A Synthesis of the Galápagos

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Natural History, Human Conflict, and the Destiny of an Archipelago

By

Guillermo Paz-y-Miño-C
and Avelina Espinosa

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To the Ecuadorian people, the *galapagueños*, and everyone committed to the preservation of the Galápagos Islands.

To the scientists and naturalists who dedicate their careers to understanding the complexity of the Galápagos ecosystems and attaining harmony between *in situ* environmental protection and sustainable development, always a challenge.

To those fascinated by Charles Darwin's work and legacy. His brief exploration of the Galápagos in 1835 was historic. Over time, he and the archipelago became inseparable, bound to be understood and discussed together.

To our graduate and undergraduate students and those curious about nature, our planet, and the cosmos.

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We thank the hundreds of scientists, conservation biologists, and wildlife managers who authored the peer-reviewed articles cited in Books One and Two (789 total references). We relied on their work to synthesize, integrate, and conceptualize (1) the most recent natural history research being conducted in the Galápagos' terrestrial and aquatic environments (Books One and Two); (2) the conflicts resulting from human interactions with nature, including local population growth and tourism practices in the context of short- and long-term conservation efforts (Book Two). We also (3) make predictions about the destiny of the Galápagos' unique biodiversity and landscapes under various scenarios of climate change impacts, urbanization trends, diversification of tourism, and conservation investments (Book Two).

We thank Gordon Chancellor for permitting us to reproduce "The *HMS Beagle* in Galápagos by 17 October 1835"; a painting interpretation by John Chancellor 1981 (Book One, Chapter One). The Syndics of Cambridge University Library for allowing us to reproduce two images (the leather cover and page number 36) from Charles Darwin's 1837-8 *Notebook B: Transmutation* (Book One, Chapter One). Ecuadorian artist Geracho Arias for his paintings of "Tomás de Berlanga" (Book One, Chapter Two) and "La Baronesa" (Book Two, Chapter Five), as well as Ecuadorian ornithologist and nature artist Juan Manuel Carrión for his illustration of "Galápagos Woodpecker Finches" (Book Two, Chapter Three), and Australian photographer Ian Wiese for the aerial image of

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Several of the historic photographs in Book One, Chapter Seven, are broadly available online at multiple depositories, as we provide links in Appendix A (Book One). We highlight that book author and historian John Woram compiled a great initial collection of these images on his Galápagos website (www.galapagos.to), unfortunately no longer available.

We acknowledge the significance of having interacted with thousands of students in our science courses (field work, laboratories, and classrooms). We are proud that many of them, graduate and undergraduate, are now researchers in academia at world-renowned institutions.

During the first year of the COVID-19 pandemic, in 2020, caused by coronavirus SARS-CoV-2, we spent much time at our home in Rhode Island, social distancing and working intensely on this project. We followed the daily statistics on global cases, fatalities, recovered patients, and financial sequels of the disease; we shared that information on social media and discussed it with our colleagues and friends. Looking back, SARS-CoV-2 transformed our communities, and Galápagos was no exception. Tourism, the main or only source of income for thousands of galapagueños, ceased [visitors dropped from 271,000 in 2019 to 73,000 in 2020; ≈80% of the local economy depended on tourism at that time, with $356 US million/year generated by tourism alone]; airports and ports closed, except for transporting essentials; islanders became even more isolated; visiting scientists, students, and tourists were trapped for months in the islands. From February 2020 to September 2021, 1,485 cases of coronavirus were accounted for in the archipelago and 17 deaths (Ecuador's total cases 503,767, and 32,351 deaths). We address these struggles in Book Two, Chapter Eight, *Earth's Wounds: Their Impact on the Fragile Islands*.

Books One and Two are our third and fourth academic volumes printed at Cambridge Scholars Publishing, United Kingdom.

Thanks to all.

PREFACE

There are hundreds of books and thousands of scientific articles about Galápagos. Our books One (*Arrivals of Life to the Galápagos*) and Two (*A Synthesis of the Galápagos*) are syntheses. In them, we integrate and conceptualize (1) the most recent natural history research being conducted in the archipelago's terrestrial and aquatic environments. (2) The conflicts resulting from human interactions with nature, including local population growth and tourism practices, in the context of short- and long-term conservation efforts. And (3) make predictions about the destiny of the Galápagos' unique biodiversity and landscapes under various scenarios of climate-change impacts, urbanization trends, diversification of tourism, and conservation investments.

There is no place on Earth like the Galápagos Islands. Since their accidental discovery by Fray Tomás de Berlanga in 1535, Charles Darwin's exploration of the archipelago's geology and life forms in 1835, and UNESCO's 1979 declaration as World Heritage, the *yªs de galapagos* [name assigned to the archipelago in the 1565 *Portolan Chart of the Pacific Coast from Guatemala to Northern Perú*] have become central to natural history studies and, more recently, research programs on the interactions between humans and the islands' fragile ecosystems.

In our two volumes, we merge historical events with contemporary conservation struggles or trends in scientific research. For example, in Book One, Chapter Two (*Adrift: A Tale of a Bishop and His Crew*), Berlanga's 1535 descriptions that, upon arrival at the unknown islands, his "*men found nothing but sea lions, and turtles and galápagos* [the giant tortoises] *so big that each could carry a man on top*", are linked to the 1600s-1800s cultural disregard for the giant tortoises, which, in turn, led to centuries of "slaughtering of the galápagos" for their meat and oil. Such practices, combined with habitats' alterations (via human settlements, agriculture) or introduced invasive species (rats, goats), caused extinctions of tortoises in the islands of Charles (Floreana or Santa María), Abington (Pinta), and Barrington (Santa Fé). Later in Book Two (Chapter Seven, *Homo the Caretaker*), we examine how, in contemporary times, since the creation of the Galápagos National Park (1959, in operation 1968) and the Charles Darwin Foundation (1959), the wellbeing of giant tortoises has improved. Successful reintroduction programs are underway, as are the restoration of habitats and the eradication of introduced invasive species.

This integration approach of past events and modern scientific debates is characteristic of both books. Here is another example: In Book One, Chapter One (*Charles Darwin, the Great Monsters, and a Little World within Itself*), Darwin's realization, once back in England, that his 1835 observations of the mockingbirds' variability among islands in the Galápagos meant that species could change (a novel view in the 1800s) is connected to his 1837 famous "I think" sketch of a little tree depicting the emergence of new genera from a common ancestor. And these two facts are, in turn, linked to the only diagram of the *Origin of Species* of 1859, a "more complex tree", in which Darwin elaborates on the mechanism responsible for such change: natural selection. Yet, we continue with Ernst Mayr's 1977 (zoologist at Harvard University) take on Darwin's thinking and how the idea of evolution by means of natural selection was conceptualized. With this introductory narrative, the reader of Book Two, *A Synthesis of the Galápagos*, should be able to understand more complex concepts examined in other chapters, such as introgressive hybridization, in which members of distinctive species, say Darwin's finches, mix (hybridize) and their descendants give origin–in just a few generations–to new lineages (Book Two, Chapter One, section *Finches Hybridize or Split into Morphs*), something Darwin never imagined [as per the few generations involved] but that modern scientists have documented in Galápagos.

We aim at revealing our passion for both Galápagos' history and the most recent discoveries in the archipelago and its marine reserve, and we do it comparatively. We discuss historical cartographic work, 1600s-onwards, along with modern satellite imaging of the islands (Book One, Chapter Three, *Mapping the Bewitched: Silhouettes Visible from Space*); or the presence of lineages of organisms older than the origin of the current islands, beyond 3-4-million years ago and, in some cases, up to 20-million years ago (Book One, Chapter Five, *The Arrivals of Life: Biogeographic Affinities, Taxa Older than the Islands, and Deep Ancestry*); or the presence of whaling vessels in the archipelago, during the 1600s-1800s, that led to the hunting of sperm whales for their oil, blubber or spermaceti (Book One, Chapter Six, *Moby Dick and the Slaughtering of the Leviathans*); or the richness of shark species as transient-apex or resident mesopredators, which, themselves are being hunted illegally for their fins (Book Two, Chapter Two, section *Thirty-Five Species of Sharks and Counting*; Book Two, Chapter Seven, section *The Global Decline of Shark Populations*). In *Homo the Caretaker* (Book Two, Chapter Seven), we bring optimism to the reader about Galápagos' future–although we do it realistically–by discussing dozens of conservation programs taking place in the archipelago, under the supervision of the Galápagos National Park and in coordination with the Charles Darwin Foundation [among numerous NGOs], and with the goal of preserving the terrestrial environments and magnificent marine reserve for future generations.

We have written and conceptualized Books One and Two for a broad audience, from professors in academia to university and college instructors, and to postdoctoral fellows, graduate students, or research undergraduates. Another target audience are study-abroad and international field-trip instructors and their students who travel to Galápagos from all over the world. Modern explorers of our planet, particularly of spectacular nature reserves like Galápagos, could consider our volumes comprehensive. Science writers and policymakers will find in them useful information to discuss and debate about imminent environmental threats to afflict the Galápagos as a consequence of human population growth, tourism practices, and climate change. For that, we examine the superb work of hundreds of scientists, conservation biologists, and wildlife managers who authored the peer-reviewed articles cited in this book (789 total references) and summarize their data in 516 figures (including within them >1,400 subfigures) and 21 tables.

The length and chapter organization make the books suitable for graduate seminars and/or laboratory discussions facilitated by a principal investigator; keep in mind that some chapters are extensive (e.g. Book Two, Chapter Two, *Crowded Shores, Murky Waters, and the Open Sea*; Book Two, Chapter Four, *Microbes and Viruses, Always Present*). Because both books and their chapters increase in complexity, we recommend the reader explore them in order. However, we have also organized the material to be read independently by chapter (i.e. by the more experienced reader). For that reason, throughout both books, we deliberately reinforce concepts and summarize content (e.g. meaning of acronyms, synopsis of figures, tables, and data from previous sections) and frequently advise the reader to explore figures in a specific manner. We include dialog boxes to highlight the central message of the figures and/or expedite the interpretation of the statistics.

Structure of Book ONE: Arrivals of Life to the Galápagos

The complete title of Book One is *Arrivals of Life to the Galápagos: On Berlanga's Worthless Isles, Darwin's Great Monsters, Melville's Leviathans,* *and World War II*. The book has ten chapters that include 255 figures, 4 tables, and 342 references.

We begin with Darwin's arrival in Galápagos in September 1835 and set the record straight (**Chapter One**): Robert FitzRoy, Captain of Her Majesty's Ship (HMS) Beagle and head of the vessel's surveying voyage around the world (1831 to 1836), which included the exploration of the Galápagos Islands, had requested and been granted by the British Admiralty permission to bring Mr. Darwin–as naturalist–on board. Four years later, Darwin wrote in *Journal of Researchers* (1839) "*The natural history of this archipelago is very remarkable: it seems to be a little world within itself; the greater number of its inhabitants, both vegetable and animal, being found nowhere else*". The Beagle's voyage, FitzRoy's command, Darwin's brilliance, and the uniqueness of the Galápagos Islands all merged in history. The notion of evolution by means of natural selection, which Darwin conceptualized later in life (*The Origin* 1859), can now be broadly applied to nature. The "*great monsters*" and "*a little world within itself*", as he referred to the giant tortoises and the isles (1839), are now exemplars of natural history. Today, the theory of evolution by means of natural selection is attributed to both Charles Darwin and Alfred Russell Wallace (co-discoverers of natural selection). Ever since Darwin and Wallace, however, our collective understanding of evolution has changed significantly at the molecular, genetic, organismal, ecosystem, global, and cosmic levels.

In **Chapter Two**, we travel back in time 300 years, to 1535, when Tomás de Berlanga–Bishop of Panama–and his crew arrived adrift in unknown islands. In a colorful letter to Carlos/Charles I King of Spain, dated April 26, 1535, the Bishop wrote: "*IT seemed right to me to let Your Majesty know about the course of my trip since I departed from Panama, on the twenty-third of February of the current year* [1535]... [Our] *ship sailed with very good breezes for seven days, and the pilot kept course near land and* [then] *we had calm for six days; the currents were so strong, and engulfed us in such a way, that on Wednesday the tenth of March we sighted an island* [likely today's Española/Hood]*; and, because on board there was water for only two more days, it was agreed to take down the lifeboat and go on land for water and grass for the horses. And once there, the men found nothing but sea lions, and turtles and galápagos* [gəˈläpəˌgəs=the giant tortoises] *so big that each could carry a man on top, and many iguanas that look like serpents*..." Berlanga's adventure helps us introduce readers to the Galápagos Giant Tortoises (*Chelonoidis* spp.), their morphs (saddleback or dome), and modern phylogenetic reconstructions. We dedicate an entire section to the *Slaughtering of the* *"gálapagos"* (1600s-1800s) and connect that past to the current (21st century) illegal trade of baby tortoises.

From Berlanga's fortuitous discovery of the isles to the first reliable chart of the "*Galápagos Islands*" by Captain Robert FitzRoy and the Officers of HMS Beagle in 1836, every attempt to map the Galápagos was sketchy (surveying methods were incipient). Plus, the islands were known for having intricate geography, places to get lost, and ambush-buccaneers, which deterred meticulous exploration of the landscape and even led to fables: Spaniard conquistadores Pedro de Alvarado and Diego de Rivadeneira–among others–referred to them as "*Encantadas*" or "*Enchanted*". A depiction later adopted by novelist Herman Melville in *The Encantadas or, Enchanted Isles* (1854-6). Thus, enchanted or bewitched, the islands became awkwardly yet beautifully illustrated numerous times, from the 1500s to 1800s; something we discuss in **Chapter Three**. In section *Islands with Many Names*, we contrast Ambrose Cowley's (British buccaneer) 1684 English nomenclature with that of Captain Alonso de Torres y Guerra's (Spain) of 1793 (Spanish names), e.g., *Albemarle Island* vs. *Santa Gertrudis* or nowadays Isabela. In section *The First Charts and Maps*, we provide images of the 1565 *Portolan Chart of the Pacific Coast from Guatemala to Northern Peru* [with sketches of *y*^{a}*s de galapagos*], as well as *The Gallapagos Islands* (1684) by Ambrose Cowley, and many others, including Samuel Dunn's 1787 *South America as Divided amongst the Spaniards and the Portuguese, the French and the Dutch*, which included The *I*^{s}*. Gallapagos or Inchanted Iflands*; James Colnett's *Chart of the Galapagos, Surveyed in the Merchant-Ship Rattler, and Drawn by Capt: of the Royal Navy, in 1793-1794*; David Porter's 1823 *Gallapagos Islands*; and finally Robert FitzRoy's and the Officers of HMS Beagle 1836 first reliable map of the *Galápagos Islands*. We close the chapter by discussing *Images Generated by Modern Technologies*, state-of-the-art satellite imagery, and provide *Practical and Didactic Sketches of Today's Archipelago*.

In *Tectonics, Volcanoes, Lava Rocks, Caves, and Soils* (**Chapter Four**), we discuss the geological essence of the Galápagos Archipelago. From Planet Earth's tectonic plates to Galápagos' location on the Nazca Plate and its boundaries with the Cocos Plate (North), South America Plate (East), and Pacific Plate (West). We examine the suspected mechanism for the origin of *A 139-Million-Year-Old Hotspot*, the magma source that fuels the Galápagos' volcanoes. The current islands are young (0.032-4 million years), but the hotspot dates back to the early Cretaceous. The Galápagos platform–where the islands rest–moves East (on top of Nazca); its islands age and sink in the same direction; and some turn into sizable seamounts (bottom-of-the-ocean paleo islands). The latter are–and were–ubiquitous in the Galápagos platform and its proximate or distant ridges (i.e. Wolf-Darwin Lineament, Genovesa Ridge, Carnegie, or Cocos ridges). In the geologic past, some seamounts were islands with caldera-volcanoes located just above or nearby the hotspot. The islands' geological past and present, combined with their current geographic location (equator, proximity to Central and South America) and interactions with the ocean (currents, seasonality), are crucial to understanding their biological processes and patterns, as well as the biogeographic affinities of their life forms with respect to recent or deep ancestry (terrestrial and marine environments). Other sections in the chapter include: *Caldera-Volcanoes and Volcanoes without Calderas*; *Spectacular Summits*; *Floreana: A Late-Stage Volcano*; *Lava-Tube Caves or "Pyroducts"* (their formation and commonness across islands); and *Soil-Sampling: Younger vs. Older Islands*.

In **Chapter Five** (*The Arrivals of Life: Biogeographic Affinities, Taxa Older than the Islands, and Deep Ancestry*), we introduce readers to Galápagos' biogeogaphy by first discussing *Turbulent Waters* [central to "arrivals of life forms" carried by ocean currents] and *Hypotheses about the Origins of the Galápagos Biota*. Three working hypotheses explain such origins: *Hi* overwater dispersal from the mainland–in which organisms flew, swam, or were carried to the islands by ocean currents; *Hii* stepping-stone dispersal from the mainland (a variant of *Hi*)–in which organisms dispersed via the now-submerged paleo islands, or seamounts, and made it to the current archipelago after "stepping" from older to younger seamounts; and *Hiii* metapopulation vicariance–in which groups of organisms originated *in situ* during the breakup of widespread ancestral populations (in the deep geological past). We rely on *Exemplar Terrestrial and Marine Taxa* to account for the origin and diversification of: Galápagos'/Darwin's finches; Galápagos penguins; giant tortoises; land and marine iguanas; lava lizards; leaf-toed geckos; land snakes or "racer snakes"; sea lions and fur seals; "flightless" weevils; carpenter bees; sand spiders; land snails; as well as snapdragon shrubs; prickly-pear trees; and *Scalesia*: Darwin's giant daisies. We dedicate an entire section to *Zooming Out: Deep Ancestry*, in which we remind readers that *although many taxa–perhaps the majority–arrived to the Galápagos via dispersal from the proximate or distant mainland, not all did*! We close the chapter by examining *Introduced Species: 1535 Onwards*.

Just as much as Berlanga's, Darwin's, or FitzRoy's historic presence in Galápagos–among other explorers, surveyors, or cartographers of the 17th to 19th centuries–Melville's quasi-silent arrival in the archipelago turned, too, monumental. Herman Melville arrived in Galápagos as a whaler on board the whaling ship Acushnet, in 1841, ten years before the publication of his masterpiece *Moby-Dick; or, The Whale* (1851). By 1854-6, he had authored *The Encantadas or, Enchanted Isles*, a collection of ten literary sketches set in the Galápagos. We discuss Melville's relevance to Galápagos in **Chapter Six** (*Moby-Dick and the Slaughtering of the Leviathans*) and link his story to global whaling, whalers, and whales. Whales were hunted for their oil, spermaceti, meat, bones, baleen, teeth, and ambergris. Sperm-whale oil (waxy and thick) burned brightly and was ideal for lanterns; it was also used as lubricant. In the archives of American whaling, the Galápagos were cataloged as Ground 38. Historically, the North Atlantic was industrially whaled first (early 1700s onwards), and its whales became considerably reduced (early 1800s); over time, whaleships needed to find new grounds in all other oceans. By 1840-1850 (The Golden Age), whaling became global, with particular intensity in the Pacific: Japan, Hawai'i, and along the equator from West to East–the latter where Ground 38 was located. Thus, whalers sailed longer distances and remained at sea for months or years. The ecocide of the "leviathans" was on, but it was only acknowledged in the 20th century! We look at *Whales Captured in Galápagos Waters* (1761 to 1920) and discuss *The Whaling Paradox (1800s versus 1900s) and How Whales Learned to Outsmart Whalers* (=the fact that global whaling declined by the late 1800s, however, it recovered by the 1950s and reached historic catches, at rates never documented before, by the 1960s). Additional sections in Chapter Six include: *Spatial and Seasonal Distribution of Whalers and Whales*; and *Whale Falls, Whale Pumps, and Whale Absence*.

One of the most intricate periods in modern Galápagos history took place during the 1940s, which we examine in *Baltra: World War II and the Geopolitics to Control "The Rock"* (**Chapter Seven**). By the end of the 1800s, the Galápagos Archipelago had gained geopolitical value due to its strategic location in the Tropical Eastern Pacific and with respect to the soon-to-be-constructed Panama Canal. Ecuador was approached by England (early 1900s), France (1898), and the United States (1899) to negotiate the islands as either payment for Ecuador's debt with England (after England financed Ecuador's war of independence with Spain), purchase an island for France, or lease one island for the United States. In 1911, the US proposed another lease–for 99-years, which was not accepted by Ecuador. After the Japanese attack on Pearl Harbor in 1941, Ecuador signed an agreement with the United States for the establishment, in 1942, of US military bases in Seymour (Baltra or "The Rock") Island (Galápagos) and Salinas (mainland Ecuador) to protect the Panama Canal and its surroundings. By 1944, the United States had prepared a draft of a "*bilateral agreement for the leasing of* [military] *bases on Ecuadorian territory over a period of 99 years*". The idea was not accepted by Ecuador, and two years later, in 1946, Ecuador requested the US "*withdrawal from Galápagos*". The US officially returned Baltra to Ecuador on July 1, 1946. All American personnel had left Galápagos by 1948. "The Rock" of the 1940s is nowadays a memory of WWII as well as a symbol of sovereignty–for Ecuador–with a complex past. Geopolitically, however, the destiny of the Tropical Eastern Pacific–and its multiple strategic locations, including the Galápagos Archipelago–will remain uncertain. Regional or global interests in this particular geographic space could manifest again in response to circumstantial change.

In **Chapter Eight** (*Galápagos versus Other Archipelagos*), we contrast the Galápagos Islands with global island groups (i.e. hotspot, oceanic islands). We rely on island biogeography as a conceptual framework for such comparisons. The General Dynamic Model of Island Biogeography (GDM) suggests that the "life cycle of hotspot islands" determines how the processes and patterns of taxa immigration, speciation, and extinction take place: (1) For the duration of their life cycles, hotspot islands or archipelagos are expected to go through emergence, development, and subsidence. (2) Because younger islands offer more vacant ecological niches than old islands, higher species richness should be expected in the former than the latter. (3) Despite the initial origin of the islands' taxa (from another island or the continent), there is a trend (not always met) in which older islands in an archipelago contribute with colonists to younger islands ("progression rule"). Younger islands–or islands in general–can act as "sinks", siphoning migrants from older islands (or the continent). "Reverse colonization" (back to the source) is possible. (4) The MacArthur and Wilson equilibrium model, central to the classical *Theory of Island Biogeography* (ToIB), is part of GDM since taxa migration and extinction, as well as island or archipelago size and distance from the mainland, play a role in an island's life cycle. (5) The GDM model incorporates gene flow within and between islands/archipelagos into the evolution of lineages and speciation, as well as (6) the impact of human activities that cause extinctions on islands/archipelagos. (7) GDM integrates geodynamics with evolutionary and ecological variables to decipher the drivers of biodiversity patterns on islands/archipelagos, diversification trends, emergence of lineages, evolution of traits or syndromes typical to islands/archipelagos (e.g. flight-loss, naïveté toward predators, secondary-woodiness in plants, body-size change). GDM aims at (8) surpassing the "static" premises of classical ToIB and turning island biogeography into a comprehensive field of scientific inquiry. Additional sections in Chapter Eight include: *Habitat Heterogeneity and Archipelago Configuration*; *Taxonomic vs. Morphological Diversity in Archipelag*os; *Trait Evolution, Predators, and Island Age*; *Fish Assemblages in Tropical-Islands Reefs*; *Deep-Ocean Fishes and Invertebrates in the Tropical Eastern Pacific*; *Coral Species Richness/Dissimilarity Across Pacific Reefs*; and *Extinctions on Islands versus Continents*.

In **Chapter Nine** (*Galápagos versus Hawai'i: Lessons to Never Forget*), we focus our attention on contrasting two exemplar volcanic archipelagos: Galápagos and Hawai'i. We begin by stating: if you travel to Galápagos, you will be one in 271 thousand visitors in a single year; if you travel to Hawai'i, you will be one in 10.4 million. The current local population in the former is 25 thousand (density 3 people per km^2), and in the latter, 1.47 million (83 people per km^2). [1 km^2=0.386 sq mi]. In Galápagos, 96% of the land is protected by law (archipelago's area 7,900 km^2/3,050 sq mi); in Hawai'i, only 5% (archipelago's area 16,636 km^2/6,423 sq mi). Extinctions of endemic species or subspecies in the Galápagos have occurred in the recent past, e.g., giant tortoises on various islands, but in Hawai'i, extinctions have been historically numerous and geographically ubiquitous. We highlight that both Galápagos and Hawai'i were once uninhabited–by humans. How did they drift apart in terms of environmental transformations? How did Galápagos remain relatively well preserved while Hawai'i turned into one of the world's red flags of species losses and nature's wounds? The simplistic answer–not less factual–is differential human presence over time! For Galápagos, limited human development (1500s onwards) and exploitation of the land (tied to the harshness of the milieu), as well as protective legislation, have been central to its conservation. For Hawai'i, by contrast, centuries of human settlements (first Polynesians arrived in the 300s or 500s) and growth have substantially modified the fertile archipelago. Indeed, as oceanic islands, Galápagos are today's good example of environmental safeguarding on Earth, whereas Hawai'i is a textbook case of nature's alterations and losses. If Galápagos chooses the path of fast, unsustainable change, urban crowding leading to occupation of additional land, and eco-unfriendly tourism (amusement, entertainment), or if it is persuaded by local or international investors to mimic or resemble Hawai'i's socio-economic trajectory, its destiny will be comparable. It will be a matter of time.

In **Chapter Ten** (*Content of Companion Book "A Synthesis of the Galápagos"*), we introduce readers to Book Two and explain the connection between both volumes. Galápagos' human history and natural history are intertwined. The environmentally sound administration, preservation, and management of the Galápagos' fragile terrestrial and aquatic ecosystems will only be possible if humans learn to coexist with nature. Any departure from this premise will lead to the unsuccessful long-term survival of Galápagos as a matchless World Heritage Site.

Structure of Book TWO: A Synthesis of the Galápagos

The complete title of Book Two is *A Synthesis of the Galápagos: Natural History, Human Conflict, and the Destiny of an Archipelago*. The book has ten chapters that include 261 figures, 17 tables, and 447 references.

Galápagos' seasonality–often called the "hot" and "cool" seasons–is discussed in **Chapter One**, *Cacti on Rocky Grounds and Forests in the Highlands' Mist*. We begin with a traditional sketch of Galápagos' "vegetation zones", which depicts Santa Cruz (*Indefatigable*) Island as an exemplar of the archipelago. This approach has didactic and historical value. However, we quickly switch emphasis to the modern understanding of Galápagos vegetation cover, which relies on merging satellite imagery with high-resolution drone imagery, groundwork, and visual confirmation of the landscape. We provide maps for all major islands. Galápagos' vegetation cover is complex and contingent on island ontogeny, size, altitude, and weather/climate patterns. Half of the archipelago (53%) is covered by native ecosystems; 43% corresponds to recent or old/er lava flows; 3% is agricultural land (particularly in Santa Cruz, San Cristóbal, Isabela, and Floreana Islands); and 1% is urban settings. These environments are the *stage of natural history* on which: *Giants* [tortoises] *Migrate to the Highlands' Mist*; *Finches Hybridize or Split into Morphs*; *Spiny Tribulus Fruits Disperse or Deter Bird Predators*; and *Mockingbirds Battle Old and New Parasites*. We examine outstanding studies conducted by world-class researchers.

In **Chapter Two** (*Crowded Shores, Murky Waters, and the Open Sea*), we leave the rocky grounds of the lowlands and highlands and venture into Galápagos' marine environments. We explore *A Uniquely Well-Preserved Mangrove Forest*, which covers one-third (35%) of the Galápagos coastline, or about 37 km^2/14 sq mi. It may not seem like much area, but mangroves are vital ecosystems. They contribute to carbon fixation (above and below ground), habitat and reproduction sites for terrestrial and marine organisms, and natural protection to coastal areas subject to intertidal cycles. In section *Rookeries of Sea Lions and Their Pups*, we alert readers that Galápagos' sea lion populations are declining. Climate change will increasingly impact sea lions due to extreme weather fluctuations, higher air/sea surface temperatures that will disrupt nutrient cycles and fish-food availability for marine-mammal predators, or sea level rise that will cover breeding areas–for colonies–ashore. In section *Marine Iguanas Shrink to Survive El Niño*, we discuss attempts to explain (=hypotheses) how and why these reptiles shrink (up to 20% reduction in body size) during stressful environmental conditions, e.g., hot years when algal productivity declines (i.e. iguanas' food). In section *A Cormorant that Became Flightless*, we explain the evolutionary and genetic basis for the loss of flight in Galápagos' "patocuervos" (*Phalacrocorax harrisi*). Chapter Two is extensive and has multiple sections: *A Green Sea Turtle with Relatives Everywhere*; *Tiger Sharks Come to Hunt, Green Sea Turtles to Nest*; *Oceanic Bioregions and the Cycles of Life*; *Darwin and Wolf: Source of Coral Larvae*; *Interactions between Coral Reefs and Sharks*; and our favorite *Thirty-Five Species of Sharks and Counting*, which includes illustrations of all known Galápagos' sharks.

Endemism (=uniqueness in occurrence) and rareness (=infrequent occurrence) of taxa are typical of oceanic islands. As Darwin explains in *The Origin* of 1859: "*several islands of the Galapagos... are tenanted... in a quite marvellous manner, by very closely related species; so that the inhabitants of each... island, though mostly distinct, are related in an incomparably closer degree to each other than to the inhabitants of any other part of the world...* [T]*he... species formed in* [these] *islands have not quickly spread to the other islands. But the islands, though in sight of each other, are separated by deep arms of the sea... The currents of the sea are rapid and sweep across the archipelago... so that the islands are far more... separated from each other than they appear to be on a map*". In **Chapter Three**, *Endemism, Rareness, and Endemic Creatures of the Isles*, we characterize endemism in Darwinian islands (formed de novo, never in contact with the source of taxa colonist; e.g. Galápagos) versus fragment islands (formed after separation from the mainland, insularization; e.g. Madagascar). We discuss concepts such as phylogenetic endemism, neo-, paleo-, mix-, or super-endemism, as well as the effects of an archipelago's spatial structure on its species diversity and endemism. We examine comparatively endemism on islands versus mainland. Sections in Chapter Three include: *A Glimpse of Galápagos' Endemics*; *Endemism and Seed-Dispersal in Galápagos' Angiosperms*; *Endemism in Galápagos' Birds*; *Endemism in Iconic Galápagos' Vertebrates*; *Endemism, Landscape, and Adaptive Radiation in Galápagos'/Darwin's Finches*; *Endemism and Hybridization in Galápagos Mockingbirds*; *Endemic Island Rodents*; *Endemism in Galápagos' Beetles*; *Endemism in Galápagos' Spiders*; and *Endemism in Galápagos' Marine Organisms*.

The least studied or understood organisms in Galápagos–the microscopic life forms and their viruses–have been around since the archipelago's formation. We dedicate almost 100 pages of Book Two to *Microbes and Viruses, Always Present* (**Chapter Four**). We begin with section *Sorcerer II and the Global Ocean Sampling* (GOS). In it, we summarize the outcomes of the *Sorcerer II* [=sailing research vessel] expedition 2003-2005, which, according to GOS, was "*inspired by the voyages of Darwin on the HMS Beagle and Captain George Nares* [Royal Navy officer and explorer of the Arctic] *on the HMS Challenger during the 19th Century*". GOS aimed at sampling genes and large sections of genomes from ocean microbial communities (not organisms themselves, but their genetic material). The vessel surveyed Galápagos from February 4 to March 2, 2004. This section is followed by *Zooming In: Bacterioplankton Communities in Galápagos*, in which we examine microbial communities from three contrasting sites: Bolívar Channel, Rock Redonda, and Cowley Islet. We continue with *Dominant Viruses' Groups: Emphasis Galápagos*, data also produced by *Sorcerer II*; and later discuss extensively *Microbes as Indicators of Galápagos Coral Reefs' Health*. Our favorite section is *Hydrothermal Vents and Their Microbial Communities*. Chemosynthetic microbes [not photosynthetic] are the foundation of deep-ocean hydrothermal-vent ecosystems. Hydrothermal vents form along ocean ridges. They were confirmed to exist in 1977, when the submersible *Alvin* reached 2,700-m (9,000-ft) deep and its crew spotted numerous vent fields at the Galápagos Rift. Hydrothermal vent fields are full of life. Scientists have documented 592 species and 332 genera of organisms distributed across 63 world-exemplar vent fields. Based on taxa composition similarity, researchers hypothesize the existence of 6 global biogeographic provinces of deep-sea hydrothermal-vent organisms: Northwest Pacific, Northeast Pacific, Mid-Atlantic Ridge, Northern East Pacific Rise (where the Galápagos Spreading Center and its vents are located), Southwest Pacific, and South East Pacific Rise. Additional sections in Chapter Four include: *Microbes at Volcanoes' Fumarole Fields*; *Microbes in the Guts of Galápagos'/Darwin's Finches*; *Vampire Finches and their Specialized Gut Microbiomes*; *The Gut Microbiomes of Land vs. Marine Iguanas*; *Pathogenic Microbes: Plasmodium and Haemoproteus*; and *Resistance to Antibiotics in Galápagos Microbes*.

In **Chapters Five** (*Homo the Settler*), **Six** (*Homo the Explorer, the Sightseer*), and **Seven** (*Homo the Caretaker*), we address human conflicts (fast population growth, urban expansion, and intense tourism) and human solutions (long-term restoration and sustainable development programs) in

Galápagos. The main message of these chapters can be summarized as follows: (1) If most of the Galápagos' ecosystems remain legally protected and restoration and reintroduction programs continue, the essence of the archipelago has a chance to make it into the future. (2) If the State of Ecuador continues to own and administer the land under low-impact development ideals, the exceptionally unique Galápagos will be exposed to manageable habitat alteration. (3) If human presence in the islands remains at low numbers and density, Galápagos could persist long-term. (4) If tourism continues to be eco-friendly, small-scale, and respectful of both the fragile terrestrial/marine habitats as well as the local people, Galápagos could offer for centuries the possibility of being explored by those who love and value nature. But (5) if Galápagos chooses the path of fast unsustainable change, urban crowding leading to occupation of additional land, and eco-unfriendly tourism (amusement, entertainment), or if it is persuaded by local or international investors to mimic or resemble other oceanic, volcanic archipelagos discussed in Books One and/or Two [e.g. Hawai'i, Cape Verde, Canaries, Madeira & Selvagens, Azores, Seychelles, Mascarenes, including in some cases their mall-shopping, spring-break, or night-life tourism; or their outdoor recreation practices and water sports: windsurfing, kiteboarding, jet-skiing, parasailing, wakeboarding, waterskiing, bumper-tube riding, fly-boarding with hydro-flight aqua-jet propulsion or jet-pack flying], its destiny will be comparable. It will be a matter of time.

In **Chapter Eight**, we address *Earth's Wounds: Their Impact on the Fragile Islands*. We focus our discussions on: *Extreme Weather and Its Sequels*; *Impacts of Climate Change on Coral Reefs*; *The "Human Factor" on Islands' Vegetation*; *Invasive Species at World-Heritage Sites*; *World-Experts' Views on Invasive Species*; *SARS-CoV-2: An Alien Invasive Virus*; *Synopsis of Common Threats to Islands' Taxa*; *Extinctions among Galápagos'/Darwin's Finches*; *Wildlife Trade: Tortoises and Iguanas for Sale*; *Wildlife Roadkills: Homo the Driver in Galápagos*; *Oceans' Microplastics Reach Galápagos*; *Microplastics in the Guts and Tissues of Marine Life: Coastal Ecuador and Galápagos*; *Macroplastics Present in All Galápagos Islands*; *Plastics Ingested and Up Taken By All Trophic Levels*; and *Microbes in the Plastisphere*.

Earth is the only planet we have. For millennia [perhaps for hundreds of thousands of years], humans have transformed the planet, altered its habitats, and caused species' extinctions. Metaphorically, we refer to these occurrences as Earth's wounds. Yet Galápagos persists, although in the context of an environmentally wounded Earth. The archipelago's fragile marine and terrestrial organisms still venture into the ocean's depths or the volcanoes' calderas. How long will these islands remain home to astonishing endemic life? Will Galápagos survive Earth's wounds? The *little world within itself*–as Darwin described it in 1839–is, too, the only one we have.

In *The Destiny of an Archipelago* (**Chapter Nine**), we reason that Galápagos, the volcanic archipelago, will persist for millions of years into the future. As long as the hotspot beneath the islands remains active, it will continue to fuel them with magma. New volcanoes will rise while the present ones gradually drift to the East on top of the Nazca Plate, become dormant, and sink to the bottom of the ocean as seamounts. If left alone and undisturbed [i.e. the islands and their biological cycles], ecological and evolutionary processes will go on in terrestrial and aquatic environments. *Opuntia* and candelabra cactuses will grow as imposing trees. Their fruits will be eaten by birds and reptiles, which will disperse the seeds all over. The finches will adaptively radiate into newer lineages; some will hybridize with seemingly distant phylogenetic relatives. The giant tortoises will vigorously migrate to the highlands of the tall islands during the hot-rainy season, where they will find plenty of browsing grounds. The land iguanas will reach the calderas of the volcanoes and compete for nesting sites, while their offshore counterparts, the marine iguanas, will dive even deeper to feast on the algae growing on the submerged lava rocks. Tiger sharks will come to hunt while green sea turtles, their favorite prey, swim along the sandy beaches looking for suitable places to lay eggs. Whale sharks will gently cruise along the water surface with their mouths open, attempting to filter minute organisms. Killer whale orcas will keep on ambushing other whales or catching distracted sea lions and fur seals. And entire deep-sea hydrothermal vent communities will manage to thrive in the dark, powered by hot water and chemosynthesis rather than sunlight. Their microbes and viruses; their giant *Riftia* worms, clams, and mussels; and their crabs, octopuses, and blind fishes will endure and rule in the blackest depths. But the immediate, 21st-century destiny of the Encantadas will be in the hands of *Homo*, the maker of the Anthropocene. Climate change; large-scale predatory fishing in the vicinity of the Galápagos Marine Reserve; macro- and microplastics in the ocean, permeating all trophic levels; unmanageable local population growth; increasing eco-unfriendly tourism; wildlife trade of baby giant tortoises, which are smuggled for the global market; illegal drug trafficking in the Tropical Eastern Pacific that has targeted the archipelago to step-stone on its way to international consumers; and geopolitical instability in the region (part of it derived from drug trafficking) pose unprecedented threats to the Galápagos.

We close Chapter Nine by asking yet again and trying to answer the following questions: Will this World Heritage Site be the one that forever survives? Will Galápagos be different? Will its caretakers and policymakers not mimic the mistakes that nature custodians have made in other volcanic archipelagos, where pristine ecosystems and endemic wildlife have substantially disappeared while being replaced by large towns and cities, conventional tourism resorts, highways, and introduced species? Will the Galápagos' people, Ecuador, and the world commit to safeguarding and managing the archipelago and its marine reserve so that sound sustainable development practices limit human population expansion on the islands, sponsor solely eco-friendly tourism, and secure revenue fairness for the residents?

Regardless of whether humans survive the Anthropocene or global catastrophic events, ecological and evolutionary processes will continue in future Galápagos archipelagos, of course on a planet already scarred by human presence. But these realities can inspire us to pledge our existence to the health of the Earth. Darwin's *little world within itself*, the spectacular Galápagos Archipelago, is worth saving forever.

In *Berlanga, Darwin, Melville, and Galápagos During World War II* (the very short **Chapter Ten**), we remind readers about the existence of Book One and the connections between Books One and Two.

Guillermo Paz-y-Miño-C
Avelina Espinosa

CHAPTER ONE

CACTI ON ROCKY GROUNDS AND FORESTS IN THE HIGHLANDS' MIST

Naturalists and scientists have traditionally sketched Galápagos' "vegetation zones" using Santa Cruz (*Indefatigable*) Island as an exemplar of the archipelago (Fig. 1.1; e.g. Black 1973; Itow 1992; Mueller-Dombois 2002; Rial et al. 2017). The approach continues to be didactic and of historical value (i.e. Santa Cruz is one of the most studied islands; currently the most populated; the Charles Darwin Research Station and offices of the Galápagos National Park were first established on Santa Cruz). Modern research, however, demonstrates that vegetation cover is complex and characteristic of each island (this chapter). As discussed in Book One, Chapter Eight, the "life cycle" (ontogeny) of an island (or volcanic archipelago) determines the fate of taxa arrivals, speciation, and extinction (see Figs. 8.10 and 8.11, Book One, Chapter Eight). Thus, vegetation cover is, too, expected to correlate with island ontogeny.

Look at Fig. 1.1, which includes a top- and lateral-view (North to the left; South to the right) of Santa Cruz Island. On both views, five vegetation (or climatic) zones are sketched: littoral (coastal); arid lowlands (with conspicuous *Opuntia* tree-like life form); transition (with *Psidium* trees or shrubs); moist uplands (*Scalesia* trees; *Frullania* liverworts; *Miconia* shrubs); and highlands. Note the differential slope on the North (leeward, dryer) and South (windward, rainy) sides of the island. On the North side, the arid lowlands reach 300-m/980-ft elevation; the transition zone continues up to about 500-m/1,640-ft elevation; the moist uplands up to 600-m/1,970-ft; and the highlands with Cerro [hill, mount] Crocker up to 864-m/2,835-ft. By contrast, on the South side of Santa Cruz, the arid lowlands quickly merge into the transition zone, which itself merges into the moist uplands (Fig. 1.1, bottom). Researchers emphasize that all these habitats have been altered by humans, particularly the transition and moist uplands (agriculture, introduced taxa; Trueman and d'Ozouville 2010).

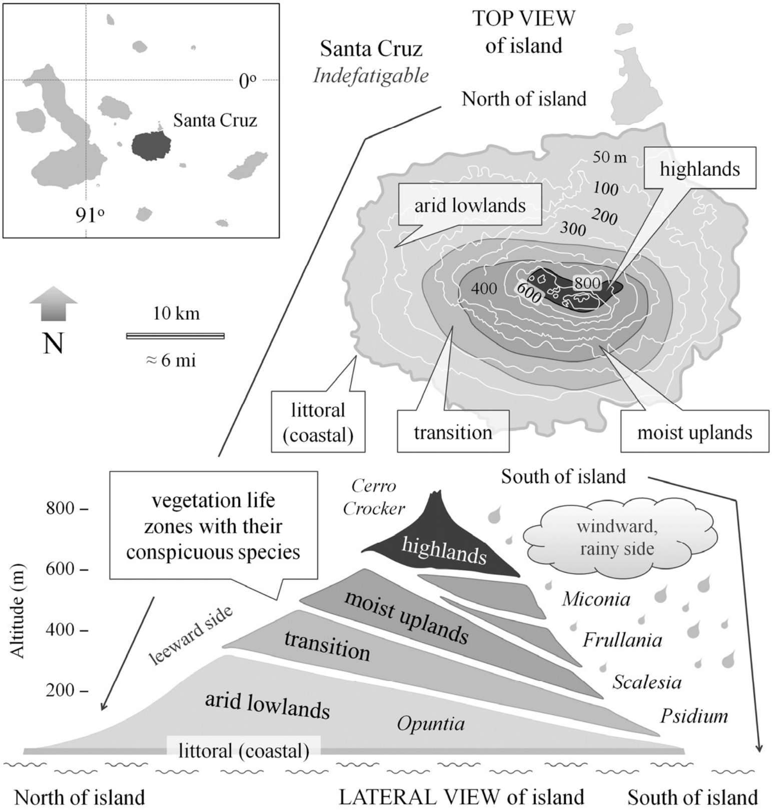

Fig. 1.1 Didactic, historic characterization of vegetation (climatic) zones in Santa Cruz (*Indefatigable*) Island. Design: G. Paz-y-Miño-C; redrawn and modified after a sample of sources, including Black (1973); Itow (1992); Mueller-Dombois (2002); Rial et al. (2017).

In Figs. 1.2 to 1.5, we offer a sample of vegetation images that are typical of some Galápagos habitats, including notes on their natural history. They illustrate contrasting environments (deciduous forests, evergreen forests, dense forests, shrublands, and wetlands) and islands (Santa Cruz, Isabela, Rábida, and Fernandina). Note that the flora of the Galápagos is relatively well known (comprehensive work in Wiggins and Porter 1971; McMullen 1999). Our focus here is to characterize seasonal weather affecting vegetation cycles (after Trueman and d'Ozouville 2010); outline vegetation cover (after Rivas-Torres et al. 2018; Moity et al. 2019); and discuss relevant natural-history case studies of exemplar taxa.