Paleogeography of the Galápagos Islands and Biogeographical Implications

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Abstract

Owing to both their historical and modern importance in evolutionary and biogeographic studies, the paleogeography of the Galápagos is examined in light of a modern understanding of eustatic sea level changes, volcanic growth, age determinations, and volcano subsidence. New age determinations and bathymetric data are reported and used to assess the Holocene paleogeography of the archipelago. The theories of hotspot tectonics and volcanic-island subsidence are also applied to estimate the distribution of islands for the past 5 million years. The ages of emergence of the Galápagos Islands decrease to the west and are consistent with the Nazca Plate moving 59 km/M.y. to the east. The islands subside proportionately to the square root of their age, leading to their eventual drowning. Sea level today is 125 m higher than it was just 20,000 years ago, leading to the drowning of many islets and several major islands, and the isolation of several of the major islands which had been interconnected. The geographic template for studies of the organismal colonization and dispersal within the archipelago has changed drastically over the past 20,000 years. The integrated area of the Galápagos Islands was much greater during the Pleistocene than it is today. Although many more islets existed, some of the major islands were connected. Over the past 5 million years, at least 7 major islands have existed within the archipelago, and the cumulative area of the islands has been at least 50% of that today. The use of the present-day map of the Galápagos to deduce biological processes that take 10^5 to 10^6 y will yield incorrect results. Island age is found to be an important control on the number of native and unique endemic species on the islands, although it is subordinate to island area. These relationships indicate that the age effect is most important shortly after emergence of an island. This new paleogeographic model highlights the importance of vicariance in the archipelago's biogeography.

Keywords: Island biogeography, island biodiversity, paleogeography, island ages, island colonization, island subsidence, vicariance

The Galápagos archipelago has served as a testing ground for evolutionary theory since Darwin's visit in 1835, owing to the islands' rich endemic biota. Recent studies have quantified evolutionary rates and colonization patterns on the basis of genetic studies (e.g., Wyles & Sarich, 1983; Rassman, 1997; Caccone *et al*., 2002; Luciano *et al*., 2003; Parent & Crespi, 2006; Grant & Grant, 2007; Jordan & Snell, 2008). An important issue for such studies is the dynamic nature of the geography in the Galápagos over evolutionary timescales, owing to relatively rapid geologic processes of plate tectonics, volcanism, subsidence and sea level change. Although we are sure that the Galápagos Islands are a dynamic geologic environment on evolutionary timeframes, the details of the changes in island paleogeography are uncertain. This paper presents our best estimates for the patterns of emergence of the Galápagos Islands and updates the previous reconstruction of Geist (1996).

Patterns of island emergence within archipelagos result from the interaction of island-building geological processes, erosion, and fluctuations in sea level. In the Galápagos, the primary island-building processes are related to volcanism and, rarely, uplifts caused by tectonic faulting. Other processes, such as the accumulation of corals, have not occurred in this region. To evaluate the paleogeography of the archipelago, we have combined analyses of the ages of islands and seamounts with the spatial patterns of topographic relief. The age of the islands, spatial patterns of seafloor depth, and estimates of fluctuations in sea level are combined to provide a geographic history of the archipelago.

The Galápagos are a chain of volcanic hotspot islands, that is they result from a melting anomaly in the Earth's upper mantle, one that is not directly tied to plate tectonics. The mantle plume which causes the hotspot has been imaged by seismic tomography, both on local (Villagomez *et al*., 2007) and global scales (Montelli *et al*., 2004), and it extends to the lower part of the mantle's transition zone at 700 km depth (Hooft *et al*., 2003). All of the Galápagos Islands currently lie on the Nazca Plate, but the archipelago lies just south of the Galápagos Spreading Center, which forms the boundary between the Cocos and Nazca plates (Fig. 1).

The main part of the Galápagos archipelago lies in shallow water created by the broad Galápagos platform, which formed by volcanism resulting from the hotspot (Fig. 1; Geist *et al*., 2008). The Carnegie Ridge lies to the east of the Galápagos platform and extends to the South American continent. Most historical eruptions have occurred in the western part of the archipelago, on Islas Fernandina and Isabela, whereas the major central and eastern islands are morphologically older, consistent with the eastward motion of the Nazca Plate. The northern islands (Islas Genovesa, Marchena, Pinta, Wolf, and Darwin) can be thought of as a separate volcanic province, because they lie off of the main Galápagos platform. They are thought to have originated from hotspot-derived plume material flowing within the mantle towards the Galápagos Spreading Center (Harpp *et al*., 2002; Harpp & Geist, 2002). They are not typical hotspot islands, but instead owe their origin to the proximity of the hotspot to the Galápagos Spreading Center.

Estimating the Age of Emergence

With the exception of a few minor islets (most notably Islotes Plazas, North Seymour, and Mosquera) and Isla Baltra, all of the Galápagos Islands formed by volcanic construction, whereby the islands have emerged and grown by the superposition of lava flows and volcanic ash on top of preexisting volcanic rocks. Thus, the most straightforward way to determine the age of emergence of an island is to measure the age of its oldest subaerial lava. This problem is far from straightforward, however, because all the oldest subaerially erupted lavas are covered by lavas produced during subsequent eruptions (most of the minor islands are monogenetic, hence do not have this problem). Because of the arid climate and resulting lack of fluvial erosion throughout most of the archipelago, the older, underlying lavas are never exposed in valleys. Thus, only the youngest subaerial volcanic rocks are exposed, and they provide a *minimum* age of emergence of an island. Furthermore, as discussed below, determining the ages of Galápagos lavas is problematic.

Plate Tectonic Estimates

A simple method of estimating the ages of the individual islands is provided by hotspot theory, which supposes that islands form by the passage of a plate over a fixed source of magma, the "hotspot" (Wilson, 1963). Age of emergence can then be calculated by dividing the distance between an old island and the present location of the hotspot by the velocity of the Nazca plate. The technique requires that the velocity of the Nazca plate, relative to the "fixed" Galápagos hotspot, is accurately known, and it assumes that each island emerged in the vicinity of the hotspot, which is currently located between Fernandina and Cerro Azul volcanoes (Hooft *et al*., 2003). Because there are so few island chains on the Nazca plate, and the plate subducts beneath the Andes while relatively young, the velocity of the Nazca plate relative to the Galápagos hotspot is poorly known. Also, volcanism around the Galápagos is very widely dispersed, owing to interaction of the hotspot with the Galápagos Spreading Center, so the islands and submarine volcanoes do not form a single geographic trace or age progression (O'Connor *et al*., 2007). Unlike velocities relative to the hotspots, velocities of plates relative to one another are well known from measurements of the seafloor's paleomagnetism, the orientation of transform faults, seismicity, and direct measurement by GPS.

Gripp & Gordon (2002) estimated plate velocities relative to hotspots using ages and trends of Pacific hotspot-derived volcanoes and the well-constrained relative plate motions. This inversion predicts 22 km/My of motion of the Nazca plate in the hotspot reference frame in the Galápagos region (Fig. 3). However, recent studies have shown that the Hawaiian hotspot has migrated relative to the earth's magnetic poles, which calls into question whether hotspots move relative to each other (Tarduno *et al*., 2003). Other studies have demonstrated motion of the Pacific "family" of hotspots relative to the Atlantic-Indian family (Molnar & Stock, 1987). If the Pacific hotspots do not provide a fixed reference frame, then the velocity of the Nazca Plate over the Galápagos hotspot may be substantially different from 22 km/My. For example, another set of hotspot data yields an estimated velocity of 52 km/My. (Wang & Wang, 2006), and O'Connor *et al.* (2007) have proposed a progression rate of 59 km/My on the basis of age determinations from the Carnegie Ridge. The Connor *et al*. (2007) velocity is within uncertainty of the current velocity of the Galápagos Islands toward South America (as measured by GPS; Angermann *et al*., 1999) and is most consistent with global geodynamic constraints (Schellart *et al*., 2008). Thus, we adopt the value of 59 km/My for plate tectonic estimates of island age.

Direct Age Measurements of Lavas

The standard method of determining the ages of lavas is the potassium-argon method (or its variant, $^{39}Ar/^{40}Ar$, where ^{39}Ar is a product of ^{40}K in irradiated samples; MacDougall & Harrison, 1988). Unfortunately, Galápagos magmas have very low potassium contents, so ages younger than one million years are difficult to determine, and this is a critical age span for the western half of the archipelago. More problematically, the rocks which record emergence of an island are not exposed, and volcanism can last for > two million years after emergence on some islands (e.g. Geist *et al*., 1986).

^{14}C data are sparse from the Galápagos. In our experience, organic carbon is rarely preserved beneath lava flows, owing to the slow soil development on the active volcanoes. Most of the existing ^{14}C age determinations are from bones found in caves (Steadman *et al*., 1991) and lake sediments (Colinvaux, 1972; Riedinger et al., 2002)).

The earth's magnetic polarity reversed 779,000 ± 2000 years ago (Singer & Pringle, 1996), and the polarity is robustly recorded in basaltic lava flows as they cool. Paleomagnetic measurements of lavas have been made on all of the major islands. All of the lava flows measured from Isabela, Fernandina, Genovesa, Pinta, Marchena, and Santiago are normally polarized (Cox & Dalrymple, 1966; Cox, 1971; Swanson *et al*., 1974; Cullen *et al*., 1987; Vicenzi *et al*., 1990; Geist *et al*., 1994; Reynolds *et al*., 1996;

Naumann & Geist, 2000; Geist *et al*., 2002; Harpp *et al*., 2002; Geist *et al*., 2005a). Santa Cruz, Baltra, Floreana, Espanola, Santa Fe, and San Cristobal all have reversely polarized lavas (Bow, 1979; Geist *et al*., 1985; Geist *et al*., 1986; Bow & Geist, 1992).

Another age-determination technique uses cosmic-ray produced ^{3}He to determine the age of Galápagos lavas (Kurz & Geist, 1999). These "exposure" ages determine time that the surface of a lava flow (specifically the olivine crystals, which retain the cosmogenic ^{3}He) has been exposed to high-energy cosmic rays (Kurz, 1986a,b; Kurz *et al*., 1990, 1994). The method assumes that lava flow surfaces have been preserved and exposed since eruption and production rates have been consistent over time. Thus, they provide minimum ages if there has been any weathering, erosion, or shielding. Samples from the Galápagos have been subjected to numerous relative age tests and reproducibility (different samples from the same flow) and have been shown to be very reliable (Kurz & Geist, 1999). In terms of island emergence, the technique has been proven most useful for small islands, most of which grow by a single eruption, and for constraining eruption rates on the larger volcanoes.

The oldest rocks exposed on Islas Isabela and Fernandina are barely old enough for K-Ar dating, and only the young surficial lavas can be dated by the ^{3}He exposure method. These volcanoes erupt frequently enough that a combination of the historical record, exposure ages, and mapping of single eruptive units (for volume estimation) permit calculation of their eruption rates. The age of emergence can then be estimated by dividing the volume of the volcano by the volumetric eruption rates, by extrapolating constant eruption rates back in time (Naumann & Geist, 2000; Kurz *et al*., 2005).

Estimating Spatial Patterns of Seafloor Depth

The bathymetry of the Galápagos Archipelago was digitized using hydrographic/ bathymetric maps from the United States Defense Mapping Agency and el Instituto Oceanográphico de la Armada (Ecuador). Eight DMA maps and twenty-four INOCAR maps were digitized and geo-referenced in ArcView 3.2a (ESRI, Inc., Redlands, Ca.). Fine-scale bathymetry from locations of interest was measured in 1999 by deploying a digital depth finder from either a small inflatable raft or R/V Prima and traversing these areas. The sonar was interfaced with a Garmin 235 GPS, and data were downloaded every two seconds to a portable computer. The combined data set comprises 104,231 bathymetric data points. Grid construction uses the Inverse Distance Weighted (IDW) method, with 12 nearest neighbors and no barriers.

Analytical Methods

All previously published K-Ar, ^{14}C, and ^{3}He exposure age determinations from the Galápagos Islands and surrounding seamounts have been compiled in a database (Table S1). Each age determination was critically assessed on the basis of relative ages from geologic relationships, the amount of radiogenic argon, and the spectra of ages determined by incremental heating.

Six new samples of basalt from the Galápagos Islands were analyzed for argon isotopes in the laboratory of Dr. Robert Duncan at Oregon State University using methods reported by Sinton *et al*. (1996). The samples were irradiated at the Oregon State University TRIGA Reactor (OSTR) facility. Argon extraction was done under vacuum after the system was baked out to remove extraneous gases. During analysis, samples were heated in molybdenum crucibles by radio frequency induction in a temperature-controlled furnace. Samples were first preheated to 450°C to release atmospheric argon. Gas produced in this heating step was not analyzed. The samples were then heated in incremental steps of 200°C from 600°C to 1400°C. An Associated Electrical Industries (AEI) MS-10S mass spectrometer was used to measure relative abundances of ^{40}Ar, ^{39}Ar, ^{37}Ar, and ^{36}Ar. Both isochron and plateau ages were calculated (Table 2).

Seven samples for helium isotope analyses were collected from the upper 4 cm of lavas whose primary flow surfaces are well exposed (Table 2). Olivine or pyroxene phenocrysts were separated from coarsely crushed rock. Each mineral separate was crushed in vacuum to measure the inherited magmatic helium isotopic composition. The crushed samples were then fused in an ultra-high vacuum resistance furnace to release the cosmogenic helium. Data were collected by mass spectrometry for both the crushing and fusion steps according to methods reported by Kurz (1986a,b).

Olivine from G99-5 (Islote Sombrero Chino) was split into two samples, one pure and the other "dirty", and analyzed separately, in order to evaluate the importance of clean mineral separates. Phenocrysts in the "dirty" sample (G99-5D) contain abundant melt inclusions, were encrusted with lithic groundmass, and displayed red to orange discoloration. The results are indistinguishable, suggesting that this is not an important factor. Sample G99-11, from Roca Beagle Sur, was also analyzed twice: once using olivine phenocrysts (G99-11(ol)), and once with clinopyroxene phenocrysts (G99-11(cpx)), and are also within analytical error. Exposure ages were calculated using a sea level, high latitude production rate of 120 atoms/gram/year and the scaling factors of Lal (1991), yielding a sea level production rate at the equatorial Galápagos of 72 atoms/gram/year. This production rate is used for consistency with earlier studies (Kurz and Geist, 1999). The uncertainties given in Table 2 are calculated as the quadrature sum of analytical uncertainties and do not reflect uncertainties in this absolute production rate.

Results

The critical data for biogeographic and historical studies are the age of emergence of an island and its history of isolation. Because each island presents its own unique issues, they are discussed individually in Appendix I. Islets that are satellites to the major islands are discussed with the major islands. Uncertainty of emergence ages is difficult to assess quantitatively, because there no direct rock record of an island's emergence, so our best estimates for realistic maximum and minimum ages of emergence are reported (Table 2).

Long-Term Subsidence of the Galápagos Islands

Islands subside as they are carried away from a hotspot, because the Earth's lithospheric plates cool and contract as they move away from the hot melting anomaly (Detrick & Crough, 1978). There are complicating effects to a simple model of lithospheric subsidence, particularly due to flexural loading of the lithosphere, which creates a "moat" surrounding the volcanic load and a flexural arch outboard of the moat (e.g. Watts, 2001). The Galápagos moat and bulge are best developed to the southwest of Isabela, owing to the massive load of the largest island in the archipelago (Fig. 1). The moat is approximately 300 m deeper than ambient depth in this area (although it is partly filled in by sediment and thus actually greater in depth), and the bulge is about 200 m shallower. Thus, one would predict that volcanoes might be 300 m "too deep" if they were overriding the moat ~ 40 km downstream of Isabela and 200 m "too shallow" as they override the arch ~ 50 km further downstream. Feighner & Richards (1995), however, showed that the central and eastern islands are not flexurally supported, nor is the northern part of the archipelago. Thus, we do not assess the effect of flexural topography in the central archipelago.

Thermal subsidence of the oceanic lithosphere as it is carried away from a hotspot is fairly well understood: the depth increases proportionally to the square root of time. This relationship has been shown to be true for a number of hotspot swells (the broad anomalously shallow seafloor around the leading edge of hotspots; Detrick & Crough, 1978) and island chains (Caplan-Auerbach *et al*., 2000). In fact, the elevation of the largest Galápagos volcanoes along the central axis (Islas Fernandina, Alcedo, Santa Cruz, Santa Fe, and San Cristobal), along with the largest seamounts to the east of the archipelago, form an excellent fit to the curve:

$$z = -1.13 * \sqrt{t} + 1979 \qquad (1)$$

(Fig. 4) where z is height in meters and t is the oldest reliable age determined from each volcano (in years; seamount data from Sinton *et al*., 1996). This equates to a subsidence rate of:

$$\frac{dz}{dt} = -0.57 * t^{-\frac{1}{2}} \qquad (2)$$

so a zero-age volcano subsides about a half meter per year, and a million year old volcano subsides about a half millimeter per year.

The thermal contraction model assumes that when the volcanoes start subsiding, they have the same elevation (1979 m), i.e. that the Galápagos hotspot has been producing magma at equivalent rates for the past several million years. We also ignore erosion and sediment cover.

The entire Galápagos platform is subsiding at about the same rate as the volcanoes. We assume a plate velocity of 59 km/M.y. and estimate the average elevation of the crest of the platform by constructing topographic cross sections, avoiding the islands and seamounts, every 1° of longitude. Sediment accumulation is more important on the flat platform surface than on sloped seamounts, and we assume a sedimentation rate of 7 cm/K.y. (Lea et al., 2006). There is an excellent linear relationship (R^2 = 0.89) between the square root of age and elevation of the platform, by:

$$z = -1.14 * \sqrt{t} + 933 \qquad (3)$$

The correspondence between this subsidence rate (-1.14 $m/y^{0.5}$) and that of the volcanoes' summits (-1.13 $m/y^{0.5}$ from equation 1) indicates a region-wide contraction of the lithosphere.

The Pleistocene Galápagos

Over the past 3 million years, which is nearly the entire emergent history of the present Galápagos Islands, there have been approximately 36 glacial advances separated by interglacials (reviewed by Huybers, 2007). When polar ice caps expand, sea level drops: during the last glacial maximum about 19,000 years ago, eustatic sea level was 121 ± 5 m lower than it is today (Fairbanks, 1989; Lambeck & Chappell, 2001).

There is evidence that during the last interglacial, sea level was 6 to 9 m higher than it is today. Also, during an interglacial at 420 ka, sea level may have been as much as 21 m higher than today (Hearty *et al.*, 2007). Both of these rises in sea level would have flooded most of the minor islets, but all of the major islands would have remained emergent, although reduced in size.

If we take Santa Cruz to be 2.3 Ma, it has subsided 7 m due to lithospheric contraction since the last glacial maximum, and the older islands to the east even less than this. Islands to the west, which likely emerged ~ 1 Ma, have subsided about 10 m in the past 20,000 years. Figure 5 shows a paleogeographic map of the Galápagos as they were 20,000 years ago, taking into account eustatic sea level change and applying the detailed bathymetric data collected in this study.

The Pleistocene Galápagos were very different than those today (Fig. 5). There were many more islands, the cumulative subaerial area of the archipelago was greater, and many of the islands were connected by land bridges. At least four major islands and dozens of islets have drowned in the past 20,000 years, presumably accompanied by extinction of unique endemic organisms. The greatest uncertainty of the map we present is the proposed connection of Isabela to both Fernandina and Santa Cruz. Both of these are uncertain because large volumes of lava have been erupted in these areas over the past 20,000 years. It is certain, however, that even if the islands never coalesced, they were much closer to one another.

There were more islets between Islas Santiago and Santa Cruz during the Pleistocene than currently exist (Fig. 6). We interpret these bathymetric highs as young satellite volcanoes, related to volcanic activity on the east side of Santiago. Daphne Major may have been connected to Santa Cruz by a narrow isthmus, but the bathymetry in this area is insufficient. Also, the satellite islands around Santa Cruz, including North Seymour, Baltra, the Guy Fawkes, Venecia, and Eden were all part of Santa Cruz (Fig. 6). A similar situation existed at Floreana (Fig. 7): Caldwell and Enderby were connected to the main island, while Gardner and Watson formed a single isolated islet.

The Proto-Galápagos

Grant & Grant (1996) have provided a paleogeography of the Galápagos using the drowned islands of Christie *et al*. (1992), but otherwise not accounting for subsidence. Beyond the most recent glacial period, the paleogeography of the Galápagos becomes more uncertain. We present a reconstruction that is certainly incorrect in its details but presents a plausible paleogeography for the Galápagos for the past 5 million years.

For the reconstructions (Fig. 8), we first assume that the hotspot is located in the vicinity of Fernandina, as discussed above. Second, we assume that the summits of the volcanoes are subsiding according to equation 1. Third, we assume that the Galápagos platform offshore the islands subsides at half this rate. Fourth, we use a constant plate velocity of 59 km/My. Fifth, any volcano with dated activity at any time period is indicated as such, and we assume that volcanoes located within 50 km of the western margin of the paleoarchipelago are active. Sixth, the paleoshorelines are assumed to follow embayments and ridges, keeping the shorelines smooth.

At 1 Ma, Santiago, Rabida, and Pinzon volcanoes were newly emergent, perhaps in a geometry comparable to Wolf, Darwin, and Alcedo volcanoes today (Fig. 8). Floreana and Santa Cruz were in waning activity. Several islands existed that are now drowned, including Wittmer seamount to the southeast of Floreana (Figs. 1, 7). Although we have sketched a single mega-island in the west at 1 Ma (Fig. 8), it is equally likely that the volcanoes were separated by narrow passages of water. At least 9 major islands existed.

At 2 Ma, the big western island was an amalgamation of Santa Cruz and Floreana, which were in peak activity, whereas San Cristobal was in a waning phase (but these lavas completely covered any older rocks). We estimate that 11 major islands existed. At 3 Ma, we speculate that there was a western island made of four active volcanoes, but 9 major islands were emergent, of which only San Cristobal and Espanola still exist. The predicted subsidence in this case has been verified: two prominent seamounts to the north and northeast of San Cristobal have subaerial lavas (Christie *et al*., 1992). One of these (PL11) was dredged from 1309 to 702 m depth, indicating substantial subsidence.

At 5 Ma, we estimate that there were seven islands, none of which exist anymore, because they have subsided beneath sea level. Lavas from several seamounts have textures indicative of subaerial weathering (Christie *et al*., 1992) and ages slightly greater than 5 Ma, confirming the subsidence model. Volcanic activity was focused in the southern part of the archipelago, in a region similar to today's setting of Cerro Azul and Sierra Negra (Fig. 8).

An additional complication is that at this time, the Galápagos Spreading Center was closer to the hotspot than it is today (Wilson & Hey, 1995), which could have caused many permutations to these reconstructions, but in mostly unpredictable ways. In fact, the Galápagos Spreading Center may have directly overlain the hotspot, as has been hypothesized by Harpp & White (2001) on the basis of lava compositions. Unfortunately, there is nothing in the geologic record that permits evaluation of past motion between the spreading center and the hotspot. When the ridge and hotspot were closer, total output of magma from the Galápagos hotspot might have been greater, because of the higher heat flow in the mantle close to the ridge, and the fact that the lithosphere is thinner near the ridge, causing greater extents of melting of the plume. But at the same time, half of the archipelago would have lain on the Cocos Plate. We predict that there are drowned islands starting at about 5 Ma on the Cocos Plate, too, but as of yet, there is no direct evidence of this.

Implications for Biogeography

A general dynamic model (GDM) of island biogeography, which relates the species richness of an island to its age, has been proposed (Whittaker et al. 2008). The findings of our work support several aspects of the GDM as it applies to the Galápagos, but we also propose an important modification. The GDM (Whittaker et al., 2008) predicts that a number of measures of biological diversity are a function of both island area and island age by the equation (referred to as ATT^2):

$$Diversity = a + b(Time) + c(Time)^2 + d(\log(Area))$$

Diversity is measured by several parameters, including species richness (SR), the number of single-island endemic species (nSIE), and the proportion of single-island endemics (pSIE).

We test the GDM with a Galápagos data set, which includes the ages reported herein and island areas (Snell et al. 1996). Our approach is different from that of Whittaker et al. (2008), because we have also included small islands (< 1000 ha), whose ages are assessed by both direct dating and geologic relationships to nearby large islands. Our species-richness and single-island endemic data comprise native vertebrate and plant species from Tye et al. (2002), who exclude introduced organisms and invertebrates.

Multiple regression shows that the ATT^2 relationship does not apply to either species richness or local speciation in the Galápagos: island area accounts for most of the statistical significance (Table 3). The discrepancy between our findings and those of Whittaker et al. (2008) are partly attributable to different data sets, most importantly their exclusion of small (<1000 ha) islands. Whittaker et al. (2008) also used the ages reported in Geist (1996), which are less accurate than the emergence ages used here, but this is not a significant factor. Also, they analyzed insects, small-order insects, and plants separately, instead of a single index of species richness, but our results are confirmed when we analyze plant and vertebrates separately.

We propose a modification to the GDM. Whitakker et al. (2008) recognized the possibility that the age effect is most important early in the history of an island, as habitat (principally soil formation from fresh lava) develops and colonization takes place. Our data support the hypothesis that islands reach their maximum size in a geologic instant, and colonization occurs at decelerating rates but continues through much of the life of an island. According to this hypothesis:

$$\log(SR) = a + b * \log(Area) + c * \log(Time)$$

Multiple regression of this equation to the Galápagos data set yields greater statistical significance than the ATT^2 model (Table 3), with P values for both independent variables << 0.001 and an adjusted $r^2 = 0.84$. The implication, of course, is that the increase in species richness of an island decelerates with time. Although the GDM pattern suggests that species richness might decrease as an island gets very old, that effect may be entirely accounted for by the decrease in area of an island as it subsides.

Part of the GDM predicts that the rate of speciation changes with time, and an implication of ATT^2 is that there is a maximum speciation rate in the mid-life of an island. Application of this hypothesis is problematic using nSIE and pSIE data in the Galápagos, because the main area effect for SIE is a threshold in size: so far as is known, no Galápagos island smaller than 499 ha includes a unique endemic plant or vertebrate species and most islands with SIE's are >800 ha. The ATT^2 regression is, in fact, worse than that for area alone (Table 3). Island age does appear to play a factor, however, when it is weighted to the early stages of emergence and growth. Regression of the relationship:

$$nSEI = a + b * \log(Area) + c * \log(Time)$$

has a significantly higher adjusted r^2 than either log(Area) alone or ATT^2 (0.63 vs. 0.50 and 0.48). Likewise, there is slight better fit in regressions using the term pSEI and island age, although the small differences are probably not meaningful.

We conclude that island age plays an important role in the Galápagos for both island biodiversity and speciation. The logarithmic relationship indicates that the age effect is most important when the island is young and growing. Species richness may also decay as the island subsides, but this is mostly because the island's area decreases.

Implications for Phylogeography

As recently as 1985, evolution of the Galápagos biota has been proposed as being limited to the past 4 to 5 million years, an estimated age of Espanola island (Hickman and Lipps, 1985), despite the well-known tendency of oceanic islands to subside below sea level over time. The discovery by Christie et al. (1992) of drowned islands on the

Carnegie Ridge proved that a set of proto-Galápagos Islands existed at least 9 million, and perhaps as long as 14 million years ago (Werner et al., 1999). However, an unanswered question remains: do we know for certain that Galápagos Islands have existed continuously for this entire interval? Or was there a period during which all of the volcanoes were submerged, requiring terrestrial evolution to restart when younger islands emerged? The largest gap between reliably dated volcanoes along the central axis of the archipelago is between 2.6 Ma (San Cristobal) and 5.3 Ma (seamount at 86° 07'; Fig. 4). Equation 1 predicts that the seamount stood 189 m above sea level when San Cristobal emerged, thus this model predicts that islands formed temporally continuous stepping stones. In fact, our more regional reconstruction suggests that the cumulative island area was at least half that of the present archipelago at 5 Ma, with at least 7 major islands. We therefore conclude that the proto-Galápagos Islands were originally colonized at least 9 Ma, and terrestrial evolution has proceeded since at least that time.

This conclusion is consistent with estimates of the divergence of island lineages from mainland ancestors on the basis of molecular data. For example, divergence between the Galápagos tortoise and the mainland taxon *G. chilensis* is estimated to be between 6 and 12 Ma (Caccone et al., 2002). Divergence between land and marine iguanas is believed to be < 10 Ma (Rassmann, 1997), and that between *Galapaganus* beetles and mainland relatives > 7 Ma (Sequeira et al., 2008). Even within island lineages there has been divergence as long ago as 5.7 Ma when *Rosada* (pink) land iguanas diverged from the more typical yellow form (Gentile et al. 2009).

Interestingly, no island lineages are proposed to have diverged from continental ancestors or nearest relatives > 12 Ma (Parent et al., 2008). It is notable that the only seamount that falls significantly below our subsidence model is the oldest one, which is 9 Ma (Fig. 4). We speculate that the initial elevation of Galápagos volcanoes was significantly lower than 1868 m prior to 9 Ma, and a continuous chain of volcanoes did not emerge above sea level much before 9 Ma. Prior to ~ 8 Ma, the archipelago was in a different tectonic setting: it was a ridge-centered hotspot (Wilson and Hey, 1995; Sallares and Charvis, 2003), and before that time, the hotspot was on the Cocos Plate. Although there is no direct geologic evidence bearing directly on this issue, it is possible that while the hotspot underlay the ridge or the Cocos Plate, there was a time when no volcanoes were emergent. Detailed marine surveys and drilling of 9 to 14 Ma seamounts on both the Cocos and Carnegie Ridges would be required to test this hypothesis.

The Progression Rule

The progression rule (Wagner and Funk, 1995) predicts that biotic lineages should progress with age of the islands, in the Galápagos from east to west. The phylogenetic data from the Galápagos are inconsistent with respect to the progression rule, however. Although tortoises follow a pattern of east-to-west dispersal (Caccone et al., 2002), Darwin's finches do not (Grant and Grant, 2007), nor do flightless weevils (Sequeira et al., 2008). Most strikingly, a recently discovered terrestrial iguana species is basal with respect to the other iguanas of the archipelago (Gentile et al., 2009), yet it inhabits the second youngest major island in the archipelago (Table 2).

Because the Galápagos Islands are widespread in two dimensions, and many islands are approximately equidistant to continental sources, younger islands are as likely to be colonized by continental organisms as older islands, and organisms do not simply migrate along a linear path from older to younger islands. Also, the phylogenetic data indicate that organisms do not simply migrate to nearest-neighbor (next youngest) islands. Phylogenetic interpretations from tortoises suggest, for example, that the Pinta tortoise is most closely related to that of Espanola (Caccone et al., 1999), instead of a nearer or slightly older island. It is thought that Darwin's finches originally colonized the islands 2 to 3 Ma (Grant and Grant, 2007), when 9 to 11 major islands existed, any one of which could have been colonized, and from which the original populations may have radiated; most of those islands no longer exist, thus determining the island-by-island progression over this time frame is virtually impossible.

Our paleogeographic model predicts that at least 7 major islands have existed at any one time for at least the past 5 million years. Thus, at 5 Ma, there are nearly 5000 different sequences by which all of the islands would become sequentially colonized from an original colony on just one island. When a new island emerged, any of the older islands might serve as a colonizing source, and the problem of evolutionary sequence becomes increasingly complex. Our view is that in areas like the Galápagos, where the islands do not form a linear chain, colonization and dispersal are not so much a series of stepping stones as they are a game of checkers on a board whose geometry changes every 100,000 years.

Dispersal and Vicariance

A central question of biogeographical theory debates the relative influence of vicariant events (the spatial or ecological fragmentation of a population) and dispersal (the colonization of new habitat) in the distribution and evolution of biological diversity (Escudero et al 2009, Hickerson & Meyer 2008, Cowie & Holland 2006, de Queiroz 2005). We use Galápagos Lava Lizards (*Microlophus spp*.), one of the most widely distributed vertebrates in the archipelago (Stone et al 2002), to examine the biological impacts of our paleogeographical model on that debate.

Previous analyses of the evolution of *Microlophus* species conclude that dispersal to newly emergent islands leads to the genetic divergence required for speciation (Benavides et al. 2009, 2007; Kizirian et al. 2004; Heise 1998; Lopez et al. 1992; Wright 1983). Geographical and ecological vicariance has been limited to explanations of intrapopulation and intraspecific variation (Jordan & Snell 2008; 2002; Jordan et al. 2008, 2005; Miles et al. 2001, Snell et al. 1988), but the results presented here suggest that vicariance may also be important for speciation in the island setting.

There is no question that the two colonizations of the Galápagos by *Microlophus* several million years ago occurred by dispersal from South America. Once in Galápagos, however, lava lizards radiated into 9 species within two lineages (Benavides et al. 2009). We interpret the divergence within the eastern lineage of *M. bivitatu*s (San Cristobal) and *M. habeli* (Marchena) as attributable to dispersal, as our paleogeographic model shows no contiguous terrestrial surface between the regions of San Cristobal and Marchena (Figure 8). Likewise, within the western lineage, the split between *M. delanonis* (Espanola) and the remaining species requires a dispersal event from the region of Espanola to the central Galápagos, as no contiguous terrestrial surface has ever connected these areas, and the divergence of *M. pacificus* (Pinta) requires dispersal for the same reason. In contrast, the possible existence of a large central island covering Floreana, Santa Cruz, Rabida, Santiago, Pinzon, and possibly Santa Fe approximately 1 million years ago suggests that the remaining 5 species (*M. albemarlensis* [Fernandina & Isabela], *M. grayii* [Floreana], *M. duncanensis* [Pinzon], *M. jacobi* [Santiago], and *M. indefatigabilis* [Santa Cruz &

Santa Fe]) speciated in response to vicariant events that resulted in population fragmentation and disruption of gene flow. Further vicariant fragmentation has led to significant disruption of gene flow and caused molecular evolution within the *M. indefatigabilis* complex during the Pleistocene (Jordan & Snell 2008), and we conclude that process accounts for the evolution of half of the species diversity within Galápagos lava lizards.

Conclusions

The minimum age of the emergence of an island can be estimated in two ways, depending on the age of the island (Table 2). For young islands, the best approach is to measure the modern growth rate of the island and extrapolate that back in time for the subaerial volume of the island. For islands older than about 1 Ma, the minimum emergence age is taken as the oldest reliable age determination from that island. The maximum estimate of emergence age is on the basis of plate tectonic theory (Table 1).

The Pleistocene Galápagos had a much greater area than the present islands. Land bridges existed between a few of the major islands, and many more minor islands and islets were exposed. We hypothesize that between 1 and 5 Ma, at least 19 major Galápagos Islands formerly existed but are currently submerged (Fig. 8). These are in addition to the 13 that exist today. Owing to the competition between subsidence and island growth, the subset of islands existing at any given time is complex, but the reconstructions suggest that at least seven major islands have existed since 5 Ma, permitting the opportunity for allopatric speciation of terrestrial organisms. For any model for dispersal, colonization, speciation, and radiation that involves island geography more that 20,000 years ago, the current map of the Galápagos Islands is completely irrelevant.

The phylogeography of the Galápagos is complicated by this dynamically changing template. Nearly any of the islands can be colonized from continental or other island sources, and the broad array of islands means that the sequence of dispersal has many possible geometries. The age of emergence of an island is a second-order control on the species richness compared to island area. Island age plays a more important role early in its history, presumably because of habitat development and open ecological niches. Partial submergence of large islands suggests that vicariance may be a more important mechanism for island biogeography than previously thought.

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Appendix I: Emergence Ages of the Individual Galápagos Islands

Isla Fernandina

Isla Fernandina is the most active volcano in the archipelago (Simkin & Siebert, 1991), it most closely overlies the core of the Galápagos hotspot (Hooft *et al.*, 2003; Villagomez *et al.*, 2007), and it is the westernmost volcano. Thus, Fernandina is predicted to be youngest major island in the archipelago. All exposed rocks on Fernandina are too young to perform age determinations by the K-Ar method.

Kurz *et al.* (2005) have determined ^{3}He exposure ages for many of the exposed lava flows on Isla Fernandina, and using the volumes of the lava flows, estimate an eruption rate of 5 x 10^6 m^3/y for the past 1000 years. If this rate has been steady (an extrapolation which may be incorrect), then the present subaerial volume of Fernandina (175 km^3) has been constructed in the past 35,000 years.

In addition to the assumption of constant growth rate, another complication is that when lava is piled on a volcano, the entire crust sinks into the mantle by the action of isostasy. For simple Airy compensation (Watts, 2001), if the crust is built entirely from above, then the volcano subsides ~ 4 m for every 1 m of growth. Isostatic response occurs over a time scale of thousands of years (Watts, 2001), thus it is likely to have an impact on Fernandina's growth. The morphology of the upper part of Fernandina's west flank as revealed in submarine sonar images (Fig. 2) is interpreted to result from subsidence of the island (Geist *et al.*, 2006). Thus, Kurz *et al.*'s (2005) growth rate calculation represents a minimum emergence age, because some of the eruptive growth of the volcano is taken up by isostatic subsidence.

The best evidence for subsidence of an island is a drowned shoreline, but none are known within the Galåpagos. In the absence of drowned shorelines whose ages are known, the amount of subsidence for every increment of growth is poorly constrained. The western volcanoes are not in perfect isostatic equilibrium, because they are flexurally supported by the Nazca plate (Feighner & Richards, 1995). Also, the weight of the erupted rocks can be partly compensated for by low-density intrusions, which build the crust from below. If the crust has grown only from above, and Fernandina has achieved perfect compensation, then the island emerged 140 ka according to Kurz *et al.*'s (2005) growth rates. In fact, we know that the western islands are flexurally supported (Feighner & Richards, 1995), and the Galápagos crust grows largely by intrusion into the mid and lower crust (Geist *et al.*, 1998; Lyons *et al.*, 2007), so this is likely a gross overestimate. For example, a petrologically based estimate of the ratio of unerupted : erupted magma is 2 : 1 (Geist *et al*., 1998), yielding a reasonable maximum emergence age of 70 ka.

Isla Isabela

Isla Isabela is constructed by the coalescence of six separate shield volcanoes. In all probability, each of these volcanoes started off as an isolated island, and each was later connected to its nearest neighbor by isthmuses of lava. It is not possible to estimate at what point in time any of the connections were made. Naumann & Geist (2000) estimated emergence ages of 350 ka for Cerro Azul, 535 ka for Sierra Negra, and 313 ka for Alcedo. These estimates were based on K-Ar age determinations from lava flows sampled at the base of each caldera (which are the oldest lavas exposed on any of these volcanoes), exposure dating of surficial lavas, and a model for the volumetric growth of the volcano. They assume a constant growth rate, extrapolated beyond the actual data (no more than 100,000 ka).

A similar calculation for Wolf volcano yields an estimated age of emergence of 380 ka, although the ages of the lavas exposed in Wolf's caldera wall are more uncertain (Geist *et al*., 2005). Work on Darwin volcano is underway, but its morphological similarity to Alcedo and lack of historical eruptions suggest it may be of similar age. Volcan Ecuador grew very rapidly at about 100 ka before it underwent sector collapse (Geist *et al*., 2002). It is a much smaller volcano than the others on Isabela, so if eruption rates are similar, it emerged much later than the other volcanoes of Isabela.

None of these calculations of emergence age from the growth rate account for subsidence. The true emergence ages could be at least twice the estimate reported above, if the volcanoes subsided as they grew.

Isla Santiago

Isla Santiago has had two historical eruptions (Simkin & Siebert, 1994) but is certainly in declining growth. If Santiago emerged at the present day hotspot center, which is assumed to near present-day Isla Fernandina, and the plate velocity of O'Connor *et al*. (2007) is valid, then it emerged 1.4 Ma. All of the exposed lavas on Santiago are normally polarized, and the oldest reliable age determination is from the north coast, morphologically the oldest part of the island, and yields 770 ± 120 ka (Swanson *et al*., 1974). Because of its declining growth rate as it is carried away from the hotspot, linear extrapolation of recent eruption rates to emergence yields excessively old ages. Probably the best estimate for Santiago's emergence age comes from Islas Rabida and Pinzon. Those volcanoes lie in the same part of the archipelago as Santiago, and some of their lavas resemble those of Santiago compositionally (Swanson *et al*., 1974; Baitis, 1976). Unlike Santiago, recent lavas do not cover the main phase of volcanism. Islas Rabida and Pinzon yield ages clustering around 1 Ma (Table S1). That is likely a minimum age of emergence, because all of these volcanoes have subsided since they grew to their peak elevations.

Several of the satellite islets around Santiago have ages measurements (Table 2). These are all monogenetic centers, so the measured ages are likely also the ages of emergence. Islote Sombrero Chino yields exposure ages of 13 ± 0.8 ka. Roca Bainbridge #3 yields an exposure age of 9.7 ± 0.6 ka, consistent with a radiocarbon age of ~ 7.13 ka from lake sediments (calendar years; Reidinger *et al*., 2002). No reliable age has been determined for Bartolome, but on the basis of weathering and soil development it is equivalent in age to these islets. Rocas Beagle are tuff cones and significantly older, with a mean ^{3}He exposure age of 316 ± 12 ka.

Islote Daphne Major is of special significance, owing to the long term biological studies there (e.g. Grant & Grant, 2007). We assume that Islote Daphne Major is a volcanic satellite of Santiago: it is one of many monogenetic volcanoes that lie along a submarine ridge that extends to Santiago. The compositions of its lavas are similar to others erupted from both Islas Santiago and Santa Cruz, but Islote Daphne Major is eroded less than any of the satellite volcanoes around Isla Santa Cruz (but more than some of Isla Santiago's satellites: Rocas Bainbridge, for example). A sample of lava from the crater of Islote Daphne Major yields an exposure age of 23.3 ± 1 ka, clearly linking it to young volcanism from Santiago. An attempt to determine its age by ^{39}Ar/^{40}Ar failed (Table 2).

Isla Pinzon

If Isla Pinzon emerged near the present location of Isla Fernandina, and the plate velocity of O'Connor *et al*. (2007) is correct, it is 1.7 Ma. Five samples of lava yield K-Ar ages that are within uncertainty of 1.0 Ma (Swanson *et al*., 1974; White *et al*., 1993). A single lava yields an age of 1.4 ± 0.08 Ma, which has not yet been replicated. The age of emergence is thus older than 1.0 Ma, because there is little doubt that the volcano has subsided and is largely constructed of older unexposed lavas. If volcanism on Pinzon lasted as long as that on Alcedo, for example, then its emergence age would be 1.3 Ma.

Isla Rabida

If Isla Rabida emerged at the leading edge of the hotspot track, its emergence age is 1.6 Ma. All three reliable K-Ar ages from Rabida are within uncertainty of 1.0 Ma (Swanson *et al*., 1974). This is the minimum age of emergence, as the volcano has no doubt subsided, submerging older subaerial lavas. For reasoning similar to that of Pinzon, the minimum age of emergence is estimated to be 1.3 Ma.

Isla Santa Cruz

The oldest reliable age determination from Isla Santa Cruz is 1.12 ± 0.02 Ma (White *et al*., 1993). This sample comes from a sequence of lavas on the island's northeast side, which records the emergence and progradation of that shoreline (Bow, 1979). Santa Cruz is one of the largest volcanoes in the archipelago, and there is little doubt that it has subsided, probably > 500 m. A young phase of volcanic rocks < 500 ka covers the entire highlands of the volcano, so volcanism lasted at least one million years on Santa Cruz and may well have lasted twice that. The hotspot estimate for Santa Cruz's emergence is 2.3 Ma.

Many small satellite islands surround Santa Cruz. Baltra, Mosquera, North Seymour, and Las Plazas are all fault block islands, meaning they were lifted above the sea by faulting after they were mostly built by submarine volcanism. The timing of faulting and emergence is only constrained to be younger than the age determinations. A Baltra lava has a K-Ar age of 1.37 ± 0.16 Ma (Cox & Dalrymple, 1966), which is just slightly older than the oldest dated activity on Santa Cruz. Mosquera and North Seymour are as geologically related to Baltra, thus likely have equivalent emergence ages. Uplifted submarine lavas on Las Plazas are nearly coeval, with an age of 1.31 ± 0.10.

Bowditch Norte and Sur are islets off the northwest coast of Santa Cruz (Snell *et al*., 1996), formed by the inflated front of relatively young lava. A ^{3}He exposure age indicates that it is at least 302 ± 10 ka, similar to exposure ages for the lavas around Santa Cruz (Kurz & Geist, 1999). The Islotes Guy Fawkes are a chain of erosional remnants of tuff cones with a similar exposure age of 298 ± 10 ka. An imprecise ^{39}Ar/^{40}Ar plateau age is 1.01 ± 0.35 Ma (Table 2), indicating that the islets may be coeval with the growth of the northeastern part of Santa Cruz. Islote Venecia has the same origin as Bowditch and yields remarkably similar results: a ^{3}He exposure age of 232 ± 8 ka and a ^{39}Ar/^{40}Ar age of 1.42 ± 0.29 Ma. Likewise, Isolete Eden, another tuff cone west of Santa Cruz has an ^{39}Ar/^{40}Ar plateau age of 1.6 ± 0.8 Ma.

Isla Floreana

About 1/3 of the surficial lavas on Floreana are reversely polarized, indicating that the waning stage of growth of Floreana began at least 800 ka (Bow & Geist, 1992). Hotspot theory suggests that Floreana should be ~ 2.3 Ma if it emerged in the western Galápagos, using the plate velocity of 59 km/My (O'Connor *et al*. (2007). The oldest reliable K-Ar age is 1.50 ± 0.08 Ma (White *et al*., 1993), but the unusual compositions of Floreana lavas suggest that they may have erupted in a rejuvenated phase of volcanism (Bow & Geist, 1992; Lyons *et al*., 2007). This phase of volcanism has continued to at least 26 ± 7 ka, the youngest dated lava on Floreana (Kurz & Geist, 1999).

Floreana's satellite islands are tuff cones that formed when magma erupted through shallow seawater. A lava from Isolete Enderby has a $^{39}Ar/^{40}Ar$ age of 370 ± 19 ka, whereas Gardner Islet was coeval with the older lavas exposed on Floreana, at 1.13 ± 0.28 Ma.

Isla Santa Fe

It was originally reported that Santa Fe is constructed of uplifted submarine lavas (Williams & McBirney, 1969), but it has since been shown that most of its lavas were subaerial (Geist *et al*., 1985). Santa Fe has the oldest precisely dated lavas in the archipelago, at 2.85 ± 0.06 Ma, as well as several other determinations nearly that old (Bailey, 1976; Geist *et al*., 1985; White *et al*., 1993). Hotspot theory suggests an emergence age of 2.9 Ma. The correspondence of the determined ages and O'Connor *et al*.'s (2007) plate velocity estimate indicates that the Nazca Plate moves no faster than 59 km/My, unless Santa Fe erupted "upstream" of the hotspot center, which is exceedingly unlikely.

Isla San Cristobal

Hotspot theory suggests that San Cristobal and Española should be the oldest islands in the archipelago, because they are the easternmost. San Cristobal should be 4 Ma if it emerged near Fernandina, but the oldest measured age is 2.35 ± 0.03 Ma (Geist *et al*., 1986). Volcanism terminated about 700 ka on the southwestern half of the island but continued to near present on the northeastern half (Cox, 1972; Geist *et al*., 1986). It is possible that the two halves of the volcano were at one time separate by a narrow channel.

Isla Española

At one time, Española was also thought to consist of uplifted submarine lavas (McBirney & Williams, 1969), but it was later shown to be a subaerial volcano (Hall *et al*., 1983). Hotspot theory suggests that Española is 3.5 Ma, but unfortunately Española's activity remains poorly dated. The oldest age determination with small uncertainty is 2.77 ± 0.04 Ma (White *et al*., 1993). Bailey (1976) determined ages of 3.04 ± 0.11 Ma and 3.31 ± 0.36 Ma. Thus, the determined ages are consistent with an age of emergence of at least 3.0 Ma.

Islas Genovesa, Pinta, and Marchena

The northern Galápagos cannot have originated in a straightforward manner from the Galápagos hotspot, as they lie far off the Galápagos platform and the hotspot track. Instead, they likely have formed by a combination of tectonic stresses related to the Galápagos Spreading Center and flow of mantle plume material from the hotspot to the spreading center (Harpp & Geist, 2002; Harpp *et al*., 2002). All three of these islands have very young unvegetated and poorly weathered lavas, and Marchena erupted in 1992.

All K-Ar ages from the northern islands are notable for the paucity of radiogenic ^{40}Ar, thus are imprecise. Cullen & McBirney (1987) estimated that Pinta emerged about 700 ka, on the basis of an imprecise K-Ar age of 890 ± 240 ka and the normal magnetic polarity of all of its lavas. The oldest age determination from Marchena is 560 ± 40 ka (White *et al*., 1993). Age determinations of Genovesa lavas are especially difficult, because they are very poor in potassium. Harpp *et al*. (2002) estimated a minimum age of emergence of 350 ka.

Islas Wolf and Darwin

These islands are small caps on mostly submarine volcanoes. Two lavas from Isla Darwin are within uncertainty at 400 ka, whereas those from Isla Wolf are notably older, with ages of 1.60 ± 0.07 Ma and 0.88 ± 0.13 Ma (White *et al*., 1993). Dredged lavas from the submarine part of Wolf volcano suggest an age of 0.8 Ma for the entire volcano (Sinton *et al*., 1996).

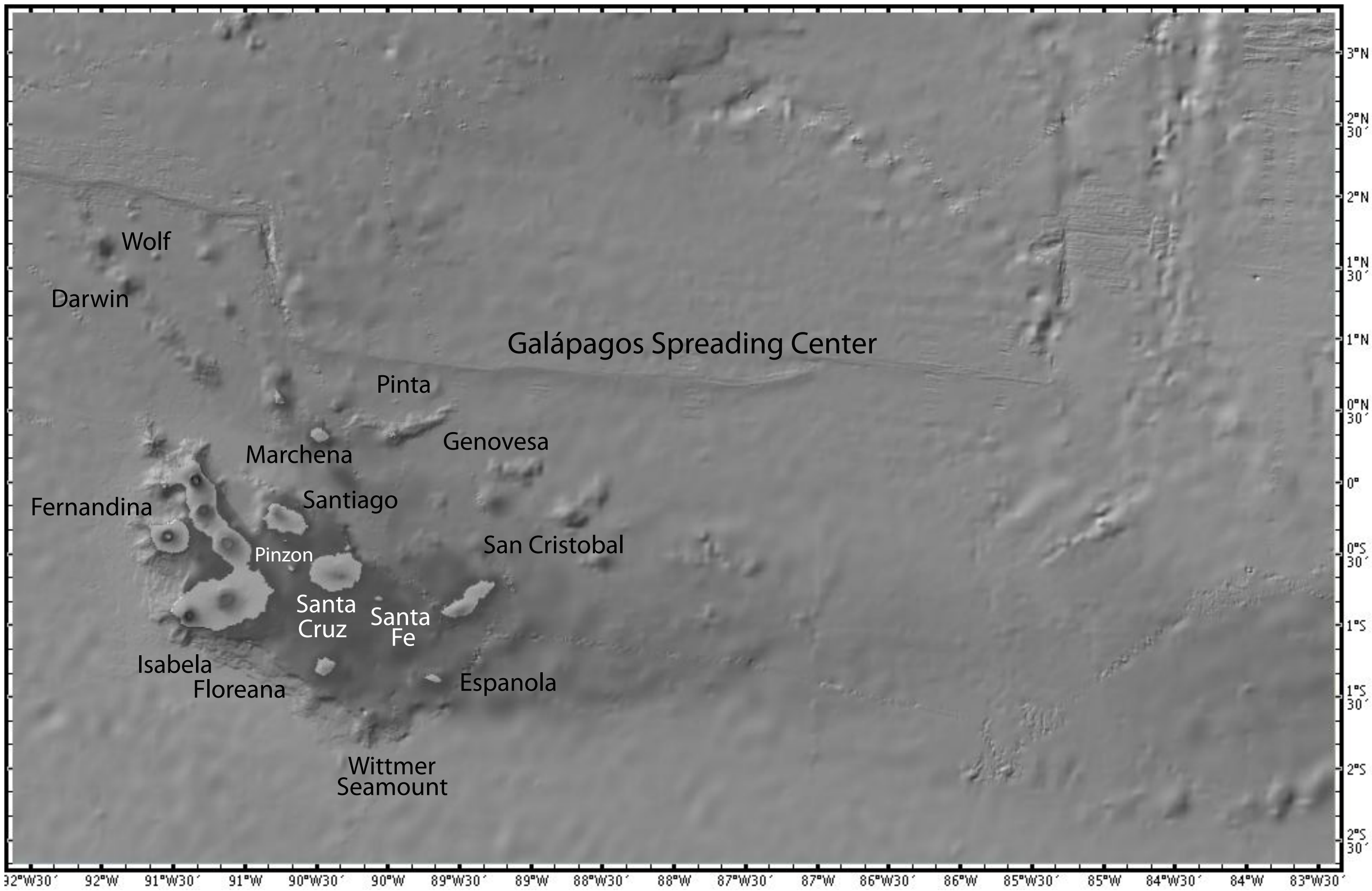


Figure 1: Bathymetric and topographic map of the Galapagos archipelago and surrounding geographic features. Darkened submarine region highlights water depth < 500 m, the Galapagos platform.

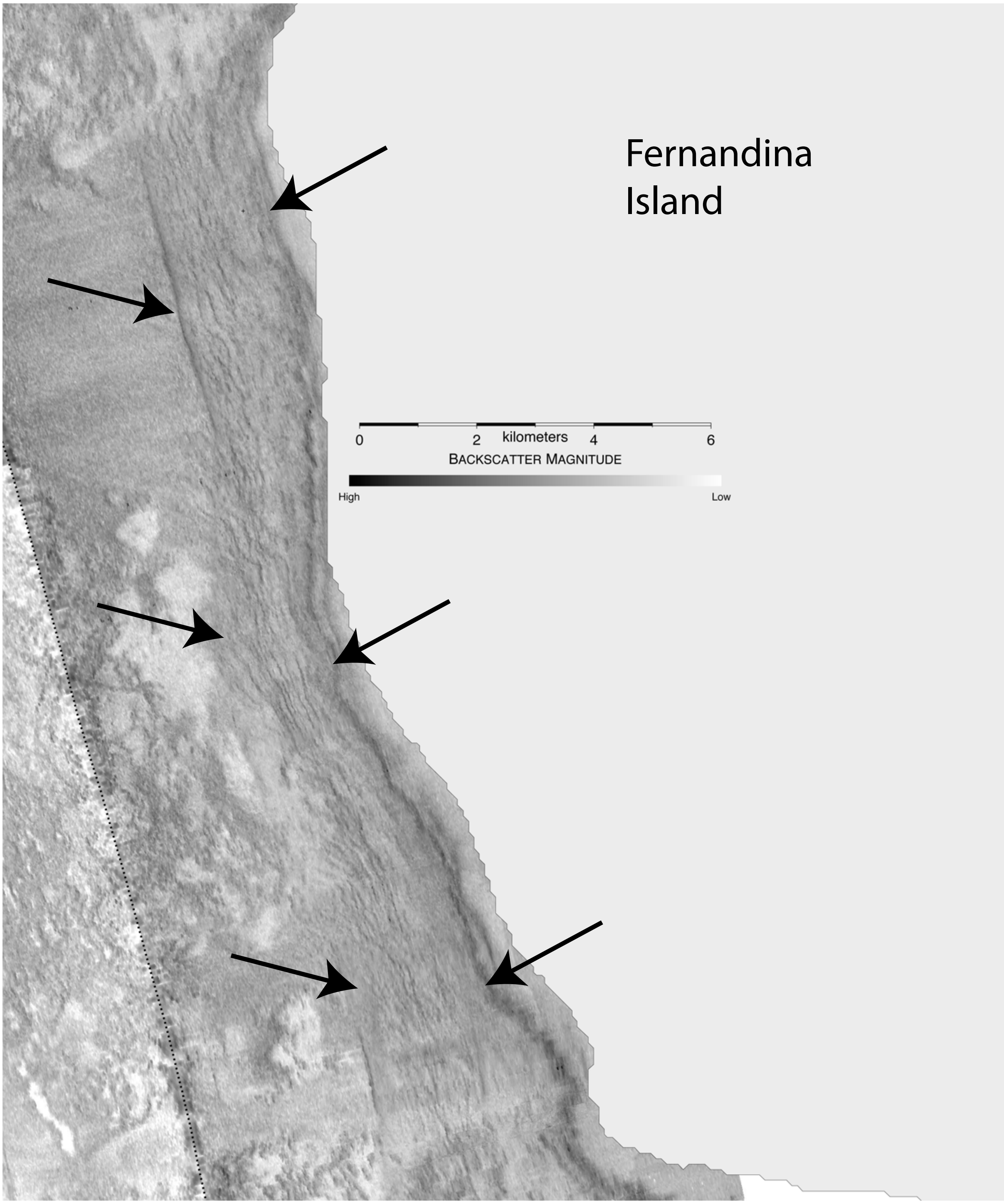


Figure 2: Sidescan sonar image of the west coast of Fernandina, from Geist et al. (2006). Image is processed so stronger sonar reflectivity appears darker. Arrows outline the top and bottom of thinly stratified formation, which has been interpreted as subsided subaerial and coastal plain lavas (Geist et al., 2006). The bottom of the stratified unit is at 1300 m water depth.

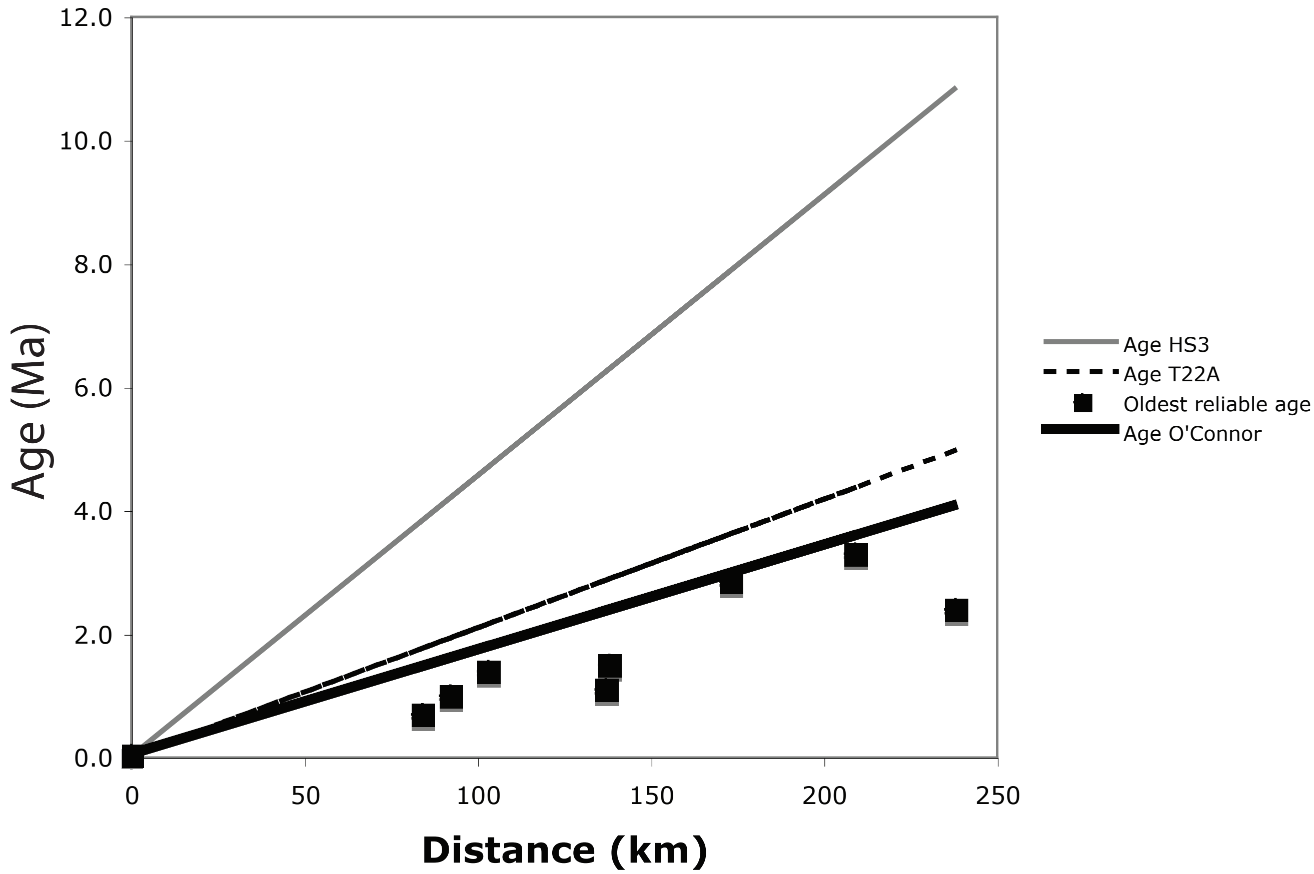


Figure 3: Velocity of the Nazca plate in the Galápagos region by several different models. HS3 is the model of Gripp and Gordon (2002); TS22 is that of Wang and Wang (2006). The 59 km/m.y. velocity of O'Connor et al. (2007) best fits the oldest age deterninations from the islands. By our model, the minimum emergence age of an island is represented by the black square, and the maximum by the O'Connor et al. velocity.

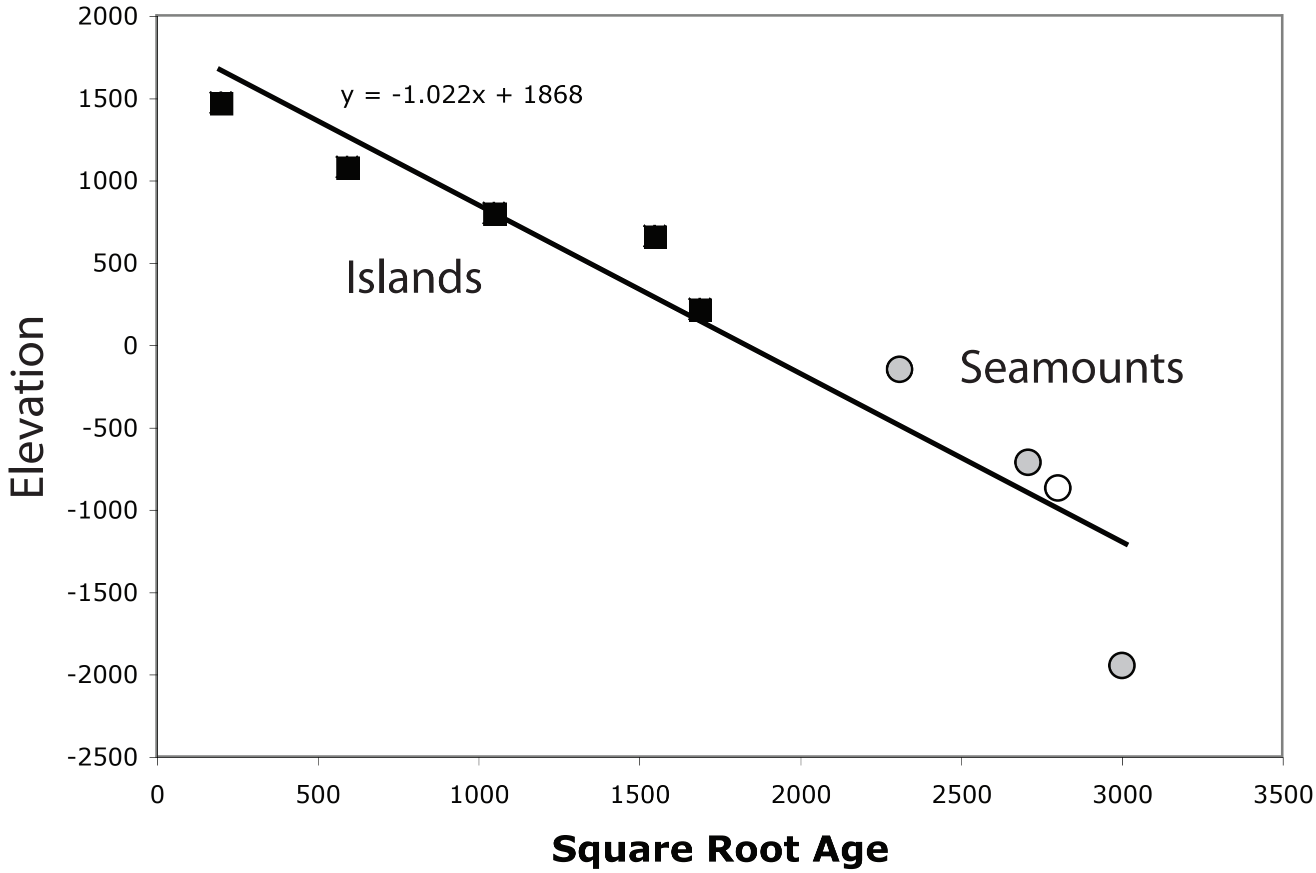


Figure 4: Subsidence model for the Galapagos Islands and seamounts. Black squares are the major volcanoes along the central axis of the archipelago: Fernandina, Alcedo, Santa Cruz, Santa Fe, and San Cristobal. Circles are seamounts, and filled circles indicate those with clasts indicative of coastal erosion (Christie et al., 1993). Note that the anomalously deep 9 Ma volcano lies well to the south of the hotspot trace axis.

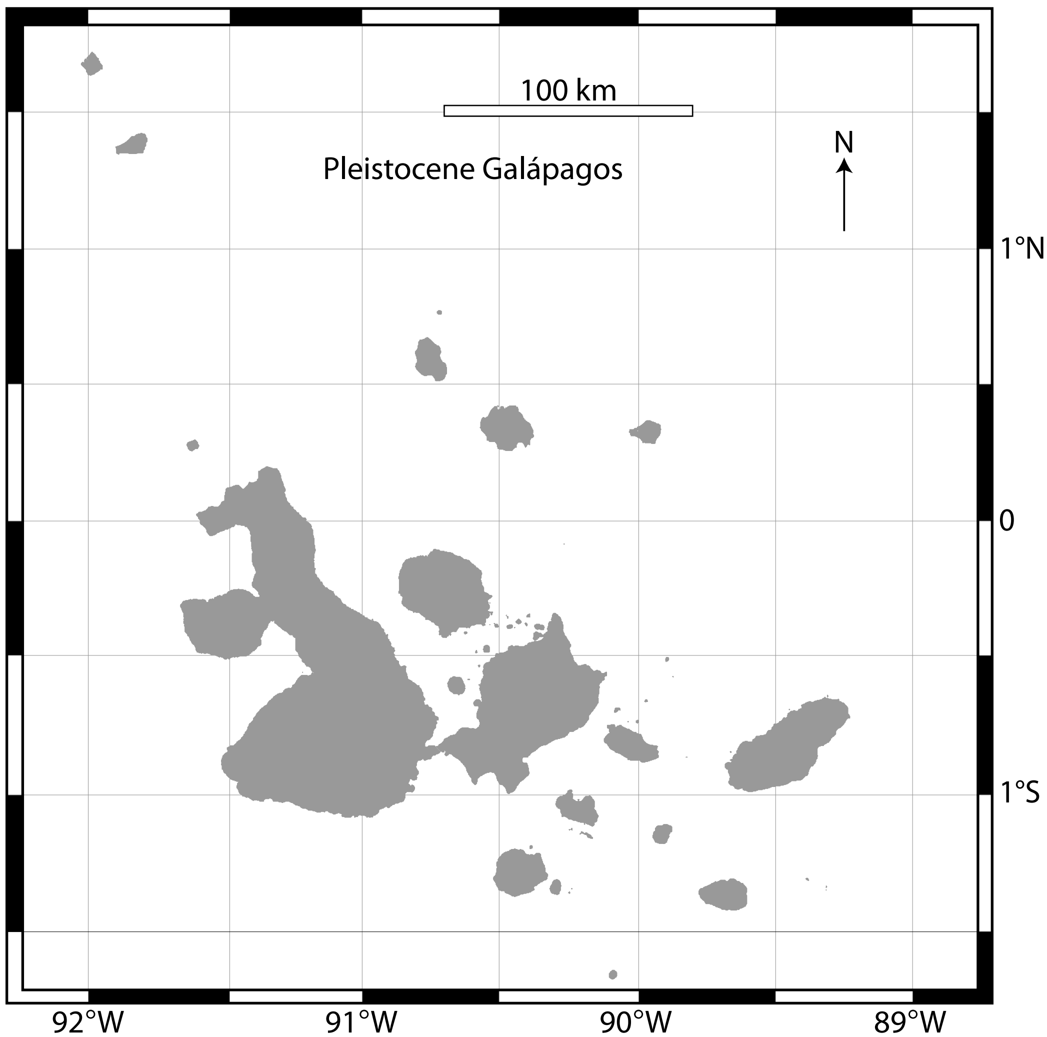


Figure 5: Model of the Galapagos at the last glacial maxiumum, similar to that produced by Grant and Grant (1996). Map was produced by contouring bathymetric data at 125 m. This model ignores volcanic growth in the western archipelago and lithospheric subsidence, which should lower relative sea level a few meters in the central archipelago. Details of the area around Santa Cruz-Santiago are in Figure 6 and Floreana in Figure 7.

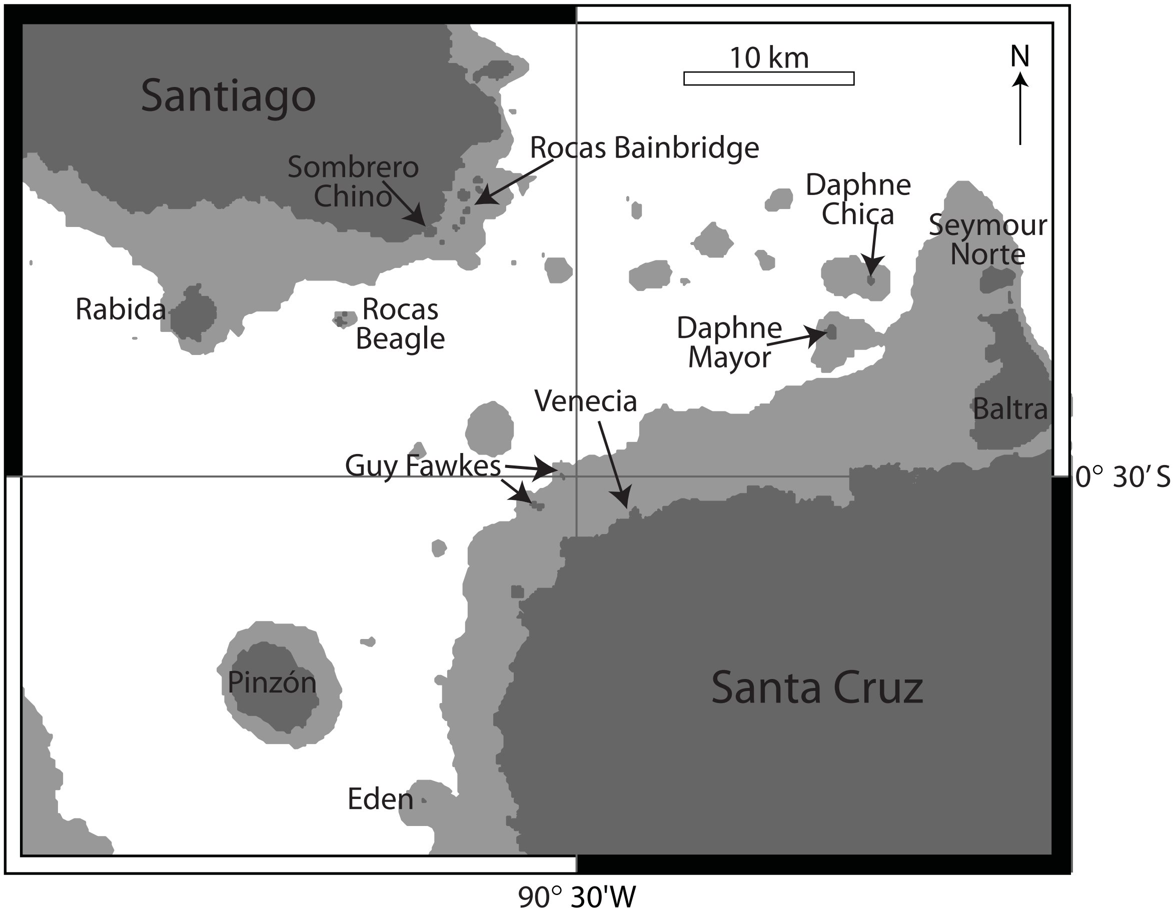


Figure 6: Closeup of Pleistocene model of the region between Santa Cruz and Santiago Islands.

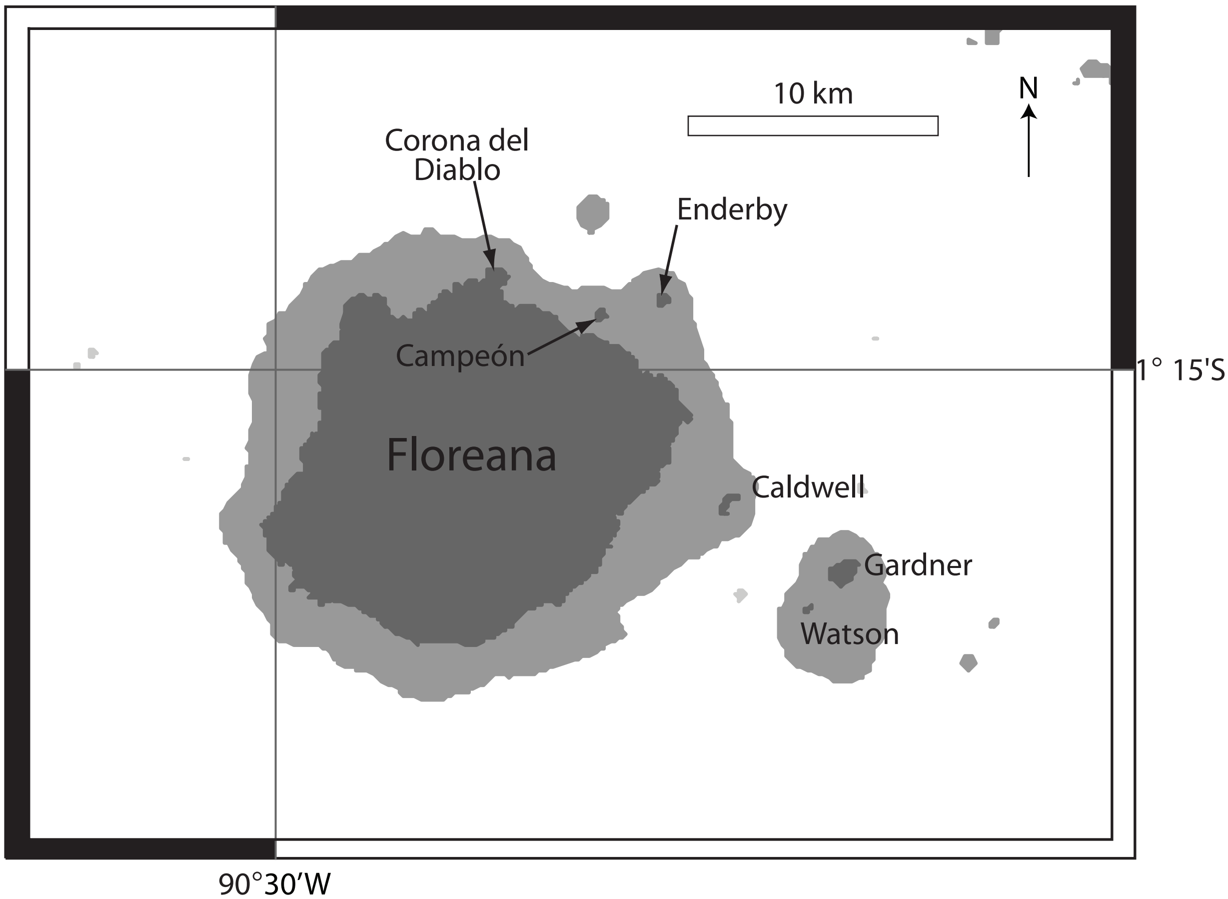


Figure 7: Closeup of Pleistocene model of the region around Floreana Island.

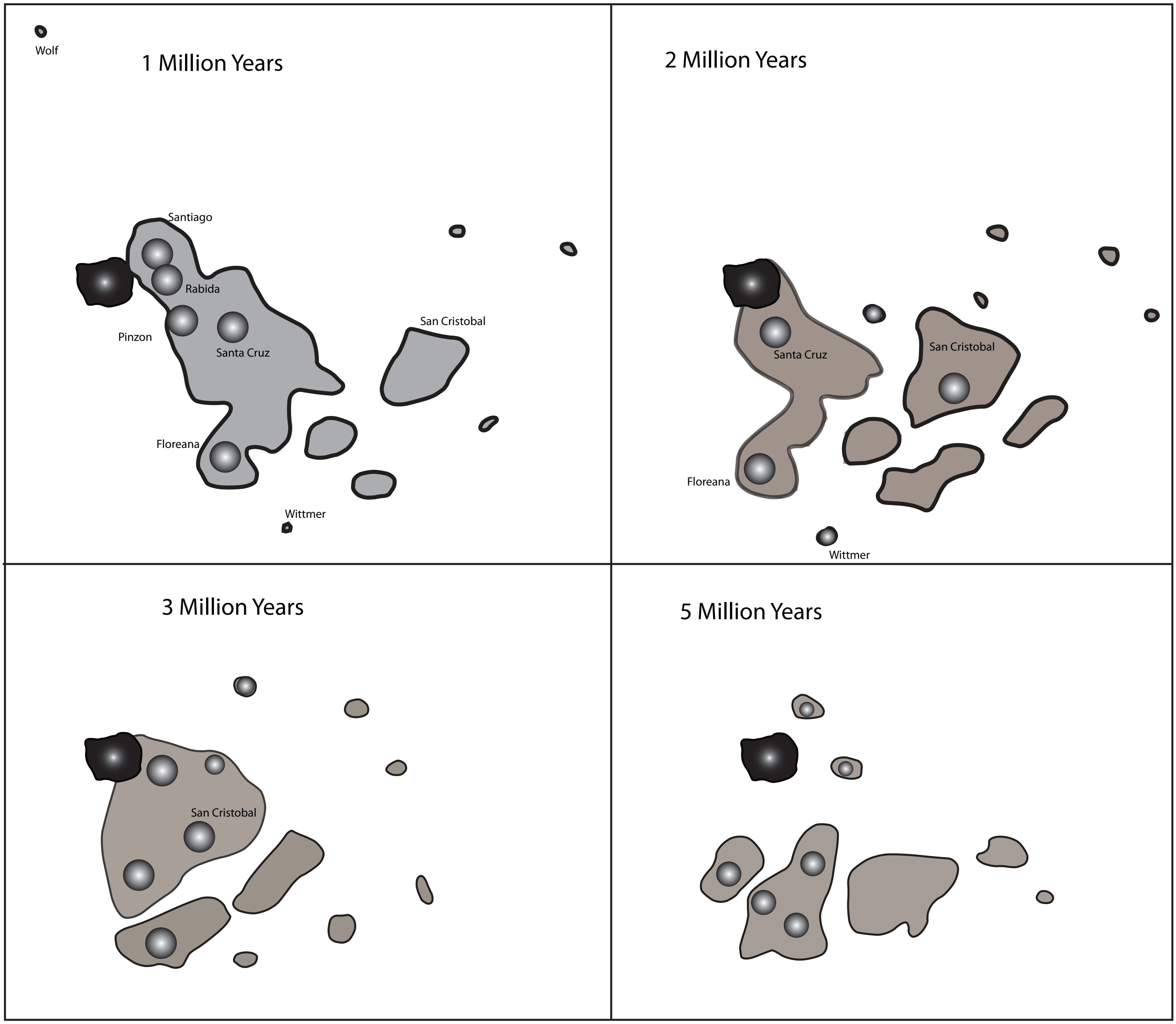
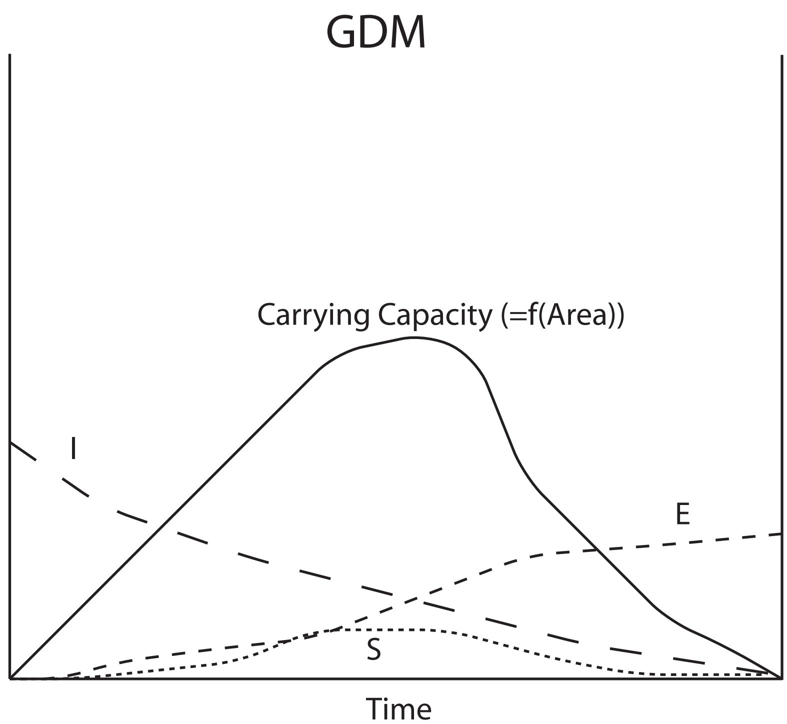


Figure 8: Proposed paleogeography of the Galapagos, from 1 to 5 Ma. Dark-colored Fernandina island provides a fixed reference frame only, as Fernandina did not exist at any of these times. Volcanoes that were active in each increment are indicated by the shadowed circles. Emergent volcanoes that are still islands are named.



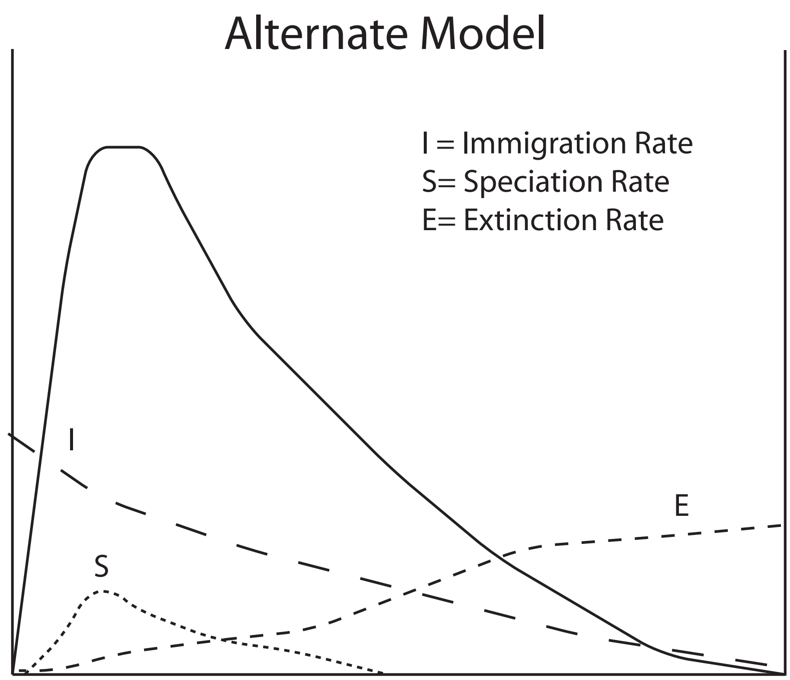


Figure 9: (top) Variation of immigration, extinction, and speciation rates with an islands' age, according to the General Dynamic Model (Whittaker et al., 2008). (Bottom) The model proposed in this work.

Table 1: New age determinations for Galapagos lavas.

Sample	Location	Latitude	Longitude	elevation (meters asl)	3He/4He (R/Ra) (crush)	1 sigma	weight (grams)	4He (ncc STP/g)	3He/4He (R/Ra) (melt)	1 sigma	3Hec (atoms/g)	1 sig	Age(Ka)	1 sigma
G99-2	Bowditch	0° 31' 50.00" S	90° 31' 00.00" W	2	8.26	0.71	0.19052	6.393	95.5	0.6	2.07E+07	3.27E+05	303.3	4.8
G99-5	Isla Sombrero Chino	0° 22' 12.00" S	90° 34' 48.00" W	15	8.75	0.28	0.29063	1.733	22.5	0.5	8.85E+05	4.79E+04	12.8	0.7
G99-5D	Isla Sombrero Chino			15	9.35	0.18	0.24357	1.513	25.3	0.6	8.96E+05	5.32E+04	13.0	0.8
G99-6	Roca Bainbridge #3	0° 22' 02.00" S	90° 34' 12.00" W	3	13.20	1.32	0.28375	1.132	29.1	0.4	6.69E+05	4.71E+04	9.8	0.7
G99-8	Isla Vanecia	0° 31' 02.10" S	90° 28' 30.42" W	5	8.89	0.25	0.22340	2.346	191.5	1.2	1.59E+07	3.75E+05	232.5	5.5
G99-9	Islote Guy Fawkes Este	0° 29' 56.52" S	90° 30' 47.22" W	11	11.91	3.64	0.25255	0.606	921.1	7.1	2.05E+07	1.38E+06	297.5	20.1
G99-11(cpx)	Roca Beagle Sur	0° 25' 05.10" S	90° 37' 50.04" W	50	22.51	6.64	0.18360	5.975	117.8	0.6	2.12E+07	4.68E+05	298.3	6.6
G99-11(ol)	Roca Beagle Sur			50	8.00	1.00	0.09614	1.043	583.3	4.8	2.23E+07	2.28E+06	314.6	12.0
G99-12	Isla Daphne Mayor	0° 25' 17.46" S	90° 22' 19.26" W	55	7.467	0.36	0.21760	2.625	23.8	0.3	1.60E+06	5.63E+04	22.5	0.8

Unless otherwise noted, all samples are olivine (ol) mineral separates
Units of 4He are nano-cc STP/gram
Several of the crushed/magmatic 3He/4He ratios are highly uncertain due to low gas contents

Sample	Island Name	Latitude	Longitude	Plateau Age	Isochron Age
G99-1	Isla Eden	0° 33' 36.00" S	90° 32' 24.00" W	1.65 ± 0.82 Ma	3.39 ± 0.89 Ma
G99-8	Isla Venecia	0° 31' 02.10" S	90° 28' 30.42" W	1.42 ± 0.29 Ma	1.31 ± 0.37 Ma
G99-10	Islote Guy Fawkes Sur	0° 30' 56.10" S	90° 31' 38.82" W	1.01 ± 0.35 Ma	0.68 ± 0.32 Ma
G99-12	Isla Daphne Mayor	0° 25' 17.46" S	90° 22' 19.26" W	45 ± 19 Ma	21 ± 25 Ma
FL99-2	Isla Enderby	1° 14' 00.60" S	90° 21' 49.02" W	0.37 ± 0.19 Ma	0.36 ± 0.20 Ma
FL99-4	Isla Gardner—Floreana	1° 19' 45.12" S	91° 17' 37.26" W	1.13 ± 0.28 Ma	0.76 ± 0.51 Ma

Table 2: Estimates of the emergence ages of the major Galápagos Islands.

	Minimum Emergence Ma	**Maximum Emergence Ma**
Fernandina	0.035	0.07
Isabela	0.5	0.8
Santiago	0.8	1.4
Pinzon	1.3	1.7
Rabida	1.3	1.6
Santa Cruz	1.1	2.3
Floreana	1.5	2.3
Santa Fe	2.9	2.9
San Cristobal	2.4	4.0
Espanola	3.0	3.5
Pinta	0.7	?
Marchena	0.6	?
Genovesa	0.3	?
Wolf	1.0	?
Darwin	0.4	?

Table 3: Parameters from multiple regressions of diversity data with island area (A) and age (T). Parameters labelled WTL are from Whittaker et al., 2008. The first three regressions use untransformed indices of diversity. The last set of parameters regresses for log of the species richness.

	ATT2		logA		LogA+LogT		LogD, LogT, LogA	
	Adjusted R2	**F**	**Adjusted R2**	**F**	**Adjusted R2**	**F**	**Adjusted R2**	**F**
Species Richness								
Insects WTL	0.73	35	0.61					
Small order Insects WTL	0.68	25	0.57					
Beetles WTL	0.76	42	0.62					
Plants WTL	0.79	50	0.72					
Verts + Plants	0.65	33	0.65	99	**0.66**	52	**0.84**	127
nSIE								
Insects WTL	0.53	9	0.41					
Small order Insects WTL	0.31	5	ns					
Beetles WTL	0.64	12	0.57					
Plants WTL	0.73	16	0.42					
Verts + Plants	0.48	17	0.50	53	**0.63**	45		
pSIE								
Insects WTL	0.4	27	0.34					
Small order Insects WTL	0.04	14	ns					
Beetles WTL	0.6	19	0.41					
Plants WTL	0.64	12	0.29					
Verts + Plants	0.65	34	0.66	100	**0.67**	53		