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.

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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
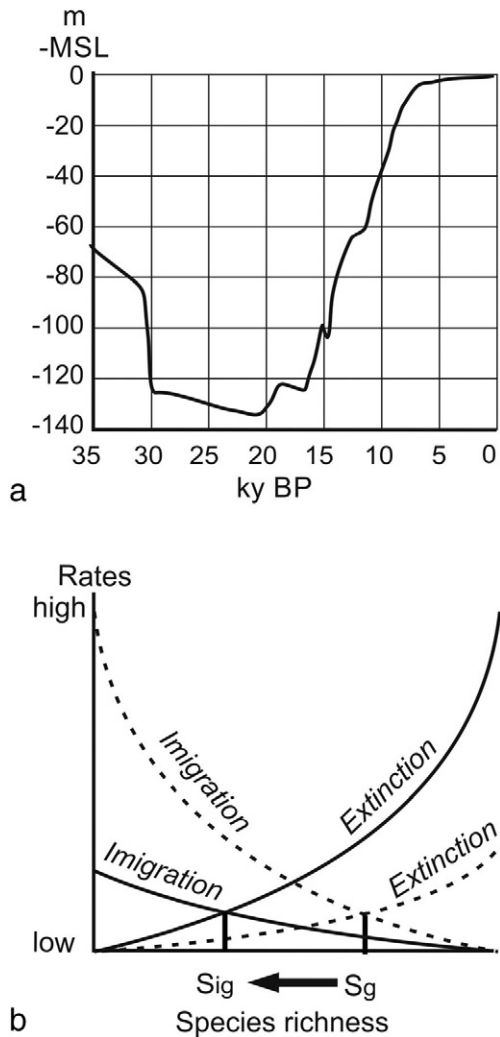
Fig. 1. a) Eustatic sea-level change during the last 35 kyr (Lambeck et al. 2014) b) Effects of different area sizes and isolation on migration and extinction rates as a result of glacial lowstands (indented lines) and interglacial high sealevel stands (solid lines) (Fernández-Palacios et al., 2015). 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,

the isolation periods of gene pools during high interglacial sea levels may have led to phylogenetic splits (Ali and Aitchison, 2014; Rijsdijk et al., 2014; Fernández-Palacios et al., 2015). Given the repetitiveness of glacial cycles and the fact that biota have endured ten glaciations during the Quaternary, it may be argued that insular species, especially endemics, have become resilient to sea-level changes and their associated range contractions and gene pool fragmentations (Rijsdijk et al., 2014; Weigelt et al., 2016). While it seems obvious that sea-level-mediated change on islands must affect biota, including their evolution and distribution, it is still unclear when and how biota are affected by sea-level-driven geographic change. This is mainly because the magnitude and rates of change that islands underwent is poorly understood. Recently, it has become possible to quantify rates of geographical changes in islands generated by sea-level alteration in continental settings, taking into account the geophysical complexity involved by modeling local sea-level-rise curves (see below).

1.2. Study area - the submergence of the Aegean archipelago

The Mediterranean basin constitutes a major global-biodiversity hotspot and hosts thousands of continental islands (Blondel and Aronson, 1999). Specifically, the Aegean Sea consists of approximately 7800 islands, dominated by small islands, islets and rock pinnacles smaller than 1 km² (Triantis et al., 2008b; Triantis and Mylonas, 2009). The Aegean Islands may be divided into five major biogeographic regions, which responded differently to sea-level rise (Fig. 2). The first region includes the Cyclades, a group of shelf islands off the eastern coast of mainland Greece. They were segregated from the mainland tectonically in the Middle Pleistocene (Foufopoulos and Ives, 1999). During the last ice age the currently >55 islands (larger than 1 km²) were merged into what is called the "Mega-Cyclades palaeo-island", which fragmented into an archipelago of islands during the subsequent sea-level rise at the end of the ice age (Kapsimalis et al., 2009). The second region includes the East Aegean Islands (i.e., the Dodecanese), a group of former palaeo-peninsular islands lying on the Anatolian shelf, off western Turkey. There are some exceptions such as the island of Astypalaia, which is palaeogeographically part of the Cyclades in the Central Aegean (for further details see Kougioumoutzis et al., 2016). These islands arose when landbridges drowned and peninsulas became separated from Asia Minor by sea level rise <20 kyr BP (Van Andel and Shackleton, 1982; Perissoratis and Conispoliatis, 2003). The third region, the South-Aegean Island Arc, is an insular chain extending from south-east Peloponnese towards south-west Asia Minor (i.e., Crete, Karpathos, Kythira, Rodos and their adjacent islets). This island arc
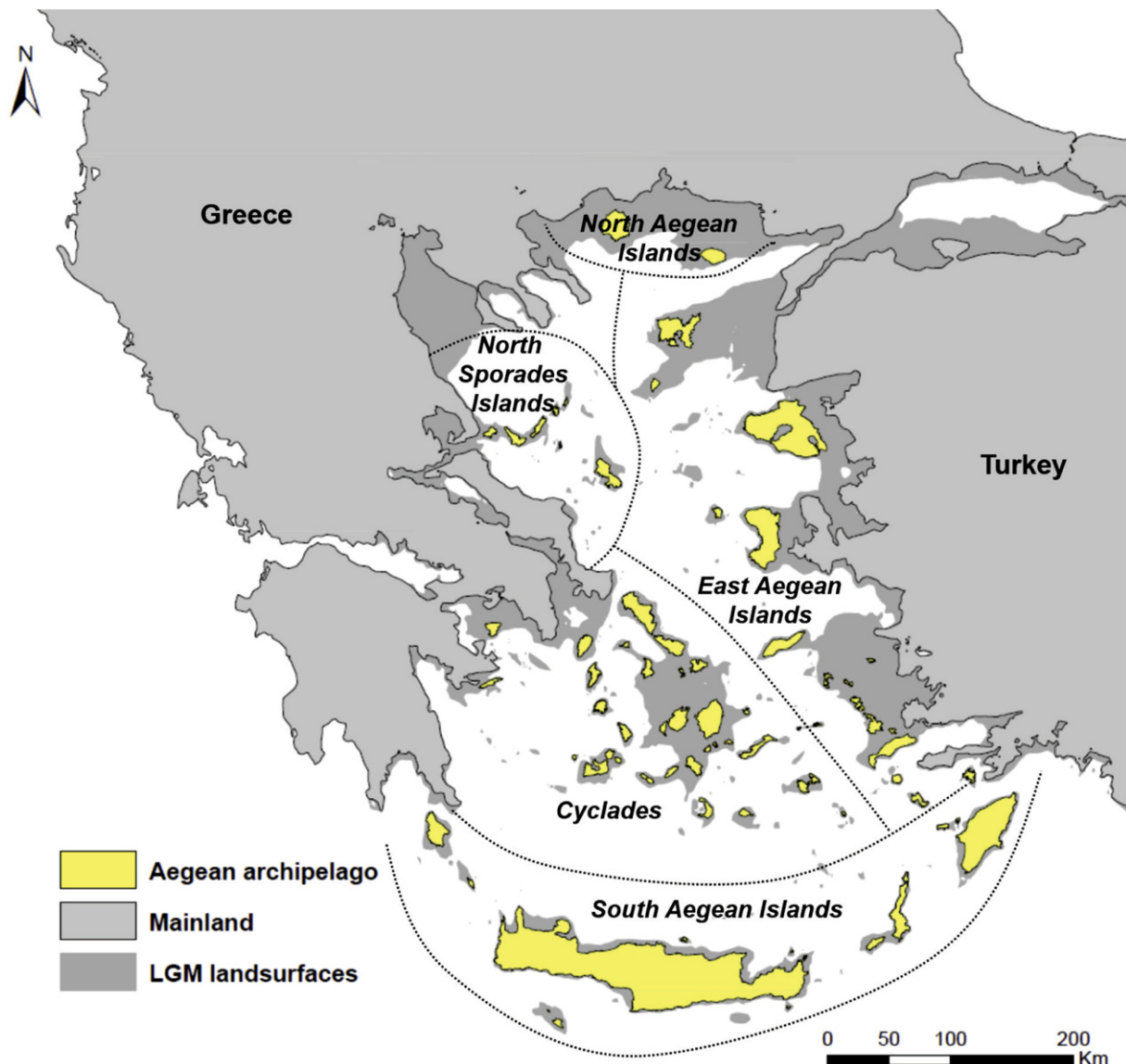

Fig. 2. Map of the Aegean Sea and biogeographic regions (in italics).

formed tectonically during the Pliocene, with many of its islands remaining isolated during sea-level change (Poulakakis et al., 2005). The fourth region, the West Aegean Islands (i.e., the Northern Sporades), situated off east Greece, is a landmass that separated from the mainland during the Pliocene (Dermitzakis, 1990). It includes former peninsulas that were connected to Europe during the LGM and had become isolated by sea-level rise (see Foufopoulos and Ives, 1999). The North Aegean Islands (i.e., Thasos, Samothraki) is the fifth group comprising the former palaeo-peninsular islands situated on the northern coast of Greece. Despite their close geographical proximity, the North Aegean Islands have very low affinities with the other Aegean Island groups and form a distinctly different biogeographical region (Kougioumoutzis et al., 2016). This could be attributed to the isolation of Thasos and Samothraki from northern Greece during the latter phases of the LGM (Kougioumoutzis et al., 2016; Sakellariou and Galanidou, 2016).

The Aegean archipelago has an extremely complex palaeogeographic history and is environmentally heterogeneous, with a high geological and biological diversity and endemism (e.g. Strid, 1996; Dennis et al., 2000; Sfenthourakis and Legakis, 2001; Chatzimanolis et al., 2003; Blondel et al., 2010), and therefore represents a natural laboratory for biogeographic studies (e.g. Lymberakis et al., 2007; Poulakakis et al., 2008; Lymberakis and Poulakakis, 2010; Simaiakis et al., 2012a; Parmakelis et al., 2013; Kougioumoutzis et al., 2014). Molecular studies have highlighted and elucidated the role of geological dynamics influencing the biogeography of species in the Aegean archipelago (e.g. Beerli et al., 1996; Gantenbein and Largiadèr, 2002; Bittkau and Comes, 2009; Poulakakis et al., 2005; Parmakelis et al., 2013; Douris et al., 2007; Lymberakis et al., 2007; Comes et al., 2008; Simaiakis et al., 2012a). The present biodiversity of the Aegean archipelago reflects the submergence and re-emergence of landmasses, due to tectonic, volcanic and marine sea-level change events. The alternating cycles of submergence and emergence of land bridges are considered a central driver in the evolutionary history of the Aegean species through the isolation and re-connection of the insular populations (see Poulakakis et al., 2005, 2008). Due to the large variation of its submerged topography, geographically the Aegean archipelago underwent a spatiotemporally differential response to sea-level change (Triantis et al., 2008c; Triantis and Mylonas, 2009; Kapsimalis et al., 2009). The sea-level rise since the LGM led to a complex and dramatic change of continental-island areas and continental coastlines of the Aegean Sea (Pavlopoulos et al., 2012). Islands submerged or were reduced in size and often fragmented, and peninsulas were disconnected from the mainland (Pirazzoli et al., 1989; Dermitzakis, 1990; Beerli et al., 1996; Foufopoulos and Ives, 1999; Lambeck and Purcell, 2005; Kapsimalis et al., 2009).

Foufopoulos and Ives (1999) were among the first to identify statistical associations between life-history traits and extinction rates in the submerged Aegean islands. They calculated the extinction rates of turtle and squamate species across islands, using radiocarbon-date-validated sea-level-rise reconstructions and detailed bathymetric maps. Although this innovative study disclosed the potential of such quantification, the analysis was based on partly outdated approaches. The process of quantifying the geographic effects of sea-level rise for continental islands requires a geophysically based model of sea-level change (Kendall et al., 2005, Milne and Mitrovica, 2008). While the global eustatic sea-level rise since 21 kyr BP averages 120 m, at a local scale, the rate and height of sea-level change was affected locally by water-loading effects and crust flexibility, gravitational effects of continental glaciations, and the flooded surface's morphology (Lambeck and Purcell, 2005; Kendall et al., 2005; Milne and Mitrovica, 2008) (see Fig. S1 in Appendix A). These geographic factors resulted in a complex local sea-level-rise pattern in the Aegean Sea (Beerli et al., 1996; Lambeck, 1996; Geraga et al., 2010).

1.3. Aim

This study has three aims. Firstly to quantify the magnitude and rates of geographic change during the last sea-level-rise episode

(21 kyr BP–present) for different parts of the Aegean archipelago. Secondly to develop an Area-Distance-Change (ADC) typology of islands to distinguish islands that changed more and at a faster rate (in terms of area and distance to mainland) from those that changed less and at a slower rate. And thirdly to illustrate that both the detailed quantification and the ADC typology can enhance our understanding of biogeographic patterns in the Aegean archipelago, we aim to discuss these results to derive a set of hypotheses on the role of sea-level change shaping and affecting the biogeography, species-richness patterns and genetic makeup of biota in a continental setting.

2. Methods

2.1. Quantifying geographic changes resulting from sea-level fluctuations

The LGM was characterized by continental ice-sheets expansions over North America and Eurasia. At the same time, Greenland and Antarctic ice sheets were larger and thicker than today. If the world ocean were to behave like a bathtub, as stated by the concept of "eustasy" (Suess, 1906), the LGM sea level would be observed everywhere at 130–140 m below present msl. However, geological sea-level indicators from different sites in the World show that the post-LGM sea-level change was regionally varying (Peltier, 2004; Khan et al., 2015; Rovere et al., 2016). Ice-proximal locations were characterized by several hundred meters sea-level drop since the LGM, while far-field sites experienced a sea-level rise that closely resembles the hypothetical eustatic curve (Khan et al., 2015). The spatial variability of sea-level change is a consequence of Earth deformability under ice and water load variations (Rovere et al., 2016). The latter, in fact, trigger solid Earth and gravitational responses that work to restore the isostatic equilibrium. Furthermore, continental ice sheets and oceans experience a mutual gravitational pull. Therefore, when ice sheets melt, the pull vanishes and sea surface drops in the proximity of the former ice sheets, while it rises and exceeds the eustatic value at the antipodes (Spada and Stocchi, 2007; Rovere et al., 2016). The combination and interrelation of solid Earth, gravitational as well as rotational processes that accompany and follow surface water-load readjustment is known as glacial and hydro isostatic adjustment (hereafter GIA; Milne and Mitrovica, 2008; Spada and Stocchi, 2007; Rovere et al., 2016). According to GIA, any ice-sheets-driven sea-level change that is recorded by surface geological features should be addressed as local relative sea-level change because it stems from the variation of the local mean sea surface with respect to the local deforming solid Earth surface.

As a result of GIA, relative sea-levels in the Aegean Sea during the LGM averaged 120 m lower than present but exceeded 140 m below the present sea surface in the central Mediterranean (Beerli et al., 1996; Lambeck and Purcell, 2005). Detailed geographical reconstructions were made of the post-LGM change in the Aegean and Eastern Mediterranean islands, using GIA models (Lambeck, 1996). However, in order to quantify the rates and the magnitude of geographic change for (small) islands and peninsulas, we required at least a 10-fold higher resolution (0.01°) grid, for both topography and bathymetry. We modeled the Generalized sea-level equation (GSLE) by applying the numerical scheme from Kendall et al. (2005, page 692) in a Fortran 90 program. The open-source sea-level Equation solver SELEN 2.9 provided useful routines for decomposing the global ice-sheet model and calculating the ice- and water-load-induced solid Earth and gravitational response (Spada and Stocchi, 2007; Spada et al., 2012). It uses a pixelation scheme by Tegmark (1996) and the library SHTOOLS to decompose and synthesize spherical harmonic functions (Wieczorek, 2012). We employed ICE-5G ice-sheet model on top of a Maxwell viscoelastic Earth model (Spada and Stocchi, 2007) that is characterized by VM-2 mantle viscosity profile (Peltier, 2004). ICE-5G was created and improved through time by changing ice thickness in space and time in order to minimize the differences between predictive relative sea-level curves and observations, using the aforementioned VM-2 profile

(Peltier, 2004). The digital elevation model (DEM) used was DEMSRE3a with a resolution of 1/120 arc degrees (approximate a resolution of 1 km^2), with the WGS 84 geoid as datum (Hengl and Reuter, 2012). This DEM was based on a combination of the shuttle-radar-topography mission (SRTM 30+; for further details see Becker et al., 2009) and the 1 arc-minute global-relief model ETOPO (Amante and Eakins, 2009). The pixel sampling resolution was set at 306,252 pixels around the Earth, the maximum spherical harmonic degree and order was set at 256. We calculated the palaeo-topography by adjusting the present day DEMSRE3a for the calculated changes in relative sea-level for each time step using the Quantum GIS 1.8.0 raster calculator (Quantum GIS development group, 2012). This palaeo-topography was reclassified into land (topography ≥ 0) and sea (topography < 0) using 'reclassify grid values' from SAGA GIS (SAGA GIS development group, 2011). The grid was polygonized using GDAL (Warmerdam, 2013), which allowed for area calculations in Quantum GIS. The vectors were loaded in PostGIS, and distance between vectors was queried using its built-in shortest distance calculator (PostGIS Project Steering Committee, 2013). We assume the geophysical system was in isostatic equilibrium during the LGM, which is not realistic given relaxation times and delayed responses of mantle and crust. Furthermore, we assumed that tectonic change and sedimentation since the last 21 kyr can be neglected, as they modify <10% our relative sea-level-rise curve. Fortran 90 program of Generalized sea-level equation (GSLE) was based on Kendall et al. (2005, page 692). For help or information contact the authors.

2.2. Construction of Area-Distance Change (ADC) typology

With the SELEN geophysical based model for sea-level change over the last 21 kyr (Kendall et al., 2005, Milne and Mitrovica, 2008), we produced one time slice for each 1000 year interval since 21 kyr ago (see Fig. S1 in Appendix A). We used these grids to calculate four geographic change metrics per island for all islands >1 km^2: (1) area contraction (%), (2) distance increase (%), (3) the percentage rate of island-area decrease (%/kyr), and, (4) the percentage rate of distance-to-mainland increase (%/kyr). Note that, for palaeo-peninsular islands, all aforementioned values were calculated after the separation of the island from the adjacent mainland. We used these calculations to plot for each island how much and how fast area reduced and distance to continents increased. For each category, we found the frequencies at which three island types fell into 33 percentile classes of low, intermediate and high change. The island types included those that had not fragmented, but simply shrunk since the LGM (true islands), peninsulas that had become islands (peninsular islands), and mega-islands that divided into several smaller islands (fragmented islands). Based on the four geographic change metrics, we constructed nine island categories of Area-Distance Change (ADC) (Table 1a). For each metric we applied the 33 percentiles to split the island into three classes: low, intermediate and high change (Table 1b). In this typology the ADC-type 1 islands represent the least and slowest changes and ADC-type 9 islands represent the greatest and fastest changes.

3. Results

3.1. Geographic changes in the Aegean archipelago

The model output confirms that after the LGM, because of geophysical effects, the degree of sea-level change varied spatially along the Aegean Sea (see Fig. S2 in Appendix A). During the LGM (21 kyr BP), the sea level in the Aegean Sea ranged between −145 m below the present level near Crete ans −120 m at the Northern Aegean Sea coasts. At 16 kyr BP, sea levels had risen 20 m in the southern Aegean Sea and up to 10 m near the northern Aegean coast. The consequences of these spatially different changes were, however, relatively minor for most islands, including the Cyclades. At 11 kyr BP the sea level had risen by >85 m in the whole Aegean Sea, dramatically altering the geography of the region. During the following period, towards 6 kyr BP, sea level rose another 35 m. However, this barely affected the geography of the area, although a few peninsulas became islands in the northern and eastern Aegean.

The sea-level rise, from 21 kyr BP to present time, reduced the total area of the islands by >70%, from 83,000 to 22,000 km^2 (Fig. 3a). Fragmentation and isolation increased considerably, as did the number of islands larger than 1 km^2, caused by the splitting up of larger islands and by islands detaching from peninsulas (when land bridges submerged). The number of islands (larger than 1 km^2) increased by ca. 44% (from ca. 125 to >180 - Fig. 3b). We reconstructed the chronology of the fragmentation and timings of the onset of separation and transgression events since the LGM (21 kyr BP) of the Aegean Sea (see Table S1 in Appendix B). Most of the change (in the order of 90%)

Table 1

a) Qualitative typology of islands based on four criteria related to magnitude and rates of changes in area and distance to nearest continent: (1) %A$_L$: total percentage of area loss, (2) %rA: percentage rate of area change (%/kyr), (3) DF: factor of distance change (D$_{Pr}$/D$_{Pa}$), where D$_{Pr}$ is the present-day distance from the nearest mainland or island mass in km and D$_{Pa}$ is the past distance from the nearest mainland or island mass in km, (4) %rD: percentage rate of distance change (%/kyr). b) Quantitative criteria for the typology classes.

(a)	Type	Magnitude and rate of changes
	1	Islands with low changes in area and distance to the continent and slow rates of area and distance changes.
	2	Islands with low changes in area and distance to the continent and moderate rates of area and/or distance changes.
	3	Islands with low changes in area and distance to the continent and fast rates of area and/or distance changes.
	4	Islands with intermediate changes in area and/or distance to the continent and slow rates of area and distance changes.
	5	Islands with intermediate changes in area and/or distance to the continent and moderate rates of area and/or distance changes.
	6	Islands with intermediate changes in area and/or distance to the continent and fast rates of area and/or distance changes.
	7	Islands with large changes in area and/or distance to the continent and slow rates of area and distance changes.
	8	Islands with large changes in area and/or distance to the continent and moderate rates of area and/or distance changes.
	9	Islands with large changes in area and/or distance to the continent and fast rates of area and/or distance changes.

(b)	Type	%Area	Condition	%Distance	Rate	%Area change	Condition	%Distance change
	1	<60	and	<158	Slow	<11	and	<11
	2	<60	and	<158	Moderate	11–18	and/or[**]	11–18
	3	<60	and	<158	Fast	>18	and/or	>18
	4	60–95	and/or	158–500	Slow	<11	and	<11
	5	60–95	and/or[*]	158–500	Moderate	11–18	and/or[**]	11–18
	6	60–95	and/or[*]	158–500	Fast	>18	and/or	>18
	7	>95	and/or	>500	Slow	<11	and	<11
	8	>95	and/or	>500	Moderate	11–18	and/or[**]	11–18
	9	>95	and/or	>500	Fast	>18	and/or	>18

[*] But neither are large.
[**] But neither are fast.

occurred within the period of 16 to 11 kyr BP, when we also find the fastest change, with a sea-level rise of 12 m/kyr (Fig. 1a). The submergence and fragmentation of the Mega-Cyclades was a major event in the Aegean Sea. The total area reduction for the Mega-Cyclades was 75% (the total area of this palaeo-island was reduced from 10,750 km^2 to 3250 km^2 - Fig. 3c), while the number of islands >1 km^2 increased from 32 to 55. The period when most of the new islands were created, lies between 17 and 6 kyr BP (Fig. 3d).

3.1.1. Area change

Individual islands show widely different spatiotemporal responses to sea-level rise (Fig. 4). The Aegean islands reduced considerably in size, from 20% to >90%, as a result of the sea-level rise since 21 kyr BP. Fragmented palaeo-islands dominate the class of highest area reductions and are underrepresented in the classes of lowest area change. True islands are never found within the highest class (Fig. 4a). The duration of the fastest area loss varied, but occurred mainly between 11 and 2 yr. The rates of area loss varied across the Aegean islands, with islands larger than 20 km^2 changing between 11%/kyr to 22%/kyr, and smaller islands, mainly fragments, from >22% up to 90% (Fig. 4b). Most true and fragmented islands fell into the category with low area-change rates. Only a few of the peninsular islands fell into this low area-change class, and few true islands fell in the class with highest rates of change (Fig. 4b).

3.1.2. Distance change

The increase in distance to the mainland varied greatly, ranging from 9% to >50%, and occurred mainly in the same time periods as area changes (Fig. 4c). The island types (more or less) distribute evenly between the three distance-increase classes, except that the proportion of true islands was somewhat lower in the class with the highest distance increase. Distance-increase rates varied between 10%/kyr and 40%/kyr for the larger islands (>20 km^2), whereas the smallest islands, usually fragments, had the fastest rates of change (>40–45%/kyr) (Fig. 4d). All island types occurred in all distance-change-rate classes, but fragmented islands dominated the group of relative slow change rates. In general, true and fragmented islands exhibit lower distance-change rates than peninsular islands, which are underrepresented in the class with the lowest area-reduction rates. True islands, however, are underrepresented in the class with the highest area-reduction rates (Fig. 4d).

3.2. ADC-typology

The ADC-typology classification scheme reveals large spatial variations between islands (Fig. 4e). The frequency distribution of islands points towards the intermediate ADC-type 5 and at the highest ADC-type classes 8 and 9. True islands show the lowest variability between ADC-classes, dominating type 5, although they are also represented in the lower classes. Fragmented islands, show the largest variability, but are dominating the high ADC-types 8 and 9. Palaeo-peninsulas are represented both in the lowest and highest ADC-type classes.

4. Discussion

4.1. Geographic changes in the Aegean archipelago

The results from this study (see Figs. 2 to 4) provide a quantification of the magnitude and rate of geographic change in the Aegean Sea. Most of the sea-level rise induced large-scale change in the Aegean, and in particular in the Mega-Cyclades island complex. The durations of largest area and distance changes differ greatly between the islands, ranging from 11 kyr to 2 kyr. This variation is mainly caused by the variation in sea-floor topography (bathymetry) and relative sea-level rise. Our reconstruction of the fragmentation of the Mega-Cyclades coincides largely with an earlier reconstruction (Kapsimalis et al., 2009), but differs in the details concerning the timing of fragmentation and the duration of

change. The differences are largely due to the application of an updated GSLE model, which incorporates the effects of horizontal coastlines variations (Milne and Mitrovica, 2008), to a different mantle viscosity profile and to ICE-5G ice-sheets chronology (Peltier, 2004).

The response of organisms to geographic change may be species specific, depending on dispersal traits, physiology and body size, and is thus species and scale dependent. Impact on island communities is expected when the rates of area or distance change exceed their adaptive potential. For elephants, for example, area reductions associated with major habitat reductions directly reduce the carrying capacity for their populations (Van der Geer et al., 2014), whereas the same effects for invertebrates may be ignorable. Whether distance increase affects species diversity depends on species' range expansion abilities (Dennis et al., 2000; Panitsa et al., 2010; Kougioumoutzis and Tiniakou, 2014; Papadopoulou et al., 2009). While changes in distances to the continent may be critical to maintain gene flow for terrestrial landlocked or habitat-specialist species, they would probably not greatly affect species with flight abilities (Claramunt et al., 2012). Soil invertebrates, typically with limited range-expansion abilities, may however be affected by relatively small distance changes. Biota may also differ in their responses to rates of change. For some species, the changes may be sufficiently slow to allow for adaptations, successfully re-equilibrating to smaller areas or larger distances, whereas other species may become extinct under the same conditions. Lastly, one may speculate that most insular endemics are better adapted to frequent area losses and isolation increases than native species which originate from the continent (Comes et al., 2008; Kisel and Barraclough, 2010; Rijsdijk et al., 2014; Weigelt et al., 2016). Therefore, extinction rates may have been lower for insular endemic species than for native species. Continental species stranded on islands, especially former peninsulas, may have been less resilient to area reduction. This is especially so when combined with distance increase, which impeded gene flow from the continent (Hoelzel et al., 2002; Losos and Ricklefs, 2010). It may, therefore, be important to discern between native and endemic species when assessing the responses of different species to sea-level changes, especially when addressing why certain species are missing from the central Aegean archipelago (Rechinger, 1950).

4.2. Hypotheses for future evaluation

4.2.1. Island-area reduction hypotheses

According to the Glacial Sensitive Model, rising sea levels led to island-area reductions and distance increases, causing increased extinction rates and reduced migration rates. Ultimately, this resulted in lowered species equilibria and induced community relaxations, thus rendering insular populations more prone to extinction (Whittaker and Fernández-Palacios, 2007; Fernández-Palacios et al., 2015). If a community has not equilibrated to the new situation, the community is considered in extinction debt, meaning that the new smaller area provides insufficient resources for all species in the community to persist, predicting future extinctions. We expect native populations on high ADC-islands, with the greatest area reductions (ADC-types 7–9), to have suffered the proportionally highest number of extinctions and also having the highest extinction debts. For example, the lower species diversity of the Cyclades, compared to the other island phytogeographic areas of the Aegean (Kougioumoutzis and Tiniakou, 2014), could be attributed to ADC-type 7–9 islands of the Cyclades. Also genetic bottlenecks (Comes et al., 2008) and lower genetic fitness (Abdelkrim et al., 2005) indicate that these islands do not host a relaxed flora (Kougioumoutzis et al., 2014).

We expect that more extinctions occurred on high ADC-islands, which abruptly reduced significantly in size. Species on low ADC-islands with smaller area reductions are expected to have suffered fewer extinctions and to show smaller genetic bottlenecks. On slow changing islands (over more than >10 kyr) there may be more time for native
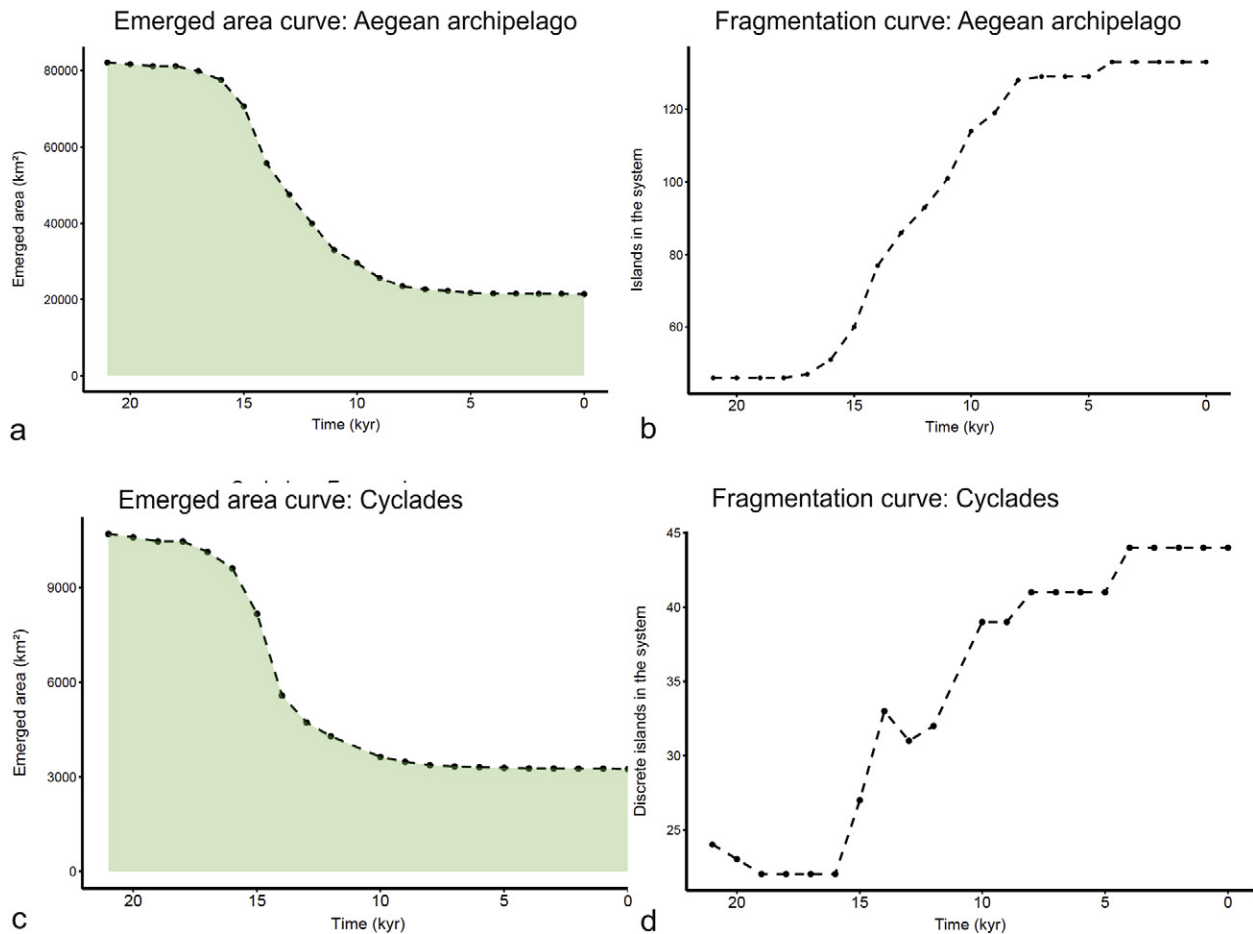
Fig. 3. a) Decrease in emerged area in km^2 and b) increase in the number of islands due to the sea-level rise since 21 kyr for the whole Aegean archipelago. c) Decrease in emerged area in km^2 and b) increase in the number of islands due to sea-level rise since 21 kyr for the Mega-Cyclades.

species to adapt, resulting in fewer extinctions than on islands where change occurred relatively rapidly (<3 kyr).

In terms of speciation, cyclic island-area increases during sea-level low stands may also have promoted speciation through adaptive radiations, as more niche space became available (Price and Elliott-Fisk, 2004; Gavrilets and Vose, 2005; Kisel and Barraclough, 2010; Papadopoulou et al., 2011). This leads to the hypothesis that islands which were larger in the past should contain disproportionally more endemics or subspecies than islands that remain close to the same size (Weigelt et al., 2016).

### 4.2.2. Distance increase hypotheses

It is likely that with relatively small distance changes in islands far from the coast (e.g. Crete), and/or with absolute small distance changes altogether (e.g. Rodos), effects on colonization probabilities are minimal for many native species. On the other hand, given an exponential or logistic distance-decay of the probability of a successful air-over-sea dispersal (e.g. pollen, seeds, beetles), just a doubling of a small distance may have negative effects on gene-flow rates, which over time may affect insular populations (Papadopoulou et al., 2009). Therefore, we expect high ADC-islands, where distances to other islands or continents have increased the most (>20%), to have fewer native species than islands with lower distance increases. Distance increase should affect

good dispersers less, for example, birds or wind dispersed plants (Whittaker and Fernández-Palacios, 2007). Moreover, we expect islands that experienced fast distance increases to have lower species richness (because of increased extinction rates) than islands where the distances to continents increased slowly.

4.2.3. Palaeo-peninsular hypotheses

Palaeo-peninsular islands are generally considered supersaturated with species, showing higher ratios of island-to-mainland species numbers than expected from their areas alone (Newmark, 1987). Studies indicate that the degree of hyper-saturation is negatively correlated with time since isolation, which points to successful relaxation into new equilibria (Wilcox, 1978). Continental species absent from palaeo-peninsular islands are generally regarded as having become extinct after separation from the continent (Diamond, 1972; Foufopoulos and Ives, 1999). We hypothesize, therefore, that the highest extinction rates for native continental species occurred on Aegean palaeo-peninsular islands that were rapidly separated (<2 kyr) from the continent. Conversely, palaeo-peninsular islands that took longer to isolate (>5 kyr) may have shown lower extinction rates. The slower separation rates may have aided stranded continental species to adapt to insular conditions; for instance, by morphological changes, as in the *Nigella arvensis* complex (Comes et al., 2008). Palaeo-peninsular islands that were

Fig. 4. Left hand side panels: Maps of change per island in the Aegean Sea; Right hand side panels: island frequency bar diagrams showing 33% quantiles of islands per change class. a) Area reduction by sea-level rise since the Late Glacial Maximum (21 kyr BP) b) Distance increase by sea-level rise c) Rates of percentage area change per kyr d) Rates of distance increase per kyr. e) Area-Distance Change (ADC-) Typology showing the relative degree of change of area and distance to the continent per island in the Aegean Sea. Red islands are in the highest class (9) of ADC-change and dark green islands in the lowest (1) ADC-class. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
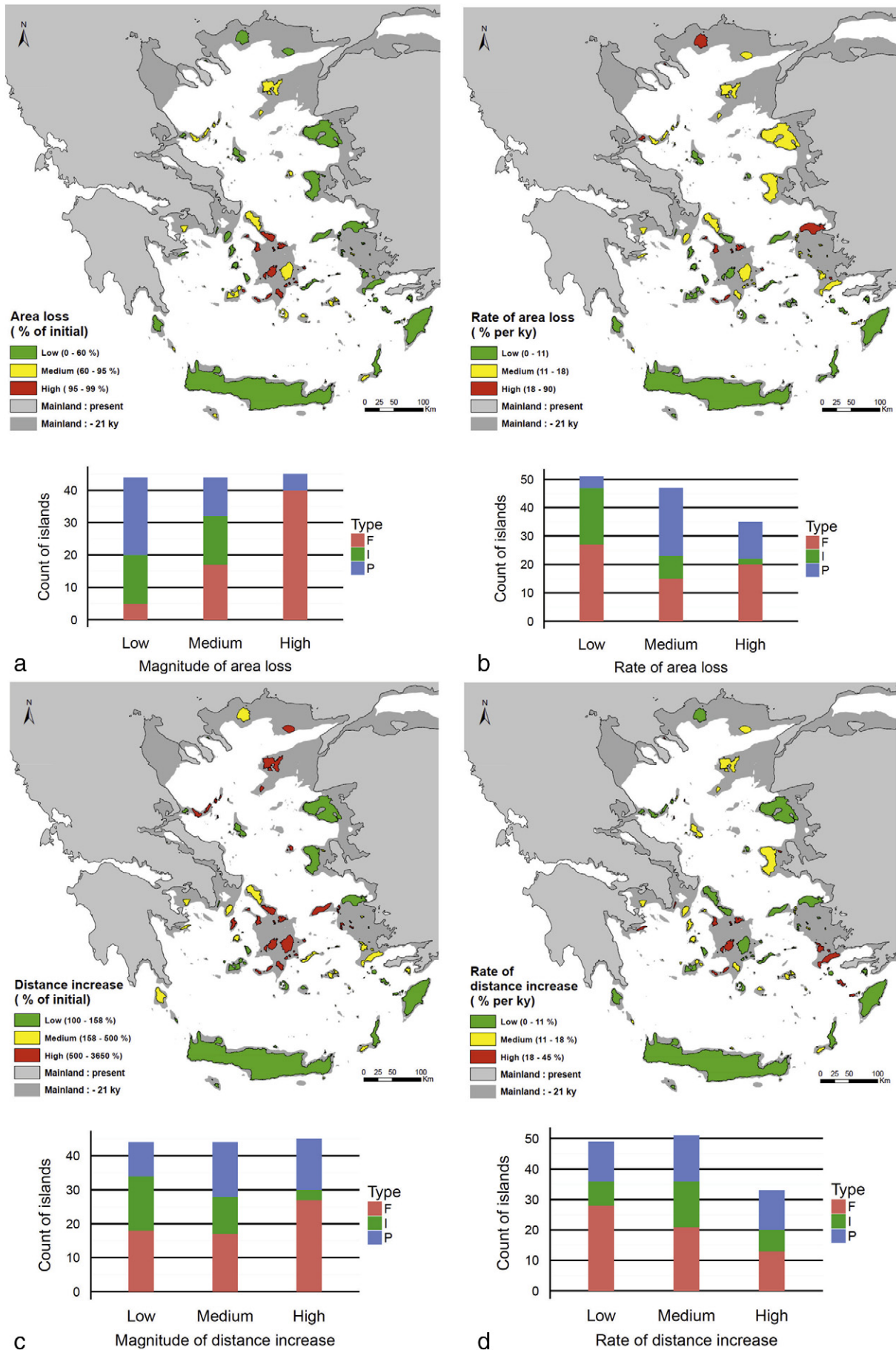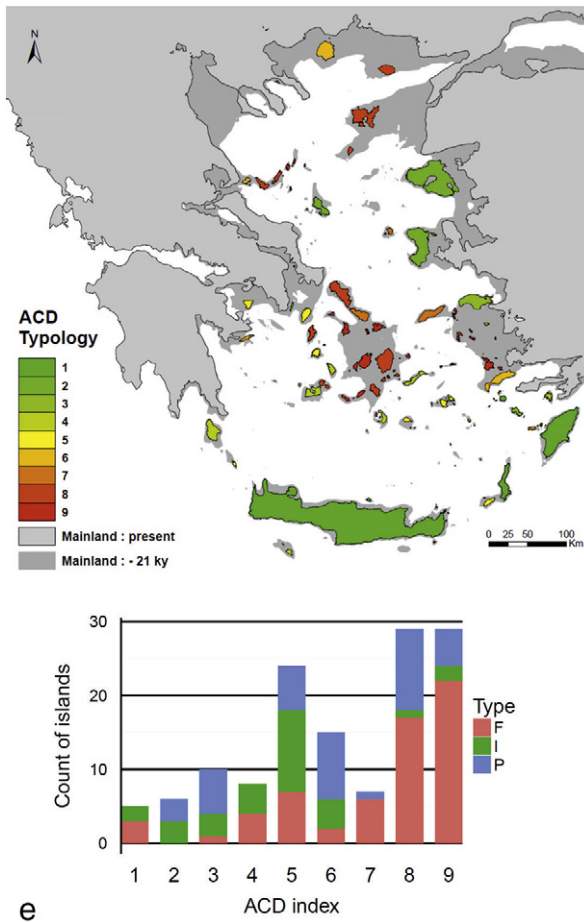
Fig. 4 (*continued*).

separated early during sea-level rise (>15 kyr) may be relatively richer in endemic species than islands separated more recently due to extirpations of native species on the latter (<5 kyr). In addition, species on the former island type may have been better adapted to insular conditions. We should also expect palaeo-peninsular islands that were separated more recently (<5 kyr) to contain larger numbers of recent invasive species. Finally, we expect that species diversity on smaller islands is relaxing proportionally more and faster than on larger islands. We propose that this must be a consequence of increasing minimum-area effects (see Tjørve and Turner, 2009) on smaller islands. Therefore, small palaeo-peninsular islands should have close to the same species richness as other small islands of similar size, whereas larger palaeo-peninsular islands should have considerably more species than true islands of similar size.

4.2.4. z-value hypotheses

The geographically diverse effects of sea-level rise should be expected to be reflected in differences in the exponent (*z*-value) of the power-law species-area relationship. For SARs of palaeo-peninsular islands we expect the species increase to level off more slowly with area (i.e. have lower *z*-values) than for other islands in the Aegean Sea (Simaiakis et al., 2012b, c; Tjørve and Tjørve, 2008), even if present-day's isolation patterns are more or less the same for both types of islands. Higher ADC-islands with larger area reductions are also expected to exhibit higher *z*-values, as compared to lower ADC-islands with lower area reductions. In addition, higher *z*-values should be observed in higher ADC-islands, which have experienced longer distance increases than lower ADC-

islands. These three hypotheses rest on the assumption that present day species diversities have not already achieved equilibrium.

4.2.5. Fragmented island hypotheses

Island complexes like the Mega-Cyclades represent a special case, because they are classified as high ADC-islands, although their area reduction is generated by island-fragments separated from larger areas (Fig. 5). Like the separation of palaeo-peninsular islands from the mainland, the fragmentation of larger islands occurred within a few thousand years and led to very rapid and large area reductions.

Populations were broken up with the fragmentation of the palaeo-islands. This clearly affected species distribution on these islands, causing higher species nestedness (e.g., Kougioumoutzis et al., 2014), more sub-species populations and higher degrees of multiple island endemics (Rijsdijk et al., 2014) in fragmented islands compared to non-fragmented islands. The combined effects of area reductions and distance increases impact individual populations on every island fragment but differ greatly between them. The timing of separation events also differ between islands, leading to a fragmentation chronology paralleled by responses from fragmented species pools (Foufopoulos and Ives, 1999). In this way the fragmentation sequence of the islands may be reflected in the phylogenies.

Fragmentation cycles may have also promoted allopatric speciation, by splitting gene pools into subpopulations which promotes genetic diversification (Qian and Ricklefs, 2000).

5. Conclusions

Recently, there has been a call for a more comprehensive theory in biogeography that includes spatiotemporal dynamics on shorter time-scales (<100 kyr) driven by environmental change, including climate and sea-level change, affecting habitats and distances to source pools (Heaney, 2000; Whittaker et al., 2008; Fernández-Palacios et al., 2015; Weigelt et al., 2016). The Glacial-Sensitive Equilibrium model predicts a dynamic species richness and a genetic response to the dynamic changes in geography associated with sea-level change (Fernández-Palacios et al., 2015). Central questions following from this model are related to the extent to which insular species are sensitive to the magnitude and rates of area and isolation change, as well as the thresholds of change are that affect species richness and their genetic makeup. To provide the framework for future works we designed a geo-physical based workflow to assess the magnitude and rates of geographic change over the last sea-level-rise episode (21 kyr BP–present), involving 120 m of rise over 10 kyr within the Aegean archipelago. We noted that the geographic change in the Aegean occurred in tandem with the largest magnitude and rates of sea-level rise between 16 and 8 kyr BP (Figs. 3 & 4). The total area loss for the whole archipelago was 80%, and for the Cyclades the surface loss was 75%. Our island analyses of single islands indicate a large and varied spatiotemporal response in geographic change, with area losses ranging from 20% to >90% and distance to mainland increasing from 9% to 30% for each. We have constructed an Area-Distance Change (ADC) island specific typology (Table 1). This may be used in future studies to test how rates of area contraction, distance increase and increased isolation affected species richness, their distribution, and their genetic makeup (Fig. 5). The biogeographic and genetic effects of sea-level-mediated geographic change on biota vary between biota, depending on their traits. We predict stronger effects on islands with higher ADC, including higher extinction debts, stronger bottlenecks, more genetic variety within species pools, more multiple endemics and shared species on fragments and higher *z*-values in the power-law species-area relationship. The widely varying spatiotemporal response to sea-level rise on islands in the Aegean Sea makes for an ideal research area where we may test whether species actually equilibrated and evolved under natural speciation rates relative to the magnitude of geographic change caused by sea-level rise.
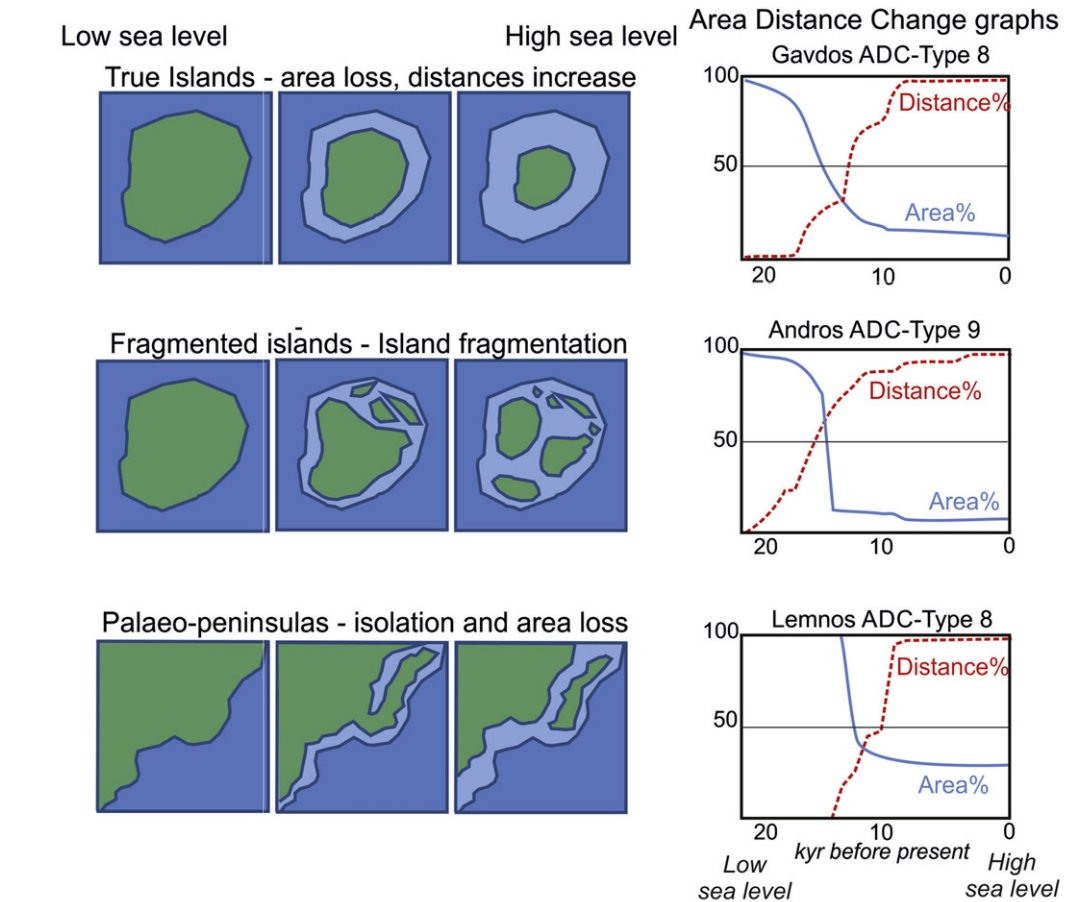
ADC-1		ADC-9
Minor, slow	**Geographic changes**	**Major, fast**
Higher Imigration, lower extinction rates	Imigration /Extinction rates	Lower Immigration, higher extinction rates
Small	Extinction Debt	Big
Proportionally higher	Species richness	Proportionally lower
Rapidly at new equilibrium	Relaxation dynamics	Potentially out of equilibrium
Proportionally lower	Proportion of endemics	Proportionally higher
Proportionally lower	Speciation rates	Proportionally higher
Lower z-values	z-values	Higher z-values

Fig. 5. Visual abstract of our model.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2017.02.002.

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