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Towards a glacial-sensitive model of island biogeography

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ABSTRACT:

Although the role that Pleistocene glacial cycles have played in shaping the present biota of oceanic islands worldwide has long been recognized, their geographic, biogeographic and ecological implications have not yet been fully incorporated within existing biogeographical models. Here we summarize the different types of impacts that glacial cycles may have had on oceanic islands, including cyclic changes in climate, shifts in marine currents and wind regimes and, especially, cycles of sea level change. The latter have affected geographic parameters, such as island area, isolation and elevation. They have also influenced archipelago configurations via island fusion and fission, and cycles of seamount emergence and submergence. We hypothesize that these sea level cycles have had significant impacts on the biogeographical processes shaping oceanic island biotas, influencing rates and patterns of immigration and extinction and hence species richness. Here we provide a first step toward the development of a glacial-sensitive model of island biogeography, representing a tentative temporal evolution of those biogeographic parameters during the last glacial cycle. From this reasoning we attempt to derive predictions regarding the imprint of sea level cycles on genetic, demographic, or biogeographical patterns within remote island biotas.

Keywords: climate change, extinction, immigration, island biogeography, island theory, oceanic islands, Pleistocene, sea level fluctuations, species richness.

INTRODUCTION

The dynamic equilibrium model

Following its introduction by MacArthur & Wilson (1963, 1967), the Equilibrium Theory of Island Biogeography (ETIB) became the ruling paradigm in island biogeography. The theory asserts that in general, islands tend towards a state of equilibrium between three fundamental processes, immigration, speciation, and extinction, which generate predictable patterns of species diversity and turnover on islands. Rates of these processes are posited to vary in response to distance from source pools (influencing immigration rates) and island area (influencing extinction rates). Although speciation rate was hypothesized to increase as a contribution to island diversity in remote, large (oceanic) islands (MacArthur & Wilson, 1963: page 378), it was not included in their famous graphical model and thus nearly forgotten by most users of their theory.

The appreciation of the utility of the ETIB as a strict explanatory model for species diversity patterns has been mixed (e.g. Gilbert 1980, Schoener 2010) and its equilibrium hypothesis, as originally defined, has even been argued to be unfalsifiable (Simberloff 1976) (see Warren *et al.* (2015) for a comprehensive synthesis). One of the strengths of the ETIB is its simplicity, yet this is also a limitation as it fails to incorporate the interplay of several other environmental factors that impact on species diversity on oceanic islands. A number of additions (or extensions) to the ETIB have been proposed to increase its realism. These modifications include the "rescue effect", which states that a lower degree of isolation also decreases the extinction rate by immigrants reinforcing extinction-prone populations (Brown & Kodric-Brown, 1977; Wright, 1985), and the "target-area effect", which states that larger area (island size) also affects immigration rate by the island becoming a larger target for passive or active immigrants (Gilpin & Diamond, 1976; Lomolino, 1990).

Towards disequilibrium models

Although explicit in MacArthur & Wilson's (1963, 1967) theorization, and thus far from being a new realization, more recently several authors (Heaney, 2000; Lomolino 2000) have highlighted the importance of speciation, which across large timescales (several Myr) modifies both the effect of distance and area on species richness, and endemic species richness in particular. Evolutionary dynamics act both through the inherent ontogeny of the speciation process itself and through changes in island geography (e.g. Johnson *et al.*, 2000; Stuessy, 2007; Whittaker *et al.*, 2008; Chen & He, 2009; Rosindell & Phillimore, 2011). On hot-spot islands (such as the Azores, Canaries, Galápagos, and Hawaii), the speciation rate over time is expected to be a unimodal ("humpbacked") pattern because of the limited lifetime of the islands themselves (e.g. Stuessy, 2007; Whittaker *et al.*, 2008). However, during such lengthy time periods, most oceanic islands experience important and often cyclical geological and climatic changes that will influence the biological processes. The changes in island geography involve not only size changes, but also formation of land bridges (Heaney, 2000), the merging or breaking-up of islands (Ali & Aitchison, 2014; Rijsdijk *et al*., 2014), or the completion of hot-spot oceanic island life cycles from emersion to submergence (Whittaker *et al*., 2008, 2010). Accordingly, Heaney (1986) proposed a dynamic-disequilibrium model in which the equilibrium in species richness is rarely achieved on islands, because of constantly changing physical conditions (geological activity and climate changes). The notion of the spatiotemporal dynamics of island geography together with the speciation processes signals the transition from equilibrium to disequilibrium models of island biogeography (see Heaney *et al*., 2013).

Island ontogeny and the General Dynamic Model of Oceanic Island Biogeography

The ETIB (MacArthur & Wilson, 1967) plus further embellishments (Brown & Kodric-Brown, 1977; Lomolino, 1990), as well as speciation-sensitive models (Heaney, 2000; Lomolino, 2000), approximate islands as static entities, with constant values of area, isolation, and archipelagic configuration through time. In practice, even very young volcanic islands can vary their geographical attributes in a very short time (for instance, Surtsey, which emerged in 1963, has already lost half of its area), while dynamism is the general rule over longer, geological, time scales (>10 Kyr), where regional geologic processes affect oceanic islands (island ontogeny) and supra-regional or even global climatic processes (Pleistocene glacial cycles) seriously compromise the perception of static islands (Heaney *et al.,* 2013).

Although several authors have underlined the consequences of past geological and climatic dynamism in island biodiversity (e.g. MacArthur & Wilson, 1967; Diamond, 1972; Wilcox, 1978; Price & Elliott-Fisk, 2004), arguably the first island biogeographic model to include a temporal element was Whittaker *et al*.'s (2008, 2010) General Dynamic Model (GDM), where the concept of oceanic island evolution (ontogenetic stages sensu Stuessy, 2007) was introduced.

In the GDM, which is primarily focussed on hotspot oceanic islands, island age is considered as a key factor determining species diversity, while variation in the speciation rate is driven largely by the availability of non-occupied ecological niches, which is highest during the early stages of the island's development, when the species numbers have not yet reached their maximum carrying capacity. Species numbers, and richness and proportions of single island endemics, are therefore predicted to follow a hump-shaped trend, increasing during island emergence (youth), attaining the zenith at maturity (maximum topographic complexity, when intra-island allogenesis is at a peak) and finally decreasing during island submergence (senescence), resulting in a *guyot* (Wilson, 1969). Although positive evidence supports the general validity of this model (Bunnefeld & Philimore 2012, Cameron et al., 2013), the GDM remains a simplified representation of island (geological and biological) dynamics and does not explain all the complexity (Borges & Hortal, 2009).

Environmental processes affecting insular dynamics

Islands in oceanic settings are highly dynamic entities, subject to different major geologic-climatic processes, which vary in origin and time scale, and it is well known that these processes influence species diversity patterns (Whittaker and Fernandez-Palacios, 2007). From the longer-lasting to more ephemeral these processes include (Table 1): (i) continental drift (plate tectonics), which extends over ten to hundreds of millions of years; (ii) oceanic island ontogeny, extending from tens to a few million years; (iii) sea level transgression/ regression cycles linked to the glacial cycles (Pleistocene glaciations), extending from 10s to 100s of thousands of years; and finally (iv) volcanic activity occurring in time frames from weeks to decades. Plate tectonics and island ontogeny affecting evolutionary processes over millions of years form one extreme of the time scale of insular dynamics. The biogeographic and evolutionary effects of plate tectonics spanning up to 100 millions of years, as a result of translocation of islands and continental fragments and the formation of new arc islands, involving vicariance effects and affecting gene flow and evolution are well known (e.g. Gaina et al., 1998; Kearey et al., 2009). The hot-spot oceanic island ontogeny cycle spans generally a shorter period up to 10s of Myrs and how this dynamics affects species richness is currently under investigation. On the other extreme of the time scale and particularly associated with oceanic islands are anomalous extreme events that act on ecological time scales (days; weeks) related to volcanic activity (e.g. sterilization events, Whittaker *et al.,* 1989) or geomorphological processes (e.g. landslides, Whelan & Kelletat, 2003). Such extreme events may destroy mature ecosystems and directly cause species extinctions within weeks, but new pristine terrain created by these processes will offer new opportunities for species to thrive in areas of reduced interspecific competition. In between these evolutionary and ecological time scales, the effects of glacial cycles and related sea level oscillations over 1000s of years affect all islands and their biota globally (Table 1, Fig. 1). Sea level fluctuations driven by glacial cycles occurred with periodicities of *c.* 40 –100 kyr during the last 2.6 Myr (Bintanja *et al.,* 2005; 2008; Rohling *et al.,* 2009, 2010). The impact of these processes is particularly relevant for the continental-shelf islands, which comprise most islands within the world's seas (Fernández-Palacios, 2010). Where the water depth separating them from their respective continent is shallow enough (< about 120 m) these land-bridge islands reiteratively join and become isolated from the continents in response to eustatic changes in sea level (e.g. British Isles, Taiwan). The biogeographic implications of these cycles of isolation and amalgamation have long been recognized (e.g. Diamond, 1972; Wilcox, 1978; Price & Elliott-Fisk, 2004; Whittaker & Fernández-Palacios, 2007).

Aims of the paper

It is evident that the island biodiversity we observe today results from geological and climatic processes that have modified the environment and the geographical island settings over ecological and evolutionary time scales. Herein we set out to incorporate the effects of these processes into a revised depiction of island theory, following the call by Lomolino (2000) for adding complexity to island biogeographic models. Thus, the purpose of this contribution is to provide a hypothesis of how various Pleistocene events may have shaped island biodiversity in the past, presenting as well a set of testable predictions (see Box) that can be derived from it.

BIOGEOGRAPHICAL CONSEQUENCES OF PLEISTOCENE GLACIAL EVENTS

As a consequence of the glacial cycles, three main types of geographic processes with biogeographic consequences can be distinguished on marine (land-bridge, micro-continental and true oceanic) islands: (a) sea level changes causing alterations in island areas, elevation, isolation and archipelagic configurations; (b) changes in climatic variables such as temperature and precipitation, which drive changes in elevational distributions of species and ecosystems; and finally (c) shifts in the direction, frequency and intensity of marine currents and wind systems influencing the connectivity of island systems with other land masses (Table 2).

Changes in the geographic configurations of islands in relation to sea level transgression/regression cycles

Land-bridge islands are continental peninsulas that achieve their insular status in interglacial periods after sea level rise, although some may have been connected during every major glacial episode and some only perhaps once or twice when the very lowest levels have been reached. Studies dealing with the impact of glaciations have mostly focused on the ‘relaxation’ (reduction of richness to a new equilibrium) of their biotas following the most recent vicariance event (Diamond, 1972; Wilcox, 1978). Examples include the Sunda islands (Sumatra, Java or Borneo), which were connected to Indochina and the Malaysian peninsular through Sundaland, the currently submerged South China Sea platform (occupying 1.8 M km^2; Wang *et al.*, 2009); the now submerged Sahul continent, comprising New Guinea, Australia and Tasmania, and the connection of mainland Britain with continental Europe through the low lying tundra of Doggerland in the North Sea (Voris, 2000; Shennan & Horton, 2002). Wallace (1880) documented this extensively in his *Island Life*.

In contrast to land-bridge islands, oceanic islands remain insular (or submerge and emerge as islands) during the glacial cycles, but their areas, configuration and isolation change over time depending on both the inherent geological dynamics of the islands and archipelagos and on their bathymetric configuration (e.g. Ali & Aitchison, 2014). In general, sea level regressions cause limited increase of area for steep-sloped young islands (Fig. 2), but for older, eroded volcanic islands, the effect of sea level cycles can be pronounced. These islands often are surrounded by shallow submarine platforms formed by extensive marine erosion and transportation. Thus, large area increases are expected during sea level regressions, potentially resulting in the fusion of two or more neighbouring islands, as has happened in the Canaries with the appearance of Mahan: the result of the fusion of Lanzarote, Fuerteventura and nearby islets (Fig. 3) (Fernández-Palacios *et al.,* 2011).

Examples of true oceanic islands subject to doubling in area during Pleistocene sea level minima, include: in the Macaronesian region, the Canarian example (above), Santa Maria (Azores), Porto Santo (Madeira), Boa Vista, and Maio (Cape Verde). Cases of island fusion also include Lauri-insula (the merging of Pico and Faial in the Azores), Pleistocene Madeira (Madeira and Desertas in Madeira), and the North-Western Pleistocene Island (Sao Vicente, Santa Luzia, Branco and Raso) in Cape Verde (Rijsdijk *et al.*, 2014). In the Caribbean, the present Leeward islands of St. Martin, Anguilla, and St. Barthelemy (today summing to 200 km^2) would have formed the St. Martin Bank, a single island of approximately 6000 km^2 (Woods & Sergile, 2009). In the East Pacific, during the LGM (last glacial maximum), the central Galápagos islands would have been considerably larger, but without coalescing into a single massif. Nevertheless, Ali & Aitchison (2014) suggest the main Galápagos islands (Santa Cruz, Santiago, Isabela and Fernandina) formed a single large island as a result of an extreme low sea level stand around 255 ka. In the Central Pacific, the Hawaiian islands of Moloka‘i, Lana‘i, Maui and Kaho‘olawe were joined during the mid-Pleistocene, forming Maui Nui. As the area underwent tectonic subsidence, the islands became isolated during high sea stands of interglacial periods starting around 0.6 Ma. However, during low sea stands, the islands reunited (Price & Elliot-Fisk, 2004). Finally, in the western Indian Ocean, many islands would have been much larger during the LGM: the Seychelles, today comprising several islands and islets summing 220 km^2 would have formed a single landmass (Granitic Seychelles) of >40 000 km^2 (Warren *et al*., 2009) (Table 3). Here we expect that nearby islands subject to fusion/fission cycles will share more species than comparable island groups that were never physically linked (Prediction 2 a in the Box). But on the other hand, we expect as well that genetic analyses will evidence that divergence has occurred among populations that were split (allopatry) when islands separated during the interglacial periods (Prediction 2 b).

Sea mounts residing in relative shallow waters would have emerged during a regression, leading to a primary colonization process lasting up to a few thousand years, depending on the duration of the low stand and the sea mount depth. These sea mounts would submerge again during the following transgression, leading to the extinction of all their terrestrial biota (Prediction 3 b). The temporary existence of sea mounts must have improved connectivity within archipelagos, between archipelagos, and between mainlands and archipelagos. Examples from the eastern Atlantic Ocean include Formigas (in Azores), Ormonde, Ampere and Siene (in Madeira) or Dacia, Conception, and Amanay (in the Canaries) (Fernández-Palacios *et al.*, 2011). In the Indian Ocean the LGM sea level drop resulted in the emergence of the submarine banks of Saya de Malha and Nazareth, located between the Seychelles and Mascarenes in the Madagascan region, forming land areas of approximately 26 500 and 22 000 km^2, respectively (Warren *et al.*, 2009).

Such changes in area and isolation over the course of the last glacial cycle (i.e. from the last one, the Eemian, 130–120 ka, to the present interglacial, the Holocene, 11–0 ka), as exemplified for the Canaries in Figures 2 and 3, should greatly affect colonization rates and possibly cause a rescue effect, preventing extinctions, as well as a target-area effect enhancing immigration (Predictions 1 a and 1 b). In summary, sea level change will, on an island-by-island basis, have affected area, shape, maximum elevation, isolation, connectivity, coastal perimeters, and the elevational distribution of the zonal ecosystems, potentially including the emergence and disappearance of the highest summit ecosystems (see below). We may therefore infer that these changes will have had a significant role in rates and patterns of species colonization and extinction, thus driving changes in distributions and in evolutionary forcing. Furthermore, Holocene sea level variation, caused by glacial melting since the end of the Last Glaciation, has forced the displacement of lowland vegetation, as exemplified by the retreat and expansion of mangroves in the Cook Islands (Ellison, 1994) and Tonga (Fall, 2005), the formation of coastal plains and associated wetland vegetation in Hawaii (Athens & Ward, 1993), the replacement of littoral forests by heath and grasslands in Madagascar (Virah-Sawmy *et al.,* 2009), and the eventual presence of wetland vegetation in coastal lowlands in Mauritius (de Boer *et al.,* 2014).

Shifts in climate factors controlling the elevational distribution of zonal ecosystems

Vegetation changes favoured by climate amelioration since the end of the Late Glacial have been best documented for high-latitude and high-elevation islands, involving e.g. forest expansion (McGlone, 2002; Hannon *et al*., 2003), and the establishment of modern vegetation after ice retreat (Miller *et al*., 2005).

Patterns of elevational migration of plant species following climate change are reflected by pollen sequences in high islands including Madagascar (2876 m a.s.l., Gasse & van Campo, 1998), New Guinea (4884 m a.s.l., Haberle, 1998), Corsica (2706 m a.s.l., Reille et al., 1999), Maui (3055 m a.s.l., Burney *et al.,* 1995) and Taiwan (3952 m a.s.l., Liew *et al.,* 2006). However, such vertical displacements of vegetation may be limited on islands, especially in the lower ones. In Mauritius (828 m a.s.l.), alternation from wet to drier periods resulted in high turnover of mountain forest species. Since the late glacial, vegetation shifted from a stable open forest to a series of forest transitions, occurring during the early Holocene, and finally to a new stable closed-stratified forest from the mid–late Holocene (de Boer *et al.,* 2013). The shift in vegetation at the onset of the Holocene was initially driven by climate but then followed by natural forest dynamics as shown by the fast replacement of tree species in the pollen diagram. This forest succession has been proposed as an alternative mechanism to elevational migration in response to climate change for islands that present a relatively low elevation (de Boer *et al.,* 2013).

In oceanic islands, the variation in the main climatic factors (such as mean annual temperature or annual precipitation) in combination with the glacial cycles must have enforced the elevational redistribution of the species and ecosystem ranges (Prediction 4 a). In contrast to at least some continental contexts, the potential for vertical migration on high volcanic islands should limit the number of extinctions during periods of climate change. This inference is consistent with the observation that in several cases palaeo-endemic species have persisted on oceanic islands, relatively unchanged while disappearing from their source regions. Examples include the laurel-forest tree species that colonized

Macaronesia from Europe (Postigo Mijarra *et al*., 2009), or the tree-fern thicket species of St. Helena that reached this island from Africa, although they were later extinguished there due to climate aridification (Cronk, 1992).

Even without changes in temperature regime, sea level declines of up to 120 m would increase the overall elevation range of any island by an equivalent amount. However, besides the sea level drop, the temperatures decreased significantly (Braconnot *et al*., 2007), so that two factors, sea level fall and regional temperature drops coinciding with it, should be considered. A new summit ecosystem may emerge on an island when a glaciation causes the temperatures to decrease. Here pre-adapted species will be favoured in the colonization of these new emerged summits, whether located in the same or a different island. As a counterpoint to the foregoing, rising temperatures during interglacial periods may be expected to result in the reduction or disappearance of prevailing summit ecosystems (Fernández-Palacios *et al.*, 2014), so that some very rare species should present signs of having experienced a demographic collapse caused by climate-driven range contraction (Prediction 4 b). We predict as well that on some islands presently lacking ice sheets, geomorphological evidence will reveal their presence in the past (Prediction 4 c). However, on islands with maximum elevations above the climatic snow line, both the timberline and the snow line are pushed synchronously upwards (during interglacials) or downwards (during glacials), so that the upper elevational zones shift up and down without entirely disappearing at any point, while experiencing changing total area and degree of habitat fragmentation.

Such zonal shifts are largely temperature-driven but are also affected by changes in precipitation and cloud cover. Furthermore, temporal shifts between wetter and dryer conditions may in addition allow for the immigration or extinction of species or even the appearance or disappearance of vegetation formations or whole ecosystems. Finally, on conically shaped volcanic islands in particular, simultaneously rising sea levels and upward shifted climatic zones may be expected to have led to both a reduction of total surface area and an upslope shift of ecological zones, resulting in a reduction of both lowland and upland habitat areas and likely in a reduction of carrying capacity for some biota (Fig. 6).

Shifts in direction, frequency and intensity of marine currents and wind systems affecting the connectivity of the target islands

It has long been argued that glacial events may have played a significant role in opening new windows of opportunity for long-distance dispersal (LDD), temporarily allowing for dispersal routes that may appear otherwise unlikely (Wallace, 1880). In the Canarian region, where synoptic climate is presently dominated by the North-Eastern trade winds and the North-East Canarian marine current, an opposing dispersal route may have existed during the last glacial period (Rognon & Coudé-Gaussen, 1996). This route, created by reversed winds and currents, would have facilitated the colonization of the African continent from the Canaries, and thus may offer an explanation for the origin of some African endemic species intermingled within Macaronesian phylogenetic clades (termed boomerangs) (Carine *et al.*, 2004; Caujapé-Castells, 2004; Fernández-Palacios *et al.*, 2013) (Predictions 3 a and 5 a).

Recently published coupled-model simulation for the Last Glacial Maximum predict a substantial shift of the Northern Hemisphere Westerlies towards the equator along with a 3°C cooling at 7°N and a 6°C cooling at 11°N (Williams & Bryan, 2006). Along the same lines, Rognon & Coudé-Gausen (1996) asserted nearly two decades ago that several geomorphological features of Canarian and Maghrebian natural landscapes indicate the dominance of Westerlies wind regimes across the Madeiran-Canarian latitudes (25-30º N) during the glacial periods in the Pleistocene, due to an extreme southward shift of the Azores high pressure field because of the increased pressures exerted by the North Polar Front. Under these altered synoptic conditions, the unusual retro-colonization events from the Macaronesian islands to the continents become readily explainable. Similar shifts of westerlies in the Southern Hemisphere affecting New Zealand, the sub-Antarctic islands (McGlone *et al.*, 1995) and Tristan da Cunha (Ljung & Björck, 2007) have been reported. However, in the absence of precisely dated examples we cannot be sure if actual colonization events coincided with these periods. Finally, it should be noted that glacial events may have also modified the frequency and/or intensity of important periodic climatic events shaping the present biota and ecosystem structure and dynamics of oceanic islands, as has been recorded in recent decades in the Galápagos, under the influence of pronounced ENSO events (Tudhope *et al*., 2001).

TRAJECTORIES OF RELEVANT FACTORS DURING A GLACIAL CYCLE

To encapsulate key features of the above, we provide (Fig. 4a) a general schematic indicating the change in area, elevation and isolation of an oceanic island of middling age and stage, during the last glacial maximum. We assume in this schematic that there has been no volcanic/ geomorphic activity affecting island area or elevation and we have made no attempt to incorporate isostatic effects or island subsidence/uplift (cf. Ali & Aitchison, 2014). The schematic proposes that area and elevation are maximal, and isolation is minimal at the point of the LGM sea level minimum, which occurred around 20 ka (Lambeck *et al.,* 2002; Camoin *et al.,* 2004), with the post-glacial eustatic sea level increase generating reduced area and elevation, in tandem with increased isolation. Area and elevation are somewhat lower for the Eemian than currently, whereas that for isolation is slightly higher, indicating that during this, the previous interglacial period, the sea level was somewhat (8–10 m) higher than in the late Holocene (Camoin *et al*., 2004).

If we now recall that we often (as in the ETIB) use area as a proxy for extinction and isolation as a proxy for immigration, and also acknowledge that elevation (or altitudinal range) affects species richness, we hypothesized that accordingly with the changes of those geographical parameters, immigration, extinction, and species richness on an island have fluctuated through the last 130 Kyr as well. For this period, changes in immigration and extinction rates are hypothesized to be symmetrically opposed, with maximum immigration rates at the LGM, when extinction rates are minimal, and maximum extinction rates in the Interglacial periods when immigration rates are minimal (Fig. 4b) (Predictions 1 a and b). Species richness is expected to show a similar trajectory as the Immigration rate curve, being highest during the Glacial Maxima, and diminishing towards the Interglacial due to the occurrence of natural extinctions, caused by area reduction following sea level transgressions (Prediction 1 c). Furthermore, we hypothesised that some very rare species should present signs of having passed a demographic collapse ca. 15–12 kyr, resulting from range contraction due to sea level rise (Prediction 1 d).

It is important to say that this will mostly affect old islands that have developed a surrounding platform, due to their erosion. For young islands their area (and to a lesser degree isolation) will pass relatively little affected by the glaciations.

The same reasoning applies to guyots, with the difference that the geographic factors affecting them will depend on the sea mount–summit depth, because, in interglacial or interstadial periods, area, elevation, immigration, and species richness of terrestrial taxa will be zero, when the sea mount is submerged. Sea mounts also act as islands for marine species, and their carrying capacity of in particular the benthic communities can also be expected to change in relation to sea level change as the area of the sea mount within the photic zone changes (cf. Hart & Pearson, 2011).

Quantitative adjustments to models in the light of the foregoing would require careful estimation because the response of sea level to climate change is not instantaneous, so the correspondence between climate phase and sea level maxima or minima show some lag effects; furthermore, different cold and warm phases locked up different amounts of ice and so a sea mount might emerge in some cold periods but not all; and may disappear in some but not all warm periods (Lambeck *et al.,* 2002; Edwards, 2006). Nevertheless, we suggest that our hypothesis provides a general framework of predictions (see Box) that potentially can be tested for signals in immigration, extinction, genetic diversity, population bottlenecks and endemism.

TOWARDS A GLACIAL-SENSITIVE MODEL OF ISLAND BIOGEOGRAPHY

If we consider the implications of these changes in island properties in terms of the classic ETIB diagram of MacArthur & Wilson (1967), we may predict adjustments in the rates of immigration and extinction (Fig. 5), and by extension implications for the rates of evolutionary processes relating to the extent and degree of fragmentation, isolation and rejoining of major habitat types (not shown in Fig. 5). The main difference is that instead of representing only a “snapshot” of a single set of immigration and extinction rates of a geographically static island (MacArthur &

Wilson, 1967), this graph incorporates two sets of rates resulting from a glacial period and an interglacial period respectively, for the same island. In the first scenario, immigration rate (*I*) will be higher during the glacial period due to the lower degree of isolation of the island, both because of increased connectivity and an improved target-area effect (due to its larger size). In the second scenario, the extinction rate (*E*) will be higher during interglacial periods, both because of smaller island area and because increased isolation causes a diminished rescue effect. The projection onto abscissa from where the immigration-rate and extinction-rate curves intersect, represents the island species richness expected for the particular stage (glacial/interglacial). The projection onto the ordinate represents the expected species turnover. It should be noted that only these two intersection points are time-coherent, whereas the other two are just artefacts of the drawing procedure.

It should be clearly stated that our model only considers the impact on the biota of the island's area and the isolation shifts due to sea level fluctuations related to glacial cycles, and not the climatic conditions (and ocean/atmospheric systems) that will influence these islands during those periods. For instance, we do know that in the case of high-latitude islands, extensive ice cover during glacial periods has caused significant depressions of diversity (Alsos *et al*., 2005). On the other hand, isolation may have decreased as well due to the formation of ice bridges between islands. For instance, the extinct Falkland Islands wolf (*Dusicyon australis*), seems to have reached these islands from the Argentinian mainland through an ice bridge that was formed among them during a sea level low stand (Austin *et al*., 2013). Similarly, a role has been inferred for sea-ice-mediated colonization of Iceland by artic fox (*Alopex lagopus*) (Mellows *et al*., 2012).

In general, we consider the model to be most applicable therefore for tropical and subtropical oceanic islands during the Quaternary. This is not to say that such islands will have been entirely immune from climate change impacts during the Pleistocene. For instance, glaciers have formed on Mauna Kea (Hawaii) during cold phases (Porter, 1979), with the consequent elevational reorganization of the vegetation belts (Gavenda, 1992). Elevational movements in response to climate change have also been suggested by palaeo-ecological data elsewhere, e.g. on Oahu (Hotchkiss & Juvik, 1999), San Cristóbal (Colinvaux & Schonfield, 1976), Easter Island (Azizi & Flenley, 2008) and the Mascarenes (De Boer *et al*., 2013). Furthermore, low-lying island biotas would have little chance of escape of species towards lower elevations and several insular taxa could have gone extinct.

Nevertheless, even considering that those climatic shifts could have obscured the role of immigration and extinction processes driven by area and isolation changes, we highlight the potential importance of incorporating sea level shifts in Island Biogeography models. We hope as well that the explicit ecological, genetic, biogeographical and evolutionary predictions generated (see Box) will improve the relevance of other theoretical oceanic islands quantitative models (Whittaker *et al*., 2008, 2010; Rosindell & Phillimore, 2011; Rosindell & Harmon, 2013) recently developed.

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Biosketch:

José María Fernández-Palacios is a Canarian island ecologist and biogeographer, with a special interest in the role of recent, but also remote, history in shaping the ecosystems and biota of oceanic islands, with a special focus on the Macaronesian region. He also is active in research into the dynamics of the laurel forest, pine forest and thermophilous woodlands, as well as in the ecological restoration of those ecosystems.

Author contributions:

JMF-P, KFR and ET developed the idea and manuscript structure. KFR and SN produced Figs. 1, 2, 3 and 6, and JMF-P Figs. 4 and 5. RO, LdN and SFL revised the literature and finally, JMF-P and RJW led the writing.

Tables

Table 1: Major dynamic forces affecting marine islands. Key: - = relatively unaffected; + = moderately affected; ++ = considerably affected

Island Type	**Plate tectonics (100–1 Myr)**	**Island ontogeny (10–1 Myr)**	**Glacial cycles (100–1 Kyr)**	**Volcanic activity (< 1 Kyr)**
Continental-shelf islands	-	-	++	-
Continental fragments	++	-	+	-
Oceanic islands	+	++	+	++

Table 2: Summary of the biogeographical consequences of changes in climatic and geographic parameters related to glacial cycles.

Shifts related to Glacial cycles	**Geographical effects on island/archipelago setting**	**Biogeographical consequences**
- Sea level	- Area, elevation and isolation shifts - Fusion/fission of nearby islands - Sea mounts emersion/ submersion	- Shifts in area availability and connectivity, affecting immigration and extinction rates - Genetic dilution/allopatric speciation - Availability/unavailability of stepping stones
- Climate (temperature, precipitation)	- Shifts in the vertical temperature/precipitation gradients - Shifts in the elevation of the cloud-sea influence zone	- Elevation shifts of zonal ecosystems - Contractions/expansions of species distribution ranges - Emergence/disappearance of summit ecosystems - Species extinctions
- Marine currents and wind regimes (frequency, intensity, direction)	- Changes in mainland–archipelago, between-archipelago and within-archipelago connectivity	- Opening/closure of bizarre windows of dispersal - Boomerang events - Changes in marine species distributions

Table 3: Area increase during the Last Glaciation Maximum (LGM) in comparison with the present area for selected islands or island groups (see sources in the main text). * the increment in area implied the fusion of several current islands.

Island or island group	**Present area (km^2)**	**LGM islands**	**Approximate LGM area (km^2)**	**Times larger than present**
Isabela, St. Cruz Fernandina, islets (Galápagos)	6270	Large Isabela	10 000	1.6 *
Fuerteventura, Lanzarote, islets (Canaries)	2500	Mahan	5000	2.0 *
Maui, Lanai, Molokai (Hawaii)	2884	Maui Nui	6000	2.1 *
Boavista (Cape Verde)	600	Boavista Bank	2700	4.5
Porto Santo (Madeira)	65	Porto Santo Bank	250	3.8
Rodrigues (Mascarenes)	109	LGM Rodrigues	1200	11.0
St. Martin, Anguilla, St. Barthelemy (Lesser Antilles)	200	St. Martin Bank	6000	30.0 *
Seychelles	220	Granitic Seychelles	40 000	181.8 *

Box: Predictions of the glacial-sensitive model of Island Biogeography

[some sources with evidence supporting the predictions are given in parenthesis]

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1) Predictions linked to shifts in area and isolation

a) Immigration rate was lowest in the last interglacial (Eemian), when isolation was greatest, then rose throughout the last Glaciation until achieving its highest rate in the LGM (least isolation), before decreasing again until the start of the present interglacial (Holocene).

b) Extinction rate was highest in the last interglacial (Eemian), when island area was smallest, then dropped throughout the last Glaciation until obtaining its lowest rate in the LGM (largest area), before increasing again after the start of the present interglacial (Holocene).

c) Palaeontological and palaeocological research will make clear that several natural extinctions, caused by area reduction following sea level transgressions, occurred before human arrival to oceanic islands.

d) Some very rare extant species should present signs of having passed a demographic collapse ca. 15–12 kyr resulting from range contraction due to sea level rise (González *et al*., 2014).

2) Predictions linked to fusion/fission of islands

a) The fission of one large island into two or more smaller islands due to sea level rise will yield a high number of species shared among the once-attached islands, so that nearby islands subject to fusion/fission cycles will share more species than comparable island groups that were never physically linked (Macqueen *et al*., 2011; Rijsdijk *et al*., 2014).

b) Genetic analyses will evidence that genetic divergence has occurred among populations that were split (allopatry) when islands were separated during the interglacial periods [Bidegaray-Batista *et al.,* 2007; Ali & Aitchison, 2014].

3) Predictions linked to sea mounts emergence/submergence

a) Immigration and retrocolonization processes were favoured due to emergence of sea mounts during sea level regressions, thus enhancing connectivity.

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b) Fossil records on currently drowned seamount summits will reveal the presence (during the glacial events) of terrestrial plant species belonging to coastal ecosystems, shared with other nearby islands.

4) Predictions linked to climatic shift

a) Fossil records will reveal the elevational shift of zonal ecosystems toward island summits during interglacial events and toward coasts during glacial events (Hotchkiss & Juvik, 1999).

b) Some very rare species that are currently restricted to climatic refugia, should present signs of having experienced a demographic collapse caused by range contraction resulting from the disappearance of their ecosystem during the last deglaciation (Vaxevanidou *et al.,* 2006).

c) On some islands that presently lack ice sheets, geomorphological evidence will reveal the presence of ice sheets in the past (Porter, 1979).

5) Predictions linked to marine currents & wind regimes shifts

a) Shifts in marine currents and wind regimes have created new, bizarre dispersal windows, which should have left biotic signals in the form of retro-colonization (boomerang) events (Carine *et al.*, 2004; Caujapé-Castells, 2004).

Figure captions:

Figure 1 Global sea level change during the last 120 kyr. Generalized mean sea level (MSL) reconstruction from 120 ka based on Camoin *et al*. (2004). Regions that are uncertain in Camoin *et al*. (2004) were interpolated linearly. At period A, Eemian interglacial sea levels were 10 m higher than today; at period B, sea levels fell with the onset of the glacial epoch, and warmer periods (interstadials) alternating with colder periods (stadials) led to sea level fluctuations between –20 and –60 m; at period C, there was then a period of relative stability, although this may be an artefact of data sampling. Period D marks the extreme sea level fall during the Late Glacial Maximum (LGM); period E marks the rapid sea level rise at the end of the LGM; and period F marks the stabilization of sea levels at present-day levels.

Figure 2 Changes in selected Canary Islands' areas over the Last Glacial Cycle (Source: Rijsdijk *et al*., 2014). We merged a detailed bathymetric model, with a 1 km^2 resolution, with the sea level curve of Fig. 1. Fuerteventura merged several times with Lanzarote during the glacial period when sea levels lowered during stadial periods. While Gran Canaria increased in surface area, the area of the young island of El Hierro, did almost not change.

Figure 3 Transition from Mahan (LGM) to Fuerteventura, Lanzarote and islets (present East Canaries). The islands have undergone fission, halving their emerged area and increasing their distance to Africa due to sea level rise**.** In the inset graph the oscillation of the sea level (as in Figure 1) is represented. The last formation of Mahan and the last emergence of Amanay coincided with the Last Glacial Maximum (Period D), whereas the splitting in Lanzarote, Fuerteventura and the islets surrounding them and the submersion of Amanay began during the deglaciation period until achieving the present geographical configuration in the beginning of the Holocene (Period F). See text for a further explanation.

Figure 4 (a) Hypothesized variation of geographic parameters (area, elevation and isolation) of old oceanic islands during the most recent glacial cycle, comprising from the Eemian (130-120 Ka) to the Holocene. The trajectories have been kept simple for pedagogic reasons. In reality each of these trajectories should have been adjusted to take account of lag effects and to the precise timing of the most recent glacial ycle (see Fig. 1). (**b)** Hypothesized variation of biogeographic factors (immigration, extinction and species richness) on old oceanic islands during the most recent glacial cycle, comprising from the Eemian (130-120 Ka) to the Holocene. The trajectories have been kept simple for pedagogic reasons. In reality each of these trajectories should have been adjusted to take account of lag effects and to the precise timing of the last glacial cycle in particular parts of the world (see Fig. 1).

Figure 5 Proposed glacial-sensitive model of island biogeography. The main difference with the MacArthur & Wilson ETIB model (1967) is that instead of representing only a "snapshot" of a single set of immigration and extinction rates of initially inhabited and geographically static islands, this model incorporates two sets of rates resulting from a glacial period and an interglacial period respectively, for the same island. The projection onto abscissa from where the immigration rate (I) and extinction rate (E) curves intersect, represents the island species richness expected for this climatic context, whether a glacial or interglacial. It should be noted that only these two intersection points are time-coherent, whereas the other two are just artefacts of the drawing procedure. Although in some cases the degree of change in island area and isolation can be large, for instance, in older islands, such as the granitic Seychelles, Mahan, Boa Vista, Porto Santo, we expect this effect to be rather small in younger islands. S_{IG} and S_{GM} refer to species richness at equilibrium for the interglacial and glacial maximum, respectively; P represents the mainland species pool, which may also change in value between the two periods (not illustrated). See text for further explanation.

Figure 6 On conically shaped volcanic islands, the transition from glacial maxima, where the island area is greater, that isolation lower (inset graph as in Fig. 4a) and the species richness expected to be higher (inset graph as Fig. 5) to interglacial stages, where the island area is smaller, isolation higher (inset graph as in Fig. 4a) and species richness expected to be lower (inset graph as Fig. 5). These shifts will be linked to rising sea levels and upward shifted climatic zones, which may have resulted in a reduction of both lowland and upland habitat areas and a reduction of the carrying capacity for some biota.

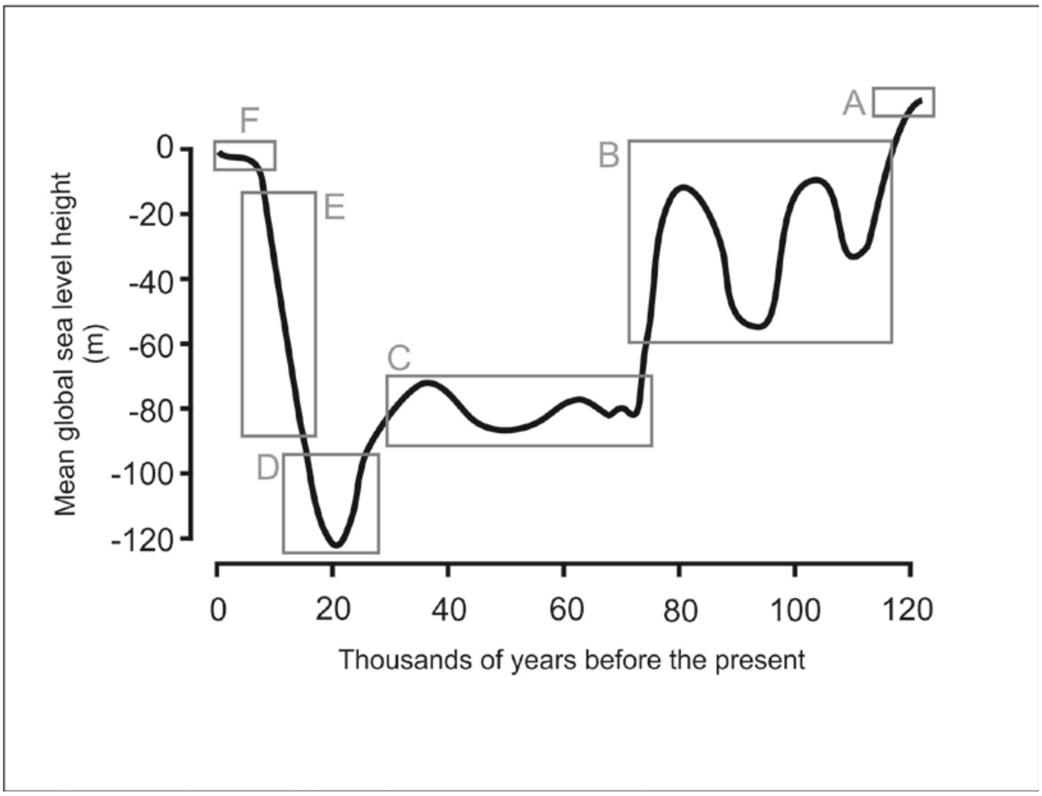

Figure 1

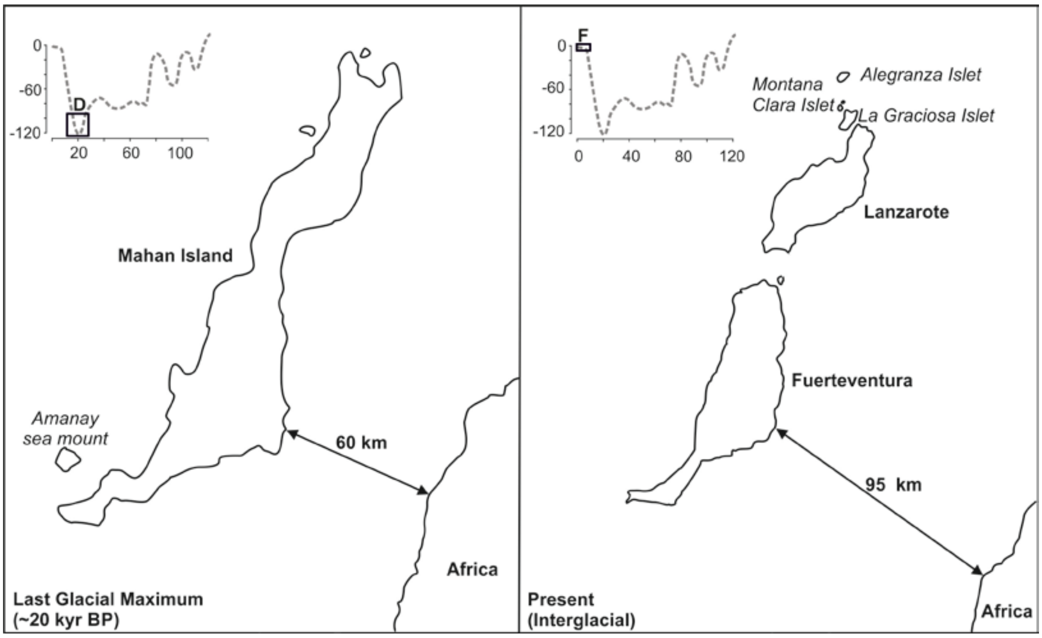

Figure 2

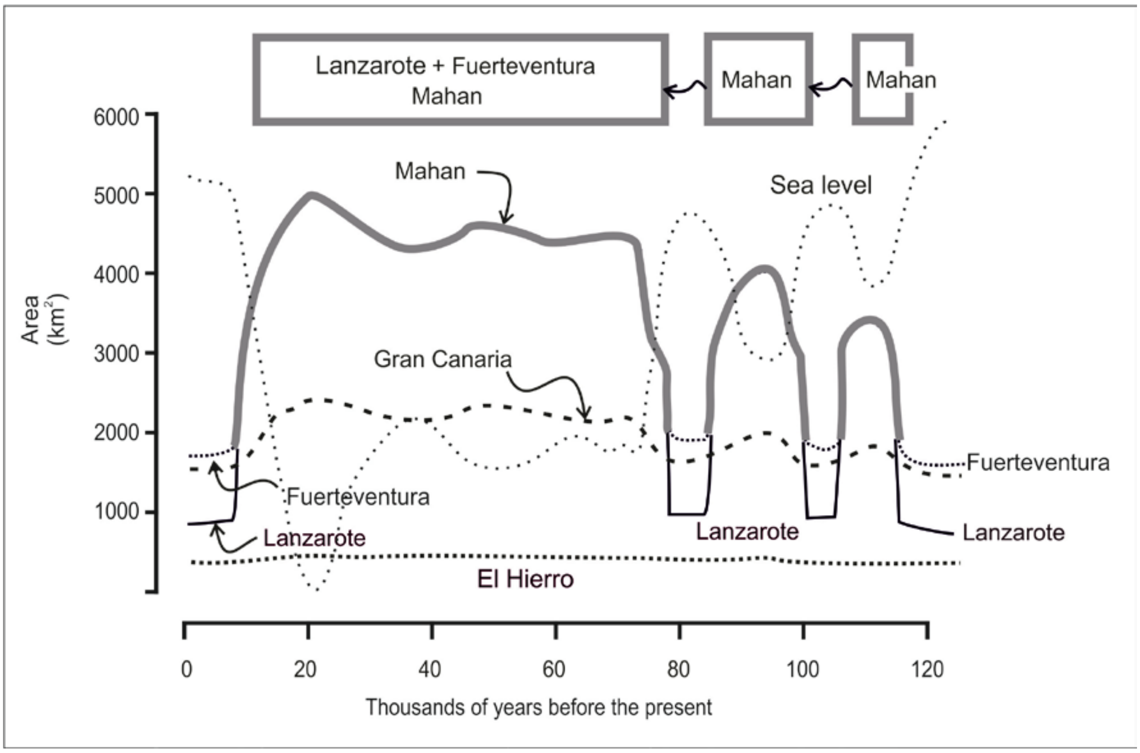

Figure 3

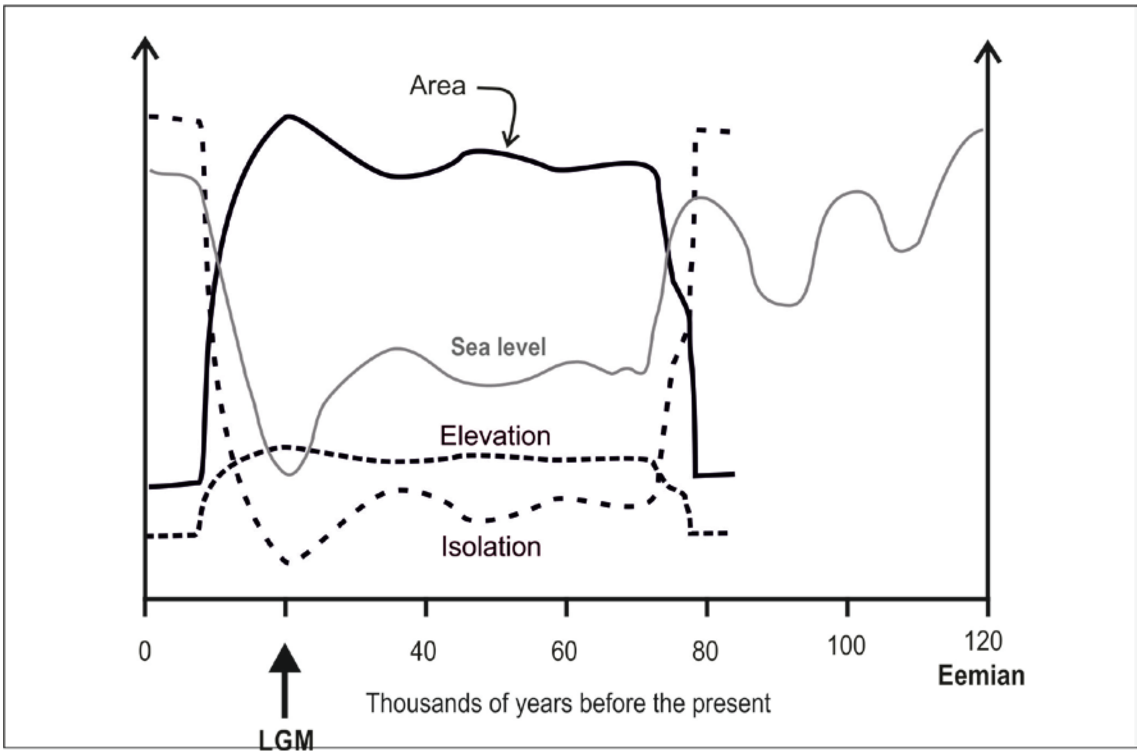

Figure 4a.

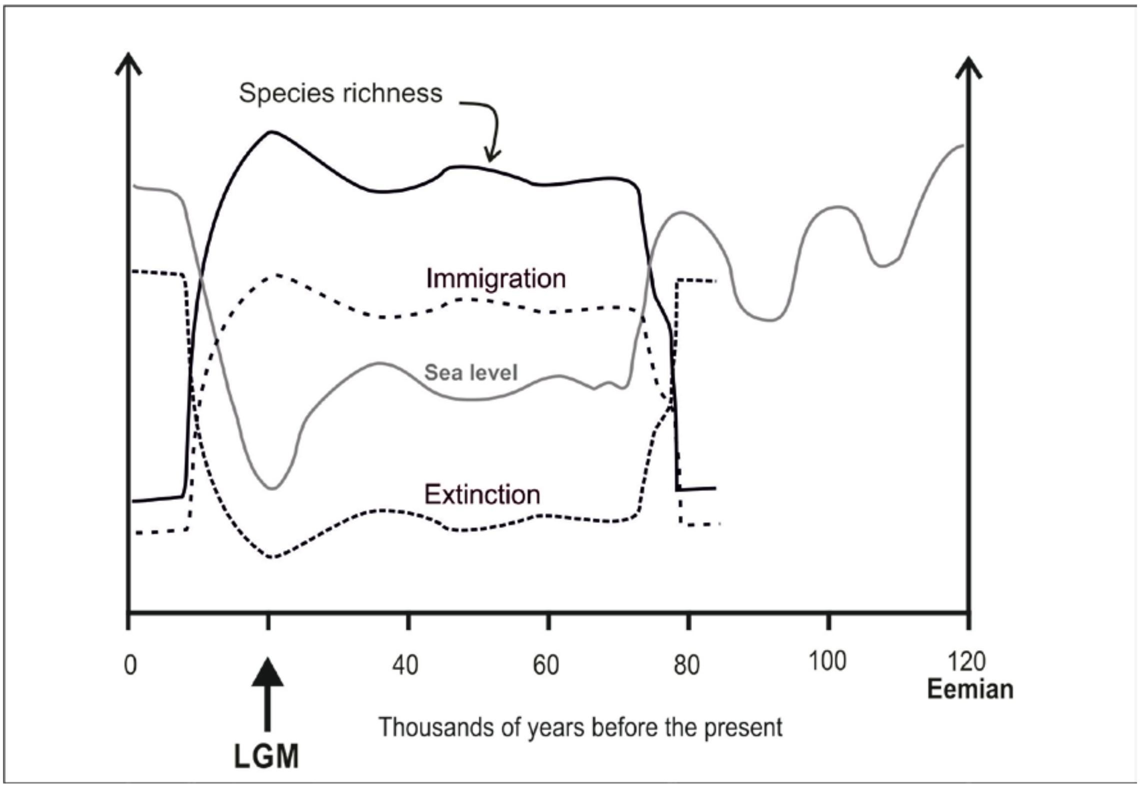

Figure 4b.

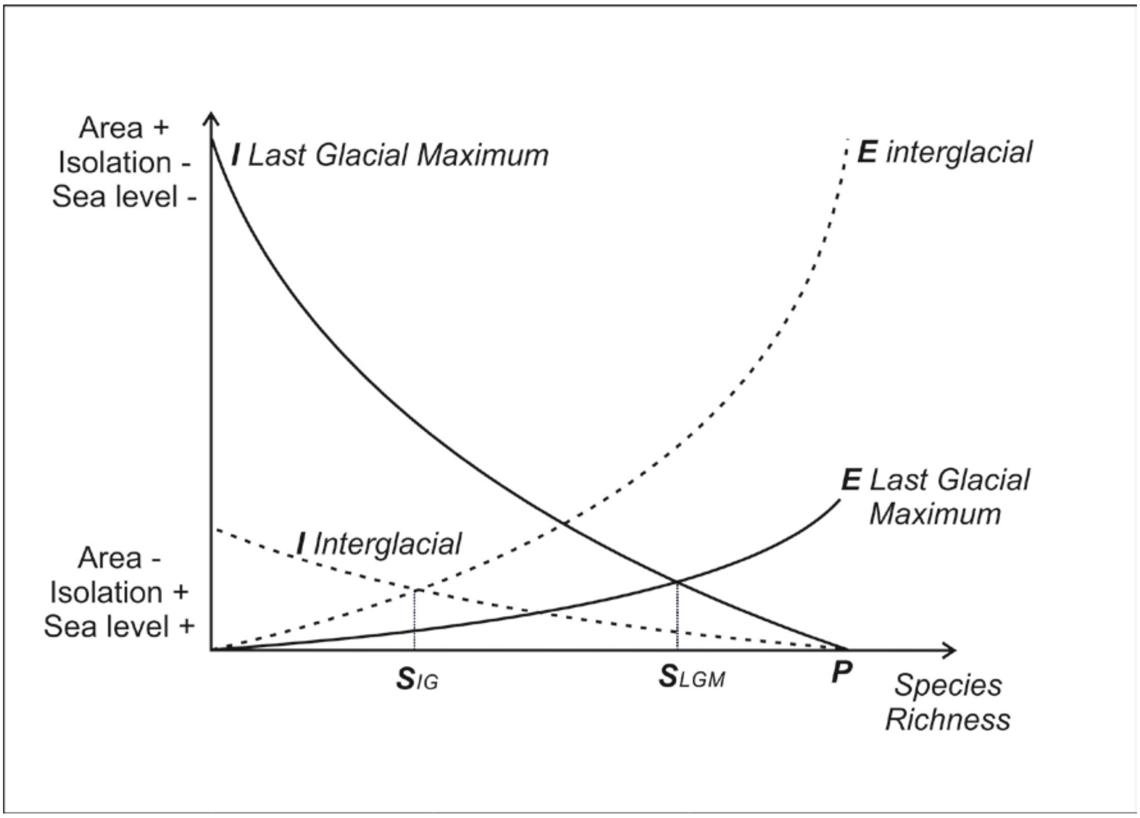

Figure 5.

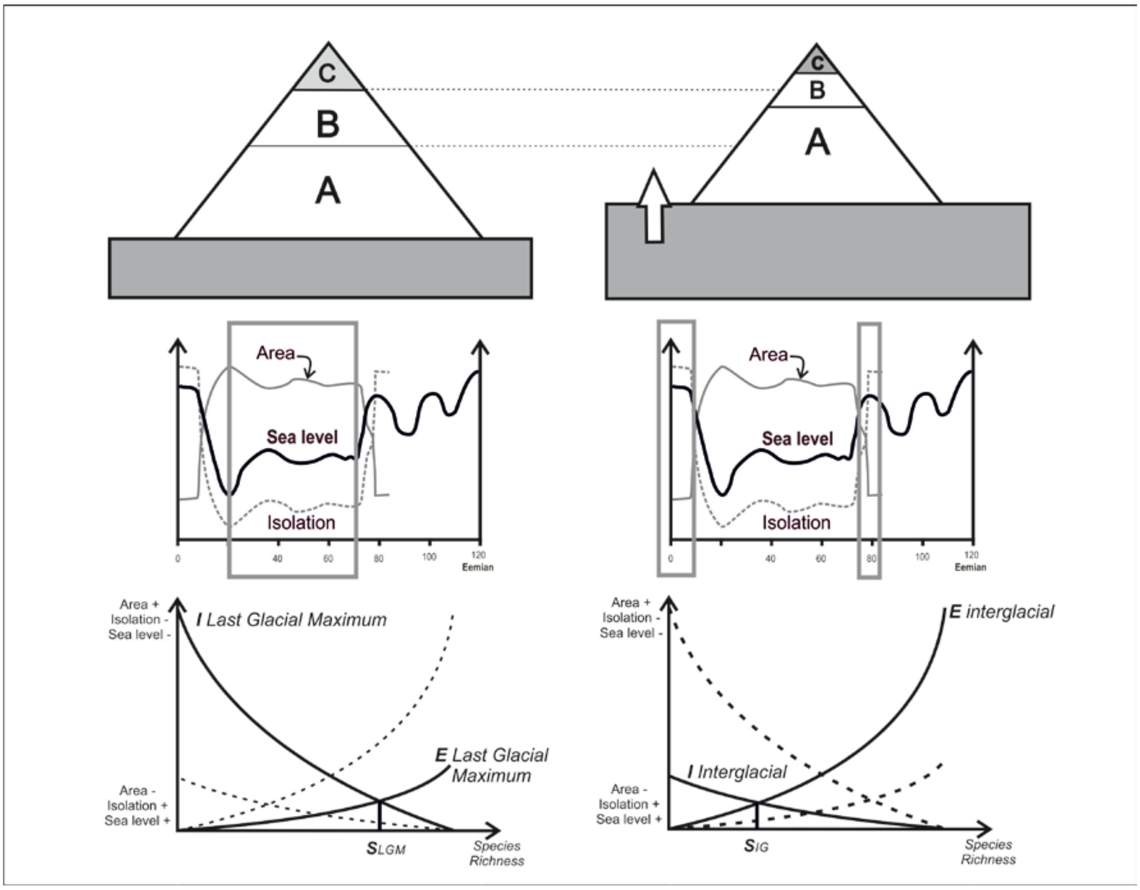
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Figure 6.