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### Modelling sea level driven change of Macaronesian archipelago configurations since 120 kyr BP

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MODELLING SEA LEVEL DRIVEN CHANGE OF  
MACARONESIAN ARCHIPELAGOS  
CONFIGURATIONS SINCE 120 KYR BP

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CLIMATE CHANGE PERSPECTIVES FROM THE ATLANTIC:  
PAST, PRESENT AND FUTURE

Jose María Fernández-Palacios, Lea de Nascimento, José Carlos Hernández,  
Sabrina Clemente, Albano González & Juan P. Díaz-González (eds.)  
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## ABSTRACT

The MacArthur and Wilson island biogeography theory relates species diversity on islands as the result of equilibrium between extinctions and colonization events which rates depend on island size and isolation. Although island size and isolation can be considered static on ecological timescales (<100 years) they are not static on longer time scales. Since the last million years sea levels fluctuate with a period of ca. 120 kyr between -120 m and up to +10 m MSL (Mean Sea Level). Due to these sea level changes islands have changed in size and ultimately may have drowned or emerged. The rate and degree of their drowning depends on island morphometry and the shape of the sea level change curve. We explore the effects of global sea level cycles on the configuration of archipelagos and volcanic islands of Macaronesia. The results indicate that the islands changed shape considerably during the last 120 kyr. Notably the period between 80 kyr and 15 kyr ago sea levels were at least 80 m lower than present and several islands now isolated were merged or were much larger than present. Recent shrinking of islands due to the sea level rise since the last glacial maximum period (20 kyr BP) led to more than 50% reductions in island size, significant loss of coastal habitat and a significant increase in isolation by the increase of distances between islands and island and continents. Island size reduction must have induced pressures especially on terrestrial insular ecosystems, inducing upward migrations and interspecies competitions, and probable extinctions. The splitting of merged islands must have led to separations of populations leading to gene flow losses for some biota. Present day islands are not representative for the mean island configurations during the last Myr but rather represent an anomaly. Islands at present are smallest and most isolated and this configuration makes the insular biota even more vulnerable to human impact.

**KEYWORDS:** island biogeography, last glacial cycle, Palaeo-Macaronesia, sea level change.

## INTRODUCTION

Since its introduction by MacArthur and Wilson (1963; 1967), the Dynamic Equilibrium Model has been the ruling paradigm in island biogeography and nature conservation. It models species abundances ( $S$ ) on an island of given size ( $A$ ) as a dynamic equilibrium between numbers of species immigrating to the islands and number of species that become extinct. It predicts that as soon as the carrying capacity ( $K$ ) of a given island is reached, some species inhabiting the islands begin to undergo extinction processes. Furthermore, it becomes harder for species to settle and survive. A dynamic equilibrium between immigration and extinction

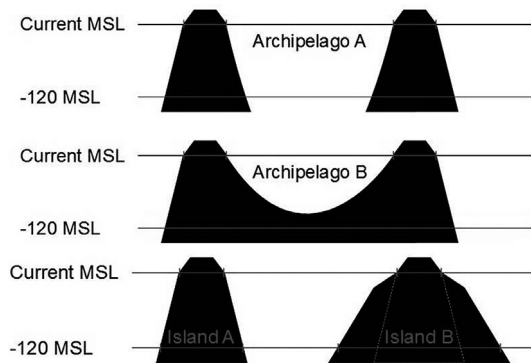


Figure 1. Basic principles of island morphology affecting size changes during sea level falls or rises. When volcanic islands are steep cones (Island A), surface change is minimal. When islands are relatively flat surface (Island B) change is large. A land bridge may emerge during sea level fall between islands of Archipelago B.

numbers is reached, resulting in an island equilibrium number of species ( $S^*$ ).  $S^*$  has a log linear relationship between area ( $A$ ) and distance to continents ( $D$ ). Size in this model approximates the carrying capacity ( $K$ ) of islands, with larger islands holding more species. The dynamic equilibrium model assumes however that island and archipelagos are static through time, i.e. they remain static in size and configuration. Although island size and isolation can be considered static on ecological timescales ( $<100$  years) they are not static on longer time scales ( $>1$  kyr). Following the calls by Heaney (2000; 2007) and Brown and Lomolino (2000) to develop a comprehensive theory for oceanic island biogeography that unifies ecological and evolutionary biogeography, Whittaker, Fernández-Palacios and coauthors (2001; 2007; 2008) evaluated the role of island ontogeny on explaining biodiversity. They pointed out that volcanic islands are dynamic on evolutionary time scales ( $>100$  kyr). On these longer time scales evolutionary processes, migration and extinction rates are affected by island ontogeny and plate tectonics. Here size and thus  $K$  is modified by island ontogeny which changes during a complete cycle of the islands emergence (youth), erosion (maturity) and final submergence (old age) as volcanism ceased (Fig. 1).  $K$  therefore follows a hump-shaped trend, increasing during island youth and finally decreasing during islands senescence. Based on this, Whittaker *et al.* (2007; 2008) postulated their General Dynamic Model (GDM) whereby terrestrial single-island endemic species (SIE) on evolutionary time scales show a parabolic relationship with Time ( $T$ ):

$$\text{Number SIE} = \log A + aT + aT^2$$

For a number of islands and taxa they demonstrated that the abundance of SIEs is significantly correlated in the GDM (Whittaker *et al.*, 2008). These findings strongly suggest that SIEs abundances are to a large degree controlled by island age.

#### TOWARDS A MODEL THAT INCLUDES SEA LEVEL DYNAMICS

At «sub-evolutionary» time scales, between 1 kyr and 100 kyr, island sizes (A) and archipelago configurations are not static either. Due to the rise and fall of sea levels islands may shrink or expand dramatically, resulting in a dynamically changing of A and K and thus affecting biota on islands and biota migrating between islands (Warren *et al.*, 2010; Fernández-Palacios *et al.*, 2011). Furthermore, currently drowned seamounts may emerge and submerge due to sea level fluctuations, opening or closing specific dispersal routes within or among archipelagos as well as among archipelagos and the closest continents (García-Talavera, 1999; Ávila, 2000; Ávila and Malaquías, 2003). Natural sea level change results by long term climatic change, driven by astronomical cycles. The Serbian civil engineer and mathematician Milutin Milankovi (1879–1958), suggested in the 1940s that climatic cycles were driven by the cumulative effects of the shape of the earth's orbit around the sun (eccentricity), and changes in the inclination of the earth axis towards the sun (precession and obliquity). As a result of the interplay between these astronomic variables the net radiation the Earth receives varies leading to natural climate change cycles. While Milankovi theory of climate change was not accepted until decades after his demise, the theory has been proven correctly to explain the periodicity and intensity of climatic change cycles (Hays *et al.*, 1976; Imbrie and Imbrie, 1980). With the emergence of radiometric dating methods and their application in sea level dynamic research since the 1960s it has been found that major cycles of sea level rise follow those of climatic change. Oxygen isotopic analyses on marine microfossils in marine cores have provided continuous records of global sea level cycles from 5 Myr ago until present (Lisiecki and Raymo, 2005). Spectral analysis of these cycles confirmed that they are superimposed astronomical cycles. Due to the superimposition of the precession, eccentricity and obliquity cycles the amplitude and duration of sea level fluctuations changes through time. During the Pliocene (before 2.6 Ma) climatic change cycles were dominated by the precession cycles (22 kyr) leading to low magnitude short duration cycles of climate change (Lisiecki and Raymo, 2005). With the onset of the Quaternary 2.6 Myr ago climatic cycles were driven by obliquity with amplitudes of global temperatures and periodicity increasing to 41 kyr. Climatic change has become most extreme since 0.9 Myr ago when they became eccentricity forced with 100 kyr cycles (Ruddiman, 2003). As a result, ice ages lasting 100 kyr alternate with interglacials lasting ca. 10 kyr coinciding with low and high sea level stands respectively. During the glacial maxima when ice sheets reached their largest

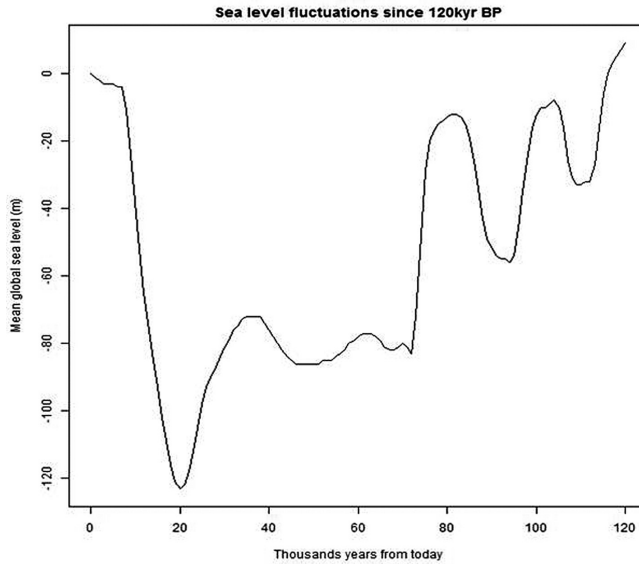


Figure 2. Sea level change reconstruction since 120 ka BP based on Camoin *et al.* (2004). Regions that are uncertain in Camoin *et al.* (2004) are here linearly interpolated.

extent, sea levels fell -120 to -130 m below present Mean Sea Level (MSL). Highest sea levels were reached during interglacials of up to +10 m MSL during the last interglacial. Based on radiometric dating of stalagmites in caves and corals that drowned and emerged during the last sea level cycle global sea level fluctuation since 120 kyr BP and especially since 10 kyr ago are reconstructed in detail (Fig. 2) (Cutler *et al.*, 2003; Zinke *et al.*, 2003; Camoin *et al.*, 2004). The last sea level cycle (Fig. 2) commenced 120 kyr ago with a relative short high stand during the pre-last interglacial lasting 10 kyr. During the subsequent glacial (120 to 70 kyr BP) sea levels fell and fluctuated between -20 and -60 m MSL. This period was followed by an extreme rapid fall of 10.6 (m/kyr) to -80 m MSL lasting 40 kyr followed by a further fall to -120 m MSL during the glacial maximum (40 to 16 kyr BP) (Cutler *et al.*, 2003). From ca. 19 kyr ago sea levels started to rise initially very rapidly 7 m/kyr until 7 kyr ago, when sea level rise decelerated to ca. 1 m/kyr. Global sea level stabilized and reached present levels ca. 2500 years ago (Zinke *et al.*, 2003; Camoin *et al.*, 2004). The last very rapid phase of sea level rise must have had major repercussions for terrestrial species on drowning islands. It is intriguing and biogeographically relevant to realize that current interglacial sea level at 0 m MSL is anomalously high for the Quaternary, and that ca. -60 m MSL is the mean for the last glacial interglacial cycle.

The rate and degree of surface change, drowning or emerging of islands depends on island morphometry and the shape of the sea level change curve. Depending on the morphometry of the drowned part of the islands the effect of sea level rise in size reduction and isolation can be more or less profound (Fig. 1, see below). Hence the effect of sea level change on volcanic islands differs among islands. In addition, for terrestrial species the connectivity between islands (and between island and mainland) decreases as a consequence of submerged topographical variability. Also seamounts currently submerged, when within a depth of 120 m were islands during the glacial forming important additional stepping stones (e.g. Warren *et al.*, 2010). Thus, both the marine and terrestrial biota of islands and archipelagos must have been affected by these changes (e.g. Ávila *et al.*, 2008; Fernández-Palacios *et al.*, 2011; Ávila, this volume).

In order to assess the effect of sea level induced change of islands on biota and biodiversity, and add the sea level history as an explaining variable to the GDM, we constructed a GIS (Geographical Information System) based algorithm that is able to reconstruct palaeo island sizes and island configurations and to derive quantitative metrics that can be used to investigate the role of sea level change on biota configurations (Rijsdijk *et al.*, submitted). Using merged digital elevation models of topography and bathymetry, volcanic island configuration change driven by sea level change is modelled over the last sea level cycle (120 kyr – present). We present here the sea-level driven change of island areas and archipelagos configuration during the last glaciation cycle for the Macaronesian biogeographic region (the North-East Atlantic volcanic archipelagos of Azores, Madeira, the Canaries and Cape Verde). We discuss some important biogeographical implications of those sea level changes and the potential to implement the model to extend the GDM.

## MATERIAL AND METHODS

We developed a novel way of modelling palaeo island change and deriving geomorphometrical metrics using the Free and Open Source software for statistical computing R in combination with the OSGeo software FWTools and GIS (Rijsdijk *et al.*, submitted). The link between GIS and R operations is established via various R libraries (RSAGA, RODBC, rgdal) (Bivand *et al.*, 2008). SAGA GIS has been used for manipulation and calculations within spatial grids, while R is the central programming environment which stands on-top of the external GIS applications (Hengl, 2009). In the resulting model island size and archipelago configuration change are driven by one sea level cycle (from 120 kyr to present). In the following sections, it will be described how island metrics are calculated and which palaeo-island configuration maps are created with the algorithm.



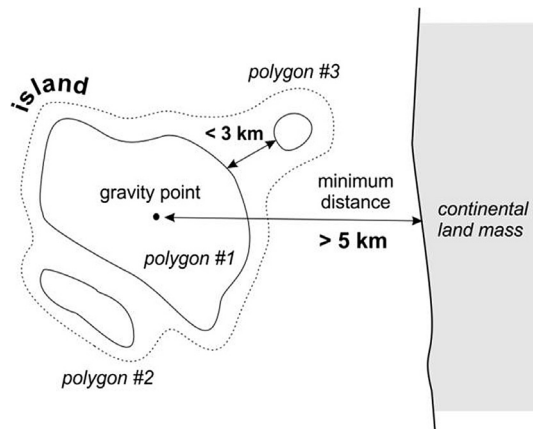


Figure 3. In order to model surface changes of islands it is crucial to employ a morphometric definition of an island that can be used in an algorithm. Here an island is considered a separate entity when (at current MSL) the area of its bounding box is larger than 3 km<sup>2</sup>, and the distance of its gravity point to a continent is larger than 5 km and its minimum boundary distance to another island or continent is larger than 3 km (see Table 1 for a complete description of island classification).

TABLE 1. Criteria for defining polygons as separate islands (area and distance are measured at current MSL).				
Classification	Area (km <sup>2</sup> ) of polygon bounding box		Distance (km) to edge of other polygon	Species data
One polygon classified as separate island:	> 3	AND	>3 km	AND Species data is gathered for separate polygon
Several polygons classified as largest island			< 3km (including 'stepping stones')	AND Species data is gathered for polygons
Polygons are omitted	< 3	AND	> 3 km	OR Species data is not available for polygon

## ISLAND DEFINITIONS

The island administrative boundaries from the global administrative areas database (GADM, courtesy of Robert Hijmans and colleagues) were used to obtain present day island boundary polygons and derive present island surface areas for Macaronesian islands. Missing island boundaries were digitized manually from the high-resolution Ikonos images of Google Earth. In GIS terms, an island is defined as a collection of closed polygons representing land mass. To reduce computer calculation time, the minimum size for polygons to be included in the analysis as separate island was set to 3 km<sup>2</sup> (see Fig. 3 and Table 1 for the island classification rules). Reconstructed sizes are based on raster calculations with a cell size of 1 km<sup>2</sup>. The resulting generalization error increases with island size decreasing, therefore areas of small islands (<10 km<sup>2</sup>) are significantly over-estimated, with the most extreme case representing an island of 1 km<sup>2</sup> of which the boundaries overlap with four grid cells.

## MODELLING PALAEO-ISLAND EXTENTS

In order to derive the distances from oceanic islands to the nearest continents, we used the World Vector Shoreline dataset at scale 1:250,000 to construct a grid of closest distances from points (oceanic islands) to continents (Fig. 4, [www.worldgrids.org](http://www.worldgrids.org)). Distance to closest island as a grid was derived iteratively for each island using buffer distance operations in a Geographic Information System (GIS) software (SAGA GIS, System for Automated Geoscientific Analyses, <http://www.saga-gis.org>). In order to obtain the required metrics from palaeo-extents of islands we merged a terrestrial digital elevation model (DEM), based mainly on data from the Shuttle Radar Topography Mission (SRTM) with a detailed bathymetric model (Becker *et al.*, 2009), both on a 1 km<sup>2</sup> resolution. This merged topographic and bathymetric DEM model is used to calculate the palaeo-island extents at various sea level heights through R-algorithms and SAGA GIS (Bivand *et al.*, 2008; Hengl, 2009) (Fig. 5). The palaeo-BioIslands GIS (pBIG) model we developed produces maps of the palaeo-extent of islands and palaeo-configurations for selected time windows of the four archipelagos of Macaronesia. For all palaeo-configurations maps area created with buffer distances from each island to the nearest other islands and emerged seamounts within the same archipelago. Surfaces and configurations are calculated for each of the 120 time steps with intervals of 1 kyr. The resulting area and distance maps are used to construct island indices that reflect the change in island size and archipelago configuration. The pBIG model does not take into account the changes in shape of islands that may result by landslides or volcanic activity.

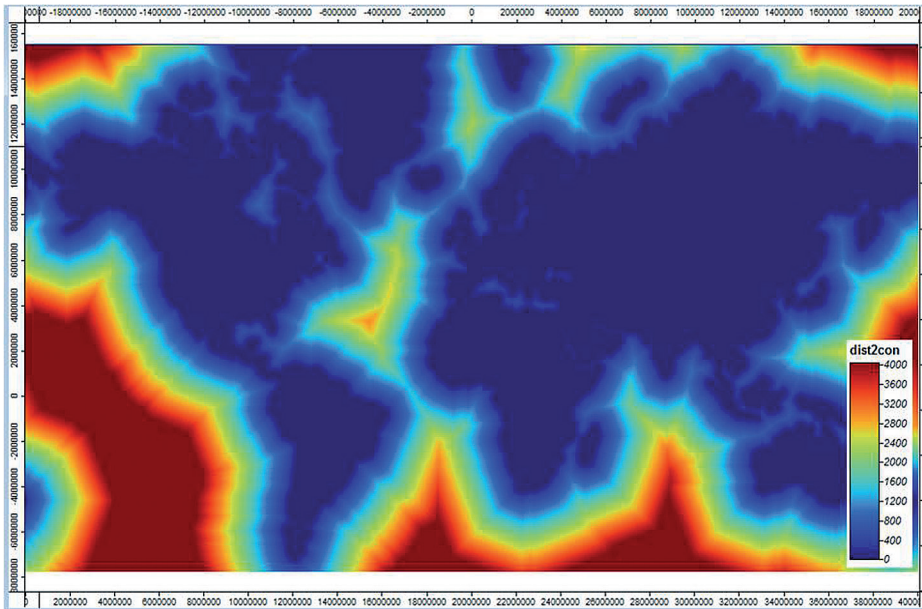


Figure 4. Distance to continents buffer grid (source: [www.worldgrids.org](http://www.worldgrids.org)). In order to obtain the required metrics from palaeo-extents of islands we merged a terrestrial digital elevation model (DEM), based mainly on data from the Shuttle Radar Topography Mission (SRTM) with a detailed bathymetric model, both on a 1 km<sup>2</sup> resolution.

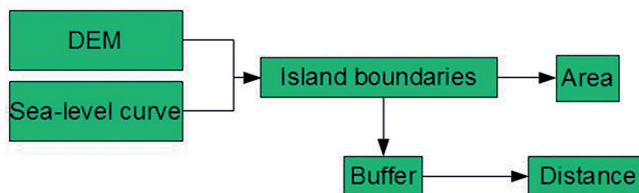


Figure 5. Flow diagram with processing steps for calculating distance and area. These steps are carried out for each island per 1 kyr during 120 kyr. In turn, the resulting area and distance maps are used to calculate island indices.

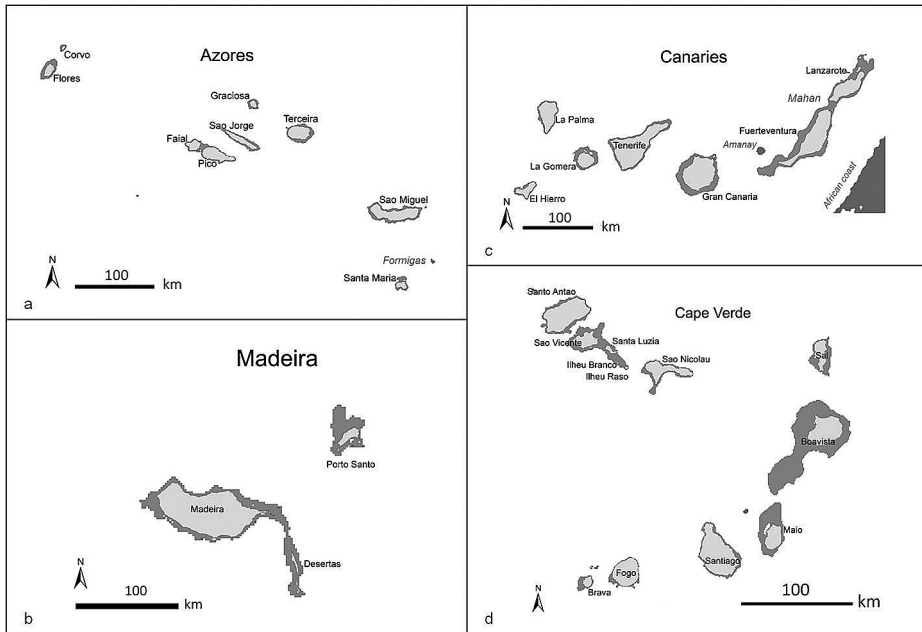


Figure 6. Surface change maps of a) Azores, b) Madeira, c) Canaries, and d) Cape Verde (Rijsdijk *et al.*, submitted). The light grey area represent the current island area, the dark grey shaded area reflects the maximum extensions of the islands during the glacial extreme low MSL stand 21 ka BP (-120 m below current level). Grey letters are names of palaeo-islands that emerged or were merged during the last glacial period. a) Azores, b) Madeira, c) Canaries, d) Cape Verde.

## RESULTS

### MORPHOMETRIC RESULTS

Within these reconstructions we focus upon the effects on island geometry for the last 80 kyr and the Holocene sea level rise (see Fig. 2), because from this period onward islands expanded and shrunk in sizes maximally. From 80 kyr ago sea level dropped with the highest rates recorded of 10.6 m/kyr to -80 m MSL. Then it remained stable for 40 kyr after it dropped another 40 m to -120 m MSL during the last glacial maximum (Cutler *et al.*, 2003). Then it rose very fast from 10 kyr ago at a rate of ca. 6 m/kyr to reach its present level at 0 m MSL ca. 2.5 kyr ago (Camoin *et al.*, 2004). The fast sea level rise from ca. 19 kyr ago led to abrupt separations of merged islands within several millennia and maximum shrinkage of areas.

Since the LGM most islands of the Azores shrunk between 20 and 50% during the Holocene sea level rise (Figs 6a and 7a). The islands of Faial (173 km<sup>2</sup>)

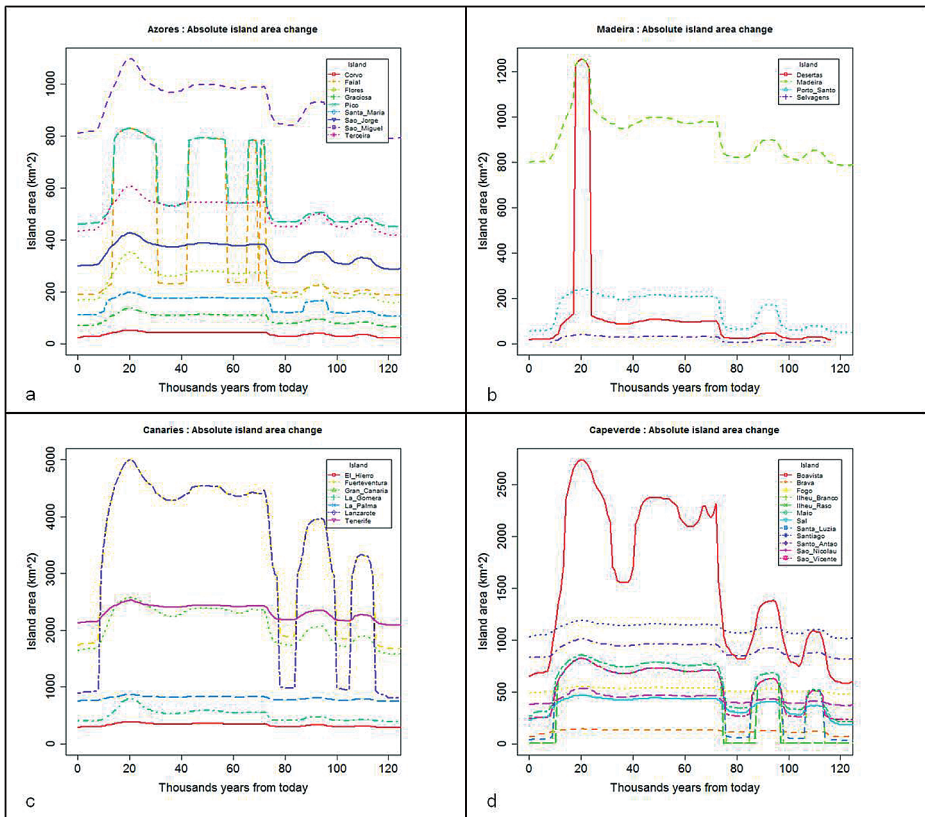


Figure 7. Absolute island area changes for Macaronesian islands since 120 kyr ago (Rijsdijk *et al.*, submitted).

and Pico (444 km<sup>2</sup>) were merged for a period of ca. 16 kyr between 30 and 14 kyr ago to form Laurinsula (the name derives from Laurel forests which at that time covered the land), an island of circa 800 km<sup>2</sup>. Also between 57 and 43 ka BP and 72 and 66 ka BP these islands were connected (except for a short interval around 70 ka BP). In addition the present-day Formigas islets, with a maximum height of only 14 m and an area of just 0.01 km<sup>2</sup>, were during the LGM much larger (~40 km<sup>2</sup>) and higher (130–140m) (Ávila, 2005).

Madeira (742 km<sup>2</sup>) increased for more than 50% in size during the LGM reaching 1256 km<sup>2</sup> (Figs 6b and 7b). The main event here is the connection of Desertas (Ilheu de Chão, Deserta Grande and Bugio, comprising together 14 km<sup>2</sup>) to Madeira during the LGM between 23 kyr and 18 kyr ago. However, within

a single millennium, Desertas abruptly became separated from Madeira again, some 18 kyr ago. Between 72 and 13 ka BP, Porto Santo (today 43 km<sup>2</sup>) was ca. five times larger than present (reaching 240 km<sup>2</sup> during the LGM).

The most significant event in the Canary Islands (Figs 6c and 7c), which happened between 77 and 9 ka BP during the LGM, was the merging of Fuerteventura (1677 km<sup>2</sup>) and Lanzarote (850 km<sup>2</sup>), as well the islets located North of Lanzarote (Alegranza, Montaña Clara and La Graciosa) or North of Fuerteventura (Isla de Lobos), into a single larger island, called today Mahan (García-Talavera, 1999), that was larger than 5000 km<sup>2</sup>. North to the western tip of Mahan, some 15 km from its coast, a present-day seamount called Amanay was emerged during glaciation times, achieving in the LGM an area of ca. 200 km<sup>2</sup> and an altitude of ca. 100 m. The distance between Fuerteventura and Gran Canaria increased from 55 km during the LGM to 87 km at present. The distance from the African coast to Mahan was only 56 km during the LGM versus today's 96 km separating Fuerteventura and the Saharan coast. Finally, also noteworthy for this archipelago is that during the LGM, the island of La Gomera (373 km<sup>2</sup>) was nearly twice its current size, whereas Gran Canaria (1574 km<sup>2</sup>) was over 1.5 times larger than today.

Finally, the Cape Verde experienced the most radical size and configuration changes in the last glaciation cycle among the Macaronesian archipelagos (Figs 6d and 7d). Four windward islands (São Vicente, Santa Luzia, Ilhéu Branco and Ilhéu Raso) were merged to form a large island between 74 kyr and 13 kyr ago of up to 830 km<sup>2</sup> during the LGM. These merged islands approached Santo Antão for less than 5 km (currently 12 km). Most significantly the distance between island São Nicolau and Santo Antão, currently ca. 75 km, was in this period through the merged islands less than 5 km. The island Boa Vista (632 km<sup>2</sup>) was on average 3.5 times larger than today between 72 and 14 kyr ago (maximum of ca. 2750 km<sup>2</sup> during LGM). During this period the island Maio (today 273 km<sup>2</sup>) was more than 850 km<sup>2</sup>, and the distance from Maio to Boa Vista was reduced to less than 7.5 km, compared to its present 77 km isolation.

## DISCUSSION

### SEA LEVEL CURVES AND LOCAL VARIATION

Due to various geological factors volcanic islands may sink or rise independent of global sea level change inducing a regional relative sea level rise or fall. It is therefore important to assess in how far these factors affected Macaronesian islands. When oceanic volcanoes become inactive they load the lithosphere which as a result may flex downward, leading to the sinking of the volcano (Whittaker *et al.*, 2008). On the other hand the loading of the lithosphere by newly formed volcanoes may induce uplift of older volcanoes that are situated on the same tectonic

moat (Menéndez *et al.*, 2008). Other factors inducing uplift include for instance lithosphere flexure as a result of tectonic plate collision (Menéndez *et al.*, 2008), reheating of the lithosphere above hotspots (Crough, 1978), lithospheric flexing and bulging around the point of loading (Grig and Jones, 1997), and upwelling mantle plume dynamics (Davies, 1988; Morgan *et al.*, 1995; Ribe and Christensen, 1999). Recently Ramalho *et al.* (2010) relate the uplift of Cape Verdean islands to expanding laccoliths that formed underneath marine sediments and volcanic edifice. Menéndez *et al.* (2008) mention erosive removal of terrestrial sediments (large-scale landslides) may lead to a decrease in loading and result in vertical uplift of the lithosphere. Empirical data for Macaronesian archipelagos suggests these factors all have less than 10% effect on the last sea level cycle from 120 kyr to present. In the Canarias, raised Pliocene sea level markers such as pillow lavas indicate maximum mean uplift rates between 0.022 and 0.024 m/kyr (Meco *et al.*, 2002; Zazo *et al.*, 2003; Menéndez *et al.*, 2008). These local uplift rates are not significantly modifying the eustatic sea level rise curves for the last 120 kyr. Zazo *et al.* (2003) derive mean uplift rates from Marine Isotope Stage 5e highstands in the Canarias and Baleares ranging between +0.046 and -0.007 m/kyr, these rates amount at maximum to ca. 5 m height differences over 120 kyr and can be considered insignificant in affecting the palaeo insular shape change patterns presented here. A sequence of Middle Pleistocene (330 ka BP) to Holocene marine terraces on Sal island in the Cape Verdean archipelago ranges between +50 and +2 m MSL indicate a maximum uplift rate of 0.14 m/kyr, or 14 m/100 kyr (Zazo *et al.*, 2007; Ramalho *et al.*, 2010). If correctly dated and interpreted this may be significant affecting island shapes given the «sensitivity» to sea level change of the relatively low Cape Verdean islands (see Figs 6d and 7d). Other factors that lead to regional deviations of the global sea level curve is the global redistribution of melt water in the oceans leading to ocean water loading effects of the lithosphere and differential crustal flexing (Lambeck and Chappel, 2001; Milne and Mitrovica, 2008; see Gehrels and Long, 2008 for a review). The precise effects and amounts of vertical movement vary across the globe as a function of crustal rigidity, mantle rheology and water distribution. However effects that are recorded within the (sub-)tropical zone are generally in order of several meters during the last maximum sea level rise of 120 m suggesting the total contribution of this component is minor. A final effect is that melt water is not evenly distributed across the globe, but as a function of the dynamic interplay between the gravity pull of ice sheets and the ocean water mass. As the volume of water in the oceans increases due to polar ice sheet melting at the same time, the strength of the gravity pull from the ice sheet decreases. The overall effect is a regionally different response but overall resulting in faster sea-level rise in areas distal from the melting source (Milne and Mitrovica, 2008). While the archipelagos nearby the African continents seem rather insensitive to this effect, the Azores are located in the middle of the Atlantic Ocean, representing an area that was sensitive to these effects (>15 m differences during LGM) and consequently sea



level reconstructions must be interpreted carefully. Although the individual effects of local factors modifying island shape-change may be limited during one sea level cycle (120 kyr), their combined effects may complicate sea level based reconstructions of palaeo-islands and hence local assessment of these combined effects on the global eustatic sea level curve is crucial for precise reconstructions of island area and archipelago configurations.

#### BIOGEOGRAPHIC IMPLICATIONS

The present island area, and related features, such as shape, altitude, isolation or geographic configuration of archipelagos represent transitory stages that result by two long-term dynamic processes, 1) the ontogenetic history of the volcanic islands themselves, lasting millions of years (Whittaker *et al.*, 2007; 2008), and 2) the incidence of the Pleistocene Glaciation cycles, lasting hundreds of millennia (Warren *et al.*, 2010; Fernández-Palacios *et al.*, 2011; Ávila, this volume; Rijdsdijk *et al.*, submitted). It is therefore indispensable to take these processes into account for a correct interpretation of the biogeographical, ecological and evolutionary processes shaping present-day insular biotic assemblages, as well as their constituting species distributions and geographical affinities. As these processes progressively transform islands and archipelagos, these dynamically changing geographical conditions will create spatiotemporal dynamic biogeographical contexts, to which the species and ecosystems will have to adapt. The degree of emergence and submergence of volcanic islands due to sea level fluctuations will depend on their age or «ontogenetic stage» (cf. Whittaker *et al.*, 2007; 2008). The older (>4 Myr) islands of archipelagos, which are in the mature or senile stages, are more sensitive to sea level changes than the younger and steeper islands. The older islands have generally more extensive submarine topography and marine platforms due to post volcanic subsidence, and longer periods of subaerial and marine erosion and reef building. Examples include Santa Maria in the Azores, Porto Santo in Madeira, Fuerteventura or Lanzarote in the Canaries, or Maio and Boa Vista in the Cape Verde. In contrast, the younger immature islands of the archipelagos are minimally affected by the sea level changes due to their steep submarine topography, for example, Corvo in Azores, El Hierro and La Palma in the Canaries or Fogo in Cape Verde.

As demonstrated, the volcanic archipelagos comprising Macaronesia constitute an outstanding example that illustrates how Quaternary sea level rise and retreat cycles can significantly alter the islands geographic characteristics that are controlling colonization processes, for instance, by decreasing significantly the inter-insular and island-mainland isolations in the Last Glaciation Maximum, or by merging different islands (Faial with Pico, Madeira with Desertas, Lanzarote with Fuerteventura and related islets or São Vicente, Santa Lucia, Branco and Raso) (Figs 6 and 7). Furthermore, the emergence and submergence of shallow



seamounts with summits less than 120 m below present sea-level (e.g., Ormonde seamount, Gorringer Bank, Seine seamount, Dacia seamount, etc.), by acting as biological stepping stones must have repeatedly opened or locked dispersal routes within archipelagos, between archipelagos and between archipelagos and the mainland (Ávila and Malaquías, 2003; Fernández-Palacios *et al.*, 2011; Warren *et al.*, 2010).

Of course, sea level driven changes of islands and archipelagos were adjoined by significant changes in climate (temperature, precipitation, wind and marine currents regimes) on the islands (see Hooghiemstra *et al.*, this volume). As temperature increased during interglacial periods, islands contracted in size and previously merged islands became separated leading to inland and upward (to the cooler summits) migration of terrestrial species and ecosystems (see Hooghiemstra *et al.*, this volume). During glacials species migrated back towards the expanded coasts. Both climate change and sea level induced change led to a continuous biotic rearrangement of insular communities on the islands. In contrast to continents insular biota could not migrate to extensive hinterlands and were forced to endure these changes. This may have resulted into extinctions of single island endemics, local extirpations of species on some islands, or increase in resilience of insular species (Rijsdijk *et al.*, 2009; Hooghiemstra *et al.*, this volume). Furthermore, the expansion of the islands, doubling in sizes (Santa Maria, Azores or La Gomera, Canaries), by three times increases (Fuerteventura and Lanzarote, Canaries) or even more than three times increases (Formigas, Azores; Porto Santo, Madeira or Boa Vista, Cape Verde), must have created new opportunities for colonizers, but on the other hand also increased significantly the competition for space when the island shrunk during interglacials. Sea level driven island and archipelago changes did affect islands globally, consequently interpreting present insular species composition or population genetic traits in terms of present-day islands' or archipelagos' geographical features, i.e. considering area, carrying capacity, and isolation as static variables, may lead to erroneous interpretations. New island biogeographical theories must include the whole spectrum of spatiotemporal changes in area, carrying capacity and isolation and assess to what degree this affected biota in the past and how it will affect them in the future.

#### FURTHER WORK

Further work will use a modified version of pBIG to assess with generalized linear models (GLM's) what role palaeo-island size/configurations may play in explaining biodiversity patterns on islands. pBIG will be modified with R algorithms that automatically analyses species data sets in relation to various abiotic explanatory variables including indices that are derived from palaeo-extents of islands and archipelagos. For this purpose data sets of insular species that have comparative dispersal traits should be collected. However, biodiversity data from

volcanic islands covering most islands of an archipelago are scarce, or are at least poorly disclosed. A BioIslands.org data portal has been set-up to collect species data of islands supplied by experts. This allows building up data sets of various islands that allow for statistical assessments. A further objective is to network researchers and research organizations actively involved in insular biodiversity research and gather enough world data to develop more accurate (global) models of island biodiversity. We call upon colleagues to join this initiative and supply insular species data of volcanic island archipelagos ([www.BioIslands.org](http://www.BioIslands.org), see below).

## CONCLUSIONS

We have outlined a PalaeoGIS based methodology to reconstruct past island size changes and archipelago changes driven by sea level fluctuations. The method is successfully applied for four Macaronesian archipelagos (Azores, Madeira, the Canaries and Cape Verde) (Fig. 6) (Rijsdijk *et al.*, submitted). The results indicate that islands changed shape considerably during the last 120 kyr. Notably in the period between 80 kyr and 15 kyr ago, several islands now isolated were merged or were much larger than present. Ecologically and biogeographically the recent shrinking of islands due to the sea level rise since the last glacial maximum period (20 kyr) led in some cases to more than 50% reductions in island size, significant loss of coastal habitat and a significant increase in isolation by the increase of distances between islands and island continents. Every island and archipelago has its own specific morphometric change history as a function of its shape and the local sea level fluctuations. For instance, young volcanic islands characterized by steep conical submarine slopes (such as El Hierro or La Palma in The Canaries) have smaller area or shape changes compared to relatively flat old islands (such as Boa Vista in Cape Verde) that changed significantly their areas. In addition, the presence of submerged topography during sea level fall induced merging of isolated islands in a larger one, such as Lanzarote merged with Fuerteventura in the Canaries. The island size reduction must have induced pressures on the insular ecosystems, inducing upward migration and interspecies competition. The split of merged island must have led to separations of populations leading to gene flow losses for some biota. Critically the present day configurations, island sizes and isolation is not representative for the mean island configurations during the last Myr but rather represents an anomaly that only represents ca. 10% of the past Myr. Islands at present are smallest and most isolated and this configuration makes the insular biota even more vulnerable to human impact. The pBIG sea level algorithm we present here can be used to include past MSL as an explanatory variable for current biodiversity patterns on oceanic islands. We set up the BioIsland.org initiative to collect abundance data from insular species to statistically and qualitatively assess in what respect past sea level configurations must have affected biota, ecosystems and biodiversity.

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