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Oceanic islands and climate: a multi-criteria model of drivers of change to select key conservation areas in Galapagos

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Abstract

The unique marine and terrestrial ecosystems of the Galapagos Islands are highly vulnerable to human-based drivers of change, including the introduction of invasive species, unsustainable tourism, illegal fishing, overexploitation of ecosystem services and climate change. These drivers can interact with climate-based drivers such as El Niño Southern Oscillation (ENSO) at multiple temporal and spatial scales, exacerbating their negative impacts on already fragile ecosystems and the socioeconomic system of the Archipelago. In this review, we performed a literature review based on published literature from 1945 to 2020 and local and global climate databases to analyze drivers of change in the Galapagos. We developed and applied a spatial impact assessment model to identify high ecological value areas with high sensitivity and exposure scores to environmental change drivers. We identified 13 priority HEVA that encompass ca. 23% (14,715 km^2) of the Galapagos Archipelago, distributed in nearly 3% of the Galapagos Marine Reserve and 20% Galapagos National Park. Current and future impacts are likely to concentrate on the inhabited islands' highlands, whereas marine impacts concentrate along most of the Galapagos islands' shorelines. These results are important for guiding the design and implementation of adaptation measures aimed at increasing ecosystem resilience and human adaptive capacity in the face of global environmental change. Overall, these results will be valuable in their application for preserving Galapagos biota, securing the provision of vital ecosystem services for resident human populations, and sustaining the nature-based tourism industry.

Keywords: Island ecosystems, global environmental changes, impact assessment, high ecological value areas, adaptation.

1. Introduction

Climate change represents one of the main threats to the conservation and sustainable use of marine and terrestrial biodiversity worldwide (Mantyka-Pringle et al. 2012). Oceanic islands are especially vulnerable to this global climatic driver due to the fragility of their ecosystems, which are the result of complex evolutionary, geological, and environmental processes (Harter et al. 2015). The geographic isolation of oceanic islands, in combination with the long-term stability of the environmental conditions and natural selection, have promoted high levels of endemic and native species (Jansson 2003; Fordham and Brook 2010). Thus, evolutionary processes shaping island communities have originated insular species with unique behavioral and life-history traits, and ecological relationships suited to stable conditions. Insular species exhibit intrinsic characteristics that make them susceptible to habitat disturbance, including narrow ecological niches, natural restricted distributions, reduced competitive ability and predator awareness, and behavioral or habitat specializations (Cronk 1997; Fordham and Brook 2010; Sodhi et al. 2004). These ecological features make islands ecosystems highly vulnerable to invasive species, whose colonization after natural or human-induced disturbances is facilitated by the absence of predators and low levels of interspecific competition (Vilà et al. 2011; Harter et al. 2015).

Climate change in combination with invasive species will exacerbate the degradation of islands ecosystems (Keener et al. 2012; Hernández-Delgado 2015; Braje et al. 2017). Physical (e.g. rising air temperature, sea-level rise) and chemical changes (e.g. ocean acidification, O_2 concentration declines) can affect both the composition and biodiversity of insular communities and the various functions of the ecosystem, transforming their structure (Keener et al. 2012; Ferreira et al. 2016; Harter et al. 2015). For example, rising sea surface temperature (SST) will result in increased rainfall that affects both low- and highland ecosystems, which likewise will alter plant growth, community structure, promotes erosion, and provides better conditions for invasive species (Trueman and D'Ozouville 2010; Larrea Oña and Di Carlo 2011).

Climate change is occurring faster than expected by the scientific community (IPCC 2014; Smith et al. 2015), potentially exceeding the adaptive capacity and resilience of island ecosystems. This is happening in a context, in which most of these unique ecosystems are already degraded by a growing number of drivers of change, increasing the vulnerability of native and endemic species to climate change (Fordham and Brook 2010; Smale et al. 2019; Castrejón and Charles 2020).

The Galapagos Islands are located in the Eastern Tropical Pacific (ETP), 960 km west of mainland Ecuador (Fig. 1). This volcanic archipelago is located in the confluence of three major seasonally varying warm and cool water oceanic current systems, and it is strongly affected by El Niño Southern Oscillation (ENSO), whose main influence area is the Equatorial Pacific Ocean (Liu et al. 2013; Glynn et al. 2018). Hence, the singular location of Galapagos makes it a unique place to assess the potential impacts of climate variability on the demography and life-history traits of Galapagos biota.

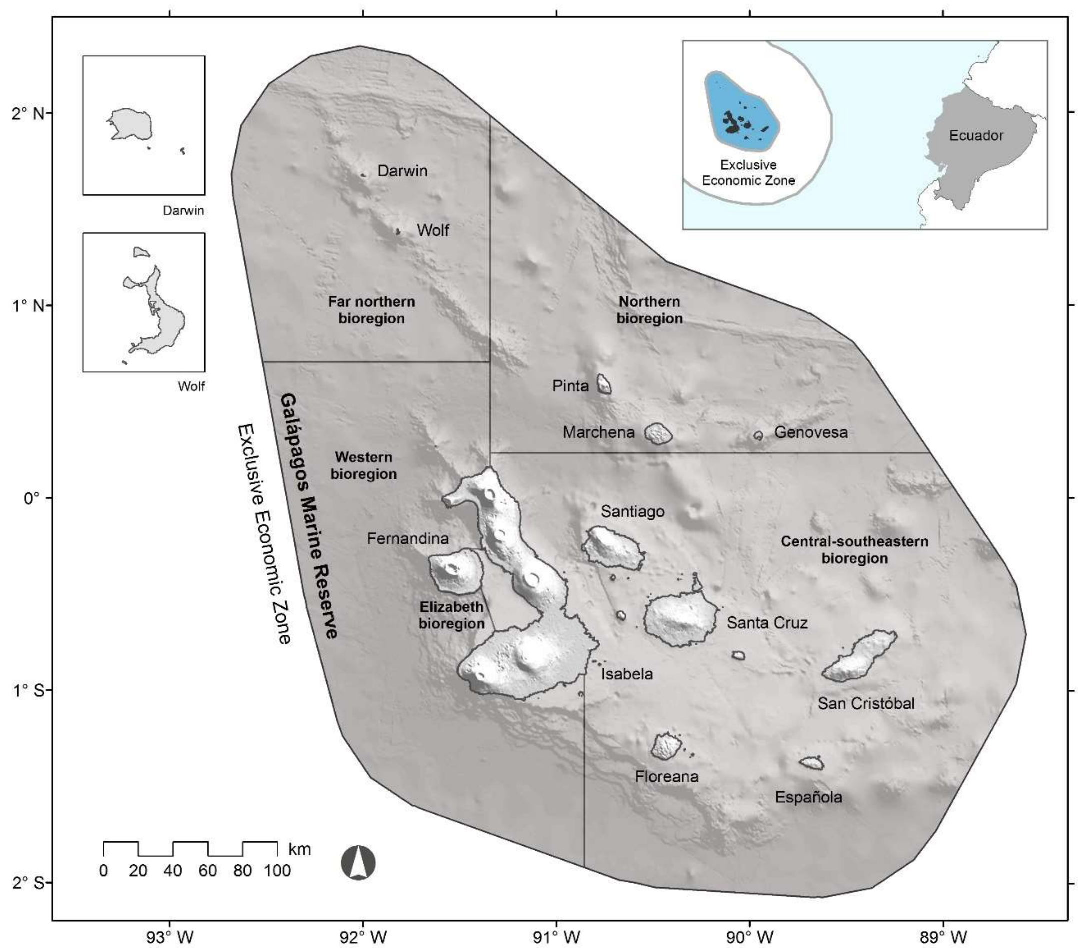

Figure 1. Map of the Galápagos Islands, with inset showing location of the archipelago relative to continental Ecuador. Surrounding lines denote the Galapagos Marine Reserve with its five bioregions as described by Edgar et al., 2004a: Far-Northern, Northern, Central-southeastern, Western and Elizabeth.

The strong differences in oceanographic conditions across the archipelago have produced broad-scale and marine biogeographical patterns not observed in other parts of the world (Edgar et al. 2004a; Riegl et al. 2019a; Schiller et al. 2014). These unique features have made the Galapagos a nature-based tourism destination upon which the local economy depends on (Mathis and Rose. 2016). It generates annual revenues of USD 450 million, representing ca. 20% of Ecuador´s tourism gross domestic product, and ca. 80% of the local economy (Pizzitutti et al. 2017).

However, tourism has produced negative effects on the Galapagos natural environment, including the introduction of new invasive species, an increasing amount of waste and growing use of local limited resources, mainly drinking water (Toral-Granda et al. 2017; Epler 2007; Larrea Oña and Di Carlo 2011; Pizzitutti et al. 2017). Besides the increasing number of tourists and invasive species, the Galapagos Islands face several other drivers of change, such as marine pollution, overfishing, and illegal fishing (Schiller et al. 2014; Alava et al. 2014; Salinas-De-León et al. 2020). All of these drivers of change can interact at multiple temporal and spatial scales with ENSO and climate change (Crain et al. 2008; Mantyka-Pringle et al. 2012; Harvey et al. 2013; Graham et al. 2011; Genner et al. 2010; Mouillot et al. 2013) exacerbating their impacts and threatening even more an already fragile system.

The global importance of the Galapagos Islands for biodiversity conservation and the high sensitivity of tropical island systems to drivers of change highlights the need to identify priority areas where conservation and management actions can be implemented to mitigate human impacts while increasing ecosystems resilience (Moreira et al. 2018; Cuesta et al. 2017; Fajardo et al. 2014; Kareiva et al. 2011). In this review, we discuss the main drivers of change that threaten the unique marine and terrestrial ecosystems of Galapagos. Then, we perform a spatial-impact assessment model of the Galapagos archipelago to identify high ecological value areas (HEVA), which we define as areas of intrinsic biotic importance (singularity), highly exposed to climate change impacts and other human drivers, using available climate databases and a literature review of published literature. This spatial analysis is based on observed and expected changes in the terrestrial and marine ecosystems of the Galapagos Islands. Finally, within the obtained HEVA, and with the overarching goal of supporting policymaking and informing about conservation actions, we select specific HEVA that should be prioritized to develop ecosystem-based adaptation measures (EBA)[1].

2. The Galapagos Islands

The archipelago is divided into five marine bioregions, referred to as Far-Northern, Northern, South-Eastern, Western and Elizabeth (Fig. 1) (Edgar et al. 2004a). Each bioregion has distinctive reef fish and macro-invertebrate assemblages, which are unique combinations of species derived from Indo-Pacific, Panamanian, Peruvian, and endemic source areas (Edgar et al. 2004a). The abundance and distribution of these communities are strongly affected by the confluence of warm currents from the north and cool waters from the southwest (Riegl et al. 2019a). The western and central-south sections are characterized by colder upwelling conditions (Edgar et al. 2004a), while the northern sections exhibit higher SST than the central archipelago. However, the northern sections also exhibit persistent intrusions of colder and more nutrient-rich waters (Kislik et al. 2017; Riegl et al. 2019b).

Galapagos comprises approximately 234 islands, islets, and rocks with a total land area and coastline of ca. 7 985 km and 1667 km (DPNG 2014), which are enclosed in a multiple-use area (MPA) of nearly 138,000 km^2, the Galapagos Marine Reserve (GMR) (Fig. 1) (Heylings et al. 2002). The GMR encompasses a variety of ecosystems, ranging from coral reefs, coral communities, and mangroves along the shorelines (Glynn et al. 2018; Moity et al. 2019; Tanner et al. 2019) to rocky reefs and

[1]An EBA is a measure designed to simultaneously reduce poverty, protect or restore biodiversity and ecosystem services, and remove atmospheric greenhouse gases. Therefore, an EBA integrates the use of biodiversity and ecosystem services into an overall strategy to help people adapt to the adverse impacts of climate variability and change (Scarano et al., 2017). EBAs are particularly relevant for Galapagos to safeguard one of most the important biodiversity and climate change hotspots in the world.

newly discovered kelp-forests on seabeds throughout the archipelago (Buglass 2018; Buglass et al. 2017; Eddy et al. 2019; Graham et al. 2007; Okey et al. 2004; Tompkins and Wolff 2016).

The GMR provides habitat for over 2,900 fish species, aquatic invertebrates, and marine mammals, 20% of which are endemic (Schiller et al. 2014). The marine diversity in the GMR ranges from emblematic pelagic megafauna species such as whale sharks and mantas to endemic corals, groupers and coral reef fish (Acuña-Marrero et al. 2018; Acuña-Marrero et al. 2014; Edgar et al. 2004a; Glynn et al. 2018; Hearn et al. 2014). Ecosystems within the GMR are important in the lifecycle of top predators that support shark diversity, shark nurseries, and other demersal ray-finned fishes (Hearn et al. 2010; Llerena et al. 2015; Salinas-De-León et al. 2015; Peñaherrera-Palma et al. 2017). The marine ecosystems of the GMR also provide important services to humans. This occurs mainly through fish productivity, where species such as red spiny lobster, sea cucumber, and demersal Serranids are particularly exploited by artisanal fisheries (Hearn and Toral-Granda 2007, Hearn et al. 2005; Castrejón 2011).

Among the terrestrial environment, islands and islets exhibit a deserted landscape rather than a tropical forest typical of equatorial latitudes. Plants depend mostly on sporadic rain from December to June. However, islands higher than ~200 m can permanently have a dense fog (Porter 1979). The spatial variation of rainfall with altitude creates a vegetation zonation pattern of three main regions in the Galapagos Islands: (1) the dry lowlands, also referred as the arid zone, which occupies the majority of the archipelago (83% of total land area); (2) the transition zones; and the (3) humid zone or the highlands (Larrea Oña and Di Carlo 2011).

Regarding plant community assemblages, up to seven vegetation zones can be recognized (from lower to higher altitudes): (1) litoral, (2) arid, (3) transition, (4) *Scalesia*, (5) Brown, (6) *Miconia* and (7) Fern Sedge zone. The plant biodiversity in each vegetation zone is adapted to the existing micro-climate conditions (Hamann 2001; Porter 1979). Smaller and lower islands typically have only littoral and arid/dry zones; seven of the islands are high enough to support humid zone ecosystems (Tye and Francisco-Ortega 2011).

The Galapagos Islands harbor over 600 plant species, of which 30% are endemic (Galapagos-Conservancy 2021) and mostly in the arid zone (Porter 1979). The humid zone has higher productivity due to its higher rainfall, which provides habitat for many native and endemic species (Larrea Oña and Di Carlo 2011). However, the humid zone is mostly degraded on inhabited islands due to land-use and invasive plant species impacts (Laso et al. 2020; Watson et al. 2009). Protected land areas are managed by the Galapagos National Park (GNP), which covers 97% of the land area in the archipelago (GNP 2020)

3. Drivers of change

The Galapagos archipelago, like many tropical islands, is a system highly sensitive to human impacts (Fordham and Brook 2010) and is affected by climate dynamics (Grant and Grant 2006). The intrinsic sensitivity of the Galapagos has increased in recent decades due to the effects of the following drivers of change: (1) climate change, (2) unsustainable tourism and local population growth, (3) overfishing and illegal, undeclared and unregulated (IUU) fishing, (4) invasive species (Defeo et al. 2013;

Castrejón and Charles 2020; Salinas-De-León et al. 2020). Throughout this article, we refer to drivers of change as any natural or human-induced stressor that causes a change in ecosystems, as defined in Nelson et al. (2006) and Carpenter et al. (2006). The combined impacts of these drivers pose an unprecedented threat to the Galapagos system (Salinas-De-León et al. 2020).

3.1 Climate: Galapagos climate, El Niño-Southern Oscillation (ENSO), current, and future trends.

3.1.1 Galapagos climate

The Galapagos climate is a product of the interaction of oceanic currents surrounding the islands and the winds from the southeast (Trueman and D'Ozouville, 2010). The influence of currents and winds is governed by interactions of the Inter-Tropical Convergence Zone (ITCZ) and the El Niño Southern Oscillation (ENSO) (Houvenaghel, 1974; Sachs and Ladd, 2010). Specifically, the ITCZ migration influences the main bi-seasonal characteristics of currents and winds of the Islands, whereas ENSO regulates yearly decadal fluctuations (Hamann, 1979, 1985; Hartten and Gage, 2000). For most of the year, the ITCZ is located north of the archipelago and the southeast trade winds blow across the Galapagos, bringing cooled air from over the cold upwelled waters of the south pole. When the ITCZ migrates southwards closer to the Galapagos, the trade winds are reduced and warmer ocean currents from the north arrive at the archipelago (Alpert 1946).

The seasonality of the ITCZ combined with the topography of the archipelago results in two seasons: a warm, rainy season (January to May) and a cool, dry season (June to December) (Colinvaux 1972; Hamann 1979; Itow 2003). During the warm, rainy season, evaporation due to high SST leads to orographic rainfall that increases with altitude; thus, the lowlands only receive a marginal amount of rainfall and stay dry while the highlands become significantly humid (Hamann 1979; Snell and Rea 1999; Trueman and D'Ozouville 2010). Each island's size, altitude, and exposure to wind determines the amount and seasonality of rainfall received. Furthermore, during the cool, dry season the air is lowered in temperature by the ocean surface and is trapped below masses of warmer air, creating condensation. Condensation occurs above 250 m altitude and creates heavy mists and drizzle that are blown inland from the ocean, shifted upwards by the mountains, and consequently cooled, resulting in more intense rainfall in the highlands (Hamann 1979; Sachs and Ladd 2010; Trueman and D'Ozouville 2010).

3.1.2 El Niño-Southern Oscillation (ENSO)

The Eastern Tropical Pacific (ETP) exhibits inter-annual SST variability that is dominated by the ENSO cycles (Wang and Fiedler 2006). El Niño (warm phase) events are characterized by high SST, a lack of west-to-east thermal gradient across the surface of the Pacific, and a weakening of the easterly trade winds (Snell and Rea 1999). In Galapagos, El Niño produces high air temperatures, sustained high SST, increased rainfall, and a longer than usual warm season, whereas La Niña (cold phase) events result in abnormally cold conditions and drought (Sachs and Ladd 2010). Past strong El Niño events (1975-76, 1982-83, 1993-84, and 1997-98) triggered dramatic effects on both marine and terrestrial ecosystems (Snell and Rea 1999; Trueman and D'Ozouville 2010; Defeo et al. 2013; Martin et al. 2017). For example, the El Niño 1982-83 decimated populations of endemic species, such as the Galapagos penguins (*Spheniscus mendiculus*), which are still recovering (Laurie 1985; Robinson and Del Pino 1985; Trillmich and Limberger 1985). Coral reefs suffered intensely during this period, with 98% of corals being wiped out by coral bleaching (Glynn, 1994; Lessios et al., 1983; Robinson, 1985) followed by a significant decrease in marine species diversity (Edgar et al. 2010; Stein Grove 1985). During El Niño events the bottom of the food chain is also impacted by ENSO, as phytoplankton concentrations can decrease substantially (33-46%) as a result of high temperatures in the archipelago, leading to community-level reductions in biomass (Wolff et al. 2012).

The impact of ENSO events also extends to terrestrial ecosystems and communities. Heavy rainfall characteristic of El Niño can trigger massive increases in herbaceous plants, which can then stimulate increased abundances of exotic invasive species and vines (Larrea Oña and Di Carlo 2011). Over-flooding can also result in increased mortality for resident species, such as for arboreal plants (Aldaz and Tye 1999; Tye and Aldaz 1999) that have trunks smothered by vines (Hamann 1985; Tye and Aldaz 1999) and giant tortoises that die due to injury or drowning in flooded ravines (Marquez et al. 2008). Land birds (e.g. finches) are also negatively affected by El Niño events due to the intensity of perturbations and because high rainfall triggers more intense parasitism (Dudaniec et al. 2007; Fessl and Tebbich 2002; Grant et al. 2000). Despite the occurrence of ENSO events in the Galapagos for thousands of years, strong El Niño events are unusual (see Fig. 2 - Riegl et al., 2019a). However, evidence suggests that El Niño events have increased in intensity and frequency over the last two decades due to warmer SSTs (Conroy et al. 2010, 2008; Rustic et al. 2015; Thompson et al. 2017).

3.1.3 Observed climatic trends

Mean air temperature has increased by ~0.5ºC since the late 1980s, in both lowland and highland regions (Fig. S1), as suggested by data from the National Meteorological and Hydrological Institute (INAMHI) climatological stations on the islands of Santa Cruz and San Cristobal, Ecuador. This increase in mean air temperature is higher during the warm/wet season on the coast in the cool/dry season (1.3 vs. 0.1 ºC respectively) (Fig. S1). In contrast to this increasing trend in mean air temperature, precipitation records from 1981 to 2017 suggest a decreasing trend across the archipelago, particularly in arid coastal areas (Fig. S2). Critically, the first two decades of this century are on average ~40% drier than those during the decade of 1981-1990 (Fig. S3). Despite this overall decreasing trend in precipitation in the archipelago, records from 2002 to 2017 suggest the precipitation pattern has not changed significantly in the coastal region of Santa Cruz and San Cristobal islands (Fig. S3). This supports the hypothesis that ENSO events, particularly those from 1982-83 and 1997-98, have influenced the time series and prevented a clear interpretation of climatic trends. Although records from the islands of Santa Cruz and San Cristobal are essential in understanding climatic patterns, their variation due to island topology and exposure to oceanographic and climatic variables, highlights the need to establish several more climatic stations in this region in order to understand climate variability throughout the entire archipelago.

In contrast to the data provided by the Santa Cruz and San Cristobal islands' climate stations, a time series analysis using monthly datasets of CHELSA (Karger et al. 2017) from the last 34 years (1979 to 2013) covering the entire extent of the Galapagos Islands, showed a small decrease of 0.06ºC in mean annual air temperature (Fig. S4A). These patterns of precipitation and air temperature demonstrate spatial variability, particularly with elevation (Fig. S4B-C). Data from this time series shows that annual precipitation across all of the Galapagos Islands ranges from 557 mm to 1324 mm and follows a clear positive trend along the elevation gradient. The upper areas (above 368 m asl) of the islands receive a mean annual rainfall of 909 mm, whereas lower areas (below 51 m asl) are exposed to an annual rainfall that can get up to 749 mm (Fig. S4B). In contrast to the positive trend in precipitation with elevation, the air temperature has a negative trend with elevation in the Galapagos Islands, with an adiabatic lapse rate of 0.55 °C per 100 meters. The thermal amplitude spans from a mean air condition of 24°C at sea level to as cold as 15°C at 1600 m AMSL at the mountain summits of Santa Cruz, San Cristobal, or Isabela (Fig. S4C).

Within the GMR, SST for the period 2002-2018 shows a clear warming trend. Data from MODIS interannual variability shows an increase in diurnal and nocturnal SST at a rate of 0.06 °C year (Fig. S5A). This finding is in agreement with other reports suggesting that the equatorial Pacific has warmed 0.4º-0.8º over the last 40 years (IPCC 2007) and that greater increases in SST are expected in this region due to greenhouse warming (Cai et al. 2018, 2015). However, due to the prevailing oceanic currents having differences depending on the particular region of the Galapagos Islands being examined, SST anomalies for the GMR have contrasting patterns (Fig. S5B). For the period 2002 to 2018, the Far-Northern and Northern bioregions have received the highest warming (up to 2.3°C increase), whereas the Western bioregion has received the highest cooling (-5.7°C decrease) (Fig. S5B). Coastal areas around Floreana, Española, and San Cristóbal have also shown increased SST anomalies.

3.1.4 Projected changes in climate

The Climate Model Intercomparison Project (CMIP5) simulates a historical and future broad warming in the Eastern Pacific over the past century (Coats and Karnauskas 2017). However, small-scale temporal and spatial variability may be dominated by natural fluctuations in the climate system or with phenomena such as El Niño. Nonetheless, for the Galapagos Islands, Global Circulation Models (GCMs) generally project warmer and wetter future conditions, consistent with current observations (Liu et al. 2013; Rial et al. 2017; Sachs and Ladd 2010).

Climatology projections, based on CHELSA grids (Karger et al. 2017) of mean annual air temperature and precipitation derived from 5 GCM models (CSIRO-MK3-6-0, HADGEM2-CC, HADGEM2-ES, MIROC-ESM-CHEM and MRI-CGCM3) for two RCPs scenarios (RCP4.5, RCP 8.5), suggest that there will be significant anomalies in both temperature and precipitation for the year 2050 (period 2020-2060), with considerable differences between the RCP scenarios (Fig. S6). Temperature is expected to increase 6.2% up to 14.5%, in the RCP 4.5 and 8.5 respectively. This increase will be heterogeneous across the islands, with humid zones in the western islands showing the greatest increase (Fig. S6A). Precipitation projections also suggest a relative increase on all the islands (30.3% up to 50.2%), with greater increases in the highlands of Santa Cruz, Fernandina, and central/southern Isabela (Fig. S6B-C). Projected increases in annual rainfall are accentuated along the elevation gradient as major deviations from current conditions and are located at the upper elevation range, with a mean annual increase of 1.2% (i.e. 10.6 mm) (Fig. S7A). Precipitation is also predicted to increase in different transitions and arid zones throughout all islands. Relatively high precipitation increments are projected for the arid lowlands of the southern slopes of Floreana, Southern Isabela, and Santa Cruz. The arid ecosystems of Española, Marchena, Genovesa, Pinta, Santa Fe, and Pinzón will also be highly exposed to increased precipitation (Fig. S6B-C). These results are concordant with other Santa Cruz-based projections, which suggest air temperature will increase throughout the 21st century (1.8-5 °C and 3-5 °C for annual max. and min. air temperatures, respectively) while precipitation will accentuate its seasonal variation (2.5-4.5 mm per-day increase in the rainy season and up-to 3 mm per-day reduction in the dry season) (CAF 2019).

The ETP is expected to have increased SSTs due to greenhouse warming, suggesting an increase in ENSO frequency and intensity (Cai et al. 2018, 2015). The dynamic downscaling of the impact of climate change on the ocean circulation dynamics in the Galapagos Islands projects an increase of a near 2°C rising trend in SST anomaly in the El Niño 3.4 region for the period 2001–2050 (Liu et al. 2013). The observed warming trends in the dynamic model show that the entire Galápagos region is significantly affected by global climate change, yet the degree of exposition is not homogeneous across the archipelago. The upwelling region to the west of the Isabela Island shows relatively slower warming trends compared to the eastern Galápagos region (Liu et al. 2013).

The observed negative effects of El Niño indicate that an interaction between climate change and ENSO could pose a grave threat to the Galapagos Islands. The coupled impacts of both stressors could profoundly impact previously affected ecosystems and species (Boersma and Rebstock 2014; Salazar and Denkinger 2010), augment colonization dynamics of invasive exotic species (Ellis-Soto et al. 2017), disrupt ecological processes such as ocean productivity (Sachs and Ladd 2010) and fishing resources (Castrejón and Charles 2020), and change water regulation capacity through the altering of soil organic carbon stocks (Rial et al. 2017). Lastly, upward trends in sea levels are projected to continue throughout the twenty-first century (Nerem et al. 2018) and the sea level in the Galapagos has been slowly rising (~10 cm since 1985) (Fig. S7B). Sea level rise in the Galapagos Islands could increase the risk of coastal flooding and impact tourism and infrastructure, along with reducing marine and terrestrial habitats such as shallow reefs, mangroves, and nesting sites for marine iguanas and turtles (Larrea Oña and Di Carlo 2011).

The observed trends and future projections discussed above indicate a progressive divergence of current climate conditions in the Galapagos Islands from past confidence intervals characterized by climatic variables in this region. Continued increases in sea surface and air temperature coupled with more intense and erratic ENSO events may lead to a climate system in the Galapagos Islands with increased seasonality and stronger spatial heterogeneity (Wolff 2010).

3.2 Overfishing and Illegal Undeclared and Unregulated (IUU) fishing

Marine ecosystems provide a diverse array of services utilized by humans, including the support of fisheries (Barbier 2017). Fisheries are of paramount importance due to their roles in food security and sustaining livelihoods (Bell et al. 2018). However, the ecosystems that provide these services are threatened by climate change and human activities, reducing the benefits they can provide (Smale et al. 2019). Human activities that threaten these ecosystems service include overfishing of target species, which continues to be a persistent and growing problem, and poor water quality as a product of harmful algal blooms, offshore pollution, and oxygen depletion from land-based runoff and infrastructure (Barbier 2017).

The marine life of the Galapagos Islands has been commercially exploited since the late 18th century, markedly with the hunting of Galapagos fur seals (*Arctocephalus galapagoensis*) (Townsend 1934), and local sperm whales (*Physeter macrocephalus*), which have never recovered from whaling activities (Cantor et al. 2017; Whitehead et al. 1997). Finfish fisheries in the Galapagos date back to the early 19th century (Castrejón 2011) and commercial fisheries were permanently established in 1945, where the main target species was the Galapagos grouper (*Mycteroperca olfax*), or locally referred to as *bacalao* (Schiller et al. 2014). Ecuadorian industrial fisheries are prevented from fishing within the borders of the GMR and are only allowed to operate within the exclusive economic zone (EEZ), an area that extends from outside of the GMR border to 320 km. Most of the legal and illegal fishing that occurs within and around the GMR comprises tunas and sharks (Carr et al. 2013; Schiller et al. 2014). The most important target species caught by the Ecuadorian industrial and artisanal fishing fleet are the skipjack, yellowfin, and bigeye tuna (*Katsuwonus pelamis*, *Thunnus albacares*, and *Thunnus obesus*, respectively) and mahi-mahi (*Coryphaena hippurus*) (Schiller et al. 2014; Castrejón 2020a). Sharks are caught incidentally in the tuna and mahi-mahi fishery, and together with IUU fishing, represent one of the main threats for shark conservation (Castrejón 2020b). The legal framework of Ecuador prohibits shark finning and commercial exploitation of sharks nationwide. In mainland Ecuador the landing and trading of sharks are permitted only in those cases when these species are caught incidentally and as long as they are landed whole (fins and body). In contrast, the capture, landing, and trading of sharks are prohibited in the

GMR, even if they were caught incidentally. Despite these measures, thousands of sharks are landed annually on the main fishing ports of mainland Ecuador, suggesting the existence of a fishery within the Ecuadorian EEZ that targets sharks illegally, including the GMR (Carr et al. 2013; Alava et al. 2017; Alava and Paladines 2017). Hence, the estimated landings of sharks very likely represent only a fraction of the total landings for this region (Schiller et al. 2014).

Galapagos artisanal fisheries target at least 68 fish species from 27 families (Schiller et al. 2014; Zimmerhackel et al. 2015). Exploited fishes are both demersal and pelagic and largely consist of serranids, tuna, wahoo, labrids, and mullets (Castrejón 2011). Galapagos fisheries also target invertebrates, mostly spiny and slipper lobsters (*Panulirus penicillatus*, *Panulirus gracilis*, and *Scyllarides astori*) (Bustamante et al. 2000; Hearn and Toral-Granda 2007). The brown sea cucumber (*Isotichorpus fuscus*) is also harvested, but this fishery has remained closed since 2015. However, at least three other species (*Stichopus horrens, Holothuria kefersteini, and H. atra*) are illegally caught (Toral-Granda 2008).

The Galapagos Marine Reserve is a sanctuary for heavily exploited fish like tuna and sharks, which migrate consistently to and from the reserve (Acuña-Marrero et al. 2017; Hearn et al. 2016; Boerder et al. 2017). The maintenance of the GMR is beneficial for both industrial and artisanal fisheries, as it increases fish productivity both outside and inside the reserve (Boerder et al. 2017; Bucaram et al. 2018). However, the overexploitation, incidental catch, and illegal fishing, produced by Ecuadorian and foreign industrial and artisanal fisheries established along GMR' boundaries (Boerder et al. 2017), reduce the effectiveness of the GMR to ensure the recovery of these commercial and protected species (Alava et al. 2017; Alava and Paladines 2017; Castrejón 2020b).

To mitigate the impacts of human activities on the GMR and to ensure the sustainability of Galapagos small-scale fisheries, marine zoning plan was implemented (between 2000 and 2006) in combination with a co-management regime, and the allocation of exclusive fishing rights to local small-scale fishers (Heylings et al. 2002; Castrejón and Charles 2013). Approximately, 18% of the Galapagos coastline were declared as no-take zones, whose individual size ranged from small offshore islets to a 70 km span of coast, with no offshore boundaries legally established. However, the biased location of no-take zones in areas of low abundance of the most lucrative fishery resources (i.e. sea cucumbers and spiny lobsters), combined with a lack of effective enforcement and a high rate of non-compliance, severely limited the effectiveness of Galapagos marine zoning to improve the governance and sustainability of small-scale fisheries and the conservation of Galapagos marine biodiversity (Bucaram et al. 2013; Bucaram and Hearn, 2014; Defeo et al. 2014; Edgar et al. 2004b; Moity 2018).

The sea cucumber fishery collapsed in 2006 due to overfishing (Hearn and Toral-Granda 2007; Hearn et al. 2005; Toral-Granda 2008), while large apex-level fish such as the Galapagos grouper (*M. olfax*), the white-spotted sand bass *(Paralabrax albomaculatus*), and the olive grouper (*Epinephelus cifuentesi*) show signs of overexploitation (Danulat and Edgar, 2002; Schiller et al. 2014; Usseglio et al. 2016). Groupers and sand basses exhibit declines in landings and catch-size compared to previous estimates, even in no-take zones (Burbano et al. 2014; Zimmerhackel et al.

2015; Usseglio et al. 2016). As a result, the catch composition has changed over time. Fish species previously with no economic value now are commercially exploited, including mullets (*Xenomugil thoburni* and *Mugil galapaguensis*), wahoo (*Acanthocybium solandri*), and pomfret (*Seriola rivoliana*) (Castrejón 2011; Danulat and Edgar 2002). Furthermore, the rate at which sharks are being extracted illegally from Galapagos is among the highest of any EEZ in the world (Schiller et al. 2014). Fisheries assessments and genetic studies suggest that sharks in the ETP show signs of overexploitation (Carr et al. 2013; Pazmiño et al. 2017), and thus, urgent attention to illegal and incidental catch of sharks within and around the GMR is required.

Intensive fishing coupled with the reduced distribution of several Galapagos marine species (e.g. Galapagos grouper) makes them very susceptible to extinction (Schiller et al. 2014). Overexploitation of top predators, such as groupers or sand basses, can trigger cascading effects in the trophic chain, declining Galapagos marine diversity (Ruttenberg 2001; Ruiz and Wolff 2011). Furthermore, given the ecological role of sea cucumbers as nutrient recyclers (Purcell et al. 2011), the depletion of this species probably degraded the function and structure of Galapagos marine ecosystems. The reduction of spiny lobster stocks could be linked to an increasing presence of sea urchins (e.g. *Eucidaris galapagensis*) in the subtidal zone, leading to bioerosion and detriment of coral communities (Banks 2007; Glynn et al. 2015). However, this hypothesis is uncertain considering that, after a period of overexploitation, spiny lobster stocks have shown clear signs of recovery (Defeo et al. 2014; Szuwalski et al. 2016).

3.3 Invasive species.

Invasive species have been introduced into Galapagos both deliberately and by accident, including the introduction of farm animals and plants and the accidental introduction of rats, fire ants, and the parasitic fly (*Philornis downsi*) (Toral-Granda et al. 2017; Gardener et al. 2013; Larrea Oña and Di Carlo 2011). Until 2017, there were 1575 alien species across the archipelago (Toral-Granda et al. 2017). Among these, there are ca. 870 introduced plant species, of which 16% are invasive species and 3.3% transformers species, leading to plant communities structure modification (Buddenhagen and Tye 2015; Trueman and D'Ozouville 2010). Invasive plant species not only impact native and endemic species abundance through competition and by transforming plant communities but can also be incorporated into the diet of native animals, aiding expansions in their distribution (Blake et al. 2012, 2015; Ellis-Soto et al. 2017). Invasive insects and vertebrates also cause negative impacts on native and endemic species decimating their populations. The larvae of the parasitic fly (*P. downsi*) feeds on the blood of chicks from native and endemic birds, causing high mortality rates (Deem et al. 2008; Jiménez-Uzcátegui et al. 2007; Lawson et al. 2017). Invasive fire ants predate on a variety of Galapagos wildlife, including reptiles, birds, and invertebrates (Causton et al. 2006; Herrera and Causton 2008; Wauters et al. 2018, 2017, 2016). Introduced mammalian species, mainly goats, rats, cats, and dogs, have decimated the abundance of diverse plant and animal species through predation and competition for the same ecological niches (Wiedenfeld and Jiménez-Uzcátegui 2008; Heleno et al. 2012; Renteria et al. 2012b).

The ecological impacts produced by invasive species can be exacerbated by climate oscillations that result in favorable conditions for these species (e.g., longer rainfall periods). ENSO increases rainfall season, which triggers massive growth of herbs and vines, changing the community structure of arid ecosystems and making them more susceptible to colonization by invasive species (Hamann 1985). In consequence, invasive plants have transformed entirely the composition of plant communities in the farmlands and pastures, located in the highlands of Galapagos inhabited islands (Laso et al. 2020; Watson et al. 2009) (Table S1). The increasing prevalence of pathogens and parasites during the rainfall season increases the mortality rates of bird populations, particularly of Galapagos finches and mockingbirds, by reducing their breeding and fledging success (Cimadom et al. 2014). This problem is exacerbated by rats and mice, which prey on native and endemic birds and whose abundance increases during the rainfall season.

The eradication of invasive species is extremely challenging and expensive (Renteria et al. 2012a) and projects aiming to eradicate invasive species in the Galapagos often meet a series of challenges, mainly with a lack of economic support for institutions, the denial by landowners to conduct fieldwork, or overly-ambitious projects (Gardener et al. 2010). Despite these obstacles, plant eradications are feasible, realistic, and justifiable if well-known criteria are met. Buddenhangen and Tye (2015) have reported an up to 38% success rate for eradication programs in the Galapagos. In addition, several invasive vertebrates like goats, pigs, pigeons, rats, dogs, tilapia and donkeys have been successfully eliminated from some of the islands or even from the entire archipelago (Carrion et al. 2011, 2007; Cruz et al. 2005; Phillips et al. 2012b, 2012a). The removal of these harmful species has immediate positive results on the recovery of endangered native species (Carrion et al. 2011; Donlan et al. 2007). However, the eradication of invasive species is just one of several steps in being able to restore the terrestrial ecosystems of the Galapagos Islands (see Atkinson et al. 2008, Carrion et al. 2011).

Finally, although the impacts of invasive species have been extensively studied in Galapagos terrestrial ecosystems, very little is known about marine invasions in Galapagos and the magnitude of their impacts on marine ecosystems. At least 53 introduced marine invertebrates and 33 cryptogenic invertebrates, algae and halophytes, have been reported for Galapagos, most of them were probably brought by ships (Carlton et al. 2019; Keith et al. 2015). Given that research on marine alien species in Galapagos is relatively recent and that only a subset of habitats has been assessed, this suggest that marine alien species and their impacts are substantially underestimated. Therefore, regulating institutions should implement measures to study the advancement of alien species, reduce invasion risk and minimize their impacts.

3.4 Unsustainable tourism and local population growth

Tourism is the main driver of change behind increasing demands for natural resources and population growth in the Galapagos, leading to an unsustainable development model that is fundamentally incompatible with the long-term conservation interests. In less than 10 years, the number of tourists that visit Galapagos has grown 417%, from 65,000 to 271,238 between 2000 and 2019 (Fig. S8A). Nature-based tourism is the primary economic engine of the Galapagos and generates annual revenues of USD 450,000,000 (Pizzitutti et al. 2017). This represents close to 20% of Ecuador´s tourism Gross Domestic Product (GDP) and almost 80% of the local economy (Pizzitutti et al. 2017). The international representation of the Galapagos has transformed the islands into a world-class nature-based tourist destination, receiving a staggering 271.238 visitors in 2019 (DPNG 2019).

The tourism industry has promoted demographic and economic growth for the Galapagos, resulting in ca. 30, 000 residents (Epler 2007; Walsh and Mena 2016) that depend both directly and indirectly on the tourism industry (Fig. S8B). The population growth rate in the islands is three times higher than on the Ecuadorian mainland (Pizzitutti et al. 2017), while the economy is one of the fastest-growing economies in the world. In response, the Ecuadorian Government has implemented restrictive migratory measures to avoid immigration into Galapagos. However, the resolution of this problem is more difficult than expected due to a complex intersection of economic, cultural, social, and political realities associated with the human development of inhabited islands (Brewington 2013; Epler 2007). Exponential rates of tourism arrivals have also negative feedbacks to local population, especially indirect effects on public health, as flux of migrants put increase pressure to the weak health systems, potable water network and pressure over food security (Walsh and Mena 2016; Thompson et al. 2020; Nicholas et al. 2019; Houck et al. 2020).

Human development has aroused several problems that threaten natural resources, such as with oil spills inside the marine reserve (Snell 2002), water contamination and wastewater mismanagement (Alava et al. 2014; Ragazzi et al. 2016; Wikelski et al. 1996), destruction of native ecosystems (Brewington 2013; Laso et al. 2020), touristic sites and trails overuse (Brewington 2013; Self et al. 2010), and plant and animals disturbance (Denkinger et al., 2013; French et al., 2010; Wikelski et al. 1996). One of the most pervasive byproducts of tourism is the introduction of invasive species (Nash 2009; Pizzitutti et al. 2017) (Fig. S8C), which have increased over time positively correlating with the increasing number of tourists (Toral-Granda et al. 2017). The effects of tourism have been so severe that UNESCO (United Nations Educational, Scientific and cultural Organization) added the Galapagos Islands to the list of "World Heritage in Danger" in 2007, listing uncontrolled development and mismanagement of tourism and growth in the human population as main reasons (Nash 2009). Additionally, the Galapagos conservation assessment by the IUCN was evaluated as of "significant concern" in by the 2017 World Heritage Outlook, with tourism, invasive species and climate change being the significant current threats (IUCN, 2017). Galapagos is a prime example of a protected area suffering an environmental crisis that has been generated by the over-exploitation of natural resources (Pizzitutti et al. 2017).

Overall, while the appealing combination of unique flora-and-fauna and beautiful landscapes in the Galapagos has helped boost the local economy and allowed the GNP to gain funds for its management and conservation initiatives, it has also brought problems to the archipelago. Climate change and tourism are interrelated drivers of change, as tourism contributes to climate change through the emission of greenhouse gases (GHG) related to accommodation, activities, and transport (Scott et al. 2008) and climate change disrupts ecosystem processes and the abundance and distribution of endemic species, which impacts the tourism industry. Thus, climate change scenarios in the Galapagos should be aligned with the tourism industry to mitigate the impacts and identify adaptation measures to increase both ecosystem and tourism industry resilience.

4. Projected impacts of environmental change

To select priority areas for the implementation of EBAs in the Galápagos (Colls et al. 2009), we built a spatially explicit model for impact assessment (Fig. 2). We used the concept of vulnerability for the identification of areas that would be highly sensitive and exposed to multiple drivers of change. The interaction of multiple drivers can result in additive, synergistic or antagonistic outcomes with varying degrees of negative impacts (Crain et al. 2008). However, the outcomes of multiple drivers' interactions in Galapagos' ecosystems remain unknown. Therefore, we used a simple additive model approach, where the impact of drivers' interactions is the product of their cumulative effects (Crain et al. 2008), and the magnitudes of exposure are differentiated and ranked. Our model does not pursue the precise estimation of the magnitudes of interactions but poses an approximation to the spatial distribution of different drivers and their heterogeneous and overlapped occurrence among the Galapagos Islands. Altogether, the combined magnitudes of Sensitivity and Exposure submodels were used to identify areas of potential impacts (i.e., areas of biotic and abiotic importance where multiple drivers of change co-occur) (Fig. 2, Eqn. 1). To this end, we used methods of multi-criteria and algebraic spatial modeling (Chakhar and Mousseau 2007; Dunčková et al. 2019; Greene et al. 2011; Lin 1998).

$$PotentialImpact = Sensitivity * Exposure. \qquad \text{Eqn. 1}$$

The magnitude of Sensitivity was obtained by a literature review derived from the Galapagos related-scientific literature about the impact of climate change on terrestrial and marine ecosystems. The magnitude of Exposure was obtained by combining environmental online databases (i.e., CHELSA, NOAA, land cover maps) with anthropogenic variables, such as terrestrial and marine public tourist use areas, reported targeted fishing and by-catch areas, and land-use management status. The resulting impact model represents a hypothetical trajectory of potential environmental change-related impacts on a sensitive ecological system, assuming the absence of adaptation measures (Füssel and Klein 2006). Finally, it is not within the scope of this study the quantitative validation of the model, but to illustrate the spatial occurrence of the multiple drivers of change described in our literature review. However, the results of our impact assessment model were qualitatively validated by local management authorities and stakeholders through workshops and work meetings.

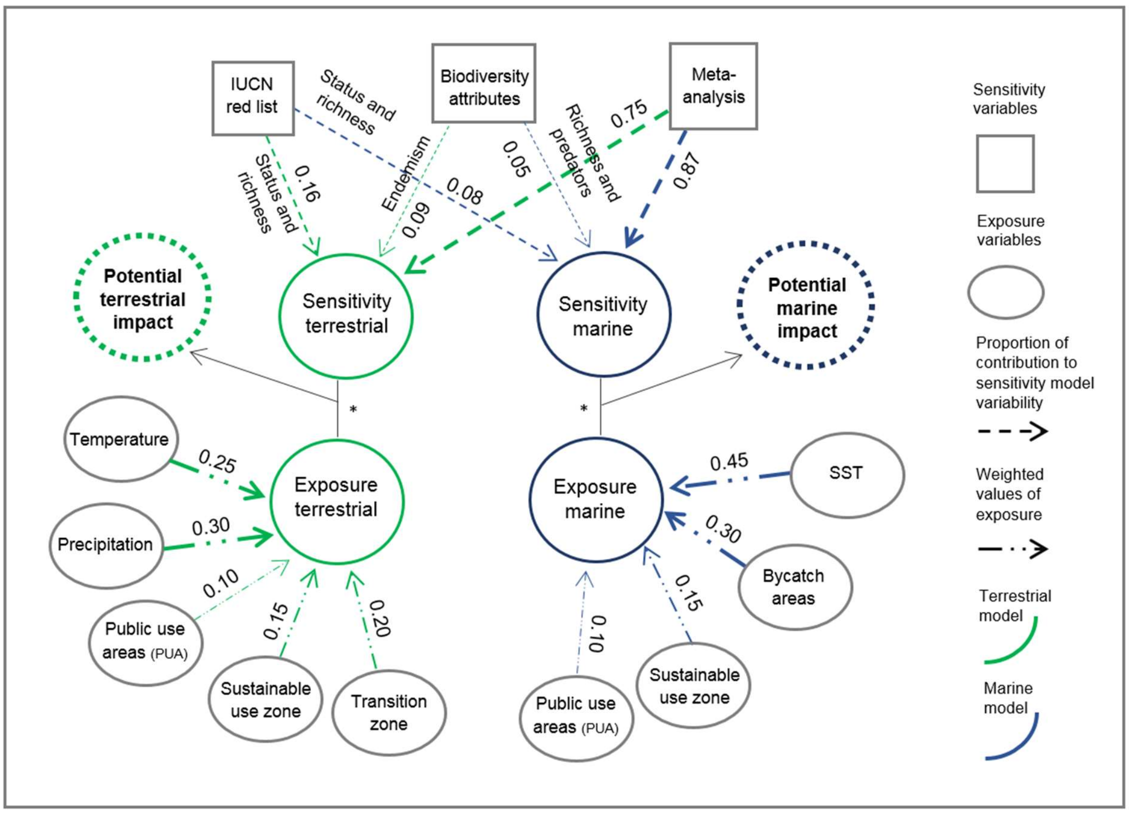

Figure 2. Diagram showing the development of the impact assessment model for the Galapagos Islands. Drivers of change and submodels that were used for estimating impacts are shown in green and blue denoting terrestrial and marine ecosystems respectively.

<u>4.1. Sensitivity analysis</u>

<u>*4.1.1 Literature review*</u>

The magnitude of sensitivity was assigned using a literature review that examined 135 published peer-reviewed studies from 1945 to 2018. We searched for Galápagos publications using the Web of Knowledge and Google Scholar and the keywords: “Galapagos”, “climate change”, and/or “environmental change”. Each study was evaluated for the following criteria: (1) invasive species impacts, (2) interactions between species, ecosystems, and services; (3) documented climate variability/change impacts of the studied population or area, (4) importance of the study area for the provision of environmental services, (5) exposure of the studied area or species to other impacts (e.g. overfishing), and (6) relevance of the studied area for the conservation and survival of a species. These criteria were scored in a binary fashion (Table S2), with a score of 1 being assigned for the respective criteria whenever any of the criteria was specified as relevant for the studied area/species in a study. In contrast, if the study did not highlight the above-mentioned criteria, a score of 0 was assigned accordingly. Studies that analyzed areas with the highest sensitivity got a maximum score of 6, only if all the criteria were met. Additionally, several publications reported quantitative attributes that were added to the score, while others lacked specific spatial references (see Supplementary materials). The final literature review score was the result of the spatial overlay of the 99 studies included in the metanalysis and the computation of an algebraic sum of the total criteria score of each study layer (Eqn. 2)

$$lit.reviewscore = \sum_{x=1}^{99} x_{criteriascore} \qquad \text{Eqn. 2}$$

4.1.2 Biodiversity attributes

We complemented our literature review by separately assigning biodiversity attributes to terrestrial and marine ecosystems. These attributes considered different areas that accounted for the number of endangered species, species richness, the proportion of terrestrial endemic plant species to total plant species richness, and marine keystone species[2] distributions.

Maps of richness of endangered species accounted for the distribution of 28 threatened Galapagos species, as cataloged by IUCN's red list. Polygons of each species' distributions were downloaded from https://www.iucnredlist.org. This variable accounted for up to 16.5 % and 7.6 % of the sensitivity model variability in the terrestrial and marine models, respectively.

For terrestrial biodiversity attributes, we included the number of endemic-plant (EP) species and mapped them on the seven vegetation zones recognized by Porter (1979), where we developed a ratio of the total 229 endemic species mapped for each vegetation zone. This variable contributed up to 9 % of the sensitivity model variability (see supplementary materials).

Furthermore, for marine biodiversity attributes, we considered the distributions of important habitats and keystone species, including top predators' density (Fig. S10). Habitats included areas of (1) sea cucumber and lobster catches (Buglass et al. 2017; Bustamante et al. 2000; Toral-Granda and Martínez 2005; Wolff et al. 2011), (2) shark nurseries (Llerena et al. 2015), (3) corals (Glynn et al. 2018), and (4) whale-shark

[2] A keystone species has a disproportionately large effect on its natural environment relative to its abundance (Paine 1995). Therefore, a keystone species plays a critical role in maintaining the structure of an ecological community, affecting many other organisms in an ecosystem, and helping to determine the types and numbers of various other species in the community.

habitat (Hearn and Roman 2016). For density and distributions of predators (PD), we included: (1) endemism and richness of sharks (Acuña-Marrero et al. 2018; Hearn et al. 2014), (2) sperm whale densities (Cantor et al. 2017), (3) tiger shark densities (Acuña-Marrero et al. 2017) and (4) hammerhead shark densities (Hearn et al. 2010; Peñaherrera-Palma et al. 2017). Polygons for each habitat and predators' density/distributions were scored with 1 whenever each was present. Marine habitats and predators' density/distributions accounted for 2.2% and 3.3% of the sensitivity model variability respectively (see Supplementary materials).

Finally, we obtained the sensitivity score as the result of the literature review plus the biodiversity attributes (Eqn. 9). Two models were obtained, one for terrestrial and the other for marine ecosystems. This output constitutes 50% of the potential impact model (Fig. 2, Eqn. 1).

$$Sensitivity = (Lit.review) + (biodiversityattributes) \quad \text{Eqn. 9}$$

<u>*4.1.3 Sensitivity results*</u>

Half of the islands had high-frequency scores (within 20 and 40) and the highest sensitivity, including Santa Cruz, San Cristobal, Santiago, and Fernandina (Fig. S11A). Among terrestrial ecosystems, the *Scalesia* zone got the highest sensitivity scores, followed by the arid and transition zones. High-frequency scores were distributed differently among the terrestrial ecosystems (Fig. S11B). Furthermore, the Western and Elizabeth bioregions obtained the highest sensitivity, while the Central-southeastern bioregion exhibited the highest frequency (Fig. S12A). Within marine ecosystems, corals and habitats of sea cucumbers and lobsters yielded the highest sensitivity, while corals and shark nurseries yielded the highest frequencies (Fig. S12B).

Our final spatial sensitivity model showed lowlands, arid zones, and mangroves as highly sensible areas (Fig. 3). The highland ecosystems of Santiago, Isabela, Santa Cruz, and San Cristobal also showed high sensitivity (Fig. 3A). Besides, the entire surface of Pinta island reported high sensitivity to environmental change stressors. Furthermore, we found sensitive areas within the GMR to be coastlines and islets from the Central-southeastern bioregion (Fig. 3B). Other sensitive areas included the Bolivar Channel, Punta Abermarle, Caleta Iguana, Punta Essex, Elizabeth Bay, Punta Moreno and Alfaro in Isabela, Darwin and Wolf islands, Leon Dormido and Punta Pitt in San Cristobal and the southeastern seabeds of Isabela and Cartago Bay.

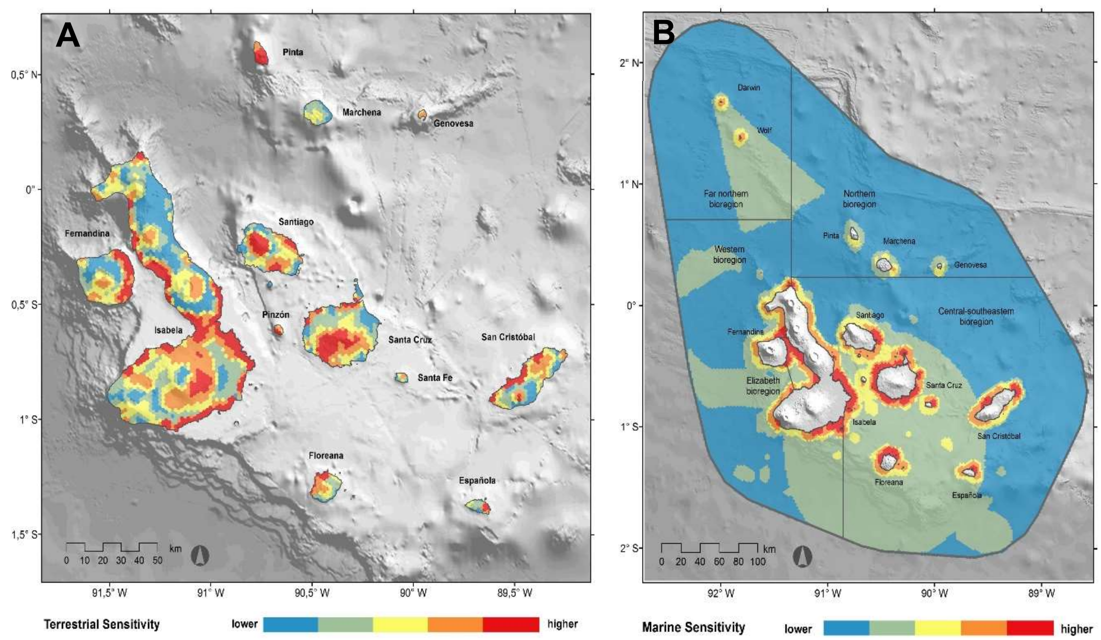

Figure 3. The estimated sensitivity of terrestrial (A) and marine (B) ecosystems. Sensitivity was calculated based on the score of the literature review, status, and richness of UICN red list species, endemism, and key species distributions. The sensitivity score is represented by hexagonal minimum mapping units of 3.46 km^2. The scores of the terrestrial model are displayed individually for each island.

4.2. Exposure analysis

To estimate exposure, we combined direct drivers of change that included our previously obtained climatic trends and projections for air temperature, annual precipitation, and SST (Fig. S5-6), the distribution of targeted-fishing and by-catch areas (Cerutti-Pereyra et al. 2020), and the magnitude of visits in tourist Public Use Areas (PUA), with indirect drivers of change expressed in the distribution of land-use and marine zones from the most recent Galapagos National Park Zoning Plan (GNP 2020; DPNG 2016; Fig. S13). This plan was designed in 2016, but it has yet to be agreed upon and enforced (see Supplementary material).

Each of the exposure inputs had different weighted values within the spatial model, according to their level of impact (see Supplementary material). The weighted values were assigned based on variables' complexities and distributions. Global drivers of change (e.g., temperature, SST) have widespread effects on the ecosystems and are more complex to mitigate, whereas local drivers (e.g., tourism, fisheries) have sequential and localized effects, defined by zoning (defined by borders) or common pool resources on ecosystems, and are less complex to mitigate (Capistrano et al. 2005). In our marine exposure submodel, we assumed that SST and bycatch have a higher impact on marine ecosystems than regulated tourism or artisanal fisheries in sustainable use areas (SST > bycatch > sustainable use areas > PUA). Furthermore, for terrestrial ecosystems, we assume, that precipitation and temperature have higher exposure values because the shifts in their temporal and spatial patterns may affect the productivity and distribution of native and invasive species. Followed by land-use zones, the potential impacts in the transition areas are higher than the ones in sustainable use and touristic areas, given by the pressures on the boundaries of other zones and remaining native ecosystems (precipitation> temperature > transition areas > sustainable use area > PUA). The exposure areas of marine and terrestrial zones account for the pressures present in these areas that affect natural ecosystems, as land-use change, admitted capacity of tourism, or over-exploitation of natural resources (e.g. fisheries).

4.2.1 Spatial Exposure Model

Our terrestrial exposure model showed that most islands have a relatively high degree of exposure, with the highest being at the highlands of Isabela, Santa Cruz, San Cristobal, Fernandina, Floreana, Santiago, and Pinta (Fig. 4A). These results reflected the spatial co-occurrence of present and future drivers of change. For example, the four populated islands had concentrated areas with high exposure in the highlands, whereas the remnants of natural ecosystems on the Galapagos are threatened by agricultural expansion, increased prevalence of invasive species, high concentration of tourism, and high exposure to temperature and precipitation anomalies (Fig. S6).

The marine exposure model revealed several exposed areas across bioregions (Fig. 4B). Marine exposure is a product of the interrelation between SST warming (Fig. S5), fishing activities susceptibility (in most of the GMR, as illustrated in the National Park Zoning of 2016), fishing bycatch (based on an experimental longline fishing study, Cerutti-Pereyra et al. 2020), and tourism. The majority of the exposed marine areas are concentrated in the Central-southeastern, Western, and Elizabeth bioregions (Fig. 3B). The areas surrounding Fernandina, between Isabela and Floreana, and the seabeds between Santiago, and between Santa Cruz and Isabela, are particularly overexposed to overfishing and bycatch, despite the delimitation of no-take zones.

The added exposure of all the above-mentioned variables illustrates that most of the GMR is exposed to several drivers of environmental change.

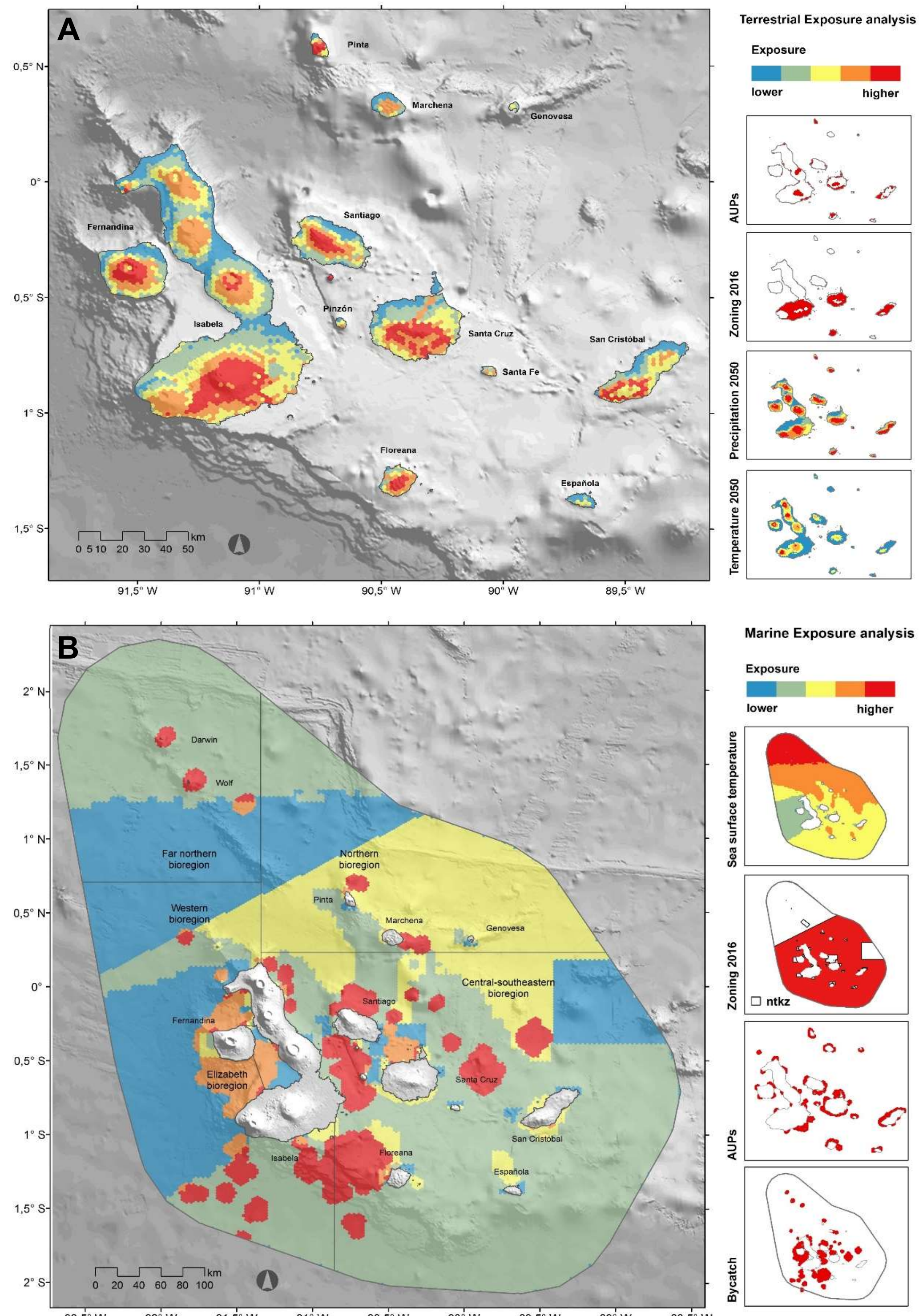

Figure 4. Exposure of ecosystems in the Galapagos. Terrestrial exposure (A) was calculated by the admitted capacity of tourism sites (PUA), the presence of sustainable

use and transition areas (Zoning 2016), and estimated changes of precipitation and temperature for 2050 (RCP 4.5). Marine exposure (B) was calculated by the admitted capacity of marine tourism sites (PUA), the presence of sustainable use areas (outside of the no-take zones, ntkz), targeted fishing and bycatch areas, and sea surface temperature trends (2002-2017). The Exposure is represented by hexagonal minimum mapping units of 3.46 km^2.

<u>4.3. Drivers of change in the Galapagos Islands: Current and future impacts</u>

Our impact assessment model identified current and future potential impacts of diverse drivers of change throughout the Galapagos Archipelago, based on the intrinsic sensitivity and degree of exposure of different bioregions, ecosystems, and islands (Fig. 5-6). The areas with higher impact scores were classified as high ecological value areas (HEVA), which are defined as areas highly sensitive and exposed to drivers of environmental change. These areas are key for environmental services provision including freshwater, fisheries, and nature-based tourism activities. HEVA with the highest impacts were concentrated on the biggest and most inhabited islands, with a clear trend towards the highlands: the *Miconia* and *Scalesia* zones containing nearly 40% of all of the HEVA (Fig. 5,7). The island of Santa Cruz exhibited the highest impact, followed by San Cristóbal, Floreana, and Isabela (Fig. 5A). Our impact assessment also identified a high concentration (ca. 20%) of HEVA in the transition and arid zones of different islands (Table S6, Fig. 5B,7). The skewed spatial distribution of the HEVA towards the inhabited islands is related to the ecological importance of the humid forested ecosystems and the high endemism from the arid zone (Fig. S10). This is coupled with a projected variability in climate (Fig. S6) and the effects of the zoning in 2016 of the highlands on the inhabited islands (Fig. S13), which are primarily used for farmlands, pastures, and tourism, resulting in an increased concentration of invasive species and a constant-increased demand for natural resources.

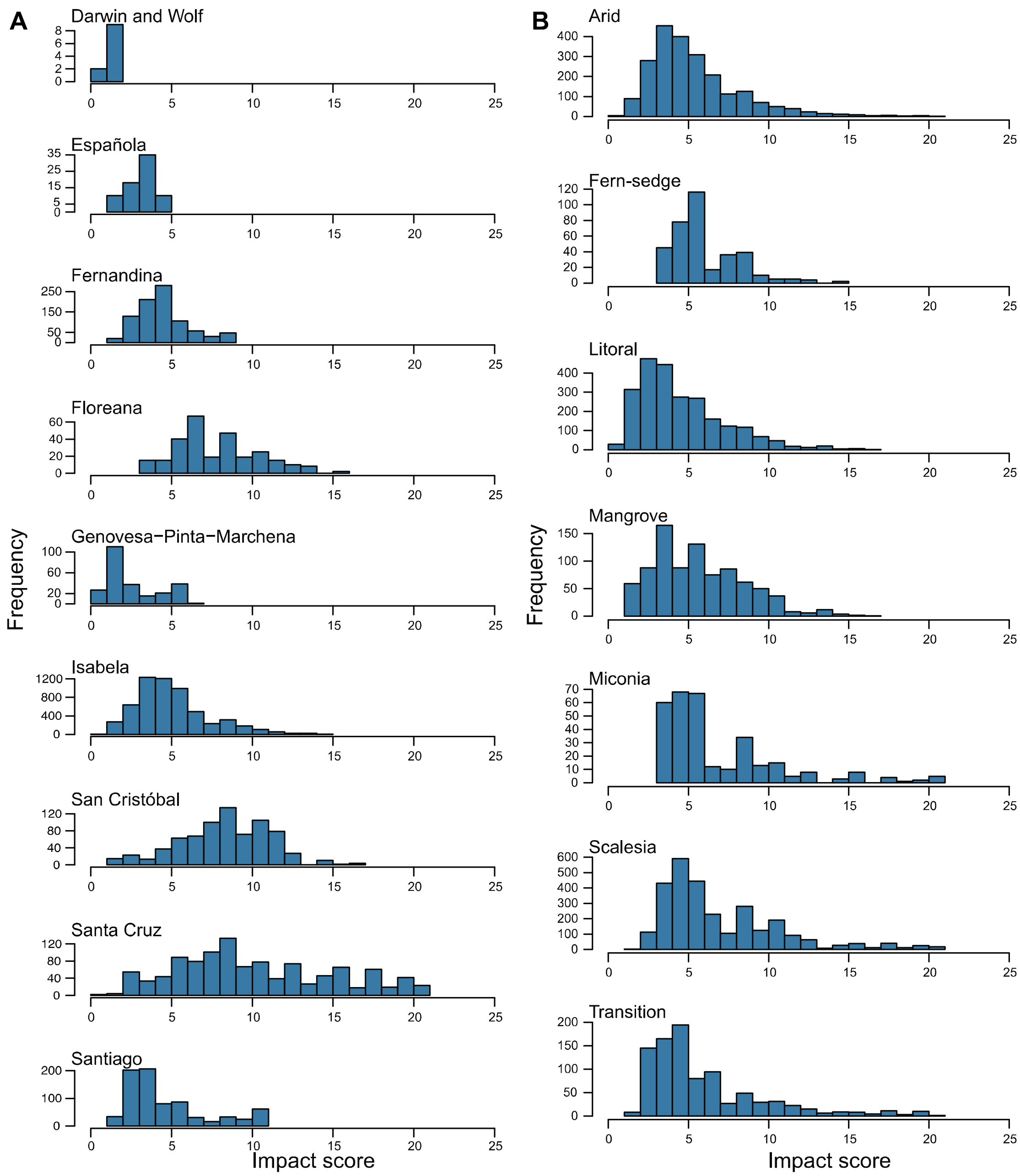

Figure 5. Magnitudes of impact for (A) islands and (B) terrestrial ecosystems. Impact scores were built for each island and terrestrial ecosystem based on the weighted values of sensitivity and exposure. Frequency denotes the number of hexagons, the minimum unit of analysis (3.46 km^2).

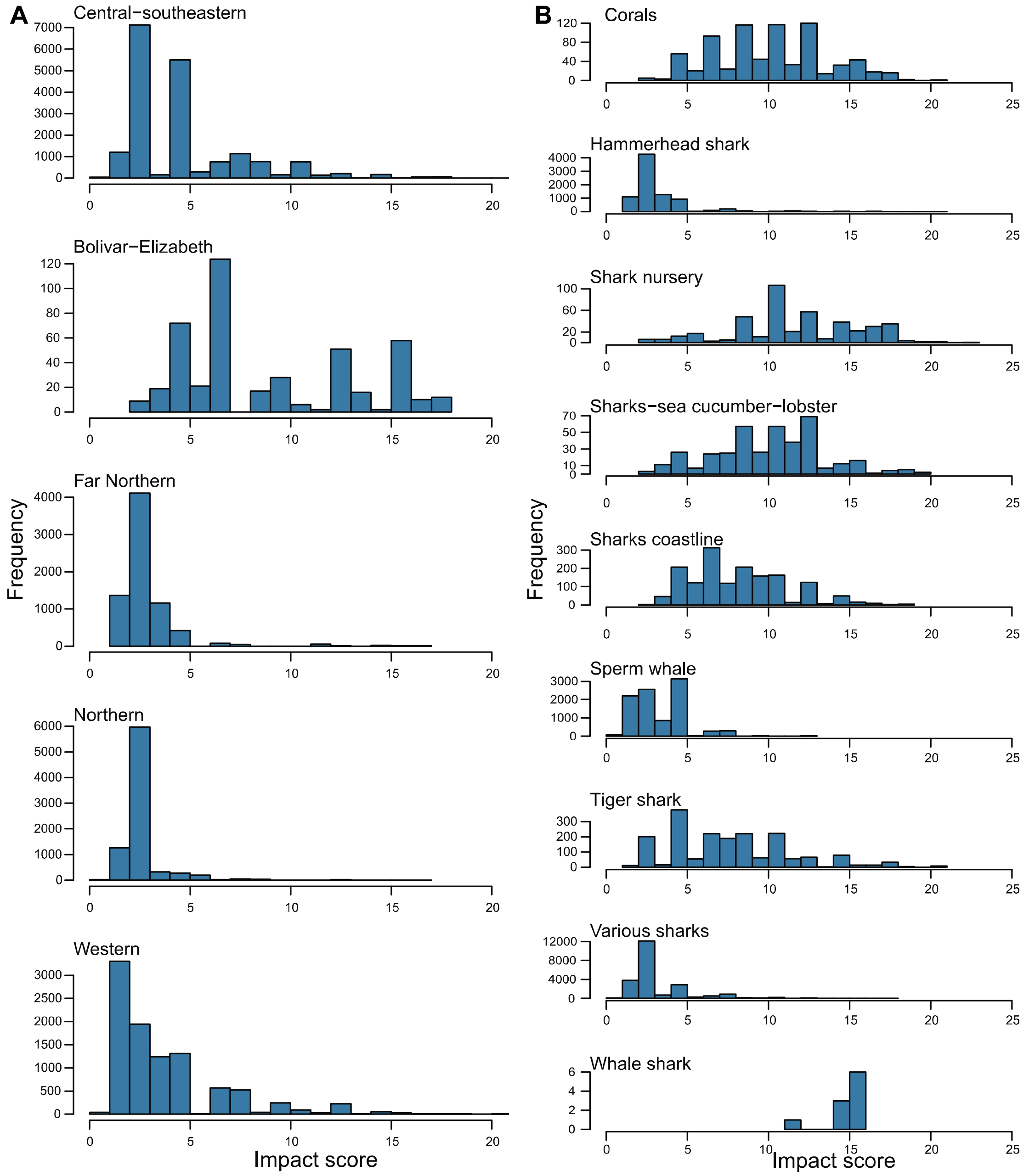

Figure 6. Magnitudes of impact for (A) bioregions and (B) marine macro-habitats. Impact scores were built for each bioregion and marine macro-habitat based on the weighted values of sensitivity and exposure. Frequency denotes the number of hexagons, the minimum unit of analysis (3.46 km^2).

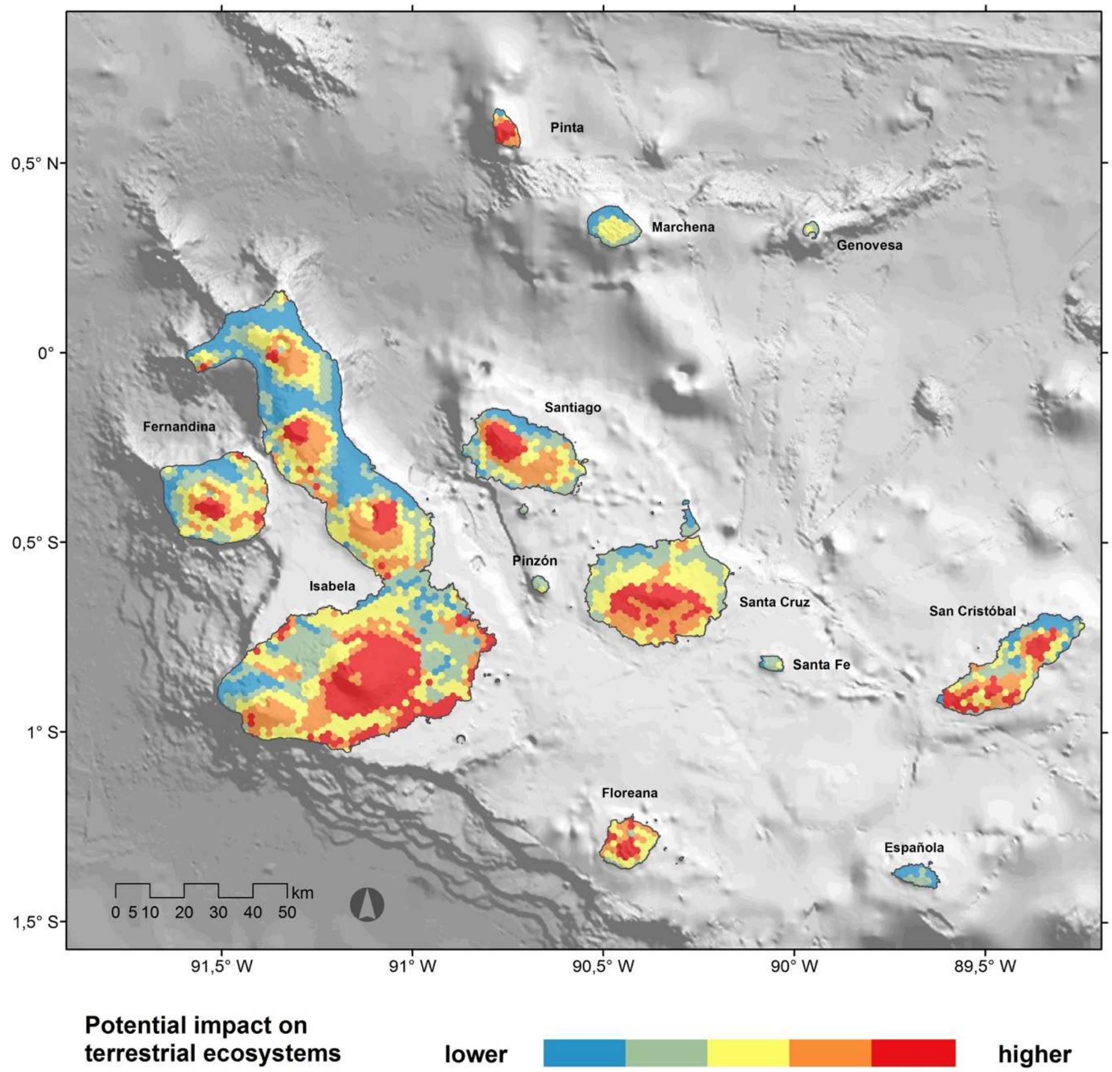

Figure 7. Projected impact on Galapagos' terrestrial ecosystems by drivers of change. Spatial analysis units are hexagons of 3.46 km^2.

Although HEVA were widespread throughout marine ecosystems in our results, there were specific regions that concentrated uneven proportions of HEVA (Fig. 6). High impacts were clustered in the Far Northern, Elizabeth, and the Central-southeastern bioregions (Fig. 6A,8). In the Western bioregion, HEVA were identified in the north and south boundaries of the Bolivar Channel and the central part of the archipelago (a marine corridor connecting Isabela, Santiago, Santa Cruz, Pinzon, and Rabida) (Fig. 8). The remaining HEVA were distributed along the islands' shorelines, whose ecological importance relies on several ecosystem services, including nature-based tourism and fisheries (Table S7). Among marine macro habitats, shark nurseries showed the highest impacts, followed by corals and the habitats of hammerhead and tiger sharks (Fig. 6B). The distribution of endemic species and macro habitats (Fig. S9-10) in areas with high sensitivity, coupled with the rise of SST (Fig. S5, Table S5) throughout the GMR, might explain the high score impacts for sharks and corals.

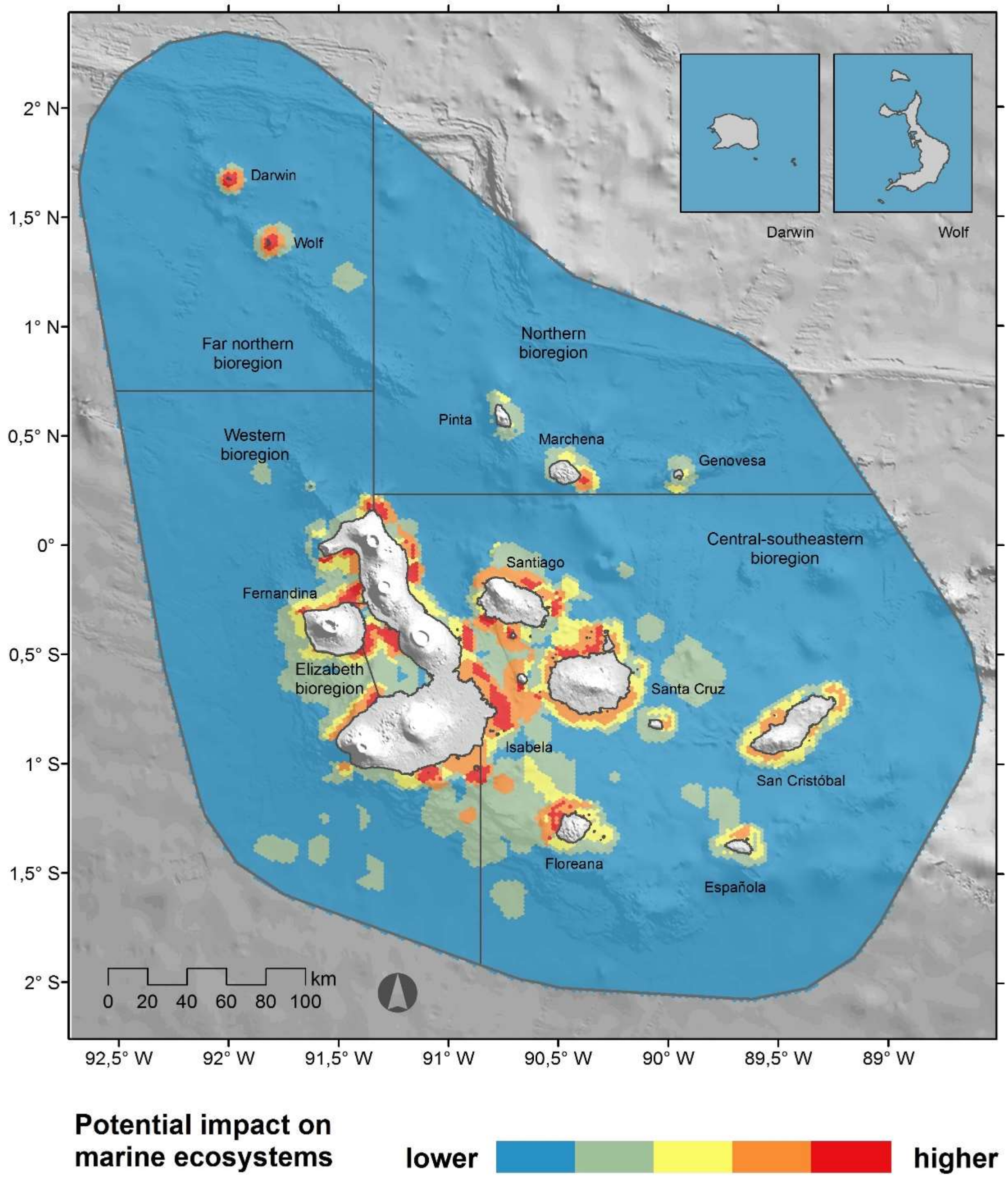

Figure 8. Projected impact on Galapagos' marine ecosystems by drivers of change. Spatial analysis units are hexagons of 3.46 km^2.

4.4 Priority High Ecological Value Areas (HEVA) and stakeholder's validation

To select HEVA that should be prioritized for implementing EBA measures aimed at increasing the resilience and adaptation capacity of the Galapagos Islands, we cross-validated our results with the assistance of technical staff and directors of the GNP during a two-day workshop held in Santa Cruz, Galapagos on February 2020. In this workshop, we used the results of our impact assessment models as inputs and chose 13 HEVA with terrestrial and marine ecosystems (Table 1, Fig. 9). Overall, the HEVA host endemic, vulnerable and critically endangered species or ecosystems with limited distribution; comprise spawning zones, shark nurseries and nesting sites for sea turtles and birds, harbor resilient coral reefs and communities, and are characterized by a high influx of tourists. Some HEVA report high diversity and biomass of marine species from different tropic guilds, are feeding grounds of multiple marine and terrestrial species, and could be considered as potential climate change refugia. Moreover, some terrestrial ecosystems within the HEVA are buffering areas around the agricultural zone, register an increasing incidence of invasive species, but also include the last remnants of the *Scalesia* forest in the humid highlands. Finally, these areas are of prime importance for local livelihoods, especially for small-scale fisheries, but some of them are highly exposed to over-fishing (For details of selected HEVA see Table S8). Each HEVA is characterized by the following criteria: (1) expected climatic variability given by the spatial distribution of terrestrial future climate models, (2) representativeness, measured as HEVA distribution among bioregions; (3) habitat connectivity across the elevation gradient (i.e., number of terrestrial macro habitats occurring on each HEVA), (4) marine habitat diversity (number of marine macro habitats), and (5) HEVA relevance for environmental services provision (e.g., tourism, fishery, freshwater provision). The HEVA selected comprise 22.7% (14,715 km^2) of the Galapagos archipelago, distributed in 2.77% (3,835 km^2) of the GMR and 19.9 % (1,592 km^2) of the GNP (the terrestrial protected area; Table 1, S8-9).

Based on the above-listed criteria, the HEVA were ranked for prioritizing the implementation of EBAs to confront climate change (Table S9-10). Four HEVA had the highest priorities: (1) Corridor Sierra Negra Volcano Isabela South, (2) Conservation area Santiago-Santa Cruz, (3) Corridor Wolf Volcano, Punta Albermarle and Cape Marshall, and (4) The Bolivar Channel and Elizabeth South (Fig. 9). These four areas comprise more than half of the marine priority HEVA and one-third of the terrestrial priority HEVA (Table 1, S8). Overall, the selected priority HEVA constitute relevant areas for the distribution and life cycle of critically endangered and endemic species and relict ecosystems (e.g. *Scalesia* forest), which are interconnected by marine and terrestrial corridors. Further, the prioritized areas are fundamental to sustain water, agriculture and fisheries provision for local inhabitants and the nature-based tourism industry.

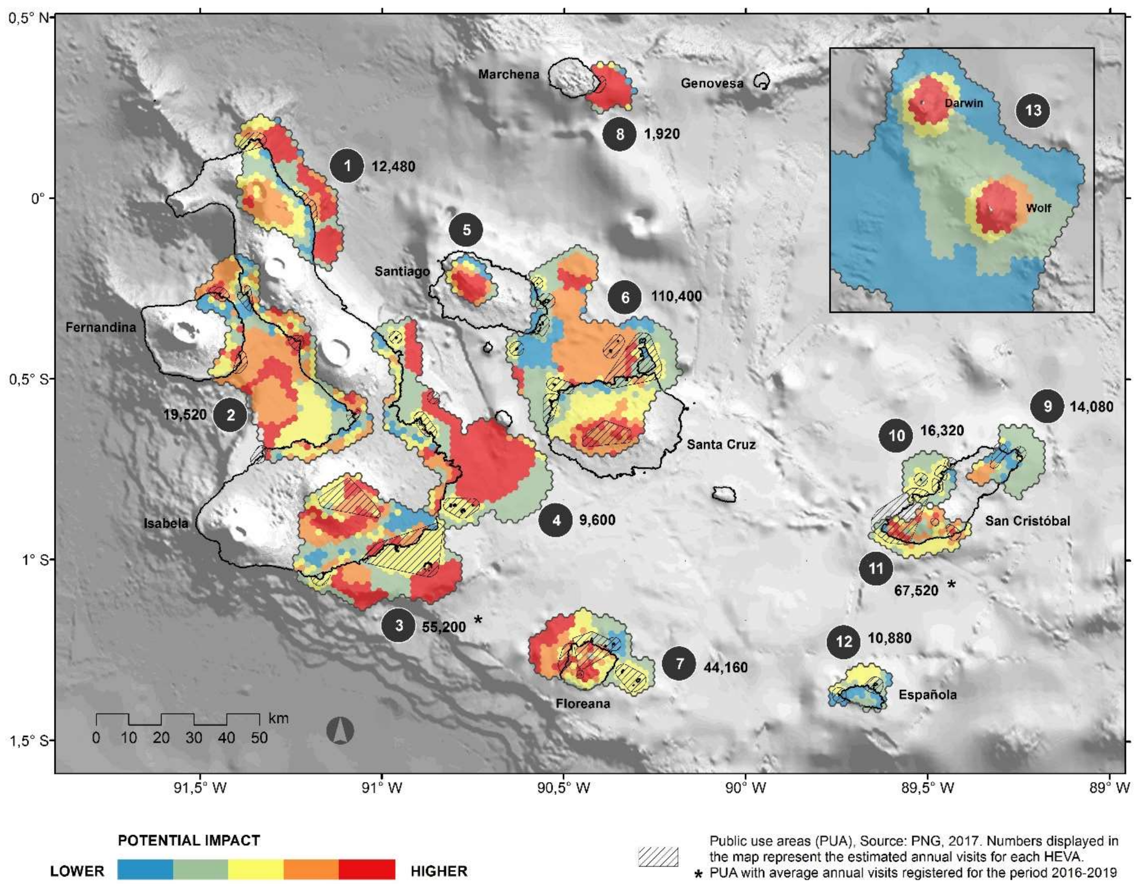

Figure 9. Priority High Ecological Value Areas (HEVA) for the development of adaptation measures against climate change. Priority HEVA are denoted as colored areas, where orange and red correspond to the fourth and fifth quintiles of the impact model score, respectively. The numbers next to the HEVA represent the estimated annual tourists at each HEVA. Stripped areas denote the admitted capacity of marine tourism sites (PUA) within HEVA. The estimated number of visitors was calculated by the ratio between the admitted capacity of visitors (CAV) and the average annual visits registered in 5 PUA (Puerto Ayora, Puerto Baquerizo Moreno, Puerto Chino, Puerto Villamil, and Sierra Negra). This may overestimate or underestimate the magnitude of visits in some areas but is an approximation of the average visits that PUA (with no data) may receive, given their actual CAV and the data in highly visited areas. Priority HEVA: (1) Corridor Wolf Volcano, Punta Albermarle and Cape Marshall, (2) The Bolivar Channel and Elizabeth South, (3) Corridor Sierra Negra Volcano Isabela South, (4) Corridor Cartago Bay – San Luis seabed, (5) Santiago highland, (6) Conservation Area Santiago-Santa Cruz, (7) Floreana and Islets, (8) Marchena coral remnants, (9) Corridor la Galapaguera – Punta Pitt, (10) León Dormido (Kicker's rock), (11) Corridor El Junco and Southern Seabeds, (12) Española and Gardner islands, and (13) Darwin and Wolf islands.

To show the impact of nature-based tourism on the islands, we overlaid the priority HEVA with the estimated potential visits of Public Use Areas (PUA; SIMAVIS 2020). We calculated the average ratio between the admitted capacity of visitors (CAV, for its

Spanish acronym) and the average annual visits registered in five PUA (Puerto Ayora, Puerto Baquerizo Moreno, Puerto Chino, Puerto Villamil, and Sierra Negra) for the period 2016-2019. Then, we estimated the number of visits for not monitored PUA given their actual CAV multiplied by the calculated average ratio (actual PUA CAV * 0.05). This approximation to the potential visits that PUA with no data may receive (given their actual CAV and the available data from highly visited areas), adds to a maximum capacity of up to 526,080 annual visitors in the entire GNP. Specifically, the priority HEVA exhibited an estimated capacity of up to 383,200 annual tourists, equivalent to more than half of the potential total annual tourists the Galapagos Islands could receive (Fig. 9, Table S8). HEVA with the highest capacity were (6) Conservation Area Santiago-Santa Cruz (110 400), (11) Corridor El Junco and Southern Seabeds (67 520), (3) Corridor Sierra Negra Volcano Isabela South (55 200) and (7) Floreana and Islets (44 160). This estimation outweighs the number of tourists registered in 2019 (Fig. S8) for the regulated tourist sites. Our estimations suggest that the high influx of tourists could be affected by drivers of change, especially in marine-related touristic activities. Besides, the estimated maximum capacity should be reevaluated concerning sustainable ecosystem capacity, as many visitors that arrive directly to the inhabited islands visit nearby tourism attractions that are not recorded in the PUA/CAV statistics (GNP, personal comment). There is a lack of records regarding tourist visits and only five PUA out of 66 keep visit records. According to our estimations, more than 200,000 visits may account for the non-monitored/regulated tourism in the islands, which may exceed the sustainable ecosystem capacity.

Table 1. Terrestrial and marine priority High Ecological Value Areas (HEVA) of the Galapagos Islands. (a) Prioritized HEVA validated by the Galapagos National Park and chosen as areas of indirect intervention and (b) 4th and 5th quintile of the potential impact model (orange and red areas in the map) from the priority HEVA chosen as direct intervention areas for EBAs. Priority HEVA: (1) Corridor Wolf Volcano, Punta Albermarle and Cape Marshall, (2) The Bolivar Channel and Elizabeth South, (3) Corridor Sierra Negra Volcano Isabela South, (4) Corridor Cartago Bay – San Luis seabed, (5) Santiago highland, (6) Conservation Area Santiago-Santa Cruz, (7) Floreana and Islets, (8) Marchena coral remnants, (9) Corridor la Galapaguera – Punta Pitt, (10) León Dormido (Kicker's rock), (11) Corridor El Junco and Southern Seabeds, (12) Española and Gardner islands, and (13) Darwin and Wolf islands.

Site ID*	Total HEVA area (km²)	Marine HEVA (km²) (a)	Total area of GMR (%) (a)	4th and 5th quintile of priority HEVA (km²) (b)	Total area of GMR (%) (b)	Terrestrial HEVA in km² (a)	Total area of islands (%) (a)	4th and 5th quintile of prioritized HEVA km² (b)	Total area of islands (%) (b)
1	915.80	477.8	0.35	366.30	0.26	438	5.48	154.2	1.93
2	1617.95	990.35	0.72	617.43	0.45	627.6	7.85	280.26	3.50
3	1448.65	657.05	0.48	489.70	0.35	791.6	9.90	388.67	4.86
4	1502.80	1189.5	0.86	633.65	0.46	313.3	3.92	121.74	1.52
5	159.35	n/a	n/a	n/a	n/a	159.35	1.99	100.34	1.25
6	2006.40	1330.4	0.96	719.15	0.52	676	8.45	283.93	3.55
7	669.25	496.95	0.36	245.70	0.18	172.3	2.15	114.18	1.43
8	156.48	156.48	0.11	141.90	0.10	n/a	n/a	n/a	n/a
9	318.05	204.55	0.15	n/a	n/a	113.5	1.42	38	0.48
10	213.90	153.9	0.11	76.12	0.06	60	0.75	n/a	n/a
11	311.03	138.33	0.10	117.80	0.09	172.7	2.16	110.7	1.38
12	193.75	132.9	0.10	51.90	0.04	60.85	0.76	n/a	n/a
13	5201.26	5201.26	3.76	375.34	0.27	n/a	n/a	n/a	n/a
Total	**14715**	**11130**	**8.05**	**3835**	**2.77**	**3585**	**44.83**	**1592**	**19.91**

Conclusions

This research presents the first study evaluating the current and potential ecological impacts of major drivers of change that threaten terrestrial and marine ecosystems of the Galapagos Islands, including climate change, unsustainable tourism and local population growth, IUU fishing, and invasive species. Our literature review, coupled with the spatial impact assessment model, identified 13 areas of high ecological value (HEVA) distributed across the Archipelago, equivalent to ca. 23% (14,715 km^2) of the marine and terrestrial habitats. These HEVA represent areas most vulnerable to climate-based and human drivers of change that threaten the conservation and sustainable use of Galapagos' marine and terrestrial biodiversity. They also constitute important areas for the distribution and life cycle of critically endangered and endemic species and relict ecosystems (e.g. *Scalesia forest*).

Our impact assessment model demonstrated that current and potential impacts over HEVA are likely to concentrate on the four inhabited islands' highlands due to their prolonged periods of transformation. Projected changes are expected to increase invasive species encroachment, potentially impacting endemic Galapagos biodiversity and freshwater availability. In contrast, areas of higher impact for marine ecosystems concentrate along shorelines of most Galapagos islands, which could profoundly affect food security and livelihoods for Galapagos artisanal fisheries and the nature-based tourism industry.

The four HEVA with the highest priority to focus ecosystem-based adaptation measures are (1) Conservation Area Santiago-Santa Cruz, (2) Corridor Sierra Negra Volcano-Isabela South, (3) Corridor Wolf Volcano, Punta Albermarle and Cape Marshall, and (4) The Bolivar Channel and Elizabeth South.

Based on this review results, we recommend to the Government of Ecuador, international cooperation, civil society organizations and productive sectors, to create strategic alliances to design, agreed upon and implement a set of ecosystem-based adaptation measures (EBA). These EBAs need to ensure the well-being of local livelihoods and the conservation of Galapagos' unique marine and terrestrial ecosystems by increasing the resilience and adaptation capacity of the Archipelago against current and future threats. Specifically, it is urgent to implement the following EBA measures: (1) Restore the humid highland ecosystems of the four inhabited islands as a means to increase freshwater provision, secure agricultural production, and reduce exotic species invasions; (2) Improve the design and effectiveness of Galapagos marine zoning, through an adaptive co-management of the Galapagos Marine Reserve to reduce IUU fishing and protect the most suitable areas to ensure commercial stocks recovery, based on climate change risk assessment; (3) strengthening marine biosecurity programs for invasive species; (4) restoring selected coral reef habitats through experimental coral breeding and exclusion areas; (5) reducing the impact of diving, anchoring and pollution related to tourism operations in selected marine HEVAS; (6) strengthening ongoing ecological monitoring programs to produce the scientific data required to understand how climate change will interact with other non-climatic drivers and how they will impact the Galapagos islands. This will support the design of scientific-sound base adaptation measures and the evaluation of their effect on increasing ecosystem resilience and human adaptive capacity.

5. Declaration of interests

The authors declare they have no known competing financial interests or personal relationships that could have appeared to influence the work in this paper.

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ANNEXES

Supplementary Methods

4.1. Sensitivity analysis

4.1.1 Meta-analysis

Twenty publications (Table S3) that reported quantitative attributes for the topic area of species diversity and ecosystem attributes, such as chlorophyll concentration and carbon stocks, added the seventh criterion to the meta-analysis. Whenever these attributes were present, the data was aggregated into quartiles and assigned a score from 1 to 4, for the lower and maximum quartile respectively (Chakhar and Mousseau, 2007). These values were added to the score given by the six above-mentioned criteria.

Only 99 out of the 135 peer-reviewed publications (Annex 1) evaluated were included in the spatially explicit model. The excluded publications lacked specific spatial references that we were unable to georeference. Georeferenced features included points, lines, and polygons. For the point and line features only, buffer areas of three and five km were calculated for land and marine objects, respectively. Buffer areas were cropped according to the feature correspondence for a specific ecosystem, the geographic object, or the altitude range (inter-algebra functions with geometric functions described in Lin 1998).

4.1.2 Biodiversity attributes

IUCN endangered species included 22 vulnerable, 3 endangered, and 3 critically endangered species (Table S4). Each species was assigned a score value according to its status: 1 for vulnerable, 1.5 for endangered, and 2 for critically endangered. The total IUCN species richness score was obtained by the spatial overlay of all the individual species' polygons and the computation of an algebraic sum of individual species' scores (Eqn. 3). The scores for this variable ranged from 1 to 21.

$$IUCNscore = \sum_{x=1}^{28} x_{speciesscore} \quad \text{Eqn. 3}$$

A ratio between the total 229 endemic species mapped in these zones was calculated and multiplied by 20, representing a weighted value that accounts for maximum variability of 20% within the sensitivity sub-model (Eqn. 4). When added to the total sensitivity score, this variable contributes up to 9 % of the sensitivity model variability. The total score for terrestrial biodiversity attributes was calculated by equation 5.

$$Endemismscore = \left(\frac{x_{EP}}{229} * 20\right) \quad \text{Eqn. 4}$$

$$Terrestrialbiodiversityattributes = (IUCN_t) + \left(\frac{x_{EP}}{229} * 20\right) \quad \text{Eqn. 5}$$

Marine biodiversity attributes were obtained by georeferencing marine-taxa distributions and habitats (MA) within the GMR using publications from the meta-analysis (Annex 1). For marine biodiveerisity attributes, polygons for each habitat were scored in a binary fashion, with a 1 being given whenever a habitat was present. An algebraic sum was computed when there was an overlap of several habitats in a given area (Eqn. 6). When added to the total sensitivity score, this variable contributed up to 2.2 % of the sensitivity model variability.

$$Habitatscore(MA) = \sum_{x=1}^{4} x_{habitatscore} \quad \text{Eqn. 6}$$

The density distribution maps were classified in quartiles and assigned a score from 1 to 4, for the lower quartile and maximum quartile respectively. A cumulative ratio between the total score of the density and distribution maps was calculated and multiplied by 50 (Eqn. 7), representing a weighted value that accounts for maximum variability of 50% within the sensitivity sub-model. When added to the total sensitivity score, this variable contributes up to 3.3 % of the sensitivity model variability. The total score for marine biodiversity attributes was calculated by Eqn. 8.

$$Densityscore = \left(\frac{PD_{Qtl}}{120} * 50\right) \quad \text{Eqn. 7}$$

$$Marinebiodiversityattributes = (IUCN_m) + MA + \left(\frac{PD_{Qtl}}{120} * 50\right) \quad \text{Eqn. 8}$$

The boundaries and categories of marine macro-habitats defined in our model are limited to the studies reviewed in the meta-analysis. This implies that some species or key predators have not been included in our model. Thus, in our sensitivity submodel, biodiversity attributes were characterized by macro-habitats and the distribution of endangered species, to define differentiated and smaller marine spatial units that complemented the meta-analysis. Because the main goal for these areas is the zoning of marine ecosystems, we assigned lower weighted values to the cumulative ratio of the occurrence of species, accounting for lower contribution to the variability of the model, than the meta-analysis (Fig. 2).

For the spatial sensitivity model, all inputs were assigned to a vector grid of hexagonal spatial units of 4 km^2 (Ardron et al. 2010). We did this to convert the multi-polygon output of the multicriteria map algebra to homogeneous spatial units that could be useful for future marine and land use planning. To this end, we computed a spatial join (one-to-many) by calculating the quantile-3 of the sensitivity score of the multiple polygons contained in each hexagon.

4.2. Exposure analysis

The analysis included the sustainable use (SU) and transition (TR) zones and excluded, the conservation and intangible zones. Sustainable use areas are characterized by a regulated exploitation status, where activities such as artisanal fisheries, nonmetallic mining, selective logging and hunting are allowed. The transition zone includes all the areas in the expansion limit between agricultural-urban areas outside the park and other zoning categories; activities such as artisanal fisheries, nonmetallic mining, selective logging and the construction of public infrastructure are also allowed (GNP 2021; DPNG 2016). Its main function is to buffer the effects from agricultural expansion and other extractive activities, however, observed trends of land-use change have shown the potential expansion of agriculture in these areas (Laso et al., 2020). As defined in the Galapagos land use plan, transition zones are characterized by higher human intervention and less ecological integrity, followed by the sustainable use, conservation and intangibles zones, where the latter exhibits the least human intervention and the highest ecological integrity (DPNG, 2016). Thus, the ecosystems within or closer to the transition zone are more exposed than the ones within the sustainable use category (see Eqn. 10). Tourism is allowed in three of the zones except in the Intangible zone, but the tourism is restricted only to PUA; thus, the areas where TR and PUA or SU and PUA are observed, represent the combined exposure of the ecosystems to a high influx of tourists and other potential extractive activities (listed above). For example, areas on the southern coast of Isabela include a highly visited PUA overlapped with the SU zone where artisanal fisheries are developed.

For the terrestrial model, the exposure variables were weighted as follows: tourism (PUA, 0.10), sustainable use (SU, 0.15), transition (TR, 0.20), precipitation (P, 0.30), and temperature (T, 0.25) (Eqn. 10), while for the marine model, the exposure variables were weighted as follows; tourism (PUA, 0.10), sustainable use (SU, 0.15), target and bycatch (BY, 0.30), and sea surface temperature (SST, 0.45) (Eqn.11).

Finally, the data for each quantitative variable was classified in quintiles and assigned a value from 1 for the lower quintile and 5 for the maximum quintile. For the zoning variables, the areas were assigned the maximum value of 5. Then, the quintile value for all the variables was multiplied by the weighted value accordingly.

$$TerrestrialExposure = PUA * 0.10 + SU * 0.15 + TR * 0.20 + T * 0.25 + P * 0.30$$

Eqn. 10

$$MarineExposure = PUA * 0.10 + SU * 015 + BY * 0.30 + SST * 0.45$$

Eqn. 11

Both vector and raster inputs were also converted to a vector grid of hexagonal spatial units of 4 km^2 (Ardron et al., 2010). For the categorical data, we computed a spatial join one-to-one with the hexagonal grid, while for the quantitative data we computed a spatial join of one-to-many.

4.2.1 Spatial Exposure Model

Our terrestrial exposure model showed that most islands have a relatively high degree of exposure, with the highest being at the highlands of Isabela, Santa Cruz, San Cristobal, Fernandina, Floreana, Santiago, and Pinta (Fig. 4A). These results reflected the spatial co-occurrence of present and future drivers of change. For example, the four populated islands had concentrated areas with high exposure in the highlands, whereas the remnants of natural ecosystems on the Galapagos are threatened by agricultural expansion, increased prevalence of invasive species, high concentration of tourism, and high exposure to temperature and precipitation anomalies (Fig. S6).

The marine exposure model revealed several exposed areas across bioregions (Fig. 4B). Marine exposure is a product of the interrelation between SST warming (Fig. S5), fishing activities susceptibility (in most of the GMR, as illustrated in the National Park Zoning of 2016), fishing bycatch (based on an experimental longline fishing study, Cerutti-Pereyra et al., 2020), and tourism. The majority of the exposed marine areas are concentrated in the Central-southeastern, Western, and Elizabeth bioregions (Fig. 3B). The areas surrounding Fernandina, between Isabela and Floreana, and the seabeds between Santiago, and between Santa Cruz and Isabela, are particularly overexposed to overfishing and bycatch, despite the delimitation of no-take zones. The added exposure of all the above-mentioned variables illustrates that most of the GMR is exposed to several drivers of environmental change.

Supplementary Tables

Table S1: Actual and potential *Scalesia* forest area based on Itow 1995; 2003. The actual distribution was derived from the Landcover map from 2010 of the Galapagos islands (Trueman and Ozouville 2010). The potential distribution was derived following Itow description of Scalesia habitats. Environmental variables (elevation, slope, aspect) were used to develop a potentially suitable map using algebraic spatial modeling.

Actual and potential habitat	Area (km²)	Potential area for *Scalesia* forest (%)
Actual agricultural area – potential *Scalesia* habitat	113.01	15.83
Actual invasive species – potential *Scalesia* habitat	56.09	7.86
Actual native deciduous ecosystem – potential *Scalesia* habitat	237.09	33.22
Actual native humid ecosystem – potential *Scalesia* habitat	307.6	43.09
Total	713.79	100.00

Table S2: Meta-analysis criteria

Criteria	Description	Type of data
Invasive species	The studied area is vulnerable to invasive species	binary
Ecosystem interactions	The study accounts for critical interactions between species, ecosystems and services	binary
High CC impact	The study reports high vulnerability to climate change of the studied population or area	binary
Environmental services	The studied area or specie provides environmental services	binary
Other impacts	The studied area is exposed to other impacts	binary
Other impacts txt	Other impacts are described	nominal
Biotic relevance	The studied area is relevant for the conservation and survival of a specie	binary
Biota type	Studied species	nominal
Quantitative values	Specific values referring to species richness, chlorophyll concentration, carbon stocks, among others	nominal

Table S3. Studies with quantitative attributes

Author	Quantitative attribute
(Banks 2007)	Number of threatened taxa
(Cantor *et al.* 2017)	Distribution density of sperm whale
(Bucaram *et al.* 2013)	Fishing effort
(Bustamante *et al.* 2000)	Lobster catches
(Edgar *et al.* 2010)	Threatened species
(Riegl *et al.* 2019)	Colony diameter size trends in corals
(Tanner *et al.* 2019)	Stored soil carbon in mangroves
(Trueman *et al.* 2014)	Degree of biotic novelty
(Porter 1979)	Number of *Scalesia* species
(Watson *et al.* 2009)	Percentage modified by human activities of the six vegetation zones
(Cerutti-Pereyra *et al.* 2020)	Density of byctach, target and bycatch hotspots
(Edgar *et al.* 2004)	Fish richness and endemism
(Edgar *et al.* 2008)	Number of threatened marine species
(Glynn *et al.* 2018)	Condition of coral reefs and communities
(Jiménez-uzcátegui *et al.* 2007)	Threatened and endemic terrestrial species

(Kislik *et al.* 2017)	Chlorophyll, SST and photosynthetic active radiation
(Lamb *et al.* 2018)	Species affected by ulcerative skin disease
(Lawson *et al.* 2017)	Status of mangrove finch population
(Acuña-marrero *et al.* 2018)	Sharks abundance and richness
(Llerena *et al.* 2015)	Confirmed and probable shark nursery grounds

Table S4: List of Galapagos IUCN species

Species	**IUCN status**
Dermochelys coriaceae	VU
Nesoryzomys narboroughi	VU
Stegastes beebei	VU
Arctocephalus galapagoensis	EN
Umbrina galapagorum	VU
Nesoryzomys fernandinae	VU
Odontoscion eurymesops	VU
Eisenia galapagensis	VU
Pseudalsophis slevini	VU
Nesoryzomys darwini	EX
Prionotus miles	VU
Starksia galapagensis	VU
Aegialomys galapagoensis	VU
Progne modesta	EN
Ogilbia galapagoensis	VU
Blutaparon rigidum	EX

Xyrichtys victori	VU
Nannopterum harrisi	VU
Lythrypnus gilberti	VU
Bifurcaria galapaensis	CR
Arcos poecilophthalmus	VU
Nesoryzomys swarthi	VU
Lepidonectes corallicola	VU
Azurina eupalama	CR
Pterodroma phaeopgygia	CR
Laterallus spilonota	VU
Buteo galapagoensis	VU
Spheniscus mendiculus	EN

Table S5: Bioregions projected temperature variability (in increasing order)

Region	ΔT increase			Percentage of territory
	mean	min	max	
North-eastern islands	6.5	6.3	7.4	2.6
Southern islands	6.6	6.3	7.1	3
Central-eastern islands	6.7	6.4	7.9	27.5
Southeastern Isabela	6.8	6.4	8.7	33
Fernandina and Isabela (northwest and southwest)	7.1	6.4	10.6	34

Table S6: Impacted locations in terrestrial ecosystems

Island	Highland	Lowland
Fernandina	La Cumbre volcano	Eastern lowlands in the north and south (Punta Espinosa and Mangle Point)
Isabela	Wolf, Darwin, Alcedo, Cerro Azul and Sierra Negra volcanoes	Tortoise Breeding station, the Wall of Tears, Los Tuneles, Wetlands, Flamingoes Lake, Tintoreras and Puerto Villamil
Santiago	West highlands	East lowlands
Pinta	All of the small humid zone	All southern lowlands and most of the north.
Santa Cruz	Los Gemelos craters, the Tortoise Reserve, Half Moon, and Crocker Hill.	Garrapatero beach, the Lava Tunnels, Charles Darwin Station, Tortuga Bay, El Chato and Puerto Ayora city.
Floreana	Alieri Hill and Asilo de la Paz	Baroness Viewing point, Lobería, Post Office Bay, Puerto Velasco Ibarra.
San Cristobal	Galapaguera, El Junco Lake, Cerro Colorado.	Puerto Chino beach, Loberia Beach

Table S7: Impacted locations in marine ecosystems

Bioregion	Area	Touristic sites (marine-related activities)
Far northern bioregion	All surrounding areas of Darwin and Wolf islands	All
Northern bioregion	Eastern shorelines of Marchena	Espejo Point
Elizabeth	High impacts in the north and southern parts of the bolivar Channel	Urbina Bay, Tagus Cove
Western	Shorelines of the north, south, and west of Isabela. Western shorelines of Fernandina	Moreno Point, Albemarle point, Vicente Roca Point, Cristobal Point
Central-southeastern	A marine corridor between Isabela, Santiago, Santa Cruz, Pinzon, and Rabida. Scattered shorelines of all islands in this region	Buccaneer Cove, Cowley point, Rabida, Guy Fawkes, Nameless Rock, Baegle Bartholomew island, Daphne Island, Cousins Rock, Sullivan Bay, Black Turtle Cove, Bachas beach, Tortuga Bays, mosquera islet, Carrion Point, Devil's crown, Champion, Enderby, Coromoran Point, Post Office Bay, Gardner Bay, Kicker's rock, Punta Pitt, Wreck bay

Table S8. Landscape and Ecological attributes of the priority HEVA.

Priority HEVA	Description
1. Corridor Wolf Volcano – Punta Abermarle – Cape Marshall	This corridor encompasses both terrestrial and marine ecosystems. First, the Wolf volcano area is classified as intangible owing to its conservation value (GNP, 2021). Its humid zone hosts an endemic and vulnerable *Scalesia* species (*S. microcephala*) (Itow, 1995). Second, the Wolf-volcano area is also exceptional, as it hosts the endemic-vulnerable Wolf Volcano Giant-tortoise (*Chelonoidis becki*) and the critically endangered pink-land iguana (*Conolophus marthae*) that only occurs in northern Isabela (Caccone et al., 2017; Gentile et al., 2016). Besides, this area harbors exceptional tortoise populations which are descendants from translocated tortoises from all around the archipelago during the whaling era (Tapia et al., 2017). The giant tortoise restoration initiative (GTRI) has found tortoises from this region with genetic ancestry from already-extinct tortoise species (*C. abingdonii* from Pinta and *C. niger* from Floreana), and this has led to pioneer efforts in saving such species. Down from Wolf-volcano, other impacted areas in this corridor include the northeastern coasts of Isabela, which are home to sharks, shark nurseries, and corals. These coasts also include two famous sites that are exclusively dedicated to marine tourist activities (i.e. Albermarle Point in the north and Cape Marshall further south), adding up a total of 12, 489 tourists per year. Finally, one of the major natural threats to this corridor is the Wolf volcano itself, due to its constant activity, where the last eruption recorded was on May 2015.
2. The Bolivar Channel – Elizabeth South	This priority HEVA expands from the northern limit of the Bolivar channel and extends southwards including an expanded area of Elizabeth Bay bioregion next to Isabela. Most of this priority HEVA involves marine areas, although tourist sites on land are located in Punta Espinosa and Mangle point (north and south respectively) in Floreana while Tagus Cove and Urbina bay in Isabela. The Bolivar Channel/Elizabeth Bay area is considered as the bioregion with the greatest density in endemic species of the Galapagos (Edgar et al., 2004) and it has the greatest phytoplankton productivity throughout the archipelago (Kislik et al., 2017). It has enormous diversity and biomass of fish species inhabiting different habitats (open water, rocky reef, sand bottom) from different trophic guilds (predators, detritivores, planktivores, omnivores) (Ruiz and Wolff, 2011). This ecosystem also harbors several endemic filter feeders such as ahermatypic corals (*Tubastraea faulkneri* and *T. tagusensis*), a rare endemic scallop species (*Nodipecten magnificus*), and several species of lobsters (*Panulirus penicillatus*, *P. gracilis* and *P. femoristriga*, *Scyllarides astori*) (Ruiz and Wolff, 2011). This is also the feeding ground of endangered and endemic species such as the Galapagos penguin (*Speniscus mendiculus*), the flightless cormorant (*Phalacrocorax harrisi*), the Galapagos grouper (*M. olfax*), the sea lion (*Zalophus wollebaeki*), and the Galapagos- and white-tip reef shark (*Carcharhinus galapagensis*, *Triaenodon obesus* respectively). Finally, the last population of the critically endangered mangrove finch (*Camarhynchus heliobates*) inhabits mangrove forests of the island Isabela (Fessl et al., 2010). Furthermore, this HEVA exhibits the least SST increase anomalies from 2002 to 2017, maintaining temperatures below 25C from (Fig. S5). The prevalence of cool SSTs could qualify this region to be considered as a "climate change refugia" and highlighting its importance in the implementation of EBAs. Also, conservation attention should be devoted to this region, as it has been suggested as one of the regions that can experience harmful algal blooms (Kislik et al., 2017). Approximately, 19,520 estimated annual tourists visit this HEVA every year.
3. Corridor Sierra Negra Volcano – Isabela South	The Sierra Negra volcano area is a valuable ecosystem due to the presence of *Scalesia* forests (*S. cordata* and *S. microcephala*) and tree-less highlands (Hamann, 2001; Itow, 2003; Walsh et al., 2008). It is one of the most important

Priority HEVA	Description
	tourist attractions from southern Isabela. However, this area is also in direct contact with the agricultural zone, which has transformed land cover and increased the incidence of plant invasions (Gardener et al., 2013). For example, the invasive guava species (*Psidium guajava*) has expanded greatly outside of the agricultural zone owing to its sprouting ability after cutting and burning and its aided dispersion by feral cows, horses, and donkeys that run wild around the volcano (Itow, 2003). Furthermore, the agricultural zone and its surrounding area, which are adjacent to the Sierra Negra volcano, are greatly covered by invasive plants (Laso et al., 2020). Additionally, the combination of introduced species with historical exploitation of giant tortoises has led to the classification of the endemic Sierra Negra giant tortoise (*C. guntheri*) as critically endangered by the IUCN, owing to its low population numbers and its restrained recovery (Cayot et al., 2018). This corridor also includes the southern coasts of Isabela, which harbors coral ecosystems, key nesting sites for green sea turtles (*Chelonia mydas*), and the home range of the local tiger shark populations (Acuña-Marrero et al., 2017; Glynn et al., 2018; Seminoff et al., 2008; Zárate et al., 2013). Besides, this priority HEVA contains several public use areas, in the lowlands and coasts, that add up to a total of 56,377 estimated annual tourists.
4. Corridor Cartago Bay – San Luis seabed	This marine corridor expands throughout the half southeastern part of Isabela. Its shorelines, around and adjacent to Cartago Bay, have important mangroves forests, shark nurseries, and habitats (Acuña-Marrero et al., 2018; Llerena et al., 2015; Tanner et al., 2019). It has several touristic attractions, particularly for marine activities such as Cowley Islet, Punta Alfaro, and Cuatro Hermanos next to Isabela, and Nameless Rock in western Santa Cruz. Between Isabela, Pinzón, and Santa Cruz island, there is the San Luis seabed, an important site where kelp forests have been recently been discovered in the Galapagos (Buglass, 2018). The poor scientific knowledge of this region highlights its importance for conservation and research, as climate change threatens to impact this region with warmer temperatures. Approximately, 15,360 estimated annual tourists visit this HEVA every year.
5. Santiago highland	Similar to other highlands in the Galapagos, these areas are predicted to be impacted by higher temperatures and precipitation that are products of climate change. The highlands and surrounding areas of Santiago island support two shrub *Scalesia species*, *S. atractyloides* and *S. stewartii*, and a tree species *S. pedunculata* (Itow, 1995). Santiago highlands are also the last regions where populations of the critically endangered Santiago Giant Tortoise, *Chelonoidis darwini*, still roam free. Because of its conservation value, Santiago highlands are classified as an intangible area, thus there are no touristic sites around. Despite the conservation value of this region, it is still a recovering ecosystem due to several mammal species degrading the island during the last century. Several invasive mammal species have been extirpated (Carrion et al., 2007), however, invasive plant species like the hill raspberry still transform the island, (Renteria et al., 2012b).
6. Conservation area Santiago – Santa Cruz	This priority HEVA exhibits several key marine and terrestrial ecosystems expanding from the east coast of Santiago to the north and central parts of Santa Cruz. The shorelines of both islands in this area harbor corals reefs, coral communities, and shark nurseries. The area between the islands is also the home range of apex predators such as the tiger and hammerhead sharks. Besides, one of the highest concentrations of sharks has been reported northeast of Santa Cruz (Acuña-Marrero et al., 2018; Acuña-Marrero et al., 2017). The terrestrial ecosystem of Santa Cruz includes transition, humid, and very humid zones. One tree, the *Scalesia* species (*S. pedunculata*), and two shrub species (*S. crockeri* and *S. aspera*) occur here. Santa Cruz highlands contain three forests each of endemic plants

Priority HEVA	Description
	(*S. pedunculata* forests, *Zanthoxylum fagara* forests, and *Miconia robinsoniana* scrubs), which together are found nowhere else on the Galapagos, except on San Cristobal. These ecosystems have been severely transformed/degraded and are currently displaced to the north of Santa Cruz as highlands. They are used for farmlands and pastures and native communities are surrounded by assemblages of invasive species (Itow, 2003; Laso et al., 2020). Critically, these forests occupy now only 1% of their original distribution (Rivas-Torres et al., 2018). Santa Cruz highlands are also important for the critically endangered Santa Cruz and Don Fausto's Giant Tortoises (*Chelonoidis porteri* and *C. donfaustoi* respectively) because they arrive at the highlands from the lowlands as part of their annual migration- yet farms and invasive plants block their normal passages (Blake et al., 2015, 2012). Furthermore, the accelerated development of Puerto Ayora has increased the risk of newly introduced species and the pressures on local resources and municipalities. Thus, the interaction of these stressors with climate change impacts can be highly detrimental. As a result of the vibrant marine life, there is a great concentration of tourist attractions. Around Santiago, tourists visit Cousin Rock, Sullivan Bay, Bartolome, and Chinese Hat. Toward the south, tourists visit Daphne, North Seymour, Mosquera, and Baltra Islands; and in the coastline of Santa Cruz, other sites include Carrion Point, Bachas Beach, Black Turtle Cove, Dragon Hill, and Whale Bay. The highlands of Santa Cruz also have famous touristic destinations like Twin Craters, El Chato, Mesa Hill, Crocker Hill, Half Moon, City Santa Rosa, and several other private sites. Altogether, a staggering number of ca.110,400 tourists visit this HEVA every year, evidencing the need of focusing mitigation measures against climate change in this region.
7. Floreana and Islets	Floreana priority HEVA includes most of Floreana Island surface and marine ecosystems from the west, north, and east of the Island. Marine regions around Floreana have experienced increased-SST anomalies (Fig. S5) and are predicted to continue that trend along with the rest of the Pacific region, while the surface of the island is also predicted to experience changes in precipitation (Fig. S6). Floreana marine ecosystems are particularly important, as they are habitats for recovering corals communities (including one of the two sites of the endemic-critically-endangered coral *Tubastraea floreana* (Banks, 2007), sharks, sea cucumber, lobsters, the Galapagos penguin, green turtle nesting sites, several marine endemic species, and megafauna species commonly captured as bycatch (Cerutti-Pereyra et al., 2020; Zárate et al., 2013). In addition, the marine region to the west of Floreana also exhibits high primary productivity (Kislik et al., 2017; Tompkins and Wolff, 2016). Terrestrial ecosystems in Floreana have been the most devastated among the islands in Galapagos. This is partly because Floreana was the first Island to be colonized, hence the exploitation of its natural resources has been longer than that of other islands. The native vegetation of the highlands, used for farmlands and pastures, has been transformed not only by humans but also by plant-invasive species like *Psidium guajaba*. *S. pedunculata* forests are found in Floreana today very sparsely. Although goats were completely removed in 2007, its terrestrial ecosystems are no longer ideal to support Floreana's native wildlife. The endemic Floreana Giant tortoise species (*Chelonoidis niger*) is extinct. Current efforts focus on restoring native snakes and several bird species (Galapagos-Conservancy, 2021). Altogether, predicted impacts of climate change will affect tourism in Floreana. Several touristic sites for marine-related activities occur in this priority HEVA, including (from east to west) Gardner, Caldwell, Champion and Enderby

Priority HEVA	Description
	Islands, and Devil's crown crater. Tourists also visit Cormorant Point, Baroness Viewpoint, and the Post Office Bay and Loberia beach. Touristic sites on land include the city of Puerto Velasco Ibarra, Pajas Hill, and Alieri Hill. Overall, estimates of 44,160 annual tourists visit this HEVA every year.
8. Marchena coral remnants	This marine priority HEVA consists mainly of corals and seabed ecosystems present in the east area of Marchena. Corals in Marchena Island are suggested to have shown good recruitment and regeneration in the last 30 years after the 1982-83 ENSO event (Glynn et al., 2018; Manzello et al., 2014). An important coral species is *Porites lobata*, a reef builder, which thrives in Marchena coast and healthy populations are only present in two other localities (Darwin and Wolf islands). Corals *Porites lobata* and *Psammocora stellata*, both present in Marchena, are important owing to its resilience to warming events (Glynn et al., 2018; Vera and Banks, 2009). However, Marchena corals are also experiencing declines and diseases (Riegl et al., 2019b; Vera and Banks, 2009) highlighting the need for conservation measures for these ecosystems. Additionally, it has been suggested that fish and macroinvertebrates from Marchena, Pinta, and Genovesa islands are different from the ones from the central and southern islands, as these communities contain more oceanic species (Edgar et al., 2004a). Marchena does not have touristic sites on land and only Punta Espejo on its coast, which is used for marine-related activities for 1,920 estimated annual tourists.
9. Corridor La Galapaguera – Punta Pitt	This HEVA encompasses the northeastern terrestrial and marine ecosystems of San Cristobal. La Galapaguera Natural protected area is located at the northern tip of San Cristobal and is the only spot where the endangered San Cristobal Giant tortoise, *Geochelone chatamensis*, roams free. It is also one of the few spots where you can find the San Cristobal endemic plant, *Clandrinia galapagosa,* and several other native and endemic plant species. Another site, Punta Pitt, is a noticeable touristic attraction due to several coastal birds (including the three species of boobies and two species of frigates) nesting within this area. Conservation of the marine iguanas in these regions is encouraged because research has shown that marine iguanas in this region exhibit low densities but high genetic distinctiveness (Rassmann, 1996; Steinfartz et al., 2009) from populations in other islands. Besides, corals that live nearby Punta Pitt are among the few corals that have shown signs of recovery, having low abundances of the Galapagos urchin, *E. galapagensis,* which drives bioerosion throughout the Galapagos (Glynn et al., 2015). An estimated 14,080 annual tourists visit this corridor annually.
10. Leon Dormido (Kicker's Rock)	This HEVA includes several sites on the coastline of San Cristobal and the famous Leon Dormido formation. Leon Dormido is a key habitat for juvenile Galapagos sharks (Hearn et al., 2014) and one of the few sites where the vulnerable gastropod *Neorapana grandis* can be found (Banks, 2007). It is also where new records of octocorals species have been reported (Breedy et al., 2009). The shoreline of San Cristobal is important for corals, shark nurseries, sea cucumbers, and lobsters. The region also harbors several endangered taxa, including the red algae *Pseudolaingia hancockii*, Galapagos sea lion, marine iguana, green turtle (Edgar et al., 2008), and it is habitat for individuals and mother/calf pairs of at least three whale species (blue, bryde's, and humpack whales) (Biggs et al., 2017). Along the coast of this HEVA, there are several touristic sites (from east to west): Punta Pucuna, Punta Dedo, Witch Hill, Stephens Bay, Punta Bassa, and Lobos island. Approximately, 16,320 tourists visit this HEVA per year.
11. Corridor El Junco and	This corridor includes the highlands and lowlands of southern San Cristobal and its shoreline, which includes the

Priority HEVA	Description
southern seabeds	south-facing seabeds. El Junco is a freshwater lake located in the highlands of San Cristobal and aside from being a tourist destination, it provides fresh water to local human populations. Diverse endemic plants can be found in this HEVA, such as *Miconia* bushes (*Miconia robinsoniana*) and endemic tree ferns (*Cyathea weatherbyana*), and it provides habitats to birds such as the white-cheeked pintail ducks, common gallinules and the endemic Chatham mockingbird (*Mimus melatonis*). However, despite the efforts to preserve the El Junco Lake, it is surrounded by farms and invasive species, particularly by guava and pomarosa trees (*P. guajaba* and *Syzygium jambos.* respectively) (Laso et al., 2020). The highlands of San Cristobal are almost completely transformed (>90%) due to anthropogenic change (Watson et al., 2009). Thus, the conservation of remaining native ecosystems is of paramount importance. This corridor encompasses several touristic sites, the Interpretation Center, El Junco Lake, Cerro Colorado Reserve, Tortoise Breeding Center, and the city of Puerto Baquerizo Moreno. A total of 25,133 tourists visit this HEVA per year.
12. Española and Gardner islands	This HEVA encompasses Española and its northern shores. Española is a small-flattened island and home to several endemic species. A few include the vulnerable Española mockingbird (*Mimus macdonaldi*), Española lava-lizard (*Microlophus delanonis*), the critically endangered waved albatross (*Phoebastria irrorata*), and the critically endangered Española Giant-Tortoise (*Chelonoidis hoodensis*). Previous El Niño years have proven to be detrimental for seabirds of Española (Valle et al., 1987), as higher temperatures decrease primary productivity and cause declines in smaller-prey fish. Torrential rainfall also destroys nesting sites and climate change threatens to have negative impacts on the breeding success of these species. Besides, the Española northern coast harbors corals and seabeds that are likely to also be affected by climate change. Española touristic sites include Gardner Bay and Gardner Island, Tortuga Rock, and Punta Suarez. Approximately, 10,880 tourists visit this HEVA annually.
13. Darwin and Wolf islands	Darwin and Wolf Islands comprise the highest biomass of sharks in the Galapagos. They are known to possess marine predator aggregations and they are the only islands on the archipelago that still resemble near-natural states (Acuña-Marrero et al., 2018; Ruiz et al., 2016). These islands, due to their unique locations, are also home to coral reefs and coral communities that are recovering and have not been heavily degraded by past El Niño events (Riegl et al., 2019a, 2019b). Darwin Island is home of the only surviving true coral reef in the Galapagos (Wellington reef) (Glynn et al., 2018) and one of the few places where whale sharks can be seen (Hearn et al., 2016). These islands are also spawning zones for the threatened Galapagos grouper, *M. olfax* (Salinas-De-León et al., 2015). Owing to their high species richness, these islands are also important for small-scale fisheries and recreational diving. Climate change is predicted to affect these marine ecosystems with an increase in ocean temperature. A warmer ocean would change the primary productivity affecting all of the trophic chains in this region. Less available food coupled with the pressure of overfishing and pollution, which is already affecting some parts of this territory (Ruiz et al., 2016), could make this ecosystem less resilient to variable weather conditions.

Table S9: Selected priority high ecological value areas (HEVA) in the Galapagos National Park and the Galapagos Marine Reserve for the implementation of ecosystem-based adaptation measures (EBA).

Priority HEVA Site ID*	Climatic heterogeneity (1)																		Bioregions (2)						Connectivity of environmental gradients and habitat singularity (3, 4)			Environmental services (5)				Total score (g)
	delta T regions						P relative increase						**SST anomalies**						FN	N	E	W	CS	**score (d)**	N terrestrial macro habitats	N marine macro habitats	**score (e)**	T	F	W	**score (f)**	
	1	2	3	4	5	score (a)	Q1	Q2	Q3	Q4	Q5	**score (b)**	Q1	Q2	Q3	Q4	Q5	**score (c)**														
1					5	**5**	1					**1**		2	3			**2.5**				x	x	**2**	6	5	**11**	1	1		**2**	**23.5**
2				4	5	**4.5**		2	3	4	5	**3.5**	1					**1**			x	x		**2**	3	6	**9**	1	1		**2**	**22**
3				4		**4**		2	3	4		**3**		2	3			**2.5**				x	x	**2**	7	3	**10**	1	1	1	**3**	**24.5**
4				4		**4**				4	5	**4.5**	1	2				**1.5**					x	**1**	3	4	**7**	1	1		**2**	20
5			3			**3**	1	2				**1.5**													4		**4**			1	**1**	9.5
6			3			**3**			3	4	5	**4**	1	2	3			**2**					x	**1**	6	7	**13**	1	1	1	**3**	**26**
7		2				**2**	1	2	3	4		**2.5**			3	4		**3.5**					x	**1**	5	4	**9**	1	1	1	**3**	21
8	1					**1**									3	4		**3.5**		x				**1**		2	**2**	1	1		**2**	9.5
9			3			**3**		2	3	4		**3**			3			**3**					x	**1**	5	4	**9**	1		1	**2**	21
10			3			**3**		2	3			**2.5**	1					**1**					x	**1**	3	5	**8**	1			**1**	16.5
11			3			**3**		2	3	4	5	**3.5**	1		3	4		**2.7**					x	**1**	6	3	**9**	1		1	**2**	21.2
12		2				**2**				4	5	**4.5**			3	4		**3.5**					x	**1**	1	3	**4**	1	1		**2**	17
13																	5	**5**	x					**1**		4	**4**	1	1		**2**	12

*Priority landscapes: 1) Corridor Wolf Volcano, Punta Albermarle and Cape Marshall, 2) The Bolivar Channel and Elizabeth South, 3) Corridor Sierra Negra Volcano Isabela South, 4) Corridor Cartago Bay – San Luis seabed, 5) Santiago highland, 6) Conservation area Santiago-Santa Cruz, 7) Floreana and islets, 8) Marchena coral remnants, 9) Corridor la Galapaguera – Punta Pitt, 10) León Dormido (Kicker's rock), 11) Corridor El Junco and southern seabeds, 12) Española and Gardner islands and 13) Darwin and Wolf islands. Assessment criteria for the prioritization of potential impacted areas, T= tourism, F= fishery, W= water.

Tabla S10. Spatial statistics of priority HEVA.

	Impact (marine)					Impact (terrestrial)				
site ID	**N**	**mean**	**sd**	**min**	**max**	**N**	**mean**	**sd**	**min**	**max**
1	153	10.72	3.54	2.1	22.25	144	3.81	1.38	1.1	8.25
2	338	9.48	4.56	2.25	17.75	233	4.51	1.38	1.6	8.25
3	207	11.19	3.61	4.2	20.5	251	7.92	2.51	1.6	14.4
4	376	10.91	3.62	4.2	19	131	4.44	1.89	1.3	9.6
5						46	7.73	3.08	2.1	11
6	416	9.53	3.35	2.7	20.5	254	8.79	5.23	0.85	20.75
7	155	10.68	2.98	4.2	19.5	72	7.43	2.69	3.4	15.5
8	47	9.84	3.59	2.55	16.6					
9	67	8.49	1.53	5.4	10.5	40	7.37	3.2	2.25	12
10	51	9.92	2.85	4.2	13	25	7.03	1.74	1.7	9
11	52	9.25	1.43	5.6	12.2	61	10.06	2.68	5	17
12	47	8.51	1.87	5.4	13	31	3.22	0.9	1.1	4.5
13	1502	3.73	2.51	1.8	16.6					
	Exposure index (marine)					**Exposure index (terrestrial)**				
site ID	N	mean	sd	min	max	N	mean	sd	min	max
1	153	3.12	0.67	1.2	4.45	144	1.78	0.66	0.55	2.75
2	338	2.45	0.9	0.45	3.65	233	1.36	0.38	0.55	2.2
3	207	2.85	0.63	1.65	4.1	251	2.84	0.68	0.85	4.8
4	376	2.85	0.74	1.2	3.9	131	1.31	0.46	0.55	2.4
5						46	2.23	0.52	1.05	2.75
6	416	2.52	0.75	1.35	4.1	254	2.06	0.93	0.55	4.15
7	155	2.65	0.72	1.35	4.05	72	2.61	0.81	1.05	4.45
8	47	3.8	0.57	2.1	4.15					
9	67	2	0.22	1.35	2.3	40	2.12	0.76	0.75	3.2
10	51	2.33	0.23	1.65	2.6	25	1.62	0.24	0.85	1.85
11	52	2.53	0.32	1.4	3.05	61	3.08	0.73	1.35	4.25
12	47	2.08	0.43	1.35	2.6	31	1.61	0.45	0.55	2.25
13	1502	2.25	0.5	1.8	4.15					
	Sensitivity index (marine)					**Sensitivity index (terrestrial)**				
site ID	**N**	**mean**	**sd**	**min**	**max**	**N**	**mean**	**sd**	**min**	**max**
1	153	3.44	0.85	1	5	144	2.19	0.5	2	4
2	338	3.96	1.13	2	5	233	3.44	0.98	2	5
3	207	3.96	1.07	2	5	251	2.81	0.72	1	5
4	376	3.86	0.91	2	5	131	3.45	0.98	1	5
5						46	3.33	0.82	2	4
6	416	3.87	0.97	2	5	254	4.04	0.96	1	5
7	155	4.12	0.82	2	5	72	2.99	1.08	2	5
8	47	2.57	0.83	1	4					
9	67	4.27	0.73	3	5	40	3.45	0.64	2	4
10	51	4.2	0.96	2	5	25	4.32	0.9	2	5
11	52	3.67	0.47	3	4	61	3.3	0.56	2	4
12	47	4.13	0.61	3	5	31	2	0	2	2
13	1502	1.59	0.67	1	4					
	Sensitivity score (marine)					**Sensitivity score (terrestrial)**				

site ID	N	mean	sd	min	max	N	mean	sd	min	max
1	153	58.12	13.37	27.17	83.00	144	29.88	6.12	22.87	58.34
		Sensitivity score (marine)					**Sensitivity score (terrestrial)**			
site ID	**N**	**mean**	**sd**	**min**	**max**	**N**	**mean**	**sd**	**min**	**max**
2	338	73.53	27.12	28.29	139.13	233	45.99	13.52	26.98	86.49
3	207	69.17	18.80	36.17	98.59	251	36.88	7.03	20.9	59.11
4	376	65.46	16.93	37.00	94.33	131	44.27	11.88	14.21	72.25
5						46	42.51	8.60	27.49	53.04
6	416	67.31	19.81	28.17	110.13	254	53.29	13.70	14.86	82.84
7	155	74.27	22.23	36.67	124.58	72	40.34	14.28	22.36	80.02
8	47	44.19	10.63	20.92	60.96					
9	67	75.53	15.58	43.58	103.25	40	42.04	4.89	31.67	47.92
10	51	72.85	18.61	33.00	94.67	25	56.65	12.50	32.36	74.51
11	52	62.80	7.73	43.42	76.80	61	41.39	5.49	33.01	54.35
12	47	71.07	12.65	45.58	93.00	31	27.25	2.47	22.86	33.66
13	1502	30.09	7.83	24.58	73.83					

The sensitivity index is a value between 1 and 5 given by the distribution of sensitivity score in quintiles, whereas sensitivity score is the added value of the variables accounted in the sensitivity analysis. N= number of spatial units (hexagons of 3.46 km^2). Site ID = priority HEVA ID shown in Tables 1 and 2

Supplementary Figures

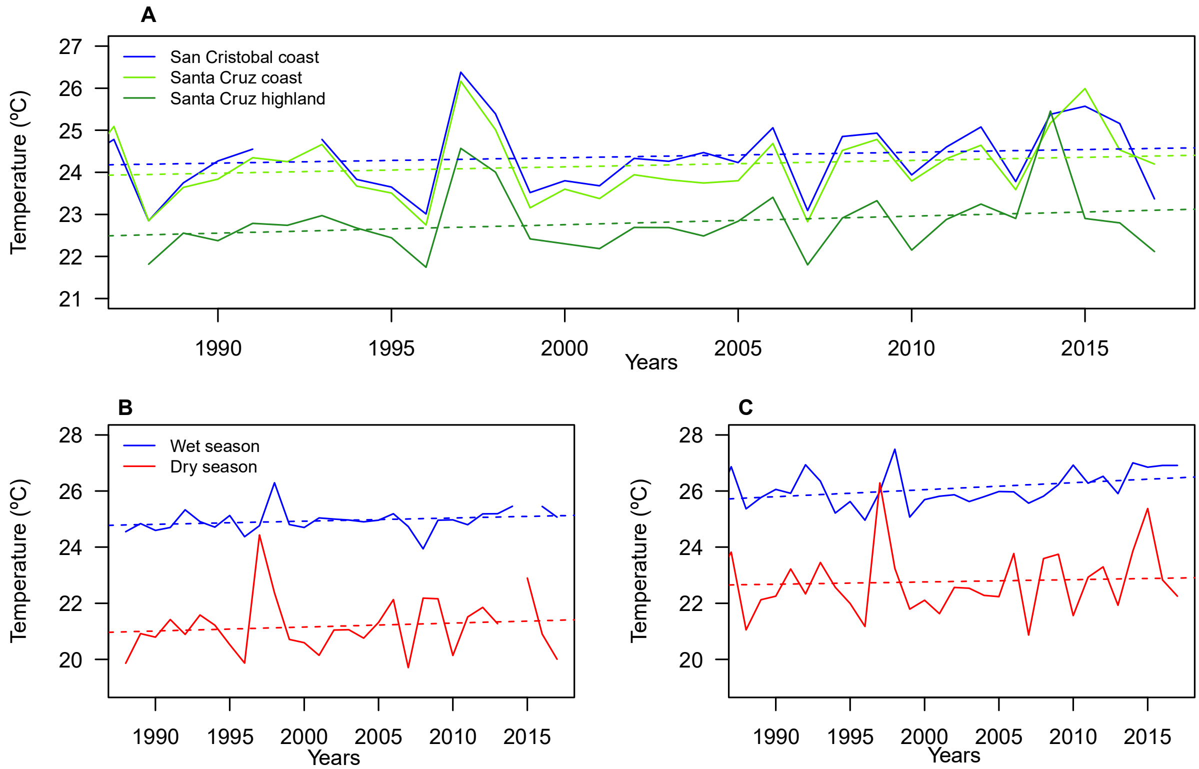

Figure S1. Mean annual temperature: (A) mean temperature and temperature trends (1988-2017) at coastal and highland stations. Seasonality temperatures observed in Santa Cruz, highland (B) and coastal (C) stations. Data from the National Meteorological and Hydrological Institute (INAMHI), Ecuador.

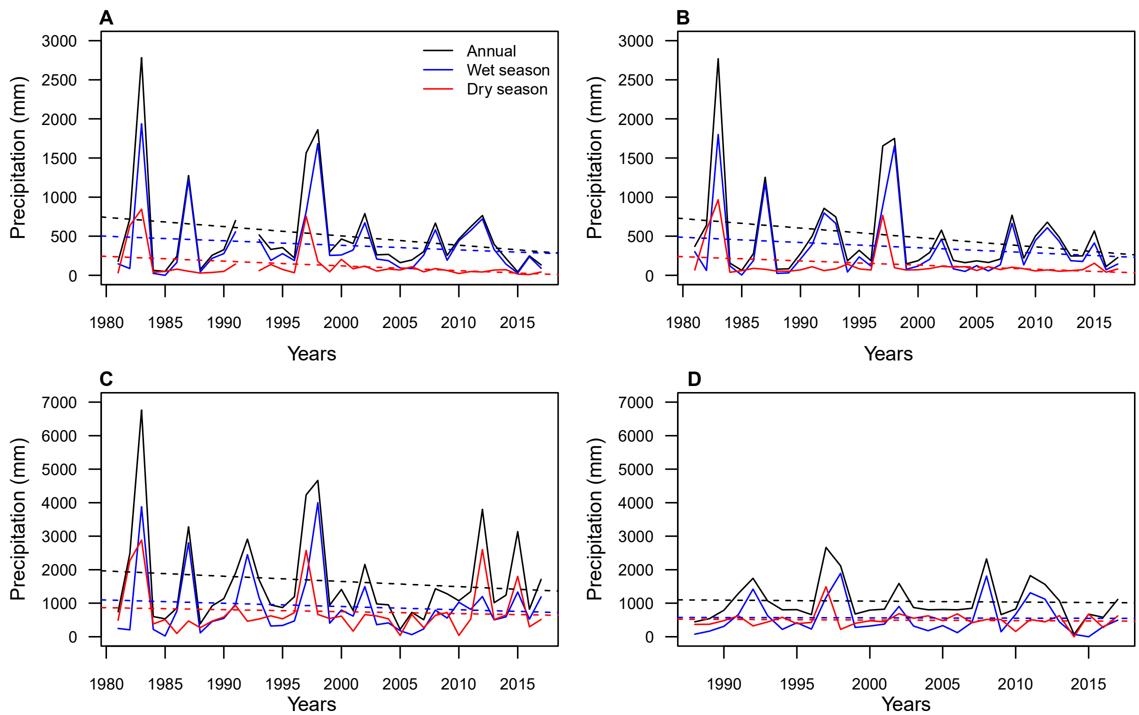

Figure S2. Mean annual and seasonal precipitation observed in San Cristobal (A & C) and Santa Cruz (B &D) at coastal (A-B) and highland (C-D) stations between 1981 and 2017. Data from the National Meteorological and Hydrological Institute (INAMHI), Ecuador.

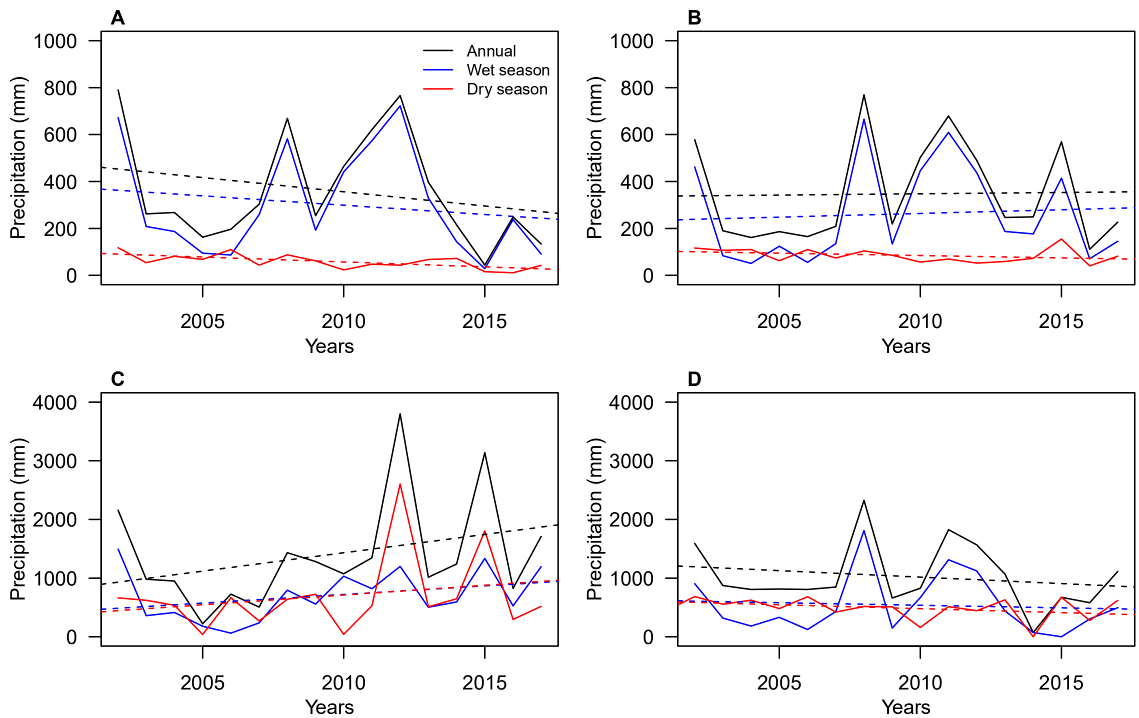

Figure S3. Mean annual and seasonal precipitation observed in San Cristobal (A & C) and Santa Cruz (B & D) at coastal (A-B) and highland (C-D) stations between 2002 and 2017. Data from the National Meteorological and Hydrological Institute (INAMHI), Ecuador.

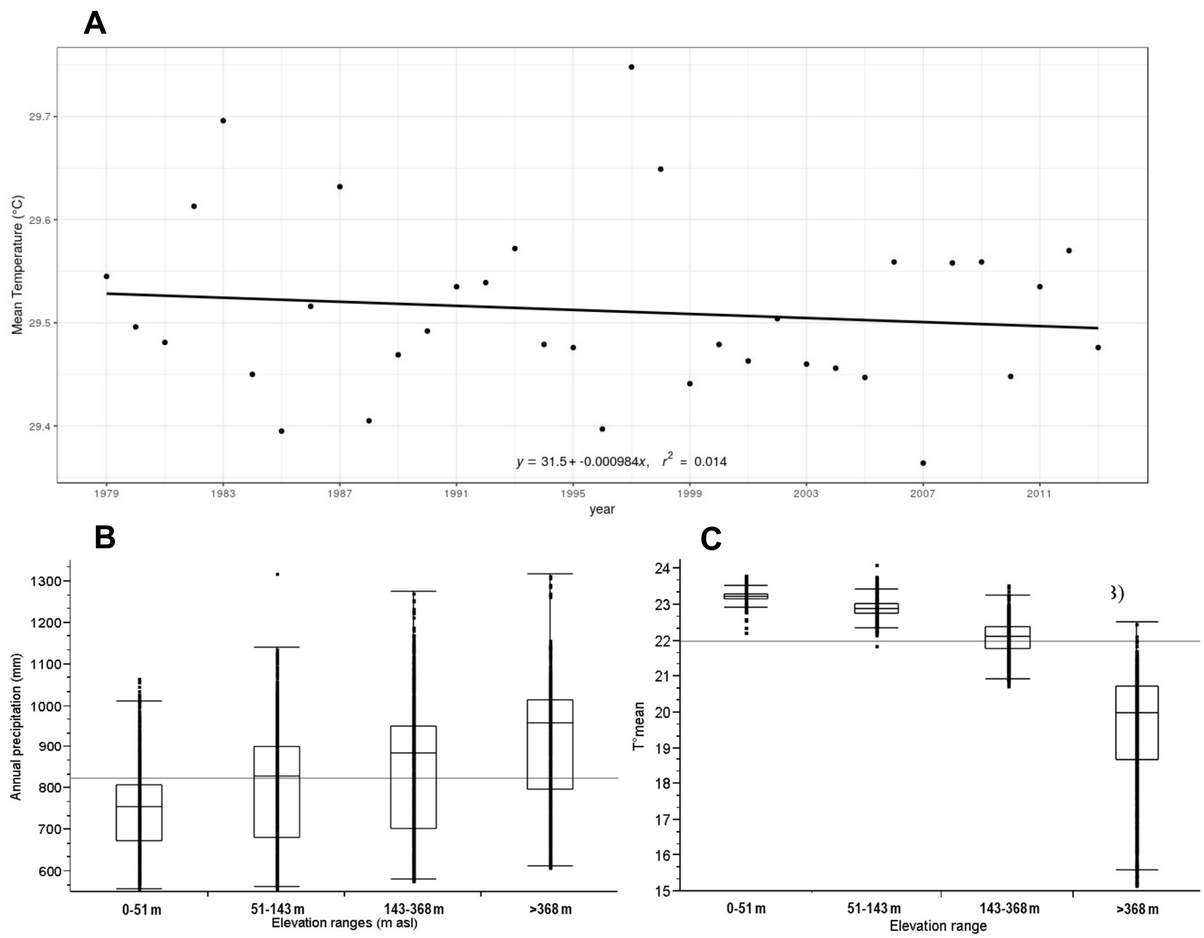

Figure S4. (A) CHELSA time-series analysis of mean annual air temperature from 1979 to 2011, based on monthly temperature files. A mean cell statistic was obtained between 5 models, CSIRO-MK3-6-0, HADGEM2-CC, HADGEM2-ES, MIROC-ESM-CHEM and MRI-CGCM3. (B) Annual precipitation and (C) mean air temperature for the period 1977-2013 along the elevation gradient in the Galápagos Islands. Elevation ranges were defined based on quartile frequencies derived from a 1km^2 SRTM elevation model. Climate data were derived from CHELSA datasets.

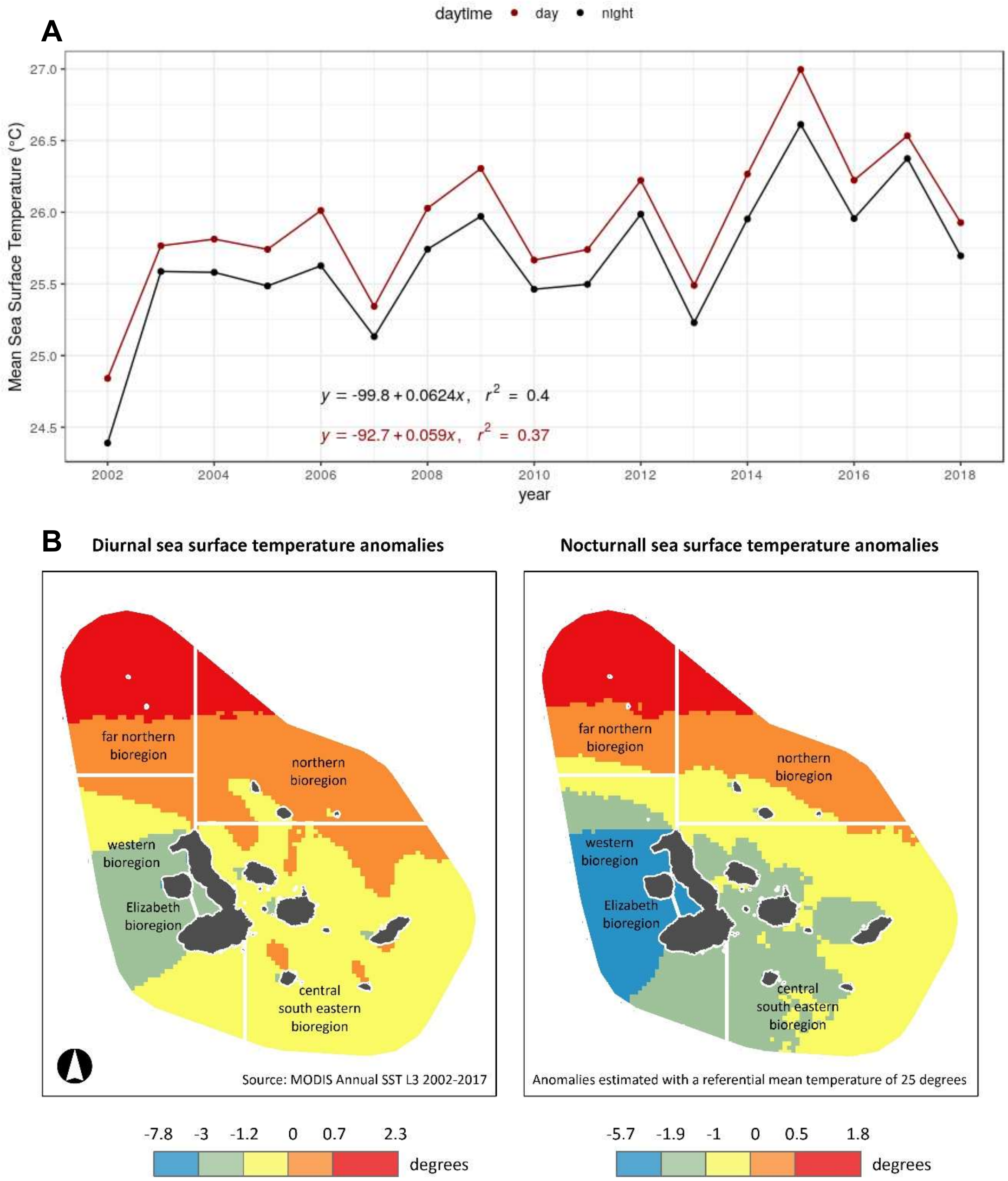

Figure S5. (A) Mean Interannual SST. Data obtained from SST MODIS L3 from 2002 to 2017. (B) Mean diurnal and nocturnal SST anomaly from MODIS L3 2002-2017. For sea surface temperature, we used the annual SST MODIS L3 product (period 2002 to 2017). A statistical analysis was performed to the whole time series data set to understand the interannual variability in SST. Since an increasing trend in SST was observed, we used a reference mean surface temperature of 25 °C, calculated from the 2002 image for the GMR, to estimate the temperature anomalies for the whole dataset. We then calculated the difference between the reference temperature and the grid values for each year. Finally, we calculated the mean anomaly between 16 images from 2002 to 2017.

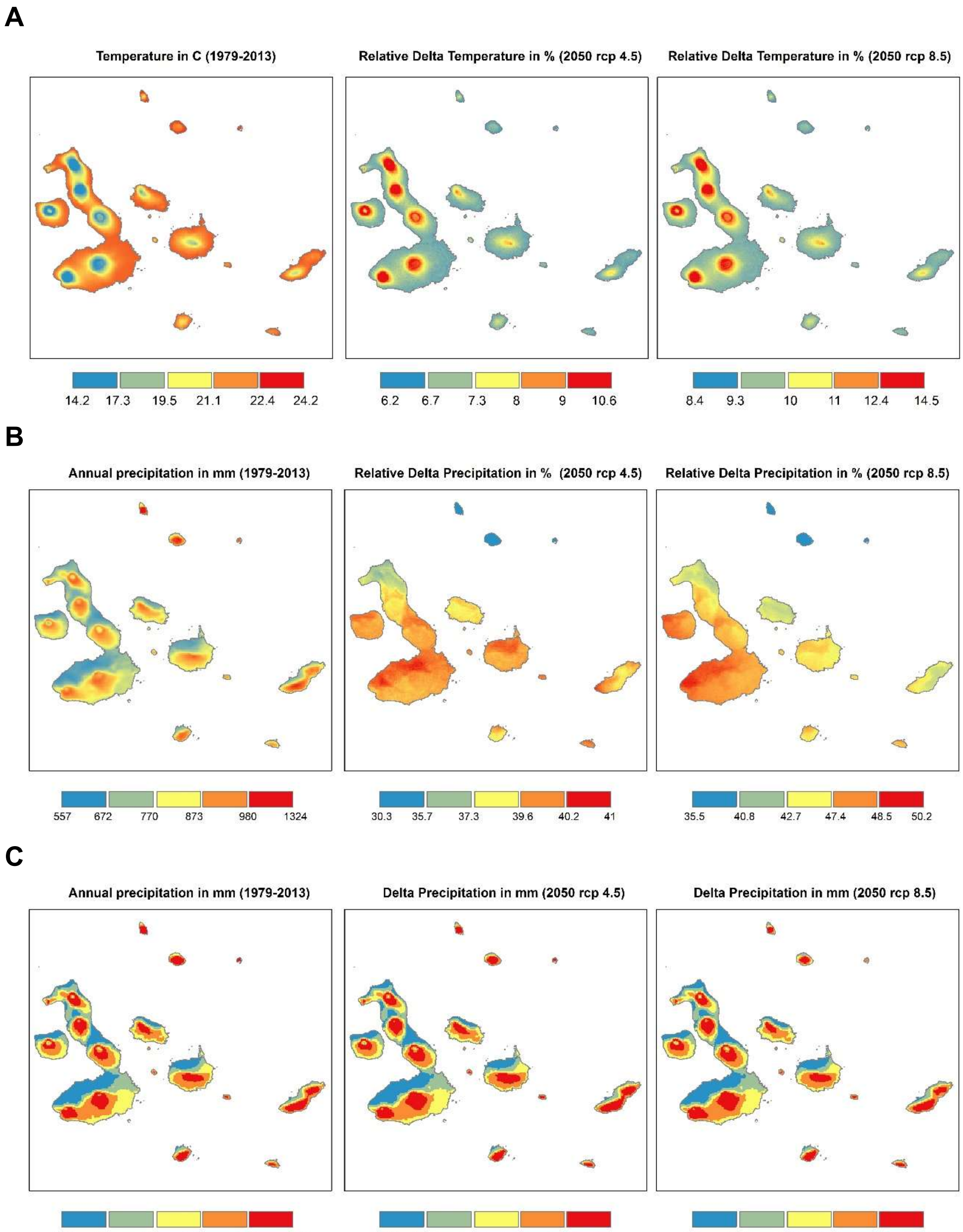

Figure S6. CHELSA climatologies of previous (1979-2013) and future years. (A) Temperature scenarios, (B) relative delta, and (C) absolute delta precipitation scenarios with 4.5 and 8.5 concentration pathways. Warm colors indicate greater changes in comparison to the 1979-2013 reference. For terrestrial temperature and precipitation, we used the Future Downscaled (CMIP5) CHELSA (Climatologies at high resolution for the earth's land surface areas) climatologies for 2050, 4.5 and 8.5 concentration pathways. Monthly temperature and precipitation were used to calculate the mean annual temperature and total annual precipitation. A mean cell statistic was obtained between 5 models, CSIRO-MK3-6-0, HADGEM2-CC, HADGEM2-ES, MIROC-ESM-CHEM and MRI-CGCM3. For comparing actual scenarios with future scenarios, we used the monthly dataset of CHELSA Climatologies 1979-2013 as the reference climate scenario to calculate the anomalies in temperature and precipitation between 1979-2013 and 2050 (Fig. S3-4). For temperature, delta T, was calculated as a percentage anomaly whereas for precipitation, delta P, was calculated as the difference between the future and actual values. The reference climate was also analyzed on an annual time scale as the future climate scenarios.

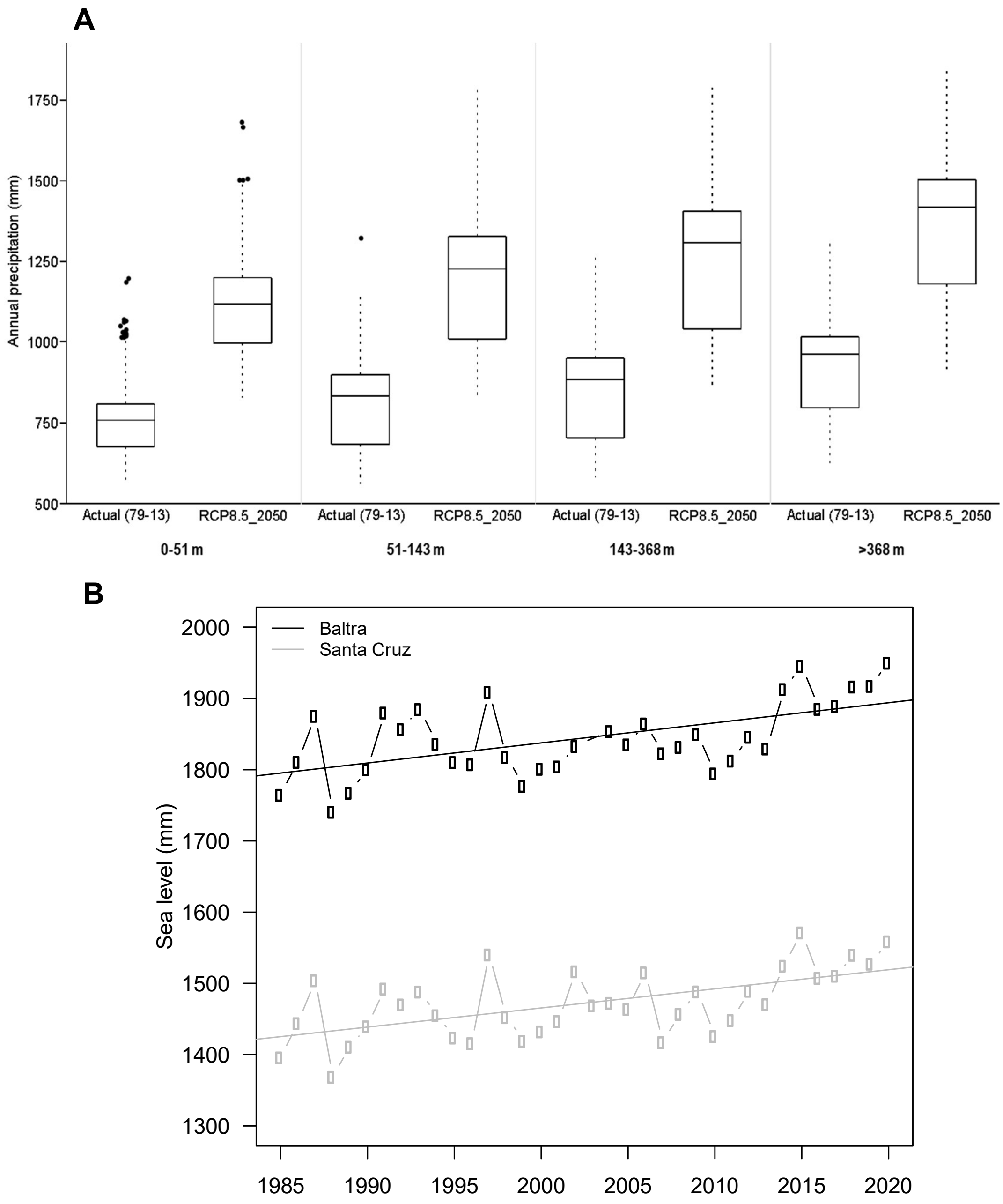

Figure S7. (A) Projected increases in annual precipitation (2050) with 8.5 concentration pathways at different altitudes. (B) Sea level change in Galapagos. Data obtained from the climatological database of the University of Hawaii Sea

Level Center (https://uhslc.soest.hawaii.edu/), based on meteorological stations of Baltra and Santa Cruz islands. Because ENSO events result in highly anomalous records hindering possible trends, records from the 95% and 2,5% quartiles were removed for this analysis.

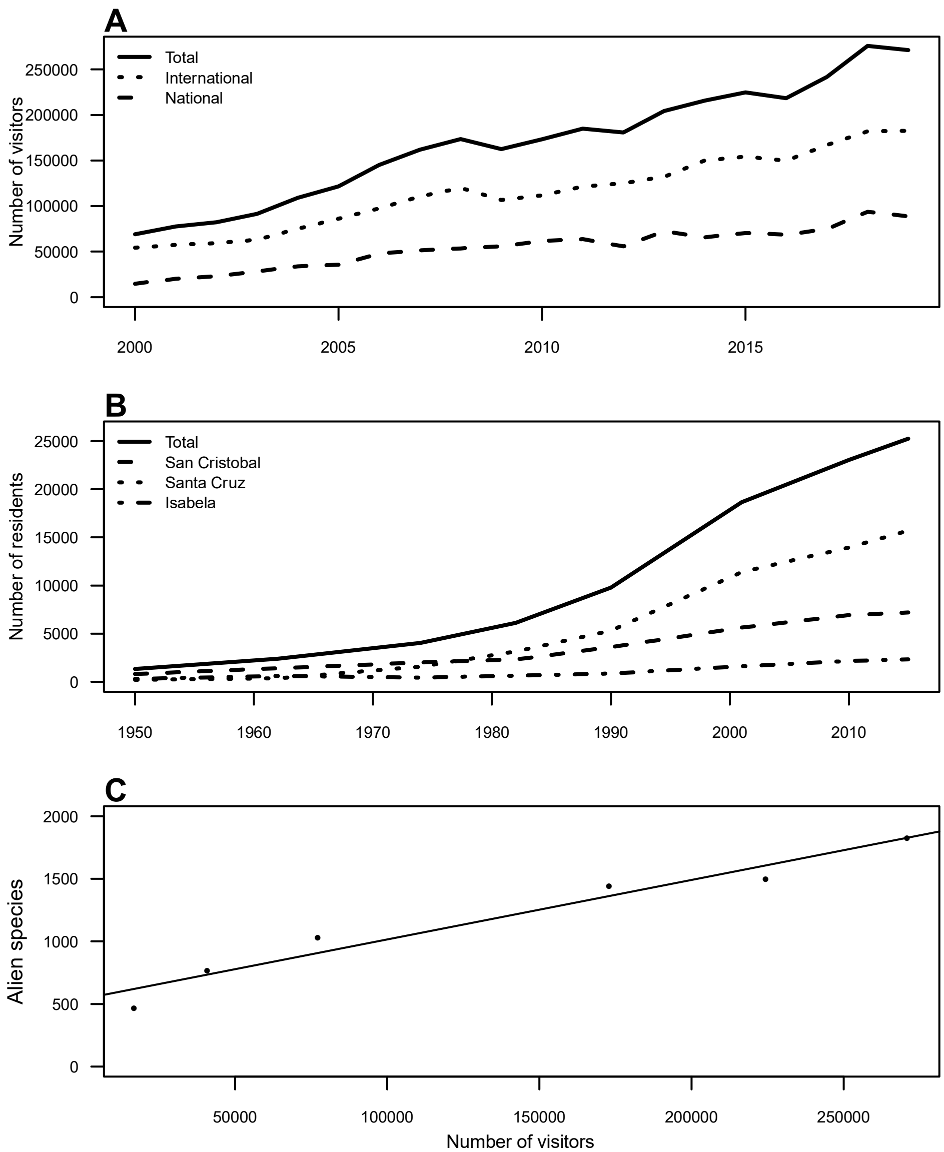

Figure S8. (A) Annual number of tourists that visited Galapagos between 2000 and 2019, according to tourism statistics collected by the Directorate of the Galapagos National Park, (B) Number of Galapagos residents between 1950 and 2015 (https://www.arcgis.com/apps/Cascade/index.html?appid=fc8f4824b1324fc1afa7ddff510db292), (C) Alien species in relation with the number of tourists. Up to 2015 there were 1504 alien species and 224755 visitors (Toral-Granda *et al.* 2017). Using the number of visitors of 2019, we predicted the numbers of alien species.

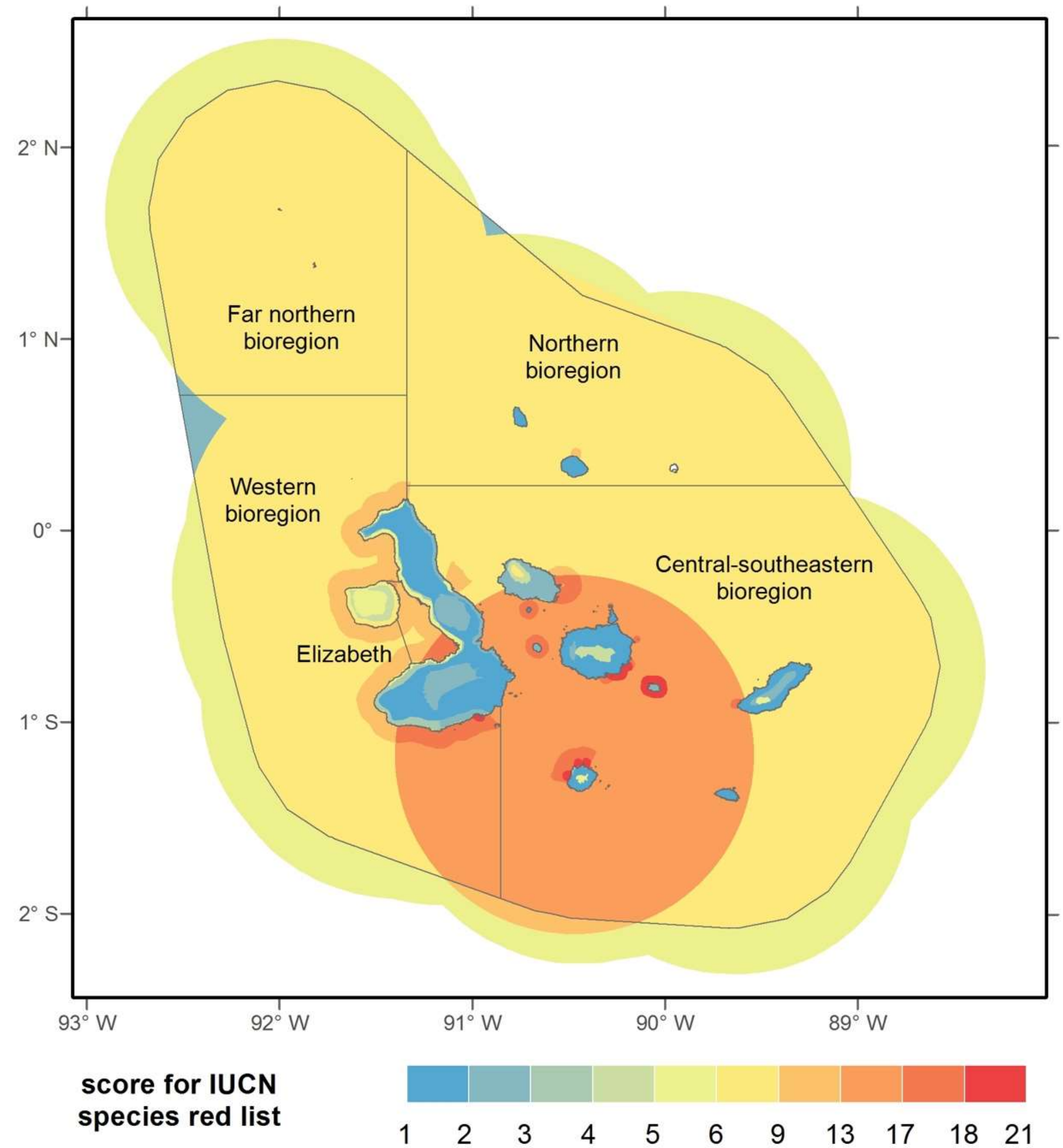

Figure S9. Distribution of 28 threatened Galapagos species (terrestrial and marine) according to IUCN's red list. Warmer colors indicate an overlap of the home-range of different threatened species.

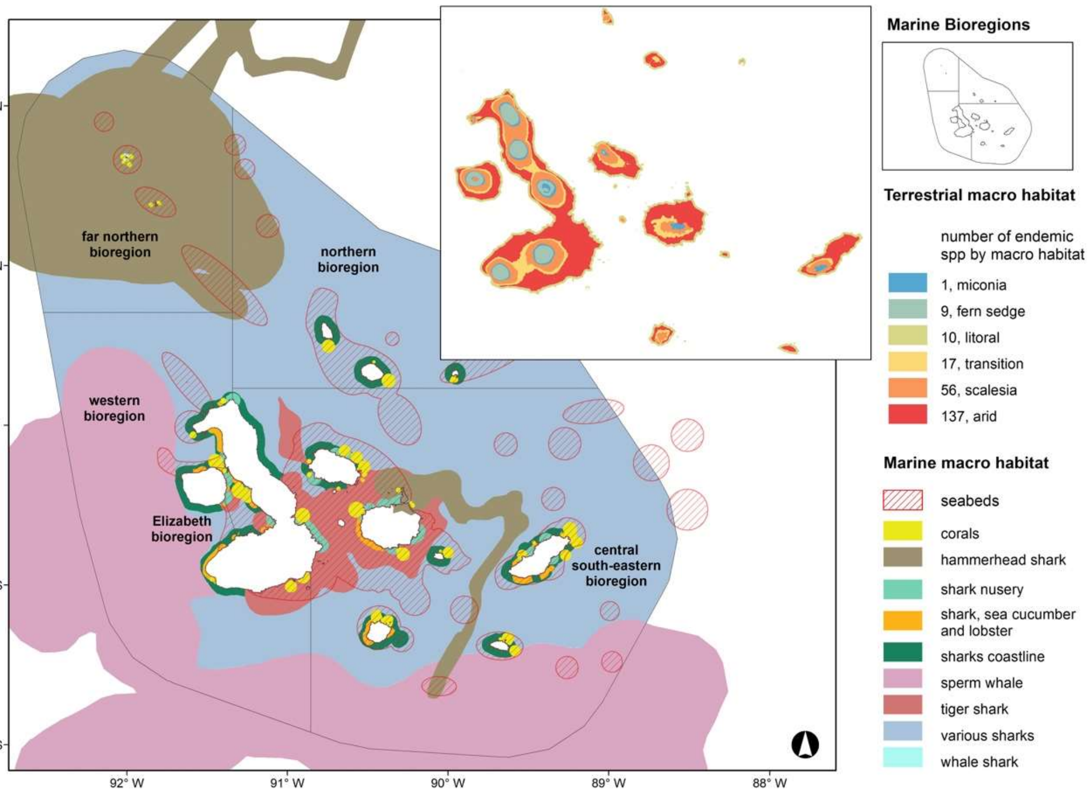

Figure S10. Terrestrial and marine macro-habitats included in the sensitivity model. For the terrestrial model, we used the macro-habitats described by Itow. (1995). Higher vegetation endemism is represented by warmer colors. For the marine macro-habitats, we included the reported distribution of predators, shark nurseries, and catchment areas of species of economic importance (sea cucumbers and spiny lobsters). The marine-macro habitats included in our analysis are limited to the species studied in the articles used for the meta-analysis.

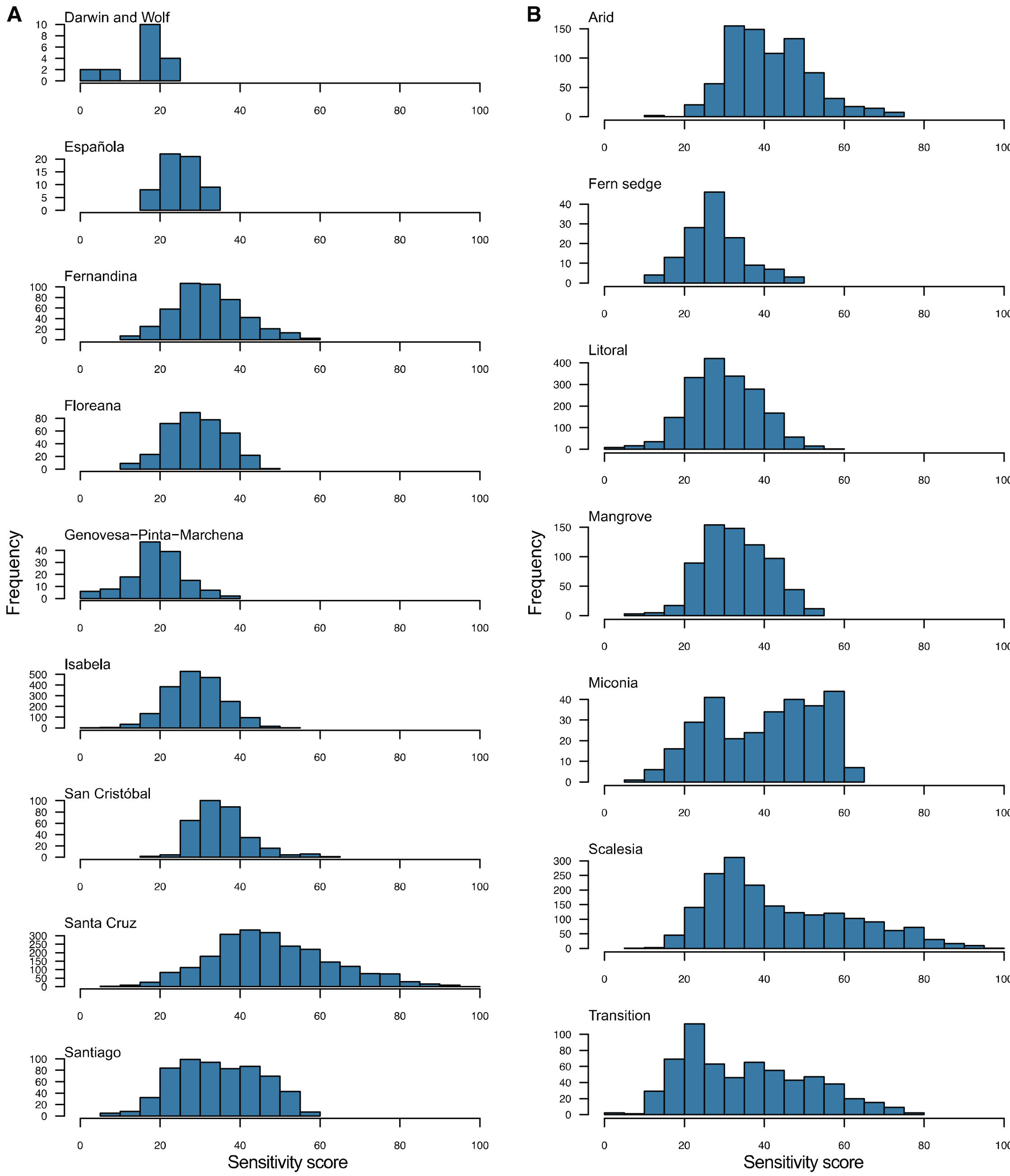

Figure S11. Magnitudes of sensitivity for (A) whole islands and (B) insular ecosystems in the archipelago. Sensitivity scores were calculated for each island and terrestrial ecosystem, based on the added magnitudes of the meta-analysis score and terrestrial biodiversity attributes. Frequency denotes the number of polygons product of the algebraic map sum of the meta-analysis and biodiversity attributes.

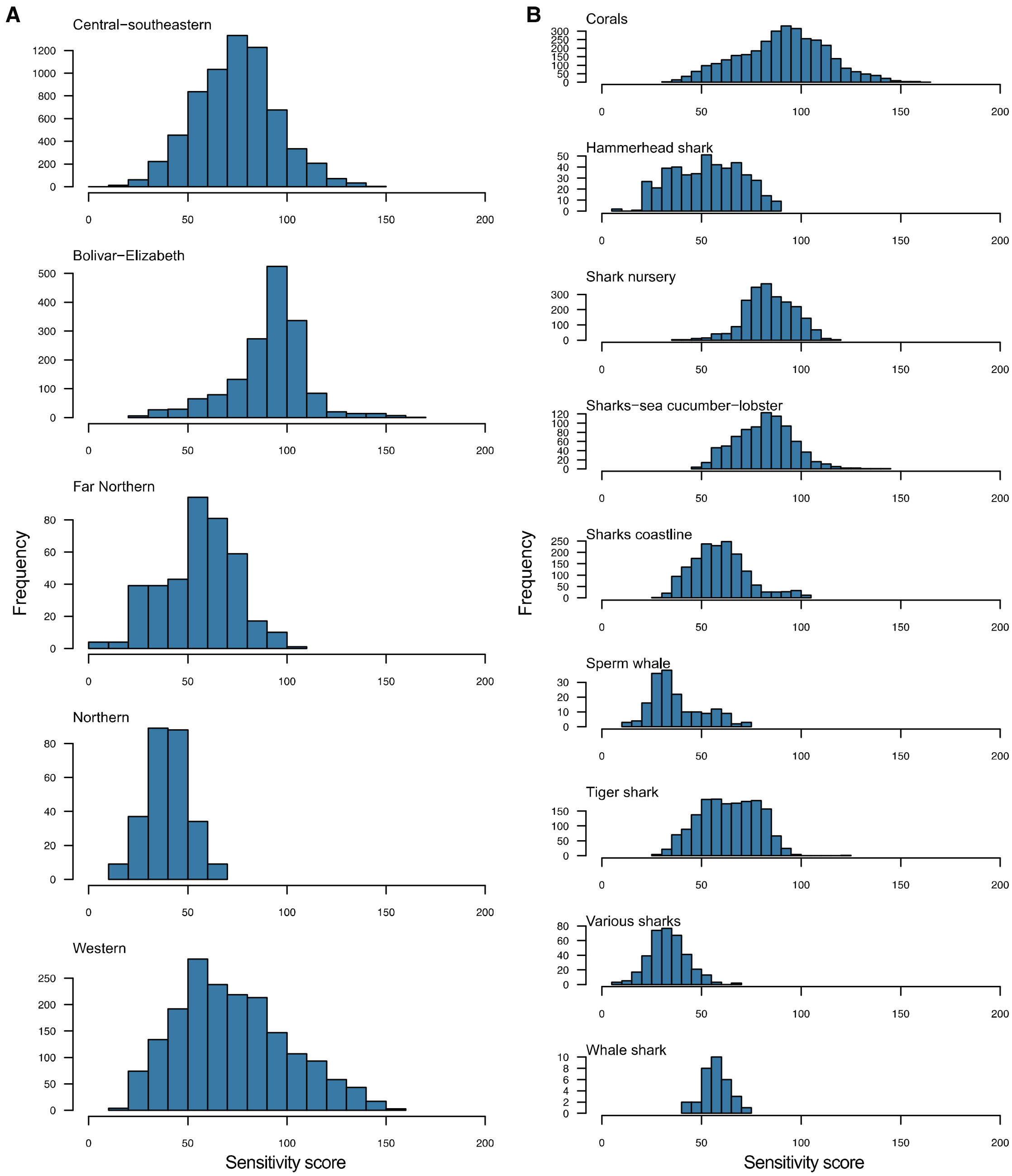

Figure S12. Magnitudes of sensitivity for (A) bioregions and (B) marine distributions of important habitats and keystone species. Sensitivity score was calculated for each bioregion and macro-habitat based on the added magnitudes of the meta-analysis score and marine biodiversity attributes. Frequency denotes the number of polygons product of the algebraic map sum of the meta-analysis and biodiversity attributes.

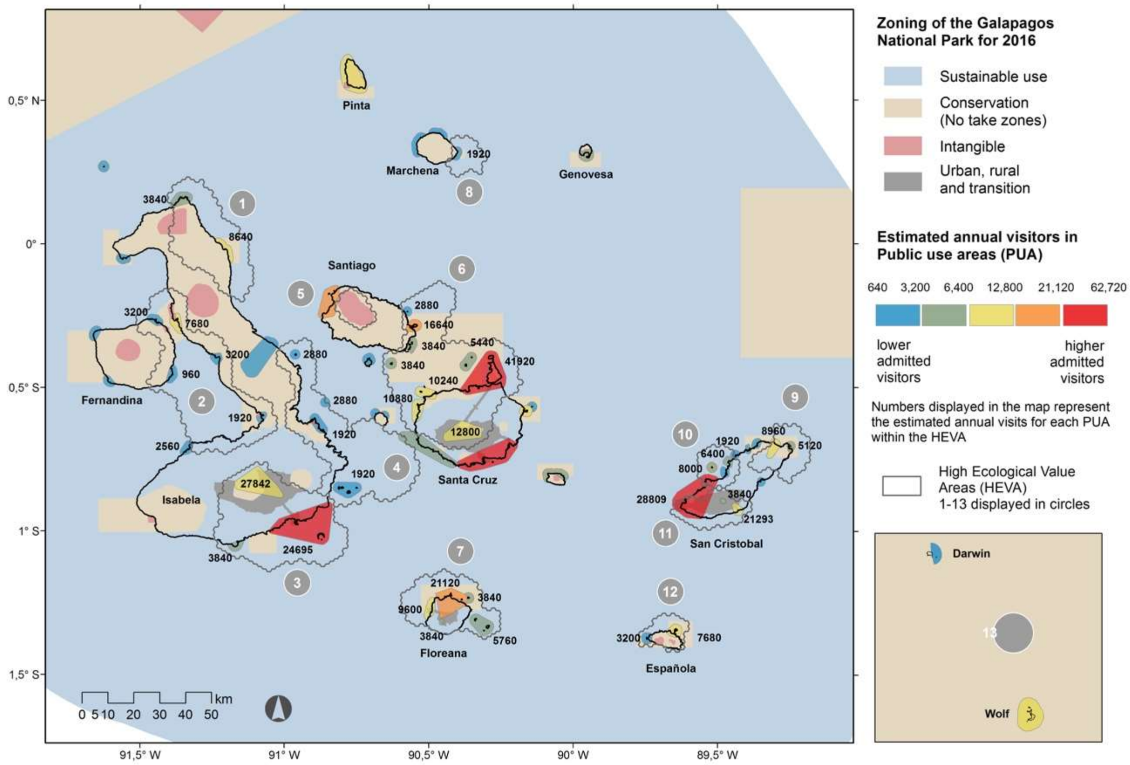

Figure S13. Map of the Galapagos Islands showing the number of tourists at each public use area (PUA) designated for tourism and the new zoning of the Galapagos National Park and Galapagos Marine Reserve approved in March 2016 (DPNG, 2016). Priority HEVA: (1) Corridor Wolf Volcano, Punta Albermarle and Cape Marshall, (2) The Bolivar Channel and Elizabeth South, (3) Corridor Sierra Negra Volcano Isabela South, (4) Corridor Cartago Bay – San Luis seabed, (5) Santiago highland, (6) Conservation area Santiago-Santa Cruz, (7) Floreana and islets, 8) Marchena coral remnants, (9) Corridor la Galapaguera – Punta Pitt, (10) León Dormido (Kicker's rock), (11) Corridor El Junco and southern seabeds, (12) Española and Gardner islands, and (13) Darwin and Wolf islands.