Chapter 2
Genetic Consequences of Invasive Species in the Galapagos Islands

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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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M.L. Torres, C.F. Mena (eds.), *Understanding Invasive Species in the Galapagos Islands*, Social and Ecological Interactions in the Galapagos Islands,
https://doi.org/10.1007/978-3-319-67177-2_2

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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