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Geographic changes in the Aegean Sea since the Last Glacial Maximum: Postulating biogeographic effects of sea-level rise on islands

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ABSTRACT

In order to assess how the last sea level rise affected the Aegean archipelago, we quantified the magnitude and rate of geographic change for the Aegean islands during the last sea-level-rise episode (21 kyr BP–present) with a spatially explicit geophysical model. An island-specific Area-Distance-Change (ADC) typology was constructed, with higher ADC values representing a higher degree of change. The highest fragmentation rates of the Aegean archipelago occurred in tandem with the largest rates of sea-level-rise occurring between 17 kyr and 7 kyr ago. Sea-level rise resulted in an area loss for the Aegean archipelago of approximately 70%. Spatiotemporal differences in sea-level changes across the Aegean Sea and irregular bathymetry produced a variety of island surface-area loss responses, with area losses ranging from 20% to >90% per island. In addition, sea-level rise led to increased island isolation, increasing distances of islands to continents to >200% for some islands. We discuss how rates of area contractions and distance increases may have affected biotas, their evolutionary history and genetics. Five testable hypotheses are proposed to guide future research. We hypothesize that islands with higher ADC-values will exhibit higher degrees of community hyper-saturation, more local extinctions, larger genetic bottlenecks, higher genetic diversity within species pools, more endemics and shared species on continental fragments and higher *z*-values of the power-law species-area relationship. The developed typology and the quantified geographic response to sea-level rise of continental islands, as in the Aegean Sea, present an ideal research framework to test biogeographic and evolutionary hypotheses assessing the role of rates of area and distance change affecting biota.

1. Introduction

1.1. Sea-level rise

Since the Last Glacial Maximum (LGM; ca 21 kyr BP), global average sea levels have risen by >120 m (Cutler et al., 2003; Lambeck et al., 2014). During this period mean rates of sea-level rise was ca. 6 m per 1000 years. These higher limit values are comparable to the rates predicted by modeled scenarios for present day and near future human-induced sea-level change (Fig. 1a; IPCC, 2013). Vast areas were flooded, palaeo-islands and land bridges submerged, peninsulas transformed into islands, and islands were fragmented into smaller entities. Sea-level rise led to reductions in island areas and increases in distances to the mainland, causing higher isolation (Rijsdijk et al., 2014). While it is clear that the geographic changes resulting from sea-level rise must have affected insular biotas, their biogeography, evolution, and gene pools (Diamond, 1972; Wilcox, 1978; Heaney, 1986, 2000, 2007; Louys et al., 2007; Whittaker et al., 2010; Fernández-Palacios et al., 2011, 2015; Ali and Aitchison, 2014; Rijsdijk et al., 2014), the actual impact is difficult to determine. Sea-level changes may explain discrepancies between predicted and observed spatial patterns of species diversity on islands as modeled by species-area relationships (e.g. Simberloff, 1976; Rosenzweig, 1995; Whittaker, 1998; Connor and

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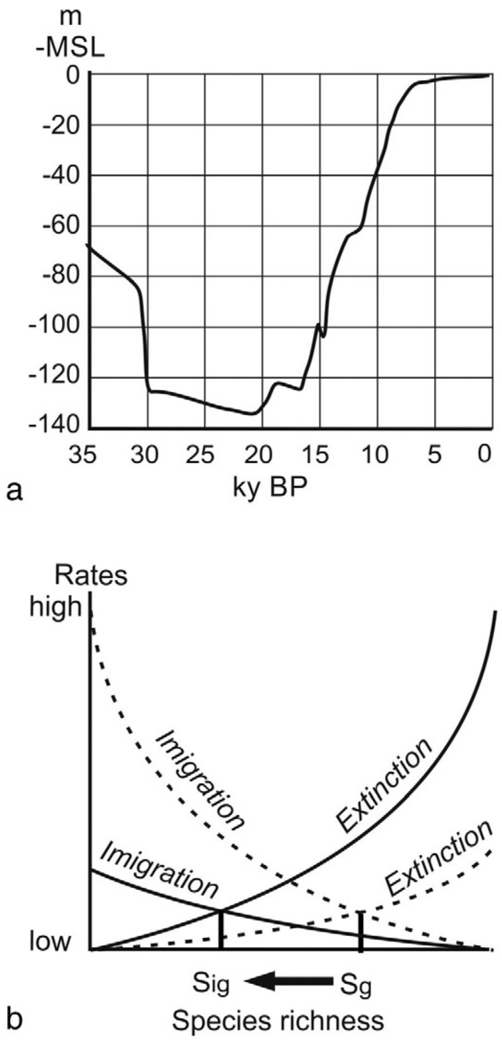

Fig. 1. a) Eustatic sea-level change during the last 35 kyr (Lambeck et al. 2014) b) Effects of different area sizes and isolation on migration and extinction rates as a result of glacial lowstands (indented lines) and interglacial high sealevel stands (solid lines) (Fernández-Palacios et al., 2015). During interglacials when sea-levels are high, equilibrium species richness (Sig) is lower due to smaller area size and higher isolation than during glacials (Sg), when sea-levels are low.

McCoy, 2000; Qian and Ricklefs, 2000; Triantis et al., 2008a; Whittaker et al., 2008). Here, we use an explicit geophysical model to quantify sea-level changes that account for glacial- and hydro-isostatic adjustment (Spada and Stocchi, 2007). Accordingly, our topographic reconstructions stem from regionally varying solid Earth deformations and geoid variations that accompanied the melting of LGM continental ice sheets. Furthermore, we present hypotheses in the light of biogeographic patterns for future research.

1.1.1. Sea-level rise and species richness

The species-area relationship (SAR) describes how the cumulative number of species changes with an increase in the area studied (Tjørve and Tjørve, 2017). SARs are used to forecast extinction from habitat loss (Triantis et al., 2010), and should also predict changes in species numbers caused by past and present sea-level rise. Many models have been suggested to fit SARs (see e.g. Tjørve, 2003, 2009), although both island (or isolated habitat patches) SARs and sample-area (or mainland) SARs are commonly expected to be described by the power law:

$$S = cA^z, \tag{1}$$

where S is the number of species, A is area, c and z are parameters. Preston (1962) proposed a canonical (universal) value for the z-parameter of 0.26, though fitting the power model to empirical data shows that the z-value varies systematically (Rosenzweig, 1998) around this figure. Although the generality of the SAR has proven valid, the precise underlying biological mechanisms and the shape of this relationship, especially the variation in z, are still debated (Rosenzweig, 1995; Ricklefs and Lovette, 1999; Triantis et al., 2003, 2012; Turner and Tjørve, 2005; Whittaker and Fernández-Palacios, 2007). However, recent theories propose a SAR with three distinct phases (i.e. triphasic) in log-log space (e.g. Hubbell, 2001; McGill and Collins, 2003; Rosindell et al., 2011). MacArthur and Wilson's (1963, 1967) equilibrium theory of island biogeography (ETIB) explains the island SAR as a balance between species immigration and extinction, where islands nearer to the mainland (or other islands) have higher immigration rates than distant ones, and smaller islands have higher extinction rates than larger islands. Since the inception of the ETIB, a number of authors (Simberloff, 1974; Heaney, 1986, 2000; Bush and Whittaker, 1993) have argued that long term equilibria are rarely achieved on islands, because of the constantly changing physical conditions (e.g. volcanic activity, climate change). For this, they advocated discussing a dynamic-disequilibrium (Heaney, 2000), or more recently a General Dynamic Model (Whittaker et al., 2008). Lately, the effects of sea-level change on species richness have been addressed in a Glacial Sensitive Model variant of the ETIB (Fernández-Palacios et al., 2015). In this Glacial Sensitive Model (GSM), it is argued that species richness rarely reaches equilibrium, as it is constantly in transition due to glacial – interglacial sea-level cycles, with high species numbers during sea-level low stands, when islands are largest and distances are shortest and vice versa (Fig. 1b). Although the premise of a disequilibrium is emphasized in the GSM, it assumes equilibria are reached during and after the geographic change occurred. A key question that arises is: how long does it take before equilibria are reached following sea-level fluctuations?

1.1.2. Sea-level rise and speciation

With increasing distances to continents the opportunity for allopatric speciation increases through cladogenesis, and leads to high endemic species richness, whereby colonizing species separated from their sister species and evolved into new species, such as the Galapagos finches (Heaney, 2000; Lomolino, 2001; Gillespie and Baldwin, 2009). Endemic species-richness patterns are related to the age and evolution of islands (e.g., Heaney, 2000; Lomolino, 2000; Johnson et al., 2000; Stuessy, 2007; Whittaker et al., 2008; Chen and He, 2009; Rosindell and Phillimore, 2011; Steinbauer et al., 2013). Changes in island geography over millions of years affected evolutionary dynamics (e.g., Johnson et al., 2000; Stuessy, 2007; Whittaker et al., 2008; Chen and He, 2009; Rosindell and Phillimore, 2011). This realization led to the recent formulation of the General Dynamic Model (GDM), which postulates that endemic species-richness variation on islands mirrors a parabolic trend related to size change of volcanic oceanic islands over millions of years, reflecting their initial volcanic emergence, their maximum size, and final submergence of islands at the end of their life cycle (Whittaker and Fernández-Palacios, 2007; Whittaker et al., 2008, 2010). There is, however, evidence that evolutionary processes are also influenced by geographic changes over shorter time spans, encompassing sea-level cycles. Sea-level changes may affect colonization, with alternating cycles of merging of species during sea-level low stands and isolation of populations during high stands (Ali and Aitchison, 2014; Rijsdijk et al., 2014; Weigelt et al., 2016). This geographically mediated cyclic dynamic led to the idea of islands becoming species pumps (Qian and Ricklefs, 2000; Price and Elliott-Fisk, 2004; Gavrilets and Vose, 2005; Kisel and Barraclough, 2010; Papadopoulou et al., 2011). Gene pools repeatedly broke up because of sea-level rises (causing a higher degree of insularity and longer distances between islands) and resulted in increases in the genetic variability of populations (Bidegaray-Batista et al., 2007; Ali and Aitchison, 2014). Thus,