Social and Ecological Interactions in the Galapagos Islands

Stephen J. Walsh
Carlos F. Mena *Editors*

Science and Conservation in the Galapagos Islands

Frameworks & Perspectives

Springer

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Foreword

Introduction to the Galapagos Initiative

On May 16, 2011, the Galapagos Science Center (GSC), on San Cristobal Island in the Galapagos Archipelago of Ecuador, was dedicated by delegations led by Chancellor Santiago Gangotena, Universidad San Francisco de Quito (USFQ), Ecuador, and Chancellor Holden Thorp, University of North Carolina at Chapel Hill (UNC), USA. The dedication marked a significant and conspicuous point in the USFQ–UNC relationship, initially developed around the Galapagos Initiative—an interdisciplinary program of research, education, and community outreach and engagement that examines the social, terrestrial, and marine subsystems of the Galapagos Islands. Scientists from the social, natural, spatial, and computational sciences have come together from both campuses, as well as from international institutions, to participate in the Galapagos Initiative, developed and led by Carlos F. Mena at USFQ and Stephen J. Walsh at UNC, codirectors of the Galapagos Science Center. With the full support of their respective campuses, USFQ and UNC have combined talents and expertise in a unique partnership to create the Galapagos Science Center and to address the social and ecological sustainability of the Galapagos Islands.

The Galapagos Science Center is equipped with four research and education laboratories: Microbiology, Marine Ecology, Terrestrial Ecology, and Spatial Analysis and Modeling. In addition, the facility includes faculty, student, and staff offices, a conference room, a community classroom, and associated space for equipment, experiments, and education and community outreach programs. The Galapagos Science Center is also equipped with a sophisticated cyber infrastructure, staffed with full-time professionals, and linked to the local community and the archipelago more generally.

Through Study Abroad programs, UNC also is linking undergraduate students to the Galapagos Science Center, working through the USFQ Galapagos Academic Institute for Arts and Sciences (GAIAS), directed by Diego Quiroga and Carlos Valle. In additional several master's theses and doctoral dissertations have been completed through the Galapagos Initiative on an array of topics including local fisheries, institutions and policies, mangroves, and land use and tourism. Several others are underway. The Galapagos Science Center has also attracted a diverse and talented group of research faculty and educators from the respective campuses who are addressing collaborative topics that extend across the sciences and resonate throughout the Galapagos Islands, and well beyond. In addition, projects are being conducted in close association with the Galapagos National Park, institutes and agencies of the Ecuadorian government, and several NGOs in the Galapagos Islands.

Introduction to the Series and the Book to Launch the Series

Motivated to understand the social, terrestrial, and marine subsystems of the Galapagos Island and their social–ecological interactions, we have created a book series titled *Social and Ecological Interactions in the Galapagos Islands* that will be published by Springer Science and Business Media, beginning with this initial book. We anticipate the publication of at least one volume each year on an array of topics that collectively examine science, conservation, population, health, and environment in the Galapagos Islands. This initial book to launch the series is titled *Science and Conservation in the Galapagos Islands: Frameworks and Perspectives.* It is designed to provide a broad description of the many challenges and opportunities for examining the Galapagos Islands through multiple lenses that offer a freshness of view and perspective, where the human dimension is clearly linked to the environment through the perspective that we call "*Island Biocomplexity*." *Island Biocomplexity* combines social–ecological coevolution and adaptive resilience with a new island ecology that incorporates human impacts in coupled natural-human systems. *Island Biocomplexity* also encompasses the interactions within and among ecological systems, the physical systems on which they depend, and the human systems with which they interact (Michener et al. 2003; Walsh et al. 2011).

This theoretical approach accommodates an enhanced understanding of the linked and integrative effects of people and environment and the nature of feedbacks that create nonlinear system dynamics, improved pattern–process understanding, and explicit linkages between the social, terrestrial, and marine subsystems of the Galapagos Islands, achieved through an integrated systems perspective (Gonzalez et al. 2008; Miller et al. 2010; Mena et al. 2011). This initial book creates a broad foundation for the more focused volumes to follow that will be developed by guest editors, responding to questions that resonate in science, conservation, and society.

In this book, we draw together scholars, predominately from the University of North Carolina at Chapel Hill and the Universidad San Francisco de Quito, as well as scientists from collaborating institutions. Collectively, these authors describe conditions, challenges, and changes in the Galapagos Islands as viewed through multiple frameworks and perspectives that include Evolutionary Biology, Complexity Theory and Agent-Based Models, Political Ecology, Landscape Ecology, Sustainability Science, Marine Conservation, Invasive Species, Water Quality, Household Livelihoods, Land Use Dynamics, Tourism, Political Institutions, Nutrition and Health, and History as context for the Galapagos

Islands as a special and contested place. Future book topics will be shaped by the interests and ideas developed by the coeditors and by the series editorial board, listed below:

Chapel Hill, NC, USA — Stephen J. Walsh
Quito, Ecuador — Carlos F. Mena

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Preface

The Galapagos Archipelago has been the source of inspiration to many individuals, and over the human history of the archipelago, many different views and opinions have been the source of debate around the world. I will not try to match those brilliant minds who have done great jobs in portraying Galapagos for the benefit of mankind, but I will try to tell my story and my history, and perhaps through my eyes the reader will feel the same passion that has driven me and forged my efforts to contribute to the maintenance and improvement of the conservation of this unique archipelago, a place that I have the honor to call home.

The authors of the chapters in this book are a perfect example of that passion that Galapagos inspires in all of us. In each chapter there is a tremendous amount of research, which is the result of dedicated passion for Galapagos, and perhaps together we might find a way to better understand the concept of sustainability that is so badly needed worldwide.

I was born on Floreana Island, of the four inhabited ones, the smaller island, both geographically and in the number of people living there. I believe I was born with an interest in the natural history of the islands, not in a conscious way, but very interested in all terrestrial life forms that occur on the island. Since my childhood, I have witnessed great changes in the islands; positive ones and some others not so positive. But one constant element over the years has been the tremendous resilience of the native and endemic species to cope with those changes—from feeding habits, behavioral choices to settle on new habitats, ability to cope with the arrival of new species, the street lights, traffic noise, speed boats, oil spills, and to the many visitors who constantly arrive to see the natural wonders that apparently inspired Charles Darwin in the thinking of the theory of evolution.

Also, another constant element that I have witnessed is the status of conservation of the Galapagos Islands that gets better each year. The Galapagos are one of the last few well-conserved tropical archipelagos in the world, which is home to numerous endemic species, and since Darwin's 1835 visit, the archipelago has been the focus of critical research on natural selection and evolution. This extraordinary archipelago has inspired countless visitors, and I'm not going to try to rewrite any of those descriptions, but instead narrate the changes that I have witnessed during my life, which in turn relates to the well-researched chapters that the different authors have put together in this book. Some of those chapters are the results of research that has been overlooked in the past; needed research, indeed, if we are to manage Galapagos as a socio-ecosystem, which has been the case since 1832 when Ecuador took possession of the islands. Since then, the islands have gone through a series of changes that have shaped the present, and I'm sure, the future of the archipelago.

Galapagos was one of the first World Heritage Sites inscribed by UNESCO in 1978, because of the archipelago's outstanding universal value and its integrity as a complete ecosystem that can ensure ecological and evolutionary processes. World Heritage recognition was extended to the Galapagos Marine Reserve in 2001, because of its endemic diversity, multifaceted oceanic currents, unusual biogeography, and complex marine communities that are linked to the terrestrial ecosystems.

The Galapagos Archipelago has been in the eye of the world due to its unique endemic species and, in the last century, the world has come to believe that Galapagos will not survive, thus sending expeditions to collect as many samples as possible of the endemic species to save them in collections cabinets for future generations. So far, the status of conservation of the archipelago is better than a century ago. But it is also true that the threats that the Galapagos faces are greater than before.

Islands are ecologically, economically, politically, and socially different from the rest of the world. In reality, islands should be kept "at risk" forever due to the loss of the original isolation that is the basis for the existence of the endemic species as well as those evolutionary processes that are so strong in isolated islands. We (*homo sapiens*) have been able to break those natural barriers. Today, the Galapagos Islands are visited by several planes each day, and also by several cargo boats each month. In each of those events, as it has been in the past, new species arrive that are aided by the easy transportation to the islands. And, there is an ever-increasing risk that with each plane or each boat, new invasive species could arrive and settle in the archipelago. The effects of globalization are not always good and, in this case, it could be the tipping point for the future of Galapagos.

I have been able to witness changes in Galapagos during my life. Since I'm one of the fortunate ones to have the honor to be a "native" growing up and working in what I call home, it has allowed me to observe and be part of a series of positive and negative changes. I'll describe some of them, but in reality each chapter in this book is a sample of how changes are occurring in the Galapagos and their possible meaning to the Galapagos.

I have experienced a life of change in the Galapagos: from no electricity to cable TV, through eventual contacts with the outside world, to now over 150,000 visitors each year; from a mail system that took several months if not years for letters and packages to arrive, to Internet and e-mail systems; from the happiness to know that Lonesome George was found, to his death as I write these words; and from the discovery of the pink iguana, a large vertebrate that is totally new to science. The islands have gone from introducing herbivores to eradicating them, as one of the most successful projects worldwide; from elementary schools to universities; and from importing skills to exporting advice in many areas and to many parts of the world. These changes show that Galapagos is a growing community aware of its unique environment and that Ecuador and the world are still keeping an interest in and care for this unique archipelago.

I truly hope that this series of publications will help to disseminate the challenges that Galapagos faces and will be a great tool to the decision-making process to have a better Galapagos for future generations. The death of Lonesome George should remind us that extinctions are forever, and, therefore, we should be inspired to do all that we can and more to prevent future losses of unique species.

Galapagos, Ecuador Felipe Cruz

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Abbreviations

ABM	Agent-based model
ADAR	Airborne data acquisition and registration
ALI	Advanced land imager data
ANOVA	Analysis of variance
ASTER	Advanced spaceborne thermal emission and reflection
AVIRIS	Airborne visible/infrared imaging spectrometer
CAS	California Academy of Sciences
CDF	Charles Darwin Foundation
CDRS	Charles Darwin Research Station
CITES	International Convention for the Trade of Endangered Species
DEM	Digital elevation model
ENSO	El Niño southern oscillation
EOL	Encyclopedia of life
ETP	Eastern tropical pacific
FUNDAR	Foundation for Alternative Responsible Development
GAIAS	USFQ Galapagos Academic Institute for Arts and Sciences
GMR	Galapagos Marine Reserve
GNP	Galapagos National Park
GNPS	Galapagos National Park Service
GSC	Galapagos Science Center
INEC	Instituto Nacional de Estadistica y Censo
INEFAN	Institute of Forests and Natural Areas
INGALA	Galapagos National Institute
IPCC	Intergovernmental Panel on Climate Change
IUCN	International Union for the Conservation of Nature
IWC	International Whaling Commission

JICA	Japan International Cooperation Agency
MODIS	Moderate resolution imaging spectroradiometer
MTMF	Mixture-tuned matched filter
NGO	Nongovernmental organization
OBIA	Object-based image analysis
SICGAL	Quarantine and inspection system for Galapagos
SST	Sea surface temperatures
UNC	University of North Carolina at Chapel Hill
UNESCO	United Nations Educational, Scientific and Cultural Organization
USAID	United States Agency for International Development
USFQ	Universidad San Francisco de Quito
WWF	World Wildlife Fund

Chapter 1
Science and Conservation in the Galapagos Islands

Carlos A. Valle

Introduction

Darwin's Theory of Evolution, more than any other scientific theory, has changed our fundamental understanding of the living world and our own conception of human nature. It is no surprise that it has been considered the most revolutionary idea in modern science (Mayr 1982). The Galapagos Islands played a central role in the development of science, particularly for the field modernly known as evolutionary biology. It was mainly his observations on the species of this isolated group of islands in the Pacific that later led Darwin to doubt the chief concept of the time on the immutability of species and to reflect and develop his ideas about the origin of species and, subsequently, his theory of evolution by natural selection (Sulloway 1982). Ever since Darwin's memorable trip to the Galapagos Islands 175 years ago in September 1835, and the publication of his theory in 1859, a large number of naturalists and scientists have visited the Galapagos eager to test Darwin's observations and theory. The Swiss-American naturalist, Louis Agassiz of Harvard University, who visited the Galapagos in 1872; the German geologist Theodor Wolf, who visited twice, in 1875 and 1878; and George Bauer, who traveled there in 1891, are among the most renowned scientists in Darwin's time to visit the Galapagos (Larson 2001). During the twentieth century, two of the best known expeditions were the ones led by William Beebe, in 1923 and 1925, and the California Academy of Sciences expedition in 1905–1906 led by Rollo Beck (Larson 2001; Quiroga 2009).

Scientific research in the Galapagos was pioneered by Lack (1947), Bowman (1963, 1979) and Eibl-Eibesfeldt (1958). Thereafter, several dozen naturalists and scientists from around the world have visited and conducted research on Galapagos

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on a wide variety of subjects. Some came to fulfill an academic requirement like a dissertation, while a few others made the Galapagos their veritable home (e.g., see Quiroga 2009). Among the latter, there are celebrities like Peter and Rosemary Grant, now at Princeton University, who have visited the Galapagos for several months every single year for nearly 40 years since 1973 when their study of Darwin's finches began. Others include Tjitte de Vries, of the Universidad Católica del Ecuador, who pioneered research on the endemic Galapagos hawk (*Buteo galapagoensis*), now, in collaboration with Patty Parker of the University of Saint Louis; Fritz Trillmich, of the University of Bielefeld, Germany, who researched the Galapagos fur seal (*Arctocephalus galapagoensis*) and the Galapagos sea lion (*Zalophus wollebaeki*); Andrew Laurie, whose work on the marine iguana (*Amblyrhynchus cristatus*) was continued and expanded by Martin Wikelski of the University of Konstanz; Tom Fritts, who researched the giant tortoises; Howard and Heidi Snell, who worked on land iguanas (*Conolophus subcristatus* and *C. pallidus*) and lava lizards (*Microlophus* spp.); and David Anderson, who carried out research on siblicide of the Nazca Booby (*Sula granti*) and the ecology of the Galapagos boobies (*Sula* spp.). Lately, a new generation of studies that takes advantage of modern molecular techniques has led to an explosion of phylogenetic and phylogeographic studies that are clarifying our understanding of ecological and evolutionary processes, particularly, the processes and mechanisms of speciation, both in time and space.

The Galapagos Archipelago is one of the most studied places on Earth, even though much of its species' ecological and evolutionary processes still remain unknown. In the marine realm, very little is known about the intertidal, subtidal, and pelagic species and populations, as well as their communities' and ecosystems' ecology and evolutionary processes. The terrestrial biota has been better studied, but, even so, the knowledge base is strongly biased toward the most conspicuous and charismatic species, such as reptiles and some groups of birds. Among plants, only a few flowering plants have been relatively well studied, while very little is known about cryptic species such as cryptogamic plants (especially mosses and lichens).

Here, I briefly summarize some of the most relevant aspects of the natural history of the Galapagos by pointing out a few selected case studies that describe the most important research findings in different fields of the natural sciences studies conducted there. This mini review also addresses the conservation status and threats as well as the conservation achievements in the islands.

Geological Research

Darwin can be considered the first geologist to observe and describe the geology of the Galapagos and to correctly affirm their geological youth and volcanic origin (emerging from the ocean) as oceanic islands that had not been in contact with continental landmasses. Referring to the geology of the Galapagos, he once wrote, "We are led to believe that within a period, geologically recent, the unbroken ocean was here spread out." Modern geological research—aside from petrology and geochemical studies of basalts (e.g., Williams 1966; Williams and McBirney 1979; McBirney and Williams 1969; Swanson et al. 1974) and volcanology (Simkin and Howard 1970; Simkin 1984)—has focused mainly on the origin and age of the islands using several dating techniques including paleomagnetic polarities (geomagnetic reversals), geomorphology analyses, and radioactive potassium–argon dating (Cox 1971, 1983; Geist 1996). Modern radiometric work estimated that Española Island is about 3.3 million years old (Bailey 1976) and that the oldest islands of the archipelago range from about 2 to 3 million years old (Geist 2009).

Estimates of the ages of individual islands vary a lot, but the latest studies estimate the age of the oldest current extant islands (i.e., San Cristobal or Española) at about 3.5 million years and only about 60,000–300,000 years for Fernandina Island (Bailey 1976; Geist 1996). Once again, Darwin was correct when he inferred that the islands emerged from the unbroken ocean, as their origin is currently explained by hot spot and plate tectonic theories. Plate tectonics—the theory that continents move—was first proposed by de Candolle, a French biogeographer, who was originally discredited for his idea. However, it was formally proposed by Alfred Wegener in 1912 and was only gradually accepted after nearly 50 years, mostly due to paleomagnetic evidence. The hot spot theory, on the other hand, is a recent one and refers to a huge and extremely hot solid, but plastic, column of rock that probably rises from the deep mantle due to radioactive enrichment (and radioactive heat). The column (mantle plume) rises due to thermal buoyancy, melts near the surface owing to decompression, and breaks the Earth's crust from beneath, giving rise to a shield volcano like those found in the Galapagos, Hawaii, and other oceanic archipelagos.

The Galapagos settles over the Nazca plate that moves eastward to South America and runs under the South American continental plate along the so-called subduction zone. The islands travel from their center of origin (the Galapagos hot spot under Fernandina Island) at a variable rate between 2 and 7 cm per year. That has created a rough age gradient with a cluster of oldest islands in the east, a cluster of middle-aged islands in the center, and still another cluster of the youngest islands in the west of the archipelago (Simkin 1984). Although most of the Galapagos Islands owe their origin to the mantle hot spot, the origin of the two northernmost islands (Darwin and Wolf) and the three northwestern islands (Pinta, Marchena, and Genovesa) is likely related to the Galapagos ridge, the Nazca-Cocos plates spreading zone, which is located north of the Galapagos Islands (Geist 2009). Current marine geological exploration (Christie et al. 1992) has corroborated the hypotheses, first advanced by biologists (Wyles and Sarich 1983), that the older sunken Galapagos Islands may have been in existence for at least 10 million years. By now, most geologists and biologists working in the Galapagos readily accept that as the Nazca plate moves eastward and the islands travel away from the hot spot, they decrease in altitude—apparently owing to the cooling and contraction of the crust—and eventually subside (Geist 2009). Recent evidence about the genetic distance between the marine and land iguanas, and especially the new species of land iguana (Gentile et al. 2009), provides further support for the currently drawn Galapagos Islands and an older origin of the archipelago.

Climate and Oceanographic Research

The Galapagos Islands are located where several marine currents converge, modifying what should be basically a tropical climate into a predominantly dry region during most of the year (Palmer and Pyle 1966). Such a geographical and oceanographic setting makes these islands attractive for oceanographers and climate scientists interested in the study of Earth's paleoclimate and for those attempting to understand and predict current climatic phenomena with a global impact, such as the El Niño–Southern Oscillation (ENSO) (e.g., Wyrtki 1975; Houvenaghel 1984; Cane 1983). The El Niño event, and its usual counterpart La Niña, affect the terrestrial and marine Galapagos biota in particular ways. During the conditions associated with El Niño (high sea surface temperature and a heavy rainy season), terrestrial organisms feast, breed freely, improve survival, and increase population sizes, while marine organisms fast and stop breeding, die, and decline in population. However, the reverse is true during the drop in sea surface temperature and drought conditions associated with La Niña (e.g., see Robinson and del Pino 1985).

Global-scale research has tremendously advanced our understanding of how the Earth's climate has changed over millions of years. Astronomic evidence and glacial–interglacial cycles, as well as local changes in landmass connectivity associated with plate tectonics, attest to the major climatic changes that the Earth has undergone on a global scale (e.g., Zachos et al. 2001; Ferodov et al. 2006). Thus, the opening and closing of the Isthmus of Panama had major consequences on the patterns of atmospheric and ocean circulation in the eastern Pacific (Cronin and Dowsett 1996). From these studies, it has been inferred how the climate of the Galapagos has changed over the last 10 million years from when the islands had a warmer and more humid tropical climate as compared to today.

Furthermore, studies conducted on the Galapagos Islands themselves have also improved our understanding of the climate both in these islands and at larger geographic scales, including the eastern Pacific. Most paleoclimate research on the Galapagos is based on analyses of sediment cores from a number of lakes but mainly at Junco Lake on San Cristobal Island, Lake Arcturus on Genovesa Island, and the lake on Bainbridge Rock islet near Santiago Island. Pollen stratigraphy and geochemical and mineralogical analyses of sediment cores and C^{14} dating (Colinvaux 1968, 1972; Colinvaux and Schofield 1976a, b), carbon/nitrogen ratios, and isotopic hydrogen and oxygen analyses (Riedinger et al. 2002) have opened a window that has allowed us to picture the history of climatic changes in the Galapagos and the whole eastern Pacific Ocean. These studies provide evidence that during the last 50,000 years, the climate of the Galapagos has undergone profound changes in temperature and precipitation, in association with the Northern Hemisphere ice-age cycles. The islands were dry during glaciations and humid and rainy during interglacial periods, such as the present (Colinvaux 1984), and the frequency of El Niño events started increasing during the last 2,500 years, particularly in the last 1,000 years (Riedinger et al. 2002; Conroy et al. 2008). Research on lake sediments continues today with modern and improved devices and methods; research on El Niño and the climate dynamics of the Galapagos has also been tracked by studies of marine organisms including coral (Shen et al. 1992; Urban et al. 2000) and foraminifera (Lea et al. 2006). One of the major effects of climate change associated with glacial and interglacial cycles in the Galapagos relates to changes in sea levels. Sea level rises (interglacial) and falls (glacial) of over 100 m (Lambeck and Chappell 2001) are presumed to have affected levels of isolation, as well as the size and shape of the islands (Grant and Grant 2008); changes, that in turn, are expected to have affected evolutionary patterns and processes. In summary, global local-scale climate studies have shown that climate of the Galapagos has been highly dynamic and has changed dramatically over geological and evolutionary time scales.

Research on Ecology and Evolutionary Biology

Research on Ecology

Ecological research in the Galapagos is mainly of autoecological character and has focused on geographic distribution, demography, and the behavioral ecology of the most conspicuous species of terrestrial vertebrates (Bowman 1984; Clark 1984; Eibl-Eibesfeldt 1984a, b; de Vries 1984; Grant 1984, 1999; Grant and Grant 2008; Harris 1984; Trillmich 1984; de Roy 2009) and a few species of vascular plants (Eliasson 1984; Porter 1984; Tye 2007, 2008). Even so, several gaps remain regarding the ecology of these relatively well-studied groups, and even less is known about most species of terrestrial invertebrates and most vascular and nonvascular plants, as well as most marine organisms. Furthermore, except for a few marine studies (Withman and Smith 2003; Edgar et al. 2004) and a handful of terrestrial organisms (Abbott and Abbott 1978; Schluter 1986; Schluter and Grant 1984; Schluter et al. 1985; Grant and Grant 2006), ecological research in the Galapagos has severely neglected community ecology at the ecosystem level, with almost a complete lack of in-depth studies about interspecific interaction at the community level and its role on the structuring of natural communities. Thus, we know very little about ecological processes such as pollination, seed dispersal, symbiotic interactions (e.g., parasitism, commensalism), competition, predation, decomposition, predator-/herbivore-mediated coexistence, and the occurrence and role of ecological guilds.

Research on Evolutionary Biology

A volcanic, highly isolated, oceanic archipelago like the Galapagos that was never connected to the mainland is expected to have been devoid of terrestrial life when it emerged from the ocean. The terrestrial life now inhabiting these islands, as well as those organisms now extinct, got there from somewhere else and became rapidly and effectively isolated from their parental populations. These two aspects of colonization and further isolation have profoundly shaped the ecological and evolutionary history of the Galapagos organisms through a three-step process involving (1) organisms' arrival, (2) establishment (colonization) in their new habitat, and (3) in situ evolution (i.e., adaptive and nonadaptive genetic and phenotypic divergence, speciation, evolutionary radiation).

Arrival of Organisms to the Archipelago

Arrival requires transportation to the islands from somewhere else, and 1,000 km of ocean represents a major ecological barrier for a vast number of organisms. A key factor for dispersal and arrival was the organisms' vagility (dispersal ability), which is dependent upon their intrinsic dispersal abilities (i.e., production of small propagules that disperse easily or are easy to transport by winds or by animals) and their ability to survive a long journey through the ocean. Organisms reached the islands by three means of dispersal: through the ocean, either by floating and drifting with the ocean currents (passive dispersal) or swimming (active dispersal); through the air, taking advantage of the trade winds blowing from southeast and northwest; or by attaching themselves to other organisms (e.g., birds). Many organisms, including several types of invertebrates (snails, arthropods) and vertebrates (lizards, snakes, and even poor-flying birds like rails), may have reached the islands on those masses of vegetation that usually get to the ocean when continental rivers overflow during the rainy season and then drift into the open ocean. Duncan Porter (1976) inferred the mean of transportation for the 378 indigenous ancestral taxa that colonized the Galapagos and suggests that birds may have been the vector for about 60% (of these, 64% in the digestive tract, 21% attached to feathers, and 15% attached to mud on the legs), while 32% were transported by the wind and 9% by the sea.

Establishment of Organisms in the Archipelago

Getting to the Galapagos was only part of the process; colonization required the establishment of a viable population. It can be inferred that many successful arrivals did not lead to a successful colonization due to a number of factors, including (1) the ecological successional stage of the island, (2) reproductive viability, and (3) demographic (population) viability. Many organisms may have been prevented from settling after not finding a suitable habitat upon arrival. For example, as we can see today on a barren lava flow, only a few pioneer species (e.g., lichens and few other plants) would be expected to have established themselves first, while the more habitat-demanding species would have had to wait for conditions that were more suitable. For organisms with strict sexual reproduction (most animals and monoecious plants), an unavoidable condition for establishment was arriving with a mate, or in a small flock with individuals of both sexes (as may be the case of the birds), or a fertilized female. Populations that are too small and isolated, such as those that just have colonized a remote archipelago from one single flock, a fertilized female, or a single asexual individual, run a high risk of extinction due to stochastic factors (including genetic, demographic, and environmental), as well as the occurrence of natural catastrophes (Lande 1980; Lande and Barrowclough 1987).

Evolution in the Galapagos Archipelago

Perhaps the most prevalent biological feature of isolated oceanic archipelagos is the high level of endemism among every native taxonomic group. Insular endemics evolve from a mainland-colonizing ancestor either through *linear evolution*, when a colonizing ancestor transforms into a new insular species, or through an *evolutionary radiation*, when either an ancestral colonizer or an insular endemic splits further into several new species.

In the Galapagos Islands, most species that colonized the archipelago have evolved at least into single endemic taxa including subspecies, species, and genera (see Baert 2000; Peck 1996; Tye et al. 2002). Endemics at the species level included mammals (~88%), birds (52%), reptiles (100%), fishes and algae (~20–30%) insects (47%), other terrestrial invertebrates (53%) and vascular plants (32%), bryophytes (mosses, liverworts; ~10%), lichens (~7%), and pteridophytes (ferns; ~4%). Examples of a single colonizing ancestor evolving into a new species (an insular endemic) abound, including the two species of sea lions, the Galapagos penguin (*Spheniscus mendiculus*), the flightless cormorant (*Phalacrocorax harrisi*), and several others. A lower number of colonizers evolved even further and underwent evolutionary radiation when a single colonizing species evolved into several new endemic species. The best examples of evolutionary radiation, most of them derived from a single colonizing event (i.e., monophyletic groups), include land snails of the genus *Bulimulus* (71 species, all endemic, perhaps the most spectacular example of adaptive radiation), Darwin's finches (15 species), and giant tortoises (originally about 15 species). Among plants, the genus *Scalesia* (Asteraceae; 15 species, 19 taxa including subspecies and varieties) and *Alternanthera* (Amaranthaceae; 14 species and 20 taxa), *Opuntia* (Cactaceae; six species and 14 varieties, from two independent colonizations).

The geological youth of the Galapagos Archipelago, together with the high level of endemism among all taxonomic groups that colonized it, implies that evolution in the Galapagos has generally proceeded rapidly particularly among those species that have evolved into different species through the process of linear evolution. The rate of evolution (speciation) has been even more dramatic among those groups that have radiated into many species from a single ancestor that colonized the islands.

The process of colonization and evolution of all organisms in the Galapagos fits nicely into the *founder effect speciation* model first suggested by Huxley (1938) and formally proposed by Mayr (1954). That is, a new species arises when a new population is founded in a remote isolated place, usually by a small group on immigrants. Under such a model, theoretically, there are a number of ecological and genetic factors and