Social and Ecological Interactions in the Galapagos Islands

María de Lourdes Torres
Carlos F. Mena *Editors*

Understanding Invasive Species in the Galapagos Islands

From the Molecular to the Landscape

Springer

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Series Editors

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Series Preface

Galapagos Book Series, "Social and Ecological Sustainability in the Galapagos Islands"

In May 2011, the University of North Carolina (UNC) at Chapel Hill, USA, and the Universidad San Francisco de Quito (USFQ), Ecuador, jointly dedicated the Galapagos Science Center, an education, research, and community outreach facility on San Cristobal Island in the Galapagos Archipelago of Ecuador. The building dedication was the culmination of an emerging partnership between UNC and USFQ that began several years earlier through a 2006 invitation to Carlos Mena and Steve Walsh to assist the Galapagos National Park and The Nature Conservancy in a remote sensing assessment of land cover/land use change throughout the archipelago. Leveraging related work in the Ecuadorian Amazon, Carlos Mena (USFQ Professor of Life and Environmental Sciences) and Steve Walsh (UNC Lyle V. Jones Distinguished Professor of Geography), Co-Directors of the Galapagos Science Center, traveled throughout the islands using preprocessed satellite imagery and spectral and geospatial equipment to validate preliminary analyses of the Galapagos with a focus on invasive plant species. Since that project, Mena and Walsh have continued to regularly engage the Galapagos Islands, coordinating research conducted at the Galapagos Science Center by faculty, staff, and students from both campuses as well as by collaborating scientists from institutions around the globe who together seek to understand the social, terrestrial, and marine subsystems in the Galapagos Islands and their linked and integrative effects. Now with nearly 50 permitted Park projects operating at the Galapagos Science Center and a diversity of scientific topics being studied using a host of theories and practices, innovative work continues in an assortment of compelling and vital ways. The state-of-the-art facilities at the Galapagos Science Center include nearly 20,000 ft^2 of space that supports four laboratories (i.e., Microbiology and Genetics, Terrestrial Ecology, Marine Ecology, and Geospatial Modeling and Analysis), operated through a permanent administrative and technical staff, to support science, conservation, and sustainability in the Galapagos Islands. In addition, students enroll in classes taught by UNC and USFQ faculty as well as conduct research to complete their undergraduate honors theses, graduate theses, and doctoral dissertation. And several scientists at the Galapagos Science Center engage the community on topics including water and pathogens, nutrition and public health, tourism and community development, marine ecology and oceanography, and invasive species.

From these beginnings and with the general intention of developing a Galapagos Book Series to document our scientific findings, highlight special needs, and describe novel approaches to addressing special social-ecological challenges to the conservation and sustainability of the Galapagos Islands, the Springer Book Series was launched through its inaugural book, *Science and Conservation in the Galapagos Islands*: *Frameworks & Perspectives*, edited by Steve Walsh and Carlos Mena and published by Springer in 2013. The series has continued to expand, with books, for instance, on Evolution, the Galapagos Marine Reserve, and Darwin and Darwinism. Now with considerable pleasure we welcome, *Understanding Invasive Species in the Galapagos Islands*, edited by Maria de Lourdes Torres and Carlos Mena. The editors, along with the invited authors, have documented the multi-scale character of invasive species in the Galapagos Islands that extends from the molecular to the landscape level. A variety of questions are framed across space–time scales, and a diversity of analytical approaches are used to examine invasive species, the drivers of expansion and eradication, social-ecological factors, and future trajectories.

The general goal of the Galapagos Book Series is to examine topics that are important in the Galapagos Islands but also vital to island ecosystems around the globe. Increasingly, viewing islands as a coupled human–natural system offers a more holistic perspective for framing the many challenges to island conservation and sustainability, but the perspective also acknowledges the important context of history, human population, migration of plants, animals, and people, development, disturbances, and the evolution and adaptation of species (human and otherwise) on islands to changing social and ecological circumstances. This book offers new and compelling insights and further adds to the Galapagos Book Series in important ways.

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

Preface

How can we define an invasive species? What is its history? How is it that they come to dominate and transform ecosystems? These and many other questions are relevant when trying to understand the behavior of invasive species—primarily in fragile ecosystems such as islands—and the social and economic impact of invasions.

The behavior of species introduced in oceanic islands has been—and remains—an enigma and probably represents one of the most fascinating concerns in island conservation. For a long time, the discussion has been about how a proper management of these species should achieve two main goals: (a) eradication of the species to recover affected ecosystems and (b) conservation of endemic species. But the discussion has also taken on other nuances since there are voices suggesting that an invasive species, when already adapted to an ecosystem, forms an integral part of it and that its eradication would in itself be against conservation. On the other hand, some invasive species are not only part of the biological compound of the island ecosystems, but they also form part of the social and cultural history of the inhabited islands—some of these identified by the local inhabitants as species of real or potential economic value.

The study of the Galapagos Islands is intrinsically interdisciplinary, as is shown in the book series Social and Ecological Sustainability in the Galapagos Islands, which now covers five books. Book 1, *Science and Conservation in the Galapagos Islands: Frameworks & Perspectives*, Stephen J. Walsh and Carlos F. Mena, editors (2013), is a review of the different disciplinary perspectives that have been used to understand social and ecological processes in the Galapagos Islands. Book 2, *Evolution from the Galapagos: Two Centuries after Darwin*, Gabriel Trueba and Carlos Montufar, editors (2013), devotes its pages to advance key topics in the theory of evolution. Book 3, *The Galapagos Marine Reserve: A Dynamic Social–Ecological System*, Judith Denkinger and Luis Vinueza (2014), compiles a set of chapters covering key aspects of the vulnerability, dynamics, and island sustainability of coastal and marine ecosystems. *Darwin, Darwinism and Conservation in the Galapagos Islands*, book 4, edited by Quiroga and Sevilla (2016), places into cultural and historical contexts the notion of the Galapagos as a living laboratory and how Darwin's theory contributed to the construction of the conservation and management of this archipelago. Finally, this book—number 5—compiles a set of chapters which review different perspectives on the study of invasive species in the Galapagos Islands and discuss theoretical backgrounds and methods used to identify, map, and eradicate exotic plants and animal species. This publication sees invasive species as one component within larger social and ecological systems, which need to be better understood in order to have stronger solutions when dealing with management of invasives.

So, defining an invasive species is not an easy task, and neither is defining the species' roles in different ecosystems. This is why we believe that this book, *Understanding Invasive Species in the Galapagos Islands: From the Molecular to the Landscape*, will contribute to the discussion of this fascinating topic.

Quito, Ecuador

María de Lourdes Torres
Carlos F. Mena

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Introduced Species and the Threats to the Galapagos

Diego Quiroga

Oceanic islands possess some of our planet's most unique and diverse organisms, yet these organisms are also very vulnerable to introduced animals and plants. The Galapagos has experienced rapid ecological and social transformations that have created opportunities for new invasive species to arrive. It is important to understand the biological and social processes that underline the spread of some of the invasive species and some possible solutions to manage the archipelago's unique ecosystems. New ways of conceptualizing invasive species need to be explored, and novel forms of dealing with their threats have to be discussed.

Oceanic Islands and Introduced Species

Islands constitute only 5% of the Earth's total area, yet it is there where an important part of the planet's biodiversity exists and where many threatened and endangered species live. Invasive viruses, bacteria, parasites, insects, plants, and animals are major drivers of biodiversity loss and ecosystem degradation on islands. As these invasive organisms reduce—and even eliminate—the population of endemic and native flora and fauna, islands' species are becoming homogenized with those in the rest of the world.

Species adapted to live on oceanic islands have a unique set of characteristics that differ in many ways from those of their ancestors, who often reside in nearby continents. These unique conditions generate the disharmonic biota that characterizes the fauna and flora of remote and isolated oceanic islands, in which some sorts of species are usually missing, such as large terrestrial predators like felines, bears, and canines, and there are no large grazing animals such as large mammalian herbivores

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(Simberloff 2013). Characteristic of oceanic islands includes the change of size of some animals and plants—resulting in island dwarfism and gigantism—and the loss of the capacity for flight among birds and insects. Besides morphological and physiological adaptations to islands, there are also behavioral characteristics, such as tameness, since many of the animals are not threatened by predators. Oceanic animals often have not developed immune responses, given that they are not exposed to many of the diseases that their mainland relatives encounter. There is the possibility of niches not being completely filled, and this idea of the empty niche has been used to explain adaptive radiation among many of the endemic organisms in the case of oceanic islands (Simberloff 2013).

The geographical filters that separate these islands from the mainland create the special character of the native and endemic species and also explain the reasons why the organisms that live there often are vulnerable to introduced and invasive species. Islands have experienced 64% of IUCN-listed extinctions and have 45% of IUCN-listed critically endangered species (Keitt et al. 2011). When terrestrial predators, even relatively small ones such as rats, cats, and the small Indian mongoose, are introduced, native and endemic species can be exterminated. Introduced grazers can also have devastating effects, as with the grazers introduced by Norwegians in South Georgia in the early twentieth century, which damaged the native lichens and grasses. Another characteristic of oceanic islands is the recurrently small animal and plant populations, which increase these organisms' vulnerability to external physical events, such as El Niño or hurricanes. This is the case of some bird populations in the Galapagos, with 1500 penguins as a mean population size between 1993 and 2004 (Vargas et al. 2007), 1679 flightless cormorants (Bird Life International 2013), no more than 100 mangrove finches in 2009 (Fessl et al. 2010), and a small remnant of around 168 mockingbirds of Floreana that survive on the small islets of Champion and Gardner (Jiménez-Uzcátegui et al. 2011). The low numbers evidence these populations' vulnerability, which is particularly worrisome when we take into account their exposure to the 1982–1983 El Niño event, during which the population of many seabirds in the Galapagos Islands—such as the Galapagos penguin (*Spheniscus mendiculus*) and the flightless cormorant (*Nannopterum harrisi*)—did not breed. The cormorant and penguin populations were reduced by 49 and 77%, respectively (Valle and Coulter 1987).

In some cases, people intentionally introduce species to islands, but often they are introduced unintentionally as is the case of animal and plant species that free ride on ships and boats.

Examples of these unintentional introductions include geckoes, rats, insects, and many plants. Rats have spread onto many oceanic islands. Three species of rats have been introduced to 90% of the islands. They prey on seabirds (eggs, chicks, and adults) and are opportunistic feeders and very adaptable to new environments. They can be blamed for seabird extirpation and population decline (Jones et al. 2008; Oppel et al. 2011). In the case of the Galapagos, many of these unintentional introductions were brought on by early explorers, pirates, and whalers between the fifteenth and eighteenth centuries. Some plants, however, were introduced to the Galapagos on purpose as is the case of blackberry and guava, and so were animals such as goats, cattle, donkeys, dogs, and cats. In some cases, species were introduced to oceanic islands on purpose with the aim of eliminating other species, an effort that is often counterproductive. For example, on Hawaii, Society Islands, and other islands of the Pacific, the rosy wolfsnail—from Florida and Central America—was introduced to lower the population of the giant African snail. The attempt failed and the rosy wolfsnail caused the extinction of at least 50 species of terrestrial snails (Simberloff 2013). Cats are often introduced as pets and they have decimated bird and reptile populations. A dramatic case is that of cats having been introduced in the sub-Antarctic Marion Islands in the Southern Indian Ocean in 1949, and currently each cat is estimated to kill 213 birds a year, totaling of over 400,000 birds a year (Whittaker 1998).

There are several mechanisms that account for the success of invasive species over the native flora and fauna, including niche displacement, when the introduced species displaces the native one, and competitive exclusion, when the invasive species completely eliminates the native one (Crowell and Pimm 1976; Simberloff 2013). Not all introduced species become a threat; some authors have mentioned the "one in ten" rule (Richardson and Pyšek 2006), arguing that of every ten introduced organisms, one will become invasive. Although not a very exact number, this ratio does give an idea of how common invasive species are. One of the reasons why invasive species are successful is that they become associated with other invasive species, thus increasing the capacity of each organism to create harm and what has been referred to as an invasional meltdown (Simberloff and Von Holle 1999). The association of introduced species with native and nonnative species is one of the most complex and poorly understood effects of rapidly spreading invasive plants and animals.

An example of introduced species association is the case of pathogens that are transmitted by introduced vectors. In Hawaii, introduced mosquitoes have transmitted avian pox and avian malaria to the native birds, contributing to the extinction of several species and threating many others (Whittaker 1998; Simberloff 2013). In the case of the Galapagos, an example of association exists between *Rubus niveus* (blackberry) and *Psidium guajava* (common guava) seeds, which are dispersed not only by introduced herbivores such as pigs, cattle, and donkeys but also by native animals like finches and mockingbirds. These relationships between introduced species and native ones question the idea that plants create long-lasting relations that are necessary and fixed by years of evolution. New relationships between species are created in nature all the time in relatively short timespans, demonstrating that evolution is based—to a large extent—on opportunistic and unpredictable interactions.

Insects introduced in islands can also have very negative effects and are often good example of detrimental interaction between invasive organisms. One dramatic example of invasive insects annihilating a whole population of islands' organisms is that of the crazy ant (*Anoplolepis gracilipes*) that caused a catastrophic ecosystem shift on the Christmas Islands in the southeastern Indian Ocean, where they killed off one of the keystone species of the island, the red land crab (O'Dowd et al. 2003). Hybridization is another threat to the endemic flora and fauna. There are many examples from oceanic islands where hybridization has resulted in introgression, which can eventually lead to the extinction of endemic species. In the case of the Galapagos, there are several possible cases, which include tomatoes, lantana, grasses, geckos, guava, cotton, moths, wasps, ants, and rats (see Chaps. 1 and 2 of this book).

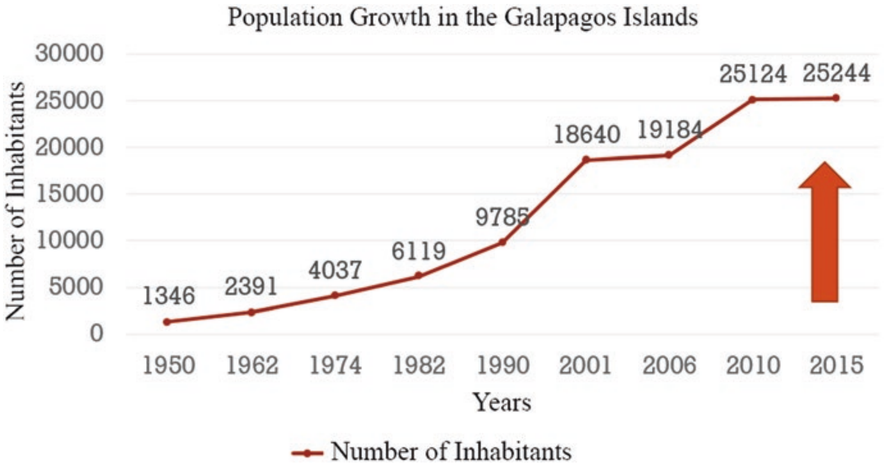
Many invasive species take opportunistic advantage of degraded ecosystems, and rather than being the drivers of change, they benefit from changes occurring due to other anthropogenic causes. These disturbed habitats are the result of human intervention—as when fields are open for agriculture or for urban expansion. The existence of these disturbed environments is an important factor that explains why introduced species spread so quickly. Because of all of these conditions, the extinction rate on oceanic islands is approximately 100 times higher after human colonization than before human arrival.

Galapagos Economic and Social Changes

In the relatively short history of human occupation, the Galapagos Islands have experienced several cycles of economic and ecological transformations (González et al. 2008). Galapagos is one of the few relatively large archipelagos that had not been impacted by humans before the Europeans arrived in 1535. After those early visits, the archipelago endured the impact of several extractive ventures (González et al. 2008; Quiroga 2009). Once the Spaniards lost interest in the islands, pirates and privateers used the Galapagos as a safe haven from which they could launch attacks on Spanish ports and ships and where they could hide from the enemy that was defending the South American coastline. It is during their visits that some of the early invasive species such as rats and goats—and probably some of the plants—were introduced. Whalers and pirates brought goats and rats to many of the islands. Goats were introduced in different times during the history of Galapagos, and they have been reported in most of the islands since 1685. They were reported in Santiago in 1813 and 1900, Floreana in 1832, Isabela in 1897 and 1968, and San Cristobal and Santa Cruz in 1847. In the nineteenth century, British whalers at first and later American whalers also used the Galapagos as a resting place and brought more introduced species and also took with them tortoises, which can survive for a long time on their ships, a characteristic that allowed these poor animals to be used as a source of fresh meat for pirates and whalers as they traveled around the world.

In 1832, the Galapagos was claimed as part of the territory of Ecuador, and Jose Villamil arrived with a group of colonists—mostly people who had trouble with the law—to colonize the archipelago (Latorre 2001). When Charles Darwin visited the Galapagos in 1835, he mentioned some 200–300 people living in Floreana and described some 17 species that had already been introduced to the islands (Gardener et al. 2013). The colonization of the Galapagos by Ecuadorians was also the cause of new introductions. Villamil introduced dogs to San Cristobal and Isabela in some of his hunting expeditions, and he left the animals on the islands (Latorre 2001; Reponen 2013). During the nineteenth century, Manuel J. Cobos established sugarcane and coffee plantations and a cattle farm in San Cristobal. Many animals were introduced by Villamil, and later by Cobos, including donkeys, pigs, cats, and birds such as chickens (Latorre 2001; Fernando Astudillo, personal communication). In their efforts to colonize and create useful landscapes, they introduced animals and plants that would reproduce the conditions on the mainland.

It was not until in the twentieth century, however, that the rate of introductions increased in a significant way. During the first half of the twentieth century, Galapagos remained relatively isolated with few cargo ships arriving to the islands each year. This pattern changed in the 1960s as fisheries and tourism started to increase the rate of connectivity between the Galapagos and the mainland (Grenier 2007; Watkins and Cruz 2007; Quiroga 2009). Currently, the economy in Galapagos is in the midst of rapid transformation (Quiroga 2013), changing from one based on the production of goods, such as agriculture and fishing, to a service economy, i.e., tourism and public sector. Large numbers of travelers started arriving to the Galapagos when cruise ships began taking tourists around the islands in the late 1960s. The increasing flow of people to Galapagos was in part the result of the use of the airport in Baltra, originally constructed by the USA during World War II to bring tourists to the islands. As tourism grew, so did the number of cargo ships and the demand for all kinds of modern goods imported from the mainland. The rate of goods and people arriving from the mainland has accelerated during the twenty-first century; from 2011 to 2015, there has been a 25% increase in the number of imported goods to the islands, and Galapagos has become the Ecuadorian province with the highest consumption per capita (Sampedro 2017). Tourism is the main engine driving the Galapagos economy. In 2004, it was reported that tourism employs 40% of the residents and represents almost 65% of the local economy (Kerr et al. 2004). In 2016, Pizzitutti et al. estimated that nearly 60% of residents are associated with tourism and that tourism accounts for nearly 80% of the local economy. Corresponding with the increase in the demand for goods and services caused by tourism, there has also been an increase in the number of people living on the islands. From 1990 to 2010, Galapagos had a population growth rate of 4.8%, and the 2010 census showed that 65% of the people had not been born in the islands.



(Taken from Sampedro 2017)

The increase in the number of tourists traveling to Galapagos has also meant that local inhabitants have moved from the highlands where agriculture occurs to the towns in the lowlands where most of the tourism companies are based. From 2006 to 2015, there was an important decrease of almost 40% in the number of people working in the agricultural area (INEC 2006, 2014). The rural sector accounted for 42% of the population in 1974 and only 17% in 2010. This movement of people, especially young people, away from agriculture sectors of the inhabited islands into the lowland towns where the ports are—and where tourism and other service jobs are growing—has meant that many of the areas that were cleared to allow for more agriculture have been abandoned (Walsh et al. 2008; Quiroga 2013). Many of these abandoned agricultural fields, where the native vegetation such as *Scalesia* had been removed, have become ideal places for the establishment of invasive species.

Galapagos and Introduced Species

The list of introduced plants in the Galapagos is expanding at a rapid rate. At the moment, there are almost 900 species of plants—found in 46 islands—that are considered introduced. Most of them, 560, were introduced for agricultural purposes and 94 were accidental introductions; only four species have been eradicated. Most of them have been introduced over the last 30–50 years (Buddenhagen 2006; Gardener et al. 2013; Guézou et al. 2016). It has been calculated that 332 of these plant species have been naturalized and 32 of them are invasive (Jaramillo and Guezou 2012; Tye 2001). The list now also includes some marine plant introductions such as a brown alga (*Asparagopsis taxiformis*). The worst invasive plant species in the Galapagos originated in the inhabited areas and are aggressive displacing other plants and affecting the native flora. They include *Rubus niveus* (blackberry), *Psidium guajava* (common guava), *Lantana camara* (multicolored lantana) and several *Passiflora* spp. (passion fruit). Many of them are transformer species and very difficult to eradicate. *Rubus niveus* is considered by many to be the worst alien plant species in the Galapagos. It was introduced for agricultural purposes in Santa Cristobal Island in the early 1970s and was later found on other islands, including Floreana, Santa Cruz, Isabela, and Santiago (Renteria et al. 2012). The cinchona or quinine tree (*Cinchona pubescens*) has become a major problem in Santa Cruz, where at least 11,000 ha has been detected. This tree reduces not only native plant species richness but also the abundance of animals such as the Galapagos rail (*Laterallus spilonotus*) (Jaeger et al. 2007; Gardener et al. 2013). Paradoxically, some introduced species in Galapagos such as the cinchona tree have become endangered in their original habitat.

Until 2006, there were 463 species of introduced insects, 52 of which are considered to be highly invasive, threatening the endemic flora and fauna. These invasive species include fire ants (*Wasmannia auropunctata* and *Solenopsis geminata*), wasps (*Polistes v. and versicolor*), cottony cushion scale (*Icerya purchasi*), and a bird ectoparasite (*Philornis downsi*) (Causton et al. 2006). *Philornis* is among the most worrisome of all the invasive invertebrates at the moment, as it is threatening some of the unique endemic birds of the island. By 2014, the number of introduced invertebrates had reached 762 taxa (Causton et al. 2014). The fire ant—which has a very negative impact on native biota—has been eradicated in many small islands in the Galapagos (Wauters et al. 2014) but will be very difficult to eradicate in the larger and inhabited islands. Most invertebrates probably arrived aboard ships carrying food and products from the mainland, and some introduced invertebrates probably arrived in commercial airplanes as well as in private boats and airplanes. Although many invertebrates were brought to the Galapagos unintentionally, a few were brought intentionally. Such is the case of the recent introduction of the giant African snail (*Achatina fulica*), a species brought to Galapagos in the erroneous belief that it could be commercialized as an ingredient of beauty creams (Causton et al. 2014).

There are 41 taxa of vertebrates reported from the Galapagos (Jiménez-Uzcátegui et al. 2016). One species of bird, smooth-billed ani (*Crotophaga ani*), was introduced by cattle ranchers because of the mistaken belief that it eats ticks. One species of frog (*Scinax quinquefasciatus*), one species of freshwater fish—tilapia—that was introduced to El Junco Lake in San Cristobal but has apparently been successfully eliminated, and many mammals have been detected on the islands.

At the moment, the most important threat comes from rats and some pets such as dogs and cats. For a long time, it was assumed that introduced rats eliminated the endemic rice rats in many islands of the Galapagos. Of the seven species that existed, there are only four extant species. One was discovered in Fernandina (*Nesoryzomys fernandinae)*, and the other (*Nesoryzomys swarthi*) was discovered in 1997, on Santiago (Dowler et al. 2000). This rat is the only one of four remaining Galapagos rats of the original 12 species that lived in the same island as the introduced rat (Harris and Macdonald 2007). It is probable that rats were brought to Galapagos by pirates and/or whalers during the seventeenth or eighteenth centuries. It is believed that introduced rats prey on eggs and the hatchlings of birds and reptiles (Clark 1981). However, research suggested a diet based mostly on plants (98%) and some arthropods (2%) (Riofrio-Lazo and Paez-Rosas 2015). Dogs are other mammals introduced to the Galapagos over a century ago. Introduced dogs have been known to feed on marine iguana, Galapagos penguin, juvenile sea lion, fur seal, brown pelican, and blue-footed booby (Barnett and Rudd 1983; Reponen et al. 2014). As mentioned above, cats also have the potential to cause great harm in oceanic islands. Cats were introduced by ships visiting the islands and by colonists, as pets. Historically, they have been present on the five inhabited islands (Baltra, Santa Cruz, San Cristobal, Floreana, and Isabela) as well as in unpopulated areas of northern Isabela (Konecny 1987; Stone et al. 1994).

It is not always possible to ascertain when parasites were first introduced to the islands; in some cases, it is not adequate to assume that they were introduced by humans. Thus, for example, it was discovered that the black salt-marsh mosquito (*Aedes taeniorhynchus*)—found in many of the islands—colonized the Galapagos naturally before the arrival of humans (Bataille et al. 2009). It has adapted well to the Galapagos and is capable of feeding on reptiles, a characteristic not found among its continental relatives. Evidence also exists of the constant introduction of the mosquito *Culex quinquefasciatus*—a vector for diseases such as avian malaria and West Nile fever—and the ongoing movement of mosquitoes between islands, probably by the transportation mechanisms of tourist cruise ships and interisland boat services (Bataille et al. 2009).

Other threatening species include *Aedes aegypti,* which transmits yellow fever, dengue fever, Zika, and chikungunya. Some of these diseases have already affected the human inhabitants of Galapagos. Since they are vectors for avian malaria and West Nile virus—and penguins in the genus *Spheniscus* are highly susceptible to these diseases—these insects represent a potential new threat for the Galapagos penguins. Some of these viruses have been in the Galapagos for at least 100 years. A study of samples collected since 1899 by Patricia Parker et al. detected cutaneous lesions consistent with *Avipoxvirus* (Parker et al. 2011). AVP is known to cause symptoms like pustules full of pus lining the skin on the infected birds. It has been detected that the APV in the Galapagos has increased dramatically between 2000 and 2009 (Whiteman et al. 2005; Zylberberg et al. 2012). The *Plasmodium* blood parasite has also been found in Galapagos penguins (Levin et al. 2009).

The most sensitive and worrisome pathogens are those that could affect sea lions. Canine distemper is a viral disease that kills 50% of dogs it infects and has been known to jump from domestic animals to seals and sea lions. In the year 2000, over 10,000 Caspian seals died off the coast of Kazakhstan due to cross-species distemper infections (Kuiken et al. 2006). In the Galapagos, antibodies against parvovirus, parainfluenza virus, adenovirus, and distemper virus were present in dogs. Antibodies against panleukopenia virus, *Toxoplasma gondii*, calicivirus, and herpesvirus were detected in cats (Levy et al. 2008).

Eradication of Invasive Species

Fortunately, given the conditions of oceanic islands—such as isolation—there have also been many successful eradication campaigns of invasive plants, animals, and insects. Eradication is more feasible on islands than on continents. Glen et al. (2013), based on a global analysis of 1224 successful eradications of invasive plants and animals, determined that 808 of them were on islands, where small size and isolation can be a positive characteristic. On oceanic islands, there have been successful campaigns to eradicate vertebrates (Keitt et al. 2011; Oppel et al. 2011). Most of these campaigns have taken place on non-inhabited islands (Schoener et al. 2005; Oppel et al. 2011). Galapagos is still considered to be a relatively pristine archipelago, with 95% of its prehuman biodiversity remaining (Bensted-Smith 2002).

There have been several examples of successful elimination of introduced and invasive species in the Galapagos. Rats, dogs, and cats in some of the smaller islands (Baltra Island) represented the best case for the eradication of cats, followed by a land iguana reintroduction (Carrion et al. 2007). Cats were eliminated using

Tomahawk and Victor traps, poison baits, and rifle shots. In the case of dogs, eradication by the GNP began in 1981 on Isabela by shooting and applying poison inside donkey carcasses (Barnett and Rudd 1983). There has been some success in rodent eradications on small- and medium-sized islands such as Rabida and Pinzon. A total of 34 hawks was removed from Pinzon and 40 iguanas were captured in Plaza Sur (Galapagos Conservancy Blog n.d.). The poison was engineered with a strong anticoagulant that makes the rats dry and disintegrate in less than 8 days without a stench (Galapagos Conservancy Blog n.d.). There are now reports that newly hatched tortoises were spotted in Pinzon. The scientist James Gibbs posted that he encountered some 100–300 saddleback tortoises in the island, which evidences an important recovery (Nicholls 2015). Pigs (Cruz et al. 2005) and donkeys (Carrion et al. 2007) are large mammals that have also been successfully eradicated in the Galapagos.

Some of the most successful examples of eradication of mammals in the world come from the Galapagos. Given its magnitude and impact, the most important example of a large-scale eradication is that of the elimination of the goats from Santiago, Isabela, and other islands (Carrion et al. 2007; Márquez et al. 2010). By placing tracking devices in the so-called Judas goat, often sterilized female goats on induced heat, hunters could track and eliminate large quantities of goats and pigs. Project Isabela became the largest island restoration effort to date, removing 140,000 goats from 500,000 ha for a cost of US$10.5 million. Some 79,000 goats were also removed from Santiago Island from approximately 58,000 ha, at a cost of more than US$6 million (Cruz et al. 2009; Carrion et al. 2011).

There are other examples of successful eradications from the Galapagos Islands, one of which includes the use of biological controls to eliminate the cottony cushion scale. In 2002, a biological control program was implemented in the Galapagos by the Charles Darwin Foundation and the Galapagos National Park, as the Australian ladybug *Rodolia cardinalis* was released to control the invasive cottony cushion scale, *Icerya purchasi,* which had been affecting more than 60 plant species. *Rodolia cardinalis* moved quickly and was efficient in reducing and controlling the invasive scale. In 2009, the ladybug was found in seven of the islands surveyed that had the cottony cushion scale, where it successfully eliminated the scale from most of these islands (Alvarez et al. 2012). Most of the plants are now free of cottony cushion scale.

Despite all these successes, there are still many problems with the process and the concepts behind eliminating invasive species. Often, the local people oppose the eradication project for several reasons. Lack of involvement of locals in the design and implementation of the projects has played a role in the failure of some campaigns around the world and in the Galapagos. There has been opposition by the local population on the grounds of violation of animal rights, or because dangerous toxins were used (Oppel et al. 2011). In the case of the Galapagos, the people see some of the species as useful and they do not want them to disappear. Such is the case of trees like cedrela (*Cedrela odorata*) used for construction. Some opposition is also based on ideological reasons; thus, the fishermen opposed some of the eradication efforts in part because they thought that these efforts were a waste of money that could have been used for other purposes and because they resented the conservationist groups and GNP authorities in charge of the campaigns. There is often a lack of community involvement in these efforts. Opposition is especially strong in the case of pet animals such as dogs, cats, fish, and exotic birds but also in the case of farm animals.

In the Galapagos, the population of dogs is theoretically controlled; they are supposed to be neutered and spayed and are not allowed to be brought in from the mainland. However, the reality is different. New dogs appear on inhabited islands all the time, especially large purebreds, which their owners proudly take for walks in the town. It is thought that these animals are often illegally brought by cargo boats. At the moment, there are several public and private institutions working on neutering and spaying the pets. NGOs such as Sea Shepherd, Animal Balance, and Darwin Animal Doctors work to round up feral cats and dogs and bring volunteer veterinarians to spay and neuter the domestic cats and dogs. Galapagos Preservation Society's (GPS) mission is to protect the islands' fragile ecosystems and endemic species by humanely removing and rehoming nonnative animals.

The process of eliminating introduced species is open to many unpredictable outcomes, which has led to ambiguous results when it comes to the elimination of many species. There are instances of ambiguous triumphs in the Galapagos, where the elimination of one invasive species results in the growth of other invasive species. Often there was an overgrowth of invasive plant species after goats and other herbivores were eliminated. As a result of the success of the goat eradication project in some of the islands—such as the highlands of Santiago—blackberry (*Rubus niveus*) has not only started to grow but is now spread by naive birds (Carrion et al. 2011). In the case of islands like Pinta, where the giant tortoises became extinct, managers have resorted to introduction of sterilized species of tortoises from Española Island (Quiroga and Rivas 2017).

Some have criticized the eradication efforts as being expensive and often unsuccessful. A study by Gardener et al. (2010) documented that of 30 projects, only four were successful: the successful ones were all in a net area of less than 1 ha, on land with a single owner and that did not have persistent seed banks. Blackberry is one of the most difficult plants to eliminate in the Galapagos. More than one million dollars has been spent in the eradication of 34 plant species, and four were successfully eradicated (Vince 2011). The eradication of these four species occurred mainly because the population of these invasive species was small and they were localized in very specific areas.

The lack of success in elimination processes with many invasive species has resulted in people suggesting that it is better to maintain some of the invasive species, at least in the cases where their elimination is impractical or economically impossible. For some, the idea of novel ecosystems means embracing introduced species (Vince 2011). For this reason, it has been mentioned that it is necessary to determine a target at which some introduced species should be maintained. Studies have shown a significant difference in native species richness and vegetation structure associated with *R. niveus*. The idea is that there is a threshold value. Renteria et al. have suggested a conservative maximum of 40% *R. niveus* cover, which could be a sustainable target for managers (Renteria et al. 2012). Another complication is that some introduced species may have beneficial effects and provide the local people with some important ecosystem services. Furthermore, some introduced species now have positive effects on some native and endemic species, as is the case of guava, which supports endemic and native epiphytes and is used to give shade to cattle, and cedrela, used for construction.

Given these ambiguous results in the fight against invasive species, the lack of success in some cases, and the expense incurred, some authors have suggested that the best way to handle resilient invasive species is to manage and control these novel ecosystems (Hobbs et al. 2006; Gardener et al. 2010). Species, some authors argue, should not be judged by their origins, i.e., what is important is the ecological functions of species and not where species are from (Davis et al. 2011). The idea of novel ecosystems has been recently criticized as not being well formulated, that it gives the sensation of giving up the fight against invasive species and that there are no explicit irreversible ecological thresholds, whereas in reality many ecosystems are successfully being conserved and restored (Murcia et al. 2014).

Some authors have questioned the extent to which the fight to restore pristine environments is based on objective scientific evidence and represents bias-free concerns or whether restoration decisions are more the result of political, cultural, and economic interests and considerations that lie behind the apparently neutral façade of conservation efforts. They question the way conservationists conceive the war against invasive species under the premise that one can restore ecosystems to their pristine conditions. The idea of recreating pristine environments is seen as unrealistic—or in many cases impossible—because we do not know enough about these often-imagined pristine environments. Elliot (1997) argues that it is fallacious idea that humans can restore natural areas that have already been transformed. Restoration is impossible both because of historical reasons, as in art, a replica can never be the same as the original for it has a different genesis, and also for practical reasons given the unpredictable and changing nature of environments to replicate a particular complex system. Katz (1992, 1997) maintains that the anthropocentric idea humans have about their power and right to restore and manage nature is misleading. He argues that once humans restore an area, the area loses its naturalness and becomes artificial and an artifact. As economic and social globalization during the Anthropocene generates homogenous landscapes, we try to restore some specific environments that we consider unique and special by creating artificial replicas of assumed pristine areas. Increasingly, many natural parks and protected areas around the world, such as the parks in Africa, Europe, North America, and places in Latin America like the Galapagos, are becoming highly managed areas, losing their naturalness in this process, and becoming some type of large zoos for tourists and some scientists to enjoy, photograph, and study.

Daniel Botkin (2012) has questioned the paradigm that maintains nature as a balanced system. Uncertainty, threshold changes, and unlocked relationships are now becoming common metaphors to understand nature. The recreation of pristine, untouched, and to some extent unchanging environments is contrary to the evolutionary processes that created these environments (Quiroga and Rivas 2017).

The Galapagos has been constructed as a natural laboratory where the majority of the evolutionary processes are still in place. This construct has meant that any change in the Galapagos from this original—albeit to a large extent unknown—state requires that managers must intervene to restore the imaginary pristine environments. The effort to restore the Galapagos has brought about successful and unsuccessful attempts to eliminate introduced species. The paradox lies in that, in order to restore the Galapagos to the point where evolutionary processes are guaranteed, it is necessary to stop and freeze some of the Darwinian evolutionary process that restoration is meant to insure. Since this restoration is often imperfect—and results in uncontrolled and unpredictable consequences—an ever more intensely managed ecological system is being created.

Invasive species represent one of the most difficult challenges facing the Galapagos. As in many oceanic islands, the same characteristics that make their organisms unique make them vulnerable to introductions. There are many successful examples of combating introduced species on islands and in the Galapagos but also many failures. New paradigms and ideas need to be explored in order to use the limited resources in a more effective way, and we need to question some of the traditional ways of understanding and managing the problem if we are to successfully deal with the threats that invasive species pose for the biodiversity of the Galapagos.

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Part I
From the Molecular

Chapter 1
A Preliminary Assessment of the Genetic Diversity and Population Structure of Guava, *Psidium guajava*, in San Cristobal

María de Lourdes Torres and Bernardo Gutiérrez

The Importance of Genetic Diversity on the Fitness and Success of Invasive Species

Our current knowledge on the genetics of invasiveness is limited, but it has allowed us to identify a set of genetic factors that influence the ability of a species to adapt to new environments and become invasive. Numerous studies have analyzed various aspects of the genetic composition of invasive species in different settings, allowing researchers to establish some base hypotheses (reviewed by Sakai et al. 2001 and Lee 2002). Based on the studies of both invasive and noninvasive species, an association between genetic diversity and fitness has been observed, as higher levels of genetic diversity positively correlate with better response to selection and higher population fitness. Low levels of genetic diversity, on the other hand, tend to have negative effects on fitness, as genetic drift and inbreeding depression can take a toll on the population's gene pool and reduce its ability to respond and adapt to new or changing environments (Reed and Frankham 2003).

The effects of reduced genetic diversity in a population are particularly important when dealing with invasive organisms, since these scenarios tend to include a bottleneck for the invading species. An invasion can be described as a rapid evolutionary event, and as such, it is dependent on random processes like genetic drift and nonrandom processes like natural selection. On the former, it is noteworthy that

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invasive populations tend to be small subsets of the original populations, and this "sampling" process provides a certain degree of randomness in the selection of the founding genetic pool during an invasive event. As a result, the invasive population represents, to different extents, just a fraction of the complete genetic pool of the original source population. This reduction in the genetic diversity of the invasive population is what is commonly known as a bottleneck, a phenomenon that can also be observed in species where small populations survive catastrophic events or species under extinction processes (Nei et al. 1975).

The process of new ecosystem colonization follows a determined path that can be clearly separated into two distinct phases. In the early stages of invasion, members of an original population disperse into a new environment and are immediately subject to selection, where the most adaptable individuals survive the challenges that are presented by the new habitat. This first phase places the invasive species under a bottleneck, where part of the original genetic diversity can be lost due to purifying selection. In a later stage of the invasion, the surviving individuals must compete in the new environment to establish their niche by gradually adapting to the new environmental factors (climate, photoperiod, etc.) while competing with resident species (Lee 2002).

It may sound paradoxical that a population under such heavy selective pressures could succeed in the new environment, even to the point of displacing and compromising the survival of local species. It is a widely accepted fact that invasive species are one of the main causes for the loss of biodiversity worldwide, only second to habitat destruction (Scalera et al. 2012). However, specific processes contribute to the potential success of some invasive species. Numerous phenomena at the genetic level are key determinants of a successful invasion, including epistasis, genetic trade-offs that work in favor of an adaptation to the new environment, large genetic rearrangements that can result beneficial for the invasive species, and the action of specific genes on the overall fitness of said species (Lee 2002). The occurrence of such events, however, is dependent on the species' additive and epistatic genetic variances in the first place. It has been proposed that both components of genetic variance play key roles in exposing genetic elements to the action of natural selection, whether they encode for desired traits or affect key regulatory networks that have a major impact on individual or group fitness (Lee 2002).

It is also important to understand that invasiveness in island environments is a unique phenomenon itself, as it presents a distinct scenario in which individuals are placed under stringent separation from the original population with minimum gene flow between the island and the source. This situation follows the same bottleneck concept previously described and has a profound effect on the allelic frequencies of specific genes. As a general rule, gene alleles that increase the organism's fitness in the new environment may become more frequent in the population gene pool by the action of natural selection, while neutral or detrimental alleles become rare or disappear altogether, generating an overall reduction of gene diversity (Frankham 1997). As a direct consequence, we can observe that at the time of introduction, and for a time span following colonization, island populations can undergo a period of constant genetic diversity reduction. This process is exacerbated by the intense genetic drift and inbreeding depression associated with the small sizes of the founding populations. Posterior stages in the population's history may alter these allelic frequencies as new mutations and migration events can occur (Frankham 1997).

Nonetheless, island ecosystems still host an observable competition between endemic and invasive species, where the genetic makeup of each serves as the basis for their potential survival. Endemic island populations also tend to have reduced genetic diversity when compared to their mainland counterparts or to other island non-endemic species, and this can be reflected in reduced phenotypic and quantitative genetic variation (Frankham 1997). It has been proposed that this reduced diversity can partially account for the vulnerability of endemic island populations, where the effective inbreeding coefficients have been found to be demonstrably higher (Frankham 1998) and where genetic drift can also have negative effects (especially in populations found in small islands with little habitat heterogeneity) (Stuessy et al. 2014). On the other hand, multiple factors are associated with the success of an invasive species, and no clear patterns between invasion success, number of introduction events, origin of the invading individuals, and heterogeneity of the founding gene pool have been established (Novak and Mack 2005). These phenomena highlight the vulnerability of endemic island populations, especially when they are forced to rapidly adapt to the selective pressures of competing with invasive species, a process that has been continually observed in the Galapagos Islands for the past century (Jäger et al. 2009; Mauchamp 1997).

The Case of Guava (*Psidium guajava* L.) as an Invasive Species in the Galapagos Islands

The insular ecosystems of the Galapagos Islands have long been under threat due to the presence of numerous invasive species from a wide range of taxa, including plants, reptiles, and mammals (Novak and Mack 2005). Invasive plant species are of particular interest due to their rapid propagation and the displacement effects that they may exert upon endemic and native species. The 2013 census for plant species in the Galapagos Islands reports a total of 1581 different species of vascular plants in the islands (Jaramillo Díaz and Guézou 2013). In addition, the latest endemic plant species reports mention 560 species classified as native, where 180 of these (32% of all native plants) are classified as endemic (Tye 2002). A partial analysis of these native plants shows that at least 54 different species are vulnerable under the IUCN parameters, a number that could rise with more complete data (Tye 2002). These numbers are contrasted by a total of 815 different species considered to be introduced plant species, 273 of which are naturalized species that reproduce without human intervention, and 509 are still cultivated species (Guézou et al. 2014). Considering the numerous reported cases of the negative effects that invasive species have induced on the local biodiversity of the Galapagos Islands (Novak and Mack 2005), it can be inferred that the presence of these competing invasive species accounts for a considerable portion of those observations, especially due to the aggressiveness of some of the introduced plant and animal species. Even when the direct effects of introduced animal species (such as rats, feral cats, and goats) are more directly observable, several invasive plant species also have drastic effects on the biodiversity of the islands (Jäger et al. 2009).

A large portion of the introduced plant species are a direct consequence of the permanent settling of human populations in the archipelago, a process that has formally been acknowledged since 1869. However, sporadic presence of humans has also been reported since before the official discovery of the islands in 1535, as different seafaring groups used the Galapagos Islands as temporary resupply stations and safe havens (Slevin 1959). Whether it was by deliberate action or as an accident, a large number of species were introduced to the islands as a direct consequence of human activities in the archipelago. This phenomenon saw an increase of plant species with the establishment of permanent populations in the four currently inhabited islands: Santa Cruz (including the military base and civilian airport in the adjacent island of Baltra), San Cristobal, Isabela, and Floreana. Early introduced species included a series of edible fruits and vegetables (Mauchamp 1997), which were commonly established in the humid areas of the islands due to more favorable environmental conditions (Tye 1999).

During those early colonization stages, the guava tree (*Psidium guajava* L.) was introduced on the islands, and by the early twentieth century, it was already reported as having escaped the agricultural fields into the wild (Yadava 1996). Commonly known as “guayaba” in Spanish-speaking countries, *P. guajava* is a fruit crop endemic to the tropical regions of South America and has been distributed to numerous other countries of tropical and subtropical climate (Yadava 1996). This economically important species belongs to the Myrtaceae family and is commonly sought after for its fruits, which are consumed fresh or as processed food products (Yadava 1996). It is an allogamous species, characterized by an open pollination reproductive cycle, a trait that tends to maintain high genetic diversity levels, reduces introgression, and maximizes outcrossing (up to 40% of all pollination is estimated to be outcrossing) between populations (Nakasone and Paull 1998). This species has proven itself a particularly efficient invader of the islands’ ecosystems, as its fruit production facilitated the dispersion of its seeds across long distances by the action of birds, small mammals, or other local animals (Tye 1999). It also presented a particularly negative effect on the native ecosystems because of the effects that woody plants can have on local flora. These plant species are responsible for dramatic habitat alterations in large portions of the Galapagos Islands due to their role in shading their surroundings (therefore altering light access for other small-sized plant species), the prevention of seedling germination through soil structure alteration, and the overall displacement of local species (Jäger et al. 2007). The presence of invasive woody plant species can also be a hindrance for the restoration of native vegetation, as the invaders can disrupt the composition of the local endemic seed bank, and their abrupt elimination can favor the propagation of fast-growing grasses that displace the normally diversified vegetation (Loh and Daehler 2008).

The wide distribution patterns of *P. guajava* on the islands and the distinct and observable habitat alteration that they have generated make this species a matter of serious concern for the conservation efforts in the islands. The species is currently used by local farmers as a perimeter delimitation tree in agricultural fields, but its presence can be observed in more remote locations as well. This escape from the agricultural fields was possible by the naturalization of the species and its ability to survive and propagate without direct human intervention. Over 40,000 ha of the archipelago land surface are populated by guava trees, an area that includes a large portion of the humid highland environments of the San Cristobal Island and a considerable portion of Isabela Island (Lawesson and Ortiz 1990). Santa Cruz, the island that sustains the largest human population in the archipelago, also presents widespread distribution of escaped guava trees in wild environments, specifically in the fern-sedge zone (Jäger et al. 2007).

The current situation of the species in the Galapagos Islands makes its study an imperative priority, as an adequate understanding of its biological capabilities and genetic composition can aid in the development of efficient control practices and policies, aimed at protecting the most vulnerable species that dwell in the archipelago.

Studying the Genetic Diversity of Invasive *P. guajava* in San Cristobal and Its Effects on the Endemic Guayabillo (*Psidium galapageium*)

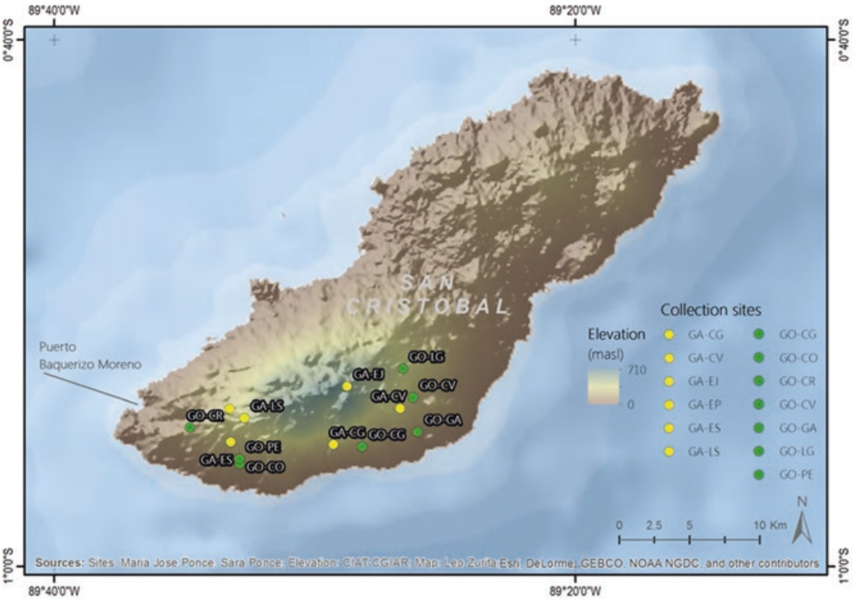
Genetic diversity analysis is one of the most powerful tools that evolutionary biologists and population geneticists have to elucidate a species' evolutionary history, its current ecological role, and its potential for survival in the long term. The development of robust research methodologies in molecular biology has been a strong incentive for the use of genetic data as a way of establishing relationships between individuals and drawing conclusions on their biological and ecological status. Based on these principles, our research group focused on the use of molecular markers for the characterization of the genetic diversity of *P. guajava* in one of the inhabited islands in the Galapagos archipelago, San Cristobal.

Genetic diversity studies have been performed based on the use of specific molecular markers which quantify the genetic variations found between individuals of various populations or species. This methodology, therefore, requires a considerable amount of genetic information, obtained from the largest possible coverage of the organism's complete genome. Historically, the technical limitations of performing such feats and obtaining sufficient amounts of information were overcome by the use of molecular biology techniques that scanned through large numbers of genome-wide distributed markers. The development of new high-throughput sequencing technologies, such as whole genome sequencing (WGS), has rendered many of these previous tools close to obsolete, as newer methods allow for a rapid and efficient analysis of numerous single nucleotide polymorphisms (SNPs) in a genome (an approach that can be executed through protocols such as genotype by sequencing (GBS) or SNP array genotyping) (Ellegren 2014).

An alternative approach that is still widely used for genetic diversity studies is based on the analysis of microsatellite regions commonly found in nuclear or plastid genomes. These regions, commonly known as simple sequence repeats (SSRs), are made up of small motifs (a motif can be a combination of two to four nucleotides in a microsatellite region) that are repeated multiple times in tandem. They present polymorphic variations based on the number of tandem repeats of the motifs that make up their sequence. The variation in the number of repetitions of each motif is a process that occurs during DNA replication, as the enzymes that handle the copying process of the genome can introduce insertions and deletions in these sequences (especially in highly repetitive regions). For this reason, microsatellite regions are highly variable between individuals while still being conserved within lineages. In addition, most SSRs are noncoding elements, which suggest that they evolve in a nearly neutral fashion, providing an unbiased model of molecular evolution. These markers are analyzed through PCR amplification of their respective loci, and polymorphisms between individuals are scored as different-sized amplification fragments (Weber and May 1989). They have proven to be exceptionally reproducible in laboratory settings, as a specific PCR reaction targets a single locus for all of the individuals being analyzed. They also allow the user to determine the identity by state of individual alleles for each locus, which makes a direct estimation of allelic frequencies possible and allows the indirect estimation of the genetic diversity and population genetic parameters (Ellegren 2004).

Given the advantages that SSR markers provide, the genetic diversity of a guava sample taken from the island of San Cristobal was evaluated and compared to a smaller control sample, taken from continental Ecuador. The San Cristobal sample included 94 guava individuals collected from six different locations in the island's humid agricultural fields (Fig. 1.1). The continental control sample included 18 individuals that were collected from an altitude gradient ranging from the valley of Tumbaco (adjacent to the capital city of Quito) in the northern highlands to the coastal region in the province of Manabí (from 2200 masl to sea level). A total of 17 different loci were analyzed for these samples, with specific primers obtained from a previous *Psidium guajava* study (Kanupriya et al. 2011). The PCR products were observed through polyacrylamide gel electrophoresis (PAGE), and specific alleles for each sample were scored into codominant matrixes for posterior data analysis. Once all samples were genotyped, we evaluated the relationship between all samples, their genetic similarity, the overall genetic diversity for both populations, and, finally, the presence of specific population structure in the island of San Cristobal.

The results, as expected, show a considerable gene pool reduction for the San Cristobal *P. guajava* population when compared to the continental sample. The percentage of polymorphic loci in the island populations ranged from 41% to 47%, while the continental sample presented 71% polymorphic loci. The average number of alleles appeared to be less divergent between samples (17.88 alleles per locus for the continent versus 15.22 alleles per locus for the island populations), but the



Sources: Sites: Maria Jose Ponce, Sara Ponce. Elevation: CIAT-CGIAR. Map: Leo Zurita Esri, DeLorme, GEBCO, NOAA NGDC, and other contributors

Fig. 1.1 Sampling sites for guayaba and guayabillo individuals in San Cristobal Island, in the Galapagos archipelago. Guayaba (*Psidium guajava*) collection sites (yellow marks) include Cerro Gato (GA-CG), Cerro Verde (GA-CV), the El Junco lagoon (GA-EJ), El Progreso (GA-EP), El Socavon (GA-ES), and La Soledad (GA-LS). Guayabillo (*Psidium galapageium*) collection sites (green marks) include Cerro Gato (GO-CG), Camino a Opuntias (GO-CO), Centro de Reciclaje (GO-CR), Cerro Verde (GO-CV), Galapaguera (GO-GA), Las Goteras (GO-LG), and Perimetral (GO-PE)

number of exclusive alleles was definitely greater for the continent sample, where a total of 18 exclusive alleles were found, in contrast to only 2 exclusive alleles in the San Cristobal populations. These data represent a classic "loss at foundation" effect in the island sample, which is also evident when we analyze an indirect measure of genetic diversity (Frankham 1997). The observed heterozygosity is more than 50% higher for the continental sample ($H_o = 0.252 \pm 0.065$) when compared to the average observed heterozygosity on the island populations ($H_o = 0.153 \pm 0.014$), indicating that there is a clear reduction in the genetic diversity of *P. guajava* in the island of San Cristobal when compared to the continental populations.

A more profound analysis of the genetic similarities between individuals also indicates a clear distinction between the island and continental populations, as shown through a clustering analysis using Euclidean distances in a principal coordinates analysis (PCoA) (Fig. 1.2). However, when clustering patterns are analyzed through a phenogram using the neighbor-joining method (Saitou and Nei 1987) (Fig. 1.3), these analyses also reveal an additional level of structure, as the samples that were collected in the island of San Cristobal tend to separate into two groups: one of them clusters most individuals sampled from the southernmost locations in the island's humid agricultural ecosystems, and the other tends to group individuals

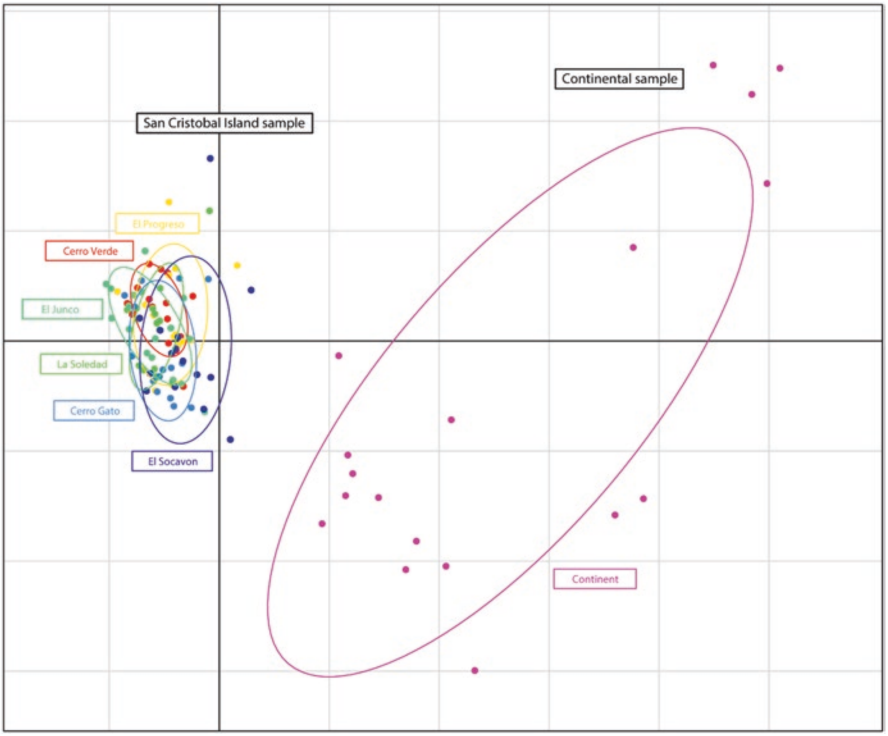


Fig. 1.2 Principal component analysis (PCoA) of *Psidium guajava* samples analyzed with SSR markers reveals a clear separation of the continental samples, when compared with the individuals from San Cristobal Island, Galapagos

from the sampling sites located to the north of the main road that transects San Cristobal's humid region (Fig. 1.1). It should be noted that this clustering is not absolute, as individuals from the southernmost locations (green branches) group together with individuals in the northern group (gray shading) and vice versa (individuals from the northern group, in black branches, group within the southernmost group, in light green shading) (Fig. 1.3). This subtle separation may be a direct product of three possible phenomena: multiple introductions of *P. guajava* on the island, an ongoing adaptive process through diversifying selection, or a distinct interruption of gene flow between both clusters combined with the effects of genetic drift. Under any of the three scenarios, it is clear that the island's *P. guajava* individuals share genetic similarities which are not observed when compared to the continental sample.

These phenomena can be further characterized by analyzing the genetic distances between locations, taking into account the fixed alleles of each sample. This is performed through the estimation of F_{ST} genetic distances, which can discern the presence of separate populations—with distinct gene pools—where gene flow between populations is minimized (Weir and Cockerham 1984). These results

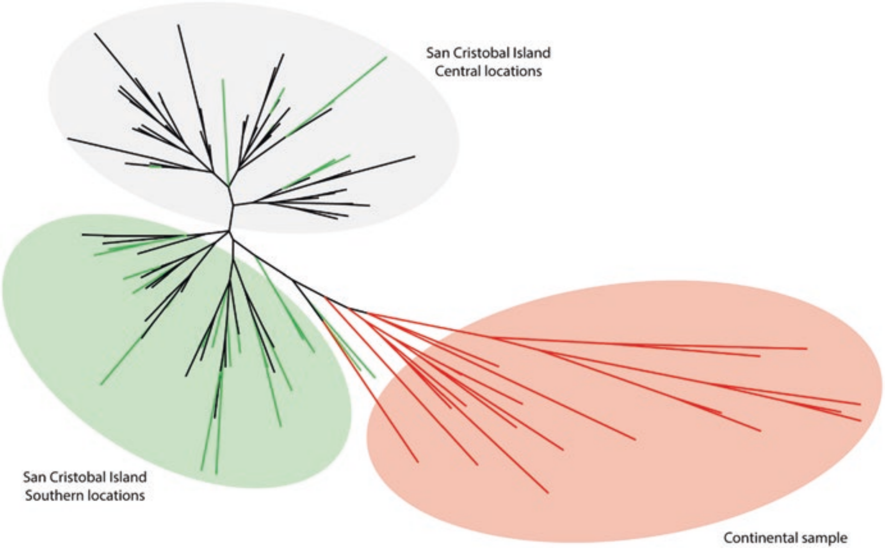


Fig. 1.3 A dendrogram constructed using the unweighed neighbor-joining (NJ) method shows a clear genetic separation of continental guava plants and an apparent distinction between individuals from the central sampling locations (El Progreso, Cerro Verde, El Junco, and La Soledad) and the southern sampling locations (Cerro Gato and El Socavon). Line color indicates origin of samples (red for continental samples, black for San Cristobal Island central locations, and green for San Cristobal Island southern locations), and circles indicate observed groups that were formed

Table 1.1 Wright's pairwise F_{ST} distances between *Psidium guajava* individuals collected from six locations in San Cristobal Island, Galapagos, and a collection from continental Ecuador

	Cerro Verde	El Progreso	La Soledad	El Junco	Cerro Gato	El Socavon
Cerro Verde	–					
El Progreso	0.080	–				
La Soledad	0.080	0.033	–			
El Junco	0.052	0.031	0.023	–		
Cerro Gato	0.100	0.046	0.051	0.066	–	
El Socavon	0.083	0.051	0.058	0.062	0.029	–

(Table 1.1) suggest that the individuals from the locations of Socavon and Cerro Gato (in the southernmost areas of the sampled region) and from the locations of El Junco and La Soledad (the two northernmost sampled locations) (Fig. 1.1) show reduced genetic distances between them. However, a certain degree of genetic similarity (whether it's a product of common ancestry or gene flow) cannot be ruled out between the individuals from all sampling locations in the island. This homogeneity in the San Cristobal *P. guajava* gene pool and its implications in the species' population structure throughout the island were further explored through the use of Bayesian inference methods (Pritchard et al. 2000), which revealed that the continental sample presents a considerably different identity from the island population,

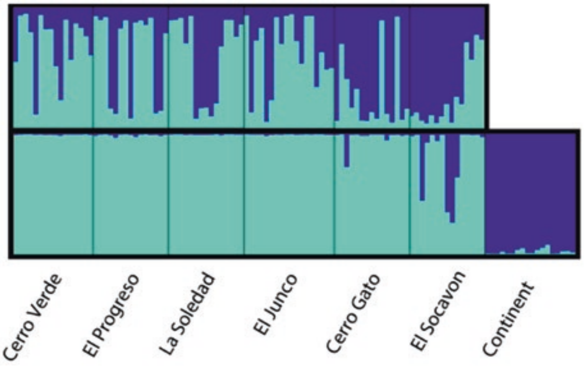


Fig. 1.4 Bayesian inference methods applied in the software *structure* (Hamrick et al. 1993) reveal a high reduction in gene flow between the continental and island guava samples (lower panel) while suggesting a subtle genetic cutoff between the southernmost locations of Cerro Gato and El Socavon and the rest of the individuals in San Cristobal (upper panel)

with slight similarities observed in individuals sampled from the southernmost locations of Cerro Gato and Socavon (Fig. 1.4). Moreover, this analysis still suggests that genetic similarities exist between the individuals in the island, regardless of their location (Fig. 1.4). This phenomenon could be explained by widespread migration or gene flow between individuals from different locations, which would be expected for an allogamous species in which individuals from different locations could engage in cross-pollination. Migration, in the form of seed dispersal through the action of different animals or human mobility (whether deliberate or accidental), would also allow individuals to breach the geographical barriers through the germination of plants in locations at great distances from their progenitors (Hamrick et al. 1993; Nathan et al. 2008). Nonetheless, it can still be argued that some differences are observable between the island's guava populations through these graphics (again, comparing the genetic identities for the individuals at Cerro Gato and Socavon, which tend to be assigned to the predominantly purple lineage, compared to their northern counterparts, assigned to the predominantly cyan lineage), suggesting that, despite an extensive homogenization, a certain degree of genetic differentiation exists among the island's guava populations. These differences could be explained either by multiple introductions of *P. guajava* in San Cristobal or by an ongoing diversification process. If multiple introductions occurred, there is still a subtle distinction between two ancestral lines, which contribute to the maintenance of a certain degree of genetic diversity for the species in this island. On the other hand, the possibility for diversification of a population derived from a single introduction event could occur through positive selection on one or multiple sites in the island (driven by specific environmental conditions for each region, such as climatic factors and soil composition) or as a product of genetic drift and a lack of gene flow between populations. This scenario could imply that an adaptive process is occurring within these populations, where the standing genetic diversity for the originally

Table 1.2 Wright's pairwise F_{ST} distances between *Psidium galapageium* individuals collected from seven locations in San Cristobal Island, Galapagos

	Camino a Opuntias	Perimetral	Cerro Gato	Galapaguera	Centro de Reciclaje	Cerro Verde	Las Goteras
Camino a Opuntias	–						
Perimetral	0.018	–					
Cerro Gato	0.127	0.127	–				
Galapaguera	0.038	0.033	0.132	–			
Centro de Reciclaje	0.022	0.028	0.192	0.047	–		
Cerro Verde	0.161	0.167	0.067	0.143	0.222	–	
Las Goteras	0.093	0.106	0.126	0.066	0.098	0.124	–

introduced population would have provided *P. guajava* with a sufficiently diverse genetic toolbox to allow it to adapt to different microenvironments inside the island.

Our current data provide a considerable description of the diversity of *P. guajava* in a single island of the archipelago, but the implications of its effects over other endemic species remain unclear. An interesting hypothesis has been formulated on the effects that *P. guajava* could have over the populations of another endemic member of its genus, *Psidium galapageium*. Locally known as guayabillo and considered the "endemic guayaba", this species sometimes shares the physical space with guava trees and perhaps even a niche in the island's ecosystems (McMullen 1999). This would place both species under direct competition and could be an important factor in the evolution of these populations in San Cristobal. Furthermore, the extensive interspecific hybridization phenomena that have been observed in island ecosystems suggest that the generation of hybrids could also be possible (Ellstrand and Schierenbeck 2000).

To explore these hypotheses, our group collected *P. galapageium* samples from seven locations in the island's humid and transitionary ecosystems (Fig. 1.1). These samples were analyzed with nine heterologous SSR markers (all of them previously used for *P. guajava*), in order to perform similar genetic analyses as the ones described for the island's guava trees. The results show that the endemic guayabillo displays a considerably higher standing genetic diversity when compared to *P. guajava* in San Cristobal ($H_o = 0.472 \pm 0.043$), as might be expected for an endemic species. Genetic distance analyses also show that F_{ST} values between various sampling sites tend to be higher for *P. galapageium* populations (Table 1.2), attributable to longer diversification times for these populations (although differences in seed and pollen dispersal between both species could also explain these differences) (Cain et al. 2000). Clustering and population structure analyses show that populations like the ones on Cerro Gato differ from the rest of the island, but as with *P. guajava*, there is no evidence for a defined population structure, and extensive diversification in San Cristobal also appears to be scarce for *P. galapageium* (data not shown). Overall, the results suggest that there is an evident difference between the genetic diversity of the guava and guayabillo gene pools in the island, but the lack of clearly defined populations appears to be a common feature for both species.

The Future of *P. guajava* in the Galapagos Islands: From Interspecific Hybrids to the Social Implications of an Invasive Species

Based on our knowledge of the genetics of invasiveness and the current status of the *P. guajava* populations in the Galapagos Islands, we cannot rule out their potential for further propagation. Any disregard for the control policies for invasive species in the archipelago could allow them to prevail in their current habitats and even expand to new ones. However, the establishment of efficient control measures requires a deeper understanding of the biology and genetics of the species in San Cristobal and the Galapagos Islands altogether. The previously described results are part of a preliminary study of the genetic diversity of *P. guajava* and *P. galapageium* that is currently being extended to populations in the islands of Isabela and Santa Cruz, where the species are present. The genetic diversity of the populations of each individual island must be characterized if we are to fully understand the population structure of these species in the Galapagos and to infer the extent of the gene flow between individuals in the archipelago. The single-island approach fails to explain the reach of the gene flow between populations in different islands, a piece of information that is crucial for understanding the potential that different populations have to maintain highly diverse gene pools. It is also important to characterize the similarities and differences between the populations on different islands, since a combination of widespread gene flow and high genetic diversity would increase a population's ability to adapt to new environments and to compete more efficiently in their current locations. For *P. guajava*, this would make it a more aggressive threat to native and endemic species such as *P. galapageium*. The evolutionary history of *P. guajava* also depends on a broader sampling of continental populations that would allow us to identify the source for the island's current gene pool and to determine the potential number of introduction events for the species in the Galapagos Islands. A clear identification of the selective forces shaping the island's populations would also contribute to the understanding of the factors that influence both species' ability to survive in their environments and colonize new ones.

Regarding the *P. guajava* gene pool, it is important to take into account that one of the phenomena that can dramatically increase the genetic diversity of an invasive species is the interspecific hybridization between evolutionary close relatives (Lee 2002). These processes have been previously described in larger island scenarios, as in the rise of invasive olive species in Australia (Besnard et al. 2007), the formation of natural *Rubus* hybrids in Hawaii (Rendell et al. 2004), and the reported hybridization of the endemic *Psidium socorrense* with *P.* sp. *aff. sartorianum* in Isla Socorro, Mexico (López-Caamal et al. 2014). With the *P. guajava* populations in the Galapagos Islands, establishing their potential for hybridization with guayabillo is a priority, as this would clearly represent a direct threat to the diversity of the endemic species' gene pool through genetic erosion and an adaptive opportunity for the invasive species through the acquisition of beneficial traits. Preliminary analyses have been already performed using the available genetic data of both species. Using each species' unique identity as a prior, Bayesian inference methods such as the ones previously described were adapted to explore the possibility of hybrid individuals existing in San Cristobal. These preliminary results suggest that no hybridization events have yet occurred in San Cristobal, a conjecture that might be explained by biological differences between both species (flowering times, chromosome number incompatibilities, etc.) (Abott et al. 2003). Nonetheless, the implications that these hybrids would have on the ecological and evolutionary dynamics of both species make this a topic that needs to be further explored, with larger datasets and more diverse analytical methods.

All of this information represents a solid baseline that can be combined with biological and ecological data to establish regulation policies for the species. However, the establishment of control strategies is a process that needs to be implemented with the local human populations in mind. The importance for the preservation of the local biodiversity in the Galapagos Islands answers to both ecological and social needs, since land management and the restoration of natural ecosystems are critical points for the survival and economic prosperity of the inhabitants of the islands (Walsh et al. 2008). Recent studies exploring the local populations' perception of the current control and quarantine systems in the islands reveal that 91% of the local inhabitants recognize invasive species as a problem for the survival of local species, with a significantly reduced perception and recognition of this problem in the island of Isabela (Velasco 2002). The success of any species management program is directly related to the acceptance that it receives from local populations, who must work in conjunction with local authorities to guarantee its success. For this reason, it is imperative that the quantified effects of the propagation of *P. guajava* are effectively socialized with the local communities, to ensure their acceptance of the problem and their commitment to assist in all control efforts that may be undertaken.

Our current efforts have only begun to unravel the complete evolutionary and demographic history of guava in the Galapagos Islands. The study of the genetic diversity and population structure of the species (and its endemic close relatives) within the archipelago must be treated as a priority, since the analytical power of genetic data has proven to be unmatched by any other data when studying the biology and ecology of any living organism. The results that can be obtained by a deep genetic analysis of *Psidium guajava* will undoubtedly represent a powerful tool in the understanding of how this invasive tree species has managed to thrive in the Galapagos, the extent of its effects on the local flora and fauna, and the most appropriate steps that must be followed if we want to efficiently control it in the fragile ecosystem they now inhabit.

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Chapter 2
Genetic Consequences of Invasive Species in the Galapagos Islands

Jaime A. Chaves

Introduction

Human-introduced species, accidentally or intentionally, are a threat to global biodiversity, agriculture, economy, and health (Pimentel et al. 2001; Chen et al. 2011; Chown et al. 2015). Their effect can be exacerbated in isolated areas where species have evolved in the absence of such invaders (in some cases, for millions of years). Of all ecosystems on earth, those hit hardest by invasions are, without question, island ecosystems (Vilà et al. 2011). Their geographic isolation dictates the balance between colonization and extinction, where the probability of individuals reaching and surviving on a given island is governed both by the size of the island and its distance from the mainland (MacArthur and Wilson 1963). This balance is disrupted, however, when anthropogenic activity is ubiquitous. For example, accidental or intentional human introductions can eliminate the costs behind long-distance colonization, usually imposed by geographic distance, by actively moving less vagile species to insular ecosystems. This means that human-induced passive transport makes island ecosystems less isolated, thus altering the ecological connectivity in place. Once settled, introduced species can become invasive, that is, they become established and spread beyond the place of introduction and usually alter the local flora and fauna negatively in myriad of ways.

One direct negative effect invasive species can have is becoming direct predators to both plants and animals, against which preys have not developed avoidance adaptations or behaviors. Indirectly, invasive species may deplete resources used by native flora or fauna or more subtly through introgression. Introgression or interspecific hybridization of invasive species with local ones, who may not have been fully

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isolated reproductively from invasives by either pre- or post-zygotic means, could result in the loss of local genetic variants. This mechanism repeated over many generations could result in a weakening of native-species genetic integrity, a decrease in local fitness, and, ultimately, a complete erosion of the endemic genome (Sax et al. 2007; Todesco et al. 2016). Alternatively, this could also result in new species with greater invasion potential (Soltis and Soltis 2009) or even an increase in biodiversity through the incorporation of new genetic combinations, a controversial topic in conservation genetics (Hulme and Le Roux 2016; Sarrazin and Lecomte 2016). Despite the final outcome, this phenomenon is expected to depend on the genetic affinities between both forms (native and invasive): the closer these are phylogenetically to each other—and the more similar their evolutionary histories—the higher the chances that hybridization will occur. The genetic consequences of this form of invasion are just beginning to be deciphered, as novel techniques for genome-wide analyses are being implemented.

The ability of an introduced species to establish itself depends on whether it can overcome novel environmental variation experienced in a new range or if the novel area includes similar ecological conditions (e.g., niche) like in its native range. In the first case, invasive species are often subject to strong selective pressures, which could result in the unsuccessful establishment. Invasive species mostly encounter considerable environmental challenges when faced with habitats different from those in their native range (Reznick and Ghalambor 2001), raising questions about the components of the invasive species' genome that allow for a successful founding event and the overall genetic consequences for both invasive and native species. Important aspects of the understanding of this phenomenon are (1) the comparison of the genetic information available from invasive species within their native range, (2) identifying source populations for such invasions, (3) detecting possible routes of invasion, (4) estimating the time of arrival, and (5) the population genetics of founder individuals, among others.

In this chapter, I focus on describing the steps leading to the success of species invasions in the fragile ecosystem of the Galapagos Islands and the genetic consequences of such invasions. I will provide examples from Galapagos' invasions to determine whether genetic divergence of invading species is occurring among islands, whether dispersal and migration between islands are present, and whether population bottlenecks are signatures resulting from the invasion process. Most importantly, I present several recommendations that could be implemented for preventing future invasions to the islands.

Invasive Species in the Galapagos Archipelago

Introduced species represent the largest conservation threat to the Galapagos Islands (Loope et al. 1988). Most dramatic is the potential to modify the integrity of evolutionary processes on the islands, much of which is difficult to foresee or detect (Fundación Natura 1997). The Galapagos archipelago is located ca. 1000 km from the coast of Ecuador, and its geographic isolation is, with a doubt, one of the most important factors driving the extraordinary biological and evolutionary outcome on the islands. The remoteness of these islands has been an influential factor in reducing the chances for species to reach them, and few species have successfully arrived at the archipelago. Unfortunately, these same challenges have been made drastically easier to overcome by the presence of humans on the islands. The Galapagos were first discovered in 1535, and there are reports of frequent buccaneer and whaler visits as early as 1684. Human settlements started in 1807 and experienced a gradual increment shortly after the 1930s, up until its present residential population of ~30,000, plus an estimated 225,000 visitors per year (Walsh and Mena 2016). It is known that by the time Darwin visited the archipelago there were at least 20 species of plants, rats, and mice and other 12 vertebrate species that had been previously introduced (Cruz and Causton 2007), probably by early pirates and buccaneers who visited the islands persistently prior to his arrival in 1835. This suggests that the evolutionary trajectories and the genetic consequences of invasive species on the Galapagos are, relatively speaking, recent problems. These problems are exacerbated by the large logistical operations required to maintain the important number of residents and tourists. Shipments of goods from the mainland to the Galapagos have increased in frequency (i.e., 5 ships, 24 visits/ship starting in 2006) (Cruz and Causton 2007), as have tourist routes between the islands, representing additional opportunities for dispersal and transport of alien species. To date, there have been 490 species of invasive invertebrates (Causton and Sevilla 2007), 748 species of introduced plants (Tye et al. 2007), 36 species of introduced vertebrates (Jiménez-Uzcáteguia et al. 2007), 4 strains of avian malaria (*Plasmodium* sp.) (Levin et al. 2013), and avian pox (Parker et al. 2011) reported in terrestrial ecosystems of the Galapagos.

Genetic Diversity and Genetic Makeup of Introduced Species in the Galapagos

Many invasions are founded by few individuals that are able to establish themselves in new habitats different from those in which they evolved. This first step is enhanced by the ability of some invasive species to cope with, and become established under, these novel conditions (i.e., phenotypic plasticity) (Bradshaw 1965; Schlichting and Levin 1986), something that successful invasive species are better equipped for than native species (Davidson et al. 2011). These individuals carry the initial genetic composition that will be the starting point for the next generations. The low number of initial founders thus becomes a challenge, as the low levels of genetic diversity present in these few individuals (in some cases a single gravid female!) could be detrimental throughout the invasion. This is expected as reduced genetic diversity usually determines the evolutionary potential for survival. Thus, the expectation is that introduced species should experience a reduction in genetic diversity relative to their native source populations. This pattern is clearly found in the Galapagos with the recently introduced yellow fever mosquito (*Aedes aegypti*). The yellow fever mosquito, introduced in the 1990s (Bataille et al. 2009a, b), is a vector of human diseases such as dengue, yellow fever, chikungunya, West Nile virus, and the recently emerging Zika virus (Mustafa et al. 2015; Rey and Lounibos 2015; Rodriguez-Morales 2015). Genetic information obtained from mitochondrial DNA from mosquitoes collected in the two most populated islands in Galapagos (Santa Cruz and San Cristobal) suggests a severe genetic bottleneck, characteristic of either few founder individuals or a dramatic decrease in population sizes after colonization (Chaves et al. in prep). Furthermore, this study showed genetic diversity indices (haplotypic and nucleotide diversity) to be low for mosquitoes from San Cristobal but higher in Santa Cruz, compared to the samples from mainland Ecuador. One alternative explanation for the difference in genetic indices between the islands could be the possibility of multiple colonization events from the mainland affecting (increasing) genetic makeup in the Santa Cruz populations. Mosquitoes have most probably arrived in Galapagos via airplanes (commercial flights), although maritime transportation may also be a possibility. Cruz and Causton (2007) reported the arrival of 5 live mosquitoes from 46 flights to 3 islands in the Galapagos (3 in Santa Cruz and 2 in San Cristobal). In the same report, other invertebrates were found in much higher proportions, such as spiders, crickets, wasps, ants, beetles, cockroaches, and moths. It is expected then that these introductions will affect the native fauna and flora from the Galapagos with unpredictable outcomes.

Not only has mitochondrial DNA been used to detect genetic signatures in invasive species. Small fragments of repeated nuclear DNA found throughout the genome (i.e., simple sequence repeats (SSR), microsatellites) provide detailed and useful population data. The use of these techniques (known as “genetic fingerprinting”) in the Galapagos has genetically characterized the highly invasive guava tree (*Psidium guajava*) in San Cristobal; the results (reported in detail in Chap. 1 of this book) further support the generality of alien-introduced species to Galapagos containing reduced genetic diversity, where half of the total amount of genetic variability in alien individuals was found, compared to what is normally characterized in plants in mainland Ecuador. This technique has also been applied to confirm interspecific hybridization between closely related *P. guajava* and endemic *P. galapageium* as a possible outcome from its introduction (Torres, this book). Thus, the use of genetic markers (nuclear and mitochondrial DNA) is a powerful tool to explore these signatures, since these markers complement each other at exploring levels of genetic diversity in very different ways as results of their inherent natures (i.e., maternally inheritance, coalescence time).

Genetic differentiation could result from geographic isolation and the cessation of gene flow among island populations. This pattern was found in another insect introduced to the Galapagos. The parasitic fly, *Philornis downsi*, reached the islands in the last 20–40 years (Fessl et al. 2001; Causton et al. 2006) and parasitizes nestlings of most terrestrial birds in the Galapagos, posing an imminent threat to the persistence of endemic bird species (Wikelski et al. 2004). Samples from the three islands showed that flies from Santa Cruz and Isabela could be considered a single genetic cluster separate from flies from Floreana. This data, obtained from both microsatellite and mitochondrial DNA, showed that gene flow between islands was to some extent restricted although an independent colonization of Floreana could not be discarded as an alternative explanation (Dudaniec et al. 2008). The low genetic differentiation among islands contributes to the general pattern found in most studied invasive species in the Galapagos. This signature was found in the genetic makeup of *P. downsi* in Galapagos across the three islands examined, resulting most likely from a small founding population, low immigration rates, or few introduction events (Dudaniec et al. 2008). Despite the reported genetic reduction in these parasitic flies—thus posing a limitation for its persistence—*P. downsi* seems to be successfully spreading across several islands, and population numbers appear to be on the rise (Kleindorfer and Dudaniec 2016).

Identifying Source Populations, Invasion Routes, and Time of Invasion

Indirect methods that use molecular markers are commonly applied to link source populations of invasive species to their ranges and to reconstruct the colonization history and timing of such introductions. Shared ancestry of invading individuals with populations from native ranges (shared haplotypes) is usually interpreted as evidence for the point of origin of the invading form. Nevertheless, these studies are sensitive to the same issues any phylogenetic study could suffer from, where incomplete sampling could influence these inferences (see Pybus and Harvey 2000; Rabosky et al. 2008; McCormack et al. 2011; Ruane et al. 2013). This is problematic if the native range is broad or unknown, thus affecting the accuracy of the source of the invasion. One hypothesis is that species usually invade or colonize novel environments from nearby landmasses, as proposed by island biogeography theory (MacArthur and Wilson 1963). Molecular phylogenies have shown that for the Galapagos archipelago, the source of most native colonizations are indeed ancestors that have close living relatives in coastal regions in South and Central America (Caccone et al. 1999; Benavides et al. 2007; Chaves et al. 2012; Torres-Carvajal et al. 2014, 2016), with few exceptions in the Caribbean and North America (Sato et al. 1999; Arbogast et al. 2006). Nevertheless, when describing human-mediated transport of species into novel locations, this expectation may no longer be sufficient to explain the origin of invasive species.

The combined analysis of native and invasive populations of *A. aegypti* mosquitos from the Galapagos has also helped in the assessment of this invasive species' geographic origins. By analyzing the genetic diversity of mosquitoes in mainland Ecuador, Chaves et al. (in prep) described two haplotypes common in individuals from broad geographic ranges in the coastal region of mainland Ecuador. These same haplotypes were recovered in Santa Cruz Island, but only one was found in San Cristobal, linking directly to mainland populations and identifying the most probable route of arrival to the Galapagos. Several different haplotypes for *Aedes* mosquitoes are reported in other countries in Central and South America (Gorrochotegui-Escalante et al. 2002; Costa-da-Silva et al. 2005; Kraemer et al.

2015), but none of them were found in the samples from Galapagos. Most commercial flights and cargo shipments leave mainland Ecuador from the city of Guayaquil before reaching the islands, so it is suspected that these invaders originated in mainland Ecuador (Chaves et al. in prep.).

Phylogenetic studies of the common house gecko (*Hemidactylus frenatus*), a species recently introduced to the Galapagos Islands, in combination with samples from mainland South America (Ecuador and Colombia), Hawaii, Myanmar, and Papua New Guinea provide an almost complete colonization route and possible origins for this highly invasive species. The fact that haplotypes of an invasive species in the novel range are identical to the ones found in other geographic (native) ranges suggests the place of origin and the direction of dispersal routes (Torres-Carvajal et al. 2014). For the house gecko, mitochondrial *cytochrome b* and *12S* haplotypes from Hawaii, Galapagos, and mainland South America are identical to those found in Papua New Guinea, suggesting dispersal from Melanesia to South America across the Pacific Ocean (Fig. 1; Torres-Carvajal 2015). Furthermore, this long-distance dispersal seems to have happened only once, a hypothesis supported by low genetic variation and genetic distance found in South America, Hawaii, and Galapagos (Torres-Carvajal 2015). Once in South America, the house gecko probably followed a southern dispersal to Colombia first and then spread south into Ecuador and Galapagos (Torres-Carvajal 2015) with an estimated time of arrival to Galapagos occurring sometime around 2011 (Torres-Carvajal and Tapia 2011). Similarly, introduced Reissii's gecko (*P. reissii*), first seen in Santa Cruz Island (Puerto Ayora) in the 1970s (Hoogmoed 1989; Olmedo and Cayot 1994) is another common species currently found in sympatry with native geckos in at least three islands (Isabela, San Cristobal, and Santa Cruz). Phylogenetic studies comparing individuals from native range sites with samples from introduced *P. reissii* found Galapagos individuals deeply nested within the clade of specimens from several localities from coastal Ecuador and Peru (Torres-Carvajal et al. 2014). In both cases, the means for their arrival to Galapagos has not been identified by direct observations but could be attributed most likely to maritime transport via cargo vessel service from Guayaquil (Olmedo and Cayot 1994).

Oceanic islands pose additional challenges for the arrival of species by imposing harsh physiological constraints on salt-intolerant species such as amphibians. Intriguingly, the presence of the tree frog *Scinax quinquefasciatus* on the Galapagos Islands represents yet another clear example of the passive arrival of invasive species via cargo from mainland Ecuador. Phylogenetic studies of the established population of tree frogs on Isabela Island—compared to samples from populations in the lowlands of western Ecuador—showed that the Isabela tree frogs most probably arrived in two separate occasions. Three very distinct, latitudinally segregating genetic clusters exist in mainland Ecuador, and two of them were recovered in Isabela tree frogs (Pazmiño 2011). Geographically, these two clusters correspond to regions very close to the city of Guayaquil; thus, any passive transport to the port and then to Galapagos via maritime vessels could explain the arrival and establishment of this breeding population on the islands. There have been additional confirmations of tree frogs in Santa Cruz and San Cristobal Islands that became established around the same period of high precipitation, but these seem to be tightly dependent on environmental conditions, and they have not persisted as the ones found on Isabela Island (Pazmiño 2011). Further genetic studies on tree frogs from the Galapagos could provide important insights into the mechanisms (e.g., physiological plasticity) and adaptations (e.g., genes under selection) that facilitated their establishment in these physiologically challenging environments.

Closing Remarks

Although evolutionary change can happen very rapidly (a single or few generations) as a response to sudden environmental change, or by the introduction to a novel habitat, invasive species to the Galapagos show signs of between meager and no genetic change. It is possible that (1) the environmental conditions on these islands closely resemble those of the native range, (2) the genetic markers commonly used do not provide enough information to recover the signature of genetic adaptation, or (3) the relatively recent timing of invasions is the main factor limiting the accumulation of such differences. Future evolutionary genetic studies of invasive species should focus on the genetic architecture of adaptation and tolerance to novel environments, as well as on the genetic basis of phenotypic plasticity. Exhaustive genetic studies comparing native populations with invasive ones could provide insights into the pace of adaptation, the effect that novel environments have on the speed of genetic modification/adaptation during invasions, and identify which genes facilitate invasion success. Genome-wide analysis in the future could open a window to such explorations, as well as give a more accurate estimate of the timing of such events. Reporting on the speed and form in which alien species evolve before changing environments—and on the native species' response to such invasions—could not only provide important information on the new evolutionary trajectories both groups could take (see, e.g., Colautti and Barrett 2013; Stuart et al. 2014; Hulme and Le Roux 2016) but also could forecast the risk and consequences for the future of the Galapagos Islands.

It is important to address the unknown evolutionary direction of both endemic and invasive species in the face of potential interspecific hybridization or introgression in Galapagos. The stage for this phenomenon to happen is set by the genetic relatedness between several native and invasive forms (species of the same genus or same family (Table 2.1)). The list of potential candidate species pairs in Galapagos points to future research, which includes the native Galapagos guava and introduced guava tree (*P. galapageium* and *P. guajava*), three endemic Galapagos passion fruits and five introduced passion fruits (*Passiflora* spp.), endemic Galapagos lantana (*Lantana peduncularis*), and big-sage/tickberry (*L. camara* and *L. montevidensis*), among others. Animal species such as the endemic rodents (*Nesoryzomys* spp., *Aeglalomys galapagoensis*) and the introduced black rat (*Rattus rattus*), brown rat (*R. norvegicus*), and house mouse (*Mus musculus*)—all members of the same family—could be of potential interest as well as the endemic geckos (*Phyllodactylus*

Table 2.1 Closely related species pairs (genus and family level) with potential hybridization impact upon their introduction

Native/endemic species (common name)	Native distribution	Introduced/invasive species (common name)	Current distribution
Psidium galapageium var. galapageium (Galapagos guava (Guayabillo))	Fernandina, Isabela, Pinta, Santiago, Santa Cruz	*Psidium guajava* (guava)	Floreana, Isabela, San Cristobal, Santa Cruz, San Cristobal, Isabela, Santiago
Psidium galapageium var. howellii (Galapagos guava (Guayabillo))	Santa Cruz, San Cristobal		
Passiflora foetida var. galapagensis (Running pop)	Española, Floreana, Isabela, San Cristobal, Santa Cruz, Santiago	*Passiflora edulis* (passion fruit)	Floreana, Isabela, San Cristobal, Santa Cruz
Passiflora colinvauxii (Colinvaux's passion flower)	San Cristóbal, Santa Cruz	*Passiflora ligularis* (sweet granadilla)	Isabela, San Cristóbal, Santa Cruz
Passiflora tridactylites (Passion flower (manos cortas))	Española, Isabela, Pinta, Santa Cruz, Santiago	*Passiflora maliformis* (chalupa)	San Cristobal
Passiflora suberosa (Corky passion flower)	Española, Fernandina, Floreana, Isabela, Pinta, San Cristobal, Santa Cruz, Santiago	*Passiflora quadrangularis* (giant granadilla)	Floreana, Isabela, San Cristobal, Santa Cruz
Lantana peduncularis (Galapagos lantana)	Española, Fernandina, Floreana, Genovesa, Isabela, Marchena, Pinta, Pinzon, San Cristobal, Santa Cruz, Santa Fe, Santiago	*Lantana camara* (big-sage/ multicolored lantana)	Floreana, Isabela, San Cristobal, Santa Cruz
		L. montevidensis (weeping lantana)	San Cristobal, Santa Cruz
Pennisetum pauperum (Fountaingrasses)	Fernandina, Isabela, Santiago	*Pennisetum occidentale* (pasto)	San Cristobal
		Pennisetum purpureum (elephant grass)	Floreana, Isabela, San Cristobal, Santa Cruz

(continued)

Table 2.1 (continued)

Native/endemic species (common name)	Native distribution	Introduced/invasive species (common name)	Current distribution
Cenchrus platyacanthus (Buffelgrasses)	Darwin, Española, Fernandina, Floreana, Genovesa, Isabela, Marchena, Pinta, San Cristobal, Santa Cruz, Santa Fe, Santiago	*Cenchrus brownie* (slimbristle sandbur)	San Cristobal, Santa Cruz
		Cenchrus echinatus (bur grass)	Isabela, San Cristobal, Santa Cruz
		Cenchrus pilosus (abrojo)	San Cristobal, Santa Cruz
Gossypium darwinii (Darwin's cotton)	Española, Fernandina, Floreana, Isabela, Marchena, Pinta, Pinzon, San Cristobal, Santa Cruz, Santiago	*Gossypium barbadense* (Sea Island cotton)	San Cristobal, Santa Cruz
Gossypium klotzschianum (Galapagos cotton)	Isabela, Marchena, San Cristobal, Santa Cruz		
Phyllodactylus barringtonensis (Barringtonensis leaf-toed gecko)	Santa Cruz, Santa Fe	*Phyllodactylus reissii* (Reissi's gecko)	
Phyllodactylus bauri (Bauri leaf-toed gecko)	Santa Cruz, Floreana	*Hemidactylus frenatus* (common house gecko)	
Phyllodactylus darwini (Darwin's leaf-toed gecko)	San Cristobal		
Phyllodactylus galapagensis (Galapagos leaf-toed gecko)	Floreana, Isabela, Pinzon, Santa Cruz, Santa Fe		
Phyllodactylus leei (Leei gecko-San Cristobal leaf-toed gecko)	San Cristobal		
Phyllodactylus sp. 1 (Rabida leaf-toed gecko)	Fernandina, Isabela, Marchena, San Cristobal, Santa Cruz		
Phyllodactylus gilbert (Wolf leaf-toed gecko)	Wolf		

(continued)

Table 2.1 (continued)

Native/endemic species (common name)	Native distribution	Introduced/invasive species (common name)	Current distribution
Aeglalomys galapagoensis/ Oryzomys bauri (Galapagos rice rat)	Santa Fe	*Rattus rattus* (black rat)	Fernandina, Floreana, Isabela, Marchena, Pinzon, San Cristobal, Santa Cruz, Santiago
Megaoryzomys curioi (Giant Galapagos rice rat)	Santa Cruz	*Rattus norvegicus* (Norwegian brown rat)	Floreana, Isabela, San Cristobal, Santa Cruz, Santiago
Nesoryzomys darwini (+) (Darwin's Galapagos mouse)	Santa Cruz	*Mus musculus* (house mouse)	Floreana, Isabela, San Cristobal, Santa Cruz, Santiago
Nesoryzomys indefensus (+) (Indefatigable Galapagos mouse)	Santa Cruz		
Nesoryzomys narboroughi (Fernandina rice rat)	Fernandina		
Nesoryzomys swarthi (Santiago Galapagos rice rat)	Santiago		
Nesoryzomys fernandinae (Fernandina Galapagos mouse)	Fernandina		
Nesoryzomys sp.1,2,3 (Rabida and Isabela Galapagos mouse)	Santa Cruz		

(Common names and distribution follow the Charles Darwin Foundation Galapagos Species Checklist): (+) possibly extinct

spp.), invasives Reissii's (*P. reissii*), and common house geckos (*Hemidactylus frenatus*). Although this list is far from being complete, these invasive species are known to be of global concern given their high invasive biology.

Island biogeography theory predicts that the closer an island is to the mainland, the more chances the species from that range have of invading and establishing there (MacArthur and Wilson 1963). Current phylogenetic studies of invasive species from the Galapagos support this assumption and suggest that most introductions are human-mediated, albeit the limited number of invasive species' genetic data from these islands. The sole violation to island biogeography theory is the high frequency of arrival of species with limited dispersal abilities reaching remote islands like the Galapagos, facilitated by human transport. Thus, the examples presented here support a mainland Ecuador origin for the invader haplotypes found in the Galapagos.

A very different story could be revealed if the species under examination corresponded to the ones that invaded these islands before current commercial routes were in place (i.e., rats, mice). These correspond to most routes that were used by pirate ships and whalers, with little or no connection to mainland Ecuador. Nevertheless, the previous pattern is expected to hold in modern and future introductions, as transport from mainland Ecuador to the islands is only expected to increase given the human population and tourism sector demands.

There are over 1000 invasive species in the Galapagos (Causton and Sevilla 2007; Jiménez-Uzcáteguia et al. 2007; Tye et al. 2007), from which we have limited genetic data from just a handful. The few examples presented here represent the only available information on this subject to date. There is an urgent need to sample and genetically categorize as many of these invasive species as possible, as well as their potential native relatives if we want to implement sound control efforts. Understanding the genetic makeup of invasives, the connection to other populations across the islands and to the source populations, and the response of native species to these introductions are the first steps in conservation planning if preservation of the Galapagos' genetic heritage and its evolutionary potential are priorities.

Recommendations

Several actions have been taken in the last years to prevent further introduction of new species to the Galapagos, but the situation is far from being under control. Currently, the use of insecticides inside the commercial flights before landing in Galapagos might provide alternative solutions to eliminate air-borne aliens. Unfortunately, the insecticide spray is limited to the overhead compartments, leaving other areas of the airplane (e.g., bathrooms) unattended. Furthermore, the mandatory connection in the city of Guayaquil increases the potential for air-borne insects with tropical ecological adaptations that could benefit their settlements. The strict use of these insecticides and tighter control for passenger and luggage transfer in Guayaquil is very necessary. Along the same lines, the transportation of goods from the mainland to Galapagos should provide an alien-free environment during shipments. For many years, pest control and fumigating systems on docks and in cargo facilities did not exist in the routes connecting Galapagos with the mainland (primarily to the Port of Guayaquil) (Zapata and Martinetti 2010). Furthermore, quarantine measures were performed through random visual inspection, cargo was not always inside containers, and most ships lacked the infrastructure to transport goods or were in poor structural conditions (oxidized walls) (Zapata and Martinetti 2010). A series of implementations such as fumigation of vessels before departure and the use of climate-controlled storage containers were put into place in 2009 (Zapata and Martinetti 2010). These efforts might have helped with the reduction of certain types of aliens—such as insects and small vertebrates—to reach the islands; unfortunately, there have been reports of large vertebrates (e.g., Ecuadorean milk snake and green iguana) landing in Santa Cruz Island in 2014. These cases reinforce the need to implement tighter regulations before departure in the mainland and more thorough inspection of the cargo vessels. On the other end, a construction of modern loading facilities that allow a more vigilant control over cargo entering the island should be implemented, with the power to decide whether a shipment should be unloaded or not, following a series of strict regulatory requirements. Furthermore, tougher regulations should be put in place to prevent the movement of alien species via vessels' hulls. Strict controls should be enforced not only for cargo ships departing from Ecuador's mainland but also from the high number of sailing boats that visit the Galapagos and many different ports around the globe. These efforts, in combination with molecular techniques performed on-site, should contribute to an effective control protocol. For instance, the implementation of DNA barcoding approaches could help identify alien taxa upon their detection, particularly with species of challenging taxonomic nature (e.g., cryptic species). These techniques could incorporate simultaneous screening of multiple species from less obvious sources—like water and soil—via metabarcoding (Chown et al. 2015). Finally, an early warning system should be implemented in both aerial and maritime routes to detect the arrival of invasive species, accompanied by a rapid response plan in case a new invasive species is detected.

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Part II

To the Ecosystem

Chapter 3
Interactions Among Exotics: Guava and Its Associated Fauna in the Highlands of San Cristobal

Stella de la Torre, Isabel Villarruel, Anais Córdova-Páez, and Ximena Herrera-Alvarez

Introduction

Introduced species pose a severe threat to terrestrial habitats in Galapagos, a world's heritage archipelago. Alien plants are found primarily on the agricultural and urban areas of the four inhabited islands, and invasions into the protected area are particularly problematic in the humid highland zones (Snell et al. 2002; Guézou et al. 2010; Itow 2004). Currently, 866 introduced plant species are reported in Galapagos, surpassing the number of native and endemic species together (552) (Guézou et al. 2010; Tye 2000, 2002). Of these introduced species, approximately 30 are considered invasive (Hamann 1991; Itow 2004).

Invasive plant species can cause profound changes in nutrient cycles and in the community structure of native plants and animals, rapidly spreading over vast areas (Snell et al. 2002; Walsh et al. 2007; Weidenhamer and Callaway 2010). However, although invasive plants may share some common characteristics and effects, variation exists in the way ecosystems are affected by different species (Weidenhamer and Callaway 2010). To better understand the biological and social impacts of invaders, we must know how each species alters ecosystem function and how it interacts with native and introduced animals that are affected by and affect the spreading of invasives.

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The guava *Psidium guajava* L. (Myrtaceae) was introduced in Galapagos from continental Ecuador for human and livestock consumption around 1850. Currently, it is considered an invasive species that has spread in the highlands, both in agricultural areas and in the national park (Snell et al. 2002; Walsh et al. 2007). Its current spreading is related to farm abandonment (Miller et al. 2010). However, despite its economic and environmental importance, little is known about how this species is affecting nutrient cycles, nor do we understand how it affects and is affected by animal communities. A preliminary analysis carried out in the first phase of our research suggested that guava was affecting the nitrogen cycle (de la Torre 2013). If this is so, soil invertebrates could be affected by changes in nutrient dynamics. To assess the effects of guava on the community of soil invertebrates, in this study we compare carbon and nitrogen concentrations in soil and plant tissues and the structure of the community of soil invertebrates in areas with similar altitude and climate but which differ in the presence of guava. On the other hand, to analyze how guava could be affected by animal communities, we present a preliminary evaluation on the role of introduced mammals as seed dispersers of this invasive species. These results suggest that the structure of the community of soil invertebrates is affected by complex interactions among several environmental factors that are not limited to pH and nutrient availability in soils and plant tissue, but may include present and past effects of competition among introduced species of invertebrates.

Study Areas

The pasture-guava site was located at Hacienda La Tranquila, in the village of La Soledad (approx. 400 masl). Vegetation was dominated by introduced plant species, including grasses (e.g., *Paspalum dilatatum*) and guava (*Psidium guajava*) trees. Also, in Hacienda La Tranquila, we studied an area that is part of a restoration experiment with native species, including *Lecocarpus darwinii* and *Scalesia pedunculata*. This area formerly had pasture infested with guava and blackberry (*Rubus niveus*); few individuals of these two species were still present in the area. These two areas were separated by about 300 m from each other (Fig. 3.1).

Methods

Fieldwork was carried out from 2011 through 2013 for 1 month in the dry and 1 month in the rainy season by 1–3 fieldworkers. Data on soil pH and snail diversity was gathered in the dry season of 2015.

In each study site, five randomly selected 50-m transects were built. In each transect we randomly located two 1-m^2 plots, separated from each other by at least 10 m for a total of ten plots per study site (range of plot separation in a site, 10–400 m). From the approximate geometrical center of each plot, we collected one

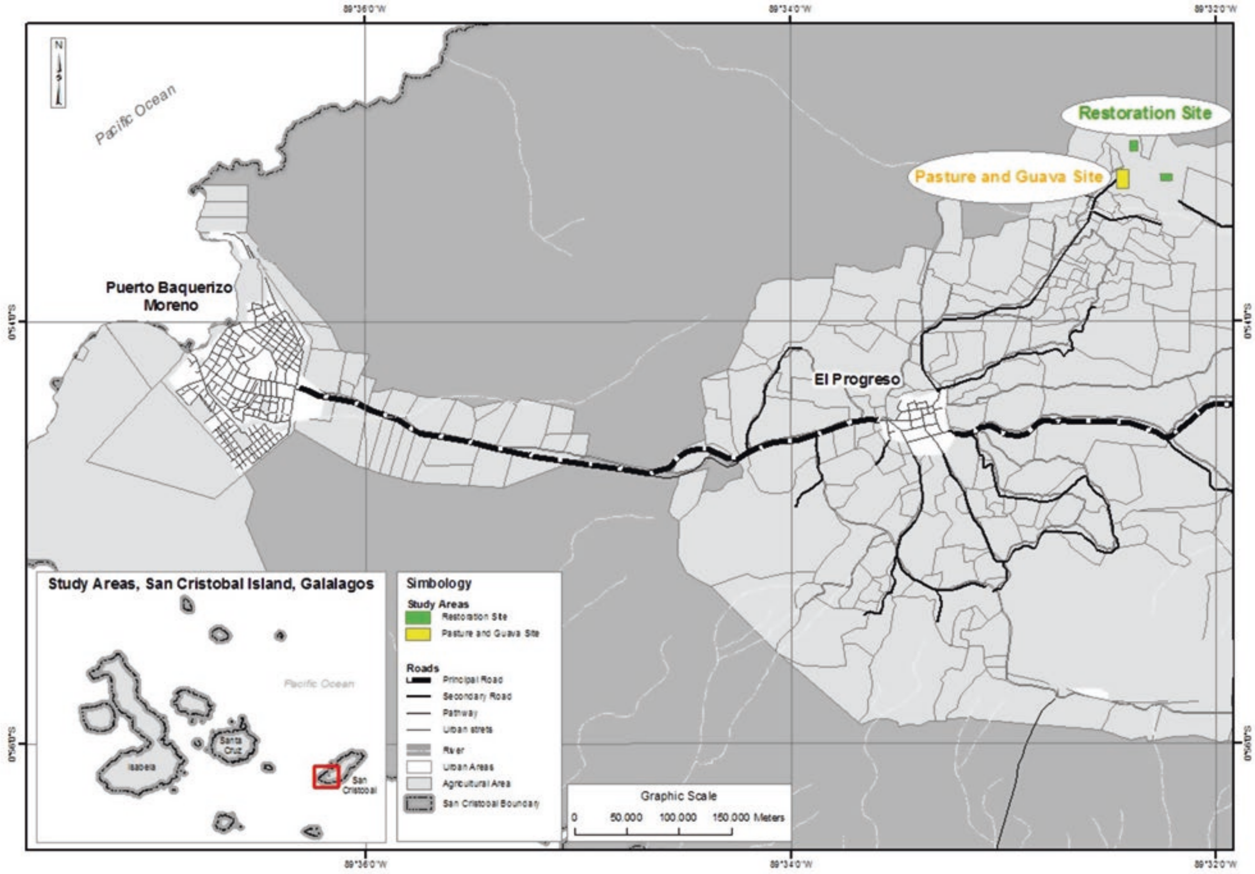


Fig. 3.1 Study areas in San Cristobal Island

soil sample from a depth of 0 to 10 cm and two samples from the adjacent vegetation (live leaves of all the species inside the plot), once in each climatic season. Soil and leaf samples were dried at ambient temperature, sieved at 2 mm (for soil), and transported to a laboratory in Quito to assay for carbon and nitrogen concentrations. Carbon concentration in leaves was calculated as 50% of the organic weight (Schlesinger 1991). Carbon concentration in soil and nitrogen concentration in soil and leaves were directly measured with Walkley-Black and Kjeldahl methods, respectively. For the statistical analyses (see below), we averaged the carbon and nitrogen concentrations of the two leaf samples and used the mean concentrations per plot per season for the calculations. The soil samples taken in the dry season of 2015 were measured for soil pH with a potentiometer (1:2.5 soil/water).

The diversity of soil invertebrates was assessed by combining three approaches. For the first one, we carried out surveys in two 25-cm^2 subplots in each of the 1-m^2 plots in the study areas. In each subplot we conducted 2–4 different surveys of soil invertebrates, from the soil surface to a depth of 5 cm, in each climatic season. Invertebrates were photographed and identified to their taxonomic order. No specimens were collected. Shannon diversity indices were calculated with the data on the number of orders and the number of individuals in each order, recorded in each survey for each subplot. For the statistical analyses (see below), we averaged the indices of the subplots and used the mean index per plot per season.

For our second and third approaches, we focused on the diversity of two key groups of soil invertebrates: ants and land snails. To assess the diversity of ants, during July–August 2013, we carried out nine surveys in each of the plots in each study area. For the surveys we used a 25-cm^2 quadrat and recorded the number of morphospecies and the number of individuals of each morphospecies that were observed inside the quadrat. When numbers were high (>20 individuals), we estimated the number of individuals with a quick (2 min) count of all the ants inside the quadrat. Individuals of each of the morphospecies were photographed in the field with a macro lens (Olympus) and then released in the same area where they were found.

Taxonomic identification of the photographs was carried out with AntWeb (www.antweb.org). For the genus *Wasmannia*, we used the taxonomic key of Wetterer and Porter (2003). The identification of the genus *Nylanderia* was carried out with the advice of Ms. Giovanni Ramón, a biologist from the Pontificia Universidad Católica del Ecuador with expertise on this group.

To assess snail diversity, we carried out two surveys during August–September 2015 in each of the plots in both study areas. For the surveys, we used a 25-cm^2 quadrat. Field identification was done to the genus or species level based on a previous study on the snail community of San Cristobal (Villarruel and de la Torre 2014). We recorded the number of live and dead snails of each species. Shannon diversity indices were calculated with the number of live individuals only and with the total number of live and dead individuals of each recorded species. We later used photographs and shells of dead individuals to confirm the taxonomic identification carried out in the field.

To evaluate the role of introduced mammals as seed dispersers of guavas, during July–August 2012, we randomly collected 24 fecal samples from cattle and 21 from horses that were using the pasture-guava area. We dried the feces in the Laboratory of Terrestrial Ecology of the Galapagos Science Center and weighted each dried fecal sample. We then counted all the guava seeds in each sample to calculate the number of seeds per gram of dried feces.

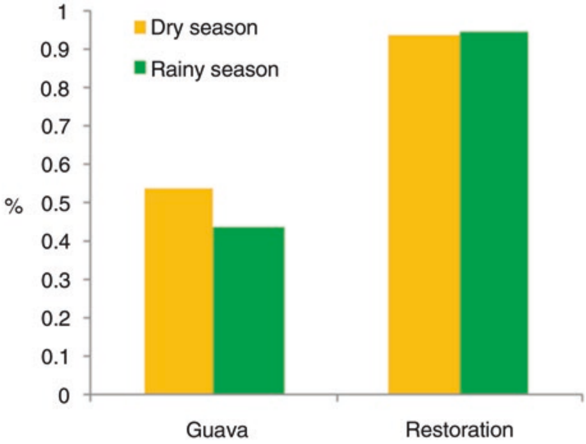
Quantitative Analyses

Two-way repeated measures ANOVAs were carried out to compare the log-transformed carbon and nitrogen concentrations and the diversity of soil invertebrates between the sites in the two climatic seasons of 2012 and 2013. We used simple linear regressions to evaluate the influence of carbon and nitrogen soil concentration on nutrient concentrations in leaves during both climatic seasons across sites. One-way ANOVAs were carried out to compare the pH of soil samples and the diversity indices of ants and snails between sites. We compared the number of seeds per gram of dried cattle and horse feces with an unpaired t-test. In the results, means are presented ± the standard deviation.

Results

We found significant differences in nitrogen concentration in the soils from the two study areas. The pasture-guava site had the lowest concentrations of nitrogen in soil in both climatic seasons (N: $F_{1,38} = 13.18$, $p = 0.0008$) (Fig. 3.2). Nitrogen concentration in leaves was also significantly lower in the pasture-guava site ($F_{1,38} = 61.65$, $p < 0.0001$) (Fig. 3.3). We found no significant differences in carbon concentration in soil and leaves (Figs. 3.4 and 3.5).

Fig. 3.2 Comparison of nitrogen concentration (%) in soil between areas and climatic seasons



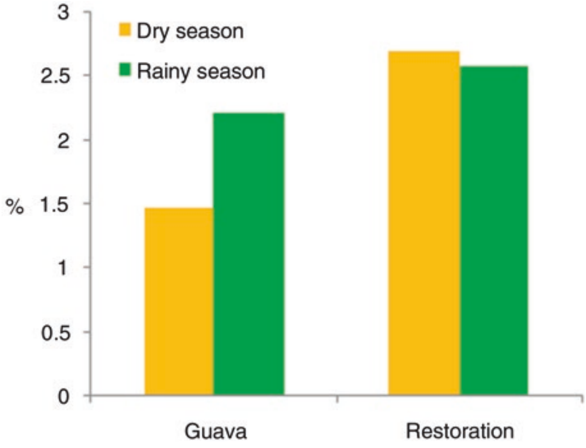


Fig. 3.3 Comparison of nitrogen concentration (%) in leaf tissue between areas and climatic seasons

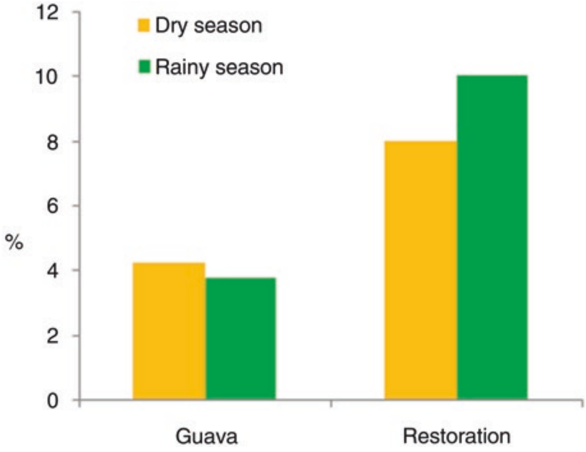


Fig. 3.4 Comparison of carbon concentration (%) in soil between areas and climatic seasons

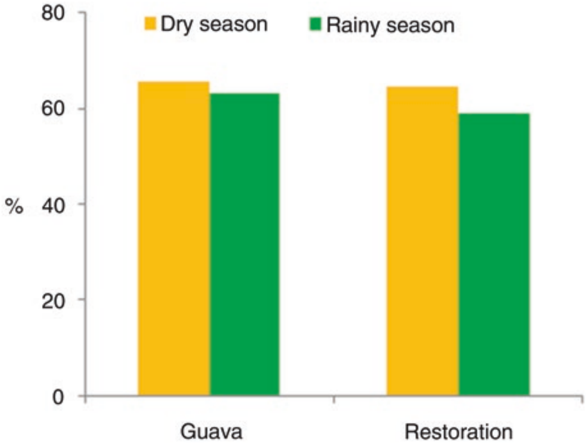


Fig. 3.5 Comparison of carbon concentration (%) in leaf tissue between areas and climatic seasons

Coefficients of determination of the regressions between soil and leaf concentrations of carbon and nitrogen were low (R^2 range, 0.0004–0.12) and nonsignificant except for the concentration of nitrogen in the dry season. In this case, the trend of a higher concentration of nitrogen in leaves as the nitrogen concentration in soil increases was weak but significant ($R^2 = 0.12$, $F_{1,38} = 5.18$, $p = 0.029$).

The soils of the pasture-guava site were significantly more acidic than the soils of the restoration site (mean pH_{guava}, 5.54 ± 0.13; mean $\text{pH}_{\text{restoration}}$, 5.92 ± 0.12) ($F_{1,18} = 46.55$, $p < 0.0001$).

We recorded a total of 16 orders of soil invertebrates in the dry and rainy season samples in the two study sites. Gastropoda (snails), Diplopoda (millipedes), and Isopoda (pill bugs) were frequently recorded. The Shannon diversity index for taxonomic orders was slightly greater in the pasture-guava site during the dry season ($H_{\text{guava-dry}} = 1.30 \pm 0.53$; $H_{\text{restoration-dry}} = 1.05 \pm 0.27$), whereas in the rainy season, the index was higher in the restoration site ($H_{\text{guava-rainy}} = 0.99 \pm 0.36$; $H_{\text{restoration-rainy}} = 1.11 \pm 0.22$). These differences, however, were not significant.

We recorded a total of ten ant species in both sites; eight were introduced species and two were "questionably native" (Table 3.1). One of the introduced species, *Tetramorium caldarium*, was the most abundant in both sites. The Shannon diversity index was slightly higher in the pasture-guava site ($H = 1.57 \pm 0.10$) than in the restoration site ($H = 1.35 \pm 0.06$); but the difference was not significant. The ratio between the abundance of introduced and native ("questionably native") ant species was higher in the pasture-guava site, where we found four introduced ants for each native ant. In the restoration site, we found a mean of 2.5 introduced ants for each native ant.

A total of seven species of snails was recorded in both sites. Most species were observed in both sites except for *Bulimulus* sp. that was recorded only in the restoration site and *Euconulus galapaganus*, which was recorded only in the pasture-guava site (Table 3.2). The two introduced species, *Subulina octona* and *Zonitoides arboreus*, were the most abundant in both sites. Native species were rare (1–2 individuals recorded per survey), and a considerable proportion of their records were shells of

Table 3.1 Ant species recorded in the study areas

Species	Restoration site	Pasture-guava site
Cyphomyrmex rimosus[a]		X
Hypoponera opaciceps[b]		X
Nylanderia sp.[a]	X	
Paratrechina vaga[a]	X	
Odontomachus bauri[b]	X	X
Rogeria curvipubens[a]	X	
Solenopsis globularia pacifica[a]	X	
Tapinoma melanocephalum[a]	X	
Tetramorium caldarium[a]	X	X
Wasmannia auropunctata[a]		X

[a] Introduced species

[b] Possibly introduced, questionably native

Table 3.2 Snail species recorded in the study areas

Species	Restoration site	Pasture-guava site
Bulimulus (Naesiotus) sp.	X	
Euconulus galapaganus		X
Habroconus sp.	X	X
Helicina nesiotica	X	X
Subulina octona[a]	X	X
Succinea sp.	X	X
Zonitoides arboreus[a]	X	X

[a] Introduced species

dead individuals, especially in the restoration site (90% of the snails recorded were dead vs. 32% in the pasture-guava site). The ratio between the number of individuals of introduced species and the number of individuals of native species was higher in the restoration site, where we found four times more individuals of introduced species than individuals of native species. In the pasture-guava site, the ratio was 3:1.

The Shannon diversity indices for those species of snails that were found alive were low and did not differ significantly between sites ($H_{\text{guava-live}} = 0.44 \pm 0.50$; $H_{\text{restoration-live}} = 0.25 \pm 0.41$). Differences in snail species diversity between areas were even smaller when adding the records of dead individuals in the calculations ($H_{\text{guava-all}} = 0.71 \pm 0.43$; $H_{\text{restoration-all}} = 0.69 \pm 0.60$).

The mean number of guava seeds per gram of dried feces was significantly higher in horse feces (3.95 seeds/g ± 3.66) than in cattle feces (0.25 seeds/g ± 0.5) ($t = 4.45$, $gl = 19$, $p = 0.0001$). Additionally, in the samples of horse feces, we found a mean of 67.3 guava seedlings ± 221.22 per sample. No guava seedlings were recorded in the fecal samples of cattle.

Discussion

Our approach to assess the effects of guava on nutrient cycling and on animal communities in the highlands of San Cristobal Island was based on comparing several related variables between adjacent sites that were similar in altitude and climatic conditions but that differed in the presence of the guava. Although we are aware that the environmental conditions of the two study sites were not exactly the same, we believe that the results of this comparison could shed light on how ecosystems function and how animal communities can be influenced by guava, allowing us to identify new and more detailed research questions.

After the first year of our research, we found preliminary evidence that areas with guava had significantly less nitrogen in plant tissues than areas with native or other introduced plant species (e.g., coffee), suggesting this species was affecting the nitrogen cycle in the islands (de la Torre 2013). Our present results of lower nitrogen concentration in soil and leaf tissues in the pasture-guava site confirm and complement this finding. Interestingly, our results do not agree with the results of other studies that have found that areas with invasive plants have higher nitrogen concentration in soil compared to areas with no invasives (Jager et al. 2013).

Higher soil nitrogen has been explained as a result of specific traits of invasives, such as greater size, higher photosynthetic rates, and effective symbiotic-based mechanisms for nutrient absorption that potentially increase the rates of decomposition and nutrient cycling (Weidenhamer and Callaway 2010). Compared to sympatric native species in the study areas, guava trees are large-sized, and although their photosynthetic rate is unknown, they have mycorrhizal fungi that increase nutrient uptake by plants and may give guava a competitive advantage over native plants (Schofield 1989).

In this scenario, it is difficult to explain the repeated pattern of low nitrogen concentration in soil that we found in our pasture-guava study site from 2011 through 2013 (analyzed in this chapter) and in 2015 (de la Torre and Villarruel in prep.). One possible explanation is that this pattern may be related to a decrease of nitrogen availability resulting from a process of soil acidification that occurred over time as a result of a high nitrogen deposition rate (Bobbink et al. 2012).

The pasture-guava study site is at least 15 years old (G. Sarigu pers. com.) and has been affected not only by nitrogen deposition related to the metabolism of the invasive plants but also by the presence of large introduced herbivorous mammals (cattle and horses), whose excretions have also contributed to nitrogen deposition in soils. In this site, soils are significantly more acidic than soils in the restoration site. A reduced pH may inhibit nitrification and decomposition rate (Bobbink et al. 2012).

The low nitrogen concentration in the soil may be related to the low concentration of this nutrient in the leaf samples from the pasture-guava site. This relationship has been reported in other studies (e.g., van Arendonk et al. 1997; Ordoñez 2010). However, the low coefficients of determination we found between nitrogen concentration in soil and leaves suggest that other environmental factors may influence nitrogen uptake by plants.

We did not find significant differences in the communities of soil invertebrates between sites with any of the three approaches we used. Both sites shared most of the taxonomic orders, which may be expected considering the broad taxonomic level being analyzed. However, when focusing on the species diversity of ants and land snails, differences in diversity were not significant either.

According to the Checklist of Galapagos Introduced Invertebrates (Causton et al. 2014), all the ant species recorded in this study are introduced (eight species) or "questionably native" (two species). The genus *Nylanderia* is not included in this list, but Herrera (2015) reported it as introduced in Galapagos. When considering the ratio of introduced vs. questionably native ant species, we found more introduced species of ants in the pasture-guava site than in the restoration site.

On the other hand, of the seven species of land snails that were recorded in this study, two species are introduced. One of these species, *Zonitoides arboreus*, is a new record for Galapagos since it is not included in the Checklist of Galapagos Introduced Invertebrates (Causton et al. 2014). Species composition of land snails was very similar between sites, but the abundance of introduced species compared to native species was higher in the restoration site. It is also remarkable that a considerable proportion of the snails that we found in both areas were dead. This proportion of dead individuals was almost three times higher in the restoration site.

These results suggest that the structure of the community of soil invertebrates is affected by complex interactions among several environmental factors that are not limited to pH and nutrient availability in soils and plant tissue, but may include present and past effects of competition among introduced species of invertebrates. The greater ratio of introduced vs. "questionably native" ant species in the pasture-guava site suggests that changed environmental conditions caused by the invasive plants may have favored the spread of introduced ants like *Wasmannia auropunctata*, which is known to outcompete and displace native ants (Lubin 1984; Global Invasive Species Database 2016). The prevalence of introduced species in the restoration site could be due to the fact that this site was formerly an area with pasture and guava; thus, changes in species composition in the ant community may have occurred when the area was dominated by introduced plants. Ant community appears to have changed slowly after introduced plants were eradicated.

In the case of land snails, the greater abundance of introduced species in both study sites also suggests that competition may be ongoing between native and introduced species. We are currently carrying out an experimental study in the highlands of San Cristobal to learn more about these possible interactions. The high number of dead snails of all species, on the other hand, could be related to seasonal changes in the species' population dynamics (Patz et al. 2000) or to specific human activities, like selective cutting and pruning, which were more frequent in the restoration site, possibly affecting the snails' habitats.

Research into the role of animals on guava dispersal in Galapagos has focused on birds (Buddenhagen and Jewell 2006). The role of cattle as seed dispersers was stated by De Vries and Black (1983) and Schofield (1989); however, we are not aware of previous studies that have quantitatively evaluated the effectiveness of cattle and horses as seed dispersers. We found a significantly higher number of seeds per gram of dried horse feces. Additionally, we only found guava seedlings in horse feces and not in fecal samples from cattle. These results suggest that horses are more effective dispersers of the guava than cattle. The significantly lower number of seeds/g of dried cattle feces, compared to horse feces, could be due to the more effective ruminant digestion of cattle that may destroy seeds when they pass through the digestive tract, but it is also possible that horses may consume more guava than cattle. A future study to assess rates of guava consumption by these species is needed to confirm this possibility.

Our results point to the complexity of the interactions between exotic plants and animals. We do have some evidence that guava is affecting carbon and nutrient cycling, possibly through acidification processes. However, since in our study area the guava was not the only introduced species, we cannot discard the possibility that at least some of these effects are caused by introduced grasses or by an interaction between guava and grass. The same is true when analyzing the effects of guava on the community of soil invertebrates. These effects are further complicated by interactions among native and introduced animals and by human intervention. What is clear from these analyses is that the combined effects of introduced plants and animals have altered the terrestrial environments in Galapagos in ways that still need to be fully understood.

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Chapter 4
A Study Contrasting Two Congener Plant Species: *Psidium guajava* (Introduced Guava) and *P. galapageium* (Galapagos Guava) in the Galapagos Islands

Hugo Valdebenito

Introduction

The study of introduced plants on oceanic islands is one of the most fascinating concerns and interests in conservation (Tye 2006; Gardener et al. 2013; Walsh and Mena 2016; Brodie et al. 2016; Celesti-Grapow et al. 2016; Helmstedt et al. 2016). New environments, low predation, isolation, and low competition by endemic species are some factors that promote the wide distribution of introduced species, affecting populations of endemic species.

In Galapagos, the problem represented by introduced organisms, especially plants, is well known (Magee et al. 2001; Itow 2004). Currently, there are over 820 introduced plant species on the islands (Tye 2000, 2002; Guézou et al. 2016), a greater number than native and endemic species together (552). Over 30 introduced plant species (Itow 2004) have been listed as the most invasive ones, with characteristics such as easy dispersal and high germination rate, which allow them to occupy large areas displacing both endemic plant and animal species alike. Among the above species, the "guava" (*Psidium guajava*) is noteworthy and was introduced around 1850 on the islands as fruit and as food resource for cattle feed. Currently, this species occupies large areas in Galapagos (>100.000 ha), including Floreana, Isabela (CA, SN), San Cristobal, and Santa Cruz islands (Walsh et al. 2007).

Both the Galapagos National Park Service and the Charles Darwin Research Station have made substantial efforts in order to control not only this species but also other introduced species, with some positive results (Tye 2002; Rentería et al.

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2006, 2012); however, more studies are needed in order to determine the structure of their communities, habitat, and nutrient cycling.

The genus *Psidium* has an additional endemic species in Galapagos, *P. galapageium*, which has two varieties, *P. galapageium* var. galapageium and *P. galapageium* var. howellii. Differences in distribution and morphology are not clear for these varieties; Porter (1969) mentions that both varieties are allopatric except for collections in Santa Cruz and that both *P. galapageium* var. galapageium and *P. galapageium* var. howellii have similar floral morphology in populations belonging to the same island, but there is heterogeneity between islands. However, the questions that remain are how well-defined (morphologically and genetically) these two varieties are and how similar with *P. guajava*. In order to explore these issues, it is necessary to determine the distribution as well as the morphological, ecological, and taxonomic relationships of these species.

On the other hand, topics such as distribution, germination rates, and methods of control have been relatively well-studied on *P. guajava* (internal reports at the Charles Darwin Station), but little has been studied regarding nutrient dynamics, decomposition rate, habitat characterization, and morphological variability. Regarding the endemic *P. galapageium*, there are no studies addressing those issues.

Finally, the genus *Psidium* in Galapagos presents the unique condition of having both an endemic and an introduced species. Naturalization and sympatry of these species can lead to a natural hybridization as has happened in Hawaii in the genus *Rubus* (Randell et al. 2004), which highlights the negative consequences of this coexistence and the importance of documenting the behavior of both species, including a study of their habitat, phenology, community structure, and dynamics of nutrients like N, C, and P.

In this chapter, some preliminary results are presented from a study which aims to evaluate the community structure, morphology, and phenology of *Psidium guajava* (introduced guava or guayaba) and *P. galapageium* var. *howellii* (Galapagos guava or guayabillo) on San Cristobal Island.

Study Areas

Fieldwork was carried out in the guayaba zone in the highlands of San Cristobal Island as well as in lowland areas within the Galapagos National Park. Vascular plants were sampled in 14 randomly placed 20 × 20 m permanent plots during the dry seasons (June–August) of 2014 and 2015, 7 for *P. guajava* with a range of different guava densities and 7 plots for *P. galapageium* at different altitudes (Fig. 4.1). The guayaba zone extends from about 200 m to the highest point of the island at approximately 650 m (pers. obs.). On the other hand, *Psidium galapageium* var. *howellii* extends from about 60 m to almost 400 m. Plant species nomenclature follows Jorgensen and León-Yáñez (1999). During the sampling period, the climate was characterized by two seasons: warm-wet rainy (December–April) and cool-dry (May–November) with

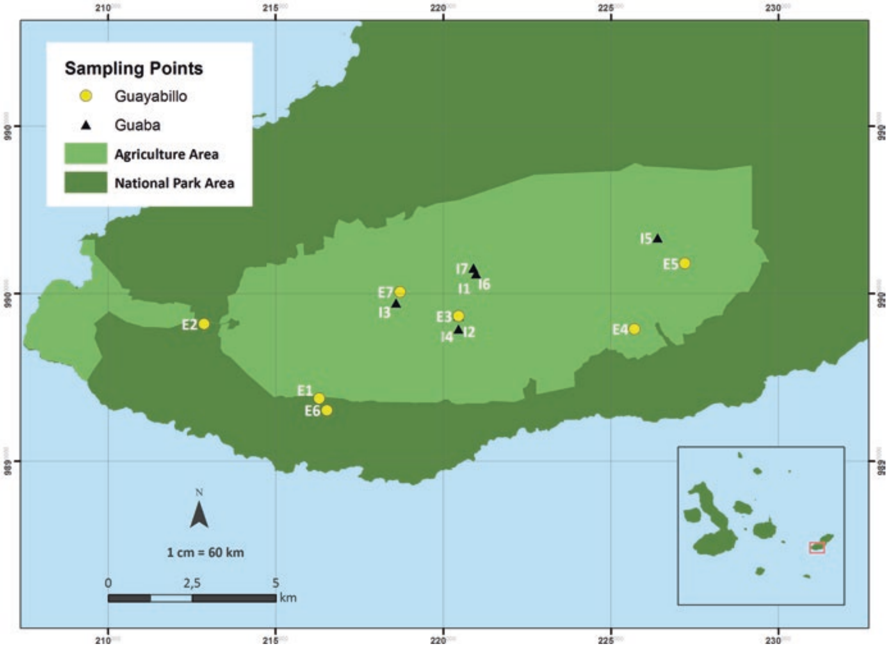

Fig. 4.1 Location of plots for *P. guajava* (I) and *P. galapageium* (E) in San Cristobal Island

some anomaly (November and December 2015 and January and February 2016 as the wettest months; Meteoblue tiempo Puerto Baquerizo Moreno).

Methods

Morphology

This investigation was based on 14 collections of both species made by the author in 2014 and 2015. Whenever possible, plant material was collected from three individuals in any given collection site. A map of collection sites can be seen in Fig. 4.1. In addition, herbarium specimens (CDS) were checked. In order to differentiate the species, 19 morphological characters were observed on 42 specimens. A list of observed characters is given in Table 4.1.

Seven characters (1, 3, 11, 12, 14, 17, 18) were measured manually using a "slide gauge," and the remaining 12 features were observed/counted. Leaf and flower measurements were made on pressed material softened by boiling water, and the diaspore measurements (14) on dried material, whereas the measurements on flowering shoots (15, 16, 19) were made on fresh material. For each specimen, measurements were made on five leaves, five flowering heads, and four diaspores, whenever possible. On most quantitative characters, an average value was obtained.

Table 4.1 Characters measured/observed to differentiate between *P. guajava* and *P. galapageium* var. galapageium

No. character	Character observed/measured
1	Flower diameter (cm)
2	Flower arrangement
3	Bud length (mm)
4	Leaf shape
5	Leaf symmetry
6	Leaf persistence
7	Leaf pubescence (above)
8	Leaf pubescence (below)
9	Leaf texture
10	Leaf color
11	Blade length (cm)
12	Blade width (cm)
13	Veins (above)
14	Fruit diameter (mm)
15	Habit
16	Trunk shape
17	Tepals length (cm)
18	Tepals width (cm)
19	Number of seeds

Community Structure

Vascular plants were sampled, as indicated above, in seven randomly placed permanent plots with a range of different *P. guajava* densities, both in the agricultural and in the Park zone. All plots were 20 × 20 m with the NE corner marked by a PVC tube. Five parallel 20 m transects were set through each plot, 5 m apart from each other. Vegetation measurements were carried out along the transects, and percentage vegetation cover was estimated for each species by the line-intercept method in 2014 and 2015 during the dry (May–December) and rainy seasons (January–April). To account for rare species, the spaces between transects were searched, and species not recorded along the transects were noted. All *Psidium guajava* and *P. galapageium* individuals in each plot were counted, and those exceeding 1.5 m in height were marked with an aluminum tag and the dbh at ca.1.5 m was measured. The percentage slope of each plot was measured with a clinometer.

For data analysis we used the Primer 6 software. Prior to analysis, species presence/absence counts and values for percentage cover (referred here as "cover") obtained from the five 20 m transects in a plot were pooled. Species richness was determined as "total number of species," which is the number of all species present in plots (7) for each species. To calculate the cover for each species (abundance), the vertical projection of the foliar cover on the transect was considered (e.g., shrubs, ferns, and frobs). The interception with the transects was measured as well, for grasses and grass-like plants, along with rosette-forming plants at the ground level.

Therefore, the total cover could exceed 100% when there was interception of overlapping canopies.

A general checklist of species was established after digital processing of the 14 sample plots. Specific abundance, frequency, diversity, species richness, and similarity among plots belonging to either *P. guajava* or *P. galapageium* was determined. Additionally, we studied compositional similarities between plant communities associated to *P. guajava* and *P. galapageium.*

Phenology

This study focused on flowering, leaf growth, and fruiting phenology of *P. guajava* and *P. galapageium* in San Cristobal Island. Information of flowering and fruiting gathered throughout this study can then be used to differentiate both species in the study area. These observations were conducted in 15 stations (Fig. 4.2), which covered different areas of San Cristobal, ranging from 60 to 650 masl. The vegetation in these areas consisted of mixed forests (*P. galapageium*) and abandoned agricultural fields and plantations (*P. guajava*).

The phenology data were gathered through surveys conducted monthly from June 2015 to April 2016. The surveys focused on observing individual trees of both species and documenting their flowering and fruiting periods. The individual trees

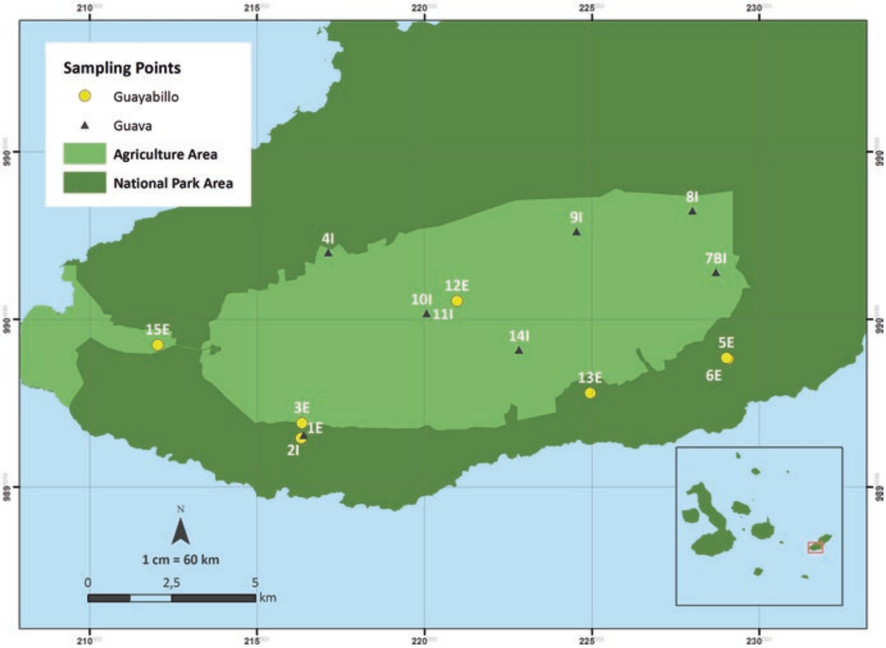

Fig. 4.2 Sampling points for the phenology study

Table 4.2 Five/point scale based on percentage of the event

Value	Percentage of the event
0	Absence of the event
1	Occasional presence of the event (1–25%)
2	Common presence of the event (25–50%)
3	Abundant presence of the event (50–75%)
4	Dominant presence of the event (75–100%)

were randomly selected based on ease of access to the area and visibility of their flowers, leaves, and fruits. Every individual tree was marked in the GPS monitor for monthly observations. When it was possible, at least three individuals—27 trees from each species—were chosen to represent a species in a specific survey area. Then the monthly average values (%) were taken for representation on the graphs, and the phenological event was visually scored along a five-point scale based on an increasing percentage of the event (Table 4.2).

To determine the intensity of monthly flowering and fruiting, the number of flowers and fruits on plants were counted with the aid of binoculars when necessary, and that figure was transformed in percentage of the event according to Table 4.2. For each sampling period, the survey plants were examined and scored as currently bearing flowers and/or fruit. Only flowers and fruits still attached to plants were included. To determine the leaf presence, the percentage of the tree covered by leaves was used. Sometimes, and especially for fruit maturation, the only evidence was fallen fruit (e.g., June for *P. galapageium*).

The following phenological events were derived in both *Psidium* species from the monthly counts of leaves, flowers, and fruits: leaf flush initiation, leaf flush completion, leaf fall initiation, leaf fall completion, leafless period, initiation of flowering, completion of flowering, time lag between start of vegetative (first-leaf flush) and reproductive (first-visible flower) phases, initiation of fruiting, completion of fruiting, fruit-fall initiation, and completion of fruit fall.

Results

Morphology

Based on 19 characters used in this study, there is a clear morphological difference between the species studied (Table 4.3). Flowers and their parts, buds, fruits, and leaves are on average smaller in *P. galapageium* var. howellii than in *P. guajava* (Table 4.3). Regarding the above features, the interspecies population variation was greater than within-individual variation in the same species. Additionally, the habit and trunk shape are different, especially in adult individuals, being more

Table 4.3 Characters observed to differentiate between *Psidium guajava* and *P. galapageium* var. howellii. Figures correspond to the range of values obtained

	Psidium guajava	*P. galapageium*
Flower diameter (cm)	2.5–3	1–1.5
Flower arrangement	1–3 flowered dichasia	Solitary
Bud length (mm)	7–10	5–5.5
Leaf shape	Ovate to ovate-lanceolate	Elliptic to ovate/suborbicular
Leaf symmetry	Slightly inequilateral	Equilateral
Blade length (cm)	5–14	1.8–5.5
Blade width (cm)	2–6	1–2.6
Habit	Small trees to 8 m	Trees or shrubs to 8 m high
Trunk shape	Young branches four-angled	Several to monopodial (adult); branches divaricate
Fruit diameter (cm)	Berry (2)	Berry (0.6–1.3)
Number of seeds	Many	4–8
Leaf pubescence (above)	Thinly pubescent to glabrate	Thinly pubescent to glabrate
Leaf pubescence (below)	Tomentose, especially on veins	Thinly pubescent to glabrate
Veins (above)	Impressed (above); prominent (below)	Impressed (above and below)
Leaf texture	Leathery	Subcoriaceous
Leaf color	Dark green	Shiny light green
Tepals length (cm)	1.1–1.8	0.4–0.6
Tepals width (cm)	0.5–1.0	0.3–0.5

monopodial and with divaricate branches on *P. galapageium*. However, there is some variation from this pattern, especially the height of the endemic species. At lowlands (100 masl), the individuals are shrubs (2–4 m), but at higher elevations (400 masl), the individuals are monopodial trees, more than 1 m wide and with branches only from the middle part and higher, and can reach a height of up to 8 m (Fig. 4.3). *P. guajava* trees are more regular in height and shape (Fig. 4.4).

Unfortunately, we did not have access to individuals (fresh material) of *Psidium galapageium* var. *galapageium* (present in Santa Cruz), and therefore we could not establish a comparison between both varieties, which seem very similar (Porter 1969).

Community Structure: Species Composition

The investigation revealed a total number of 97 different plant species (Table 4.3), and there were only six species common to both plots (*Oxalis corniculata, Desmodium incanum, Pennisetum purpureum, Peperomia galapagensis, Phyllanthus caroliniensis*, and *Pteridium aquilinum).* There were 54 species in plots with guayaba, 26 (49%) of them were native, 19 (35%) introduced, and 10 (16%) endemic. On the other hand, in plots with *P. galapageium*, there were 48 species in total, 21

Fig. 4.3 *P. galapageium* at 460 masl

(43%) native, 17 (35%) introduced, and 11 (22%) endemic. Therefore, there was no significant difference in the number of species in the different plots, but the species present on plots of either *Psidium* species were different (Table 4.4).

Vegetation and Community Analysis

There was a clear difference between both types of plots. The species that contributed most to this difference are listed in Table 4.5. Clearly, for plots with guava, the species that contributed the higher values (av. abundance and av. similarity) to

Fig. 4.4 *P. galapageium* (left) and *P. guajava* (right) at 250 masl

differentiate these plots were *Centella asiatica* (native), *Blechnum occidentale* var. *puberulum* (introduced), *Pennisetum purpureum* (introduced), and *Hypoxis decumbens* (native). On the other hand, for guayabillo plots, the more important species were *Cuphea carthagenensis* (introduced), *Lantana camara* (introduced), *Chiococca alba* (native), and *Plumbago zeylanica* (native). In addition, there was more similarity among plots with guava (34.38%) than with guayabillo (11.23%).

According to Table 4.5, the abundance of eight plant species present in guava plots was greater than the abundance of the seven most representative species in the plots of guayabillo. Even *Pteridium aquilinum,* with the lowest percentage of abundance in quadrants with guava (1.5%), had higher abundance than the most abundant species in plots with guayabillo.

There were no families better represented in either quadrat. According to the origin, there were three introduced species as the best represented in plots with *P. galapageium* and two in the guava plots. None of the species that contribute most to the differentiation of quadrats is common to both types of quadrats. This confirms the difference between the plots (Fig. 4.5).

According to the above clustering analysis, plots with guava (I) separate very clearly from those with Galapagos guava (E). Plot E7, corresponding to guayabillo, stands apart because the plot is located in a dry, rocky area with a very distinctive associated flora, where 67% of the species are native and 17% are endemics. On the other hand, plots I7 and E6 are clustered together because I7 is in a very humid area, with 74 guava trees; and the major percentage (46%) of the associated flora was

Table 4.4 Species composition in guayaba (*P. guajava*) and guayabillo (*P. galapageium*) plots

	Guayaba plots			Guayabillo plots	
Family	Species	Origin	Family	Species	Origin
Asteraceae	*Ageratum conizoides*	Native	Poaceae	*Aristida subspicata*	Endemic
Amaranthaceae	*Alternanthera halimifolia*	Native	Asclepiadaceae	*Asclepias curassavica*	Introduced
Aspleniaceae	*Asplenium auritum* var. *auriculatum*	Native	Malvaceae	*Bastardia viscosa*	Native
Aspleniaceae	*Asplenium serra* var. *imrayanum*	Native	Acanthaceae	*Blechum pyramidatum*	Native
Asteraceae	*Bidens pilosa*	Native	Crassulaceae	*Bryophyllum pinnatum*	Introduced
Asteraceae	*Blainvillea dichotoma*	Native	Burseraceae	*Bursera graveolens*	Native
Blechnaceae	*Blechnum polypodioides*	Native	Asteraceae	*Centratherum punctatum*	Introduced
Blechnaceae	*Blechnum occidentale* var. *puberulum*	Introduced	Rubiaceae	*Chiococca alba*	Native
Polypodiaceae	*Campyloneurum amphostenon*	Native	Poaceae	*Chloris virgata*	Native
Apiaceae	*Centella asiatica*	Native	Verbenaceae	*Clerodendrum molle* var. *molle*	Native
Rutaceae	*Citrus limetta*	Introduced	Euphorbiaceae	*Croton scouleri*	Endemic
Pteridaceae	*Cheilanthes microphylla*	Native	Lythraceae	*Cuphea carthagenensis*	Introduced
Capparaceae	*Cleome viscosa*	Introduced	Cyperaceae	*Cyperus anderssonii*	Endemic
Commelinaceae	*Commelina diffusa*	Native	Fabaceae	*Desmodium incanum*	Native
Asteraceae	*Conyza bonariensis*	Introduced	Euphorbiaceae	*Hippomane mancinella*	Native
Dryopteridaceae	*Megalastrum pleiosoros*	Endemic	Hypoxidaceae	*Hypoxis decumbens*	Native
Dryopteridaceae	*Ctenitis sloanei*	Native	Mimosaceae	*Inga edulis*	Introduced
Lythraceae	*Cuphea carthagenensis*	Introduced	Verbenaceae	*Lantana camara*	Introduced
Cyperaceae	*Cyperus anderssonii*	Endemic	Mimosaceae	*Leucaena leucocephala*	Introduced
Dennstaedtiaceae	*Dennstaedtia cicutaria*	Native	Asteraceae	*Macraea laricifolia*	Endemic
Fabaceae	*Desmodium incanum*	Native	Celastraceae	*Maytenus octogona*	Native
Rubiaceae	*Diodia radula*	Introduced	Cucurbitaceae	*Momordica charantia*	Introduced
Adiantaceae	*Doryopteris pedata*	Native	Oxalidaceae	*Oxalis corniculata*	Introduced
Caryophyllaceae	*Drymaria cordata*	Native	Polypodiaceae	*Pecluma dispersa*	Native
			Poaceae	*Pennisetum purpureum*	Introduced
Apiaceae	*Hydrocotyle galapagensis*	Endemic	Piperaceae	*Peperomia galapagensis*	Endemic
Dennstaedtiaceae	*Hypolepis hostilis*	Native	Euphorbiaceae	*Phyllanthus caroliniensis*	Introduced

Hypoxidaceae	*Hypoxis decumbens*	Native	Fabaceae	*Piscidia carthagenensis*	Native
Asteraceae	*Jaegeria gracilis*	Endemic	Nyctaginaceae	*Pisonia floribunda*	Endemic
Cyperaceae	*Kyllinga brevifolia*	Native	Plumbaginaceae	*Plumbago zeylanica*	Native
Verbenaceae	*Lippia strigulosa*	Native	Polygonaceae	*Polygonum hydropiperoides*	Introduced
Onagraceae	*Ludwigia leptocarpa*	Native	Mimosaceae	*Prosopis juliflora*	Native
Melastomataceae	*Miconia robinsoniana*	Endemic	Myrtaceae	*Psidium galapageium* var. *howellii*	Endemic
Davalliaceae	*Nephrolepis cordifolia*	Introduced	Myrtaceae	*Psidium guajava*	Introduced
Poaceae	*Oplismenus compositus*	Introduced	Dennstaedtiaceae	*Pteridium aquilinum*	Native
Oxalidaceae	*Oxalis corniculata*	Introduced	Cyperaceae	*Rhynchospora nervosa* ssp. *ciliata*	Native
Oxalidaceae	*Oxalis corymbosa*	Introduced	Rosaceae	*Rubus niveus*	Introduced
Poaceae	*Paspalum conjugatum*	Introduced	Rhamnaceae	*Scutia spicata* var. *pauciflora*	Endemic
Polypodiaceae	*Pecluma dispersa*	Native	Caesalpiniaceae	*Senna alata*	Introduced
Poaceae	*Pennisetum purpureum*	Introduced	Malvaceae	*Sida rhombifolia*	Introduced
Piperaceae	*Peperomia galapagensis*	Endemic	Portulacaceae	*Talinum paniculatum*	Introduced
Euphorbiaceae	*Phyllanthus caroliniensis*	Introduced	Bromeliaceae	*Tillandsia insularis*	Endemic
Pteridaceae	*Pityrogramma calomelanos* var. *calomelanos*	Native	Boraginaceae	*Tournefortia rufo-sericea*	Endemic
Plantaginaceae	*Plantago major*	Introduced	Boraginaceae	*Tournefortia psilostachya*	Native
Polypodiaceae	*Pleopeltis macrocarpa*	Native	Boraginaceae	*Tournefortia pubescens*	Endemic
Polypodiaceae	*Polypodium insularum*	Endemic	Apocynaceae	*Vallesia glabra* var. *glabra*	Native
Polypodiaceae	*Polypodium tridens*	Endemic	Fabaceae	*Vigna luteola*	Native
Asteraceae	*Pseudelephantopus spiralis*	Introduced	Sterculiaceae	*Waltheria ovata*	Native
Myrtaceae	*Psidium guajava*	Introduced	Rutaceae	*Zanthoxylum fagara*	Native
Rubiaceae	*Psychotria rufipes*	Endemic			
Dennstaedtiaceae	*Pteridium aquilinum*	Native			
Cyperaceae	*Rhynchospora nervosa ssp. ciliata*	Native			
Rosaceae	*Rubus niveus*	Introduced			
Solanaceae	*Solanum americanum*	Introduced			
Asteraceae	*Sonchus oleraceus*	Introduced			

Table 4.5 Species that contribute most to the abundance and similarity to guava (I) and guayabillo plots (E)

Species	Av. abundance (%)	Av. similarity (%)
Group I (guava plots)		
Average similarity among guava plots: 34.38		
Centella asiatica	6.22	14.83
Blechnum occidentale var. *puberulum*	2.84	4.9
Pennisetum purpureum	1.78	3.42
Hypoxis decumbens	2.29	2.78
Ageratum conizoides	1.95	2.34
Pteridium aquilinum	1.5	1.24
Hydrocotyle galapagensis	2.5	1.17
Commelina diffusa	1.54	1
Group E (guayabillo plots)		
Average similarity among guayabillo plots: 11.23		
Cuphea carthagenensis	2.33	3.17
Lantana camara	1.18	1.95
Chiococca alba	1.18	1.87
Plumbago zeylanica	0.8	0.92
Bryophyllum pinnatum	0.93	0.9
Zanthoxylum fagara	0.82	0.74
Blechum pyramidatum	0.35	0.63
Groups I and E		
Average dissimilarity = 97.06%		

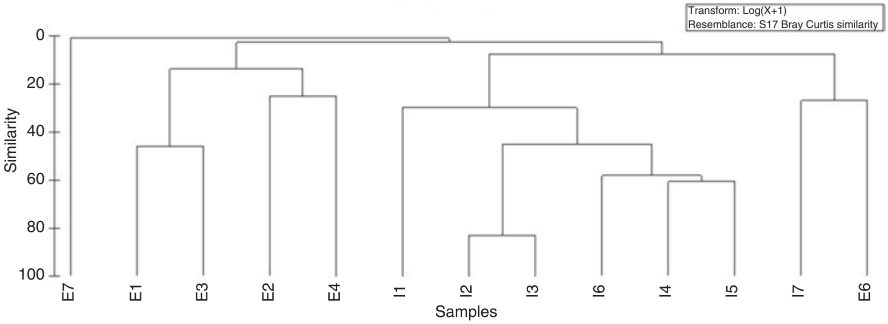

Fig. 4.5 Clustering of plots with *P. guajava* (I) and *P. galapageium* (E)

native and 23% endemics. E6 is a plot with nine guayabillo trees in a very dry and rocky area with approx. 50% of introduced species (e.g., *Lantana camara, Chloris virgata, Sida rhombifolia*). In other words, the clustering analysis sets these two plots apart because they were out of what was “normal” for these plots (fewer native species for the former and fewer introduced species for the latter).

Regarding the number of individuals per species, there were approximately 86% more individuals per species in the guava plots. There were always more individuals per species on quadrats with guava. The three quadrats with the greater number of individuals/species were I6 (22% of the total number of individuals on 22 species), I7 (22% on 16 species), and I5 (20% on 32 species). On the other hand, with less than 3% of the total number of individuals are E3 with 16 species, I1 with 9 species, and I5 with 20 species.

According to the origin, species with the greatest cover in guava plots were *Hydrocotyle galapagensis* (endemic, present in quadrats I6 and I7 covering 100%), *Centella asiatica* (native, covering 100% in plots I1, I3, I6, and I7), *Blechnum puberulum* (native, plots I2 and I3), and the native *Blechnum polypodioides* (I5). In guayabillo plots, the best represented species were the natives *Pecluma dispersa* (plot E1) and *Plumbago scandens* (plots E5 and I7).

Phenology: Flowering and Fruiting

Although the presence and the pattern of temporal change were generally consistent between sites for each species, the sites differed in the magnitude of production. For example, fruit production in *P. galapageium* was extremely variable between trees on the lowlands (100 masl) and the highlands (400 masl). Usually, flowering and fruiting occurred earlier at lower altitudes.

In general, both *P. guajava* and *P. galapageium* displayed similar phenological flowering and fruiting patterns. A complex assortment of floral buds, open flowers, fruitlets, and fruits of varying sizes was found on both species during similar periods (Figs. 4.6, 4.7, 4.8, and 4.9). The reported developmental stages include an initiation of flowering in October, with a completion of flowering in February for *P. galapageium*. The flowering for *P. guajava* began 4 months later with a peak of open flowers in February (Figs. 4.6 and 4.7). Peaks in fruit completion were in April 2016 for both species. However, *P. guajava* bore fruits in the period between August and October with no fruits during November and December when fruits were decomposed, probably due to heavy rains in November.

Leaf Phenology

Branches bore leaves during the whole year for both species. The proportion of leaf initiation, leaf completion, and leaf fall was constant during the sampling period for both species, with the exception of October and November, when leaf fall increased (Figs. 4.10 and 4.11). There was no correlation with other phenological events.

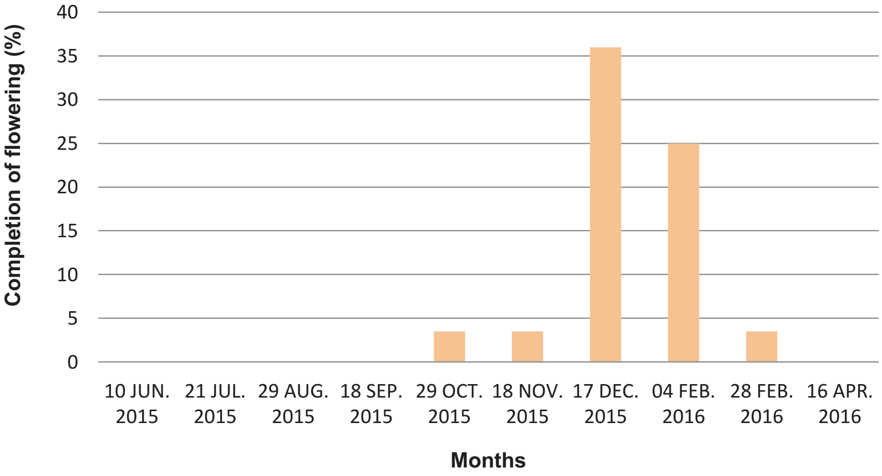

Fig. 4.6 Flowering in *P. galapageium* var. *howellii* (Galapagos guava)

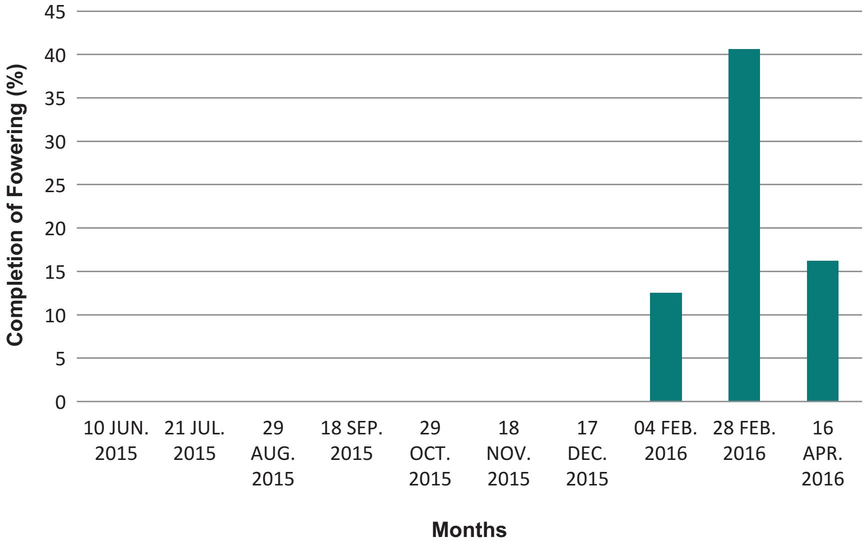

Fig. 4.7 Flowering in *P. guajava*

Discussion

Even though this study has been restricted to San Cristobal Island, the results show morphological, phenological, and community structure differences. However, more observations need to be conducted, especially regarding phenology and community structure in both *Psidium* species.

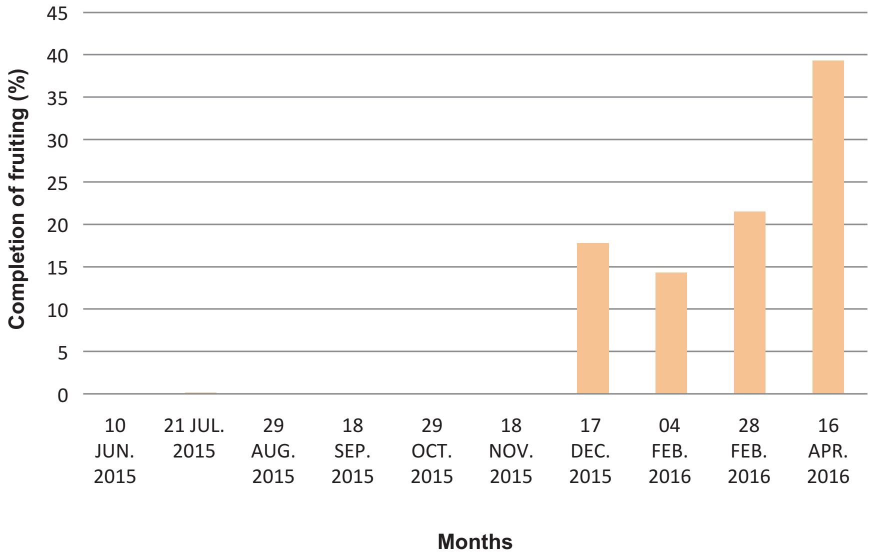

Fig. 4.8 Fruiting in *P. galapageium*

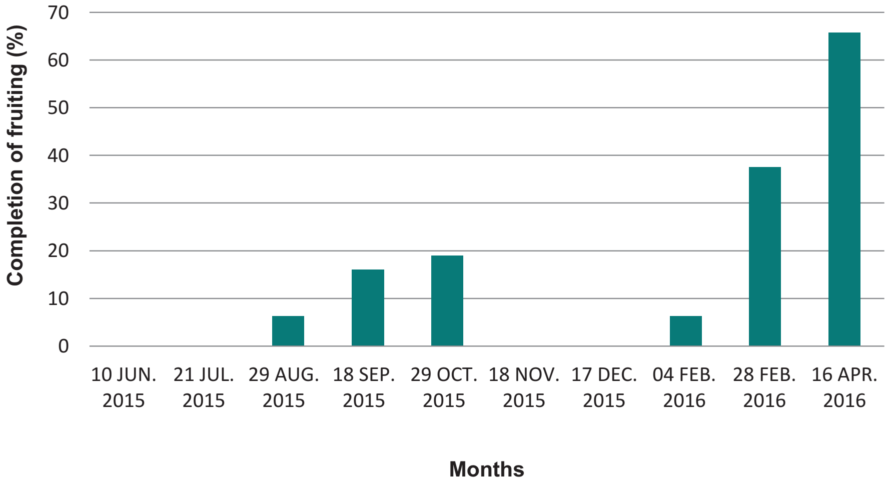

Fig. 4.9 Fruiting in *P. guajava*

Morphology

The genus *Psidium* (Myrtaceae) is represented by two species in Galapagos, *P. guajava* (introduced and invasive, a native of tropical America, and widely cultivated and well established as an escape throughout the tropics) and *P. galapageium*

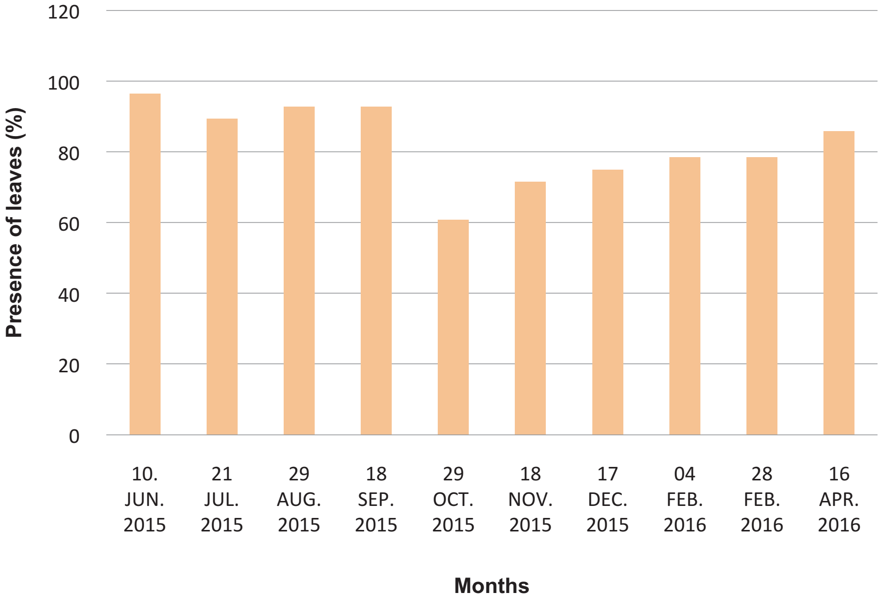

Fig. 4.10 Presence of leaves in *P. galapageium*

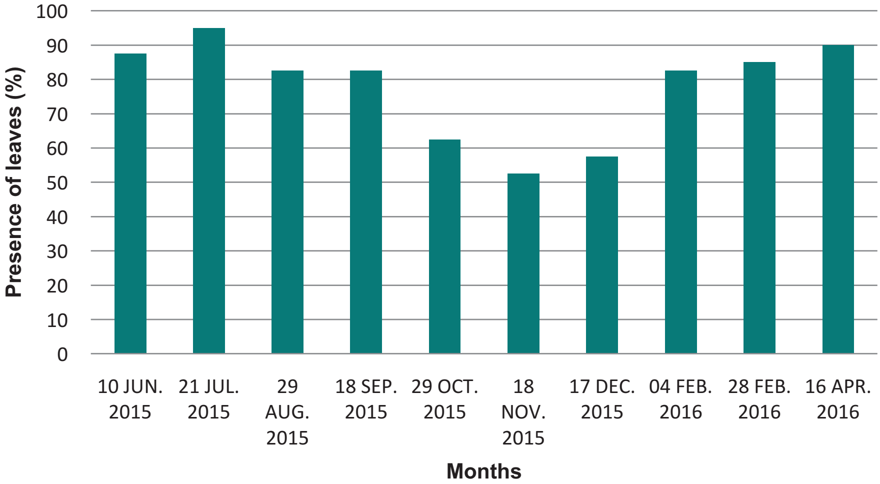

Fig. 4.11 Presence of leaves in *P. guajava*

(endemic to the Galapagos) with two varieties, *P. galapageium* var. *galapageium* and *P. galapageium* var. *howellii* (Porter 1969).

The two varieties are virtually indistinguishable in collections bearing only mature fruits. However, these two varieties are allopatric in distribution (*P*. *galapageium* var.

galapageium on Santa Cruz, Fernandina, Isabela, Santiago, and Pinta islands; *P. galapageium* var. *howellii* on San Cristobal and one population on Santa Cruz), which could be sympatric (Porter 1969). However, more field study is needed to ascertain the biological and ecological relationships between these two varieties in Santa Cruz (Porter 1969). *Psidium galapageium* var. galapageium is found at altitudes of 100–400 masl, usually at arid lowlands and moist uplands. *P. guajava* is more common at moist uplands forming dense forests. However, even though both species are sometimes found in the same areas, we did not find morphological evidence of hybrids.

An interesting annotation (Porter 1969) is that *P. galapageium* appears similar to *P. sartorianum* (Berg.) Ndzu., a widespread tropical American *Psidium* species present in forests and savannas below 1500 m from Mexico to Northern Colombia and Venezuela. Porter (1969) believes this similarity supports the assumption of independent radiation from a common ancestor in the Mexican-Central American region to Galapagos and the Socorro Islands.

Psidium species in Galapagos are probably the product of two introductions: an ancestor—most probably from Mexico and Central America—which diverged into two endemic varieties and *P. guajava* (guava) which has been introduced from mainland Ecuador. However, this hypothesis needs to be proven and a first step has been attained with this study, which is looking for the degree of similarities between *P. guajava* and one variety of *P. galapageium*.

Additionally, our results support what Porter (1969) had stated regarding morphological differences between *P. guajava* and *P. galapageium*; however, since our collections have been restricted to San Cristobal only, we have been unable to correctly assess differences between the two varieties described by Porter (1969), which are present in different islands. Therefore, further field study is needed to ascertain the biological and ecological relationships not only between these two varieties but also with *P. guajava*. Furthermore, in order to determine genetic relationships between the species of this study, there is a current research whose preliminary results are also presented in this book (see Chap. 1).

Community Structure

A primary finding of this study is that the endemic species, *P. galapageium*, shows a clear pattern of ecological differentiation with its congener *P. guajava*. The endemic guava usually grows at lower altitudes and drier areas than the introduced guava. Additionally, the associated plant communities are different on both *Psidium* species. On the other hand, *P. galapageium* occurs in habitats with higher bedrock and block cover, fewer associated species, and lower and sparser vegetation than *P. guajava*.

A marked difference between the vegetation composition present in plots with guava and guayabillo was found where only six species were common to plots of both species. The plant richness and abundance of individuals was higher in plots with guava. Interestingly, guava plots with different degrees of invasion by *Psidium guajava* showed no relationship between the degree of invasion and the number of species present. For example, while some plots had 21 guava trees, there was a maximum of 11 associated plant species (e.g., plot I2), and on the other hand, plot I5 had more than twice the guava trees (50) and presented over 30 associated plant species.

Regarding species' contribution to coverage, two species were very distinctive on guava plots, the natives *Centella asiatica* and *Blechnum occidentale* var. *puberulum* (Table 4.5). On the other hand, in plots with the endemic guava tree, two introduced species presented the major contribution to coverage, *Cuphea carthagenensis* and *Lantana camara*; the native *Chioccoca alba* also had an important contribution. This difference in species' plant composition and coverage is probably due to higher humidity with increasing altitude as well as to the soil texture, which is very dry and rocky on the lowlands and at higher altitude zones is covered by more weathered soils covered by degrees of brown soils with probably audosolic characteristics (Stoops 2014).

Comparing the vegetation structure of plots with guayabillo or guava, six out of seven guava plots had no shrubs but a herbaceous cover. On the contrary, all plots with guayabillo had shrubs and, in a lesser degree, herbs. The shrubs were *Hippomane mancinella* (poison apple), *Piscidia carthagenensis* (matazarno), *Bursera graveolens* (holy tree), *Zanthoxylum fagara* (cat's claw), and *Prosopis juliflora* (mesquite).

Regarding the location of these plots, most guava plots were located on the *Miconia* and Fern-Sedge zone, above 400 masl; the plots with the Galapagos guava were in the transition zone as well as in moist areas, from 60 to 400 masl. Perhaps the cover by shrubs represents a factor for having more herbs under guava trees and—on the other hand—more coexisting shrubs (e.g., *Miconia*) with the Galapagos guava. In other words, *Miconia* shrubs have been replaced by guava trees, and therefore herbs are "accustomed" to live under shade, and they have been living so even under an introduced species such as guava. Similarly, the distribution of Galapagos guava is in rockier and drier areas where there is not much soil, and therefore the ground conditions are more adverse for herbs but suitable for shrubs adapted to these conditions (e.g., *Hippomane mancinella*, *Piscidia carthagenensis*, *Cuphea carthagenensis*, *and Lantana camara*).

A similar situation was described by Jäger et al. (2009) in the Fern-Sedge area with the invasive *Cinchona pubescens* in Santa Cruz Island. They described that in areas of the Fern-Sedge zone covered with a high density of *Cinchona pubescens,* ferns and grasses had a sharp reduction due to the shade promoted by *Cinchona*. However, areas in the *Miconia* zone invaded by *Cinchona,* where vegetation is accustomed to the shade, presented no major changes. For example, species richness did not vary significantly either in the mean number of species per plot or in the number of species in all plots studied. In addition, they found constancy in the overall numbers as well as relative proportions of native, endemic, and introduced species over a 7-year monitoring period. They also did not detect any relationship between the number of native and endemic species and the number of introduced species in each plot during any of the sampling periods.

In our study, six of the seven plots with guava had *Miconia*, and this may be one of the reasons why the diversity of species in the plots with guava has not decreased. On the other hand, when *Miconia* had low density in plots with guava, clearly the dominant species was guava. In the pampa zone where there is no tree vegetation, forests of guava in high density may be affecting the light conditions in the ecosystem and therefore diminish the diversity of species (pers. obs.).

According to our results, further monitoring is necessary to determine whether the recorded species richness and diversity represents an ephemeral or a more permanent picture.

Phenology

No statistical tests comparing time series of the reported developmental stages were performed; thus, the means of variables reported in the figures are only indicators of the stage throughout the observed months. However, periodical empirical observations done by park rangers (J. Malaga, pers. comm.) indicate that the trends noted in the observed months are typical.

Phenotypic events in *P. galapageium* and *P. guajava* occurred in very similar times. Their flowering coincided with the first rainfall of the rainy season. Fruit formation was continuous through 3–4 months following the peak flowering. Fruit fall occurred in both species during the last 2–3 months of the fruiting phenophase. Generally, fruit fall was complete for both species between February and April. The intensity of both flowering and fruiting varied between months; flowering peaked in the early wet season, while fruiting was highest in the first half of the wet season. These peaks and lows in the intensity of flowering and fruiting tended to occur synchronously in different plots, at least for *P. guajava*, indicating that the pattern was robust within this species. Unfortunately, there are no phenological studies published that have been carried out in mainland Ecuador with which to compare these results. However, there are studies carried out in Colombia during 2008 and 2009, which indicate a similar phenological behavior as described here. In general, different events (flowering, fruiting, and leaves presence) can change from site to site as well as from year to year, but there is a range of months when the events occurred (Solarte et al. 2014). For example, in 2008, flowering occurred from March to June and then the following year from January to July. At the same time, in a different site, the same event occurred from February to April, and the following year from November to July. Therefore, guava has a rather irregular behavior that depends heavily on environmental factors such as temperature and humidity.

In the present study, leaf presence occurred in both species during the whole year with a decline in October and November coinciding with the onset of the rainy season.

In general, these phenological patterns are coincident with those observed in Santa Cruz Island by Cedeño (1990) in the same species. According to Cedeño, fruiting in *P. galapageium* occurs in March–June and November–April and flowering in October and November. It is important to mention that an El Niño climate anomaly occurred during the study period. From November 2015 to April 2016, high rainfall occurred (Meteoblue tiempo Puerto Baquerizo Moreno). Overall flowering and fruiting activity fluctuated more than normal in comparison with the results of Cedeño (1990).

Additionally, as has already been stated, the exhibited events can change from year to year due to climatic factors (e.g., El Niño event). Nonetheless, the data indicate that seasonality in climatic factors plays a major role in shaping broad community-wide phenology patterns.

Concluding Remarks

Psidium galapageium has a more restricted geographic range in San Cristobal Island, mostly limited from 100 to 400 masl, while *P. guajava* has widespread distribution from 200 to 550 masl. In addition, *P. galapageium* was found to occur in habitats with higher percentage of bedrock and block cover than *P. guajava*, which is more common in humid areas. Nevertheless, the two species have the same lifeform, and probably pollination mode (we have seen the Galapagos carpenter bee—*Xylocopa darwinii*—in flowers of both species) and dispersal mode (berry eaten by birds).

Introduced and endemic congener plant species may hybridize (Anderson and de Vicente 2010; Lehman et al. 2014). Alien-native hybridization may be detrimental to native species, especially because this process can erode the genetic integrity of the endemic species, potentially resulting in a loss of local adaptability (Bleeker et al. 2007).

Even though this study did not find morphological evidence of hybrids, still there is a risk of such phenomenon. The potential risk of hybridization events between *P. galapageium* and *P. guajava* is relatively high. First, both *Psidium* spp., at least on some sites, share similar areas. Second, both species are capable of flowering during the same time of the year. Third, both *Psidium* populations are visited by the large Galapagos carpenter bee (pers. obs.). A related species, Hawaii's carpenter bee is known to fly many kilometers to forage in that archipelago (Pasquet et al. 2008).

Finally, a larger array of ecological and biological attributes should be investigated in *P. galapageium* and *P. guajava*. Among others, it is important to study the species' reproductive biology, and we need to know if these species are interfertile and produce fertile progeny. In addition, extant populations of both species need to be screened using both morphological and molecular techniques to assess the presence/absence of hybrids and potential gene flow that may have occurred between the two species.

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Chapter 5
Quinine Tree Invasion and Control in Galapagos: A Case Study

Heinke Jäger

Introduction

The red quinine tree (*Cinchona pubescens* Vahl, synonym *C. succirubra*, Rubiaceae) is one of 23 species in the genus *Cinchona* and used to be an economically important species due to its quinine-containing bark (Andersson 1998). Therefore, it had been introduced to many parts of the world, mainly from Bolivia, Colombia, Ecuador, and Peru (Andersson 1998). The main area of introduction was the Pacific region, were quinine had been introduced to 11 islands or archipelagos (Jäger 2015) and has become invasive at least in Galapagos (Macdonald et al. 1988), Hawaii (Starr et al. 2003), Tahiti (Meyer 2004), and West Java (Junaedi and Mutaqien 2010). Quinine is now considered among the 100 worst invasive species globally (ISSG 2014).

Red quinine tree has a natural distribution from Costa Rica to Bolivia (Andersson 1998). In Galapagos, this evergreen tree with wide leaves and aromatic, lightly pink flowers reaches a maximum height of 15 m (Shimizu 1997) and a DBH of 25 cm (Jäger 2015).

Introduction of Quinine to Santa Cruz Island and Its Spread

Quinine was purposefully introduced to Santa Cruz Island in the 1940s by two farmers as a cash crop (Hamann 1974; Lundh 2006). It was originally planted in the agricultural zone of Santa Cruz at middle elevation (~250 m) (Valdebenito 1991), just below the area that now belongs to the National Park. By 1965, a few quinine plants were established "above the timber line" in the *Miconia* shrubland—dominated by the

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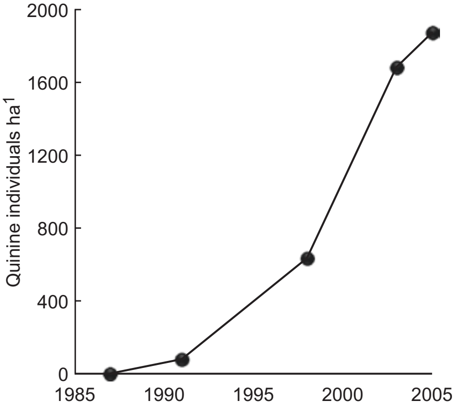
Fig. 5.1 Increase of quinine individuals per ha (not including seedlings) at "Media Luna" between 1987 and 2005 on Santa Cruz Island. Value for 1987 from Macdonald et al. (1988), for 1991 from Valdebenito (1991) and for the years 1998 to 2005 from unpubl. data



endemic *Miconia robinsoniana* Cogn—and the fern-sedge vegetation (Kastdalen 1982), as well as in semitropical forests dominated by the endemic tree *Scalesia pedunculata* Hook. f. (Shimizu 1997; Rentería et al. 2012). Quinine had completely naturalized by 1972 and could be found at an altitude of 580 m as scattered small trees between *Miconia robinsoniana* shrubs and in the central part of the island (Hamann 1974). Quinine distribution reached around 1619 ha in 1976 (Moll 1990), 4000 ha in 1987 (Ortiz and Lawesson 1987), 8500 ha in 1990 (Moll 1990), and over 11,000 ha in 2004 (Buddenhagen et al. 2004). A more recent assessment using satellite imagery estimates the current distribution as low as 1541 ha (Trueman et al. 2014), which could be due to a different method used, management actions carried out by the GNPD or a recent natural dieback of the species (see "Conclusions" at the end of this chapter).

Close to the extinct "Media Luna'" volcano, density was estimated at one individual ha^{-1} in 1987 (MacDonald et al. 1988), at 60–100 in 1991 (Valdebenito 1991) and at 1873 in 2005 (unpubl. data) (Fig. 5.1). Over a 7-year study in the highlands of Santa Cruz, the basal area of quinine trees increased from 1.0 to 4.2 m^2 ha^{-1} in the study plots, while mean quinine cover increased from 6.6% to 16.4% over the same time period. The mean density of quinine stems in 2005, including seedlings, was 2193 individuals ha^{-1} (Jäger 2015).

The successful invasion of quinine was a slow but continuous one, and it took 40 years after its introduction for its invasive character to be recognized (Ortiz and Lawesson 1987). The crop was not economically viable, and quinine production was never implemented, but quinine wood is now increasingly used for construction in the island.

Impacts of Quinine

The quinine tree was introduced to Galapagos in a formerly treeless environment, leading to significant changes in the plant communities, habitat structures, and light, water, and nutrient regimes (Jäger et al. 2007, 2009, 2013). As a consequence, quinine is now considered an ecosystem engineer (Jones et al. 1994; Jäger et al. 2009). In the highlands of Santa Cruz Island, quinine is very abundant in the vegetation zones that are dominated by ferns and sedges and by the endemic shrub *Miconia robinsoniana* Cogn, in areas where the GNPD is not actively controlling quinine. In both vegetation types, quinine is reducing species diversity and native species cover, especially that of endemic IUCN Red List species including *Justicia galapagana* Lindau and the tree fern *Cyathea weatherbyana* (C.V. Morton) (Jäger et al. 2007, 2009), as well as *Scalesia pedunculata* Hook. f. in the Scalesia zone (Shimizu 1997). A study on quinine's impacts on the microclimate showed that it reduced photosynthetic active radiation (PAR) by 87% and increased precipitation under the tree canopy by 42%, since its broad leaves intercept the heavy fog ("garua") in the highlands (Jäger et al. 2009). Quinine does not seem to resorb phosphorus from senesced leaves prior to shedding these (as common in most, if not all, tree species that shed their leaves to conserve nutrients; Killingbeck 1996), which resulted in phosphorus concentrations in the senesced leaves that were double those in mature green leaves (Jäger et al. 2013). This unusual behavior might be prompted by an increased phosphorus uptake of the quinine roots due to their association with arbuscular mycorrhizal fungi (Jäger et al. 2013). This, along with a high specific leaf area and a faster decomposition rate, suggests that *Cinchona* enhances phosphorus cycling in the soil (Jäger et al. 2013). This pattern was confirmed in a 2-year study, indicating an increase in the soil phosphorus concentration over time (unpubl. data). Whether or not increased phosphorus levels in the soil will have a negative impact on the native Galapagos flora is currently unknown. Native species are generally adapted to phosphorus-poor soils and could suffer from enhanced phosphorus levels, as shown in other ecosystems (Wassen et al. 2005). It is likely that increased phosphorus concentrations in the soils will facilitate the establishment of introduced species, which often originate from nutrient-rich soils.

Animals such as Galapagos petrel *Pterodroma phaeopygia* Salvin are also affected by the invasion of quinine, since quinine changes the habitat structure of petrel colonies, this way contributing to their habitat loss (Wiedenfeld and Jiménez Uzcátegui 2008). In addition, a study by Gibbs et al. (2003) showed that populations of Galapagos rail *Laterallus spilonotus* Gould were reduced in abundance by 31% from 2000 to 2007, which was related to an increasing quinine cover in this area (Shriver et al. 2011).

Lastly, there might also be some positive effects of the quinine trees, as they add a lichen- and liverwort-covered substrate to the system, that might provide a new habitat to otherwise locally rare epiphytic fern and orchid species (Jäger et al. 2007).

Management

Quinine has long been recognized as a potential risk to the native Galapagos flora, and for the last 35 years staff from Galapagos National Park Directorate and the Charles Darwin Foundation have worked on identifying the best method to eliminate this species (Buddenhagen et al. 2004). Some of the manual methods that have been attempted include felling and uprooting trees, but the fact that trees re-sprout from cut stumps makes these methods very inefficient (Macdonald et al. 1988; Buddenhagen et al. 2004). Several methods of herbicide application have also been tested, including basal bark, cut stump, girdle and squirt, branch filling, tree injections, and foliar spraying (Buddenhagen et al. 2004). The only method that has provided satisfying results (killing 73–100% of trees) was a hack and squirt technique where a mixture of the herbicides picloram and metsulfuron-methyl was applied to connecting machete cuts around the circumference of tree trunks (Buddenhagen et al. 2004). This method, followed by hand-pulling of smaller shoots and saplings, is now successfully applied by the GNPD in an area of approximately 310 ha between Cerro Crocker, Media Luna, Los Picachos, and Puntudo (GNPD 2009).

Experimental manual control of quinine was carried out by the GNPD in January 2005 in the fern-sedge vegetation between "Media Luna" and "El Puntudo" in an area of approximately 33 ha. Control measures consisted of uprooting large quinine trees by cutting the stems and digging up the underground stems and rootstocks with picks and machetes. Saplings and seedlings were pulled out by hand (Jäger and Kowarik 2010). These control measures were successful in significantly reducing quinine cover, but they also caused a substantial decline in native plant cover and diversity. The native plant community subsequently recovered quickly though, and plant cover reached before control levels within 2 years (Jäger and Kowarik 2010). However, the manual control actions caused severe disturbances to the surrounding vegetation and soil, probably facilitating the establishment of other introduced species, since their numbers continuously increased over the study period. The cover of introduced species was at peak levels 1 year after control, suggesting that introduced species not only established in the controlled area but that they also spread. This was especially the case with blackberry (*Rubus niveus* Thunb.), which was recorded at the end but not at the beginning of the study (Jäger and Kowarik 2010). Further monitoring would be necessary to determine whether those introduced species, which were newly recorded toward the end of the study, are only "passengers" of community change after an anthropogenic disturbance (MacDougall and Turkington 2005) or if they might establish and become invasive in the future. In addition, to guarantee a lasting success of quinine control, continuous hand-pulling of emerging seedlings over a long period would be necessary (Jäger and Kowarik 2010).

The estimated costs for the chemical control of quinine are between US$ 14 and 2225 per ha^{-1}, depending on stem density (Buddenhagen and Yánez 2005). Assuming a total invaded area of 11,000 ha, treating all existing plants at least once would require approximately 276,500 man-hours (equivalent to 150 men working for a year), which would added up to US$ 1.65 million, in 2005 (Buddenhagen and Yánez 2005). Treated areas would still have to be revisited subsequently for 1–5 years to pull out germinating seedlings, adding extra costs to this estimation.

Ironically, while no expenses or efforts are spared to rid Santa Cruz of the invasive quinine, this species (*Cinchona pubescens*) is now considered rare in its native range on mainland Ecuador (Günter et al. 2004). This species thus joins other plant species that are invasive but endangered in their native range, such as *Pinus radiata*, which is invasive, e.g., in South Africa, New Zealand, and Chile but is endangered in its native California (Lavery and Mead 1998).

What Makes Quinine Such a Successful Invader?

The main characteristic responsible for quinine's rapid spread on Santa Cruz is its abundant seed production. The youngest observed seed-producing trees are 2 years old, with a height of 1.8 m and a diameter at breast height (DBH) of 1.5 cm (unpubl. data). As in their native range (Garmendia Salvador 2005), quinine trees in Galapagos flower and produce fruits during almost all months of the year (Rentería 2002). Development from the opening of the flower to the production of mature fruits takes approximately 19 weeks (Rentería 2002), and each capsule contains from 60 to 70 seeds (J. L. Rentería, pers. comm. 2013), with a thousand-seed weight of 0.26 g (unpubl. data).

In addition, quinine seeds can germinate in dense understory vegetation or under a dense quinine canopy (Palacios 1993). Trees re-sprout from fallen and cut stems to produce vertical shoots (Macdonald et al. 1988) and grow especially well in areas that are disturbed, such as after fires (Kastdalen 1982; Jäger and Kowarik 2010). Quinine withstands extreme climatic conditions, like standing water accumulated through heavy rainfall during El Niño (pers. obs. 1998) and prolonged dry periods (Itow 2003). Furthermore, it flourishes in Galapagos despite the fact that the soils are nutrient-poor, especially in nitrogen and phosphorus (Jäger et al. 2013). One possible reason might be that quinine benefits from an increased nutrient uptake due to its association with arbuscular mycorrhizal fungi (AMF), which are observed in much greater densities than in native plant species (Schmidt and Scow 1986; Jäger et al. 2013). A study of root samples collected from adult quinine trees in Galapagos showed that roots were highly colonized with AMF (20–100%) (Serrano Tamay 2013).

Conclusions

A study has shown that the percentage of quinine cover just before control measures were applied is correlated with blackberry cover 5 years after control (unpubl. data). In other words, the more quinine cover there was before control actions were carried out, the more blackberry cover there is now. Thus, initial findings of quinine control facilitating the establishment of blackberry by Jäger and Kowarik (2010) have been confirmed. It is not recommended, therefore, to expand the current area where quinine is being controlled but rather to ensure that re-sprouting stems and germinated seedlings are constantly being pulled out by hand to avoid a reinvasion of areas devoid of the invader, which is the method currently applied by the GNPD. In addition, this follow-up control must also include hand-pulling of germinated blackberry plants. If this cannot be guaranteed, quinine populations should be left untouched. Although quinine has an adverse impact on native plant communities, its presence is preferred to that of blackberry, which has a devastating effect on the native vegetation (Rentería et al. 2012). In addition, over the last 10 years, quinine trees have shown symptoms of natural debilitation, which cause the trees to lose all but a few leaves

Fig. 5.2 Debilitated quinine (*Cinchona pubescens*) trees close to "Los Picachos" on Santa Cruz Island. Note that trees are not dead yet since they have a few green leaves that seem to persist for a long time. It is not clear yet what causes this debilitation/die-off

and severely compromise their vigor (Fig. 5.2). It is currently unknown what causes this debilitation and die-off, but it is likely a pathogen. Pathogens have been shown to accumulate in invasive plant populations over time, and this may result from multiple ecological processes, including high plant densities (Flory and Clay 2013). This can cause a decline in invader density and facilitate the recovery of native species but may also negatively influence co-occurring native species, further exacerbating the effects of the invader (Flory and Clay 2013). To test whether this is the case on Santa Cruz, fungus samples have been taken from affected quinine trees for analysis and will continue to be taken in the future. In addition, the current distribution of quinine is being mapped using the latest satellite imagery.

The quinine invasion on Santa Cruz Island exemplifies many of the complicated nuances characteristic of plant invasions on oceanic islands. Initially spreading rapidly and displacing native vegetation, it became a target of intense control measures incorporating various strategies that had been developed over the years. Although very effective in reducing quinine cover, these measures also facilitated the establishment and spread of another invader, blackberry, presenting an even more severe threat to the native vegetation. Finally, natural processes have begun to limit the extent of established quinine populations, all of which must be taken into account for current and future management decisions.

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Chapter 6

Allelopathic Impacts of the Invasive Tree *Cedrela odorata L.* (Meliaceae, Sapindales = Magnoliidae) in the Galapagos Flora

Gonzalo Rivas-Torres and María Gloria Rivas

Introduction

Non-native plant species are considered one of the main threats to native organisms, human welfare, and native ecosystems worldwide (Hejda et al. 2009). Some of the most serious negative impacts of non-native plant species are their potential to outcompete native plants and the capacity to spread quickly and colonize recipient areas, becoming invasive (sensu Richardson et al. 2000) in the introduced range (Mascaro 2011). To reduce the ecological and economic impacts of harmful introduced species, we need to understand the processes behind biological invasions. Hence, one of the main objectives of invasion ecology-IE, which appeared as a response to the significant increase of biological invasions around the globe, is to provide analytical frameworks that help understand the mechanisms enabling and

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enhancing non-native species to become invasive once they are introduced into recipient communities (Table 6.1).

One of the most known and widely tested mechanisms promoting non-native plant colonization is allelopathy or the potential that certain plant species have to produce chemical compounds that inhibit germination or growth of other species (Callaway and Aschehoug 2000). In the context of biological invasions, it is hypothesized that allelopathy allows non-native plants presenting this trait to chemically exclude coexisting neighbor native species in order to colonize new areas and to become invasive as a result (Bais et al. 2003). Allelopathic mechanisms inhibiting the establishment of native plants have been described to occur in different plant habitats, ranging from herbs and shrubs (i.e., *Brassica nigra*, Turk and Tawaha 2003) to trees (such as *Acacia pennatula,* Peguero et al. 2012). Furthermore, evidence suggests that the use of chemical weapons for plant invasions has effects not only on species but also at community level. For example, relevant investigations have shown that the use of chemical weapons may not only favor the plant responsible for the chemical production but also provide advantages to other coexisting non-native plants. These non-native neighbors could be, for example, positively affected by the absence of resident species excluded by the chemical substances (Callaway and Ridenour 2004). Allelopathic impacts can be highly significant at the population level as well, as has been recognized to explain monoculture formations of the invasive plants that present this particular trait (Hierro and Callaway 2003).

Despite of the wide range of plant habitats and ecological levels where allelopathy has been recorded to occur, there are comparatively very few studies detailing the presence of this explanatory mechanism in one of the most invaded biomes of the globe, oceanic islands. Due mainly to historical and biogeographic characteristics, such as high frequencies of non-native species introductions mediated by humans and low native species numbers, islands record a significantly higher number of non-native species compared to other biomes, making them particularly vulnerable to plant invasions (Ewel et al. 2013).

In the Galapagos Islands, for example, invasive species are nowadays one of the main problems for native biota, and some of the unique forests of the inhabited islands of this archipelago are presently dominated by invasive plants (Jaeger et al. 2007; Rivas-Torres et al. 2017). An example of a highly invasive tree, which tends to dominate the canopy of infested areas is *Cedrela odorata* L. (Meliaceae, Sapindales = Magnoliidae; hereafter also called *Cedrela*). Due to relatively fast population growth observed in the last decades in the Galapagos, the effects of *Cedrela* over native and invasive flora are under rigorous study by parallel experimental investigations (Rivas-Torres et al. 2017). One particularly interesting condition observed as a result of such studies is the fact that this tree species sheds leaves in higher proportion than native trees dominating other areas (Rivas-Torres et al. 2017). The leaves and roots of *Cedrela*—which along with the entire tree present a very pungent odor that characterizes the species—are not only exceedingly adding biomass in the site (Rivas-Torres et al. 2017) but are also in direct contact (along with potential compounds) with other native and non-native seeds and seedlings present in the immediate areas.

Table 6.1 Summary of general mechanisms and hypotheses described in literature as potential explanatory processes regarding plant invasions

Mechanism	Described and/or cited by	Examples of being reported in indexed literature as tested for the Galapagos before this chapter
1. The lack of attacks from natural enemies that are absent in the new and potentially far invasive range (a.k.a. enemy release hypothesis; ERH)	Elton (1958); Keane and Crawley (2002); Callaway et al. (2004); Maron et al. (2014)	No
2. Higher establishment probabilities of taxonomically distinct (phylogenetically separated) alien species due to trait differences with native species, which may allow niche differentiation (a.k.a. Darwin's naturalization hypothesis)	Darwin (1859); Rejmánek (1996a); Daehler (2001); Duncan and Williams (2002)	No
3. Lack of herbivores' pressure evolving in lower use of resources to protect against enemies in the invasive range (when compared to native ranges), which may provide a higher competitive ability in the new site (aka evolution of increased competitive ability; EICA)	Blossey and Notzold (1995); Blossey and Kamil (1996); Callaway and Ridenour (2004)	No
4. Higher probability of non-native species to fill niches unoccupied by native plants/species, also reducing competition for resources. The probability of filling empty niches is higher on islands because of underrepresented biotas recording low functional diversity (aka the vacant-niche hypothesis)	Rejmánek (1996b); Fine (2002); Symstad (2000)	No
5. Increased phenotypic plasticity in traits that allow higher establishment and spread rates in areas presenting new and altered characteristics. This can also be related to the higher capacity of non-natives to tolerate and cope with low resource availability	Tilman (1982); Richardson and Pyšek, (2006); Davidson et al. (2011); Funk (2013)	Yes Renteria 2011
6. Phenological differentiation of non-native species, which allows them to germinate or present flowers and fruits earlier—or in higher amounts—than natives to escape resource competition	Wainwright et al. (2012); Wolkovich et al. (2013)	Yes Heleno et al. (2013); Carrión-Tacuri et al. (2014); Campbell et al. (2015) This study
7. Higher resource availability in the recipient-invaded area than in the native range and the capacity invasive species may have to capture these resources more efficiently than native and non-native counterparts	Denslow (2003); van Kleunen et al. (2010); Funk (2013)	No

(continued)

Table 6.1 (continued)

Mechanism	Described and/or cited by	Examples of being reported in indexed literature as tested for the Galapagos before this chapter
8. Capacity of non-native species to transform abiotic and biotic conditions in the recipient sites that favor (own) and other alien plants, which may be more efficient to take advantage of such changes (aka direct and indirect facilitation)	Flory and Bauer (2014)	Yes Jaeger et al. (2009); Rivas-Torres et al. 2017
9. The appearance of novel biotic interactions that can arise after arrival of non-natives to recipient sites, like higher seed dispersal rates of invasive plants by vertebrates at the recipient sites	Mitchell et al. (2006)	Yes Buddenhagen and Jewell (2006); Guerrero and Tye (2009); Carrión-Tacuri et al. (2014); Blake et al. (2015)
10. The use of allelochemicals that reduce competitive capacity of native species in favor of non-native ones (aka allelopathy or novel weapons when tested between native and introduced ranges)	Callaway and Aschehoug (2000); Hierro and Callaway (2003)	Yes This study

In spite of the fact that this tree now covers previously native-dominated systems and it virtually mono-dominates forest stands in the Galapagos (Rivas-Torres et al. 2016; Rivas-Torres et al. 2017), no studies have directly tested if *Cedrela* presents allelopathic characteristics that could explain this highly successful invasion. Specifically in the present contribution, the results of an experimental study are presented, including native and invasive species found in sites mono-dominated by *Cedrela* in order to test if this species presents allelopathic substances, and the effect these chemicals might have over species with different origins. For instance, we were explicitly interested in testing if the potential allelopathic compounds that might be present in *Cedrela* help exclude one of the main endemic and highly threatened competitors of this tree, *Scalesia pedunculata* Hook. f. (Asteraceae, Asterales = Magnoliidae; hereafter also called *Scalesia*).

Methods

The Galapagos and the invasive plants issue. The Galapagos Islands is an archipelago formed by a group of islands of volcanic origin, located around 1000 km west of the Pacific coast of Ecuador (Fig. 6.1). The directorate of the Galapagos National Park (GNP) controls and monitors plants introduced into the protected

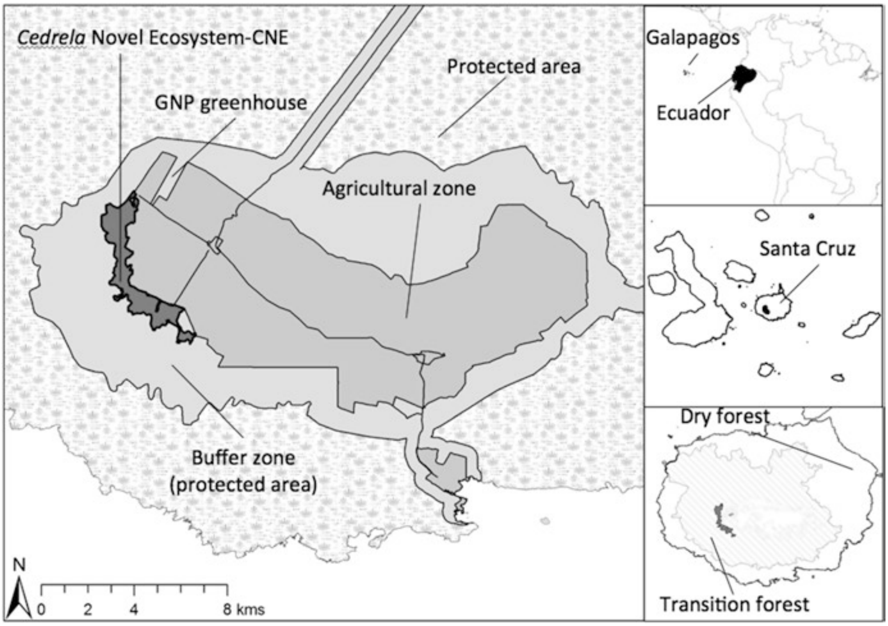

Fig. 6.1 Map showing in the upper insert (right): the location of Galapagos in front of the South American continent; and below: the location of Santa Cruz Island within the archipelago. The map also shows the land use distribution where Buffer and Protected zones are under preservation, while the Agricultural zone is under constant human pressures. *Cedrela dominated* forest (a.k.a. "Cedrela Novel Ecosystem" or Cedrela Forest, Trueman et al. 2014) is located in the south-western portion of Santa Cruz, and the GNP greenhouse is located just a few kilometers from this invaded site. For a more complete map, please visit http://institutodegeografia.org/vega-2/

area, which consists of approximately 97% of the archipelago. Human settlements are located in the remaining 3% of the land, which is also intended for agriculture and livestock (Fig. 6.1). Native organisms living in the Galapagos, as occurs in other oceanic islands, are being affected by the intentional or accidental introduction of non-native species. Updated studies on this issue report that approximately 880 plant species have been introduced to the archipelago, which is almost twice the number of natives (550, Gardener et al. 2010). In 2011, around 15% of the introduced non-native species were categorized as invasive for the archipelago (Atkinson et al. 2011). Given the number of detrimental impacts they cause to the native biota in the Galapagos, a considerable number of programs have been created to eradicate or at least contain these invasive species, presenting mixed results (Zavaleta et al. 2001; Gardener et al. 2010; Buddenhagen and Tye 2015). Nevertheless, the archipelago still has islands free of introduced species and ecosystems that exhibit adequate conservation conditions (Gardener and Grenier 2011).

Among disturbed sites, inhabited areas in the archipelago that have been historically degraded due to anthropogenic activities contain the majority of the recorded non-native and invasive plant species, which mostly occupy the wet highlands (from

~250 masl above; Mauchamp and Atkinson 2010). The highlands of Santa Cruz (the island with the largest human population in the Galapagos) have been particularly impacted by invasive species and land clearing, due to the benign climatic conditions for agroforestry practices that are recorded at higher elevations. This has resulted in the radical transformation of around 86% of the original land cover of the Santa Cruz highlands (Guézou et al. 2010; Mauchamp and Atkinson 2010; Watson et al. 2010). In spite of the high number of non-native plants and the negative impacts they cause, particularly in the Galapagos' inhabited islands, there are very few ecological studies on these organisms that provide baseline information, which could be useful for making adequate decisions and reducing the uncertainty in the managerial projects dedicated to control and eradication of invasive plants (Table 6.1).

The case of Cedrela odorata*—cedar tree—in the Galapagos. Cedrela*, also known as cedar, is a shade-tolerant tree that was introduced to Santa Cruz in the late 1940s for its timber value (Lundh 2006). Today, this tree is recorded in the four inhabited islands of the Galapagos: Santa Cruz, San Cristobal, Isabela, and Floreana. The largest population of *Cedrela* is recorded currently in Santa Cruz, where it virtually dominates an area of ~1000 hectares that extend to the southwestern portion of this island, within the "buffer zone" on the border of GNP and the agricultural land (Rivas-Torres et al. 2016; Fig. 6.1). It is supposed that the site was previously composed by species from the lowlands and highlands, among which the endemic tree *Scalesia* was dominating the native canopy (Itow 1995). *Scalesia* is one of the few endemic trees reported for the island and has been growing without much competition for many centuries until some decades ago, when the number of non-native and invasive trees proliferated in the highlands of Santa Cruz. Nowadays, *Scalesia* population for this island is reduced to only 1% of its original extent, and its local extirpation has been attributed to invasive species such as *Cedrela*, and land clearing (Mauchamp and Atkinson 2010). *Cedrela* is one of the invasive species *Scalesia* has to compete with, and this invasive tree has been extremely successful in colonizing areas previously occupied by the endemic *Scalesia* (Renteria and Buddenhagen 2006), yet the mechanisms explaining such replacement are still not clear.

In the Galapagos, *Cedrela* can grow up to 30 m tall and produce on average 40–50 wind-dispersed winged seeds per fruit (Citrón 1990). When this non-native tree fruits during the wet season (December to March), it generally sheds its leaves before the process begins, although some individuals lose their leaves in other seasons too (G. Rivas *pers. obs.*).

Testing the allelopathic effect of Cedrela in the Galapagos. To test the allelopathic effect of *Cedrela* over other native and invasive plants, eight species of both origins (native and non-native invasive, including *Scalesia* and *Cedrela*, respectively) were used in an experimental study performed on Santa Cruz Island. Four native species, namely, *Scalesia* (*S. pedunculata* Hook. f.; code name *S. pen*), *Psychotria rufipes* Hook. f. (*P. ruf*), *Psidium galapageium* Hook. f. (*P. gal*), and *Zanthoxylum fagara* (L.) Sarg. (*Z. fag*), were used as the indigenous taxa. Of these species, the first three are described as endemic and the fourth is recorded as native for the Galapagos (Guézou et al. 2014). In addition to *Cedrela*, three invasive plants were also included in the experiment: *Cestrum auriculatum* L'Hér. (code name *C. aur*), *Psidium guajava* L. (*P. gua*), and *Rubus niveus* Thunb. (*R. niv*). Code names are used in figures and tables. All these invasive species are naturally recorded in areas were *Cedrela* virtually mono-dominates the canopy (Rivas-Torres et al. 2017) and are known to cause pervasive effects over other native plants in the Galapagos (Renteria and Buddenhagen 2006).

Because it is expected that—if present—the allelopathic effects of an invasive plant might be impacting early plant stages preventing recruitment and colonization by other species (Orr et al. 2005), we tested how seeds and seedlings of other coexisting native and non-native invasive plants might be affected by *Cedrela* chemical compounds. We specifically used loose leafs and roots of this invasive tree to obtain extracts—smashing these structures in rainwater to obtain potential chemical compounds—as this is close to the actual process occurring in nature where these structures are in direct contact with either seeds or seedlings of other species. Using this method to test the effects of allelopathic chemicals over other plant species has been discussed as being a realistic approach when compared to other techniques performed under more controlled conditions, such as in laboratories (Orr et al. 2005).

Seeds from the eight different species were collected between July and December of 2012 and saved in refrigeration to guarantee the seeds were not killed after preservation. For the experiments presented here, we used seeds that showed no attacks by seed predators. Seedlings of the eight species used in this experiment were either germinated from collected seeds or obtained in the surrounding ecosystems of Santa Cruz from July 2012 to February 2013 and transported immediately to the GNP greenhouse (located in the highlands of Santa Cruz; Fig. 6.1). Seeds were maintained in a refrigerator at this same facility. For seedlings collected in the surrounding forests, we looked for individuals that germinated within the same period that the individuals germinated in the greenhouse. This means, we ensured that all seedlings of the species used here were of the same age. Because all individuals used in this experiment were younger than 2 years old, we could categorize them as seedlings. Additionally, within each species we used seedlings with similar initial height for the experiments (average size for all species = 10.16 cm; SD ± 5.53 cm). For example, *Scalesia* seedlings presented, on average, similar initial heights of individuals used to test root (15.2 cm; SD ± 5.48) and leaf (12.6 cm; SD ± 4.43) *Cedrela* extracts (methods described below) when compared to control individuals (13.7 cm; SD ± 3.81). In the greenhouse, seedlings were planted in a generic soil generally used for plant nursing and kept under the same climatic conditions. We used the pest-free and enclosed GNP greenhouse and the generic soil provided at this facility because we wanted to reduce herbivores and soil biota attacks by native enemies during the experiment. All plants were acclimated for a maximum of 2 months before starting the experiments.

To prepare leaf and root extracts that were used to water the experimental seeds and seedlings, we proceeded to collect mature leaves from branches belonging to adult individuals of *Cedrela* recorded in nearby *Cedrela*-dominated forests. Also in these forests, roots from adult *Cedrela* individuals were excavated and cut into small pieces of around 20 × 20 cm. As with the leaves, roots were collected freshly for every new extract application. Collected *Cedrela* leaves and roots were transported to the greenhouse where the fresh material was infused into rainwater recently collected at this facility. Specifically, leaves were broken into smaller pieces to occupy one-third of a 50 L plastic container. The rest of the container was filled with rainwater and left to rest for at least 3 h. The same procedure, with similar quantities, was applied for the collected *Cedrela* root material to prepare experimental infusions.

Experimental design: germination. A total of 24 plastic germination trays divided into 18 slots were filled with generic germination soil used at the greenhouse. In each of these slots, between 5 and 25 seeds of the eight different plants were sowed (Annex 1 online). Differences in seed numbers were due to the seeds' size and number of seeds per adult, that varies naturally among the target species. A total of 24 trays (3 per species) were randomly assigned to one of the three treatments: leaf extract and root extract and control (rainwater).

To test the potential effect of *Cedrela* root and leaf chemicals over germination, leaf extract was applied to eight trays (one per species; four native, four invasive) containing the seeds that were sowed before. This same scheme was applied to the eight trays assigned to be watered with the root infusion treatment. The remaining eight trays were assigned for control, meaning that they were only irrigated with rainwater. We applied the same amount of liquid measured in the trays or containers (for seedlings, see below) for each treatment to all the experimental seeds. Treatments and control were applied on a weekly basis from 15 May to 12 August 2013. The experiment ended when all the species germinated and before the emergent seedlings were already providing shade to the non-germinated seeds.

Experimental design: seedlings growth. To test the potential effect of *Cedrela* leaves and root chemicals on seedling growth, a total of 120 seedlings per species—except for *P. rufipes* which had only 105 individuals due to lack of material—were located in individual plastic containers in the same greenhouse but in separated benches. These seedlings were obtained from previously germinated or collected seedlings that were already acclimated in the greenhouse and not from the parallel germination trial. A total of 40 seedlings, or one-third of individuals per species, were randomly assigned to receive the two *Cedrela* extracts. Seedlings were planted in individual plastic containers to avoid competition with other plant individuals, which might have happened if we had used one shared tray. Each container was also far enough from the next one to avoid sun competition between seedlings. Infusions applied to seedlings were prepared exactly as described for the germination trials and applied evenly. Treatments for seedlings were applied on the same days as with the germination trials. Even though all seedlings (and seeds in the germination experiment) were under the same light and climatic conditions, seedlings (and seed trays) were moved within the greenhouse every 2 weeks to ensure that the results were not biased due to differences in any characteristic in the designated area inside the GNP facility. This area was covered with transparent plastic to prevent precipitation from altering watering regimes.

Data collection. Plastic trays containing the seeds of the target species were surveyed every week for a total of 12 weeks to record positive germination and number of germinated seeds per treatment. Meanwhile, germination time was calculated as the number of weeks until germination was observed for each seed of the target species.

In a parallel fashion, to evaluate if composition of soil in the germination trays was affected by *Cedrela* root and leaf extracts, a sample of soil was collected for only three species, namely, the same *Cedrela*, *C. auriculatum*, and *S. pedunculata*. These three species were chosen from the eight target species for soil analyses because: (1) the Galapagos does not have a certified soil laboratory; therefore, transport of samples to the continent would have become very expensive and unfeasible for all the individuals used in the experiment; (2) one of the objectives of this study was to contrast *Cedrela*—and other invasive species—against the endemic *S. pedunculata* tree competitor; and (3) in a preliminary analysis these three species showed apparent significant variation among treatments. Soil analyses were performed to the entire germination tray per treatment for these three species, because laboratory methodology required at least half a kilo (500 g) of a mixed sample to run soil tests. This might have affected replication for posterior analyses.

On the other hand, to evaluate the potential allelopathic effect of *Cedrela* over seedling development of the eight target plants, growth (measured in cm from the base to the apex of each individual) was recorded for all seedlings at each treatment for 24 weeks (from 15 May to 14 November 2013). We measured initial and final height of each seedling at the beginning and end of the experiment, respectively, and these measurements were used in the posterior analyses. We ran the experiments only for 6 months because we wanted to prevent seedlings from having stressful conditions that might impact growth due to the lack of nutrients in each container.

Additionally, after the seedling experiment ended, a subset of 30 individuals per species (10 per treatment) was randomly cropped from the original group of seedlings. Each individual (including all parts of plants from roots to leaves) of the subset was immediately dried and later weighted at the Charles Darwin Foundation herbarium facilities (Santa Cruz, Galapagos) in order to calculate if treatments affect biomass (referred as "dry weight" in our analyses) of the experimental plants.

Data analyses. To analyze treatment effects over germination percentage, time and seedlings dry weight, nonparametric multiple comparison Wilcoxon tests were performed (using JMP® software v.10.0, SAS Institute, US, 2012) for each of these parameters. This nonparametric test was chosen after testing for data parameters such as distribution and homogeneity of variance. On the other hand (due to differences in data parameters), we performed an analysis of covariance-ANCOVA (JMP® software v.10.0, SAS Institute, US, 2012) to evaluate if the two *Cedrela* treatments had any effect over seedling growth of the target species. We included initial height as the covariate in this analysis to test if this condition affected the observed results for each species. Additionally, we ran post hoc Tukey HSD tests only for species that presented a negative effect of the treatments. Because we were interested in the influence of *Cedrela* extracts (treatments) within each species, we didn't analyze growth differences among the eight target species.

In relation to soil samples, Wilcoxon tests were also used to analyze relevant physical (i.e., pH, organic matter, ion exchange, conductivity) and chemical (Ca, N, P, K, Mg, S) variables in each sample for the three different treatments.

Results: Allelopathic Effects of *Cedrela* over Germination and Growth

Germination. Overall, results showed that there is no negative effect of leaf and root infusions over germination percentage (*Z*: 0.28, $p = 0.86$, S.E. ±5.0) and seed germination time (*Z*: 1.41, *p*:0.49, S.E. ±0.18) for all the species.

Growth. Among all native plants, *Scalesia* was the only endemic species showing negative effects over seedling growth by both the leaf (SQ mean = 37.94, $p \leq 0.05$) and root (SQ mean = 32.76, $p \leq 0.05$) treatments extracted from *Cedrela*. Contrary to treatments, initial growth of *Scalesia* seedlings did not explain lower final heights of young individuals of this species (Table 6.2). *P. rufipes* was the other native species presenting significantly lower growth for the treated individuals, when compared with controls . But, initial height appears to explain better (than the applied treatments) the lower final seedling heights recorded for this endemic plant (Table 6.2). Additionally, the invasive plants *R. niveus* (SQ mean = 30.18, $p \leq 0.05$) and *C. auriculatum* (SQ mean = 31.93, $p \leq 0.05$) exhibited significantly less growth than controls when irrigated by root extracts of *Cedrela*.

Dry weight. *Scalesia* and one other resident species, namely, *P. rufipes*, showed significantly lower dry weight with the leaf and root treatments (Fig. 6.2). For instance, the dry weight of *Scalesia* was significantly lower for the individuals treated with root infusion ($Z = -1.96$, $p = 0.04$), while *P. rufipes'* dry weight was significantly affected by both the root ($Z = -2$, $p = 0.004$) and the leaf extracts from *Cedrela* ($Z = -2.32$, $p = 0.02$; Fig. 6.2). As for growth analysis, *R. niveus* presented lower biomass in seedlings irrigated with root ($Z = -3.06$, $p = 0.002$) and leaf ($Z = -2.15$, $p = 0.03$) *Cedrela* extracts when compared to controls.

Physical and chemical soil analyses. Soil samples analyzed for each treatment, obtained from the germination trays where *Cedrela*, *C. auriculatum*, and *S. pedunculata* were seeded, did not show significant differences among the relevant physical and chemical characteristics measured by this investigation (Annex 3 online).

Discussion

This study provides evidence of the allelopathic effect *Cedrela* has over at least the seedling stage of two endemic species in the Galapagos Islands. Specifically, we present here data that suggest that the leaf and root extracts of the invasive *Cedrela* tree may negatively affect growth of some native plant species, which are important

Table 6.2 Effect of *Cedrela* treatments over seedlings growth of 4 native and 4 invasive plants in Galapagos

		Native							Invasive				
	Parameter	Df	Sum Sq	F ratio	*p*	SQ mean		Parameter	Df	Sum Sq	F ratio	*p*	SQ mean
Scalesia	In. Height	1	62.115	1.54	0.217		*Cedrela*	In. height	1	72.33	2.64	0.10	
	Treatment	2	1792.9	22.23	*<0.0001*			Treatment	2	327.40	5.98	*0.0001*	
	Control					42.27		Control					23.50
	Root					***37.94***		Root					22.61
	Leaf					***32.76***		Leaf					***27.12***
Z. fag	In. Height	1	4.67	0.15	0.6979		*R. niv*	In. height	1	2.45	0.0095	0.9225	
	Treatment	2	92.35	1.49	0.2286			Treatment	2	13295.5	25.71	*<0.0001*	
								Control					49.94
								Root					***30.18***
								Leaf					54.54
P. gal	In. Height	1	116.02	3.4758	0.0648		*C. aur*	In. height	1	6.0044	0.05	0.8144	
	Treatment	2	54.18	0.8116	0.4466			Treatment	2	2215.3	10.20	*<0.0001*	
								Control					38.92
								Root					***31.93***
								Leaf					42.31
P. ruf	In. height	1	8603.99	1359.8	*<0.0001*		*P. gua*	In. height	1	1228.7	22.72	*<0.0001*	
	Treatment	2	83.38	6.58	*0.0021*			Treatment	2	233.15	2.15	0.1205	

ANCOVA results showing significant effects (*p*) on either initial height (In. height) or treatment are presented in italics. Significant Tukey tests (SQ mean) for each treatment compared with controls are presented in bold. Tukey tests are presented for species that recorded significant effects of *Cedrela* treatments only

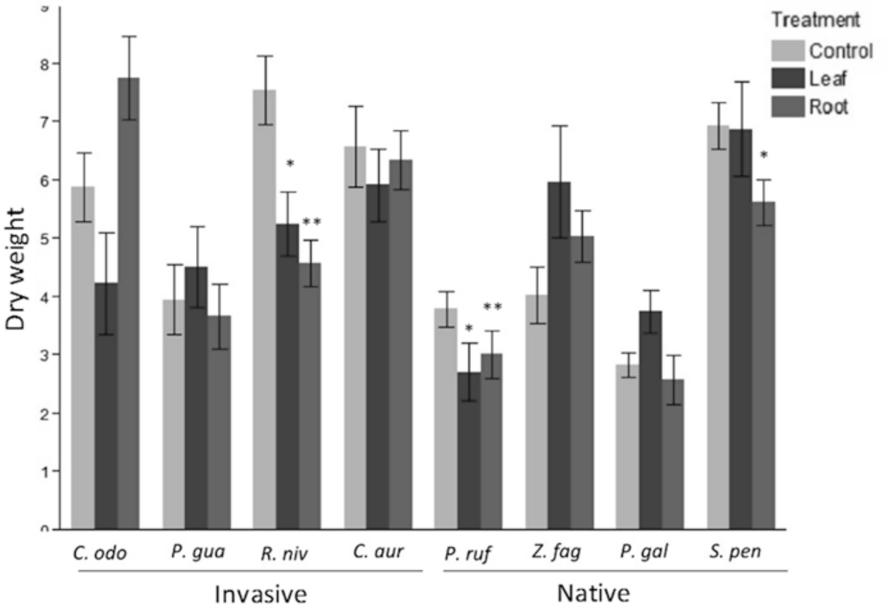

Fig. 6.2 Average dry weight (in grams) per treatment for the eight target species in this study. Note that the natives *Psychotria rufipes* (*P. ruf*) and *Scalesia pedunculata* (*S. pen*) were the only resident species to be affected by the *Cedrela* extractions. Only species with asterisks were significantly different than controls. Statistical significance: one asterisk = marginally significant or $p < 0.05$; two asterisks = significant or $p < 0.01$; and three asterisks = highly significant or $p < 0.001$

components of the resident ecosystems in this archipelago. The negative impact that *Cedrela* extracts have over *Scalesia* seedlings is particularly relevant, as this endemic tree used to dominate the highlands of Santa Cruz and is now in direct competition with this invasive plant. *Cedrela* is rapidly colonizing sites previously occupied by *Scalesia*, apparently using chemical traits as one of the mechanisms to outcompete this endemic tree at early plant stages. The negative effect of *Cedrela* extracts over *Scalesia* seedlings observed in this experiment might be caused by certain compounds found in plants presenting allelopathic traits that apparently affect root development and thus reduce initial growth of the resident plants (Butcko and Jensen 2002; Lawan et al. 2011).

Under natural conditions, *Scalesia* presents a die-off mechanism where adults of the same or similar cohorts die in synchrony, contributing to native regeneration and, mainly, allowing thousands of young *Scalesia* seedlings to have the light necessary for growing rapidly and recolonizing these recently opened areas (Itow 1995). Usually, *Scalesia* seedlings grow rapidly—in these gaps and elsewhere—in order to use the newly available light resource efficiently; but as is shown here experimentally, and for the first time in the Galapagos, *Cedrela* chemical compounds are reducing such fast initial growth. The competitive advantage at seedling stages—mediated by negative allelopathic effects—may in part explain *Cedrela*'s invasive success as has been proposed elsewhere (Hierro and Callaway 2003; Sheng et al. 2007; Imatomi et al. 2015). But, for our case study, allelopathy was only tested for early stages under controlled conditions and might not be the only invasive mechanism *Cedrela* is using to colonize and promote novel mono-dominated forests. So, other potential processes (such as those described in Table 6.1) explaining *Cedrela* invasion and the monocultures it forms in Santa Cruz (and *Scalesia* extirpation from original sites) should be tested at the actual invaded locations, at other plant ontogenies and using different experimental approaches. These new experiments should consider evaluating how some explanatory ecosystem-scale factors, their interactions (e.g., water and light availability) and species-specific variables (e.g., plant growth) affected by invasive plants, may impact native plant assemblages and explain invasive plants' colonization.

This study, for instance, also evidenced that in addition to allelopathy operating over *Scalesia* seedlings, *Cedrela*, *P. guajava*, and *C. auriculatum* invasive plants germinated in larger amounts than this endemic tree. Additionally, germination times of these three species were relatively faster than most of the native and endemic species used in this experiment. *Scalesia* presented a rapid germination, similar to the mentioned invasive species, but had a very low germination rate compared with these non-native plants (Annex 2 online). This means that invasive species such as *Cedrela*, apart from using allelopathic chemicals to diminish *Scalesia* initial growth, may have also had higher—and earlier—access to important resources for seedling recruitment, such as light and water (i.e., "phenological differentiation" Table 6.1, mechanism 6).

When the effects of allelopathy over germination are analyzed, research on other species of the Meliaceae family—including *Cedrela* genus—has suggested that several species under this same taxonomic affiliation can produce a chemical compound (also known as cedrelanolide or a photogedunin) that may be responsible for inhibiting germination of other coexisting plants (Céspedes et al. 2001). The lack of negative impacts by *Cedrela* extracts over native germination makes us speculate that this mechanism might present effects depending on the target species and might also need to be evaluated for different parameters related to seed germination traits not analyzed here. Likewise, due to logistic restrictions, we did not analyze soil chemistry for specific compounds particularly found in field sites where *Cedrela* is now dominating. Hence, our lack of findings on this regard does not mean all native and endemic seeds in the Galapagos are free from allelopathic attacks and that soils, mainly those dominated by *Cedrela*, are free of such compounds.

On the other hand, when the effects of *Cedrela* compounds are analyzed for invasive species, we found that some of these chemicals may prevent noxious plants, such as *R. niveus*, from growing rapidly as they do in conditions lacking these substances. The allelopathic negative effect of *Cedrela* over invasive weeds, such as *R. niveus*, could be tested as a potential chemical control to diminish the fast colonization pace that this very noxious invasive shrub presents in the Galapagos.

In conclusion, this study demonstrates for the first time the negative allelopathic effects an invasive species, namely, *Cedrela*, is apparently causing on seedlings stages of at least two endemic species in the Galapagos, one of them, *Scalesia,* a highly threatened tree of significant importance for the maintenance of key ecological processes operating in these unique forests. Despite the capacity to dominate the sites this tree invades, *Cedrela*'s ability to outcompete native species by using chemical weapons has not been tested before in the Galapagos or, as far as we know, in any other island recording this economically valuable tree. But, now that we know that allelopathic effects can in part explain the lack of previously dominating endemic species in invaded areas in the Galapagos, we also need to understand other explanatory mechanisms acting to aid this and other non-native species to help colonize the archipelago. Our investigation also supports the fact that invasive species—such as *Cedrela*—are presenting seed traits that could allow them to outcompete native plants, as well as faster and higher germination rates. This pattern is described as one of the widely accepted mechanisms used to explain plant invasions defined by IE and is one of the processes that has been previously recorded on these islands (Table 6.1).

Overall, the results of this chapter are expected to help GNP managers to understand that the mechanisms used by non-native plants to become invaders are diverse. The incorporation of knowledge obtained from studies like the one presented here will not only provide a better understanding of the processes involved in harmful plant invasions in the Galapagos but will also aid to prioritize and choose the best actions to control and eradicate noxious species in this unique biome.

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Chapter 7
The Hitchhiker Wave: Non-native Small Terrestrial Vertebrates in the Galapagos

Diego F. Cisneros-Heredia

Introduction

Movement of propagules of a species from its current range to a new area—i.e. extra-range dispersal—is a natural process that has been fundamental to the development of biogeographic patterns throughout Earth's history (Wilson et al. 2009). Individuals moving to new areas usually confront a different set of biotic and abiotic variables, and most dispersed individuals do not survive. However, if they are capable of surviving and adapting to the new conditions, they may establish self-sufficient populations, colonise the new areas, and even spread into nearby locations (Mack et al. 2000). In doing so, they will produce ecological transformations in the new areas, which may lead to changes in other species' populations and communities, speciation and the formation of new ecosystems (Wilson et al. 2009).

Human extra-range dispersals since the Pleistocene have produced important distribution changes across species of all taxonomic groups. Along our prehistory and history, we have aided other species' extra-range dispersals either by deliberate translocations or by ecological facilitation due to habitat changes or modification of ecological relationships (Boivin et al. 2016). Over the last few centuries, human globalisation has led to the integration of most areas of the planet. Due to transportation advancements, humans and our shipments travel faster and further than ever before. Unintentionally or deliberately, thousands of species of flora, fauna and microorganisms have been translocated to places they would never have reached on their own and beyond the biogeographic barriers that typically prevented their spread in such a timeframe (Ricciardi 2007). However, most translocated species are already adapted to anthropogenic niches (especially the ones that are unintentionally introduced), and since their new arrival areas are usually also under

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anthropogenic impact, their adaptation process and possibility of survival are increased.

Non-native species contribute to Earth's biota homogenisation, but ongoing scientific debates on the processes, effects, importance and management of non-native species are intense (Davis 2003; Brown and Sax 2004, 2005; Cassey et al. 2005; Dukes and Mooney 2004; Davis et al. 2011; Chew and Carroll 2011; Ricciardi et al. 2013; Simberloff et al. 2013; Chew 2015; Kuebbing and Simberloff 2015; Pereyra 2016; Sol 2016). Non-native species may modify biological communities and ecosystem functions by becoming, for example, predators, competitors, preys, seed dispersers, parasites, disease vectors or ecosystem engineers (Daszak et al. 2000; Crooks 2002; O'Dowd et al. 2003; Doody et al. 2009; Capps and Flecker 2013; Ricciardi et al. 2013; Simberloff et al. 2013). Non-native species may have economic, social, cultural and health impacts on human populations (Vitousek et al. 1997; Pejchar and Mooney 2009). Non-native species that are successful and spread in their new areas become invasive and have been described as major anthropogenic drivers of current changes in biodiversity (Vitousek et al. 1997; Chapin et al. 2000; Mace et al. 2005; Clavero and García-Berthou 2005; Bellard et al. 2016; Doherty et al. 2016). Yet, evidence, scientific perspectives and practical implications for this assertion are still under examination (Gurevitch and Padilla 2004a, b; Ricciardi 2004; Didham et al. 2005; MacDougall and Turkington 2005; Young and Larson 2011; Russell and Blackburn 2017).

In spatially restricted ecosystems, such as island and wetlands, the effects of invasive non-native species on native biodiversity can be severe and lead to extensive transformation of native ecosystems and even the extinction of endemic species (Davis 2003; O'Dowd et al. 2003; Blackburn et al. 2004; Mace et al. 2005; Simberloff et al. 2013). The Galapagos Islands are a region of particular interest and relevance to the issue of species introduction and invasiveness. In the most recent comprehensive review on the Galapagos non-native vertebrates, Phillips et al. (2012a) pointed out that vertebrate introductions in Galapagos are shifting away from intentionally introduced species, such as domestic mammals, towards hitchhiking species, such as reptiles (Phillips et al. 2012a). Furthermore, the authors remarked that snakes and lizards—i.e. squamate reptiles—could pose the greatest threat the Galapagos' biodiversity in the future. Like an unfortunate prediction, while Phillips and collaborators were writing their article, the common house gecko *Hemidactylus frenatus*, a lizard profiled as highly invasive, had already arrived in Galapagos (Torres-Carvajal and Tapia 2011). Despite the fact that only 5 years have passed since Phillips et al. (2012a), the panorama of non-native terrestrial vertebrates in Galapagos has changed in important ways, in particular for non-mammals. Although Phillips et al. (2012a) and previous studies have dealt with the impacts and management of non-native species in Galapagos, most studies have focused on domestic species gone feral. Very little information is available on wild non-native species that have been unintentionally introduced. Thus, in this publication, I analyse the current status of all non-native amphibians, reptiles and birds that have been reported in the Galapagos Islands, provide new evidence about their relationship with native and non-native species, comment on their invasiveness and impact potential, and propose that it is important to rethink about how we understand, manage and prevent introductions of non-native species. The new wave of introduced species in Galapagos is formed by small hitchhiker species that are easily overlooked, may travel in high numbers and are highly linked to human-made environments.

The Galapagos Islands: An Overview

The volcanic marine islands of the Galapagos archipelago are separated from the nearest mainland—the coast of Ecuador—by ca. 930 km. Nineteen main islands (>1 km^2) and over 100 islets and rocks constitute the archipelago, totalling ca. 7850 km^2 of land, spread out over ca. 430 km (straight line between the outermost islands: Darwin and Española). The largest islands are Isabela (4588 km^2), Santa Cruz (986 km^2), Fernandina (642 km^2), Santiago (585 km^2), San Cristobal (558 km^2), Floreana (173 km^2) and Marchena (130 km^2) (Snell et al. 1996).

The Galapagos are among the few Pacific islands that were not settled by aboriginal humans (Anderson et al. 2016). They were discovered by Fray Tomas de Berlanga in 1535. While pirate and whaling ships frequently visited the archipelago since the sixteenth century, the first settlement was only established in 1832. Nowadays, Santa Cruz, San Cristobal, Isabela and Floreana have human populations established on the lowlands and highlands. The main cities in each island are Puerto Ayora (Santa Cruz), Puerto Baquerizo Moreno (San Cristobal), Puerto Villamil (Isabela) and Puerto Velasco Ibarra (Floreana). There are airports in Baltra, San Cristobal and Isabela islands, with connections to Guayaquil and Tababela (Quito) airports in mainland Ecuador. All populated islands have maritime ports for passengers and freight, with connections to several international and national ports, including the Ecuadorian ports of Guayaquil, Manta and Salinas (Cruz Martínez et al. 2007).

The climate of Galapagos largely depends on the oceanic currents and winds, resulting in vegetation distribution being determined by orogenic rainfall (Jackson 1993; Wiggins and Porter 1971). On the lowlands, all islands and islets are arid and warm. A narrow belt along coastal areas, called littoral zone,[1] is dominated by salt-tolerant shrubs and small trees. Xerophytic low scrub, arborescent and shrubby cacti, thorn woodland and deciduous forest are the main vegetation on lowlands, i.e. dry zone.[1] A transition zone,[1] with taller trees, denser canopy and more mesic conditions than the dry zone, appears as elevation rises (plants here are a mix from lower and higher zones). Moist conditions exist in the higher islands above 300–600 m, where three vegetation zones have been recognised: humid zone,[1] with incremented humidity and denser vegetation dominated by evergreen species, in particular, the endemic giant daisy tree genus *Scalesia*; very humid zone, with very dense vegetation dominated by the endemic Galapagos miconia *Miconia robinsoniana*; and

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[1] The ecological classification of vegetation is based on the proposal by Wiggins and Porter (1971).

pampa zone, treeless and dominated by sedges and ferns above regional treeline. An upper dry zone[1]—a climatic inversion zone with drier conditions—exists on the Cerro Azul and Wolf volcanoes, which reach beyond 1000 m above the main cloud layer. This zone is covered by scrub vegetation dominated by *Opuntia* cacti or *Scalesia*. On the leeward side of islands, the littoral, dry and transition zones rise higher and the moister zones may be absent (Wiggins and Porter 1971). The moist zones (humid, very humid and pampa) are only present on the largest islands (i.e. Santa Cruz, San Cristobal, Pinta, Santiago, Floreana, Isabela, Fernandina). In addition to these natural vegetation zones, humans have modified large sections of the dry, transition, humid and very humid zones on the four inhabited islands, transforming them into agro-urban areas, where a large amount of non-native plant species dominate (Wiggins and Porter 1971; Guézou et al. 2010). The pampa zone has been enlarged by human activities and grazing by non-native mammals.

World famous for their biodiversity and role in the formulation of the theory of evolution by natural selection, the Galapagos Islands are home to a vast array of endemic species of flora and fauna. Galapagos biodiversity evolved in isolation from its continental counterparts. Moreover, its uniqueness is not just due to differences between insular and continental species but also due to a large level of inter-insular endemism. There are many taxa restricted to just one or few islands (Parent and Crespi 2006; Sequeira et al. 2008; Benavides et al. 2009; Hoeck et al. 2010; Poulakakis et al. 2012; Torres-Carvajal et al. 2014; MacLeod et al. 2015; Carmi et al. 2016). The Galapagos archipelago is home to no less than 211 terrestrial vertebrates, including 6 endemic species of snakes of the genus *Pseudalsophis*, 24 endemic lizards (genus *Phyllodactylus*, *Amblyrhynchus*, *Conolophus*, *Microlophus*), 12 endemic giant tortoises of the genus *Chelonoidis*, 160 species of birds (of which 46 taxa are endemic) and 9 species of mammals (of which 7 taxa are endemic).

Human population in Galapagos has increased significantly over the last decades, and transportation links carrying local travellers, tourists and supplies have facilitated the arrival of non-native species (Mauchamp 1997; Causton et al. 2006; Tye 2006; González et al. 2008; Phillips et al. 2012a). Invasive non-native species have been identified as the principal threat to biodiversity in the Galapagos terrestrial ecosystems (Causton et al. 2006). For example, feral populations of dogs *Canis familiaris*, cats *Felis catus*, pigs *Sus scrofa* and black rats *Rattus rattus* have been reported to predate upon several endemic species, causing serious declines on the populations of Galapagos tortoises *Chelonoidis* spp., Galapagos land iguanas *Conolophus subcristatus*, marine iguanas *Amblyrhynchus cristatus* and Galapagos penguins *Spheniscus mendiculus*, among others (Konecny 1987; Phillips et al. 2012a). Grazing and trampling by feral goat *Capra hircus* have depleted the populations of several native and endemic plants, including the critically endangered Santiago Scalesia *Scalesia atractyloides* and Floreana flax *Linum cratericola*, which are now at the verge of extinction (Schofield 1989; Aldaz et al. 1997; Simbana and Tye 2009). Feral cattle *Bos taurus* aided the spread of the invasive non-native common guava *Psidium guajava* and other non-native plants by habitat engineering and seed dispersion (Phillips et al. 2012a). The parasitic fly *Philornis downsi* is causing significant excess mortality in the endemic and threatened Darwin's medium tree finch *Camarhynchus pauper* (O'Connor et al. 2010). Cottony cushion scale *Icerya purchasi* has become a pest causing population declines in the endemic thin-leafed Darwin shrub *Darwiniothamnus tenuifolius* (Calderón-Álvarez et al. 2012). Ambitious programmes to control and eradicate non-native species have been established in the archipelago (e.g. Barnett 1986; Campbell et al. 2004; Cruz et al. 2005; Carrión et al. 2007).

However, ecological interactions are of a complex nature, and non-native species may in some cases contribute to maintaining ecosystem functions in ecosystems experiencing environmental change (Buckley and Catford 2016). For example, black rats have become a seed disperser of the endemic *Miconia robinsoniana* in some agricultural areas of San Cristobal Island (Riofrío-Lazo and Páez-Rosas 2015). Black rats have also become the most important prey for the Galapagos hawk *Buteo galapagoensis* since the eradication of feral goats on Santiago Island (Jaramillo et al. 2016). Non-native species may also help in managing invasive species, acting as biological controls. The vedalia beetle *Rodolia cardinalis* was deliberately introduced in Galapagos to control the spread of *Icerya purchasi* (Calderón-Álvarez et al. 2012).

Definitions

The dichotomy of native/non-native species is a predominant concept in ecology, biogeography and conservation biology (Mace et al. 2005; Lomolino et al. 2010; Simberloff et al. 2013). It has been widely adopted in analysis of the conservation of Ecuadorian biodiversity and particularly in relation to Galapagos (Josse 2001; Causton et al. 2006). However, a dichotomous approach is evidently simplistic and even artificial in any complex and dynamic system. The cornerstone term "native species" is part of an ongoing scientific and philosophical debate about its conceptual and operational definitions as well as its relevance and applicability in ecological, conservation, management, sociocultural and economic scopes (Chew and Hamilton 2011; Clavero 2014; Van Der Wal et al. 2015). A dichotomous approach is hard to make fully operational, especially in regions where it is difficult to assess the status of an archaeophyte/archaeozoan versus a native taxon or where the distinction between native and non-native taxa is not absolute (Preston et al. 2004). However, these issues are greatly controlled in Galapagos due to the isolation of the archipelago and the specific date of human arrival. Although recognising issues associated with a dichotomous approach, I—for the sake of operational straightforwardness and due to the particular nature of Galapagos geography and history—use the following working definitions (modified from Pyšek et al. 2009):

Native taxa: Those that are originated in a given area or that arrived from an area in which they are native by their own means. Their successful arrival is due to their adaptation for dispersal and survival in the physiological and ecological conditions across the dispersal routes, which are not acting as strict dispersal barriers. Complete or partial synonyms include terms like indigenous or autochthonous taxa.

Non-native taxa: Those that have arrived from an area in which they are non-native or that arrived from their native range by extrinsic dispersal mechanisms (i.e. outside of their own natural dispersal potential). These extrinsic mechanisms provide specific conditions that allow these taxa to disperse across environments that otherwise would be severe natural barriers in the same timeframe. Complete or partial synonyms include terms like alien, exotic, non-indigenous or allochthonous taxa.

To establish working definitions on the basis of ecological and biogeographic criteria only, human intervention was intentionally left out. While human extra-range dispersals do facilitate the arrival of non-native taxa via direct or indirect extrinsic mechanisms, natural colonisations and human-mediated introductions and establishments of non-native species are nevertheless similar ecological processes (Buckley and Catford 2016; Hoffmann and Courchamp 2016). Several authors have argued that geographical origin of species should not be used as the only criteria guiding management/control decisions (Buckley and Catford 2016; Hoffmann and Courchamp 2016). However, a distinction between natural colonisations and human-mediated introductions is at least partially necessary when management and control issues are involved. For example, if a species reached a new area by its own means and without the intervention extrinsic dispersal mechanisms (including without human intervention), it would most probably be able to do so repeatedly as it is evidenced that the species has the capability to disperse across natural barriers that separated its geographical origin and new areas. Any proposed regulations to control its population would be insufficient and inefficient as new arrivals would most certainly keep occurring. On the other hand, a non-native species that solely depends on human-mediated extrinsic dispersal mechanisms could be controlled by regulating the aforesaid mechanisms.

Therefore, all species that were established in the archipelago before 1535 are considered native. Species that have apparently reached the archipelago through their own means after 1535 and that have established populations because of their own successful oceanic dispersal capacities (and probably with several dispersal events) are also considered native. Due to the long distance between Galapagos and mainland (or even other islands), all non-native species in the Galapagos Islands seem to have arrived due to intentional or unintentional mediation of humans.

Non-native Amphibians, Reptiles and Birds

I report herein a total of 25 non-native amphibians, reptiles and bird species in the Galapagos archipelago. The changes, when compared to Jiménez-Uzcátegui et al. (2007) and Phillips et al. (2012a), are in part explainable by a better understanding of some species' status (see species accounts below for details) but also due to the arrival of new non-native vertebrates (I include two species not reported in previous reviews). These non-native species are equivalent to 12% of all Galapagos native amphibians, reptiles and birds. Santa Cruz and San Cristobal are the islands with the largest amount of reported non-native amphibians, reptiles and bird species (18 spp. each). Twelve species are reported in Isabela Island, three in Baltra Island and two species in Marchena and Floreana. The islands of Genovesa, Pinta, Pinzon, and Santiago each has only one reported species (Table 7.1).

In any environment, there is an introduction-invasion continuum between the arrival of a non-native species, its establishment and its shift into invasive (Mack et al. 2000; Blackburn et al. 2011; Pereyra 2016). Non-native species introduced to Galapagos are heterogeneous in terms of their establishment, spread, dominance and impact. Only a fraction of the non-native species that arrives becomes established, and an even smaller portion is able to have spreading populations—i.e. become invasive. For example, out of 754 non-native vascular plants recorded by Guézou et al. (2010) in the inhabited areas of Galapagos, 35% have established populations; and Tye et al. (2002) classified 5% of those species as invasive. As for insects, 463 non-native species were reported by Causton et al. (2006) in Galapagos, with at least 73% of them having established populations and 13% species classified as invasive.

In order to provide a straightforward evaluation of the degree of establishment of non-native amphibians, reptiles and birds in Galapagos—independent of their conservation effects—I adopt the categories proposed by McGeoch and Latombe (2016), with some modifications (Table 7.2). This typology is based on three main aspects: degree of expansion, population size and time since arrival (McGeoch and Latombe 2016). Since all non-native species were introduced to Galapagos within the last two centuries, all could be classified herein as recent. However, I differentiate between historic (the last centuries) and recent (the last decades) translocations. Also, I take into account the fact that introductions have not been synchronised and that some non-native populations are the result of more than one introduction event.

Information about establishment, spread, dominance and impacts of non-native amphibians, reptiles and birds in Galapagos biodiversity is still incomplete. Eleven non-native amphibians, reptiles and bird species reported in Galapagos did not become established (Table 7.1). Six species are established but only as domestic stock. *Columba livia*, a non-native species that was introduced as domestic and became established, was eradicated. *Gallus gallus* is the only species currently present in Galapagos with domestic and feral (or semi-feral) populations. Some feral chickens may have self-sufficient populations, but evidence is unclear. *Hemidactylus frenatus* is newly established, and self-sufficient populations are apparently small, but this species has a high potential not just to become more broadly established but to spread successfully and therefore become invasive. Monitoring is urgently needed to understand the distribution, populations and impacts of *H. frenatus*. There is evidence that one non-native amphibian, three non-native reptiles and one non-native bird are established in Galapagos, having self-sufficient populations (Table 7.1). However, they do not have the same level of establishment. *Gonatodes caudiscutatus* is classified as constrained, by having large populations but only on a very limited geographic range, apparently unable to establish new populations despite being in Galapagos for ca. 200 years. *Scinax quinquefasciatus* is considered as incipient, by having established large populations but only on a limited geographic range, yet

Table 7.1 List of non-native amphibians, reptiles and birds species in the Galapagos Islands

Suprataxa	Family	Genus	Species	Establishment status	Biogeographic origin	Arrival method	Islands
Amphibia	Bufonidae	*Rhinella*	*marina*	Non-established	Non-native	Human mediated	San Cristobal
Amphibia	Hylidae	*Scinax*	*quinquefasciatus*	Incipient	Non-native	Human mediated	Santa Cruz, San Cristobal, Isabela
Amphibia	Craugastoridae	*Pristimantis*	*unistrigatus*	Non-established	Non-native	Human mediated	Santa Cruz, Isabela
Squamata	Colubridae	*Lampropeltis*	*micropholis*	Non-established	Non-native	Human mediated	Santa Cruz
Squamata	Sphaerodactylidae	*Gonatodes*	*caudiscutatus*	Incipient	Non-native	Human mediated	Santa Cruz, San Cristobal, Baltra
Squamata	Gekkonidae	*Lepidodactylus*	*lugubris*	Successful	Non-native	Human mediated	Santa Cruz, San Cristobal, Isabela, Marchena
Squamata	Gekkonidae	*Hemidactylus*	*frenatus*	Newly established	Non-native	Human mediated	Isabela
Squamata	Phyllodactylidae	*Phyllodactylus*	*reissii*	Dispersed	Non-native	Human mediated	Santa Cruz, San Cristobal, Isabela
Squamata	Iguanidae	*Iguana*	*iguana*	Non-established	Non-native	Human mediated	Santa Cruz, San Cristobal, Isabela
Squamata	Scincidae	*Plestiodon*	*inexpectatus*	Non-established	Non-native	Human mediated	San Cristobal
Testudines	Bataguridae	*Trachemys*	*scripta*	Non-established	Non-native	Human mediated	Santa Cruz, San Cristobal
Testudines	Pelomedusidae	*Podocnemis*	*unifilis*	Non-established	Non-native	Human mediated	San Cristobal
Testudines	Testudinidae	*Chelonoidis*	*denticulata*	Non-established	Non-native	Human mediated	Santa Cruz

Suprataxa	Family	Genus	Species	Establishment status	Biogeographic origin	Arrival method	Islands
Aves	Anatidae	*Anas/Cairina*	*platyrhynchos/ moschata*	Domestic	Non-native	Human mediated	Santa Cruz, San Cristobal, Isabela
Aves	Anatidae	*Anser*	*anser*	Domestic	Non-native	Human mediated	Santa Cruz, San Cristobal
Aves	Columbidae	*Columba*	*livia*	Eradicated	Non-native	Human mediated	Santa Cruz, San Cristobal, Isabela
Aves	Cuculidae	*Crotophaga*	*ani*	Successful	Non-native	Human mediated	Santa Cruz, San Cristobal, Isabela, Floreana, Genovesa, Marchena, Pinta, Pinzon, Santiago
Aves	Phasianidae	*Coturnix*	*japonica*	Domestic	Non-native	Human mediated	Santa Cruz
Aves	Phasianidae	*Gallus*	*gallus*	Domestic | dispersed	Non-native	Human mediated	Santa Cruz, San Cristobal, Isabela, Baltra
Aves	Phasianidae	*Meleagris*	*gallopavo*	Domestic	Non-native	Human mediated	Santa Cruz, San Cristobal, Isabela
Aves	Phasianidae	*Numida*	*meleagris*	Domestic	Non-native	Human mediated	Santa Cruz, San Cristobal, Isabela
Aves	Phasianidae	*Pavo*	*muticus*	Domestic	Non-native	Human mediated	San Cristobal
Aves	Icteridae	*Quiscalus*	*mexicanus*	Non-established	Non-native	Human mediated	Santa Cruz
Aves	Thraupidae	*Sicalis*	*flaveola*	Non-established	Non-native	Human mediated	Baltra
Aves	Psittacidae	*Aratinga*	*erythrogenys*	Non-established	Non-native	Human mediated	San Cristobal

Table 7.2 Topology to evaluate the degree of establishment of non-native amphibians, reptiles and birds in Galapagos, independent of their conservation effects. It is based on McGeoch and Latombe (2016), with some modifications

Category	Degree of expansion	Population size	Time since establishment
Non-established	Intercepted	None	None
Domestic	Human dependant	Human dependant	Recent/historic
Newly established	Narrow	Small	Recent
Incipient	Narrow	Large	Recent
Dispersed	Wide	Small	Recent
Successful	Wide	Large	Recent
Eradicated	Wide/narrow	None	Recent/historic
Non common	Narrow	Small	Historic
Constrained	Narrow	Large	Historic
Sparse	Wide	Small	Historic
Highly successful	Wide	Large	Historic

it was introduced recently (ca. 40 years). *Phyllodactylus reissii* is dispersing, with a large population in Santa Cruz established ca. 40 years ago and a probably newly established population in Isabela. Finally, *Lepidodactylus lugubris* and *Crotophaga ani* are classified as successful by having large populations established on many islands. Since *L. lugubris*, *P. reissii* and *C. ani* have self-sufficient and spreading populations, they are further classified as invasive species.

Non-native Amphibians in Galapagos

Amphibians have never been able to establish by their own means in Galapagos. The absence of native amphibians in Galapagos is not surprising, as most true oceanic islands are devoid of native amphibians (Zug 2013). Generally, amphibians are poor dispersers across oceanic barriers due to their high sensitivity to osmotic stress caused by salt water at all ontogenic levels (Balinski 1981; Duellman and Trueb 1986; Bernabò et al. 2013). However, a number of frog species have physiological adaptations to tolerate salinity (Balinksi 1981; Beebee 1985; Gomez-Mestre and Tejedo 2003), and oceans are not always strict barriers to the dispersal of amphibians (Hedges et al. 1992; Vences et al. 2003, 2004; Measey et al. 2007). The oceanic islands of Mayote, São Tomé and Principe have native frogs that seemingly reached the islands by rafting through ca. 400 km from Africa (Vences et al. 2003; Measey et al. 2007; Bell et al. 2015). The Seychelles Islands are extraordinary: despite the extreme distance of ca. 1000 km from Madagascar and ca. 1300 km from Africa, they have one endemic frog species (Maddock et al. 2014). Nevertheless, and contrary to the Galapagos Islands, all oceanic islands with native frogs generally have humid terrestrial ecosystems almost next to the coastlines, where frogs would have been able to establish. In contrast, frogs that might have rafted between mainland

America and Galapagos would have reached the arid littoral and dry zones, which are inhospitable to amphibians. Actually, evidence from palynological studies has revealed that the lower areas of the islands were even drier in the past glacial (Colinvaux 1972; Colinvaux and Schofield 1976).

Three non-native frogs[2] have reached the islands (Table 7.1):

- Jiménez-Uzcátegui et al. (2007) and Phillips et al. (2012a) reported a **Western cane toad** *Rhinella horribilis* at Galapagos (as *Bufo* sp. and *Chaunus marinus*, respectively[3]). Records at the Vertebrate Collection of the Charles Darwin Research Foundation (VCCDRS; CDF 2016) show that it was discovered in a house at Puerto Baquerizo Moreno, San Cristobal Island, on 5 February 1995. This species has a large native range from southern USA to the lowlands of western Ecuador and northwestern Peru (Frost 2016). It inhabits a large variety of ecosystems and is abundant in anthropogenic areas like pastures and gardens (Zug and Zug 1979). Although it can live in arid environments, it depends on water availability for reproduction (see Zug and Zug 1979 for information on its natural history). *Rhinella horribilis* is present in Manta, Guayaquil and Tababela (Quito), areas with cargo warehouses, maritime ports and airports with connections to Galapagos (pers. obs.). Apparently, only one population of *Rhinella horribilis* may have established completely outside of its native range (in Florida, King and Krakauer 1966; Easteal 1981).[4] No information is available on potential or evidenced impacts by non-native *R. horribilis*. For comparison, the eastern cane toad *Rhinella marina* has been extensively introduced worldwide (Easteal 1981; Lever 2003) and is one of the most studied introduced species, especially in Australia. The main evidenced ecological impact of *R. marina* is the declining of Australian native predators, due to its toxicity when ingested (Shine 2010).
- Snell (2000) reported an individual of **striped robber frog** *Pristimantis unistrigatus* beside a dishwasher in a house on 17 March 2000 at Puerto Ayora, Santa Cruz Island. Phillips et al. (2012a) reported another *P. unistrigatus* from Isabela Island without providing further details. There are no specimens of *Pristimantis* at the VCCDRS. Frogs of the genus *Pristimantis* are part of the superfamily Brachycephaloidea (Frost 2016). Brachycephaloidean frogs are terrestrial breeders, laying their eggs on land, with no need of water, and eggs hatching directly

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[2] The Global Invasive Species Database (GISD 2010) erroneously reported *Eleutherodactylus coqui* at Galapagos, citing Snell and Rea (1999) as the source, yet those authors reported *Scinax quinquefasciatus*.

[3] The correct updated name of the toad that arrived to the Galapagos is *Rhinella horribilis*, assuming its origin was western Ecuador. Until recently, *R. horribilis* was a synonym of *Rhinella marina*. However, Acevedo-Rincón et al. (2016) recognised them as different species. *Rhinella marina* is now restricted to the east of the Andes. Further taxonomic changes are expected, and populations from western Ecuador could receive yet another (new) name (Vallinoto et al. 2010).

[4] The non-native populations of *Rhinella* in Florida have multiple origins, with first individuals coming from Surinam and Colombia. Toads from Surinam were probably *Rhinella marina*, while those from Colombia could be *R. horribilis* if their origin was western Colombia or *R. marina* if they came from eastern Colombia.

Fig. 7.1 Juvenile of *Scinax quinquefasciatus* at Santa Cruz Island, Galapagos. Photo: Luke Smith

into froglets, bypassing the tadpole stage. These features could provide clear advantages to establishing self-sufficient populations in islands with limited freshwater availability. Frogs of the brachycephaloidean genus *Eleutherodactylus* have established spreading populations in Hawaiian and Caribbean islands, where they arrived as hitchhikers (Kraus et al. 1999; Kraus and Campbell 2002; Lever 2003; Olson et al. 2012). However, introduced populations of *Pristimantis* are undocumented (Lever 2003, Kraus 2009), probably because most *Pristimantis* show high levels of endemism and high physiological specialisation. Nevertheless, a few species, like *P. unistrigatus*, are more widespread and have adapted to human-created habitats, showing potential to establish non-native populations if conditions for establishment are adequate. *Pristimantis unistrigatus* is native to inter-Andean highland valleys from southern Colombia to central Ecuador, where it can live in mildly arid environments with seasonal rains and thrive in agricultural lands, gardens and other artificially watered areas (Lynch 1981). It is the most common frog in urban, suburban and rural green areas of the valley of Quito, including the surroundings of air cargo warehouses and the airport (pers. obs.).

- **Fowler's snouted tree frog** *Scinax quinquefasciatus*[5] (Fig. 7.1) is the only amphibian established in the Galapagos. Snell et al. (1999) and Snell and Rea (1999) published the first reports of *S. quinquefasciatus* from Galapagos based on records from Isabela[6] and Santa Cruz islands. Although subsequent authors

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[5] This name is currently applied to different populations of *Scinax* that include at least one undescribed cryptic species (R.W. McDiarmid in litt. 2003; S. Ron pers. comm. 2013).

[6] Snell and Rea (1999) confused specimens from Isabela with "leptodactylid frogs", a common error due to the snout form and general appearance of *Scinax* frogs.

have commented on *S. quinquefasciatus* in Galapagos (Lever 2003; Jiménez-Uzcátegui et al. 2007; Phillips et al. 2012a; Zug 2013), many details about their introduction history remain unpublished. The VCCDRS (CDF 2016) holds several specimens of *S. quinquefasciatus* that offer valuable information to better contextualise its timeframe in the archipelago. The first specimen of *S. quinquefasciatus* (VCCDRS 2247) was collected on May 1973 at an unknown locality in Santa Cruz Island. Four additional specimens were collected in 1991–1992 at the dry lowlands of Santa Cruz Island, in urban areas of the town of Puerto Ayora. Between 1998 and 2013, one to four specimens were obtained in or around Puerto Ayora every year, except for 2011, when ten specimens were collected. In 2001, the first *S. quinquefasciatus* (VCCDRS 1502) was collected at humid highlands in agricultural areas of Bellavista, Santa Cruz Island, with additional single tree frogs collected in 2003, 2008, 2011 and 2013. Seven tree frogs were collected in 2000 and one in 2001 in the dry lowlands of urban Puerto Baquerizo Moreno, San Cristobal Island. No further records have been reported since.[7] All six VCCDRS specimens of *S. quinquefasciatus* from Isabela Island were collected after its confirmed establishment at the lagoons near the town of Puerto Villamil on 1998. Since *S. quinquefasciatus* is insectivorous, predation of native invertebrate fauna has been identified as a potential impact on Galapagos biodiversity (Phillips et al. 2012a), but there are no studies regarding its diet or evidence about any real impact. *Scinax quinquefasciatus* is native to the Pacific lowlands and low montane areas from southwestern Colombia to central-western Ecuador (Frost 2016). In its native distribution, *S. quinquefasciatus* occurs on a variety of habitats, as it is able to breed in small ponds in agricultural areas, herbaceous marshes and stream pools in arid zones and wetlands with low salinity in river deltas (Duellman 1971; de la Riva et al. 1997; Cisneros-Heredia 2006a; Ortega-Andrade et al. 2010; pers. obs.). It is present in urban, suburban and green rural areas of Manta and Guayaquil, including the surroundings of air cargo warehouses and the airport (pers. obs.).

Non-native Reptiles in Galapagos

Nine species of non-native reptiles have been recorded in Galapagos. All established populations are geckos—members of the squamate reptilian infra-order Gekkota. Worldwide, several species of geckos have adapted to live in anthropic or perianthropic conditions, dwelling in human-made buildings and surroundings. This close relationship has resulted in geckos being able to effectively colonise geographically distant regions by human-facilitated dispersion (Lever 2003; Gamble et al. 2008; Kraus 2009). Anthropophilic geckos are some of the most capable

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[7] Phillips et al. (2012a) reported a “Tree frog 3 (*Hyla* sp.)” reported from San Cristobal in 1990. It is possible that it corresponds to early records of *Scinax quinquefasciatus*. Due to uncertainty with the identification and lack of voucher specimens, they are not included in these analyses.

overseas dispersalists among non-volant, terrestrial vertebrates, having in some cases the largest distributions among reptiles and even attaining larger densities than in their natural habitats (Gamble et al. 2008; Ineich 2010). Presently, geckos have been introduced as non-native species far more frequently than any other lizard group (Lever 2003, Kraus 2009). Out of 503 introduction events involving gekkotan species analysed by Kraus (2009), about 45% resulted in successful population establishments, showing that geckos are among the most successful reptiles in establishing populations. Not all gekkotan families are involved, and Gekkonidae, Phyllodactylidae and Sphaerodactylidae are responsible for all introduction and establishment events in the world (Lever 2003; Kraus 2009). Non-native species of the three families are present in Galapagos.

- **Dwarf gecko** *Gonatodes caudiscutatus*[8] is found in small numbers at the town of Puerto Baquerizo Moreno,[9] San Cristobal Island, where it is restricted to moist anthropic environments. It is abundant in the agro-urban highlands of San Cristobal, in El Progreso, where it has been able to establish also in natural areas (Garman 1892; Wood 1939; Mertens 1963; Wright 1983; Hoogmoed 1989; Lundh 1998; Olmedo and Cayot 1994; pers. obs.). During a survey in June 2009, I found three specimens of *G. caudiscutatus* in gardens near Playa Man and the interpretation centre and ten specimens at orchards in El Progreso. The rarity of *G. caudiscutatus* in the lowlands is probably due to climate restrictions and predation by domestic and native species[10] (Wright 1983; Hoogmoed 1989; Olmedo and Cayot 1994; pers. obs.). There are reports of *G. caudiscutatus* in at least two other islands of Galapagos. Jimenez-Uzcátegui et al. (2007) reported it from Baltra, without further details. The VCCDRS (CDF 2016) has four specimens of *G. caudiscutatus* collected at Puerto Ayora, Santa Cruz Island: on 5 November 2003, 29 January 2006 and 20 July 2006. It is probable that a small population is already established at Santa Cruz Island. Impacts by *G. caudiscutatus* on Galapagos biodiversity are unknown but have been suspected to be slight or even non-existent (Hoogmoed 1989; Olmedo and Cayot 1994; Phillips et al. 2012a). Competition or exclusion of endemic geckos is unlikely, due to body size, habitat and microhabitat differences.[11] Although *G. caudiscutatus* is insectivorous, it

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[8] Garman (1892) described *Gonatodes collaris*, based on two specimens collected by George Baur at Wreck Bay, next to the town of Puerto Baquerizo Moreno, San Cristobal Island. Vanzolini (1965) proposed that *G. collaris* and *G. caudiscutatus* were actually synonyms, which was confirmed by Wright (1983).

[9] Several expeditions did not find *Gonatodes* in San Cristobal Island during the late 1800s and early 1900s (Cope 1889; Heller 1903; Van Denburgh 1912; Slevin 1935). Van Denburgh (1912), Slevin (1935) and Barbour and Loveridge (1929) suggested that the specimens reported by Garman (1892) were probably collected at Guayaquil, in mainland Ecuador. However, it is probable that *G. caudiscutatus* was overlooked due to its restricted distribution and low abundance in Puerto Baquerizo Moreno and low activity during the dry season.

[10] I observed San Cristobal lava lizard *Microlophus bivittatus* predating on *G. caudiscutatus* on June 2005. See account of domestic chicken *Gallus gallus* for details on a predation event on *G. caudiscutatus*.

[11] All endemic Galapagos geckos which belong to the genus *Phyllodactylus* are diurnal and noctur-

probably eats mainly non-native and widespread invertebrates, but there are no studies about its diet. *Gonatodes caudiscutatus* is native to the lowlands from central to western Ecuador and extreme northwestern Peru (Sturaro and Avila-Pires 2013). It is present in urban, suburban and green rural areas of Guayaquil, including the surroundings of air cargo warehouses and the airport (pers. obs.).

- **Peters' leaf-toed gecko** *Phyllodactylus reissii* arrived at Santa Cruz Island in the mid-1970s (Wright 1983, Hoogmoed 1989, Olmedo and Cayot 1994). Hoogmoed (1989) published a detailed study on the population in Puerto Ayora, where it was well established in the urban area (Hoogmoed 1989; Olmedo and Cayot 1994). Olmedo and Cayot (1994) reported one individual of *P. reissii* in natural areas next to Puerto Ayora (adjacent to Las Ninfas neighbourhood). On July 1997, I observed three *P. reissii* at the same area in natural vegetation. *Phyllodactylus reissii* has reached the highlands of Santa Cruz Island, at Bellavista (Phillips et al. 2012a). Torres-Carvajal and Tapia (2011) reported the first record of *P. reissii* at Puerto Villamil, Isabela Island, but the presence of an established population remains to be confirmed. During a survey in June 2009, I did not find *P. reissii* in San Cristobal Island. *Phyllodactylus reissii* inhabits dry forests and scrubland and rural, suburban and urban areas from central-western Ecuador to northwestern Peru (Dixon and Huey 1970). In Galapagos, *P. reissii* remains mostly restricted to urban, suburban and rural areas. In areas of Puerto Ayora where *P. reissii* is dominant, it appears to have displaced the endemic *P. galapagensis*, and only rarely are both together (Hoogmoed 1989; Olmedo and Cayot 1994). No information about possible exclusion mechanisms or interactions has been published.[12] If *P. reissii* would expand to natural areas, it could impact endemic *Phyllodactylus* (Hoogmoed 1989; Olmedo and Cayot 1994; Phillips et al. 2012a).
- **Mourning gecko** *Lepidodactylus lugubris* is native to Southeast Asia and islands of western Oceania (Hoogmoed and Avila-Pires 2015 and citations therein). It is a parthenogenetic species, which benefits the establishment of new populations (Kraus 2009; Phillips et al. 2012a; Hoogmoed and Avila-Pires 2015). It has become established in Northeast Asia, the west coast of South America, Oceania and Pacific Ocean islands, including Galapagos (Lever 2003; Kraus 2009; Hoogmoed and Avila-Pires 2015). *Lepidodactylus lugubris* likely arrived at Galapagos during the early 1980s[13] (Hoogmoed 1989; Olmedo and Cayot 1994).

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nal and inhabit the arid lowlands. They are scansorial and arboreal, having dorsoventrally compressed digits with greatly expanded lamellae. *Gonatodes caudiscutatus* has a smaller body size than all endemic geckos, is diurnal and mainly inhabits the humid highlands. It is terrestrial and semi-arboreal, having more restricted climbing abilities than the endemic geckos due to its cylindrical digits without expanded lamellae.

[12] At least one study on interactions between non-native and endemic geckos in Galapagos has been conducted but remains unpublished (M. Altamirano's PhD dissertation, cited by Phillips et al. 2012a).

[13] Hoogmoed (1989) published the first mention of *Lepidodactylus lugubris* in Galapagos. However, he did not find the species and cited the unpublished records obtained by John Wright at Puerto Ayora, Santa Cruz Island, in 1983.

It remained rare during the first decade[14] but subsequently became well established and expanded. Nowadays, it has fairly large self-sustained populations but only on moist environments in coastal areas—i.e. artificially watered urban areas and mangroves—in the towns of Puerto Ayora, Puerto Baquerizo Moreno and Puerto Villamil (Olmedo and Cayot 1994; Sengoku 1998; Jiménez-Uzcátegui et al. 2007, 2015; Torres-Carvajal and Tapia 2011; Phillips et al. 2012a; pers. obs.). It has also established in the town of El Progreso, where it remains restricted to human buildings and has not been found in farms (M. Altamirano, in litt. 12 June 2009). Jiménez-Uzcátegui et al. (2015) reported *L. lugubris* from Marchena Island, without further details. The consequences from the introduction of *L. lugubris* in Neotropical areas, including Galapagos, are not clear (Hoogmoed and Avila-Pires 2015). No impacts on Galapagos' biodiversity have been reported (Olmedo and Cayot 1994; Phillips et al. 2012a, b). Competitive interactions between *L. lugubris* and Galapagos endemic geckos have apparently not affected endemic species (M. Altamirano 2002 cited in Phillips et al. 2012a). Although *L. lugubris* is insectivorous, it probably eats mainly non-native and widespread invertebrates. There are no studies yet about its diet.

- **Common house gecko** *Hemidactylus frenatus* is a nocturnal species native to Southeast Asia (Lever 2003). It has invaded several areas across the planet, including many islands in the Indian and Pacific oceans and several areas of Africa and America and currently has the widest worldwide non-native distribution of its genus (Lever 2003; Kraus 2009). Torres-Carvajal and Tapia (2011) reported the first record of *H. frenatus* in Galapagos, based on five individuals found at Puerto Villamil, Isabela Island, but an established population was not confirmed. On 24 October 2016, three *H. frenatus* were recorded at Puerto Villamil, thus suggesting that an established population is indeed present in Isabela Island (T. Schramer and Y. Kalki, in litt. 2016). It seems to have also established in Puerto Baquerizo Moreno, San Cristobal Island, where over ten individuals were recorded between September and November 2016 in human buildings (T. Schramer and Y. Kalki, in litt. 2016). Due to its recent arrival, no information is available for any type of interactions or effects of *H. frenatus* on the endemic *Phyllodactylus* geckos. However, its arrival has raised concerns due to reported impacts on native fauna in other areas where it has established (Torres-Carvajal and Tapia 2011; Torres-Carvajal 2015). *Hemidactylus frenatus* has outcompeted and excluded non-native *Lepidodactylus lugubris* from several Pacific islands by competitive exclusion (Petren and Case 1998; Kraus 2009). Preliminary evidence suggests that *H. frenatus* may be also excluding *L. lugubris* in San Cristobal (T. Schramer and Y. Kalki, in litt. 2016). At the Mascarene Islands, *H. frenatus* contributed to the decline and population extirpation of endemic geckos of the genus *Nactus* (Cole et al. 2005). Furthermore, it could carry novel parasites that might impact native reptile species (Hoskin 2011).

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[14] Marinus Hoogmoed did not find *Lepidoblepharis lugubris* during his intensive surveys of Puerto Ayora in 1988 (Hoogmoed 1989; Lundh 1998).

Fig. 7.2 Specimen of *Lampropeltis micropholis* collected at Santa Rosa, Santa Cruz Island, Galapagos

- On 22 February 2014, a local inhabitant ran over a **milk snake** *Lampropeltis micropholis*[15] (Fig. 7.2) in the area of Santa Rosa, highlands of Santa Cruz Island. Photographs of the snake were quickly disseminated through social networks, and Galapagos authorities were able to recover the specimen. Four days later, the specimen was delivered and deposited at the Laboratory of Terrestrial Zoology, Universidad San Francisco de Quito (USFQ), by officials of the Ministry of Environment of Ecuador (MAE) in order to confirm its identification and preserve it as a voucher specimen. Morphology and colouration data suggest that the specimen belongs to the population distributed in the Pacific lowlands of Ecuador. In mainland Ecuador, *L. micropholis* inhabits the Pacific lowlands and Andean highlands in a large variety of ecosystems, from arid to moist habitats (Cisneros-Heredia and Touzet 2007). *Lampropeltis micropholis* is present in the surroundings of Guayaquil[16] and Quito (Williams 1988; Pérez-Santos and Moreno 1991;

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[15] Until recently, *Lampropeltis micropholis* was a subspecies of *L. triangulum*. However, Ruane et al. (2014) raised it to species status. As currently understood, *L. micropholis* occurs from western Costa Rica to Ecuador. Further taxonomic changes are expected, and populations from the highlands of Ecuador could receive yet another (new) name (J. Valencia, in litt. 2012).

[16] *Lampropeltis micropholis* is rather frequent on the highlands, even in rural and suburban areas. However, there are few specimens from the lowlands (Cisneros-Heredia and Touzet 2007; pers. obs.). Williams (1988) reported it from Guayaquil, based on a specimen collected by Edward Whimper during the 1890s. Pérez-Santos and Moreno (1991) reported the species from the province of Guayas, without providing details. Although no further information about *L. micropholis* from Guayaquil has been published, I am aware of two additional records: one individual collected ca. 18 km from Guayaquil and delivered to Jean-Marc Touzet (Fundación Herpetológica "Gustavo Orcés" FHGO) in February 1990 (Touzet JM pers. comm.) and another photographed by Keyko

Cisneros-Heredia and Touzet 2007). This snake is terrestrial and active during day and night and eats a large variety of vertebrates and invertebrates (Williams 1988). There are no records of non-native populations of *L. micropholis* established outside of its range or studies of insular populations. For comparison, a study of the diet of insular populations of *Lampropeltis polizona* at Isabel Island, Mexico, showed that they fed on different species of terrestrial lizards and nestlings of ground-nesting marine birds, including blue-footed booby *Sula nebouxii*, but avoided arboreal geckos and tree-nesting birds. The California kingsnake *Lampropeltis californiae* became established in Gran Canaria Island, where its main evidenced ecological impact is predation of endemic lizards (Rodriguez and Drummond 2000; Pether and Mateo 2007; Cabrera-Pérez et al. 2012).

- Several individuals of **green iguana** *Iguana iguana* have reached the Galapagos Islands (Cruz Martínez et al. 2007; Jiménez-Uzcátegui et al. 2007; Phillips et al. 2012a). Five specimens are deposited at the VCCDRS (CDF 2016). The earliest *I. iguana* (VCCDRS 571) was collected on 15 February 1982 at an unknown locality in Santa Cruz Island. Two additional specimens were found at a private house in the town of Puerto Ayora, Santa Cruz Island, on 14 August 2000[17] (CDF 2016). One *I. iguana* (VCCDRS 2218) was found at an unknown locality in San Cristobal Island, on 19 April 2008, while another (VCCDRS 2153) was found in Isabela Island on 14 June 2010 (CDF 2016). Cruz Martínez et al. (2007) and Phillips et al. (2012a) mentioned an *I. iguana* found walking in the streets of Puerto Baquerizo Moreno, San Cristobal Island. Another was photographed on a dock at Puerto Ayora on 13 August 2015 (Christen 2015). *Iguana iguana* is native from Mexico to Paraguay and southern Brazil (Uetz and Hošek 2016). It is very common on the littoral and lowlands of western Ecuador (Ortega-Andrade et al. 2010), including the surroundings of cargo warehouses and the air and maritime ports of Guayaquil (Cruz Martínez et al. 2007; pers. obs.). *Iguana iguana* is able to disperse between islands by ocean rafting (Censky et al. 1998). However, I agree with Jiménez-Uzcátegui et al. (2007, 2015) and Phillips et al. (2012a) in classifying it as a non-native introduced species, as there is evidence of its hitchhiking behaviour (Cruz Martínez et al. 2007). In some islands where it has been introduced, *I. iguana* has displaced the native *I. delicatissima* by hybridisation (Lever 2003; Powell and Henderson 2005; Kraus 2009; Powell et al. 2011; Vuillaume et al. 2015). Since intergeneric hybridisation has been reported in iguanas (Rassmann et al. 1997; Jančúchová-Lásková et al. 2015), the establishment of *I. iguana* in Galapagos could pose a threat for the endemic iguanas of the genus *Amblyrhynchus* and *Conolophus*.
- One **yellow-footed tortoise** *Chelonoidis denticulata* in Santa Cruz Island, one **yellow-spotted river tortoise** *Podocnemis unifilis* in San Cristobal Island and a single **common slider turtle** *Trachemys scripta* in Santa Cruz and San Cristobal islands were intercepted (Jiménez-Uzcátegui et al. 2007, 2015; Phillips et al.

Cruz at Cerro Blanco, ca. 8 km from Guayaquil (Cruz 2015).

[17] However, Jiménez-Uzcátegui et al. (2007) reported that only one *Iguana iguana* was found in Santa Cruz in 2000, while the other was found in San Cristobal.

2012a). All individuals were apparently brought to Galapagos as pets, and these three species are commonly traded as pets in mainland Ecuador (Carr and Almendáriz 1989; Cisneros-Heredia 2006b; pers. obs.). *Chelonoidis denticulata* and *P. unifilis* are native to the Amazonian lowlands. They are illegally caught and occasionally offered in pet stores of Quito and Guayaquil (pers. obs.). *Trachemys scripta* is native to the western USA and Mexico, and it is the most common pet turtle and the most widely released reptile species in the world (Kraus 2009).

- A gravid **five-lined skink** *Plestiodon inexpectatus* was intercepted as a pet in Galapagos. Jiménez-Uzcátegui et al. (2007) and Phillips et al. (2012a) cited the island of interception as San Cristobal. However, VCCDRS data indicate that it was intercepted at the Baltra airport on 26 May 2005 (CDF 2016).

Non-native Birds in Galapagos

Twelve species of non-native birds have been recorded in the Galapagos Islands (Table 7.1):

- **Domestic ducks,**[18] **domestic turkey** *Meleagris gallopavo*, **domestic goose** *Anser anser*, **domestic quail** *Coturnix japonica*,[19] **domestic guinea fowl** *Numida meleagridis* and **green peafowl** *Pavo muticus* occur in the Galapagos only in agro-urban areas under human care (Gottdenker et al. 2005; Jiménez-Uzcátegui et al. 2007; Phillips et al. 2012a). None of them have established self-sustaining populations outside of farms. The 2014 Census of Agricultural Production (CGREG 2014) reported 926 ducks and 28 turkeys, all free-range, in Santa Cruz, San Cristobal and Isabela islands (Table 7.3). While the number of turkeys declined by one-third when compared with the census of 2000, the population of ducks increased by 117% (CGREG 2014).

- **Domestic fowl or chicken** *Gallus gallus* has been introduced across the planet as domestic poultry, with over 21 billion reported in 2014 (FAO 2015). Several populations have become feral, especially in Pacific islands, including Galapagos (Phillips et al. 2012a; McGowan and Kirwan 2015). The 2014 Census of Agricultural Production (CGREG 2014) reported that 22,180 free-range and 70,750 intensive poultry chickens were in Galapagos. Domestic chickens are found in all four inhabited islands of Galapagos: Santa Cruz, San Cristobal, Floreana and Isabela (Table 7.3). While Floreana Island holds the largest number

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[18] Domestic ducks in Galapagos seem to be a mix of descendants from the mallard *Anas platyrhynchos* and the Muscovy duck *Cairina moschata*.

[19] Japanese quail *Coturnix japonica* and common quail *C. coturnix* are distinct but closely related species (Johnsgard 1988; McGowan and Kirwan 2016). *Coturnix japonica* was domesticated in eastern Asia several centuries ago, and domesticated quails are derived from *C. japonica* and its hybrids with *C. coturnix* (Guyomarc'h 2003). While *C. coturnix* is a partially migratory species, the domestic *C. japonica* lost its migratory impulse during domestication (Derégnaucourt et al. 2005; Guyomarc'h 2003).

Table 7.3 Free-range domestic chicken *Gallus gallus* in the Galapagos Islands based on data reported by the 2014 Census of Agricultural Production (CGREG 2014). Free-range chickens were defined as those allowed to move freely in outdoors. Census did not include areas where stock was raised entirely for self-consumption; thus total numbers might be slightly underestimated

Island	Number of ducks	Number of turkeys	Number of free-range chicken	Chickens per 100 inhabitants	Density in agricultural lands: chickens per 1 km^2 of agricultural land	Density in the whole island: chicken per 10 km^2 of total land area
Santa Cruz	407	3	10,340	57	108	105
San Cristobal	328	21	7286	86	131	131
Isabela	191	4	3973	147	110	9
Floreana	0	0	581	387	253	34

per inhabitant and the greatest density in agricultural lands of free-range chicken, San Cristobal and Santa Cruz are the islands with the greatest density of free-range chickens (Table 7.3). Vargas and Bensted-Smith (2000), Gottdenker et al. (2005), Wiedenfeld (2006) and Phillips et al. (2012a) reported feral (or semi-feral) populations of chickens established on the four inhabited islands. However, it remains unclear if those populations are indeed self-sufficient and truly feral—i.e. completely independent of human care.

The main potential impact of domestic chicken on native fauna is the spreading of infectious diseases to native birds (Wikelski et al. 2004; Gottdenker et al. 2005; Hernandez-Divers et al. 2008; Soos et al. 2008; GISD 2010; Deem et al. 2012). Yet, this threat has not been demonstrated, and the evidence remains theoretical and correlative (GISD 2010; Baker et al. 2014). The Global Invasive Species Database (GISD 2010) mentions that *G. gallus* could negatively impact native vertebrates, but their only reference (Varnham 2006) is anecdotal and based on a different species (green junglefowl *Gallus varius*). Phillips et al. (2012a, b) noted: "no impacts [by *G. gallus*] to the [Galapagos] native biota have been documented".

I present here the first evidence of predation on squamate reptiles by domestic chickens in Galapagos. On June 2009, I observed a hen attacking a small Galapagos racer *Pseudalsophis biserialis* in a private yard next to the road between Puerto Baquerizo Moreno and El Progreso, San Cristobal Island. The hen pecked on the snake's head and body, after which it seized the snake with its beak and started to run, chased by another hen. Eventually, the hens carrying the snake took cover inside a shed. In July 2009, I observed a hen chasing a small dwarf gecko *Gonatodes caudiscutatus*, apparently found while foraging among some leaf litter and rocks in a private yard at El Progreso, San Cristobal Island. The gecko managed to flee and hide under rocks. In July 1997, I observed a rooster pecking and eating a dead Peters' leaf-toed gecko *Phyllodactylus reissii* in a vacant urban lot at Santa Cruz Island.

Gallus gallus mainly eats seeds and other plant material, although it is an omnivorous bird. Red Junglefowl, the wild ancestor of the domestic chicken, occasionally eats lizards and snakes (Ali and Ripley 1980). Reports of attacks and predation on squamate reptiles by Domestic Chicken are rare but worldwide (Guthrie 1932, Bell 1996; Powell and Henderson 2008; Mesquita et al. 2009; Sasa et al. 2009; Rahman and Das (2013), pers. obs.). Scarcity of records would suggest that chicken predation on lizards and snakes is an opportunistic yet atypical behaviour. However, it could also be due to under-reporting and paucity of herpetologists surveying chicken yards. Free-range chickens can move over hundreds of metres away from their shelters to forage, usually towards hedges and borders where encounters with small snakes and lizards would be more prone to occur, though remaining unwitnessed.

- Four **domestic pigeon** *Columba livia* were brought to Floreana Island during the early 1970s to establish a dovecote (Harmon et al. 1987). Within the next decade, pigeons were introduced to Santa Cruz, San Cristobal and Isabela islands (Harmon et al. 1987). The population increased rapidly, and ca. 550 pigeons were present in Galapagos by 2001—most of them semi-feral or feral (Phillips et al. 2003). The main potential impact of domestic pigeon on Galapagos fauna was the spreading of the protozoan parasite *Trichomonas gallinae* to the endemic Galapagos dove *Zenaida galapagoensis* (Harmon et al. 1987; Phillips et al. 2003). Indirect evidence for this threat was anecdotal and correlative, based on the presence of the parasite in *Z. galapagoensis* on islands where pigeons occurred (and their absence in pigeon-free islands) and the decline of *Z. galapagoensis* on islands populated by pigeon (Baker et al. 2014; Wikelski et al. 2004). In 2000, on the basis of the precautionary principle, Galapagos National Park Service and Charles Darwin Research Station started an eradication programme (Phillips et al. 2012b). *Columba livia* was declared eradicated from Galapagos in 2007 (Phillips et al. 2012b).
- **Red-masked parakeet** *Psittacara erythrogenys* was reported from Puerto Baquerizo Moreno, San Cristobal Island, in April 1996 (Vargas 1996, as *Aratinga erythrogenys*). Vargas (1996) obtained reports from local inhabitants of the presence of two or three parakeets, and he observed one *P. erythrogenys* flying between the town and the surrounding natural areas. These parakeets were possibly escaped pets and probably did not establish, and they have not been reported since (Wiedenfeld 2006; Phillips et al. 2012a). *Psittacara erythrogenys* is endemic to central-western Ecuador and southwestern Peru, where it inhabits deciduous and semi-deciduous forest (Ridgely and Greenfield 2001). It is among the most common birds illegally caught and traded (Juniper and Parr 1998), and freed pets can be found almost anywhere in Ecuador (pers. obs.). There are self-sustained non-native populations of *P. erythrogenys* in Spain and the USA.
- **Smooth-billed ani** *Crotophaga ani* has naturally[20] expanded its distribution from South America to southern Florida, the Caribbean and Central America

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[20] *Crotophaga ani* expansion across America has not been mediated by humans. The species is not

during the twentieth century (Terborgh and Faaborg 1973; Terborgh et al. 1978; Quinn and Startek-Foote 2000; Payne and Kirwan 2016). Humans apparently introduced *C. ani* in the Galapagos Islands as a possible biological control against ticks (Harris 1973; Grant and Grant 1997; Phillips et al. 2012a).[21] The first records of *C. ani* in Galapagos were in 1962, at Isabela Island. It progressively expanded to all major islands of the archipelago (Harris 1973; Grant and Grant 1997; Wiedenfeld 2006; Connett et al. 2013). At present, the estimated population of *C. ani* in Galapagos is over 250,000 individuals (Connett et al. 2013). *Crotophaga ani* is mainly insectivorous, but it also consumes plant material (especially fruits) and vertebrates (including lizards, snakes, frogs, birds and mice) (Bent 1940; Skutch 1959; Olivares and Munves 1973; Rosenberg et al. 1990; Burger and Gochfeld 2001; Payne and Sorensen 2005; Repenning et al. 2009; Connett et al. 2013). Predation on animal material seems to increase during the breeding period, which coincides with the wet season, when *C. ani* apparently prefers grasshoppers and other orthopterans (Davis 1940; Payne and Sorensen 2005; Repenning et al. 2009). Hymenopteran insects, such as euglossine bees and social wasps *Polistes* spp., have been reported as part of the diet of *Crotophaga ani* (Skutch 1959; Rosenberg et al. 1990; Raw 1997; Burger and Gochfeld 2001; Repenning et al. 2009). Two studies on the diet of *C. ani* at the Santa Cruz Island showed the presence of hymenopterans. Rosenberg et al. (1990) reported hymenopterans in only 4 of 24 dissected gizzards. Connett et al. (2013) found 12 *X. darwini* in the gizzards of 12 *C. ani*, but in this case, it was the single most frequent invertebrate species.

Four potential impacts by *Crotophaga ani* on Galapagos biodiversity have been postulated (Rosenberg et al. 1990; Grant and Grant 1997, Dvorak et al. 2004; Fessl et al. 2010):

1. Propagation of invasive plants. Available evidence suggests that *Crotophaga ani* has a high potential to propagate introduced plants, including the invasive raspberry *Rubus niveus* and wild sage *Lantana camara* (Guerrero and Tye 2011).
2. Predation on native fauna. Rosenberg et al. (1990), Guerrero and Tye (2011) and Connett et al. (2013) reported predation of Galapagos native invertebrates, lizards and Darwin finch nestlings by *Crotophaga ani*.
3. Competition with native avifauna, which remains untested and speculative.
4. Introduction of avian diseases, also untested and speculative.

Nonetheless, Phillips et al. (2012a; *contra* Rosenberg et al. 1990) stated that the smooth-billed ani is "a low priority alien species, not having been attributed with any serious impacts to native species, although it is likely that it has some effects on native [fauna]".

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listed within the GISD (2010).

[21] Still, this introduction hypothesis remains an assumption, mainly based on the apparently low capacity of anis to self-disperse through long distances across oceans (Harris 1973; Grant and Vries (1993), Grant and Grant 1997; Phillips et al. 2012a).

Fig. 7.3 *Crotophaga ani* predating on Galapagos carpenter bee *Xylocopa darwini*. Photo by Zell Lundberg and Christina Mitchell

I present herein information that constitutes the first evidence of a probable major impact on an endemic invertebrate due to predation by *Crotophaga ani* (Fig. 7.3) Between 8 and 16 June 2009, I observed six groups of *C. ani* predating assiduously on Galapagos carpenter bee *Xylocopa darwini* at six different locations on San Cristobal Island. Carpenter bees in high densities were foraging on blooming trees in the dry zone, usually near the coast. I observed one group of *C. ani* over a 30-min period, and the other five groups during 15-min period each. In total, the six groups consumed 661 bees over the observation periods. Each bird captured an average of 8.5 ± 4.4 (range = 4–15) bees per 15 min. *Crotophaga ani* continued preying upon bees after each observation period ended. Despite the continuous attacks, the bees did not disperse, and more kept coming attracted by the flowers. Although large numbers of the non-native social wasp *Polistes versicolor* were also present, as well as some butterflies, *C. ani* largely ignored them.

- An individual of **saffron finch** *Sicalis flaveola* was intercepted in 2014 at Baltra Island's airport, where it arrived as a hitchhiker on an airplane from Quito (Jiménez-Uzcátegui et al. 2015). Interestingly, after its interception, it was returned to Quito where local staff misidentified it as a Galapagos endemic bird and sent it back to the archipelago[22] (Jiménez-Uzcátegui et al. 2015). In Ecuador, *S. flaveola*'s native distribution is in arid semiopen areas with scattered trees or

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[22] When it arrived to Galapagos for the second time, it was weak and died by the next day (Jiménez-Uzcátegui et al. 2015).

shrubs and agricultural areas of southwestern Ecuador, both lowlands and inter-Andean highland valleys (Ridgely and Greenfield 2001). During the twenty-first century, *S. flaveola* started to expand along central-western lowlands and northern inter-Andean highland valleys of Ecuador (Henry 2005; Buitrón and Freile 2006; Cisneros-Heredia et al. 2015). It is now a frequent species in the valley of Quito, including the surroundings of air cargo warehouses and the airport (Cisneros-Heredia et al. 2015; pers. obs.).

- Phillips et al. (2012a) and Jiménez-Uzcátegui et al. (2015) reported an individual of **great-tailed grackle** *Quiscalus mexicanus* captured at the town of Puerto Ayora, Santa Cruz Island, in 2010. However, there is a previous record of this grackle that remained unreported: one *Q. mexicanus* was filmed at Santa Cruz Island on May 2005 (Fig. 7.4). *Quiscalus mexicanus* has a broad distribution, from central USA to the Pacific coasts of Ecuador and northern Peru (Fraga 2016). It has expanded considerably its distribution along northern USA and Caribbean islands (Dinsmore and Dinsmore 1993; Wehtje 2003; Fraga 2016). *Quiscalus mexicanus* was first reported from the Caribbean islands in the mid-2000s (Mejía et al. 2009; Paulino et al. 2013; Levy 2015). Currently, it seems to be established at least in Jamaica and Hispaniola (Paulino et al. 2013; Levy 2015). Grackles have been observed to hitchhike on passenger boats (Norton 1902), and Haynes-Sutton et al. (2010) mentioned that *Q. mexicanus* probably reached Jamaica with cargo. The paucity of records of *Q. mexicanus* in islands suggests that it is a poor disperser across oceanic barriers but cargo and passenger boats may offer aid for oceanic trips. The same transport mechanism was probably used by *Q. mexicanus* to reach Galapagos (although this remains an assumption). Thus, I include this species as a non-native introduced species, rather than as a vagrant.

Fig. 7.4 *Quiscalus mexicanus* at Santa Cruz Island, Galapagos, on May 2005. Photo by Kevin Dowie (www.kevindowie.com)

Nine species of terrestrial birds recorded at Galapagos have reached the islands most probably by natural dispersion from mainland South America in recent (historic) times[23]: snowy egret *Egretta thula*, little blue heron *Egretta caerulea*, cattle egret *Bubulcus ibis*, black-bellied whistling duck *Dendrocygna autumnalis*, masked duck *Nomonyx dominicus*, paint-billed crake *Neocrex erythrops*, purple gallinule *Porphyrio martinicus*, eared dove *Zenaida auriculata*, grey-capped cuckoo *Coccyzus lansbergi* and bananaquit *Coereba flaveola* (Wiedenfeld 2006; Jiménez-Uzcátegui et al. 2015). While most of these species have few records in the archipelago, the following species have become regular visitors or have established self-sufficient populations: *Egretta thula* with several records in Santa Cruz, Isabela, Floreana and San Cristobal islands (Wiedenfeld 2006; Hendrickson et al. 2015; pers. obs. at El Junco lagoon in July 2009); *Neocrex erythrops* with nesting populations in Santa Cruz and Floreana islands and probably in San Cristobal and Isabela islands; *P. martinicus* "with long periods of residence, bordering on being a permanent resident in recent years" (Wiedenfeld 2006); and *B. ibis* with breeding colonies on the main islands and widespread across the archipelago (Wiedenfeld 2006). All of these species are considered herein as native species of Galapagos. Although some of them may have established more easily due to human habitat modification, humans did not mediate in their arrival process.

Bubulcus ibis has been commonly identified as a non-native invasive species at the Galapagos Islands. However, its arrival to the Galapagos was not human-mediated but was instead a natural colonisation based entirely on the species' adaptations to successfully disperse across oceanic routes. The original distribution of *B. ibis* included the south of the Iberian Peninsula and parts of sub-Saharan and meridional Africa. During the nineteenth century, *B. ibis* underwent an enormous expansion, and it has currently colonised all continents except Antarctica (Martínez-Vilalta and Motis 1992; Martínez-Vilalta et al. 2017). Its natural arrival to Galapagos was a matter of time, and its establishment would have happened with or without anthropic areas, since it may inhabit swamps and mangroves. The existence of agricultural areas in Galapagos only facilitated the expansion of *B. ibis* in the archipelago. Its situation is very similar to *Neocrex erythrops*, also a recent arrival that has benefited from agricultural and other anthropic areas.

Discussion

Arrival Mechanisms

Eight (32%) non-native amphibians, reptiles and birds in Galapagos arrived as domestic animals, five (20%) as pets and one (4%) as (unsuccessful) biocontrol (Table 7.1). All domestic animals, pets and biocontrols were brought to the islands

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[23] While all other bird species recorded as vagrants at Galapagos can be classified as oceanic wanderers or as stray boreal migrants (Wiedenfeld 2006; Jiménez-Uzcátegui et al. 2015)

deliberately. However, most (44%) non-native amphibians, reptiles and birds reached the Galapagos Islands as hitchhikers aboard airplanes or ships, unintentionally translocated (Table 7.1). While data for most species is not complete, this hypothesis is supported by VCCDRS specimens of *Scinax quinquefasciatus* collected on a ship at Santa Cruz and at the airport of San Cristobal and by *Sicalis flaveola* found inside of an airplane (CDF 2016).

Six hitchhiking species arrived to Galapagos before the quarantine inspection system began in June 2000, and nine species were first recorded afterwards. Among the hitchhikers, *Rhinella horribilis* is a large toad (>70 mm in old juveniles, >100 mm in adults), thus unlikely to bypass quarantine inspections. The only known record of *R. horribilis* in Galapagos was made 5 years before the quarantine system began. *Lampropeltis micropholis* and *Iguana iguana* are large reptiles (>600 mm), and both have reached Galapagos after 2000 (it is uncertain how they bypassed quarantine). In contrast, *Scinax quinquefasciatus*, *Pristimantis unistrigatus*, *Gonatodes caudiscutatus*, *Phyllodactylus reissii*, *Lepidodactylus lugubris* and *Hemidactylus frenatus* are relatively small and with rather cryptic colorations (brownish). They could thus be easily overlooked during quarantine inspections, and multiple translocations could have occurred. Gill et al. (2001) reported live interception cases of *S. quinquefasciatus* (in Ecuadorian banana shipments), *L. lugubris* and *H. frenatus* in New Zealand, showing its ability to be translocated and to survive physiological stress during long trips.

Most hitchhiking species that have reached Galapagos occur in the surroundings of air and maritime ports or of cargo warehouses. However, not all translocations come directly from ports of shipment. *Lepidodactylus lugubris* does not occur in areas with air or maritime ports in mainland Ecuador with connections to the Galapagos, including Manta, Guayaquil or Quito. *Lepidodactylus lugubris* was first recorded in mainland Ecuador at Esmeraldas in 1963 (Fugler 1966). Currently, it inhabits along the humid lowlands and foothills of northwestern Ecuador, restricted to urban and suburban areas in the provinces of Esmeraldas and Santo Domingo de los Tsachilas (Fugler 1966; Schauenberg 1968; Hoogmoed and Avila-Pires 2015). It is absent from the arid central and southwestern lowlands of Ecuador. The translocation of *L. lugubris* to Galapagos was possibly achieved via horticultural cargo coming from Esmeraldas or from other countries where the species was already present, such as Colombia or Panama[24].

Human-facilitated transportation has provided opportunities for amphibians, reptiles and birds to reach Galapagos, independent of their physiological adaptations to salinity or to long trips. However, upon arrival, they still need to withstand the arid environments of the littoral and dry zones, where freshwater is almost

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[24] The first specimen of *Lepidodactylus lugubris* from America was collected in Panama in 1916 (Fugler 1966; Hoogmoed and Avila-Pires 2015). G.K. Noble collected it during his trip for the Harvard Peruvian Expedition (Collection catalogue, Herpetology, Museum of Comparative Zoology, Harvard University). The gecko was collected just 2 years after the opening of the Panama Canal and was probably translocated on boats coming from Hawaii or Oceania (Smith and Grant 1961). By 1941, *L. lugubris* had already reached Colombia (Daza et al. 2012; Hoogmoed and Avila-Pires 2015).

absent under natural conditions on most islands. While all non-native frogs, reptiles and birds reported in Galapagos are able to survive in arid environments to some degree, at least frogs and small geckos are still dependent of some humidity. Local and regional climate changes can have an important effect on the establishment and distribution of non-native species in Galapagos (Snell and Rea 1999). Higher rainfall during El Niño events (e.g. 1997–1998 and 2009–2010) was a major factor in the establishment of *Scinax quinquefasciatus* populations in Isabela and for the expansion of *Crotophaga ani* (Snell and Rea 1999; Pazmiño 2011). El Niño in 1997–1998 increased environmental humidity and diluted salinity in the lagoons of Puerto Villamil, allowing *S. quinquefasciatus* to thrive. After the El Niño event of 2009–2010, *S. quinquefasciatus* was able to reach the humid agricultural areas of Bellavista (Pazmiño 2011).

Artificially watered green urban and suburban areas, such as parks and gardens, have played an important role in the establishment of non-native amphibians and reptiles in Galapagos. They can act as refuges for newly established species, providing resources for locally large populations and facilitating intra- and interisland dispersion across inhabited areas (Ineich 2010). All non-native geckos are mainly found in green urban and suburban areas. Genetic evidence from Isabela Island populations of *Scinax quinquefasciatus* (Pazmiño 2011) and recurring records of *S. quinquefasciatus* from Santa Cruz Island and *G. caudiscutatus* at San Cristobal suggest multiple introduction events for both species. Before El Niño's thrusts, these populations were apparently able to survive thanks to artificially watered green urban and suburban areas.[25]

Most hitchhiking amphibians and reptiles are usually translocated inside freight or dwelling within spaces and crevices of airplanes and ships. However, they can be transported inside tourist luggage too. On August 2009, a live *L. lugubris* was unintentionally translocated in my handbag from San Cristobal Island to Guayaquil. It probably entered my bag at a restaurant near the dock, since I never saw *L. lugubris* at the USFQ Galapagos campus, where I stayed. I noticed its presence after opening my bag in Guayaquil. Furthermore, this shows that non-native species translocations may work on both ways, exchanging individuals between populations of Galapagos and the continent.

Large hitchhiking reptiles and birds can accidentally enter closed areas inside freight airplanes and ships, although they are easily detected and intercepted (like the individual of *Sicalis flaveola* in Galapagos). However, probably the most common hitchhiking situation takes place when large reptiles and birds stay on decks and other exterior structures of passenger and cargo ships. They can hitchhike after the ships have gone through departure port inspections, survive for several days, remain overlooked, and swim or fly towards land before the ship reaches controls in the arrival ports. *Iguana iguana* and *Quiscalus mexicanus* have likely arrived in this

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[25] In comparison with Santa Cruz Island, the area of urban and suburban gardens in San Cristobal is reduced. This limited habitat availability is apparently the reason why *Gonatodes caudiscutatus* holds small and restricted populations in the lowlands of San Cristobal and why *Scinax quinquefasciatus* has not become established in that island (despite its first record in 2000).

way to Galapagos. Several hitchhiker bird species are known to have arrived and established in islands around the world: house sparrow *Passer domesticus* in the Canary and Maldives islands, Spanish sparrow *Passer hispaniolensis* in the Canary Islands, pale-billed myna *Acridotheres cinereus* in Borneo island, red-vented bulbul *Pycnonotus cafer* in the Marshall and Hawaii islands, house crow *Corvus splendens* in the Socotra islands and Australia and great-tailed grackle *Quiscalus mexicanus* in Jamaica (Haynes-Sutton et al. 2010; Lever 2005; Suleiman and Taleb 2010).

Vulnerable Islands

If further amphibian, reptile and bird introductions are to be stopped in Galapagos, it is important to establish the vulnerability of islands to those introductions and to understand the general profile of potential hitchhikers.

The four populated islands are the most vulnerable to translocation of non-native species because they have (1) established and active air and maritime ports, thus arrival mechanisms and dispersal events of non-native species are facilitated in repetitive occasions; (2) large flux of local population and tourists, which means large amount of baggage and freight where non-native species may hide, find adequate microenvironments to survive the oceanic dispersion and be transported to different areas of the islands; and (3) human-modified environments where anthropophilic non-natives may find suitable niches.

Isabela Island is apparently the most vulnerable island to the establishment of amphibians because of its freshwater wetlands next to the city and harbour.[26] Santa Cruz, San Cristobal and Floreana islands have coastal lagoons with significantly more salinity than Las Diablas lagoon in Isabela (Gelin and Gravez 2002); thus amphibians probably do not become easily established. The highland moist zones of all populated islands are especially vulnerable to the introduction of non-native amphibians, reptiles and birds, due to the presence of mesic environments with extensive agro-urban areas and wetlands. Furthermore, the moist zones on the highlands of Isabela are closer to the coast, making it easy for non-native species to reach a mesic environment in which to survive and establish.

Potential Hitchhikers

Intentionally introduced species, such as pets and domestic animals, are rather easy to detect and identify because they are usually conspicuous and recognisable. However, hitchhiking species are the real predicament of quarantine officials. Hitchhiking species are usually inconspicuous, difficult to identify and hard to find.

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[26] The largest coastal lagoon of Isabela, Las Diablas, is next to the town of Puerto Villamil. Its low salinity levels (6–10 gL^{-1}, Gelin and Gravez 2002) allow the reproduction of *S. quinquefasciatus*.

There is not a single set of characteristics that ascertains the potential of vertebrates to become a successful hitchhiker or to become established in insular ecosystems. Several publications have reviewed and proposed different methods for predicting introduced species. Since I am analysing three different phylogenetically diverse groups of terrestrial vertebrates, I will use basic criteria for each group, which were selected after studying the following references: Kolar and Lodge (2001), Hayes and Barry (2008), Blackburn et al. (2009), Van Wilgen and Richardson (2012) and Buckley and Catford (2016). I think this criteria set allows for fast and simple identification of potential species in mainland Ecuador that could hitchhike to Galapagos. A key factor for the control of hitchhiking species is that personnel at ports and crew in airplanes and ships receive training to correctly identify, restrain and handle non-native hitchhiking animals. Although the species lists provided herein could be improved, I hope they will provide valuable information for the Agency for Regulation and Control of Biosecurity and Quarantine for Galapagos (ABG) and other organisations involved in the conservation and management of the archipelago (including Consejo de Gobierno del Régimen Especial de Galápagos CGREG, Ministerio de Agricultura, Ganadería, Acuacultura y Pesca MAPAG, Parque Nacional Galápagos PNG, Ministerio del Ambiente MAE).

A cautionary note: some reptiles and birds from mainland Ecuador may look similar to those native to Galapagos. For example, the Galapagos endemic geckos of the genus *Phyllodactylus* could be confused with the non-native *Phyllodactylus reissii*; and the native *Setophaga petechia* has been confused in the past with the non-native *Sicalis flaveola*. Guides and manuals specifically focused on crew or control personnel should be produced to avoid confusion and reinforce control measurements.

Amphibian and reptile species with higher hitchhiking potential for Galapagos seem to be characterised by (1) having inconspicuous colouration and small to medium body size,[27] (2) being adapted to arid environments or anthropogenic areas,[28] (3) occurring frequently in the surroundings of cargo warehouses or in agricultural areas[29] and (4) living in the Pacific lowlands of central Ecuador, where habitats have environmental conditions similar to those found in the Galapagos[30] and the main ports of freight airplanes and ships to Galapagos are located.

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[27] Which contributes to their hard detection and improves their survivorship (Olson et al. 2012).

[28] Adaptation to desiccation conditions has also enhanced tolerance to salinity in some amphibians (Balinsky 1981; Wells 2007), thus making it easy for them to survive in low salinity lagoons like Las Diablas in Isabela Island. The three species of *Scinax* that have become established in islands as cargo hitchhikers have adapted to arid environments or anthropogenic areas on their native distributions: *Scinax quinquefasciatus*, *S. x-signatus* and *S. ruber* (Breuil and Ibéné 2008; Breuil 2009; Kraus 2009; Powell et al. 2011). The first two are also known to be adapted to breed in marshes with low salinity (Jiménez-Uzcátegui et al. 2007; Rios-López 2008; pers. obs.). It seems that *Scinax* species, which are able to adapt to open habitats, show some tolerance to salinity.

[29] Frogs that are common in these habitats have easy access to freight or have a great chance to be packed along with horticultural products (Kraus et al. 1999).

[30] Species that establish successful self-sufficient populations usually come from areas that have a similar climate to the jurisdiction where they are introduced (Bomford et al. 2009).

In mainland Ecuador, there are seven frog species matching this hitchhiker profile (Fig. 7.5): *Scinax quinquefasciatus*, *Pristimantis achatinus*, *Barycholos pulcher*, *Engystomops pustulatus*, *Trachycephalus jordani*, *T. typhonius* and *Rhinella horribilis*. While the first species is already established in Galapagos, the remaining five, if allowed to reach the archipelago, have a high probability of settling there. Furthermore, these species have additional advantages favouring their establishment in insular environments: *Pristimantis achatinus* and *B. pulcher* are terrestrial breeders with direct development; *E. pustulatus*, *S. quinquefasciatus* and *R. horribilis* are opportunistic breeders that can reproduce even in small puddles; and *E. pustulatus*, *T. jordani* and *T. typhonius* can inhabit extremely arid environments with low seasonal rainfall, similar to the lowlands of Galapagos. Live *T. jordani* has been intercepted as far away as the USA and New Zealand in banana shipments from mainland Ecuador (Hartweg 1955; Gill et al. 2001). Although large adult *R. horribilis* should be intercepted during quarantine, juveniles are small and inconspicuous. However, desiccation is a major mortality factor for juveniles (Zug and Zug 1979), but if they were to find shelter and wet conditions, they could survive travelling to Galapagos. There are 11 species of squamate reptiles matching the hitchhiker profile in mainland Ecuador (Fig. 7.5): *Gonatodes caudiscutatus*, *Hemidactylus frenatus*, *Phyllodactylus reissii*, *Iguana iguana*, *Lampropeltis micropholis*, *Boa constrictor*, *Dipsas elegans*, *Erythrolamprus epinephelus*, *Mastigodryas* sp. (cf.

Fig. 7.5 Species of amphibians, reptiles and birds from mainland Ecuador that could be potential hitchhikers in the Galapagos Islands

boddaerti), *Mastigodryas pulchriceps* and *Oxybelis aeneus*. The first five of these species have already been recorded in Galapagos.

Although little information is available on hitchhiker birds, at least the following features seem to profile potential hitchhiker birds to the Galapagos: (1) being adapted to arid environments or anthropogenic areas, which would allow them to survive in the lowlands of Galapagos; (2) occurring frequently in the surroundings of main ports of freight airplanes and ships to Galapagos, with higher probability of entering closed areas inside of freight airplanes and ships or wandering around boat decks; (3) habit of flying at least short distances over the sea, so they can reach departed ships; and (4) adaptability to build nests within human-made structures, thus attracting reproductive adults to the ships. Since birds are active and noticeable animals, their detection and capture should be fairly easy during quarantine procedures.

To guide such training, I provide a shortlist of birds from mainland Ecuador that match the potential hitchhiker profile (Fig. 7.5): eared dove *Zenaida auriculata*, blue-gray tanager *Thraupis episcopus*, saffron finch *Sicalis flaveola*, rufous-collared sparrow *Zonotrichia capensis*, shiny cowbird *Molothrus bonariensis*, great-tailed grackle *Quiscalus mexicanus* and house sparrow *Passer domesticus*. Of these birds, two have been already recorded at Galapagos and are discussed above. There are records of *Z. auriculata* at Champion islet, Santa Cruz and Baltra islands (Wiedenfeld 2006; Loranger 2012). Although all these areas are in or close to inhabited islands, their origin cannot be directly assigned to hitchhiking since this species is capable of oceanic dispersing (Baptista et al. 2013). Of all the birds herein listed, *M. bonariensis* could be a major threat if established in Galapagos. It is a brood parasite and can seriously affect bird species with small populations (Oppel et al. 2004). Its populations have expanded in the surroundings of the two air and maritime ports of Guayaquil and Quito (Cisneros-Heredia et al. 2015; Crespo-Pérez et al. 2016; pers. obs.).

Effects, Management and Control

Chickens have become the dominant domestic birds in all inhabited islands in Galapagos. Several studies have discussed the possible transmission of disease from chickens to native Galapagos fauna, its potential impacts and control measures (Wikelski et al. 2004; Gottdenker et al. 2005; Soos et al. 2008; Deem et al. 2012). Free-range (and feral) chickens seem to have some degree of predatory impacts on Galapagos fauna, as evidenced in this publication. However, chicken predation on endemic fauna is probably uncommon, because endemic snakes and lizards prefer dry lowland areas and most free-range and feral chickens occur in moist highland areas (CGREG 2014). In contrast, it is possible that chickens have significant impacts on the populations of the introduced gecko *Gonatodes caudiscutatus*, the only squamate reptile of Galapagos that occurs mainly in moist highland areas, i.e. agricultural lands at San Cristobal Island. Nevertheless, chicken predation probabilities increase in urban and suburban areas, where endemic snakes and endemic and non-native lizard and chickens co-occur.

Soos et al. (2008) suggested several regulatory and management procedures focused on preventing the spread of poultry diseases to wild birds, including the elimination or reduction of free-range chickens. To eliminate free-range farming could be impractical due to cultural, social and economical factors. A more plausible option would be to promote free-range poultry farming with biosecurity measures that reduce the interaction between chickens and wildlife. Some measures should include well-kept fences to prevent chickens leaving the farm and to stop them from foraging on hedges and other vegetated areas; a peripheral ring without vegetation, rocks or wreckage around the fences, coops and troughs; and clean fenced-in pastures for poultry roaming to prevent attracting wildlife inside chicken yards. These and other measures must be established and reinforced with the active participation of Galapagos poultry owners and local and national authorities dealing with agricultural practices and wildlife conservation (including ABG; Consejo de Gobierno del Régimen Especial de Galápagos (CGREG); Ministerio de Agricultura, Ganadería, Acuacultura y Pesca (MAPA); Parque Nacional Galápagos (PNG); Ministerio del Ambiente (MAE)).

Of all non-native species, *Crotophaga ani* is the only species with established, self-sufficient populations expanding into anthropic and natural areas in Galapagos. Data presented herein show that the smooth-billed ani *Crotophaga ani* can heavily predate on the Galapagos carpenter bee *Xylocopa darwini*. Large body size and slow flight of carpenter bees probably make them an easy and more nutritious prey for *C. ani*, in comparison with other similar species of invertebrates. Observations of six different groups of *C. ani* with an intensive predatory behaviour on *Xylocopa darwini* in San Cristobal Island suggest that this is not a unique habit. Furthermore, this behaviour may be widespread since *X. darwini* is known to be part of the diet of *C. ani* in Santa Cruz Island (Rosenberg et al. 1990; Connett et al. 2013). If similar patterns of predation are constant—at least during the breeding period—*C. ani* may have a severe impact on local carpenter bee populations. *Xylocopa darwini* is the only endemic bee from the archipelago (Gonzalez et al. 2010; Rasmussen et al. 2012). It is a keystone pollinator species in the islands, being the most important flower visitors and responsible for the vast majority of insect pollination in Galapagos (Linsley 1966; Linsley et al. 1966; McMullen 1985, 1989; Phillip et al. 2006; Chamorro et al. 2012). As a dominant and keystone pollinator, negative impacts on its populations may have significant effects on the plant-pollinator networks of the islands.

Eradication of established non-native populations is costly and rarely successful (Mack et al. 2000), and control policies seem to have effects only before species are widespread (Olson et al. 2012; Pitt et al. 2012). In this context, the Agency for Regulation and Control of Biosecurity and Quarantine for Galapagos (ABG) plays a decisive role in preventing new introductions of non-native amphibians, reptiles and birds in Galapagos, especially hitchhikers. Furthermore, for non-native species already established, it is important to stop new or multiple introductions of the same species, since they will increase reproductive output and genetic diversity

(Lambrinos 2004; Van Wilgen and Richardson 2012). Quarantine officers should pay particular attention to horticultural trade and temperature-controlled freight, which, because of their constant temperatures, are non-lethal for amphibians and reptiles (Work et al. 2005). Decks and exposed cargo on ships are another source of non-native species, especially large body size hitchhikers such as snakes, iguanas and birds.

If the eradication of non-native established species is of interest, the eradication programme of *Columba livia* is a successful but rather unique story (Phillips et al. 2012b). The success was due, in part, to the availability of adequate and updated knowledge about the species' natural history, distribution, ecological relationships, effects and eradication methods (Phillips et al. 2012b). In contrast, eradication attempts of other non-native species that are poorly known have been unsuccessful, e.g. *Scinax quinquefasciatus*.[31] In fact, it is probable that after a non-native species has become established and self-sufficient, management policies could be better focussed on guiding its control rather than to "undertake the daunting (and often illusory) task of eradicating them" (David et al. 2017).

Very little information has been published about the natural history of most non-native amphibians, reptiles and birds in their native distribution in mainland Ecuador. Knowledge on non-native species is paramount to understand whether their control should be a conservation goal in the archipelago and, if so, how it could be best achieved. Even the species' identity of some species is uncertain (e.g. *Rhinella horribilis*, *Scinax quinquefasciatus* and *Lampropeltis micropholis*). Furthermore, knowledge about Galapagos populations remains in many cases unpublished.[32] Most terrestrial non-native hitchhikers in the Galapagos are geckos, and their effects on Galapagos biodiversity have usually been considered as low or absent. Unfortunately, Marinus Hoogmoed's (1989) words are still valid today: "these are only speculations based on few observations". With all these restrictions, control policies are not sufficiently evidence based. Future research on non-native species should provide information on habitat and microhabitat use, physiology and growth, intra-population tolerance to abiotic and biotic factors, reproductive biology and population dynamics and diet and trophic interactions, both in Galapagos and in its native distribution.

Fundamentally, we need to rethink about how we understand, manage and prevent introductions of non-native species. Available information about non-native terrestrial vertebrates in Galapagos is still basic and not enough to even understand their natural history and general ecological patterns. We need to go beyond the paradigm that the main impact of non-native species is framed by their direct effects on native species, i.e. direct competition or predation. It is necessary to understand the

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[31] Eradication attempts by hand capture, spraying caffeine, and increasing the salinity of the lagoons were unsuccessful (Jiménez-Uzcátegui et al. 2007; Phillips et al. 2012b).

[32] For example, available knowledge about the populations of *Scinax quinquefasciatus* in Galapagos remains in two unpublished dissertations: Pazmiño (2011) described the genetic diversity and origin of the Galapagos populations of *S. quinquefasciatus*, and Vintimilla (2005) analysed the control potential of increasing water salinity.

ecosystemic effects of non-native species, for example, on nutrient dynamics and cumulative effects on food webs through trophic and non-trophic interactions (e.g. mutualisms or ecosystem engineering). We also need more research on how native species are evolving when confronted and living with non-native species, since often native species rapidly evolve traits to better tolerate or exploit invaders (David et al. 2017).

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Part III
To the Landscape

Chapter 8
Multi-scale Remote Sensing of Introduced and Invasive Species: An Overview of Approaches and Perspectives

Stephen J. Walsh

Introduction and Objectives

It is well documented that introduced and invasive species, both flora and fauna, in the Galapagos Islands of Ecuador and elsewhere around the globe, are posing considerable threats to the sustainability of native and endemic species (Levine and D'Antonio 1999, Lonsdale 1999, Dirnbock et al. 2003, Hulme 2006). By outcompeting local species, altering ecosystem goods and services, and occupying an increasingly significant geographic proportion of landscapes, waterways, and oceans, introduced and invasive species are capable of transforming the fundamental ecology of sites and altering future trajectories of change (Rejmanek 1999, Stohlgren et al. 1999, Kulmatiski et al. 2006, Farhan and Lim 2012), with implications for the sustainability of endemic and native species, including the iconic and emblematic species occurring in the Galapagos Islands (Itow 2003, Watson et al. 2010). In the Galapagos, 870 alien plant species have been recorded—34% of these species have naturalized and within this group are the invasive species (16% of evaluated) and the transformer species (3% of evaluated) (Trueman et al. 2010). Naturalized species in the Galapagos have been present in the archipelago longer than non-naturalized species (Fig. 8.1). Generally, the number of naturalized plant species has increased linearly over time on many individual islands around the globe, and the mean ratio of naturalized to native plant species across islands has changed steadily for nearly two centuries (Sax and Gaines 2003, 2008).

Controlling and managing invasive species requires new approaches and perspectives to map, monitor, and model their spread. For instance, Walsh et al. (2008) used OBIA (object-based image analysis) approaches and fused HYPERION and

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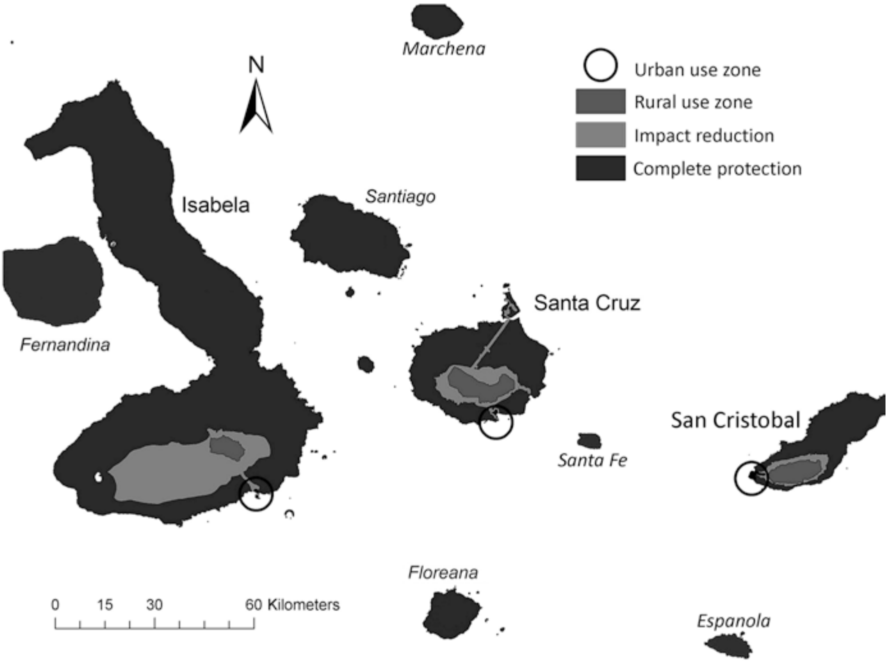

Fig. 8.1 The primary islands and communities of the Galapagos Archipelago of Ecuador

QUICKBIRD data to assess land use/land cover change as a consequence of the spread of invasive species from the agricultural zone on Isabela Island into the surrounding Galapagos National Park. Asner et al. (2006) derived spectral signatures of native, introduced, and invasive species in Hawaii using AVIRIS aircraft data as an indicator of conservation and management efforts. Ustin et al. (2002) also used AVIRIS data to take advantage of its high spectral and spatial resolutions to map invasive species in California through spectral feature mapping followed by supervised classification. Joshi et al. (2004) integrated remote sensing and geographic information systems by mapping the actual—and predicting the potential—distribution of invasive species, with an emphasis on the remote sensing of non-canopy invader species. Huang and Asner (2009) fused passive and active remote sensing systems to detect the structure and functional properties of invasive plants at different canopy levels by emphasizing the use of canopy-penetrating, LiDAR systems. Lefsky et al. (2002) described the basic functions of LiDAR for directly measuring the 3D distribution of plant canopies to estimate structural properties of vegetation for ecosystem studies, and Turner et al. (2003) indicated that the advances in the spatial and spectral resolutions of sensors, such as LiDAR, are making the direct observation of certain aspects of ecosystems increasingly feasible.

Detecting invasive species and predicting their potential distribution are also vital to coordinating management responses to plant invasions (Buddenhagen et al. 2004, Cord et al. 2010). The fusion of remote sensing data from several spatial, spectral, and temporal resolutions can support a variety of environmental models by providing vital information to predict plant distributions and the most suitable environmental conditions for their spread. Diao and Wang (2014) showed that mapping the suitable habitat of invasive species is of paramount importance to effective management. They fused remote sensing data to species distribution models to characterize species patterns by developing fine-scale environmental predictors. Heumann et al. (2011) linked remote sensing approaches and ecological modeling, i.e., *MaxEnt* (maximum entropy model), to adapt and apply the presence-only geographic species distribution model for agricultural crops to land suitability mapping. Heumann et al. (2013) also applied *MaxEnt* to characterize the suitability of occurrence of land use across a human-managed landscape through recent advances in niche-based geographic species distribution models to understand land suitability and land use decisions. The species distribution models link species presence and location information with geospatial information and use machine learning algorithms to develop nonlinear and discontinuous species-environment relationships. Results indicated that, although the natural environment is often the dominant factor in species' likelihood of occurrence, this likelihood is also influenced by household characteristics and human decision-making about the use and management of the land. For instance, in the Galapagos Islands, arriving residents as well as tourists accidentally introduce plant species through seeds that inadvertently hitchhike to the Galapagos with travelers, and immigrants also knowingly carry alien species to the Galapagos to transform the homes and gardens in ways customary to their family places on the mainland, although species control programs are in place to stem the flow of alien species to the Galapagos.

Malanson and Walsh (2013) reported on the challenges facing the Galapagos Islands as a consequence of invasive species (Hamann 1981, Ellshoff et al. 1995, Tye 2006, Jager et al. 2009) and described an array of remote sensing approaches to characterize invasive species through hyperspectral, multispectral, and hyperspatial systems that involve aircraft- and satellite-borne sensors and highlighted through pattern recognition approaches embedded in image processing software systems. Furthermore, they discussed field techniques to improve the on-the-ground efforts for mapping and monitoring invasive species. Finally, they described how eradication of invasive species could be added to an optimization model by determining the time needed to physically eradicate a plant and its effectiveness across the landscape.

In this chapter, consistent with the theme of the book, "…*from the molecular to the landscape*," a suite of satellite remote sensing systems are briefly described relative to their capacity to map and monitor land use/land cover change and introduced and invasive species; advances in unmanned aerial vehicles are assessed for local-scale mapping and spatial landscape ecology; and field methods and geospatial technologies are described for characterizing landscape types and conditions at fine spatial scales and for discrete and continuous time periods. Finally, fusion of the data secured through these collection approaches is described that integrates the multi-scale observations of introduced and invasive species to map, monitor, and model future landscape alternatives, given current conditions, spatial patterns, and social-ecological processes that serve to eradicate, mediate, or extend introduced and invasive species across the landscape.

Study Area

Politically part of Ecuador, the Galapagos Islands are 1000 km from the mainland. The population is small (~30,000 today vs. 3488 in 1972) but growing and dynamic. Tourism is also growing exponentially. In 1960, 40,000 tourists visited the islands, but the number of tourists increased to 65,000 in 2000 and 215,000 in 2015. The promise of outstanding recreational experiences for tourists increased population immigration patterns, and lucrative opportunities for those seeking better livelihoods brought about higher demands on local resources that significantly change, and often stress and degrade the social, terrestrial, and marine ecosystems of islands. With nearly two million visitors arriving in the Galapagos since 2000, the tourism sector directly employs 60% of the residents (Kerr et al. 2004, Villacis Carrillo 2013) and represents almost the entire economy. Although some islands are well-preserved and do not allow tourists, over 70% of San Cristobal and 50% of Santa Cruz, the two most populated islands, have been dramatically altered by LCLUC since 1987 (Percy et al. 2016).

It is estimated that on the populated islands, 29% of the humid and 45% of the very humid highlands have been transformed by the combined presence of invasive plants and agriculture (Watson et al. 2010). The dynamics of plant invasion depend on the combination of species and recipient environments relative to stochastic events, such as the heavy rains associated with El Niño events and drought conditions linked to La Niña events as well as land change dynamics related to the expanding human dimension in the Galapagos Islands (Itow 2003, Henderson et al. 2006). Over the past three decades in the Galapagos, the human-assisted introduction rate of introduced species has been approximately 10 species per year or some 100,000 times the natural arrival rate of introduced species (Tye 2001, 2006). It appears that the occurrence and spread of introduced species in the Galapagos may depend more on human activities and the nature of managed landscapes than on human population size per se (Tye 2006).

Approaches and Perspectives

Several sciences, most prominently the discipline of geography, has at its very core an emphasis on the fundamental importance of space-time scales of observation, measurement, and analysis for assessing social-ecological patterns, processes, and human-environment interactions (Walsh and Mena 2013). Commonly, studies are organized in a multi-scale framework in which the spatial (and/or temporal) scale above the focal scale is used as geographic context, while the scale below the focal scale is used to understand mechanisms linked to observed patterns. In remote sensing, data collected from multiple sensor systems and platforms, for example, satellites, aircraft, unmanned aerial vehicles, and geospatial field technologies, offer special opportunities for assessing spatial patterns and associated processes through a fused approach that is designed to improve our understanding of the drivers of change and the composition, condition, and behavior of target species across the landscape as well as land use/land cover types and conditions. For most landscape studies, multispectral systems afford unique perspectives to assess vegetation conditions by associating plant characteristics to specific spectral regions, for instance, plant pigmentation to the visible wavelengths, chlorophyll content to the near-infrared wavelengths, moisture content to the middle-infrared wavelengths, and temperature variability to the thermal-infrared spectral region. Multi-date image acquisition further enhances mapping and monitoring requirements by organizing image datasets into an image time series to better characterize a dynamic environment that may be altered through annual changes, phenological shifts, disturbance regimes, or land use/land cover modified by natural processes as well as the direct and indirect consequences of an expanding human dimension. Hyperspatial and hyperspectral systems are often used to accentuate the informational needs of high interest areas and periods, merged with coarser-grained data used to characterize the regional context.

With considerable amount and diversity of satellite assets now globally available through government and private sources, long-term image archives have been assembled for several systems, most notably, the LANDSAT system for Earth observation. Launched in 1972, the LANDSAT system has evolved over time, but the data are generally quite compatible, yielding an impressive image archive for long-term studies. Augmented by finer- and coarser-grained systems, such as IKONOS and QUICKBIRD data for localized studies as well as MODIS data for regional studies, systems have also been developed that emphasize hyperspatial (e.g., World View data) and hyperspectral (e.g., HYPERION) capacities. Image archives are accessed for global assessments using, for instance, the *USGS Global Visualization Viewer* (*GloVis*–http://glovis.usgs.gov), the *USGS EarthExplorer* (http://earthexplorer.usgs.gov), and the *NASA Earth Exchange* (*NEX*–https://c3.nasa.gov/nex/) web portals.

Normally, remote sensing data are fused to optimize fine- to coarse-grained analyses that represent both space and time domains. Project designs customarily involve the strategic placement of ground control sites within the nested image data set for validation of derived products through image processing for improved landscape and target characterization. Field methods vary by question and project requirements, but geo-location of sample sites is routine, as is the increasing use of intermediate-scale approaches for image acquisition and ground control that may involve the use of unmanned aerial vehicles (UAVs) as well as the placement of fixed or transient sensors placed on land and in the water as well as the use of 3D laser scanners for building ultrahigh resolution digital elevation models of target spaces and the characterization of structural information of plant communities, such as plant density, age structure, community edges, and canopy levels.

Satellite Remote Sensing Systems

Using hyperspectral remote sensing, Song et al. (2011) examined the photosynthesis rate of mangrove forests under various salinity gradients in the Galapagos Islands. Heumann et al. (2011) reports that traditional remote sensing approaches have typically failed to accurately map fringing mangroves and true mangrove species due to relatively coarse spatial resolution of applied systems and the spectral confusion with landward vegetation. Walsh et al. (2008) used QUICKBIRD and HYPERION data to characterize the areal extent of invasive plant species (*Psidium guajava*, common guava) on family farms using pixel- and object-based image analysis as well as linear and nonlinear mixture modeling to decompose classified HYPERION data into land cover/land use fractions using higher spatial resolution QUICKBIRD data for sample sites. Watson et al. (2010) used LANDSAT classifications to provide a quantitative assessment of anthropogenic degradation, defined as areas transformed by direct human activity or heavily invaded by introduced plant species.

Henderson and Dawson (2009) used a time series of NOAA AVHRR NDVI (10-day maximum value composite data) to examine the impacts of feral goat populations on vegetation dynamics on Isabela Island in the Galapagos (Fig. 8.2). Brewington (2013) also mapped vegetation responses to the invasion and eradication of feral goats on Alcedo volcano using MODIS data and the enhanced vegetation index (EVI) to assess land cover impacts from 2000 to 2010 associated with the presence of goats that were eradicated between 2004 and 2006. McCleary (2012) examined contemporary LCLUC in the communities and protected areas of Isabela Island and related observed changes to human-environment interactions. Using QUICKBIRD and WORLDVIEW-2 satellite imagery, the study relates LCLUC patterns to agricultural land abandonment, plant invasion, and forest expansion over the same period.

Unmanned Aerial Vehicles and Systems

In the relatively brief history of unmanned aerial vehicles (UAVs) applied to the mapping and monitoring of environmental conditions and systems as well as Earth resources, several benefits have been realized for landscape ecology, geography, land change science, and several other associated programs. For instance, most applications that require the use of UAVs are very local in scale, and as such, the number of repeat flights over a specified area can be controlled by the operator, taking advantage of changing environmental and illumination conditions and target discrimination from background features. Low-altitude flights allow sensors to observe the target area from several locations, changing perspectives and proximal positions as needed and potentially collecting finer spatial resolution data "on the fly" as the operator engages with the UAV. Collecting fine-scale data and aggregating them to appropriately assess defined ecological processes and landscape

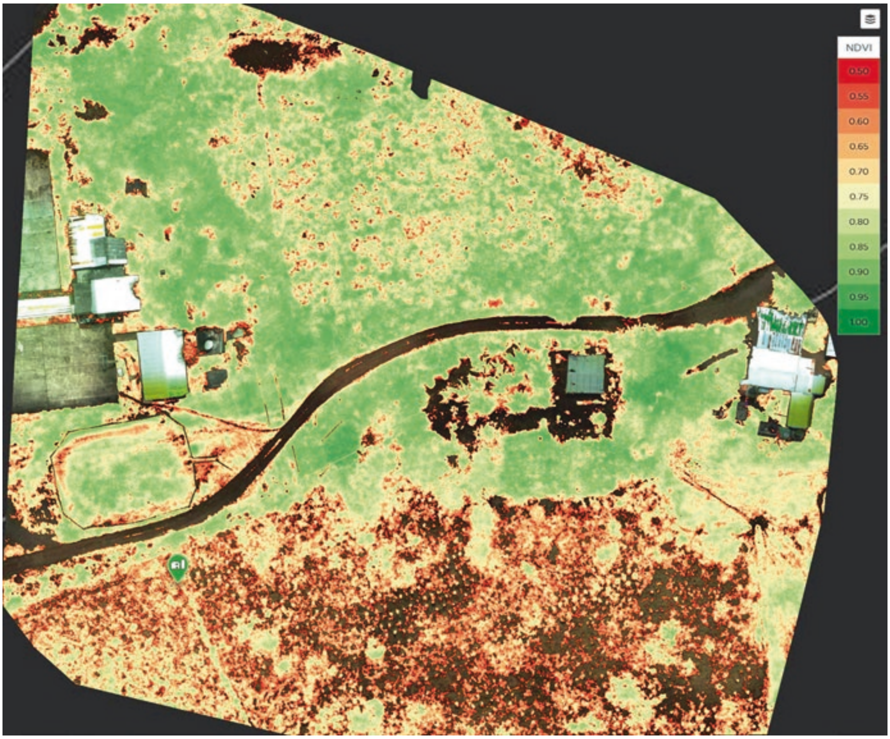

Fig. 8.2 The normalized difference vegetation index (NDVI) computed using a multispectral sensor onboard an unmanned aerial vehicle for *Hacienda Tranquilla*, San Cristobal Island, Galapagos Archipelago of Ecuador (July 2015)

features are fundamental to the importance of UAVs for landscape studies. With UAVs operating costs relatively low, the systems are generally lightweight, imaging and non-imaging payloads can be acquired, and limited cloud and shadow contamination occurs, given the ability to time local flights to optimal environmental conditions and time of the day. Anderson and Gaston (2013) discussed the ability to bridge information gaps in data-sparse locations through the use of UAVs that advance our understanding of key processes at local scales of measurement and observation. They also noted the benefits to spatial landscape ecology by focusing on studies of individual organisms and their spatial-temporal dynamics at close range, for instance, pigmentation, chlorophyll content, leaf moisture conditions, and temperature profiles of individuals and communities. Specific applications in population ecology take advantage of UAV's ability to generate a time series of abundance and/or distribution, phenological cycle of target species and canopy gap metrics, and ecosystem processes (e.g., meteorological variables, atmospheric profiling in the horizontal and vertical domains, and distribution of biotic and abiotic variables).

Operational factors in the use of UAVs are several, as described by Anderson and Gaston (2013): *platform constraints* (e.g., payload capacities and hence flying time), *sensor constraints* (e.g., limited payload size restricts users to simple sensors with few moving parts, affecting radiometric data quality and geometric stability; validation of the geometric accuracy of spatial data products), *operating constraints* (e.g., pilot flight conditions, flight restrictions imposed by civil and federal regulations), *environmental constraints* (e.g., risk of system loss in high winds, site conditions, such as dense tree canopy that may make real-time tracking difficult or prevent platform retrieval if the UAV goes off track or goes down), and *correspondence constraints* (e.g., spatial data requirements of the research question, applications need, and required minimum mapping unit of the sensor system).

Design and analytical factors affecting the use of UAVs include the robustness of sensors and platforms as additional sensors are integrated into the mapping process, such as LiDAR sensors; UAV data as ground control information, with geographic precision through onboard GPS units; scaling of data and spatial aggregation and landscape generalization; space-time dependencies of collected and processed information; temporal repeatability and periodicity vs. one-time mapping; georectification, calibration, and validation considerations; scientific data visualization and data fusion; manual interpretation vs. automated pattern recognition approaches; pixel- vs. object-based image analysis; up-scaling of imagery to environmental and social objects and processes; and data analysis alternatives, such as image classification, spatial filtering, spatial analysis, vegetation indices, change detections, and ecological pattern metrics.

Unmanned aerial vehicles (UAVs) were flown over parts of San Cristobal Island, Galapagos Archipelago of Ecuador in 4–9 July 2015. Thermal-infrared, optical-RGB, and multispectral sensors were flown on UAVs. The goals of the image reconnaissance missions were to assess the capacity of several UAV systems for coastal mapping and beach assessment, land use/land cover patterns, and urban structures in the coastal and highland environments. The flight missions involved fixed-wing as well as Quad and Hex systems that utilized optical visible, thermal-infrared, and multispectral systems (Walsh et al. 2015).

Field-Based Technologies

A host of geospatial devices and technologies are used in the field to collect primary data for analysis or to calibrate and validate derived data. In support of remote sensing image analysis, spectroradiometers, plant canopy analyzers, and 3D laser scanners (or terrestrial LiDAR) have made considerable contributions to environmental studies that seek, respectively, to define spectral response patterns of leaves and plants, characterize the leaf area index of plant canopies, and assess habitat conditions and terrain settings for the possible colonization by invasive species.

In the Galapagos, a spectral evolution PSR-1100 field portable spectroradiometer was used to link plants and patches of guava of different densities and ages to satellite imagery. The PSR-1100 has a spectral range of 320–1100 nm, a 3.0 nm spectral resolution at 600 nm, and a 1.5 nm sampling bandwidth. Spectral curves were generated for sample plant specimens in the field that extended from the visible to the near-infrared wavelengths. The typical spectral response curve for vegetation shows a relatively high green-visible wavelength response due to chlorophyll pigmentation, high near-infrared response due to healthy plant cell structure, and relatively low responses in the middle-infrared due to water absorption. The goal was to examine spectral patterns for target and background vegetation that may introduce spectral confusion at the larger satellite cell size and the integrated spectral response pattern. A Li-Cor plant canopy analyzer (LAI-2000) also was used to calculate the leaf area index from radiation measurements made with a "fish-eye" optical sensor (148° field of view) above and below the canopy to determine canopy light interception at five angles, from which LAI was computed using a model of radiative transfer in vegetative canopies. In addition, a FARO 3D laser scanner was used to examine the leading edge of guava infestation and eradication by discerning differences in plant forms, age structure, stem size and density, and the general architecture of guava plant canopies vs. other natural vegetation and cultivated crops. The raw laser scan datasets were prepared using the FARO SCENE software (FARO Technologies 2016). Preparation of the data involves importing the raw data from the scanner data storage into the SCENE software, the initial pre-processing and creation of a scan point cloud from the raw data, and finally, registering the multiple scan datasets together into a single point cloud for each study site. Walsh et al. (2008) reported that eradication of guava is most successful where stem density is relatively low and younger age plants and low-density patches occur where small islands of guava have not yet coalesced into continuous area extents or large vegetation patches.

Conclusions

The remote sensing scales—spatial, spectral, temporal, and radiometric—are fundamentally important in developing a mapping and modeling strategy to assess the composition and spatial structure of invasive plant species across the landscape and through time. Each remote sensing resolution offers special considerations in selecting an appropriate sensor system or systems to most effectively observe and/or measure the type and location of invasive species and their organizational and compositional structure at the leaf, plant, patch, or community level. The fusion of multiple remote sensing assets to extend the analysis from the local to the regional and from the visible to the near-infrared, middle-infrared, and thermal-infrared wavelengths (and beyond) has been well integrated into most landscape studies. Creating an image time series of multi-scale products is theoretically simple but often operationally difficult due to remote locations, environment characteristics of sites (e.g., clouds and shadows), and sensors that are locally managed by an on-site system operator vs. management by government or industry analysts of systems borne in satellites and/or aircraft. Field-based electronics and collected geospatial data offer considerable benefits for characterizing invasive species and habitat conditions that they prefer, but limited geographic extents of data collection are a potential limiting factor in their use, and the logistical constraints imposed by time and travel costs further retard intensive field campaigns, although the use of UAVs is revolutionizing local data collection efforts as sensor technology evolves to this new reconnaissance platform.

The use of land suitability, ecosystem, and species distribution models is important in incorporating presence-only data secured from remote sensing classifications and related approaches to develop probabilistic models of species location and spread over both time and space. The hyperspatial capacities of satellite systems such as Worldview, and now through UAVs, offer considerable improvements in modeling species distributions through an improved characterization of environmental factors and target conditions as well as the human dimension that influences invasive species distributions. The integration of geographic information systems with remote sensing and species distribution models affords special opportunities for characterizing invasive species as a consequence of extensive geospatial data available for most geographic settings; availability of hyperspatial data from satellites, aircraft, and now UAVs; and the fusion of hyperspectral data secured from remote sensing systems as well as field-based measurement technologies. Characterizing the human dimension using multi-thematic, geospatial data is crucial when species are influenced by land management decisions, land use/land cover change, and planting or eradication efforts.

While the remote sensing capacity for mapping and monitoring invasive species is improving as a consequence of increasing spatial and spectral resolutions, several challenges persist, for instance, related to the detection of sub-canopy invaders, the payload increase on UAVs, and the transformation of systems, such as LiDAR, from aircraft to the unmanned aerial vehicles. In addition, the management of large data volumes and the fusion of geometrically and spectrally diverse datasets and systems into an integrated mapping and monitoring system remain general obstacles to be overcome, particularly, related to invasive species.

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Chapter 9

Remote Sensing of Invasive Species in the Galapagos Islands: Comparison of Pixel-Based, Principal Component, and Object-Oriented Image Classification Approaches

Carolina Sampedro and Carlos F. Mena

Introduction

The Galapagos Islands are extremely vulnerable to many forms of human-related pressures, which have threatened the ecological integrity of the terrestrial and marine ecosystems (González et al. 2008). Some of the most common driving factors that act upon territory dynamics and may generate unsustainable development are extensive increase of traffic, tourism, and the resident population—which subsequently increases the demand for goods and services—as well as the arrival of invasive species. These issues seem to be repeated over and over again in the World Cultural and Natural Heritage monitoring mission reports on the Galapagos Islands (UICN 2007, 2010a, 2016). Therefore, terrestrial and marine ecosystems—especially in the inhabited islands—are degrading at an alarming rate, raising national and international concerns. In order to manage these driving factors, legal regulations and management plans have been put together by a joint effort of the Galapagos National Park Administration and the local and national authorities, as is the case of the new special law "Ley Orgánica de Regimen Especial de la Provincia de Galápagos" (Registro Oficial No. 520, 2015). Also, the efforts of private institutions, foundations, and NGOs have become key elements, having managed to launch several campaigns and projects to support conservation on the islands with international funding (González et al. 2008). For instance, over 50 million dollars were invested by governmental and

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international funds for the "Control the Invasive Species in the Galapagos Archipelago" project, which extended between 2002 and 2011 (Coello and Saunders 2011). Afterwards, the Ecuadorian government has just invested US$16,704,405 for the period of 2013–2017 in projects for the control and eradication of invasive species (Ministerio del Ambiente 2013). Nevertheless, in spite of those efforts, Galapagos was added to the World Heritage at Risk list in 2007 and, since 2010 when it was removed from the list, is still under continuous monitoring (UICN 2010b).

At the same time that millions are being invested in conservation efforts, the tourism industry has been growing at an average rate of 9.6% (Ministerio del Ambiente 2013), thus becoming the most important driver of the Galapagos economy and its rapid growth a key factor for change in the islands (Grenier 2000; Taylor et al. 2006). Such economic growth has boosted immigration from the mainland and has further increased coastal settlements and transformed them into large centers of economic activity. Tourism activities have generated abandonment of agriculture and cattle ranching, which occupied the human-use areas on the humid highlands. Therefore, the proportion of rural population in Galapagos decreased from 42% in 1974 to just 17% in 2010 (INEC 2010). In consequence, these areas are likely to become centers of establishment and propagation of invasive species, such as guava and blackberry (González et al. 2008), which will easily invade neighboring properties, including the national park restricted area. Moreover, the abandonment of agricultural lands and the establishment of new settlements in areas close to the sea has proven to increase the importation of supplies from the mainland, which in turn are the most important source of arrival of more invasive species (Cremers 2002; González et al. 2008). In this sense, it is essential for governmental authorities and other stakeholders to be able to access reliable information regarding land use and land cover dynamics. Accurate and up-to-date land use and land cover change information will allow the monitoring and assessment of spatial processes, which emerge from the highland's ecological and social processes.

Remote sensing image classification is a commonly used method to obtain land use and land cover (LULC) information from satellite images (Yan et al. 2006). Nevertheless, identifying the most appropriate approach should be based on the characteristics of each specific situation (Lu and Weng 2007), given that each classification algorithm has advantages and disadvantages. In this sense, a comparative study of different classifiers should be conducted in order to find the best classification method for a specific study area (Pal and Mather 2003, 2004; South et al. 2004). This research tries to evaluate the performance of three classification techniques for land cover mapping as well as for invasive species identification (i.e., guava) in the agricultural area of San Cristobal Island in the Galapagos: (a) pixel-based hybrid (supervised/unsupervised classification), (b) principal component pixel-based hybrid, and (c) object-oriented image hybrid classifications, as well as the evaluation of three parametric classification algorithms (maximum likelihood, Mahalanobis distance, and minimum distances). In order to assess the classifications, nine land use and land cover classes were obtained: crops, abandoned lands, coffee cultivation, wax apple fields, guava, pastures, bare soils, natural vegetation, and infrastructure.

In this context, the use of remote sensing techniques and the evaluation of different mapping methods for the identification of invasive plant species in Galapagos is essential, as it is a tool that does not necessarily require physical contact in the field (Schott 1997). This is especially important in the case of the Galapagos Islands, which have restrictions on accessibility to most of the national park areas. The three classification techniques to be evaluated in this work aim to transform satellite images into a usable geographic product (Wilkinson 2005), through finding meaningful patterns in spectral image data.

Study Area

Invasive species in the Galapagos Islands are concentrated on five islands: Santa Cruz, Isabela, San Cristobal, Floreana, and Santiago. These islands present adequate conditions for invasive species to grow, as they have high elevations and humid zones, where the problem of invasive species has become apparent with greater magnitude (Ministerio del Ambiente 2013). Also, four of them (Santa Cruz, Isabela, San Cristobal, and Floreana) are inhabited by human residents, who import supplies and develop agricultural activities. As mentioned before, the presence and sustained population growth can be directly related to the introduction of alien species, either intentionally or accidentally (González et al. 2008). In consequence, the selected study area concentrates on the highlands of San Cristobal Island, which have evident problems—especially with guava, wax apple, and blackberry—and are on the island with better logistic conditions for fieldwork.

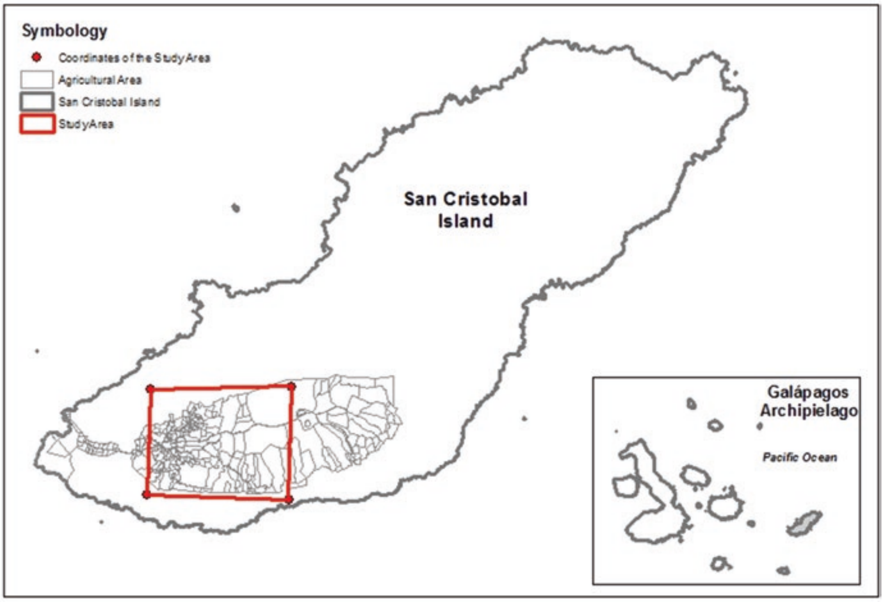

Fig. 9.1 Location of study area

The study area is located in the humid zone of the San Cristobal Island in the Galapagos Archipelago. The study area is made up of approximately 5992 ha, from which the agricultural area covers 55% and the remaining 45% are part of the national park area (Fig. 9.1). The agricultural area is subdivided into private farms owned by San Cristobal's residents, while the national park area is a restricted conservation area. The extent of the study area was limited based on the availability of up-to-date Landsat images with almost no cloud cover.

Data

This research uses a series of datasets that include ground data collected by our team, high- and mid-resolution satellite images, and secondary data from various sources.

Ground Data: The samples for land cover and land use types were collected in a field campaign, which took place in July 2011. Only 60 field sites could be recorded to inspect their land use/cover classes as a result of accessibility and budget restrictions. A stratified random sampling was made based on a first-generated classification map prepared for the field campaign; the 60 points were collected in the field with restrictions mainly of road accessibility. Afterwards, 27 validation points were selected on the high-resolution World View image, which were visually interpreted and assigned to one of the land use/cover classes already defined. As when using high-resolution information, the analyst interpretation is not only as accurate as collected ground truth data but also faster and cost-effective (Rozenstein and Karnieli 2011). Nevertheless, an even distribution for the classes was not achieved. The 87 points from different types of LULC (land use and land cover) were registered in a Universal Transverse Mercator (UTM) 15 South projection (Table 9.1).

In addition, ground control points were registered by recording points such as road intersections and property boundaries, which could be identified in the image. The ground control database accounts for ten features.

Table 9.1 Ground data collected in the field

Classes	Field points
Abandoned lands	5
Wax apple fields	11
Coffee cultivation	9
Crops	12
Guava	13
Infrastructure	4
Bare soils	0
Pasture	28
Natural vegetation	5
Total	87

Satellite Data: A Landsat ETM+ image of the study area was obtained on 21 March 2011 (WRS Path 17—Row 61) from which six multispectral bands were used (1, 2, 3, 4, 5, 7) with a resolution of 30 × 30 m. The cloud coverage corresponds to 6.57% of the scene and affects 12.2% of the study area. This area is usually covered by dense clouds; in consequence, the image was selected considering the year and its low cloud coverage in the study area. Additionally, this data is typically affected by a breakdown of one of the sensors; however, the coverage of the study area was completely unaffected by such damages.

The image was cut to fit the study area and was then masked in order to eliminate the small amount of clouds. Finally, a geometric rectification of the imagery was undertaken using a first-order polynomial with a nearest neighbor interpolation, incorporating the DEM with ten ground control points, producing an RMSE of less 0.5 pixels (7.5 m).

***Secondary Data**:* We used a high-resolution World View II image collected on 23 October 2010 with a cloud cover of 6.4%. This image covers approximately 40% of the western part of the study area. Also, a geodatabase with basic datasets, such as the island boundaries, roads, property boundaries, and agricultural boundaries, among others, was obtained from the municipality of Puerto Baquerizo Moreno.

Methods

The three stages of our methodology include pre-processing, classification, and validation components, in brackets (see the workflow in Fig. 9.2). Pre-processing included geometric rectification of the Landsat image and all other secondary data. Classification methods were adjusted using a training database obtained through field observations and a high-resolution image from World View II. During validation, assessment of classification methods was made using accuracy of nine land classes using a kappa index.

Classification Methods

Pixel-Based Hybrid Supervised/Unsupervised Classification

This approach combines an unsupervised classification algorithm, spectral signature depuration, and supervised classification algorithms (Messina et al. 2000). The values presented in Table 9.2 were selected through processing experience and literature reports (Messina and Walsh 2001; Ministerio de Medio Ambiente, S.B 2010).

During the unsupervised classification, 255 classes were established based on the fact that 255 is the most number of classes that can be selected while being able to maintain an 8-bit data structure (Messina and Walsh 2001). A preliminary attribution for each class was made through visual analysis using the World View II image.

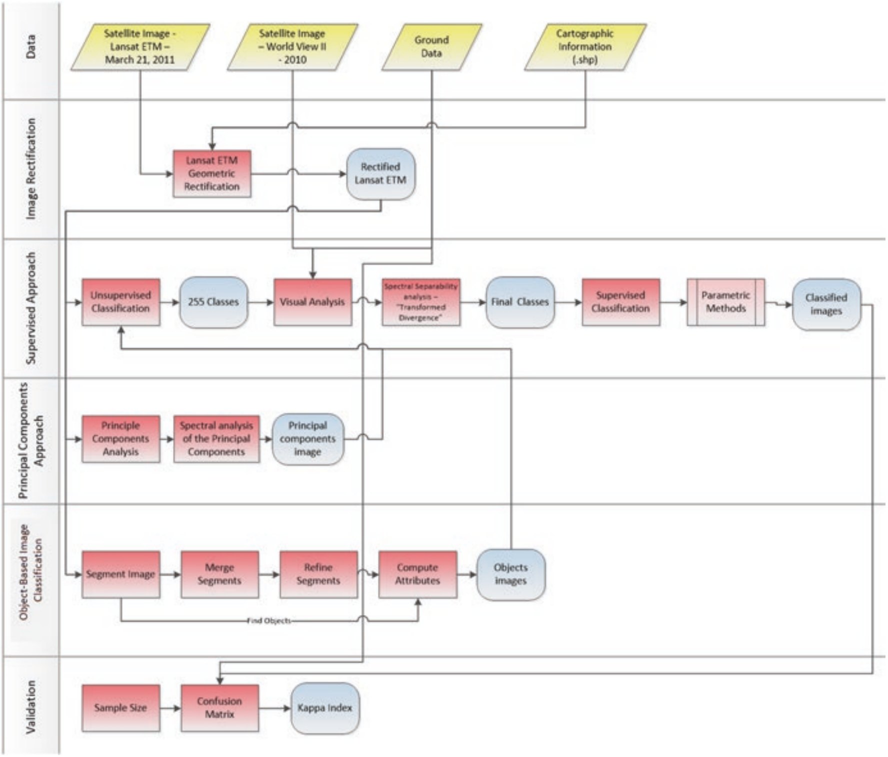

Fig. 9.2 Workflow

Table 9.2 Hybrid supervised/unsupervised classification steps

Unsupervised classification	Signature evaluation	Supervised classification
ISODATA	Evaluate separability	Input the edited signature set
255 classes	Transformed divergence	Parametric and nonparametric method
24 iterations	>1950 for acceptability	
0.98 convergence		

After unsupervised classification, the separability of the spectral signatures was analyzed using the transformed divergence method, which allowed the reduction of the original 255 spectral signatures into 36 spectral signatures or classes with a signature separability threshold of >1950, generating very limited overlap between classes (Messina and Walsh 2001). These 36 categories were assigned to 9 classes through visual analysis, which represent meaningful units of the study area: crops, abandoned lands, coffee cultivation, wax apple fields, guava, pastures, bare soils, natural vegetation, and infrastructure.

Once the statistical separable classes were identified, a supervised classification was carried out, testing the different parametric methods: Mahalanobis distance, minimum distance, and maximum likelihood. After all methods were processed in supervised classifications, a visual evaluation was performed through the overlap of the image with the training database and with secondary information from various sources. The aim of this step was to verify firsthand the consistency of the obtained information.

Principal Components with Hybrid Supervised/Unsupervised Classification

This approach uses the hybrid supervised/unsupervised classification method developed above and adds a set of bands that comes from the principal components of the original image. The principal component analysis (PCA) is a spectral enhancement technique that compresses the spectral bands and extracts new bands of data eliminating noise and redundant information through statistical algorithms (Ceballos and Bottino 1997; Erdas Inc 1999). It is important to note that the first principal component stores the maximum contents of the original data set's variance, and the second PC describes the large amount of the variance in the data that has not been described by the first PC and so on (Tayor 1977). Then, the eigenvalue of each band was analyzed, and the number of the PC bands chosen to enter into the classification analysis was determined.

Object-Based Hybrid Supervised/Unsupervised Classification

Spectral classification can be executed on a per-pixel or object-oriented basis. The per-pixel approach is the traditional classifier, which develops a signature by combining the spectra of all training-set pixels from a given feature. Thus, the resulting signature contains the contributions of all materials present in a given training-set of pixels (Myint et al. 2011). The object-oriented classifier segments the image by a merger of pixels into objects, based on specific parameters such as texture, continuity, spectral information, and others. (Desclée et al. 2006; Im et al. 2008; Myint et al. 2008). The classification is conducted based on those objects instead of an individual pixel (Myint et al. 2011).

This approach has been widely used on high-resolution images, especially in urban studies (Myint et al. 2011), but has also been used on complex landscapes such as mangroves and forests (Desclée et al. 2006; Yan et al. 2006; Xie et al. 2008; Duro et al. 2012). It has had very good results because it overcomes the problem of salt-and-pepper effects found in classification results from the traditional per-pixel approach (Xie et al. 2008).

The parameters used for the segmentation process were established for the specific area as presented in Table 9.3. These values were established based on a trial-and-error test within the different segment, merge and refine settings, trying to detect which of the different configurations in the feature extraction segmentation interface of the ENVI software better suited the grouping objects in the study area. For doing so, several spatial (area, compactness, etc.) and spectral (standard deviation of each band) parameters were considered. Also, a visual verification of the objects was part of the process. The basic premise was that objects should be as homogenous as pos-

Table 9.3 Parameter settings for the feature extraction

Phase	Parameters	Settings	Observation
Compute attributes	Segment algorithm	Intensity	
	Segment value	10	
	Merge algorithm	Full lambda schedule	Including the six image's strips
	Merge value	0	
	Texture kernel size	3	

sible. A final shapefile with all the information of the attributes was obtained from this process. Subsequently the hybrid classification was carried out.

Validation

In thematic mapping from remotely sensed data, the term "accuracy" is typically used to express the degree of "correctness" of a map or classification (Foody 2002). A thematic map derived from a classification may be considered accurate if it provides an unbiased representation of the land cover of the region it portrays (Foody 2002). Therefore, classification accuracy refers to the degree to which the derived image classification agrees with reality or conforms to the "truth" (Smits et al. 1999).

To evaluate data precision, a confusion matrix was produced using verification points established with the sample size, determined using the following formula (Magnani 1999):

$$\mathrm{ss} = \frac{Z^2 * (p) * (1-p)}{c^2}$$

where:

$Z = Z$ value → 1.96 for a 95% confidence level
$p =$ percentage → 0.5
$c =$ confidence interval → 0.01

$$\text{new ss} = \frac{\mathrm{ss}}{1 + \frac{\mathrm{ss}-1}{\mathrm{pop}}}$$

where:

Pop = population → 66,576 pixels

The sample number accounted for was 96 sample points, from which only 87 points were used due to lack of availability of primary information.

The assessments of the LULC map's classification accuracy were conducted by comparing true ground data with the classified layers (Congalton 1991). For ease of comparison between classification methods, thematic accuracy was undertaken using only the point-based reference data mentioned above. There was no consideration of any object-based accuracy assessment or accuracy measures relating to the geometric accuracy of the objects (such as location and shape) (Whiteside et al. 2011; Aguirre-Gutiérrez et al. 2012).

Accuracy assessments of all nine classifications were undertaken using confusion matrices and kappa statistics. Producer and user accuracies for each class were calculated as well as the overall kappa coefficient. The statistical significance of the difference between the kappa coefficients for the pixel-based, principal component, and object-based classifications was assessed using a marginal homogeneity test.

The kappa (K) coefficient measures the agreement between classification and ground truth pixels. A kappa value of 1 represents perfect agreement, while a value of 0 represents no agreement (ENVI EX 2009):

$$\kappa = \frac{N\sum_{i=1}^{n} m_{i,i} - \sum_{i=1}^{n}(G_i C_i)}{N^2 - \sum_{i=1}^{n}(G_i C_i)}$$

where:
i = the class number
N = the total number of classified pixels that are being compared to ground truth
$m_{i,i}$ = the number of pixels belonging to the ground truth class$_i$ that have also been classified with a class$_i$ (e.g., values found along the diagonal of the confusion matrix)
C_i = the total number of classified pixels belonging to class$_i$
G_i = the total number for ground truth pixels belonging to class$_i$

Results

This book chapter shows the comparison between three different classification methods used to identify land use and land cover and segregate invasive species in the Galapagos Islands. Figure 9.3 shows the nine classification results corresponding to the application of the three classification methods: pixel-based (PB), principal component (PC) pixel-based, and object-based (OB) and the three parametric decision rules that were applied for each classification (maximum likelihood, Mahalanobis distance, and minimum distance).

As mentioned before, the study area of the agricultural zone in San Cristobal Island is very complex due to countless social processes that have been taking place and that continue to reshape the territory. For instance, the abandonment of the agricultural farms and the rapid spread of invasive species such as guava, blackberry, and wax apple have created a very diverse landscape with a high mixture of plant composition in very small plots of land. Nonetheless, the three tested methods were able to capture the complexity of the composition of the land use and land cover structures in the area.

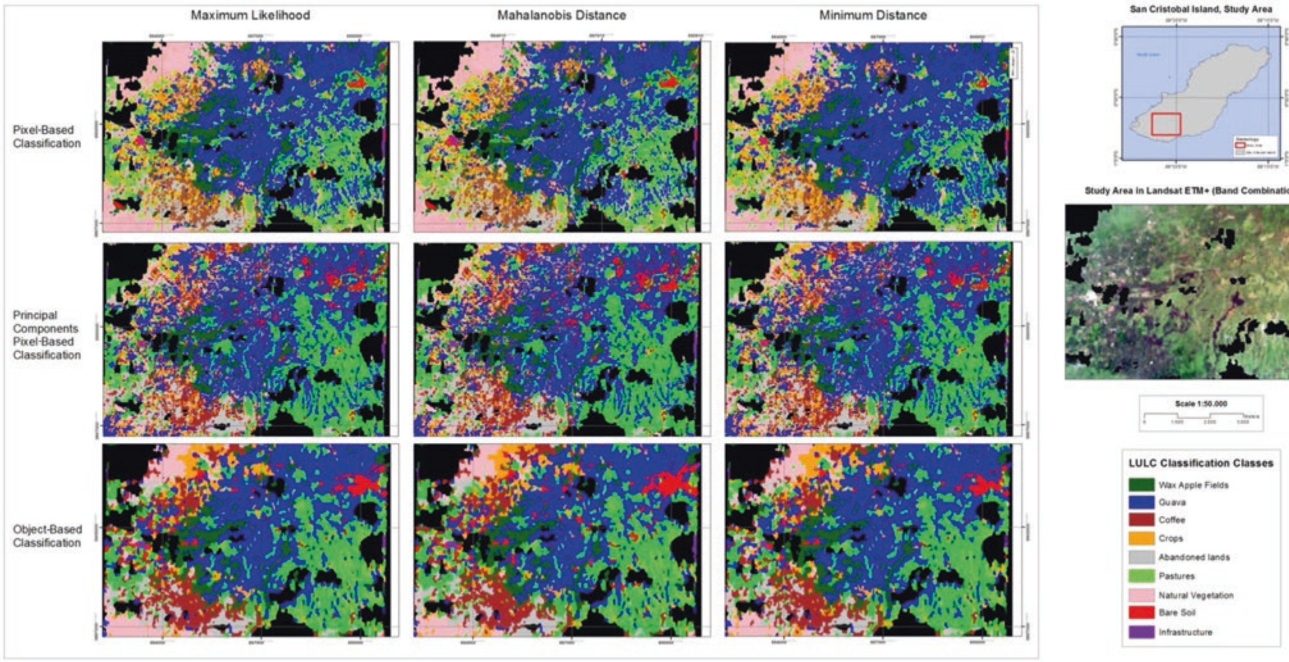

Fig. 9.3 Classification results

The segmentation of the Landsat image for the object-based analysis provided 6702 objects for classification (Fig. 9.4). The mean size of the objects was 0.89 ha, while the smallest object was 0.18 ha and the largest one was 4.41 ha.

According to Table 9.4, the results of the three classification approaches show that the land cover class occupying the largest area is “guava” (PB, 1801.14 ha; PC, 1716.48 ha; OB, 1837.92 ha), while the smallest area is “infrastructure” (PB, 21 ha; PC, 17.19 ha; OB, 18.96 ha). In addition, it is possible to identify certain differences between the areas of some classes. The area classified as “pasture” is noticeably lower in the pixel-based classification compared to the two other classification approaches. “Natural vegetation,” meanwhile, shows a higher value in the pixel-based classification compared to the other approaches. Nevertheless, the area of classes such as “infrastructure,” “guava,” and “wax apple fields” is relatively similar in the three approaches. Overall, there is consistency in the area results of the three tested approaches, as shown in Fig. 9.5.

All the above mentioned findings were supported by a visual comparison with the classification images in Fig. 9.3. It is possible to visualize the “natural vegetation” class as apparently underrepresented in the object-based classification, and especially so in the principal component pixel-based classification, while there is an apparent overrepresentation of the “pasture” classes. On the other hand, in accordance to the area values, it is possible to identify consistencies in the identification of “guava,” “wax apple fields,” and “crops” given that the three results are visually very similar.

“Natural vegetation” seems to cause confusion with other classes such as “coffee,” “pastures,” and “crops,” especially on the principal component approach. The same seems to happen with “bare soil,” which seems to be overrepresented with the principal component and object-based approaches. All these variations on classes’ representation are possible to read by a visual inspection, which is supported by the standard deviation graphic presented in Fig. 9.6. It clearly shows that “natural vegetation” and “pastures” are the ones with more variation in the area results, while “infrastructure,” “crops,” “guava,” and “wax apple” have less variation in the nine classification results.

The validation of our results is shown in Fig. 9.7, which presents the kappa index calculated for each approach. Overall, the pixel-based classification had a better outcome in all three parametric decision rules based on the kappa index (*maximum likelihood*, *0.8640*; *Mahalanobis distance*, *0.8610*; *minimum distance*, *0.7959*), which can be interpreted as a very good consistency strength according to Fleiss (1971). While the object-based classification had an underperformance compared to the other two methods (*maximum likelihood*, *0.7029*; *Mahalanobis distance*, *0.5735*; *minimum distance*, *0.5429*). “Abandoned land,” “infrastructure,” and “coffee” obtained the higher user’s and producer’s accuracy values (over 70% user’s and producer’s accuracy). It is worthwhile mentioning that there may be classes with fewer ground data samples, such as “natural vegetation,” “bare soil,” and “infrastructure,” and this evidences a possible bias in the accuracy results.

A marginal homogeneity test was used to identify if the similarity between the classification results and the reference data was statistically significant. The pixel-based classification was the approach with better outcomes, which reaffirms our

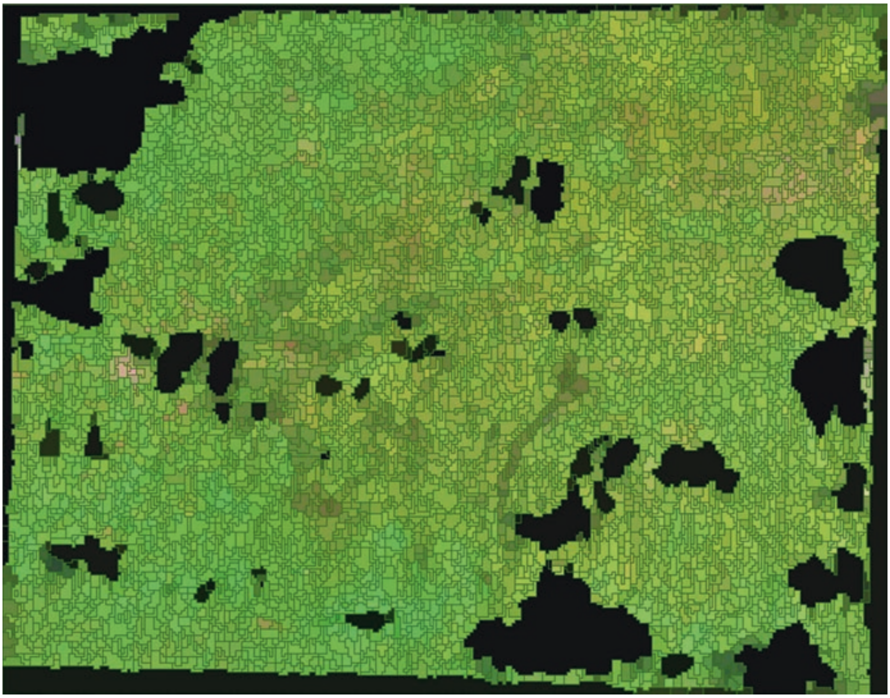

Fig. 9.4 Image segmentation result: object-based image

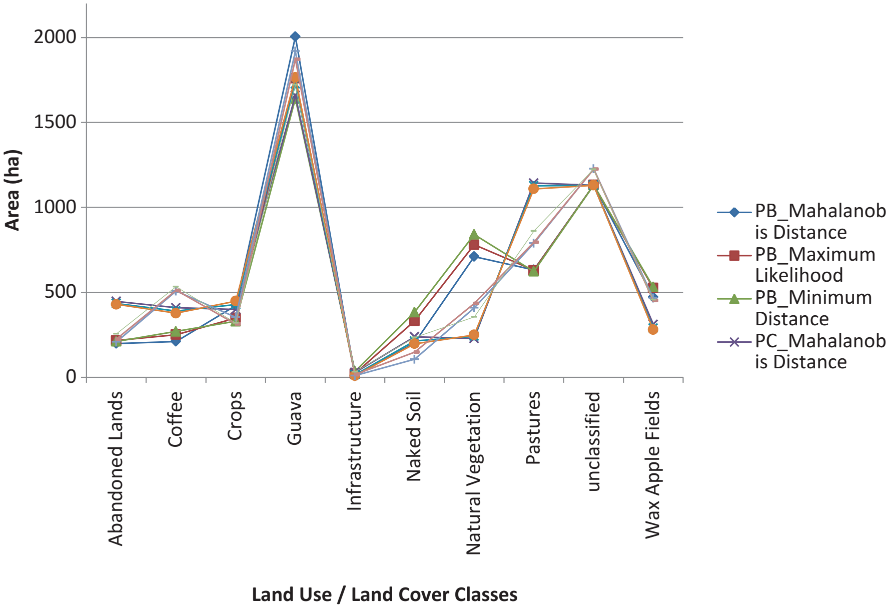

Fig. 9.5 Area values (ha) for each class, within each classification method

Table 9.4 Area (hectares) of land cover classes obtained by three methods using different selection algorithms

	Pixel-based—area (ha)				Principal components—area (ha)				Object-based—area (ha)			
	Mahalanobis distance	Maximum likelihood	Minimum distance	Mean	Mahalanobis distance	Maximum likelihood	Minimum distance	Mean	Minimum distance	Maximum likelihood	Mahalanobis distance	Mean
Abandoned lands	198.45	215.73	210.42	208.2	447.03	434.16	429.03	436.74	207.45	224.91	255.51	229.29
Coffee	210.96	250.74	269.64	243.78	409.14	389.79	376.92	391.95	507.33	511.56	532.53	517.14
Crops	422.37	348.75	329.31	366.81	398.16	427.23	448.2	424.53	353.43	313.11	319.59	328.71
Guava	2004.66	1759.23	1639.53	1801.14	1658.52	1725.93	1764.99	1716.48	1919.43	1872.54	1721.79	1837.92
Infrastructure	7.65	21.15	34.2	21	28.08	14.58	8.91	17.19	9.09	16.38	31.41	18.96
Naked soil	202.95	330.75	383.22	305.64	238.5	212.76	196.38	215.88	105.75	147.51	233.82	162.36
Natural vegetation	710.73	779.85	840.87	777.15	228.15	241.65	248.49	239.43	408.6	434.79	355.41	399.6
Pastures	632.07	629.82	622.89	628.26	1143	1127.16	1108.89	1126.35	788.4	794.61	861.21	814.74
Unclassified	1131.21	1131.3	1131.21	1131.24	1130.22	1130.22	1130.22	1130.22	1226.97	1225.08	1224.27	1225.44
Wax apple fields	470.79	524.52	530.55	508.62	311.04	288.36	279.81	293.07	465.39	451.35	456.3	457.68
Total general	*5991.84*	*5991.84*	*5991.84*	*5991.84*	*5991.84*	*5991.84*	*5991.84*	*5991.84*	*5991.84*	*5991.84*	*5991.84*	*5991.84*

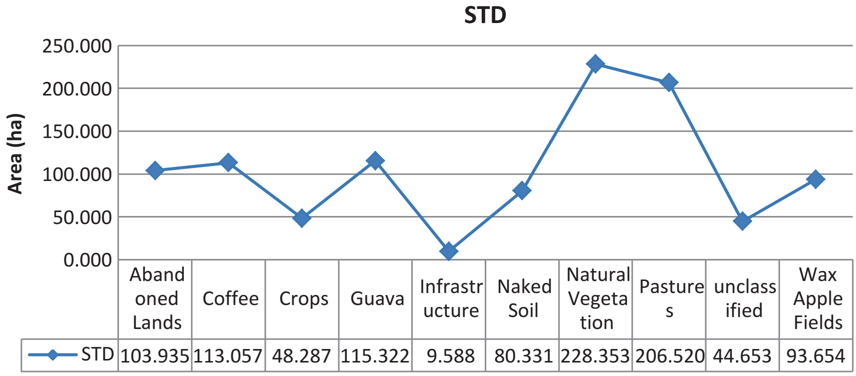

Fig. 9.6 Standard deviation of the area (ha) values for each of land use/land cover class, from the nine classification results

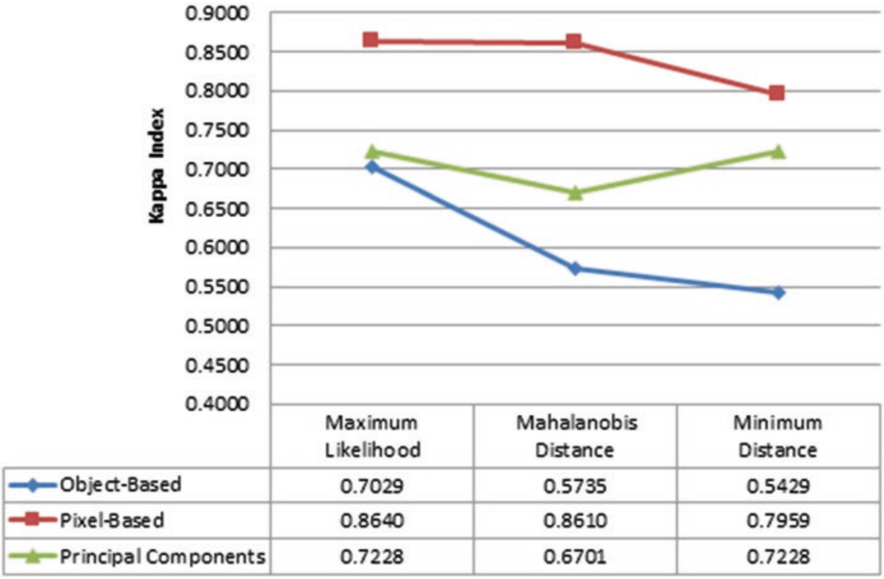

Fig. 9.7 Kappa results

findings mentioned above. Both maximum likelihood and Mahalanobis distance decision rules turned out to be statistically similar with p values of 0.2714 and 0.2714, respectively. The principal component pixel-based with Mahalanobis distance had a $p = 0.1$. The difference in overall classification results was not statistically significant ($p < 0.05$), see Table 9.5.

Specifically, in the case of the invasive species guava and wax apple, the accuracy results were over 80% for the pixel-based approach. As for the object-based and principal components, the percentage of accuracy decreased up to 50%. Result information is shown in Table 9.6.

For visual demonstration of the classification results of “guava” and “wax apple,” Fig. 9.8 shows a subset of small areas of interest. As it is possible to see, “wax apple” has a strong signature and is very well defined in all the classification meth-

Table 9.5 Marginal homogeneity significance values

Object-based	Maximum likelihood	0.0367	$p < 0.05$
	Mahalanobis distance	0.0315	$p < 0.05$
	Minimum distance	0.0067	$p < 0.05$
Pixel-based	Maximum likelihood	0.2714	$p > 0.05$
	Mahalanobis distance	0.2714	$p > 0.05$
	Minimum distance	0.0050	$p < 0.05$
Principal components	Maximum likelihood	0.0231	$p < 0.05$
	Mahalanobis distance	0.1000	$p > 0.05$
	Minimum distance	0.0231	$p < 0.05$

Table 9.6 User’s and producer’s accuracy for guava and wax apple fields

			Wax apple fields (%)	Guava (%)
Object-based	Maximum likelihood	Producer’s accuracy	83.33	61.90
		User’s accuracy	90.91	100.00
	Mahalanobis distance	Producer’s accuracy	90.00	50.00
		User’s accuracy	81.82	100.00
	Minimum distance	Producer’s accuracy	75.00	50.00
		User’s accuracy	81.82	92.31
Pixel-based	Maximum likelihood	Producer’s accuracy	83.33	81.25
		User’s accuracy	90.91	100.00
	Mahalanobis distance	Producer’s accuracy	83.33	81.25
		User’s accuracy	90.91	100.00
	Minimum distance	Producer’s accuracy	83.33	63.16
		User’s accuracy	90.91	92.31
Pixel-based—principal component	Maximum likelihood	Producer’s accuracy	100.00	54.17
		User’s accuracy	81.82	100.00
	Mahalanobis distance	Producer’s accuracy	100.00	54.17
		User’s accuracy	81.82	100.00
	Minimum distance	Producer’s accuracy	100.00	54.17
		User’s accuracy	81.82	100.00

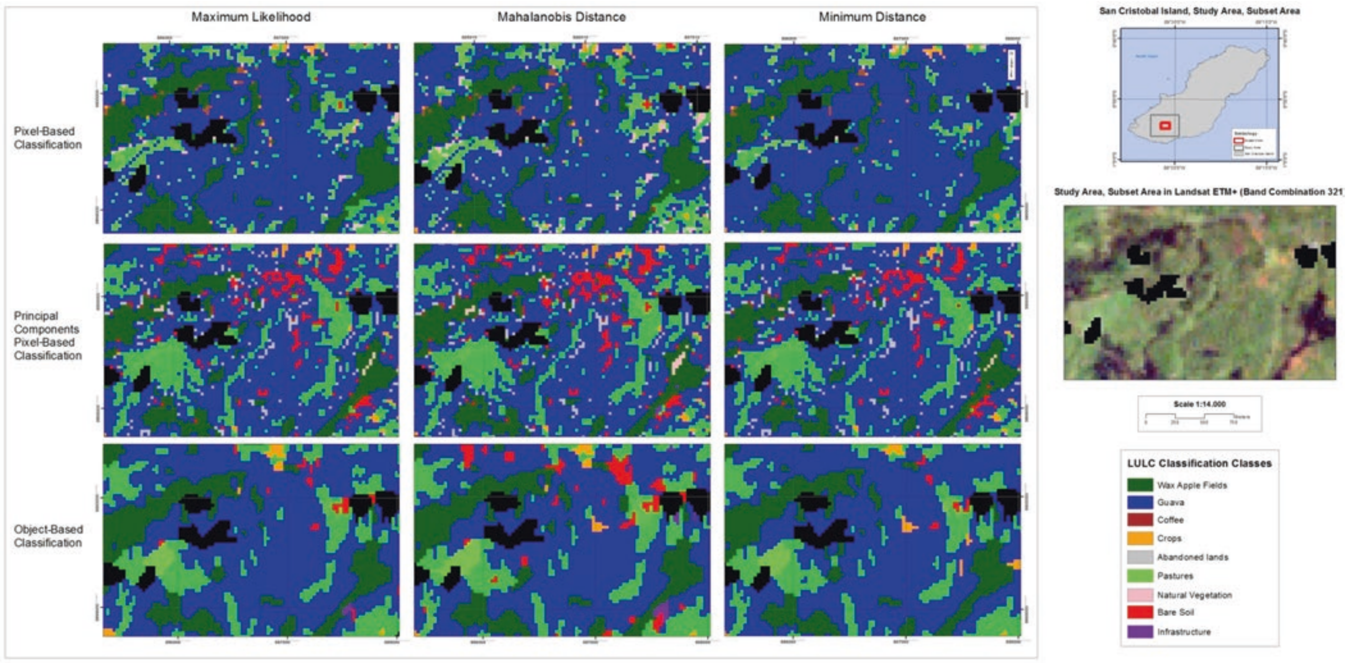

Fig. 9.8 Subset area for invasive species classification review for each of the nine results

ods. Nevertheless, pixel-based classification is the one that shows better delimitation detail of the wax apple field's area. The object-based classification presents a coarser delimitation, in which some of the border details are lost. On the other hand, the "guava" results vary; the principal component classification shows a strong salt-and-pepper effect and some confusion with the signature of "pastures," "bare soil," and "abandoned lands." The pixel-based and object-based approaches give a more solid result.

It is important to mention that these invasive species characterize for dominating big areas and allowed a medium-resolution image to capture its spectral characteristics. This is not the same for species like blackberry, which grows understory of other endemics, making it very difficult to identify, even with high-resolution images.

Conclusions

In general, the nine classification results using either pixel-based, principal component pixel- based, or object-based image classification created similar and visually acceptable representations of the land cover classes within the study area. Despite the expected "salt-and-pepper" effect in the pixel-based analysis, the pixel-based classifications offered a more generalized visual appearance and more contiguous interpretation of land cover compared to the object-based classification.

The pixel-based classification had a better outcome from evaluation than the other approaches, given that the overall accuracy of this approach presented a higher kappa than the three parametric decision rules tested. The object-based classifications had the lower kappa index for the same three tested parametric decision rules. The marginal homogeneity test performed a comparison between each classification outcome and the referential data. Despite the low sample size of the test set and associated wider confidence limits, it revealed that the obtained results reinforce the idea that the pixel-based approach using maximum likelihood or Mahalanobis distance decisions rules has a better performance than the other approaches.

The object-based approach, in this case, has a mean size object of almost 1 ha; it might contain more than one spectrally distinct land cover given that it tends to generalize the results. This particular characteristic of the object-based classifier has been recognized as a design tool to deal with the problem of environmental heterogeneity and has indeed shown to be effective for improving classification accuracy in some cases (Aplin and Atkinson 2001; Lloyd et al. 2004). The object-based approach may conceive classes as a redefined concept which transforms the traditional land cover or vegetation classes into more contextual classes (Whiteside et al. 2011) but might sometimes be difficult to apply in diverse systems.

In terms of the pixel-based approaches analyzed here, the principal component image that was created from the first two PCs, which contain 98.81% of the information, did not show the same discrimination ability than the original six-waveband information did. It might be the case that the discarded PCs may be necessary for proper discrimination of specific land cover types (Li and Yeh 1998). As a consequence, an overestimation of some classes, and underestimation of others, appears to have happened, and a visible "salt-and-pepper" effect can be seen. Meanwhile, the pixel-based approach captured the heterogeneity of the agricultural landscape with very good consistency and showed a better reading of the spectral signal of the classes compared to the other two approaches.

This methodological exercise was performed because the monitoring of land cover, using remotely sensed data, requires robust classification methods to allow accurate mapping of complex land cover and land use categories (Rodriguez-Galiano et al. 2012). The use of remote sensing techniques and the evaluation of different mapping techniques for the identification of invasive plant species in the Galapagos Island is necessary. Remote sensing technology has attracted considerable interest in the field of invasive species in recent years. It is a tool that offers proven advantages, which include a synoptic view, multispectral data, multitemporal coverage, and cost-effectiveness (Van der Meer et al. 2002). It has also proven to bring a practical approach when studying complex geographic terrain types and diverse inaccessible ecosystems like the ones present in the Galapagos Islands.

Guava, blackberry, and wax apple, among others, are several of the invasive species that threaten the sensitive ecosystem of the Galapagos Islands. Very costly efforts have been made to eradicate the mentioned species, but none have had the desired effect. Currently, management of invasive species seeks to control invaders and mitigate their impact rather than aim at eradication. Limitation of resources forces land managers to carefully plan and prioritize interventions only in areas that are most severely affected by invaders. For this important reason, information on the current and potential distribution of invaders is considered crucial for their management (Joshi 2006). For doing so, it is important to consider that these methods should be applied to broad areas, and for budget and accuracy interests, they should be based on free images (when possible) and on specific methodological procedures, which could be easily replicated by professionals in different areas.

Nevertheless, spatial and spectral information provided by moderate spatial- and spectral-resolution satellite images is insufficient to decipher the complexity of natural environments and further delineate the distribution of alien plants. Large swath width and pixel size are unique characteristics of high temporal resolution images and can frequently monitor the spread of alien plants over a broad region. However, images would capture not only the species but also other components such as untargeted plants, surface soils, and senescent vegetation which could limit the ability of images for invasive plant monitoring unless one species dominates an entire system (Huang and Asner 2009). As was mentioned before, most of the remote sensing for invasive species approaches has been oriented at species that dominate the canopy or are members of a multispecies canopy and directly reflect electromagnetic radiation. Nevertheless, other approaches should be developed to deal with invaders with different characteristics that have strong effects on the natural ecosystems, as is the case with blackberry in the Galapagos. In this sense, future investigation should focus on using different methods, which may help in identifying the presence of these types of invasive species in ecosystems.

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Chapter 10
Stakeholder Perceptions of Invasive Species and Participatory Remote Sensing in the Galapagos Islands

Laura Brewington

Introduction

The upper-elevation slopes of the larger islands in the Galapagos archipelago of Ecuador are high enough to push moisture-bearing air masses upward, bringing significant precipitation to upland areas (Perry 1984). The presence of mineral-rich volcanic soil makes these regions favorable for agriculture, and they were exploited by the islands' early settlers in the 1800s (Herrera 2008). They also proved to be easily invaded by plants introduced for cultivation, including common guava (*Psidium guajava*), a small fruit-bearing tree (Binggeli 2001). Other top plant invaders, including hill raspberry (*Rubus niveus*), elephant grass (*Pennisetum purpureum*), and rose apple (*Syzygium jambos*) have been present in the highlands for decades (GNPS 2009). The majority of the islands' nearly 900 non-native vascular plants are now found in these upland zones, which are considered to be the most degraded regions in the archipelago (Tye 2006; Guézou et al. 2010; Trueman et al. 2010).

A transformer species, common guava shades out other vegetation and alters soil composition, making it a threat to both native species and agricultural crops (Itow 2003: 53). In 1970, Itow found the plant in abundance in the agricultural zone of Isabela—the largest island in the Galapagos—with a human population of around 2500 (Itow 1971; INEC 2010). Called the archipelago's "most widespread intruder" (Schofield 1989), Walsh et al. (2008) estimated that guava covers more than 40,000 ha of southern Isabela's private and protected lands, the same figure that Stone et al. (1988) estimated two decades earlier for the total archipelago-wide area invaded by guava. Because of guava's extensive presence on Isabela, control, rather than eradication, is the most feasible management option.

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Worldwide, satellite systems have been relied on to gather spatial information about environmental change, particularly where assessments of land cover on the ground can be hindered due to private property rights, remote locations, and difficult terrain (Messina and Walsh 2001; Evans and Kelley 2004; Walsh et al. 2006). Assessments of land use and land cover change are frequently used to settle contentious debates about human impacts on local and global ecosystems (Meyer and Turner 1994; Gutman et al. 2004; Malanson et al. 2006; Walsh et al. 2008). The creation and interpretation of maps of land cover change, however, are typically in the hands of bureaucrats, environmental managers, NGOs, or outside research groups. Categories are fixed, and patterns are described according to the urgency of a particular environmental issue. One of the benefits of conducting an empirical study of landscape use is the ability to distinguish trends in ecological change and its differential impacts on particular stakeholder groups, while the incorporation of local knowledge can offer fresh insights into the causes and consequences of landscape change (Rocheleau 1995; Herlihy and Knapp 2003). By creating and comparing different interpretations of the land, participatory spatial analysis can be a rich tool to address the interests of traditionally underrepresented groups in natural resource control (Nevins 2004; Duncan and Lach 2006), disaster risk reduction (Cadag and Gaillard 2012; de Andrade and Szlafsztein 2015), land use planning (Sandström et al. 2003), and protected area management (Scholz et al. 2004; Taylor 2009).

Remote sensing analysis of land change can also reveal additional stories and a broader understanding of the social aspects of the landscape once synthesized with qualitative research (Matthews et al. 2001; Jiang 2003; Dennis et al. 2005; Brown 2006; McCall and Dunn 2012). Community-generated map products can challenge existing spatial documents or supplement management activities by incorporating local knowledge (Robbins 2003). Few studies quantitatively compare local knowledge-derived land cover classifications by separate stakeholder groups, where they diverge and why (Robbins 2001). The present study contributes to this growing body of literature that uses participatory mapping to qualitatively and quantitatively evaluate different stakeholder perceptions of land cover and the changing nature of the highlands of Isabela Island. Specifically, this study seeks to resolve (1) how different stakeholder groups “see” landscape cover and change in the Isabela highlands and (2) what competing conceptions of the landscape mean in terms of environmental management and the future of agricultural and conservation activities on Isabela.

Methods

Study Area

Isabela Island was first settled by a small group of Ecuadorian colonists in the late 1800s, who cultivated fruits and vegetables and raised livestock in the humid highlands along the southeastern-facing, windward flanks of the Sierra Negra volcano

(Perry 1984). Guava fruit contains vitamin C, fiber, and calcium, making it a desirable crop when few other nutrition sources are available, and cattle, donkeys, and pigs facilitated its rapid spread across farmland and into what is now the Galapagos National Park. Mainland prisoners were sent to the island in 1946, where many were put to work in agriculture (Gordillo and Tupiza 1989), and a wave of rural migration from Ecuador's Andean provinces occurred in the 1960s and 1970s. By the year 2000, there were 108 privately owned production units spread out over 5211 ha in Isabela's highlands (SICA-MAG 2002). Farms range in size from 0.5 to 200 ha, many of which belonged to original settlers and have since been subdivided among children and grandchildren.

Highland microclimates differentiate the production capabilities of Isabela's farms (Fig. 10.1). Those located along the western edge of the region experience a wetter, cooler climate and are generally much larger (50–200 ha) than farms to the south and east. This area was formerly used for livestock ranching but is now largely abandoned. Lower-elevation farms tend to be smaller and more intensively cultivated, and the region's drier climate facilitates a wide variety of food crops, primarily sugar cane, papaya, oranges, melons, beans, tomatoes, and greens (Chiriboga et al. 2006). A small number of farms cultivate shade-grown coffee that is exported to the mainland for processing and sale.

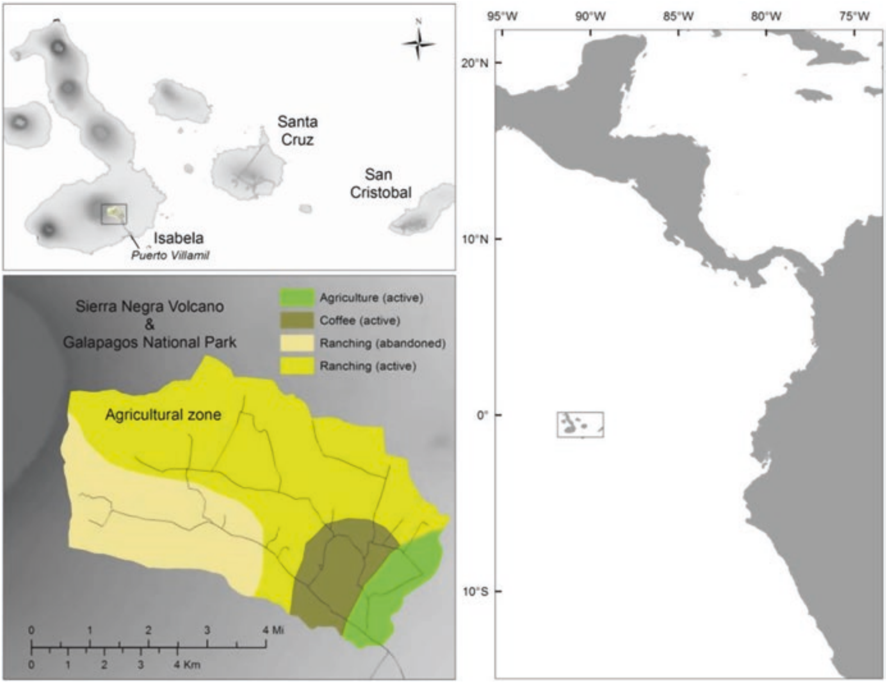

Fig. 10.1 The Galapagos archipelago and the agricultural zone of Isabela Island

Although guava has been studied and targeted for control inside Isabela's protected areas for over 30 years (Eckhardt 1972; de Vries and Black 1983; Schofield 1989; Binggeli 2001), little effort has been made to control its presence in the agricultural zone where animals eat the fruit and spread the seeds into the National Park. Invasive plant species are particularly prevalent on land used for livestock ranching. Because Isabela's farmland borders the National Park, keeping it free of invading plants and avoiding land abandonment are essential to preventing extensive spread of these pests.

In the last decade, however, Isabela began to experience considerable economic development in the small coastal village of Puerto Villamil to meet the needs of a growing tourism industry (Walsh et al. 2010). Limited local food markets simultaneously force landowners to pursue off-farm employment opportunities and create an increased demand for imported food from the Ecuadorian mainland (Vilema et al. 2003). Census data collected in 2001 and 2010 reveals declines in the number of residents and households in the Isabela Island highlands, complemented by an increase in the number of absentee landowners by almost 20% (McCleary 2013). The reduction in off-farm crop sales and increased rural-to-urban migration experienced during this timeframe follow a trend preceded by two other islands in the archipelago, Santa Cruz and San Cristobal (Rodriguez 1989; Borja and Perez 2000). McCleary (2013) found that between 2006 and 2010, land abandonment associated with a trend of rural out-migration to Puerto Villamil was a contributing factor to the expansion of the invasive plants already present.

Data Collection

Field research was carried out on Isabela Island in February and March 2010, and activities were designed to elicit information regarding highland environmental management techniques and guava control. In-depth interviews were carried out with the heads of 43 farming households identified during preliminary fieldwork in 2008 and covered household demographic and economic decision-making, land use practices, invasive species extent, and general environmental management. Interviews also clarified contrasting views and actions between the members of this stakeholder group. Most (83%) of the 43 landowners interviewed in this study live and work in Puerto Villamil during the week, reserving farm work for the weekend. A little more than half (55%) hire temporary workers from the mainland to maintain the farm while they are away. On these farms, only 2 or 3 ha are kept under cultivation at any time of the year. Of the 43 households interviewed, 15 were selected for the participatory classification exercise. They were chosen based on their above-average agricultural production and length of land tenure, a proxy for knowledge of the highland landscape and awareness of different types of vegetative cover.

Interviews and participatory classification were also conducted with 6 of the 12 National Park employees working out of the small Isabela office, who had been on the island for a minimum of 5 years and who routinely carried out monitoring, control, and eradication protocols for invasive plants in the highlands. They were accompanied during patrols of the National Park perimeter to observe the identification and removal of invasive plant species.

Ground truth sites to be used for participatory classification were selected from 80 GPS locations taken during fieldwork conducted in July and August 2008, based on their location within the spatial footprint of two satellite images over the study area. The 35 selected sites were not spatially stratified but represent a diverse set of land cover types found in the highland zone. At the end of each interview, photographs taken at each site were shown to the landowners and National Park employees, and they were asked to identify the land cover shown in the photograph. Their initial responses were assigned to a generalized set of six land cover classes, from which the majority response for each group was selected. This resulted in two classification sets per site.

Satellite Image Collection and Preprocessing

A landscape-level assessment of invasive vegetation in Isabela's highlands using satellite remote sensing was carried out by Walsh et al. (2008), who found that fine spatial resolution (3 m pixels or less) imagery was suitable for identifying patches of guava or large individual trees. Two fine-resolution satellite images, one QuickBird and one WorldView-2, were identified over the study area, images with collection dates almost exactly 6 years apart (22 October 2004 and 23 October 2010, respectively; Fig. 10.2). QuickBird and WorldView-2 sensors are linear array, push broom designs, each with a single panchromatic band and multispectral bands. The multispectral spatial pixel resolution is 2.4 m for QuickBird and 2 m for WorldView-2; therefore, they were first co-registered to each other using ENVI image processing software and ground control GPS points and resampled to a 2.4 m resolution. Then they were stacked to produce 1 image with 12 multispectral "bands," 4 from the QuickBird scene and 8 corresponding to the WorldView-2 image. Because the training samples for classification were extracted from the images to be classified, atmospheric correction was unnecessary (Song et al. 2001; Jensen 2007). Clouds and associated shadows covered a significant portion of the 2004 image and a small portion of the area of the 2010 image; these were digitized and excluded from the analysis.

Image Classification and Analysis

Because of the time difference between field and image dates, the two satellite images were compared to aerial photographs collected over the region in 2007, closer to the time when the study sites were photographed in 2008. Land cover patches containing study sites were more easily identified in the 2010 image, and

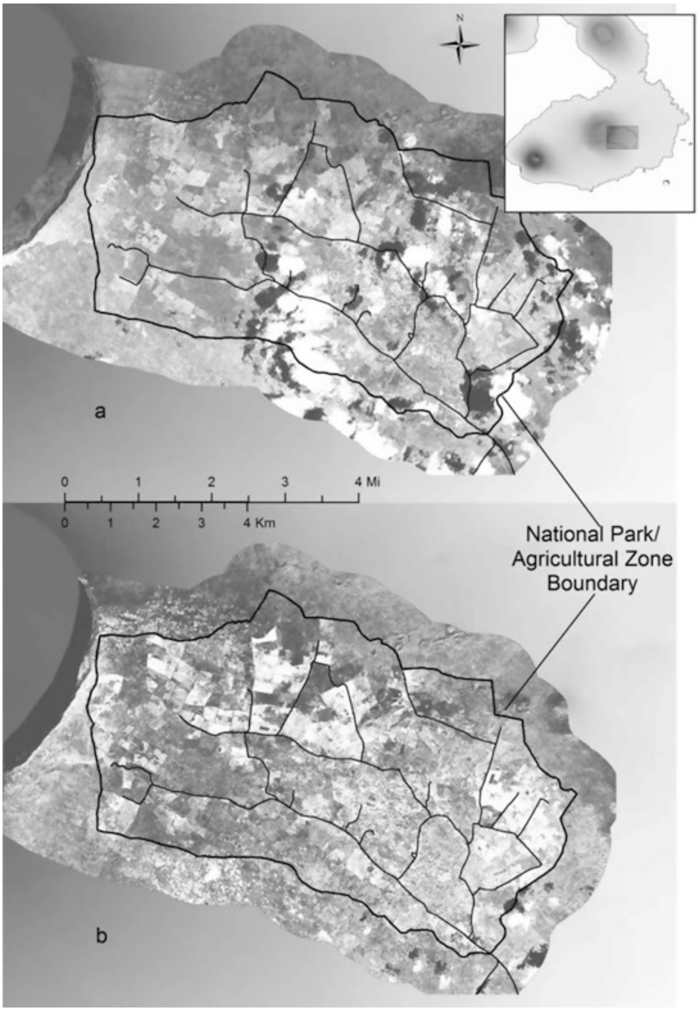

Fig. 10.2 Panchromatic bands of the (**a**) 2004 QuickBird and (**b**) 2010 WorldView-2 satellite images acquired for the Isabela Island highlands

three sites were removed due to major land cover changes between 2008 and 2010. The remaining 32 study sites were digitized into polygons that corresponded to reflectance values within the 2010 image, which was then processed using a maximum likelihood supervised classification algorithm that assumed equal prior probability of all classes. Only the multispectral bands 2, 3, 5, and 7 were used in the classification of the 2010 WorldView-2 image, as these wavelengths correspond to bands 1–4 (blue, green, red, and near-infrared) of the QuickBird image.

The classification exercise was a two-stage process, first to observe how groups of categories emerged through classification and then to reduce the number of classes to a manageable set. Participants were encouraged to assign a land cover type that they felt best represented each photograph they viewed from a broad list of types commonly found in the region. Then, based on their responses and expert knowledge of the highland zone, a final set of six general land cover classes was derived: lava, bare soil, cropland, guava, other vegetation (OV), and other introduced vegetation (OIV). The photos in which respondents identified tree plantations, for example, were assigned to the cropland category because they constitute agricultural use or income and are sometimes used to mark farm boundaries. Nonspecific vegetation types, including grasses, ferns, and shrubs, were assigned to the more general OV category; this frequently included native forest types as well. Individual species or vegetation types that participants specifically designated as introduced or invasive were assigned to OIV. Because of its extensive presence in the region, guava was frequently singled out in the photographs and was assigned its own category apart from other introduced vegetation.

The 2010 image was classified twice, producing 2 output images: 1 representing the opinions of the 15 landowners and 1 representing those of the 6 National Park respondents. The classification procedure was repeated for the 2004 image to facilitate comparative and quantitative evaluation of the change in spatial coverage and location of perceived land cover types between 2004 and 2010.

The four resulting classifications were characterized by a lack of spatial coherency, and a series of sieve, clump, and majority/minority filter procedures were run in ENVI to smooth the images. The areal coverage of each class was evaluated for all four final classified images. The land cover pairs were then cross-tabulated against one another to derive kappa indices that reflected the level of spatial agreement between corresponding categories. Because it is theorized that patterns of landscape change are tied to management practices on either side of the National Park/agricultural zone divide, GIS coverage of the boundary also allowed for spatially differentiated land cover assessments.

Results

Land Cover Classifications

The classification exercise generated two unique sets of perceptions about highland land cover. Classification results for the 2010 image are shown in Fig. 10.3. Changes in land cover area were analyzed between stakeholder groups and interpreted according to trends in agriculture and conservation in the highlands.

Responses between the two groups differed greatly, while within-group responses were highly uniform. During the exercise, landowners and National Park employees identified nearly matching guava photos, and the spatial coverage of cropland and guava matched reasonably well (Table 10.1). Agreement over what constitutes bare soil, other vegetation (OV), and other introduced vegetation (OIV) was significantly

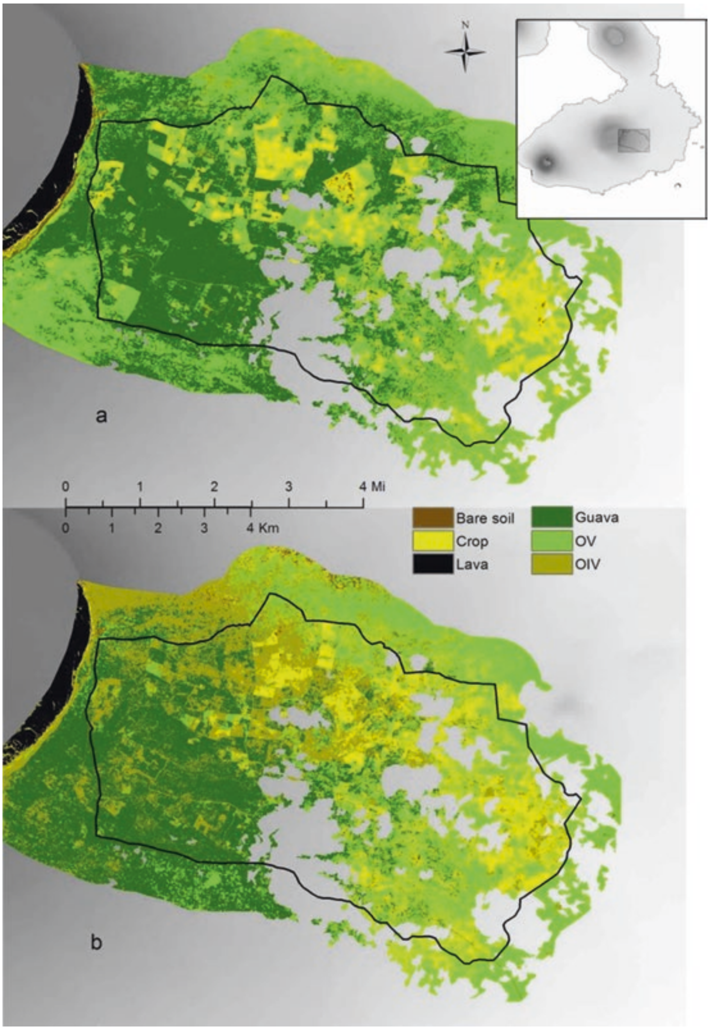

Fig. 10.3 Land cover classifications of the October 2010 satellite image of the Isabela highlands, by (**a**) landowners and (**b**) National Park employees

poorer, however. National Park employees "saw" far more OIV than do landowners, who instead identified this vegetation as OV. Overall, there was a high level of disagreement between both classifications (kappa = 0.39).

Figure 10.4 shows the spatial agreement and disagreement of guava pixels for the landowner and National Park employee classifications. The central-west portion of the image is dominated by vegetation that both landowners and National Park employees would identify as guava. This "shared" coverage is almost entirely contained within the high western elevations of the agricultural zone, a cooler area that is suitable for guava growth. This region contains a vast forest of guava trees

Table 10.1 Comparison of coverage agreement (in hectares) for the 2010 image

Category	Landowner coverage	National Park coverage	Difference (landowner–National Park)
Lava	166.55 (2%)	153.61 (2%)	12.94 (8%)
Bare soil	85.69 (1%)	46.43 (1%)	39.27 (85%)
Cropland	1068.87 (15%)	1252.93 (18%)	−184.06 (−15%)
OV	3016.18 (42%)	1651.19 (23%)	1364.99 (83%)
Guava	2715.62 (38%)	2192.46 (31%)	523.16 (24%)
OIV	39.97 (1%)	1796.27 (25%)	−1756.30 (−98%)
Total	7119.79	7119.79	

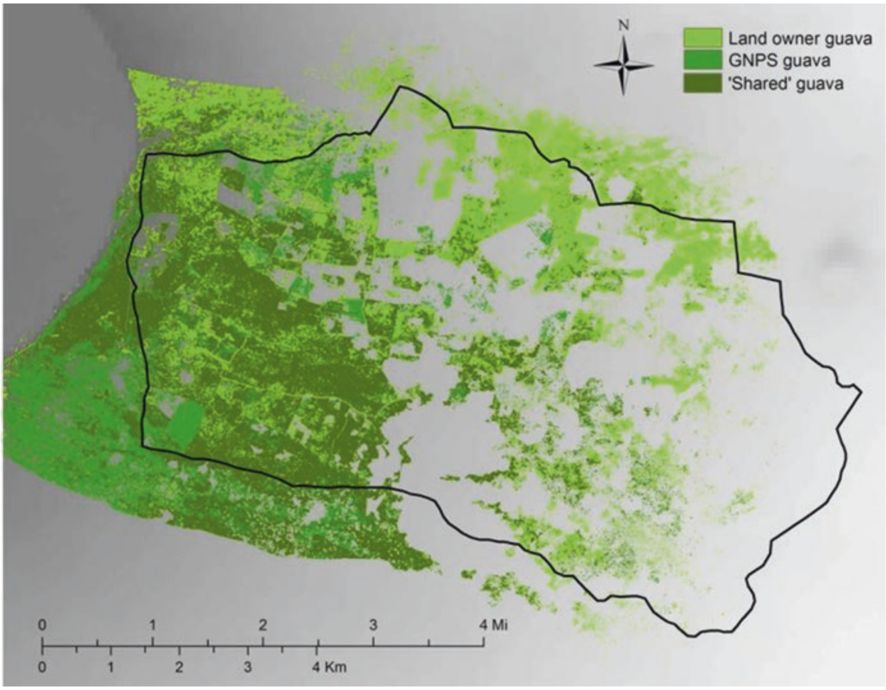

Fig. 10.4 Landowner and National Park employee perceptions of guava coverage in the 2010 image

between 3 and 4 m tall that form a dense, closed canopy. At the mid-northern edge of this dense coverage near the farm/National Park boundary, numerous seedlings are found, indicating that the invasive "front" is proceeding. The farms in this region are used primarily for livestock grazing, where landowners tend to allow trees to mature and shade out surrounding seedlings or to plant grasses in order to limit guava growth.

In the more intensive agricultural zone near the center of the image, landowners identified guava in patches that National Park employees did not. The patchy nature of guava in these areas is attributed to seed dispersal by birds and both domestic and feral animals but is also likely due to processes of land abandonment and guava succession that began in the 1970s and 1980s with the arrival of the more lucrative fishing and tourism industries (McCleary 2013). Both young and old guava in this region are interspersed with crops. The southeastern portion of the agricultural zone, because of its lower elevation and shelter from the prevailing winds, experiences a dry climate that is less favorable for guava growth. This area is also more intensely cultivated, containing a higher proportion of landowners who live in the highlands full time and operate commercial or subsistence farms.

In both classifications, areas of the National Park that are adjacent to the agricultural zone contain more guava than areas that are further away. During a site visit in 2009, the northeastern edge of the Sierra Negra crater was comprised of a mix of scrubby, non-native vegetation. According to National Park personnel, the area contained only native grasses as recently as 20 years ago (Cabrera 2008, personal communication). Since that time, trips to the crater have become popular with tourists who transport introduced seeds into the protected area on the soles of their boots or the hoofs of horses that are rented from local ranchers. As in the agricultural zone, large areas of the National Park that have not been recently cut or treated are heavily invaded by guava. The difference in the two classifications, however, stems from the fact that while landowners tended to classify only photographs that contained mature trees and young growth as guava, National Park employees also identified photographs that contained small seedlings among other shrubs and ferns as guava. Of the total guava coverage in the National Park employee classification, 54% is found inside the protected area, compared to only 30% in the landowner classification.

The unsupervised classification conducted by Walsh et al. (2008) analyzed a subset of the QuickBird 2004 image that was used in this study. They also found that guava was distributed throughout the scene, “with a large area of invasion in the southwest corner of the study area, scattered patches of invasion across the agricultural zone, and dispersed, smaller patches of invasion along the transition zone located along the border of the park.” The dense, homogenous “shared” guava patches that were identified by National Park employees and landowners in this classification correspond to regions that Walsh et al. considered well-defined areas of older guava growth and invasion. Smaller, dispersed patches within the agricultural zone that landowners in this analysis considered guava are visible in the Walsh et al. classification as well, suggesting that field knowledge and recognition of guava are especially high among landowners.

Land Cover Change

The classification exercise reveals conflicting perceptions of land cover change (Table 10.2). From the landowners’ point of view, guava coverage in 2010 actually decreased from 2004, while National Park employees perceive it as having increased. Spatially differentiated, those land cover reductions occurred primarily in the

Table 10.2 Classified land cover change between 2004 and 2010 (in hectares)

	Landowner			National Park		
Category	2004	2010	2010–2004	2004	2010	2010–2004
Lava[a]	532.89	166.55	−366.34	377.31	153.61	−223.70
Bare soil	184.45	85.69	−98.76	137.16	46.43	−90.73
Cropland	1872.03	1068.87	−803.16	554.70	1252.93	698.23
OV	1434.04	3016.18	1582.14	1362.76	1651.19	288.43
Guava	3014.23	2715.62	−298.61	1665.48	2192.46	526.98
OIV	56.10	39.97	−16.13	2994.57	1796.27	−1198.30

[a] The decrease in lava coverage in both sets of classifications is likely due to the fact that lava visible in the 2004 image has since been reclaimed by pioneer vegetation such as ferns and grasses

Table 10.3 Land cover change matrices for "cropland" and "guava" categories (in hectares)

	Landowner area (2004–2010)		National Park area (2004–2010)	
To/from category	From crop	From guava	To crop	To guava
Lava	12.19 (1%)	22.67 (1%)	41.53 (3%)	0.50 (<1%)
Bare soil	16.90 (1%)	37.96 (1%)	36.51 (3%)	14.03 (1%)
Cropland	**316.33 (17%)**	235.77 (8%)	**187.78 (15%)**	50.20 (2%)
OV	917.22 (49%)	1006.05 (33%)	442.49 (35%)	120.54 (6%)
Guava	601.27 (32%)	**1692.67 (56%)**	323.96 (26%)	**765.16 (35%)**
OIV	8.11 (<1%)	19.11 (1%)	220.38 (18%)	1241.54 (57%)
Total	1872.03	3014.23	1252.93	2192.46

Stable land cover between time periods is indicated in bold

agricultural zone according to landowners. According to the National Park employees, on the other hand, guava emerged in the National Park and the southwestern agricultural zone. If the spatial coverage of guava is seen to be in transition, then what land cover types might be replacing it?

Table 10.3 shows that the landowners' perceived transition *from* cropland and guava *to* other classes is matched by National Park employee-perceived transitions *to* cropland and guava from other classes. In fact, only 17% of cropland from 2004 was present in the 2010 landowner image, and it became OV (45%) and guava (32%). This is consistent with observed vegetation transitions on abandoned or fallow land, where grasses, shrubs, and guava seedlings often make up pioneer vegetation. The National Park employee classifications show a similar (15%) stability of the crop class, but the "new" cropland is mainly comprised of former OV and guava. This unexpected transition is likely due to the fact that the 2008 photographs containing young trees—which were used to classify the 2010 image as "cropland" according to National Park personnel input—also contained a variety of shrubs and, to a lesser extent, guava, which may have dominated the spectral signal in those same regions of the 2004 image.

Over half (56%) of the guava in the landowner classifications remained stable, while 33% transitioned into OV. This shift in crop-to-guava and guava-to-OV reflects anticipated land cover changes in areas that have been abandoned, are no longer under cultivation, or were cleared of guava and succeeded by pioneer vegetation

(OV). Landowner-defined guava actually decreased by 19% inside the National Park but appeared more widely dispersed within the agricultural zone in 2010. Compared to the landowner classifications, only 35% of National Park employee-defined guava remained stable, while 57% of its coverage in 2010 was derived from land cover previously classified as OIV. Furthermore, the majority (62%) of the National Park employee-defined guava growth occurred in the National Park. These very different understandings of species and change across the landscape likely stem from different perceptions of land use and conservation management in the Isabela highlands.

While there was a high overall level of agreement between stakeholder groups in the case of guava, the almost complementary classification of OV versus OIV calls attention to a divergence in views about native and introduced species. Landowners and National Park employees "saw" different vegetative makeup in photos that contained a variety of vegetation types. Where introduced ferns or grasses were present, National Park employees singled them out as individual introduced species, often citing the plant's common name, whereas landowners were more likely to assign them to more general categories like grasses or herbaceous vegetation. Guava was the exception to this rule in that both landowners and National Park employees identified it in photographs, even when other species or land cover types were present.

Other introduced plants like avocado and citrus trees, elephant grass, and hill raspberry illustrate the complex viewpoints that landowners have about the utility and impacts of plants that the National Park regards simply as environmentally detrimental. Elephant grass, for example, is preferred by landowners as livestock fodder because it is drought-tolerant and adapts well to poor soils, but its rapid growth makes it a threat to the National Park on the other side of the boundary. Even the presence of guava is sometimes considered positive because it provides shade and fruit for livestock, although it quickly invades open pastures. Many plant invaders are perceived as strictly negative by landowners, including most ferns, hill raspberry, and rose apple. Odd-numbered entries in Table 10.4 highlight cases where National Park employees consider an introduced plant to have a negative impact while landowners identify a positive use. Even-numbered entries exhibit shared negative views.

Several landowners had difficulty understanding the distinction drawn between introduced plants and their native counterparts. *Bryophyllum pinnatum*, they agreed, is a weed, but they were uncertain of how it had arrived or why this was relevant. This reflects the fact that awareness of the threat of introduced species among landowners in Isabela is low (79%), compared to 94% archipelago-wide (INEC-CGREG 2010). Put another way, National Park employees believe that introduced species that have the potential to impact the range, distribution, and survival of native species are ecosystem threats, while in landowner terms, a threat could be any organism, regardless of origin, as long as it somehow diminishes the productive potential or economic value of the region. Weed status for landowners does not always mean invasive, and native plants are not always welcome.

Table 10.4 Views about introduced plant impacts among National Park employees and landowners

Plant name	Stakeholder-defined impact	
	National Park	Landowners
1. Guava (*Psidium guajava*)	Invades and replaces native vegetation	Invades pasture, difficult to eradicate, provides shade and food for humans and livestock
2. Hill raspberry (*Rubus niveus*)	Chokes out native vegetation	Forms dense thickets, chokes out cultivated plants
3. Avocado (*Persea americana*)	Invades native vegetation	Provides shade and food for livestock; a cash crop
4. Ferns (*Pteridium* sp.)	Invade zones of the National Park	Form dense stands in pasture
5. Citrus trees (*Citrus* sp.)	Invade zones of the National Park	Provide shade, a cash crop
6. Rose apple (*Syzygium jambos*)	Forms dense forests, shades out native plants	Forms dense forests; prevents livestock grazing
7. Passion fruit (*Passiflora edulis*)	Chokes out native vegetation	Chokes out cultivars; food for livestock, a cash crop
8. Cathedral bells (*Bryophyllum pinnatum*)	Replaces native vegetation	Competes with grasses and cultivars for soil nutrients
9. Elephant grass (*Pennisetum purpureum*)	Competes with native vegetation, especially *Scalesia*	Assists in control of guava and raspberry; food for livestock

Discussion

Returning to the case of guava, landowners and National Park employees agree on its potential to destroy highland biodiversity and agricultural livelihoods, even if it does provide some minor benefits. However, the last three decades of guava management on Isabela Island have alienated rural community members instead of recruiting them as active participants in conservation. Such park-only policies fail to enroll landowners in the control of introduced species, which could lead to detrimental environmental effects.

Inside the boundaries of the protected area, for example, the Galapagos National Park Service has spent thousands of dollars exploring alternatives to the point application of metsulfuron and picloram herbicides, which are effective but must be applied directly to individual tree trunks or cut stumps (Rentería et al. 2006). Covering seedlings with large mats and cutting mature trees proved too expensive and labor intensive, and the use of biological controls could pose threats to the native guava variety (*Psidium galapageium*; Tye 2001). Controls are most effective in isolated patches and areas of young growth where the trees have not set fruit, making the guava “front” that is proceeding at the boundary of the park and private land a high-priority area for the National Park and highland landowners to jointly intervene. Although the National Park Service has assisted landowners in the control of hill raspberry in the past, guava control on private land is a household responsibility.

Without financial and labor assistance from the National Park, many landowners resort to using banned herbicides and, in some cases, burning, to rid their land of guava. Although prohibited, burning is a common practice in Isabela's highlands, both to promote regeneration and as a form of weed control. But fire can actually contribute to the growth of guava seedlings, as Shimizu discovered during a vegetation survey conducted in 1997. Following an intense 1994 fire that burned thousands of hectares in an uninhabited region of Isabela's highlands, new guava shoots sprouted from the base of charred trees and dead trunks. Where guava did not recover in the most severely damaged areas, dense thickets of ferns had formed as pioneer vegetation (Shimizu 1997). As a control measure, landowners often follow burning by planting elephant grass, another highly invasive (but useful) species, to serve as livestock fodder and prevent the recovery of guava.

Many Isabela landowners have found creative solutions and even uses for guava without institutional support, however. By keeping their land cleared and under production, full-time farmers avoid the problems with guava reported by landowners who cultivate only part of the year. Two Isabela farms use the wood from mature trees to make charcoal, which they sell to a growing number of restaurants in Puerto Villamil, and in 2012 a women's cooperative teamed up with Lindblad Expeditions to produce jams and marmalades from the island's fruit, including guava, for sale on Lindblad's cruise ships (Jenanyan 2012, personal communication). Some farms clear guava and plant shade-producing coffee trees that would naturally prevent the seedlings from sprouting beneath them. Others cut guava trees and seedlings several times a year, composting the weeds and planting a noninvasive species of hardwood tree to provide the farm with wood in the coming years.

Conclusion

The participatory classification exercise employed in this study to quantify land use and land cover change on Isabela Island revealed very different views and values on the landscape between landowners and National Park personnel. Competing maps of land cover in Isabela's highlands were created to quantitatively illustrate the two points of view and highlight areas of "shared" guava coverage. Spatial differences in competing land cover classifications were further articulated vis-à-vis interviews and observations, which showed qualitatively that perceptions of environmental change due to invasive plant species vary between these two stakeholder groups. The "good" or "bad" nature of introduced plants was evaluated in terms of economic and environmental goals. Two main conclusions can be drawn:

1. Remotely sensed imagery and analysis can be powerful tools for clarifying local knowledge about the landscape. National Park employee classifications found guava growth in the National Park between 2004 and 2010, but the landowner classifications only identified guava increases within the agricultural zone. Other highland areas that landowners view as productive are seen as degraded by con-

servation practitioners, suggesting that perceptions agree or disagree based on particular uses of the landscape.

2. The generation of multilayered coverage of land use and change using participatory methods could improve strategies for managing invasive species in island environments. The front of young guava that is proceeding at the edges of privately owned land and the National Park was noted by both stakeholder groups in this analysis, while competing classifications reveal important opportunities for better environmental education and the sharing of local knowledge between groups. Too often, conservation activities are handed down to landowners with little explanation of their impacts in economic terms. By involving stakeholders directly in the research process, both landowners and National Park personnel were able to play a role in the cogeneration of spatial products, unique stories about how they see, use, and care for the landscape.

In their annual review of the Galapagos as a World Heritage Site, UNESCO (2006) noted that without focused highland conservation initiatives, “controlling introduced species in the parklands of inhabited islands will always be akin to bailing out a leaking ship.” Divergent perceptions of land cover, change, and use in the Isabela Island highlands could have enormous implications for conservation in Galapagos. This analysis showed that the restoration of the National Park is high on the agenda of environmental managers, for example, but the maintenance of highland agricultural landscapes is not. In a landscape where productivity and degradation coexist, however, both of these competing conceptions about what the highlands “are” should be on the desks of policy makers. Where it is the goal of conservation practitioners to restore the island’s highland zones, the evaluation, nature, and timing of restoration schemes must incorporate the decisions that landowners are making. Current practices should be modified to reflect how ecosystem interactions differ with respect to farming and conservation activities, making it more likely that environmental management schemes will be accepted and carried out by rural community members in the long term.

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Chapter 11
A Conceptual Framework for the Management of a Highly Valued Invasive Tree in the Galapagos Islands

Gonzalo Rivas-Torres and Damian C. Adams

Introduction

The increasing movement of people and goods across the globe has allowed numerous organisms to jump natural dispersal barriers and become introduced to new sites (Work et al. 2005). In some cases, they become established, rapidly expand their populations, and become extremely noxious, causing significant ecological impacts and economic harm (Mack et al. 2000; Pimentel et al. 2000). Ecological impacts from introduced species can include significant changes in ecosystems services (Hobbs et al. 2013), and these and other impacts are extensively reviewed in other chapters of this book.

This group of ecologically and economically harmful organisms—"invasive species" (sensu Richardson et al. 2000)—represents approximately 10% of all new non-native plant introductions (Williamson and Fitter 1996). For certain invasive species, for example, those expected to cause large damages and/or those that have not yet extended their range significantly, eradication may be optimal (Simberloff 2008).

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Though rarely, in highly unique cases, eradication has been achieved (Gardener et al. 2010, 2013), including *Rubus* species in Santiago Island, Galapagos (Renteria et al. 2012), and zebra mussels in a small pond in the continental USA (Adams and Lee 2011). Efforts to eliminate invasive species have helped us understand factors that affect eradication success, which can include intrinsic ecological characteristics of the target species, such as fast growth and high offspring, insufficient budget, related logistic constraints, and social attachment by settlers (i.e., seen as beneficial or harmful; e.g., Cruz et al. 2009; Simberloff 2003).

In addition to the fairly well-described ecological impacts caused by invasive species (Daehler 2003), recent studies have focused particularly on analyzing the social impacts and related costs these introduced organisms can generate (Liu et al. 2011). For instance, there are reductions in boating and fishing caused by colonization of Eurasian watermilfoil (*Myriophyllum spicatum*) and decreased recreation (i.e., park use) due to the tree *Melaleuca quinquenervia* in the USA (Charles and Dukes 2008). These examples illustrate how invasive species can negatively impact socioeconomic values. Understanding the critical role that the broader social system plays in invasive species management may improve management effectiveness and perceived success (García-Llorente et al. 2008; Gardener et al. 2010; Kholi et al. 2008; Epanchin-Niell et al. 2010; Larson et al. 2011; Kalnicky et al. 2014; Rai and Scarborough 2014).

Despite the many examples of negative ecological, social, and economic impacts from invasive species, their management may not be beneficial for all affected stakeholders. Some invasive species clearly cause great harm and are not generally viewed as beneficial (e.g., fire ants—*Solenopsis invicta*), mainly because they were unintentionally introduced and cause significant negative damage to livestock and humans (Pimentel et al. 2001). However, a subset of invasive species was intentionally introduced for perceived social and economic benefits, and these were only later identified as invasive once their ecological effects became apparent (Kennedy and Hobbie 2004). Three notable examples include salt cedar (*Tamarix* spp.), introduced to control erosion, *M. quinquenervia* to dry up the Everglades, and kudzu (*Pueraria lobata*) for erosion control and livestock forage (Di Tomaso 1998; Webster et al. 2006). For these, and other species, there can be much less motivation to eradicate or actively manage invasions given positive public perceptions (Moyle 2001; Colautti and MacIsaac 2004; Webster et al. 2006; Pejchar and Mooney 2009; Adams et al. 2011; Davis et al. 2011).

Perceived benefits can complicate invasive species' control and management and frustrate policy interventions if diverse stakeholders have opposing views about their positive or negative impacts (Schlaepfer et al. 2011). For example, the negative effects that *Pinus* species can cause to the native ecosystems they invade are well known (Richardson and van Wilgen 2004), but in some regions (e.g., South Africa), they are highly valued for timber and non-timber forest products that support local residents (de Wit et al. 2001). While removing these trees may positively affect stream flow (Richardson and van Wilgen 2004) and diminish their ecological impact, it might result in significant economic losses to those using the trees (Turpie et al. 2003), who might oppose the control and reduction of this species.

These examples highlight the importance of understanding the social landscape in which invasive species exist, including identifying stakeholders and defining their roles and perhaps, critically, identifying which groups would view invasive species removal as beneficial or detrimental. Recent literature on social conflicts and invasive species management recognizes the need to explicitly include both ecological and socioeconomic aspects of invasive species assessments, identify impacts on diverse stakeholders, and consider policy mechanisms (e.g., incentive payments) that address their concerns (Estévez et al. 2015).

Despite a recognized need for management programs that incorporate mechanisms to reduce the negative ecological, economic, and social impacts of invasive species (e.g., Adams and Lee 2012), we often lack sufficient information to guide policy and management decisions about new invasions (e.g., Leung et al. 2002) or to understand impacts that such management projects may have on different stakeholders. However, researchers have used a variety of methods to inform these decisions despite the inherent uncertainty associated with new and potential invasions, i.e., bioeconomic modeling (e.g., Adams and Lee 2012). Such investigations are useful for gauging socioeconomic impacts and simulating the effects of potential invasive species management approaches (e.g., Lee et al. 2009; Adams et al. 2011; Adams and Lee 2012). What is most clear from these, and related studies, is that identifying the appropriate management approach requires a strong understanding of the target species' effects and impacts—ecological and otherwise. The identified negative and positive impacts can be later included in managerial decision-making that may help to reduce the risk of failure of restoration projects (Rai and Scarborough 2014).

Conceptually, this can be done using a coupled human-natural systems approach that incorporates observations on both the ecological and social systems and their interactions (Liu et al. 2007). However, in practice, this is rarely done (Pejchar and Mooney 2009; Estévez et al. 2015). Notable exceptions include analyses of the social dynamics surrounding an invasive species introduction by conceptually "mapping" local stakeholders being impacted (positively or negatively), describing the relationship among stakeholders, and analyzing the expected impacts of management alternatives on stakeholders groups (e.g., Leung et al. 2002; Richardson et al. 2009). This is a critical area of inquiry that has received insufficient attention in the scientific literature.

Here, we use descriptive analysis and survey and interview methods to understand the case of the invasive and economically important tree *Cedrela odorata* in the Galapagos Islands, Ecuador, where the tree is viewed as both beneficial and harmful to stakeholders; explore the complex social, economic, and ecological aspects of invasive species management; and identify the stakeholders that could be impacted by potential managerial actions targeting this invasive tree.

Despite the significant ecological impacts of *Cedrela* in Galapagos (see chapter by Rivas-Torres and Rivas) and its economic importance for the local timber market (Methods section), no studies have assessed the socio-environmental dynamics of *Cedrela* or the impacts of alternative *Cedrela* management approaches (e.g., *Cedrela* eradication and site restoration) on stakeholders. In the following sections, we summarize the ecological impacts of *Cedrela* to assess its biotic effects and describe the stakeholder groups engaged on this issue, including governmental agencies, local residents, and timber workers. Next, we explore the costs and benefits to stakeholder groups associated with *Cedrela* management and forest restoration and the loss of the tree as a key commodity. Finally, we present a conceptual model of the socioecological landscape that could inform *Cedrela* management by the GNP. Using this model, we compare two competing policy alternatives that are being considered for adoption: (1) continued use of *Cedrela* for the local wood products market and (2) complete extraction and eradication of *Cedrela* within the GNP (GNP Directorate 2014). Besides adding to the small but important literature on the socioecological impacts of invasive species management, this chapter also fills critical knowledge gaps about *Cedrela* impacts and alternative management approaches. Results of this study also have practical importance for the management of invasive species in the Galapagos Islands.

Methods

Background and Target Species

In the 1940s, the invasive tree *Cedrela odorata* (Meliaceae; hereafter *Cedrela*) was introduced to the farms located in the highlands of Santa Cruz Island (at the center of the Galapagos archipelago; Lundh 2006) and today is also found on the other three inhabited Galapagos islands (see chapter 6 by Rivas-Torres and Rivas in this volume for study site and species details). Within the Galapagos, *Cedrela* is a highly valued timber species for the local, on-island market. The tree is native to tropical America, ranging from central Mexico to Brazil; but despite this wide distribution, its population densities (strongly diminished by illegal and legal logging) are considered low within this native range. Ironically, although it is invasive in the Galapagos, the tree is protected from extraction and even categorized as broadly threatened and vulnerable within its native distribution (IUCN Red List 2016).

Cedrela is well known around the world for its excellent wood quality, which is one of the reasons it was exported to sites outside of its original range and introduced to many Pacific archipelagos like Hawaii and Galapagos (Cintron 1990). *Cedrela* is now the main timber resource in the Galapagos, and its wood is mostly used locally for furniture for the ~30,000 inhabitants and handicrafts for the tourism industry, which includes ~170,000 visitors to the islands (Gardener and Grenier 2011). The annual market value of *Cedrela* timber in the Galapagos local market is estimated to be US$2,000,000 (http://www.cdfdevelopment.org/our-work/biodiversityconservation.html Charles Darwin Foundation 2012), although this rough estimate represents a rare data point on the potential impacts of *Cedrela* management.

Seven decades after its intentional introduction, *Cedrela* is dominating the canopy of several forested areas and invading some of the principal ecosystems of the archipelago (Renteria and Buddenhagen 2006; Trueman et al. 2014), causing negative ecological impacts (see chapter 6 on allelopathy by Rivas-Torres and Rivas in this volume). In 2007, due to its threatened status in the American continent, the extraction of *Cedrela* was prohibited everywhere in Ecuador including the Galapagos (Ministerio del Ambiente, Acuerdo 167, Articulo 1, 2007). However, in 2009, the extraction of *Cedrela* was allowed to restart in the islands but mostly in the agricultural areas of Santa Cruz, i.e., not intensively in the protected zone where *Cedrela* dominates. Since then, the GNP has been regulating the extraction of *Cedrela*, mainly outside of the protected area by providing permits to users that specify location and timing of *Cedrela* extraction. The GNP is in the planning stages of a new rule incorporating *Cedrela* extraction into their restoration efforts (Galapagos Management Plan, Galapagos National Park Directorate 2014: 199), which presents a unique opportunity to assess how a change in the *Cedrela* market in Santa Cruz affects stakeholders.

Study Area

In the Galapagos, the biggest naturalized population of *Cedrela* (i.e., established without human intervention) exists on Santa Cruz Island, where the tree is considered invasive and is even dominating extensive areas. An ongoing project using satellite images and drones and mapping (for the first time with a peer reviewed and open methodology) the actual coverage of most invasive plants in the Galapagos (Rivas-Torres et al. 2016; http://institutodegeografia.org/vega-2/), recorded that this invasive tree now dominates a block of ~1000 hectares of continuous forest [hereafter also called "*Cedrela* forest"] in that island alone . *Cedrela* forest covers a portion of the humid highlands in the southern side of Santa Cruz at ~200 masl, around 5 km from the main site where *Cedrela* was first introduced. This forest is in the protected area, on the border ("buffer zone") that divides the developing agricultural zone with the National Park (see map on chapter 6). Given its location, the GNP has the authority to decide any actions—such as management and restoration plans—that must be taken in this invasive-dominated forest. In fact, the GNP spends on average US$132,000 per year on *Cedrela*-related restoration activities, including the operation of a greenhouse near the *Cedrela* forest that can produce 60,000 native seedlings to support restoration projects in this highly invaded zone. Outside this forest, *Cedrela* is found mainly on private lands within the "agricultural zone" in Santa Cruz and in small patches or as single individuals extending along steep hillsides. Although the GNP has a prohibition on planting or propagating *Cedrela* throughout the entire archipelago (Gardener et al. 2013), its many wind-dispersed seeds allow it to disperse naturally and colonize other ecosystems outside the block (Renteria and Buddenhagen 2006).

Ecological Data

To summarize the ecological impacts *Cedrela* may have over native and invasive plants, we tabulated the results from relevant investigations measuring invasive tree impacts (i.e., Jaeger et al. 2007) and observations by G. Rivas-Torres (and Rivas-Torres et al. 2017). Some of its main and obvious ecological impacts are related to changes in plant composition and environmental conditions of the sites this tree invades, such as changes in solar radiation to the forest understory and allelopathic effects (Rivas-Torres and Rivas' chapter 6 in this volume) that can limit growth of seedlings and juveniles.

Socioeconomic Data

Cedrela management approaches and associated costs were assessed based on in-field observations and surveys with key stakeholders. Next, we quantified the GNP's management costs for reversing the negative ecological impacts by this invasive tree (Annex 1 [Online]: Table 11.1). This quantification was performed using the Annual Operating Plan (AOP) (Galapagos National Park Directorate 2014), which is part of the Galapagos Management Plan (Galapagos National Park Directorate 2014), and includes detailed information on the yearly budget used by the GNP to perform restoration-type activities. We used the GNP's greenhouse and detailed expense database reported as part of the AOP (2015) to estimate management costs (see, e.g., Annex 1: Tables 11.1 and 11.2) and then projected the costs onto the entire ~1000 hectares which comprise the *Cedrela* forest. This invaded site was selected because it is the first likely target for restoration efforts due to GNP's control over the area and high density of *Cedrela*.

For almost 2 years, G. Rivas-Torres accompanied GNP staff and other park workers (e.g., informal loggers hired to extract *Cedrela* as part of a treatment) and observed day-to-day restoration practices and identified the primary stakeholders involved in *Cedrela* management and its wood market. We identified four primary stakeholder groups (GNP staff, handcrafters, and chainsaw and sawmill workers), which were interviewed to confirm in-field observations about their roles, to understand their participation in the *Cedrela* market and help contextualize the socioeconomic importance of *Cedrela*. Based on a series of interviews with these stakeholders, we developed a survey instrument to (1) define the involved stakeholders, (2) describe the activities they perform in the actual extraction of *Cedrela*, and (3) identify other potential users and participants of this wood market (for answers and methods details, please refer to Annex 1, Tables 11.3 and 11.4; and Annex 2, Figs. 11.4 and 11.5). The data informed a conceptual map identifying the main stakeholders for this market (Fig. 11.1).

To create the qualitative model for the Galapagos *Cedrela* market, we used three main sources: 2+ years of in-field interactions with the identified groups, the conceptual stakeholders' map (Fig. 11.1), and the relevant answers from the sur-

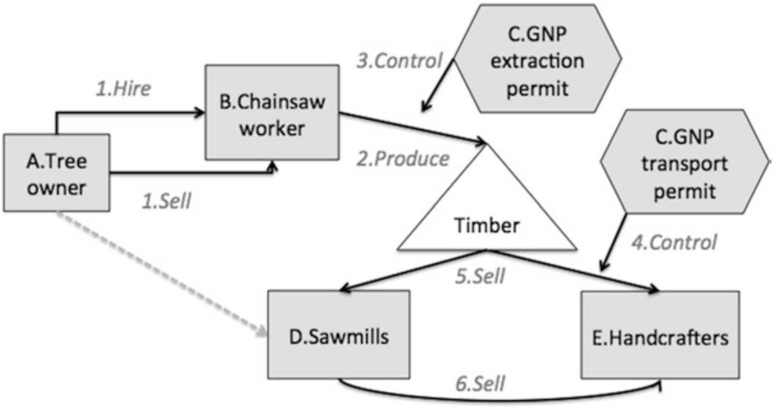

Fig. 11.1 Conceptual map denoting the five primary stakeholder groups in the *Cedrela* wood market in Santa Cruz, Galapagos Islands. The first connection links the tree owner selling the *Cedrela* tree or hiring a chainsaw worker to do the extraction. This action is followed by the production of a timber product by the chainsaw workers who obtain the logs from the felled tree onsite. At this stage, either the chainsaw worker or the previous or new owner of this timber product has the extraction and transport permit approved from the GNP, which controls the extraction process. After getting this permit, *Cedrela* logs and planks are transported and sold to either sawmills or handcrafters. The handcrafters can also buy wood from the sawmills after it has been bought from the original owner

veys, such as costs related to *Cedrela* products and how they differ between stakeholders (i.e., Annex 1, Tables 11.3 and 11.4; and Annex 2, Figs. 11.4 and 11.5). Income data from the surveys informed our predicted impacts model (Fig. 11.2). This exercise also helped identify critical information gaps that should be filled to reduce uncertainty in the decision-making process.

Status Quo and Alternative Models Assembly

According to section 2.1.2 of the Galapagos Management Plan (Galapagos National Park Directorate 2014), one of the main objectives of the GNP is to "Ensure the rational use of supply services generated by ecosystems." This objective is reinforced in subsection 2.1.2.5: "Generate and implement a comprehensive management plan on introduced timber species in coordination with relevant entities." To provide relevant information to help fulfill this objective, we assembled an alternative qualitative model that analyzed how the present model depicting the wood market status quo, and how stakeholders using *Cedrela* in Galapagos, are affected by an integrative GNP plan to manage this invasive tree. Since *Cedrela* is an invasive plant regulated by the GNP, by extension, this plan hypothetically (i.e., stated by this study but not yet implemented) also deals with controlling its extraction both inside and out of the boundaries of the protected area. We built the alternative model under

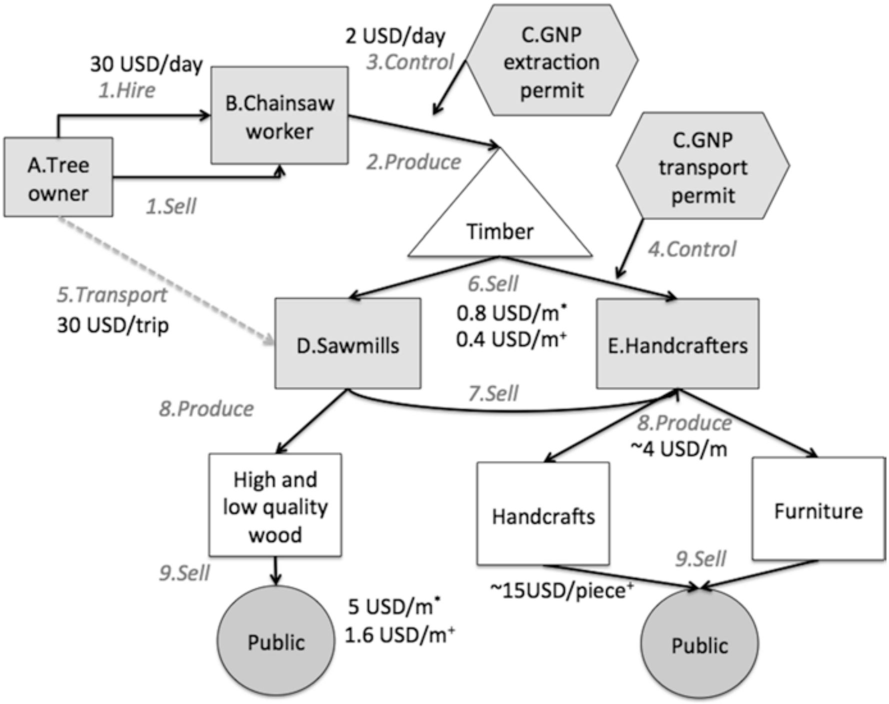

Fig. 11.2 Hypothetical qualitative model for the present *Cedrela* ("*status quo*") wood market in Santa Cruz Island, Galapagos. Stakeholders are presented in dark gray, while products are presented in white. Different steps or transitions are denoted by a number, and are presented in light gray. Prices for different steps are presented where information was available. For definition of *high quality wood and +lower quality wood please refer to notes in Annex 1 Table 11.3

the assumptions that the Park will establish a logging and management plan for the *Cedrela* forest and will also manage and control *Cedrela* planted on private lands (Fig. 11.3).

Results

We identified two main impacts related to the presence and extraction of this invasive tree. First, when *Cedrela* is present, it can significantly reduce the establishment and growth of other native canopy species (i.e., by using allelopathic mechanisms, i.e., Chapter 6 by Rivas-Torres and Rivas of this volume), and, second, when this tree is extracted, other invasive species can take over the restored sites (Jaeger and Kowarik 2010; Annex 1: Table 11.1, "Impact"). For managing the impact to native plants caused by the presence (shade) of *Cedrela*, we first determined (using available literature and restoration plans) that clear-cuts of *Cedrela*

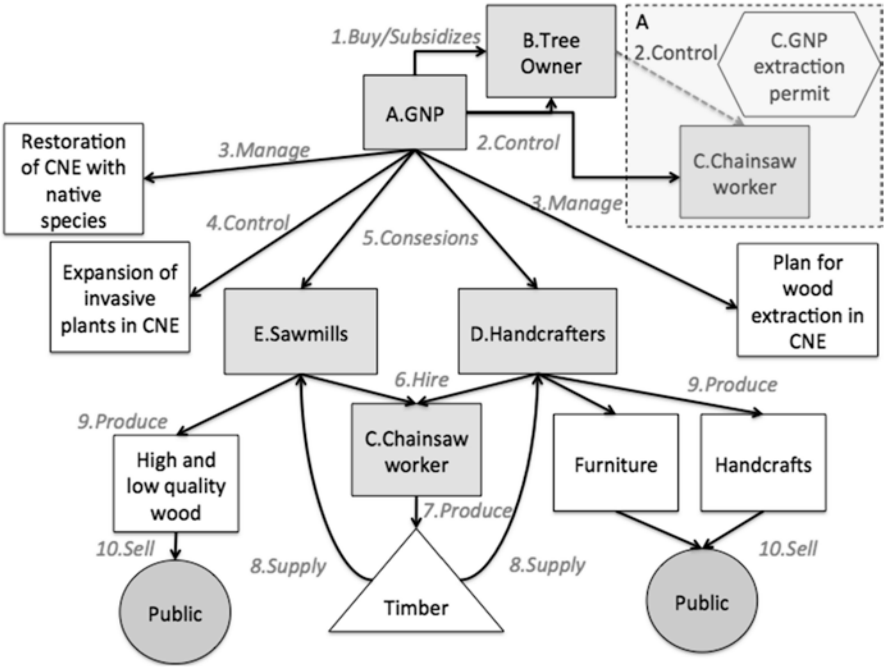

Fig. 11.3 Alternative hypothetical qualitative model for the *Cedrela* wood market in Santa Cruz Island, Galapagos. Stakeholders are presented in dark gray. Different steps or transitions are denoted by a number and are presented in black captions. This model suggests that the steps 3 and 4, i.e. the restoration of *Cedrela* novel forest, the creation of a plan to manage wood extraction and the control of the expansion of invasive plants in this and other extraction sites, should be performed by the GNP if this agency assumes the integral control of the *Cedrela* market. A box is showing the path GNP will have to take if buying a tree from the *Cedrela* owner, which will then follow a similar path as in model of Fig. 11.2

(e.g., Jaeger and Kowarik 2010), followed by reforestation with native seedlings (e.g., Gardener et al. 2009) to increase native propagules pressure (Wilkinson et al. 2005), are preferred. From an ecological perspective and considering GNP objectives, we determined that mechanical (and to a lesser extent, chemical) control is the most appropriate activity (see, e.g., Renteria et al. 2006) to reduce the establishment and expansion of other invasive species after *Cedrela* extraction.

Using the GNP Annual Operative Plan (Galapagos National Park Directorate 2014), specifically the expense section detailed per item and the greenhouse detailed expenses from the Ecosystems Unit of the GNP, we matched each item related to clear-cut of invaded areas, seedling production, reforestation with native seedlings, and mechanical and chemical control of restored areas that the GNP usually performs in other restoration projects. The values calculated for all the items of these four different activities were used to monetize and project the costs for the restoration of the ~1000 hectares that form the *Cedrela* forest. In total, we calculated that a gross amount of US$7,440,000 is necessary to clear-cut, produce the necessary seedlings to restore the extracted sites, plant native seedlings, and maintain them in initial stages, if the entire 1000 ha block of *Cedrela* forest is to be restored (Annex 1: Table 11.1).

After more than 2 years of interaction with the identified groups, the relevant answers from the surveys (Annexes 1 and 2 and more results on Annex 4) and direct discussions with GNP staff allowed us to create a preliminary stakeholders' diagram (or "systems thinking diagram," Bosch et al. 2007) that was formed mainly by five well-defined groups: private tree owners, chainsaw workers, the Galapagos National Park, sawmill workers, and handcrafters. This preliminary diagram (Fig. 11.1) was shared with and validated by GNP staff. The resulting diagram with the five defined stakeholder groups consisted of six connections. These "connections," or relations between stakeholders, are important to define because they can inform future managerial actions such as restoration or planned extraction of invasive trees and can ensure the success of such conservation initiatives (Ford-Thompson et al. 2012).

After creating the socioeconomic model for the ongoing (i.e., "status quo") *Cedrela* market (Fig. 11.2), we described the preliminary impacts of adopting a new management policy (i.e., manage and control *Cedrela* extraction inside and outside the protected GNP) and how some activities might help to ameliorate these effects. Thus, using the "status quo" conceptual model to describe these expected impacts, we identified that:

First, the GNP would have to establish some mechanisms if taking total control of *Cedrela* management, such as buying adult trees and subsidizing private owners (Dehnen-Schmutz et al. 2004), in order to stop *Cedrela*'s extraction and plantation in private lands (Fig. 11.3, step 1). If the private owners decide to sell the standing *Cedrela* trees to GNP, then this agency would have to supervise the extraction of these trees (Fig. 11.3, step 2, box A) and follow similar steps as presented in the "status quo" model (Fig. 11.3, from step 1: "hire"—onwards).

Second, to meet the actual demand for wood in the archipelago, on one hand, the GNP would have to create and implement a management plan for sustainable extraction (Richardson 1998) of *Cedrela* wood from the *Cedrela* forest (which concentrates the higher density of *Cedrela* trees) and, on the other hand, assume the costs related to the ecological restoration with the desired native species for sites where *Cedrela* would be extracted (Fig. 11.3, step 3).

Third, parallel to a restoration plan, GNP should contemplate the expansion control of other invasive species that could establish and colonize in extracted sites within the *Cedrela* forest. Experimental plots are currently established in this site to understand forest dynamics in this "novel" ecosystem.

Fourth, for those trees to be extracted from the *Cedrela* forest, GNP could arrange concession areas identified for removal to sawmills and handcrafters (Fig. 11.3, step 5), who would be in charge of obtaining the resources and hiring the personnel to extract the wood from those areas and produce the derived goods (Fig. 11.3, steps 6–10), following (more or less) the steps detailed in the first "status quo" model (Fig. 11.3). Concessions by the GNP to extract *Cedrela* within the

~1000 ha are suggested as an alternative based on the understanding that the actual *Cedrela* extraction (i.e., clear-cut to prepare the sites for restoration) represents the most expensive cost among the different activities that are necessary to restore this invaded forest (Annex 1: Table 11.1) and might be a good option to reduce the National Park's expenses.

Discussion

This analysis allowed us to identify the main stakeholders in the *Cedrela* market, assess the importance of *Cedrela* for these stakeholders and Galapagos' society and economy, and, most importantly, analyze the impacts to stakeholders if a different management alternative is implemented in this timber market. Since *Cedrela* is the main source of wood for this tropical archipelago, it is essential to create a plan to manage this highly significant timber source; but, as expected, the importance of *Cedrela* in Galapagos' society represents a potential barrier to future *Cedrela* management projects (Marshall et al. 2011). For instance, this study identified stakeholders in the *Cedrela* market, in particular the ones that depend entirely on the availability of its wood, such as handcrafters, who will be negatively affected if timber availability from this invasive species is reduced or eliminated.

After recognizing target groups that could be affected by potential management action involving *Cedrela* extraction and control (to reduce its ecological impacts), decision-makers (in this case the GNP) may want to include these stakeholders in the management process to reduce the probability of conservation project failure (Glen et al. 2013). Additionally, information and education campaigns that include impacted actors could be robust tools to inform them about the indirect and direct benefits of controlling *Cedrela* for the Galapagos community and help to engage them in an intended management project. These campaigns could also include follow-up surveys to evaluate stakeholders' perceptions about the management action of controlling *Cedrela*, information that could be included to reduce social impacts of this action and thus increase project effectiveness (García-Llorente et al. 2008). Other investigations have shown that active participation and information transfer among stakeholders are helpful to obtain sustainable logging and restoration initiatives (Larson et al. 2011) and if well-implemented might also reduce the impacts on affected social groups (García-Llorente et al. 2008).

One key factor identified by this study that might help to implement such campaigns is that, in spite of the lack of interest to get subsidies from the governmental agencies, handcrafters are open to wood alternatives that could replace *Cedrela* timber (Annex 2: Fig. 11.4). This might be advantageous if a full eradication program is intended for this timber species. In the long run, GNP should consider the eradication of *Cedrela* as this is an invasive species causing impacts within a World Heritage Site. Nevertheless, all the alternative woody species defined by handcrafters are considered non-native species (Annex 2: Fig. 11.5), and so, the use of these trees as substitutes of *Cedrela* will need to be carefully analyzed.

The resulting "status quo" model presented in this study (Fig. 11.2) identified the stakeholders that are presently part of this timber market. It depicts how chainsaw workers, sawmill workers, and handcrafters directly interact with each other (and with other stakeholders such as tree owners) and the public in general, while the GNP mainly controls the extraction and transport of wood within the Galapagos boundaries. This model also shows how prices of the different products and services offered by stakeholders can drastically change throughout the market, like the six-fold additional price a high-quality wood piece can cost in the sawmills when compared to the prices quoted by chainsaw workers. These prices can serve as a reference if the GNP agency implements logging and management programs in the *Cedrela* forest and needs to consider costs of subsidies and other economic intervention strategies to reduce the impact of a market change.

In that regard, the alternative model (Fig. 11.3) diagrams how the different stakeholders and steps would likely be affected if the GNP agency establishes an integrative plan to manage the *Cedrela* extraction in Galapagos and if it implements a logging plan for the *Cedrela* forest. The important change in this alternative model (Fig. 11.3), when compared to the "status quo" model (Fig. 11.2), is the number of activities the GNP agency would have to cover in order to acquire the control of this market. The implementation of some activities recognized to help in the efficient management of timber species like *Cedrela*, such as subsidies, education campaigns (McDermott et al. 2013), active workshops with stakeholders and society (Rea and Storrs 1999), a logging plan, and the active control of colonizing invaders in extraction sites (Jaeger and Kowarik 2010), would definitely increase the operating costs that this governmental agency would need, to manage *Cedrela* forest and *Cedrela* in general. But, after step 4 of the alternative model (Fig. 11.3), i.e., control of the expanding invasive plants in extraction sites, the Park would not need to invest significant amounts of time and money since the next stages are already established for this market.

Similar to other systems where non-native trees have invaded, *Cedrela* has greatly altered native forests in the Galapagos, and a return to native forests requires extensive—but potentially feasible—restoration efforts (Meyer and Florence 1996; Jaeger et al. 2007; Rivas-Torres et al. 2017). Such efforts, as identified by the present empirical analysis, would directly impact the GNP (activities and budget). Indeed, some have suggested that restoration using native species is the only way to restore ecological function of historical forests after tree invasion (Jaeger and Kowarik 2010). If the GNP decides to restore the *Cedrela* forest to resemble native vegetation, it will have to extract *Cedrela* trees so that other native arboreal species, such as *Scalesia pedunculata* (which co-dominated this area in the past), can reestablish in the site as a first step. Restoration of *Cedrela*-dominated sites would also mean, among other things, eradicating adult trees that are inside the agricultural land (i.e., outside the protected area) and that can produce seeds that might colonize restored sites. Due to the capacity of adult *Cedrela* trees to produce winged seeds that can colonize distant sites, we proposed that GNP also should control the production of propagules outside of the protected area, which could impact other social groups (such as tree owners) and might need to involve strategies such as buying adult trees located in private lands and subsidizing this group of stakeholders (Fig. 11.3, step 1). Opening the canopy after *Cedrela* extraction might also mean other very pervasive invasive species could colonize and outcompete native plants (Renteria 2012). If the GNP does not invest sufficient effort in controlling the colonization of noxious invasive species (such as *Rubus niveus* and *Cedrela*) on newly opened extraction sites, these weeds might then dominate the landscape. Species like *R. niveus* grow very rapidly in open areas forming dense stands, inhibiting recruitment of other plants underneath (Renteria 2012). This is why (as outlined in Annex 1: Table 11.1) the GNP will need to plant native seedlings (previously nurtured in the greenhouse) and control mechanically—or when necessary, chemically—the recruitment of other invasive plants. Relevant studies highlight that a good restoration strategy has to include post-reforestation activities (in this case control of invasive plants colonization) that will help to ensure the sustainability of the restored forest (Jaeger and Kowarik 2010; Meyer 2014). Also, for Galapagos, the mechanical control of invasive plants has been recognized as highly effective, especially when performed in the initial stages of colonization (Gardener et al. 2010; Renteria et al. 2012).

The calculations of gross costs per each activity needed to reverse *Cedrela* impacts were obtained after projecting the present costs for the same managerial actions performed by the GNP in other areas subjected to restoration. Such costs are simply for reference and would have to be adjusted in the future depending on new economic and climatic circumstances. For example, the GNP would need to define contingency plans—and budgets—in case of natural phenomena like El Niño and La Niña or climate change-related events occurring, which may significantly affect the establishment of the planted native seedlings in restored areas because of drought or excessive rain (Trueman and d'Ozouville 2010). On the other hand, positive values on the presence of *Cedrela* forest—such as refuge for some native plants and large native herbivores like the giant Galapagos turtles, which are apparently finding food in invasive-dominated areas (Blake et al. 2012)—can be also included in the balance for the evaluation of costs and benefits of *Cedrela*-dominated site restoration. It is worth mentioning that the costs presented here are only for the entire 1000 hectares that form the *Cedrela* forest, meaning the GNP will not have to invest these amounts in full when beginning with this site's management. Such costs could be covered gradually as the restoration efforts advance for the *Cedrela* forest.

It is still necessary to define if the GNP would be extracting timber from *Cedrela* forest—and/or other infested areas—until no more trees are available and invaded sites are restored and hopefully *Cedrela* is eradicated or if this agency will implement a logging plan that includes the actual crop and regeneration of *Cedrela* wood patches inside this forest that can help to supply and maintain the wood market in Galapagos. If the Park chose the latter, the costs presented in this study would increase substantially since some of the detailed activities, like the actual extraction and the post-extraction control of invaders, would have to be replicated several times per extraction patch/site and event. However, active wood production from the *Cedrela* forest could also be a significant income source for the Park, who could use the revenues from this activity for the control and management of this and other areas, and also—for instance—for subsidy payments to the private sector that might be affected by its exclusion from the *Cedrela* market. On the other hand, if the GNP chooses the former, desired *Cedrela* eradication might be achieved due to the exhaustion of this timber source, but in this case, the GNP would have to provide alternatives to the future absence of *Cedrela* timber in this closed market, which should be explored before beginning with the *Cedrela* extractions.

The two models presented here were empirically derived based on best available data and observations and on surveys that occurred over 2 years in the field, and they present the most detailed description to date of the wood market in Galapagos. The models were also verified with stakeholders. Still, these systems are not static, and future work is needed to revisit these models and revise them, perhaps including results from restoration techniques and feasibility to reconvert novel areas, different actors and users within the *Cedrela* wood market, and new socioeconomic impacts from changes in the management of the wood market for this invasive but economically valuable species. Nevertheless, we anticipate that the multidimensional analytical models here presented (i.e., that include the ecological impacts in addition to the socioeconomic aspects) will be useful for establishing conservation strategies and management priorities. These models identify which, and how, stakeholders might be impacted under alternative potential managerial scenarios, information that might be critical if new conservation programs intended to manage invasive timber species are established (Hulme 2006). They may also inform policy choices and decision-making processes for the management of other invasive timber species in the Galapagos archipelago and other highly invaded and inhabited areas where similar conservation conflicts might occur.

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Annex 1

Table 11.1 Defined impacts caused by the presence and extraction of *Cedrela odorata* on native and non-native plant species and the corresponding activities and costs that are necessary to revert them

	Impact	Management	Activity	Units	Cost[a]
1	*Cedrela* shade and addition of chemical compounds of this species to soil, significantly reduces establishment and growth of other native canopy species like *Scalesia pedunculata, Psychotria rufipes*, and *Psidium galapageium*	*Cedrela* extraction for restoration purposes	Clear-cut *Cedrela*, site cleaning, and preparation for reforestation	Hectare	US$20 per day × 3 workers × 10 days Total = $6200 per hectare = $4,960,000 for 800 hectares
		Reforestation with native seedlings	Produce seedlings[b]	Seedling	US$1.60 to produce a viable seedling × ~$500,000 needed for 800 hectares = $800,000
			Plant seedlings in the field and maintain and control restored site for native plants' survival	Seedling	US$1.68 per plant in a year × $500,000 for the 800 hectares = $840,000
2	Individual extraction of *Cedrela* adult trees significantly increases the probability of growth and establishment of other invasive plants like *Rubus niveus* and *Cestrum auriculatum*	Control of invasive species after *Cedrela* extraction	Perform mechanical and chemical control for *Cedrela* seedlings and other invasive species, establishing and colonizing after *Cedrela* extraction	Hectare	US$1.05 per hectare in a year × 800 hectares = $840,000
			GROSS TOTAL = US$ 7.440.000		

Note: [a]Costs were calculated after projecting the costs defined in the AOP of the GNP that are specified for restoration purposes
[b]Seedlings are produced in the GNP greenhouse

Table 11.2 Detailed items necessary to produce and maintain 60,720 native seedlings in the GNP Ecosystem Unit's greenhouse and reference labor and restoration costs

Input	Amount	Units	Unit Cost (US$)	Total (US$)
Compost	173	Bag	5	865
Black gravel	2	Truck	128	256
Soil	2	Truck	160	320
TS-1 (hormone, 30 kg)	345	Bag	36	12.42
Novaplex	80	Litter	20.9	1.67
Radical	40	Litter	11.4	456
Water (10.000 L)	10	Tanker	150	1.50

Input	Amount	Units	Unit Cost (US$)	Total (US$)
Subtotal				17.48
Subtotal/60,720 seedlings[a]				0.29
Materials				
Hose	17	Unit	11.59	197.05
Fumigation pump (15 L)	1	Unit	56.93	56.93
Fumigation pump (20 L)	4	Unit	70.41	281.66
Biodegradable plastic bags	600	Unit	5	3.00
Plastic sack (10 G)	12	Unit	8.41	100.99
Plastic containers	43	Unit	10.49	451.24
Large machetes (24 in.)	4	Unit	3.43	13.73
Small machetes (16 in.)	4	Unit	3	12.00
Shovel	10	Unit	17.25	172.58
Black flat plastic	50	Meter	1.89	94.76
Sacks	100	Unit	0.95	95.15
Plastic tank (250 Gl)	4	Unit	345.17	1380.68
Large plastic tank (5000 L)	4	Unit	552.28	2209.12
Subtotal				8065.89
Subtotal/60,720 seedlings				0.13
Maintenance				
Paintbrushes (1 in.)	13	Unit	1.2	15.9
Metallic brushes	8	Unit	1.9	14.9
Pressure hose	45	Meter	1.7	77.4
Irrigation hose	400	Meter	1.9	760.0
Grafting knives	5	Unit	80	399.8
White paint	10	Liter	3	29.9
Greenhouse cloth (60% × 100 m)	10	Meter	250	2500
Pruning scissors (6 in.)	12	Unit	28	342.0
Subtotal				4139.8
Subtotal/60,720 seedlings				0.07
Labor				
Public server, status 1	2	Unit	1710	3.42
Public server, status 2	2	Unit	1110	2.22
Subtotal				67.68
Subtotal/60,720 seedlings				1.11
Reforestation				
Mechanic and chemical control and reforestation (40 hectares[b])	1	Unit	1.050	42,000
Subtotal				42,000
Subtotal/60,720 seedlings				1.68
Production cost per plant				1.6

"AMOUNT" refers to the number of units necessary to produce and maintain this number of seedlings in ~1 year. This information was mainly used to define "COSTS" in Table 11.1

[a] Total plant capacity of GNP's greenhouse

[b] Reference price from restoration projects in Santa Cruz (2014)

Table 11.3 Detail of the survey questions given to four of the five identified stakeholders (not to "tree owners") of the *Cedrela* wood market in Galapagos

#	Stakeholder	Concept	Type of question	Question	Response category	Level of measurement response
1	GNP staff	ROLE	OPEN-ENDED	What is the main objective of Galapagos National Park (GNP) regarding plant-introduced species (IS)?	Fill in the blank	CONTINUOUS
2	GNP staff	ROLE	OPEN-ENDED	From your point of view, what are the main necessities for the control of IS?	Fill in the blank	CONTINUOUS
3	GNP staff	INFORMATIVE	OPEN-ENDED	What are the benefits to restore invaded native forests?	Fill in the blank	CONTINUOUS
4	GNP staff	INFORMATIVE	OPEN-ENDED	Is there an implemented system to measure the restoration benefits?	Fill in the blank	CONTINUOUS
5	GNP staff	INFORMATIVE	OPEN-ENDED	Is there an implemented system to measure the post-restoration effects?	Fill in the blank	CONTINUOUS
6	GNP staff	INFORMATIVE	OPEN-ENDED	Are there any benefits for not restoring and/or eradicating/controlling the *Cedrela* novel ecosystem?	Fill in the blank	CONTINUOUS
7	GNP staff	INFORMATIVE	OPEN-ENDED	How do you think the IS control costs could be minimized?	Fill in the blank	CONTINUOUS
8	GNP staff	INFORMATIVE	OPEN-ENDED	Is *Cedrela* a species of concern for the GNP?	Fill in the blank	CONTINUOUS
9	GNP staff	INFORMATIVE	OPEN-ENDED	What are the benefits of the *Cedrela*-dominated forest?	Fill in the blank	CONTINUOUS
10	GNP staff	INFORMATIVE	OPEN-ENDED	What are the impacts of the *Cedrela*-dominated forest?	Fill in the blank	CONTINUOUS
11	GNP staff	SUBSTITUTABILITY	OPEN-ENDED	If you are able to duplicate your budget for the control and monitoring task, what do you change in your actual planning and why?	Fill in the blank	CONTINUOUS
12	GNP staff	SUBSTITUTABILITY	OPEN-ENDED	Do you think it will be more efficient to have a major influx of money invested in the first stages for the control and monitoring of IS than the current budget schedule?	Fill in the blank	CONTINUOUS

#	Stakeholder	Concept	Type of question	Question	Response category	Level of measurement response
13	Handcrafters	PARTICIPATION	CLOSE-ENDED	Do you know of any farm or place/people who are growing timber species like sauco macho (*Citharexylum gentryi*)?	YES/NO	DICHOTOMOUS
14	Handcrafters	USE	CLOSE-ENDED	Which species do you know are planted in farms growing/managing timber products?	Cedrela	CATEGORICAL
					Guava	
					Teak	
					Cinchona	
					Laurel	
					Chanul	
					Mahogany	
					Balsa	
					Aguacate	
					Guayabillo	
15	Handcrafters	INCOME	CLOSE-ENDED	Do you sell sauco macho (*Citharexylum gentryi*)?	YES/NO	DICHOTOMOUS
16	Handcrafters	INCOME	CLOSE-ENDED	Do you sell guava (*Psidium guajava*)?	YES/NO	DICHOTOMOUS
17	Handcrafters	PARTICIPATION	CLOSE-ENDED	It is because buyers prefer other species?	YES/NO	DICHOTOMOUS
18	Handcrafters	PARTICIPATION	CLOSE-ENDED	What uses do you think the people might be giving guava wood?	Coal	CATEGORICAL
					Furniture	
					Handcrafts	
					Construction	
					Don't know	
					NO ANSWER	
19	Handcrafters	INCOME	CLOSE-ENDED	Do you mainly sell *Cedrela*?	YES/NO	DICHOTOMOUS

#	Stakeholder	Concept	Type of question	Question	Response category	Level of measurement response
20	Handcrafters	INCOME	CLOSE-ENDED	Which other woody species do you mostly sell?	Guava	CATEGORICAL
					Teak	
					Quinine	
					Laurel	
					Chanul	
					Mahogany	
					Balsa	
					Aguacate	
					NO ANSWER	
21	Handcrafters	PARTICIPATION	CLOSE-ENDED	Where do you obtain wood from these species?	Third parties	CATEGORICAL
					Own farm	
					From the continent	
					NO ANSWER	
22	Handcrafters	PARTICIPATION	CLOSE-ENDED	Where do you obtain *Cedrela* wood?	Third parties	CATEGORICAL
					Own farm	
					From the continent	
					NO ANSWER	
23	Handcrafters	INCOME	CLOSE-ENDED	For what purpose do you mostly buy or use *Cedrela* wood?	Furniture	CATEGORICAL
					Construction	
					NO ANSWER	
24	Handcrafters	SUBSTITUTABILITY	CLOSE-ENDED	Do you think there are potential substitutes for woody species such as *Cedrela*?	YES/NO	DICHOTOMOUS
25	Handcrafters	INCOME	CLOSE-ENDED	If you have *Cedrela* wood for sale, how much do you ask for a unit (define a unit)?	Fill in the blank	CATEGORICAL

#	Stakeholder	Concept	Type of question	Question	Response category	Level of measurement response
26	Handcrafters	SUBSTITUTABILITY	CLOSE-ENDED	Would you be interested in planting a different species instead of *Cedrela* if the government/local authorities offer you other plants?	YES/NO	DICHOTOMOUS
27	Handcrafters	SUBSTITUTABILITY	CLOSE-ENDED	If yes, which plant would you be willing to accept as an alternative?	Mahogany Nogal Laurel Teca Alcanfor NO ANSWER	CATEGORICAL
28	Handcrafters	SUBSTITUTABILITY	CLOSE-ENDED	Would you be interested to stop using *Cedrela* if the government/local authorities offer you to pay for it?	YES/NO	DICHOTOMOUS
29	Chainsaw	INCOME	CLOSE-ENDED	How much are you paid for a whole day's work?	Fill in the blank	CONTINUOUS
30	Chainsaw	INFORMATIVE	CLOSE-ENDED	What are the average sizes of the trees you look to cut?	Fill in the blank	CONTINUOUS
31	Chainsaw	INFORMATIVE	OPEN-ENDED	How many pieces of wood you can obtain from a tree of those dimensions?	Fill in the blank	CONTINUOUS
32	Chainsaw	INFORMATIVE	OPEN-ENDED	What is the size of wood logs do you obtain?	Fill in the blank	CONTINUOUS
33	Chainsaw/sawmill	INCOME	OPEN-ENDED	What is the price of first-quality wood[a] in USD per meter?	Fill in the blank	CONTINUOUS
34	Chainsaw/sawmill	INCOME	OPEN-ENDED	What is the price of lesser-quality wood[a] in USD per meter?	Fill in the blank	CONTINUOUS
35	Chainsaw/sawmill	INCOME	OPEN-ENDED	How much do you pay for wood transportation?	Fill in the blank	CONTINUOUS
36	Chainsaw/sawmill	INCOME	OPEN-ENDED	Is there any GNP fee you pay? If yes, how much is it?	Fill in the blank	CONTINUOUS

#	Stakeholder	Concept	Type of question	Question	Response category	Level of measurement response
37	Chainsaw/ sawmill	SUBSTITUTABILITY	OPEN-ENDED	Is there any other wood you extract or commercialize?	Fill in the blank	CONTINUOUS
38	Sawmill	INFORMATIVE	OPEN-ENDED	What is the diameter of *Cinchona* (cascarilla) that you commercialize?	Fill in the blank	CONTINUOUS
39	Sawmill	INFORMATIVE	OPEN-ENDED	What is the length of *Cinchona* (cascarilla), in meters, that you commercialize?	Fill in the blank	CONTINUOUS
40	Sawmill	INCOME	OPEN-ENDED	What is the price for a 20 cm DBH and 5-m-long log of *Cinchona* (cascarilla) in $US?	Fill in the blank	CONTINUOUS
41	Sawmill	INFORMATIVE	OPEN-ENDED	What is the diameter of bamboo that you commercialize?	Fill in the blank	CONTINUOUS
42	Sawmill	INFORMATIVE	OPEN-ENDED	What is the length of bamboo, in meters, that you commercialize?	Fill in the blank	CONTINUOUS
43	Sawmill	INCOME	OPEN-ENDED	What is the price for a meter of bamboo in $US?	Fill in the blank	CONTINUOUS

Note: [a]Lower-quality wood refers to wood pieces less than 20 cm wide and 3 m long, while good-quality wood describes wood pieces of at least 20 cm wide and 3 m long. Common species names: “guava” *Psidium guajava,* “teak” *Tectona grandis,* “quinine” *Cinchona pubescens,* “laurel” *Cordia alliodora,* “chanul” cf. *Humiriastrum*, “mahogany” *Swietenia macrophylla,* “balsa” *Ochroma pyramidale,* “aguacate” *Persea americana,* “alcanfor” *Centratherum punctatum,* “nogal” *Juglans neotropica,* “guayabillo” *Psidium galapageium,* “bamboo” *Bambusa sp*

Table 11.4 Answers for the 15 questions given to 2 chainsaw and 2 sawmill workers Question details are defined in Table 11.3, from questions 29 to 43

#	Questions	Chainsaw 1	Chainsaw 2	Sawmills 1	Sawmills 2
1	How much are you paid (in USD) for a whole day of work?	$30 USD	$30 USD	NA	NA
2	What are the average trees you look to cut?	100 DBH 15–20 m tall	NA	NA	NA
3	How many pieces of wood you can obtainfrom a tree of those dimensions?	$60	NA	NA	NA
4	What is the size of woodlogs you obtain from felled trees?	3 m by 22 cm wide	3 m by 22 cm wide	NA	NA
5	What is the price you charge for a first quality* wood piece/meter?	$0.8USD	$0.8 USD	$5 USD	$5 USD
6	What is the price you charge for a lesser quality* wood piece/meter?	$0.4 USD	$0.4 USD	$1.6 USD	$1.3 USD
7	How much do you pay for transportation?	$30 USD	$30 USD	$30 USD	$20 USD
8	Is there any fee you pay to GNP?	$2USD	$2 USD	$2 USD	$2 USD
9	Is there any other wood you extract or commercialize?	*Cinchona*	*Cinchona*	*Cinchona*	*Cinchona*, bamboo
10	What is the diameter (in centimeters) of *Cinchona* that you commercialize?	NA	NA	20 DBH	NA
11	What is the length (in meters) of *Cinchona* that you commercialize?	NA	NA	5 m	NA
12	What is the price for a log of 20 centimeters DBH and 5 meters long of *Cinchona*?	NA	NA	$40 USD	NA
13	What is the diameter of bamboo that you commercialize?	NA	NA	NA	10 cms
14	What is the length of bamboo that you commercialize?	NA	NA	NA	3 m and over
15	What is the price for a meter of bamboo?	NA	NA	$0.8 USD	NA

Note: Lower (lesser)- and good-quality wood are defined in Table 11.3

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Erratum to: Understanding Invasive Species in the Galapagos Islands From the Molecular to the Landscape

María de Lourdes Torres and Carlos F. Mena

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Conclusion and Management Implications

María de Lourdes Torres and Carlos F. Mena

The structure and function of landscapes change drastically when affected by invasive species. Genetic, evolutionary, and ecological factors are determinant when the impact and long-term implications at a given site are considered. Each natural ecosystem is the result of a long history of interactions within living organisms and between organisms and abiotic factors, which together create the landscape of a specific place. An ecosystem is a dynamic system, which continuously readjusts in response to biotic and abiotic factors, trying to maintain equilibrium and achieve different levels of complexity through time. In this scenario, when a new species is introduced, a series of changes take place at species, population, and community levels, and as a result, new landscapes arise. The important challenge is to understand how—in this new landscape—the welfare of preexisting species is affected, how the relationships between biotic and abiotic factors are modified, and what the final makeup of life networks is.

The authors of the present publication expose discussions and arguments that analyze and explain the effects of invasive species on different ecosystems, taking examples from the Galapagos Islands. Ideas of eradication of introduced species, conservation of endemic or local species, and restoration strategies of altered habitats are some of the main efforts that have been proposed—and executed—in different places. The results of these management approaches differ from case to case, but in several instances where the aggressiveness of the introduced species escapes management efforts, new approaches should be considered.e-mail: ltorres@usfq.edu.ec

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New concepts speak of coexistence between former pristine landscapes and introduced species, since eradication of the introduced species might not be feasible considering biological, financial, and social factors. Of course, these approaches will depend on the magnitude of change created by the invasive species. In some cases, these changes will allow the presence of hybrid systems in which characteristics of the original ecosystem merge with novel elements, but in other cases, where larger changes take place, novel systems could arise in which new interactions and ecosystem functions are established. If this is the case, traditional conservation and restoration strategies may need to be rethought, as is proposed here by several studies.

Another level of complexity is added when considering how invasive species have also altered human social relationships and how these species are perceived by human populations. Studies that combine information about social aspects, together with land use patterns and land change in vegetation coverage through time, show that invasive species management programs should include social considerations in terms of the impacts that such species have in the lives and activities of the people they coexist with.

Understanding Invasive Species in the Galapagos Islands: From the Molecular to the Landscape presents a journey through different views, methods, and theoretical approaches to understand how invasive species have influenced and altered and are currently shaping the landscape of the Galapagos Islands.

A starting point when discussing invasive species—and this is mentioned in almost every chapter—is isolation. Isolated areas such as island ecosystems, where species thrive in the absence of exotic influences, are the ones that most suffer the impacts of invasive species. New environments, low predation, isolation, and low competition by endemic species are some factors that promote the wide distribution of introduced species, affecting the endemic species' populations.

Several chapters in this book (Torres and Gutiérrez, Chap. 1; de la Torre et al., Chap. 3; Valdebenito, Chap. 4; Sampedro and Mena, Chap. 9; and Brewington, Chap. 10) develop different aspects of the invasion of *Psidium guajava*—commonly known as guava—in Galapagos. This species was introduced around 1850, is currently distributed, and has significant land coverage, mainly in the inhabited islands: Santa Cruz, San Cristobal, Isabela, and Floreana.

Torres and Gutiérrez, in Chap. 1, are interested in understanding the interactions that can be found between an endemic and an introduced species that are taxonomically related and share the same habitats. There are several examples of this type of relationship in the Galapagos. One is the case of *Psidium guajava* (guava, introduced species) and *Psidium galapageium* (guayabillo, endemic species). The authors studied the genetic diversity of these species in San Cristobal and found that guava presents a reduced genetic diversity—probably as consequence of a population bottleneck—which most likely occurred during their introduction into an island ecosystem. Interestingly, they also found a considerable gene pool reduction for the San Cristobal *P. guajava* population when compared to continental populations. These results support previous claims related to introduced species in a new environment, as stated in this chapter: "…the individuals that conquered the new place carried only a percentage of the gene pool of the source."

Preliminary results also show that the endemic species displays a considerably higher genetic diversity when compared to *P. guajava* in San Cristobal and that no hybrids were found. The authors emphasize the importance of extending this study to other islands to obtain definite conclusions on how taxonomically related species interact and how the invasive species affects, or does not, the endemic one. Having access to molecular data could broaden the possibilities on how to manage invasive species and how to conserve endemic species.

In Chap. 2, Chaves develops ideas on how introgression or interspecific hybridization of invasive species with local ones could result in the loss of genetic diversity and even in the complete erosion of the endemic genomes. He also describes how these processes could promote the appearance of new species with greater invasion potential, which could mean an increase in biodiversity—a controversial topic nowadays in conservation genetics and extremely relevant for Galapagos conservation.

Chaves emphasizes how molecular markers, such as microsatellites or mitochondrial DNA, can help us understand the genetic makeup of a species. He reports several studies dealing with genetic analysis, for example, the case of the parasitic fly, *Philornis downsi,* an introduced species. Using this type of analysis, Chaves examines the species' colonization history on three islands: Santa Cruz, Isabela, and Floreana. From a methodological point of view, these, and other examples, show the strength of genetic analysis to better understand the introduction history of species in ecosystem such as the Galapagos Archipelago.

De la Torre and collaborators—in Chap. 3, "Interactions Among Exotics: Guava and its Associated Fauna in the Highlands of San Cristobal"—compare the effects of guava on the community of soil invertebrates, on carbon and nitrogen concentrations in soil and plant tissues, and on the diversity of soil invertebrates, across two areas with similar altitude and climate but with different levels of presence of guava (pasture-guava and restoration). Results of this research show significantly lower nitrogen concentration in soil and leaf tissue from the pasture-guava site. The soils of the pasture-guava site were noticeably more acidic than those from the restoration site. These results are novel, since other studies cited in this chapter found that areas with invasive plants have higher nitrogen concentration in soil compared to areas with no invasive plants. The authors suggest that one possible explanation for this finding is related to a decrease of nitrogen availability resulting from a soil acidification process occurring over time as a result of a high nitrogen deposition rate.

Chapter 3 also reveals that the soil invertebrate communities did not significantly differ in either study site. Nevertheless, new and interesting information about species of ants and land snails is presented. Of the ten species of ants recorded, eight species are introduced and two are "questionably native." When the authors considered the ratio of introduced vs. questionably native ant species, they found more introduced species of ants in the pasture-guava site than in the restoration site. Seven species of land snails were also recorded, two of which were introduced, and one of these species—*Zonitoides arboreus*—is a new record for Galapagos. De la Torre and collaborators conclude: "What is clear from these analyses is that the combined effects of introduced plants and animals have altered the terrestrial environments in Galapagos in ways that still need to be fully understood." Studies such as this are necessary to recognize the interactions between invasive plants and native and introduced animals and how each species alters the ecosystem function.

In Chap. 4, Valdebenito presents some preliminary results on the community structure, morphology, and phenology of *Psidium guajava* (guava) and *Psidium galapageium* (guayabillo) on San Cristobal Island. He reports—for the first time—that *P. galapageium* has a more restricted geographic range in San Cristobal Island, mostly limited from 100 to 400 masl, while *P. guajava* has widespread distribution from 200 to 550 masl. *P. galapageium* occurs in habitats with higher percentage of bedrock and block cover than *P. guajava*, which is more common in humid areas. Nevertheless, the two species have the same life-form and probably pollination and dispersal mode as well. Another novel observation described in this chapter is related to the strong difference between the vegetation composition in plots with guava and those with guayabillo. The plant richness and abundance of individuals was higher in plots with guava.

Flowering and fruiting data for both *Psidium* species in San Cristobal are reported here for the first time. This type of information is very important, especially when estimating the possibility of hybridization between both species. Valdebenito argues that although the presence of hybrids has not been reported until now, the potential risk of hybridization events between *P. galapageium* and *P. guajava* is relatively high, mainly because both *Psidium* spp. share similar areas and both species are capable of flowering during the same season of the year. It is important to carry out reproductive biology studies on these species to learn if they are capable of producing fertile progeny and obtain conclusive information on the presence and viability of hybrids.

A paradoxical case is presented by Jäger in Chap. 5, dealing with one of the most invasive species in the Galapagos Islands, the red quinine tree, *Cinchona pubescens* Vahl (Rubiaceae). Although this species is considered rare and endangered in its native range in Ecuador, it is an aggressive invasive in Santa Cruz, producing significant changes in plant species diversity, habitat structures, and light, water, and nutrient regimes. It is clear that quinine has reduced native species cover, such as *Justicia galapagana* Lindau, the tree fern *Cyathea weatherbyana* (C.V. Morton) C.V. Morton, and *Scalesia pedunculata* Hook.f. This invasion has also affected certain animal species like the Galapagos petrel *Pterodroma phaeopygia* Salvin and the Galapagos rail *Laterallus spilonotus* Gould.

Chapter 5 describes the efforts made by the Galapagos National Park Directorate to control the spread of quinine using manual and chemical methods. Interestingly, Jäger mentions how the disturbances caused by these control measures seem to facilitate the establishment of other introduced plant species, especially blackberry (*Rubus niveus*). This situation demands a profound analysis of the control methods used and their consequences in terms of plague management and conservation efforts. In this regard, the author clearly emphasizes: "It is not recommended, therefore, to expand the current area where quinine is being controlled, but rather to ensure that re-sprouting stems and germinated seedlings are constantly being pulled out by hand to avoid a re-invasion of areas devoid of the invader, which is the method currently applied by the GNPD. In addition, this follow-up control must also include hand-pulling of germinated blackberry plants. If this cannot be guaranteed, quinine populations should be left untouched."

Another noteworthy observation presented in the same chapter is that over the last 10 years, quinine trees have shown symptoms of natural debilitation and although the causes for this are unknown, they could be assigned to the action of a pathogen. Pathogens have been shown to accumulate in invasive plant populations over time, and this may result from multiple ecological processes. The function of these "new actors" is a challenge that will have to be faced if we want to understand the role they have for introduced and endemic species.

In Chap. 6, Rivas-Torres and Rivas present the allelopathic impacts that invasives can have on island ecosystems, using as example the invasive species *Cedrela odorata L.* (Meliaceae, Sapindales = Magnoliidae) and analyzing its effects on the endemic tree *Scalesia pedunculata* Hook.f. in Santa Cruz. The authors explain that Santa Cruz highlands have suffered a radical transformation on around 86% of the original land cover due to invasive species and land clearing. *Cedrela* currently dominates an area of ~1000 ha, and *Scalesia* population for this island is reduced to only 1% of its original extent. *Cedrela* is one of the invasive species *Scalesia* has to compete with, and this invasive tree has been extremely successful in colonizing areas previously occupied by the endemic species. The mechanisms explaining such replacement are still not clear.

For the first time for Galapagos, Chap. 6 provides evidence of the allelopathic effect *Cedrela* has over at least the seedling stage of two endemic species. Rivas-Torres and Rivas discovered the negative effect of *Cedrela* extracts over *Scalesia* seedlings by certain compounds found in plants presenting allelopathic traits that apparently affect root development and thus reduce initial growth of the resident plants. Rivas-Torres and Rivas point out that they carried out experiments where allelopathy was only tested for early stages under controlled conditions and might not be the only invasive mechanism *Cedrela* uses to colonize and promote novel mono-dominated forests. Other potential processes also need to be evaluated to understand *Cedrela* invasion and the monocultures it forms in Santa Cruz and the extirpation of *Scalesia* from its original sites. Experiments including explanatory ecosystem-scale factors, their interactions (e.g., water and light availability), and species-specific variables (e.g., plant growth) should be performed to analyze the impact of invasive plants' colonization on native plant communities.

As is well known, island ecosystems record a significantly higher number of non-native species compared to other biomes, making them particularly vulnerable to plant invasions. In this context, Rivas-Torres and Rivas mention that the effects of allelopathy may be relevant, since evidence suggests that when chemical weapons are present, they affect resident plants not only at species level but also at a community level. It has been shown that the chemical weapons produced by the introduced species not only benefit themselves but also provide advantages to other coexisting non-native plants.

Cisneros-Heredia, in Chap. 7, explores the idea of “the hitchhiker wave” to understand how non-native small terrestrial vertebrates arrived in the Galapagos Archipelago. He reports a total of 25 non-native amphibians, reptiles, and bird species. This chapter reminds us of a very important fact on introduced species: human population in Galapagos has increased significantly over the last decades, and transportation links carrying local travelers, tourists, and supplies have facilitated the arrival of non-native species. Invasive non-native species have been identified as the principal threat to biodiversity in the Galapagos terrestrial ecosystems. Cisneros-Heredia shares detailed data on the distribution of non-native amphibians, reptiles, and bird species in several islands. Santa Cruz and San Cristobal are the islands with the largest amounts of reported non-native amphibians, reptiles, and bird species (18 spp. each). Twelve species are reported in Isabela, three in Baltra, and two in Marchena and Floreana. The islands of Genovesa, Pinta, Pinzon, and Santiago each have only one reported species.

Chapter 7 also presents the available information related to the introduction of three species of amphibians in Galapagos and for one of these species—*Rhinella horribilis*—a correlation between where this species is found in mainland Ecuador and areas with cargo warehouses, maritime ports, and airports with connections to Galapagos. In this way, the author suggests possible introduction routes for this species. Furthermore, Cisneros-Heredia reports on the introduction history of nine species of non-native reptiles, emphasizing that all established populations are geckos—members of the squamate reptilian infraorder Gekkota. He also discusses the 12 species of non-native birds recorded in the Galapagos Islands: chickens, ducks, and turkeys, among others. The impacts these species have on native flora are still not clear (i.e., spreading of infectious diseases to native birds).

Relevant data for conservation and management of the Galapagos are also presented in Chap. 7: 8 (32%) non-native amphibians, reptiles, and birds in Galapagos arrived as domestic animals, 5 (20%) as pets, and 1 (4%) as (unsuccessful) biocontrol. All domestic animals, pets, and biocontrols were brought to the islands deliberately. However, most (44%) non-native amphibians, reptiles, and birds reached the Galapagos Islands as hitchhikers aboard airplanes or ships, unintentionally translocated. Considering this information, it is clear that in order to prevent the introduction of more hitchhiking species in the Galapagos, a key factor is the establishment of control measures at ports and airports and the training of the crew in airplanes and ships to correctly identify, restrain, and handle non-native hitchhiking animals.

In a transition from molecular methods to a focus on ecosystems, Walsh—in Chap. 8—describes how different image analysis methods and geographic information systems contribute to the study of introduced species and their consequences at a landscape level. The author explains how the fusion of remote sensing data from several spatial, spectral, and temporal resolutions can support a variety of environmental models by providing relevant information to predict plant distributions and the most suitable environmental conditions for their spread throughout the time.

Walsh also discusses how stochastic events can influence the dynamics of plant invasion in certain environments. In Galapagos, it appears that the occurrence and spread of introduced species may depend more on human activities and the nature of managed landscapes. In this scenario, data collected from multiple sensor systems and platforms (satellites, aircraft, unmanned aerial vehicles, and geospatial field technologies) enables us to assess spatial patterns and associated processes that help us grasp the sources of change, the composition, condition, and behavior of target species across the landscape. Now, central for environmental management in Galapagos, Walsh describes how the inclusion of the human dimension, when using remote sensing methodologies, is crucial for better land management decisions, land use/land cover change analysis, and eradication projects. In this sense, new approaches in mapping, monitoring, and modeling the spread of introduced species need to include human decision-making.

In Chap. 9, Sampedro and Mena evaluate different satellite imaging methods to discriminate the spread of *Psidium guajava* or guava in San Cristobal Island. Principal components of pixel-based and object-based image classifications were used to create similar and visually acceptable representations of the land cover classes within the study area. Despite the expected "salt-and-pepper" effect in the pixel-based analysis, the pixel-based classifications offered a more generalized visual appearance and more contiguous interpretation of land cover compared to the object-based classification.

This study comments on the importance of having accurate and up-to-date land use and land cover change information, mainly of inhabited islands, where several factors—but mainly the growth of tourism activities—have promoted the abandonment of agriculture and cattle ranging areas. In consequence, these areas are likely to become centers of establishment and propagation of invasive species, such as guava and blackberry. The area of study chosen for this research is very complex, since numerous social processes are taking place, producing different landscape changes. The rapid spread of invasive species, such as guava, blackberry, and wax apple, has created a very diverse landscape, presenting small plots of land with a high mixture of plant composition. However, the three tested methods were able to capture the complexity of the composition of the land use and land cover structures of the area.

Continuing with landscape-level analysis, in Chap. 10, Brewington adds another relevant point when considering invasive species. In her research, she discusses stakeholder perceptions of invasive species and participatory remote sensing in the Galapagos Islands, focusing on Isabela. She presents data on the aggressive invasion of guava on this island, where it has been estimated that this species covers more than 40,000 ha of Isabela's southern private and protected lands. Given its extensive presence, control—rather than eradication—is the most feasible management option according to the author.

Brewington conducted interviews and performed a participatory classification exercise with two main stakeholders, landowners and National Park employees, in order to analyze their perceptions on the changes that have occurred in land use and land cover on Isabela's ecosystems. In this way, the author attempts to broaden the discussion on invasives using remote sensing images, adding narratives and including social aspects. The participatory classification exercise revealed very different views and values of the landscape between landowners and National Park personnel. For example, National Park employees could recognize areas of introduced ferns or grasses, identifying them as individual introduced species and using the plant's common name. On the other hand, landowners used more general categories like grasses or herbaceous vegetation to describe these areas. Guava was the exception: both stakeholders identified it in photographs, even when other species or land cover types were present.

A remarkable observation from Chap. 10 is the difference in perceptions found between the two stakeholder groups: while National Park employees believe that introduced species are ecosystem threats, landowners regard any organism that might diminish the productive potential or economic value of the region as a possible threat, regardless of origin. Weeds—for landowners—do not always mean invasive, and native plants are not always well seen. As Brewington puts it: "The results of this study provide compelling arguments for using participatory research methods as a tool to directly engage stakeholders in the research process and reconcile visions of productivity or degradation in shared spaces for conservation and economic activities." Importantly, in these participatory research methods, remotely sensed imagery and analysis have demonstrated to be powerful tools for clarifying local knowledge about the landscape.

In Chap. 11, Rivas-Torres and Adams also emphasize the importance of recognizing the critical role of social aspects in invasive species management. Here, the authors cite several examples that highlight the importance of the social landscape in which invasive species exist, where identifying stakeholders and defining their roles is vital. The appropriate management of introduced species in this approach includes the view of different groups identifying invasive species removal as beneficial or detrimental. Perceived benefits might complicate invasive species' control and management and frustrate policy interventions if diverse stakeholders have opposing views about their positive or negative impacts.

Rivas-Torres and Adams explore the example of the invasive tree *Cedrela odorata* and present some interesting data: *Cedrela* is now the main timber resource in the Galapagos, and its wood is mostly used locally for furniture and handicrafts for the tourism industry, representing an annual market value of around US$2,000,000. On the other hand, the GNP spends on average US$132,000 per year on *Cedrela*-related restoration activities, including the operation of a greenhouse near the *Cedrela* forest that can produce 60,000 native seedlings to support restoration projects in this highly invaded zone in Santa Cruz.

The authors use descriptive analysis, survey, and interview methods to understand the case of this invasive and economically important tree. After over 2 years of work, Rivas-Torres and Adams were able to create a preliminary stakeholder diagram conformed by five well-defined groups: private tree owners, chainsaw workers, the Galapagos National Park, sawmill workers, and handcrafters. The identification of these stakeholders is very noteworthy and helps us recognize the complex social, economic, and ecological aspects of invasive species management.

The main contribution of Chap. 11 is the presentation of two empirical models (status quo and alternative models) based on best available data and observations—and on surveys that occurred over 2 years in the field—to describe the wood market in Galapagos. The authors recognize that these systems are not static and that future work is needed to revisit these models and revise them, perhaps including results from restoration techniques and feasibility of reconverting novel areas, different actors and users within the *Cedrela* wood market, and new socioeconomic impacts from changes in the management of the market for this invasive—but economically valuable—species. However, these models do identify stakeholders who might be impacted under alternative potential managerial scenarios and anticipate how this might happen, information that could be useful if new conservation programs intended to manage invasive timber species are to be established.

Final Remarks

Considering the range of methodological approaches and scales, the chapters that make up this edited volume reinforce different aspects within the study and management of invasive species in Galapagos, including:

- The importance of genetic studies on invasive and endemic species, especially in cases where related species (invasive and endemic) are living together in a specific area, in order to identify the geographic distribution of these species' genetic diversity and establish whether hybridization events have occurred. This information could guide conservation, control, and eradication programs of the GNP.
- The importance of expanding studies regarding morphological, phenological, and community structure to better understand the interactions between related endemic and introduced species.
- The importance of remote sensing studies to have consistent programs monitoring the different areas affected by introduced/invasive species, in order to access information regarding changes of land use and land coverage through time. In recent years, remote sensing technology has proven to be efficient in the field of invasive species since it provides a synoptic view, multispectral data, and multitemporal coverage.
- The importance of healthy agricultural areas. Invasive species flourish in abandoned farms and plots outside of the control of the Galapagos National Park. Moreover, lack of local agricultural products results in food importation to satisfy local markets. Reactivation of agriculture is necessary to fight invasive species in key areas of populated islands.
- The importance of strengthening the quarantine measures established by agencies—such as the Galapagos Biosafety Agency—to better control and prevent the introduction of species coming from the mainland via air flights, goods shipments, and tourist and commercial activities.

The Galapagos Islands are a mix of complex geographic territories and diverse inaccessible ecosystems. It is unlikely that one management solution or approach to invasives will fit all islands and species. It is clear now that inhabited islands, like San Cristobal and Santa Cruz, need to emphasize control of existing invasions, while non-inhabited islands need to have an emphasis on eradication. In many cases, the Galapagos National Park has already adopted this strategy, within the limited economic resources available.

Finally, we would like to close this chapter paraphrasing Cisneros-Heredia (Chap. 7): we should go beyond the paradigm that the main impact of non-native species is framed by their direct effects on native species. We need to understand the ecosystemic effects of non-native species, for example, on nutrient dynamics and cumulative effects on food webs through trophic and non-trophic interactions, and we need to understand the role of human populations in relation to new invasions and how different future scenarios can be built for better conservation and environmental management.

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