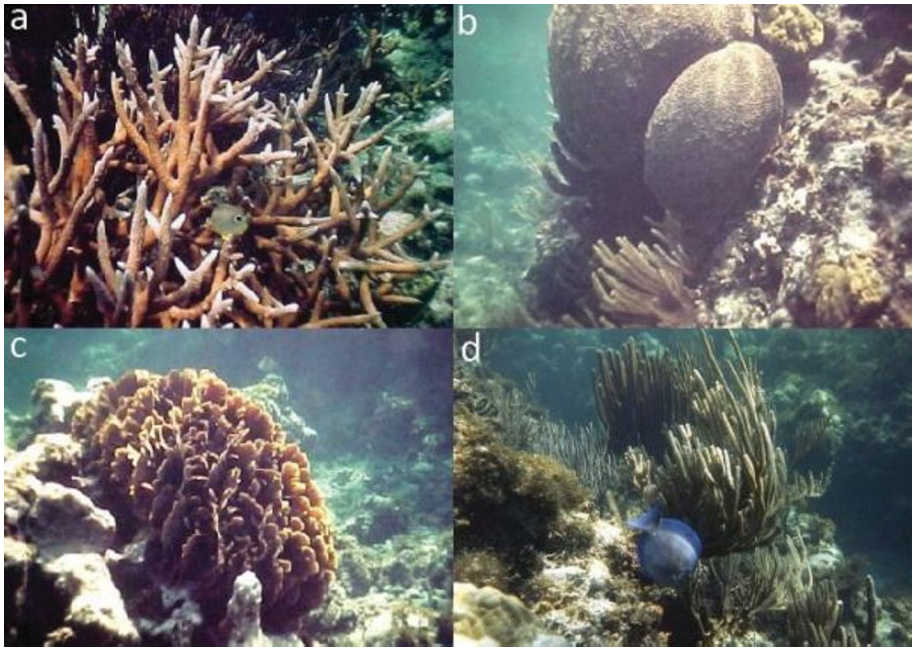


Fig. 10 Swan Island coral reefs in 1973. (**a**) Staghorn coral (*Acropora cervicornis*) (**b**) brain coral (*Pseudodiploria clivosa*) (**c**) Lettuce coral (*Agaricia agaricites*) (**d**) gorgonian coral (possibly *Eunicea tourneforti*) Credit: Donald Keith

Table 1 Some present-day species introductions (non-native species brought to the islands by human activities) in the Swan Islands

Species	Status
Mammals	
Rat (*Rattus* sp.)	Introduced, possibly in mid-1600s and by mid-1800s; invasive
Agouti (*Dasyprocta* sp.)	Introduced approximately 1980s; invasive
Domestic cat (*Felix catus*)	Introduced approximately 1850s; invasive
Goat (*Capra hircus*)	Introduced approximately 1850s; invasive
Horse (*Equus ferus caballus*)	Introduced approximately 1850s
Reptiles	
House gecko (*Hemidactylus frenatus*)	Introduced, invasive
House gecko (*Hemidactylus mabouia*)	Introduced
Curly-tailed lizard (*Leiocephalus varius*)	Introduced
Marine Life	
Lionfish (*Pterois* sp.)	Introduced early 2000s; invasive
Plants	
Many introduced non-native and invasive species including flowers, trees, shrubs and grasses	First introductions recorded early 1900s; some invasive

hurricane [56]. However, the damage noted by Keith could also have been the result, at least in part, to anthropogenic stressors at the time, such as small boat anchor damage and sewage discharge associated with the radio and weather stations present on Great Swan Island during this period. *Diadema antillarum* and large spiny lobsters were also deemed abundant by observers at the time [168] (Supplementary Fig. 4 in Supplement 2). Observers assessed the fishing around the islands at this time as "tremendous" [168], although other accounts suggest that fish were "fairly abundant" (Keith, personal observation). A wide range of predatory fish, including grouper, were still being caught by the local weather station personnel (Supplementary Fig. 4 in Supplement 2), and sharks were reported as abundant [168]. There is an anecdotal report that by around the mid-1990s,

Table 2 Some present-day species extinctions (complete disappearance of a species globally), extirpations (localized extinction), and ecological extirpations (localized reduction in abundance to the point where a species is no longer ecologically significant) in the Swan Islands

Species	Status
Mammals	
Little Swan Island hutia (*Geocapromys thoracatus*)	Abundant until 930s at least; extinct by late 1950s
Seabirds	
Brown booby (*Sula leucogaster*) Red-footed booby (*Sula sula*) Magnificent frigatebird (*Fregata magnificens*)	All species apparently extirpated from Great Swan Island by late 1800s but still present on Little Swan Island; now recolonizing Great Swan Island in small numbers
Reptiles	
Whiptail lizard (*Ameiva fuliginosa*)	Not observed since 1887; extirpated
Swan Island gecko (*Aristelliger nelsoni*)	Once very common on both islands; now endangered and possibly ecologically extirpated
Little Swan Island racer snake (*Cubophis brooksi*)	Common on Little Swan Island in 1930s; now endangered and possibly ecologically extirpated
Green turtle (*Chelonia mydas*)	Historically abundant; ecologically extirpated by 1970s
Hawksbill turtle (*Eretmochelys imbricata*)	Historically abundant; ecologically extirpated by 1970s
Loggerhead turtle (*Caretta caretta*)	Historically abundant; ecologically extirpated by 1970s
Land Mollusks	
23 species (9 endemic) collected in 1937	Likely extinct/extirpated between 1937 and 1960
Marine Life	
Staghorn coral (*Acropora cervicornis*)	Ecologically extirpated by early 2000s
Elkhorn coral (*Acropora palmata*)	Ecologically extirpated by early 2000s
Goliath grouper (*Epinephelus itajara*)	Ecologically extirpated by early 2000s

Honduran fishers participated in regular fishing trips to the Swan Islands during which they would remove large amounts of fish, lobster, and conch [146]. If so, the Swan Islands were known and targeted as a source of abundant marine resources during this period.

In 2000, the coral reefs were still reported as healthy, although the corals in shallow water were damaged, probably because of the passage over the islands of Category 5 Hurricane Mitch in 1998 (Fig. 7) [145]. Blacktip (*Carcharhinus limbatus)*, nurse (*Gingly-mostoma cirratum)*, Caribbean reef (*Carcharhinus perezi)*, and hammerhead (*Sphyrna* spp.) sharks were present around the islands [145]. It thus seems that the marine ecosystem was still reasonably intact as late as 2000, almost a century after Lowe's initial observations in 1908, although direct comparisons between these two time periods are difficult to evaluate because of the lack of quantitative information and the shifting baselines of the observers due to intergenerational loss of perspective on marine species size and abundance and overall marine ecosystem health.

7.6 2001–2024—altered landscape and marine ecosystem collapse

The species composition of the Swan Islands is now greatly altered from its natural state as a result of numerous introductions, extinctions, extirpations, and ecological extirpations of both marine and terrestrial taxa (Tables 1 and 2; Fig. 11). Many introduced plants are now present on Great Swan Island, including sago palm (*Cycas revoluta)*, mango (*Mangifera indica)*, lemon (*Citrus* sp.), Australian she-oak (*Casuarina equisetifolia)*, jocote (*Spondias purpurea)*, castor bean (*Ricinus communis)*, teak (*Tectona grandis)*, fodder grass (*Megathyrsus maximus)*, upland cotton (*Gossypium hirsutum)*, and mother of cocoa (*Gliricidia sepium*) [57]. Invasive grasses have colonized the airstrip and castor bean is reclaiming areas of previously cleared forest. Some "re-greening" is taking place on previously cleared areas of Great Swan Island characterized by the creation of a mixed secondary forest containing both native and introduced species. Rats are now

abundant on Great Swan Island along with mice, cats, and agouti; rats and cats most likely persist on Little Swan Island as well.

The composition and abundance of the terrestrial reptile fauna are now greatly changed in comparison to what Charles Townsend and George Nelson observed in 1887 and 1912/13, respectively [57, 106]. Two introduced house geckos, *Hemidactylus frenatus* and *Hemidactylus mabouia*, are now present, the former outcompeting the endemic gecko, *Aristelliger nelsoni*. Another introduced species, the Cayman curly-tailed lizard, *Leiocephalus varius*, is also now present. The endemic whiptail lizard, *Ameiva fuliginosa*, has not been observed since 1887 and can safely be confirmed extinct [106]. The endemic Little Swan Island racer snake, *Cubophis brooksi*, has not been observed since the late 1990s and is now rare or extinct [57, 98, 106]. Iguanas are currently very abundant on Great Swan Island on rocky cliffs near the ocean, in forested areas, and around buildings [57]. Germer [57] carried out the first quantitative survey of iguana abundance at the islands and calculated that there was between 18,000 and 20,000 iguana of all sizes on Great Swan Island, or approximately 74 animals per hectare. This creates a 2024 baseline against which to compare future changes in iguana abundance. Unlike in earlier times, iguana now avoid humans, diving into the ocean when approached [106]. This change in behavior is likely due to increased hunting during previous decades.

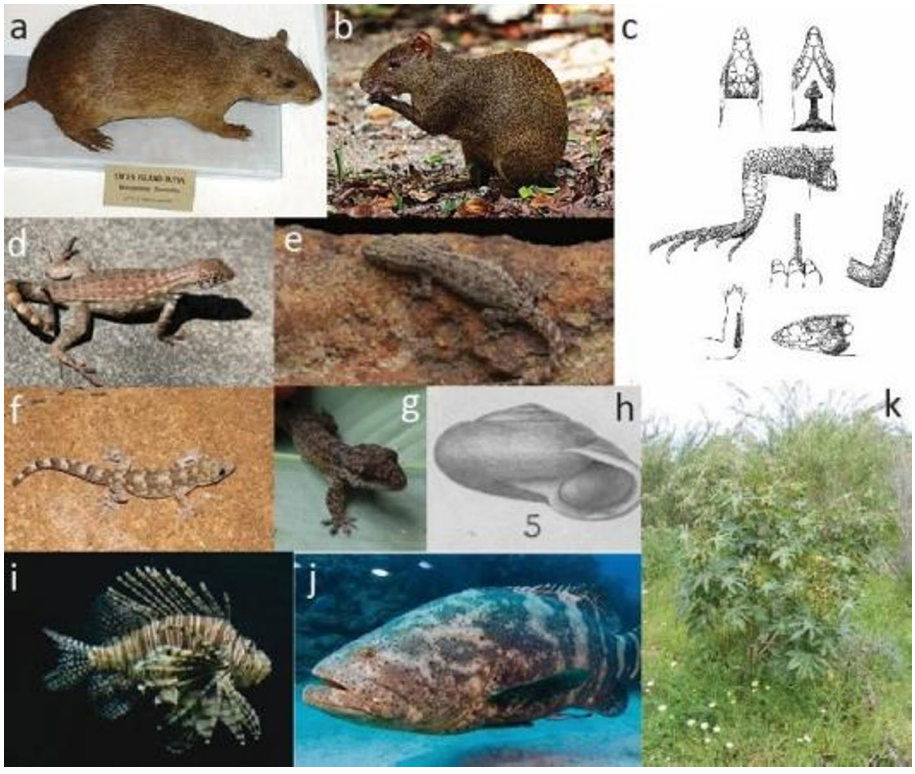


Fig. 11 Some present-day examples of introduced (I) (non-native species brought to the islands by human activities), extinct (E) (complete disappearance globally), extirpated (Ex) (locally extinct), ecologically extirpated (EEx) (reduced in abundance locally to the point where no longer ecologically significant, and endangered (En) species in the Swan Islands. **(a)** Hutia (*Geocapromys thoracatus*) (E); **(b)** Agouti (*Dasyprocta* sp.) (I) Credit: Chuck Homler/FocusOnWildlife.Me; **(c)** Whiptail lizard (*Ameiva fuliginosa*) (E) from Cope [26]; **(d)** Curly-tailed lizard (*Leiocephalus varius*) (I) Credit: Steven Mlodinow; **(e)** Gecko (*Hemidactylus frenatus*) (I) Credit: sarayoung; **(f)** Gecko (*Hemidactylus mabouia*) (I) Credit: Martin Grimm; **(g)** Gecko (*Aristelliger nelsoni*) (En) Credit: Daniel Germer; **(h)** Land snail (*Lucidella pilsbryi indecora*) (E) from Pilsbry [125]; **(i)** Lionfish (*Pterois* sp.) (I); **(j)** Goliath grouper (*Epinephelus itajara*) (EEx) Credit: Key West Aquarium; **(k)** Castor bean (*Ricinus communis*) (I) Credit: Plants of the World Online



Fig. 12 (See legend on next page.)

The historical record suggests that there have been dynamic shifts in iguana populations between Great Swan Island and Little Swan Island over the last approximately 125 years. In 1908, iguana were likely present only on Little Swan Island [95]; in 1929 they were abundant on Great Swan Island [126]; in 1960 and 2007 they were present on both

(See figure on previous page.)

Fig. 12 Changes in coral health in the Swan Islands synthesized from the archival record (1908–2024). Yellow ellipses show areas where healthy coral reefs were observed, and stars show locations where branched corals were observed. Information presented for 1908 is derived from observations made from a boat using a bathyscope and grappling hooks and by wading across reefs [95] and may not reflect the complete distribution of coral reefs and branched corals at that time. See Lowe's sketch map (Fig. 8) and Supplement 2 for more details of Lowe's observations. Information presented for 1972 is based on qualitative underwater surveys at many locations around the Swan Islands [160, 161]. See Supplementary Table 3 in Supplement 2 for detailed locational information on Tortora and Keith's surveys. Information for 2013 and 2024 is derived from quantitative transect surveys around both islands. See [68, 159] and Supplement 2 for detailed locational information on these surveys. For 2013, solid line ellipses show areas where live coral cover was about 20% (classified as "good") and dotted ellipses show areas where live coral cover was about 10% (classified as "fair"). Live coral cover at all other stations surveyed around the islands was 5% or less (classified as "poor" to "critical"). The branched corals observed in 2024 consisted of three small 5–20 cm colonies of staghorn coral showing signs of bleaching; no elkhorn coral was observed in that year

islands but most numerous on Little Swan Island [144], [151]; in 2024 they were present only on Great Swan Island in great numbers [57]. Iguana are good swimmers and can easily migrate between the two islands, but at this stage, it is not clear what might be driving these shifts in abundance between the islands, although observations made in 2007 suggest that iguana were moving from their home range on Little Swan Island to nest on Great Swan Island [144].

Small numbers of brown boobies, red-footed boobies, and a newcomer, the masked booby, *Sula dactylatra*, are now present on both islands [57]. Some magnificent frigatebirds have also persisted on Little Swan Island, along with the first record of the white-tailed tropicbird, *Phaethon lepturus* [57]. The continued presence of seabirds on the islands, although in modest numbers, is a positive development.

In 2007, sharks were reported in the channel between Great Swan Island and Little Swan Island and the reefs were still being reported as in a "good" condition, although no branching corals and goliath groupers were reported [144]. Lobster and queen conch (*Aliger gigas*) were still plentiful, and loggerhead and hawksbill turtles were observed on the reefs, and some turtle tracks were apparently observed on a beach on Great Swan Island [144], which would be the last report of any potential turtle nesting in the Swan Islands. Discounting the observational bias due to shifting baselines, which is likely significant, this is the last report of what might be considered a reasonably intact coral reef ecosystem around the Swan Islands.

In the period between 2007 and 2011/13, the coral reefs underwent a major phase shift (Fig. 12). Qualitative observations in 2011 [109]) together with quantitative surveys of corals and fish in 2011 and 2013 ([61][68]), the first quantitative reef surveys to take place in the Swan Islands, showed that most of the coral was dead and reduced to rubble, with live coral cover averaging only about 13% in 2011 and 10% in 2013, and macroalgae covered about a third of the reef surface in both years. The expedition members attributed the extensive coral damage to hurricanes. This is probable given the cluster of severe hurricanes with short return periods impacting the Swan Islands between 1998 and 2007 (Fig. 7 and Supplement 3) prior to their survey. They observed some patches of living coral and a few branching corals in the channel between the two islands, perhaps because this site is more protected from hurricane damage. Predatory fish and sharks were very rare [61]. The expedition members attributed the lack of fish to recent and intense overfishing which is quite possible but untestable given that no formal records of fishing activity or catch have ever been collected in the unmanaged ocean adjacent to the Swan Islands. However, a large contingent of fishers from Honduras were observed in the Swan Islands in 2012 [106] and there is an anecdotal report from 2008 that fishers

from the Bay of Islands were aware that marine resources were comparatively abundant in the Swan Islands [61], suggesting that targeted overfishing may well have occurred. Lionfish were present on the reefs, an invasive species that has no natural predators in the Caribbean, although groupers and sharks have been known to eat them but not yet in sufficient numbers to control their population [33, 64, 97]. Some quantitative observations taken a decade later in 2024 [159] showed that the status of the coral reefs has changed little since 2013 (Fig. 12). Live coral cover is still low and dominated by *Siderastrea siderea*, *Porites astreoides*, and *Agaricia agaricites* ([159]*). Siderastrea* spp. have life history traits, including resistance to storm damage and a higher ability to withstand sedimentation, that helps them persist in environments subject to frequent low magnitude disturbance such as temperature stress and sedimentation; *Agaricia* spp. and *Porites astreoides* exhibit "weedy" life-history traits including high sexual reproductive output that facilitates rapid colonization of open spaces following severe disturbances, such as a hurricanes [27].

This rapid phase shift in the marine ecosystem surrounding the Swan Islands after 2007 correlates with a convergence of multiple anthropogenic stressors and catastrophic events affecting both the terrestrial and marine environments of these islands, some stretching back at least 175 years, as demonstrated or inferred in our historical synthesis. These include in order of temporal onset:

- Extensive land-use change commencing in the 1850s that likely resulted in increased sedimentation and turbidity in the nearshore environment. It is well understood that these factors can negatively affect the health of corals and seagrasses by increasing nutrient load, stimulating algal growth, reducing water clarity and interfering with coral ciliary feeding [50, 78, 147].
- A significant reduction in seabird numbers because of habitat loss, predation by invasive species, and human culling, commencing in the 1850s, which likely disrupted seabird-derived nutrient flows into the nearshore environment. There is growing awareness that seabirds act as important land-sea "connector" species on oceanic islands [7, 41, 52, 60, 139]. After foraging in the adjacent ocean, they transport nutrients back to their island rookeries in the form of guano droppings. These nutrients enhance the productivity of the terrestrial flora and fauna and some also leach into the nearshore environment enhancing seagrass, coral, and fish growth and overall coral reef resilience. However, on humanized rat-infested islands with low seabird numbers, such as in the Swan Islands, this marine-terrestrial nutrient cycling process is disrupted, affecting both the terrestrial and marine environments [7, 41, 60, 94].
- A significant reduction in local populations of green, hawksbill, and loggerhead turtles from overhunting commencing in the mid-1800s and culminating in the complete loss of turtle nesting on Great Swan Island beaches by the early 2000s. This likely affected the health of the nearshore marine environment since sea turtles are known to be ecosystem engineers that have important roles in maintaining the health of seagrass beds and coral reefs [9, 77, 103, 156].
- A severe reduction in the abundance of reef fish, particularly larger herbivorous and predatory species, because of sustained overfishing by local inhabitants and big game fishers commencing in the mid-1800s and likely peaking in the 1990s and early 2000s coupled with targeted and unreported fishing by visiting fishers. The overfishing of

herbivorous fish, such as parrotfish, has been shown to be associated with increased macroalgal cover and decreased coral cover on Caribbean reefs [78].

- The likely arrival of White Band Disease which was spreading through the Caribbean sometime in the late 1970s and early 1980s which would have impacted the health of branched coral species in the Swan Islands [4, 59, 78].
- The likely decimation of the sea urchin, *Diadema antillarum*, population in 1983 due to a mass mortality event that caused population declines of up to 85–90% throughout the Caribbean [91, 93]. The culprit is still unknown, though a more recent event in 2022/23 has been attributed to the pathogenic parasite, *Philaster apodigitiformis*, which is known to occur in fish [73]. The loss of this significant herbivore likely contributed to an increased growth of macroalgae and a reduction in coral cover in the Swan Islands [2, 3].
- Arrival of invasive predatory lionfish in the early 2000s. This species is likely outcompeting native reef fish for food and space and overconsuming herbivorous reef fish that contribute to the control of macroalgal growth [62, 112].
- Ocean warming that started in the Caribbean as early as 1915 leading to an increased frequency and duration of marine heat waves in the region after the 1980s [10]. This likely resulted in increased coral bleaching events in the Swan Islands, as has been documented throughout the Caribbean [78].
- A cluster of four severe Category 4 and 5 hurricanes impacting the Swan Islands between 1998 and 2007 with very short return times of three, four and less than two years (Fig. 7), leaving little time for coral recovery between successive events. In this regard, a study of 177 coral reef sites across the Caribbean impacted by hurricanes between 1980 and 2001 revealed no evidence of recovery to a pre-storm state for at least eight years after impact [56].

We are not able to untangle the magnitude, relative importance, and interactions of these various events through time. However, it is quite possible that the cluster of severe hurricanes between 1998 and 2007 played a pivotal role in pushing the reefs, whose health was already in decline due to the synergistic effects of reduced water quality, disruption of natural land-based nutrient flows, loss of herbivores controlling macroalgal growth, coral disease, coral bleaching, and overfishing, into a collapsed algal dominated state. Gardner et al., [56] concluded from their analysis that a high rate of coral decline on many hurricane-impacted sites in the Caribbean in the 1980s was suggestive of a synergy between hurricanes and other stressors.

8 Discussion

8.1 The role of remoteness in the trajectory and extent of ecological change in the Swan Islands

Anthropogenic changes in the Caribbean commenced around 7000 years ago when Archaic Age foraging/fishing/hunting peoples began to spread through the insular Caribbean and settled many of the northern Antilles islands and began altering their landscapes and seascapes [51]. They hunted birds and perhaps some of the remaining populations of giant sloths and utilized a variety of marine resources, including manatees, sea turtles, and monk seals; invertebrates from nearshore environments; and fish from coral reefs and inshore pelagic waters, such as parrotfish, grouper, snapper, and grunts [47, 51, 101, 103, 118]. Beginning about 2500 years ago, Saladoid groups began

colonizing most eastern Caribbean islands that harkened the Ceramic Age, and in some cases may have displaced Archaic Age settlers. These new migrants introduced a number of different exotic plant and animal species and cleared native forest for horticulture and villages [51, 118, 121, 122, 131]. They also depended heavily on marine resources and in some places over-harvested fish and shellfish resources, altering the structure of nearshore marine environments [47, 51, 118, 173]. Following European incursion, the alteration of many Caribbean island terrestrial and marine ecosystems quickly accelerated in the 1600s as a result of large-scale clearance of land for timber, fuel, and agriculture; further introductions of non-native plants and animals; and overfishing and hunting [51, 77, 100, 101, 103].

The humanization of the Swan Islands followed a different trajectory from most other Caribbean islands as shown by our historical synthesis. Human impacts on these remote islands by Indigenous people during the pre-contact period and through much of the time following European incursion appear to have been minimal. Significant anthropogenic change on land was delayed until the 1850s with the start of guano mining, but accelerated rapidly from then on, resulting in deforestation on Great Swan Island; the introduction of a host of invasive plant and animal species; loss of seabirds, turtle nesting beaches, and endemic species of reptiles, land snails, and an endemic rodent. The remoteness of the Swan Islands also delayed some of the worst effects on the marine environment. For example, by the late 1800s, and probably much earlier, the coral reefs of Jamaica were severely overfished and large herbivorous and carnivorous fish were largely eliminated [77]. In contrast, Percy Lowe and his colleagues were able to capture a prodigious number of giant groupers in one morning of fishing in the Swan Islands in 1908 and appear to have specifically sought out these islands for their reputation for superb big game fishing [95]. Furthermore, large-scale coral decline in the Swan Islands lagged many other Caribbean islands. For example, the branching corals, *A. palmata* and *A. cervicornis*, became a less dominant feature at most Caribbean coral reefs starting in the 1950s–60s [28]. Around the Swan Islands, these branching corals were still reasonably abundant in the early 1970s. The loss of *Acropora* spp. dominance in the Caribbean appears to have been related at first to local effects such as population density and fertilizer use leading to coastal eutrophication [28], followed later by the regional impacts of White Band Disease, *Diadema* die off, and coral bleaching [78]. It is possible that the historically low human population following the collapse of the guano mining industry and the insignificant use of fertilizer on Great Swan Island allowed *Acropora* corals to persist for longer than elsewhere in the Caribbean. Ultimately, it appears that a confluence of local, regional, and global anthropogenic impacts and a cluster of catastrophic hurricanes between 1998 and 2007 tipped the coral reefs of the Swan Islands into collapse, and they may now be even more degraded than other reefs in the region based on the results of qualitative observations and quantitative surveys taken between 2011 and 2024 [68, 159].

8.2 Implications of historical ecological knowledge for future management of the Swan Islands

(Lowe, [95], p. 97) was the first to note that the ecology of the Swan Islands was at risk from human impacts, writing:

> *It is a thousand pities some one (sic.) does not go to Swan Island (sic.) and make a catalogue of all the native plants and trees, before they disappear beneath the onslaught of foreign interlopers and the rude effects of man's occupation. Looking back now, we exceedingly regret that we did not make collections and more notes of this indigenous flora.*

Moyne later wrote prophetically in 1938 ([113], p. 87):

> *In view of the damage done to rare species on the far larger islands of Galapagos by indiscriminate collecting on the part of fishermen and others who may hope to sell at a profit to museums, owing also to the dislocation caused to the natural fauna by the introduction of foreign animals, it seems most desirable to secure that Eastern Swan Island [Little Swan Island] be made a nature reserve. Only a few weeks previously the head man on the western island [Great Swan Island] had introduced six goats, and if these animals multiply the destruction of the flora and fauna is only a question of time.*

Weigel also saw the Swan Islands as unique and vulnerable back in 1972 writing [168]:

> *For a while at least, it [the Swan Islands] will remain one of nature's relatively unspoiled hideaways. Perhaps this was the inspiration for the sign that greets visitors at the dock—"Swan Island—Last of the Caribbean Paradises."*

More recently, McCranie and colleagues expressed their frustration over the lack of protection for the Swan Islands [106]:

> *… the Honduran governmental agency … assigned with protecting the country's natural resources has shown no interest in helping protect those natural resources on the Swan Islands… despite the Swan Islands being designated as a Marine National Park … which also includes the land areas and their terrestrial-arboreal faunal residents.*

Clearly, the concerns expressed by Lowe, Moyne, Weigel, and McCranie and his colleagues about the vulnerability of the Swan Islands have come to pass as shown by our reconstruction of their historical ecology which reveals the scale of degradation that has occurred.

The Swan Islands and their surrounding ocean are presently a legally established marine protected area (MPA), the largest in the Caribbean, comprising 1,653.73 square nautical miles (5,672 square kilometers) of ocean [83, 132, 148]. Unfortunately, this significant MPA remains largely unmanaged and lacks a strategy for its future ecological protection and restoration that considers various competing historical, cultural, and social values, as well as the appropriateness of any restoration interventions that might be used, such as control of invasive predatory and competitive species, species reintroductions, and coral restoration attempts. Developing such a strategy will be a complex task, the details of which are beyond the scope of this paper. However, we believe that an understanding of the long-term historical ecology of the Swan Islands will play an important role in this endeavour.

In the first instance, historical ecological knowledge is critical for dispelling present-day myths that the Swan Islands possess a so-called pristine marine environment. For

example, as recently as August 2025, the Swan Islands were described in the following terms:

> *These low-lying coral islands, covering just 3.1 square kilometers, represent one of the Caribbean's most pristine marine environments [86].*

Clearly, such a fallacy is misleading at best and at worst hinders the case for developing a proper management and restoration strategy.

Historical ecological knowledge will also help planners, managers and restoration ecologists better understand their inherent shifting baseline biases, fully comprehend the scale and linkages of the ecological changes that have taken place, and consider a range of possible futures for these islands. Obviously, in today's Anthropocene world, it will not be possible to restore the terrestrial and marine environments of the Swan Islands to their completely natural pre-human state or to some form of "precolonial" naturalness, nor may it be desirable to attempt to faithfully recreate a past ecosystem fidelity. However, historical ecological knowledge will help identify appropriate reference models from the Swan Islands' past that can help inform the setting of practical, suitably ambitious, restoration benchmarks as part of an overall strategy. Our historical analysis also points to the importance of ecological land-ocean linkages on the Swan Islands, which suggests that a holistic, ridge to reef approach to management and restoration will be beneficial and that any attempts to restore the coral reefs of the Swan Islands could well fail or be sub-optimal unless they are coupled with the management of the adjacent terrestrial environment.

9 Conclusions

Overall, our synthesis of historical records, visitor accounts, and both terrestrial and marine biological surveys has revealed a small group of islands that have been in flux environmentally and anthropogenically over the last five centuries and perhaps longer. While no detailed archaeological surveys have been carried out on the Swan Islands, there is suggestive evidence of pre-contact artifacts and occupation refuse. Further archaeological research could add a deep time dimension to information already gleaned from what we have compiled here. Regardless, the historical ecology narrative for these remote islands is one that mirrored the Antilles in some respects, but diverged in others, making them a useful model system for examining future natural and cultural processes over time and space [36, 46], and developing strategies for holistically restoring tropical island ecosystems as is being attempted on other islands in the Caribbean and Pacific (e.g., [41, 54, 75]).

Supplementary Information

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Supplementary Material 1

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Author contributions
PM. Conceptualization; data gathering, analysis and visualization; writing–original draft SF. Conceptualization; resources; data analysis and visualization; writing–review and editing.

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