

**Climatic and environmental drivers of extinction in Mediterranean island reptiles since the height of the last Ice Age**

By  
Samuel Kalb

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Thesis Committee:  
Professor Johannes Foufopoulos, Chair  
Professor Kenneth Rijdsdijk, University of Amsterdam



## **Abstract**

As the earth experiences an accelerating wave of climate change-driven species extinctions, it is increasingly important to understand how natural species communities respond to the dual stressors of climate and landscape modification. Island species represent an excellent system in which to study the effects of shifting climate and concomitant landscape change on wildlife populations. Reptiles in particular are ideal study organisms because they are, like most species worldwide, 1) ectotherms, making them directly susceptible to changes in the thermal environment and 2) poor dispersers, attenuating their ability to respond to environmental changes by movement or migration. In this study we take advantage of a natural long-term fragmentation process that occurred when, following the end of the last ice age, rising sea levels led to the separation of numerous Mediterranean land-bridge islands from the nearby mainland. Reptile species occurring on these islands became isolated and subject to numerous stressors such as small population sizes and an increasingly inhospitable thermal environment, and many taxa went extinct over these millennia. Because these stressors closely reflect the problems that present-day wildlife species face, they can help us understand the process of extinction and serve as a model to understand the long-term implications of anthropogenic landscape change on wildlife.

In this study, we assess how reptile population persistence on Mediterranean islands has been influenced by the interacting effects of island area, timing of fragmentation, changing climate, and changing topography, in the period since the height of the last ice age (the Last Glacial Maximum, LGM). We use bathymetry, topography, and geophysical models of sea-level rise to reconstruct the sequence and timing by which 83 islands in the Aegean and Ionian seas progressively separated from paleo-landmasses, and to characterize the topography of paleo-islands from which they fragmented. We also reconstruct the progressive sequence of local reptile population extinctions that occurred on these islands going back to the LGM. Combined with publicly available paleo-climate reconstructions, we characterize a set of landscape and climate variables for each present-day and paleo-island for which we have reconstructed extinction events. Our analysis revealed that extinction increased directly with diminishing island size and tended to accumulate linearly with increased duration of isolation. We also find that extinctions are significantly positively associated with higher warmest-season temperatures, and with higher topographic roughness, which may be a measure of diminishing resource availability. We also find that extinctions are positively associated with higher pre-fragmentation precipitation, an indication that reptile population persistence may be negatively affected by large differences between pre- and post-fragmentation vegetation lushness. These conclusions point forward to predicting, anticipating, and eventually preventing future species extinctions due to environmental change.

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## **Introduction**

### ***Rationale and Background***

In the age of anthropogenic climate change and mounting, planet-wide biodiversity loss, it is increasingly vital to understand the relative contributions and interactive relationships between the factors that drive species extinction. Complicating our understanding is that many of these processes are diffuse, large-scale, and impact the survival of populations over long periods of time, making experimental approaches difficult. While paleontological studies have aimed to understand species extinctions on geological time-scales, and have applied those findings to understanding the present-day extinction crisis (Barnosky et al. 2011), the relatively coarse quality of paleontological data has made it difficult to use that understanding to gain insight into what drives population extinctions at the meso-scale. More recently, however, studies investigating the decline of populations have focused on reconstructed population extinctions on true islands or habitat patches on time scales ranging from a few dozen to several thousand years (Newmark 1995, Halley et al. 2016).

The many population extinctions that occurred during the period of major warming and sea level rise since the height of the last ice age, often called the Last Glacial Maximum (LGM) (Barnosky et al. 2004) provide an ideal opportunity to investigate how long-term climatic changes affect species both directly and indirectly through landscape change. Global average temperatures have risen by 17 +/- 1.8 °C since the LGM (20 – 24 kybp [thousand years before present]), and global average sea levels have risen 120 +/- 10 m (Bintanja, van de Wal, and Oerlemans 2005; Lambeck et al. 2014), allowing researchers to study how biotic communities may respond to levels of climate change far exceeding the amount of warming that is likely to occur on the timescale of a human lifespan.

The breakup of land-bridge islands since the LGM provides a particularly useful setting in which to assess the influence of climate and landscape on long-term population dynamics (Diamond 1984). Island biogeography research has found that following fragmentation, communities have a full complement of species and with passing time, species are progressively lost (Pimm et al. 1993). Immediately after isolation, habitat fragments therefore have more species than what would be predicted by the species-area relationship, and are therefore considered to be super-saturated with species; their “extinction debt” is paid off through a process of progressive community relaxation (Diamond 1972; MacArthur and Wilson 1967; Wilcox 1978).

The Aegean and Ionian Sea archipelagoes in the northeastern Mediterranean harbor more than 3000 islands of various sizes, that encompass a diversity of habitats (Trichas and Legakis 1987). They are particularly well suited to island biogeography studies because they contain many land-bridge islands with well-surveyed species communities, which evidence suggests have undergone community relaxation since the LGM (Foufopoulos and Ives 1999; Valakos et al. 2008).

Reptiles are among the most sensitive taxa to climatic changes; as ectotherms, their body temperatures and life histories are highly responsive to ambient temperatures, and large climatic shifts can put reptile populations at risk of demographic collapse (Gibbons et al. 2000). Research suggests that both present-day and historical climate features may be important for determining species distributions (Simaiakis et al. 2017; Hammoud et al. 2021).

Prior research has investigated associations between the ecology and persistence of reptile populations and various bioclimatic variables. Both modern and late-Pleistocene precipitation and temperature have been associated with reptile species richness (Araujo et al. 2008), and Mediterranean reptiles have been shown to be affected by both high and low temperature extremes (Megia-Palma et al. 2020; Wishingrad and Thomson 2020). Several papers have used climate envelope modelling to explore the relative importance of present-day climate to the distributions of lizards in Mediterranean-type habitats. They have documented high importance for bioclimatic variables related to temperature, precipitation, and climatic variability (Sillero and Carratero 2013; Rodder and Shulte 2010, Silva-Rocha et al. 2015). In addition, they have shown that the relative importance of particular bioclimatic influences may vary even among closely related species (Carneiro et al. 2017).

Beyond climate, some evidence suggests a role for landscape structure on the persistence of reptile populations. Landscape heterogeneity has been significantly associated with the presence and abundance of several reptile species (Fischer et al. 2005; McElhinny et al. 2006; Brown, Dorrough, and Ramsey 2011). Both specific landforms such as large flat rocks and general topography can provide certain species with environmental refugia that allow them to survive otherwise detrimental changes in climatic conditions (Hannah et al. 2014; Pontes-da-Silva et al. 2018; Senczuk et al. 2019). For example, dominant slope aspect can influence how species respond to shifting climatic conditions by providing different levels of insolation, and ultimately altered temperature and humidity regimes (Harter et al. 2015; Schwartz, Stark, and Meiri 2019; Pavlicek et al. 2003). Similarly, elevational profile of an island has been shown to affect patterns of genetic diversity within a species (Senczuk et al. 2019).

Although there is a substantial body of research on how present-day reptile population persistence is affected and predicted by modern climate and landscape conditions, much less has been studied about the influence of paleo-climate and landscapes, and how these interactions influence reptile biology over epoch-level time-scales. Several studies have found that on islands, modern species distributions of certain taxa have been influenced by paleo-geographic features such as island area and distance to the mainland at the LGM (Weigelt et al. 2016; Simaiakis et al. 2017; Hammoud et al. 2021). The importance of island area, distance from the mainland, and (for land-bridge islands) time since isolation from the mainland in driving island biodiversity has been well known for decades (MacArthur and Wilson 1967; Wilcox 1978). However, both the time scales over which these phenomena operate, and their relative contributions to explaining island biodiversity relative to other factors, are less clear (Burkey 1995; Diamond 1972; Halley et al. 2016). In this study, we use reconstructions of climate and physiography on Mediterranean islands going back to the LGM, in conjunction with reconstructions of local extinctions of reptile populations, to examine the relative influence of area, time-since-isolation, climate, and physiography on island reptile population persistence.

### ***The Study Region and Species Communities***

Our area of focus comprises much of the Aegean and Ionian seas, two subregions of the northeastern Mediterranean, and part of a global biodiversity hotspot (Myers 2000). Part of a mountainous, rocky, and semi-arid region, the islands of the Aegean belong to the Mediterranean vegetation biome, and are covered by a patchwork of maquis, heaths, coniferous forests, and occasional coastal wetlands. The Ionian sea region is significantly more mesic than the Aegean, and is characterized by a high extent of structurally complex vegetation cover. Humans have

inhabited the region for millennia, and have had an extensive influence on the landscape and ecology through forest clearance, animal husbandry, small scale agriculture, and the construction of dry stone walls and terraces (Blondel 2006; Grove and Rackham 2003).

The region harbors a diverse herpetofauna, and given that it is located at the crossroads of three continents, its species communities consist of taxa of European, Asian, and African origins. In addition, there are also several endemic taxa; however, these are found largely on the older, deep-water islands of the region, which by definition are not included in this study. Here we consider here the 44 species (32 genera) that occur on at least one of the study islands, and which represent a sizeable portion of the reptile biodiversity of the region. While many of these taxa are widespread throughout all five of the island groups considered here, others have more limited distributions restricted to a one or two archipelagoes (Appendix A).

Most islands in the region have relatively shallow underwater saddles to the neighboring mainland, and were connected to it during the Pleistocene era's lower sea level stands. As a result of these relatively recent connections, they share with it the same reptile species communities. Following the end of the last ice age, rapidly rising global sea levels inundated low-lying coastal regions and led to the progressive isolation and eventual separation of coastal hills and peninsulas (Foufopoulos and Ives 1999). Because most reptile species in the region are poor overwater dispersers, and cannot cross even narrow water barriers, they became isolated for very long periods of time on these newly-formed islands and, with these islands often being small, eventually started going extinct in a highly predictable manner (Foufopoulos et al. 2011). Consequently, species communities on all of the study islands today are a subset of the larger species communities found on the nearby mainland (Simaiakis et al. 2017; Hammoud et al. 2021). As sea levels rose even further, fragmentation of islands progressed, leading to increasingly smaller populations and accelerating extinctions (Fig. 1).





**Figure 1.** Reconstructed Aegean and Ionian coastlines during the 7 climatic stages considered in this study spanning the last 21,500 years. Numbers denote starting date of each period. Green represents present-day landmasses and darkest blue represents sea areas at lowest sea-level stand (Last Glacial Maximum). A = Naxos, Cyclades; B = Cape Drastis, Corfu, Ionian Sea; C = Gioura, Sporades.

Although the underlying fragmentation and extinction process is the same across the region, because of the complex geography of the northeast Mediterranean Basin, the original species communities do vary somewhat between different island clusters. Furthermore, one group of islands, the Cyclades, did not derive from the fragmentation of a continental mainland, but rather from a distinct very large (10,750 km<sup>2</sup>) mainland-like paleo-island called Cycladia, which remained separated at all times by a narrow water channel from the European mainland (Fig. 1)(Simaiakis et al. 2017). Because of the large number of well-studied islands available, as well as the relative ease of reconstructing the sequence of fragmentation, along with the general lack of overwater dispersal for herpetofauna in the region, this has been an excellent system in which to reconstruct past reptile extinctions (Foufopoulos and Ives 1999) and understand the process of species extinction.

Such land-bridge islands are also prime settings in which to reconstruct local population extinction events using the principles of vicariance and parsimony. Because we know the makeup of the reptile species communities on each island, and can assume a lack of overwater dispersal for these species (Heatwole and Levins 1973; Foufopoulos and Ives 1999; Hurston et al. 2009), and because we can reconstruct the pattern of island fragmentation, we can assume that any difference in species communities among islands that were connected at the LGM is due to extinctions on one or more islands (see methods section for a complete description of extinction reconstructions).

### ***Overview and Hypothesis***

Although prior research has found some climate and landscape features that are important in explaining reptile distributions today, to our knowledge no study has yet investigated the relative influences of a set of spatially explicit climate and landscape variables on the extinctions of island reptiles over a multi-thousand year time-scale. In this study, we investigate the associations between a reconstructed sequence of local population extinctions of reptiles on Aegean and Ionian islands going back to the LGM, and the landscape and climate conditions that existed on these islands at the times the extinctions occurred. It is important to gain an understanding of the relative magnitude of climatic and environmental extinction drivers, and also to ascertain the patterns by which this process occurs over multiple millennia, in order to gain insight the long-term responses of species communities to the present-day wave of environmental change.

We use an advanced sea level rise simulation model (Hammoud et al. 2021) to model the precise timings of breaking up of paleo-islands as a result of sea level rise. The model is improved to produce the best possible estimates of break up ages by using a detailed bathymetric map of Greece (EMODnet 2021) and an advanced geological uplift raster of the Aegean (Van Der Groeve et al. in prep.). We use this raster to characterize island topography. Based on the timings of island fragmentations, we reconstruct updated historic island fragmentation cladograms showing the sequence of island splitting in five major archipelagoes. Based on the

principles of vicariance and parsimony, we use these island fragmentation cladograms to reconstruct a series of potential local extinctions of reptile populations on these islands. We use reconstructions of paleo-climatic conditions at several climatic periods going back to the LGM (Fordham et al. 2017; Brown et al. 2018) to assess the influence of climate. We hypothesize that reptile extinctions on fragmenting islands are non-random but have been driven by the interacting effects of area loss, changing temperature and precipitation, and topographic change. We build a historical environmental model to test this hypothesis and analyze the relative importance of these extrinsic factors in explaining island reptile extinctions.

## **Methods**

### ***Reconstructing ancient landscapes***

In order to reconstruct the historic extents of coastlines under lower glacial sea level positions, we used a historic coastal reconstruction workflow based on geophysical modelling of the local crust dynamics in conjunction with concurrent sea level change (De Groeve et al., submitted A). To obtain the best possible estimates for the timings of landmass fragmentation due to land-bridge drowning, we took into account the slow geological crustal uplift and downwarping rates, varying between -1 and +1 mm/year across the Aegean sea plate (De Groeve et al., in prep. B; Van der Geer et al. submitted). In addition, we used an improved and highly detailed new bathymetric map of Greece based on the European Marine Observation and Data Network (EMODnet 2021) bathymetric model (115 m x 115 m), which is a harmonized European bathymetric model integrating data from multiple resources. Where no more detailed information was available, we used the General Bathymetric Chart of the Oceans (GEBCO 2021). We merged the bathymetry raster with a digital elevation model over Europe (EU-DEM) (25 m x 25 m) (European Environmental Agency, GMES RDA 2021).

Using these newly available, fine-grained historic coastline rasters, we were able to not only quantify in high detail the location and size and moment of separation of all study islands, but also calculate a set of physiographic variables for each paleo- and present-day island. These variables were: area, average roughness (calculated as the average of each cell's largest difference in altitude from its neighboring cells), proportion of north-facing slopes (defined as number of cells on an island with an aspect  $a$  such that  $315^\circ < a < 45^\circ$ , i.e. aspect within  $45^\circ$  of true North), and proportion of south-facing slopes (number of cells with aspect  $a$  such that  $135^\circ < a < 225^\circ$ , or aspect within  $45^\circ$  of true south). These variables were calculated for the latest time-step in which an island existed, such that for intermediate paleo-islands we use the conditions just before further fragmentation into daughter islands, while for present-day islands we use present-day conditions. We also calculated each island's total duration of isolation following fragmentation of the ancestral landmass. Lastly, we also calculated what we term the "original area" of each island, calculated as the final area of its mother island right before fragmentation, and used this to calculate two metrics of area change: total area contraction (original area – final area), and average contraction (total area loss/time since isolation). A complete list of variables, and their sources and methods of calculation, can be found in Appendix C.

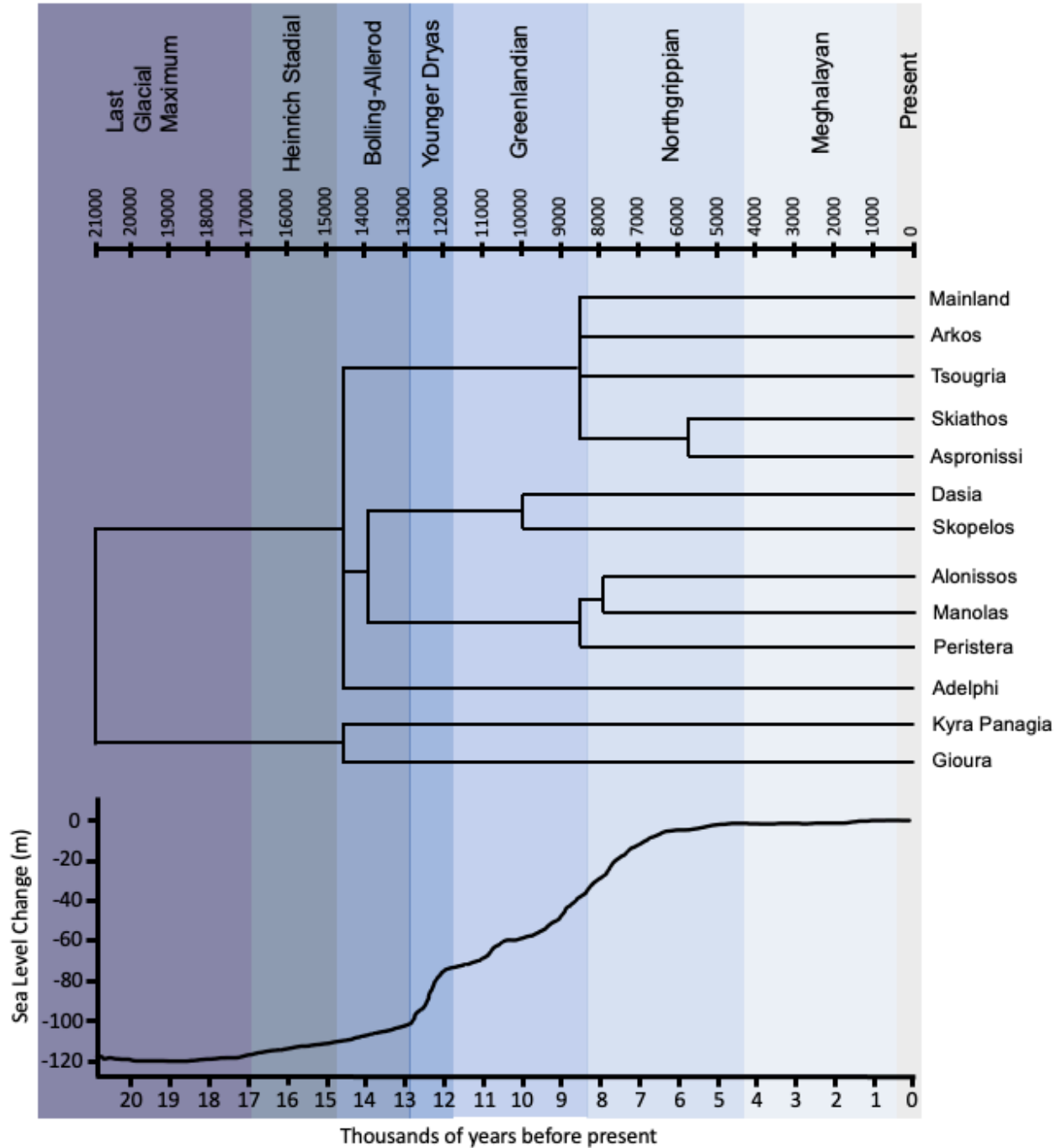
## Reconstructing extinctions

We selected a set of 83 land-bridge islands in the NE Mediterranean Basin for which high quality herpetofaunal data were available. These islands contained a total of 44 reptile taxa (Appendix A), representing a sizeable portion of the reptile species richness in the region.

Using the historic coastline rasters we developed, we were able to characterize how these islands separated from paleo-islands or the mainland since the LGM, and create a set of five island fragmentation cladograms, displaying the sequence of island separation in five of the major archipelagoes around Greece (Fig. 2): the Ionian, the Sporades, the Cyclades, the Argo-Saronic, and the East Aegean. Our historic coastline rasters were used to update and add to island fragmentation cladograms used in prior research (Foufopoulos and Ives 1999). An example cladogram displaying island fragmentation patterns along with global mean sea level rise over the climatic periods we consider is provided for the Sporades archipelago (Fig. 3), with the other 4 available in Appendix B.



**Figure 2.** The five island groups considered in this study. Each island is colored according to the percent of taxa lost relative to its ancestral mainland species community.

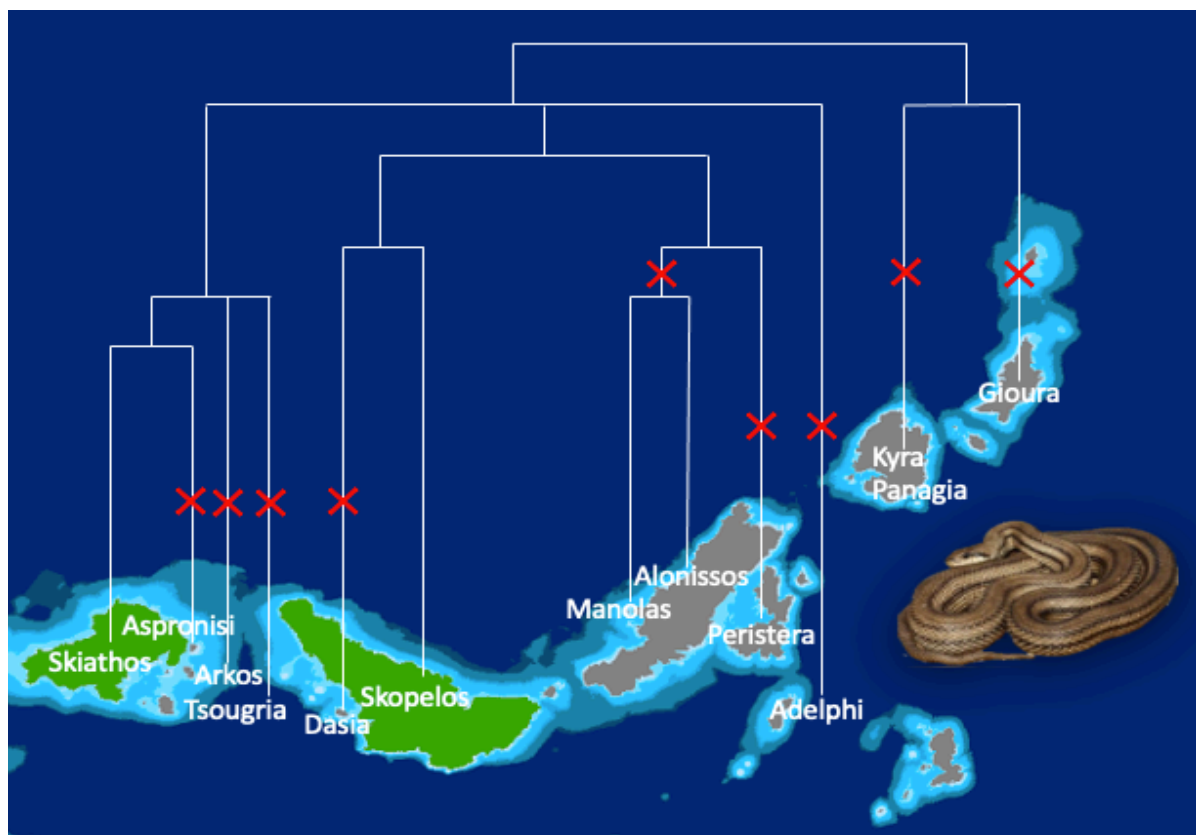


**Figure 3.** Island fragmentation cladogram displaying separation sequence of the Sporades archipelago over the 7 climatic stages considered in this study. Below, global average sea level changes occurring over the same period (Fleming et al. 1998).

Each non-terminal node (representing a paleo-island or paleo-peninsula) in these island fragmentation cladograms was given a unique name for ease of analysis (e.g. the paleo-island that contained the present-day islands of Tinos and Andros was named Tin-And). We then reconstructed the number of potential extinctions that may have occurred on each modern and

paleo-island based on present-day occurrences of each reptile species on today islands, along with the principles of vicariance and parsimony: we assume that any given paleo-island contained all the species present on each of its daughter islands. Any difference in species communities in sister islands is assumed to be due to local extinctions of certain species on one or more islands.

This simple parsimony assumption, however, is potentially problematic, as parsimony assumes that the correct reconstruction of extinctions is the one that explains current species distributions with the fewest possible number of extinction events; however, island biogeography theory has long held that smaller and longer-isolated islands should have higher extinction rates (MacArthur and Wilson 1967; Wilcox 1978). Because of this possibility, we use a principle developed by Foufopoulos and Ives (1999), which we here call “modified parsimony”. Under this technique, we assume parsimony but with the exception that a paleo-island is assumed to have been occupied by a given species even if its daughter island is unoccupied provided its sister island is occupied. This technique caused our reconstructed sequence of extinctions to be more in line with established island biogeography theory (i.e. more extinctions were reconstructed on smaller islands than under the simple parsimony method), and so further analysis used the sequence of extinctions reconstructed by modified parsimony (Fig. 4).



**Figure 4.** A set of extinctions reconstructed by modified parsimony: *Elaphe quatuorlineata* (pictured), in the Sporades archipelago. Species is present on green islands and not present on gray islands. X represents a reconstructed extinction event.

This approach also relies on the additional assumption that no colonization is occurring, and based on this important factor we removed certain species from our analysis due to the possibility of their having been introduced by humans. The following species were removed due to this possibility (Kornilios et al. 2010; Carranza and Arnold 2006): *Chalcides ocellatus*, *Hemidactylus turcicus*, and *Laudakia stellio*. We determined that colonization was not a concern for the remainder of the species considered based on several lines of evidence. Firstly, population genetic studies identify distinct reproductively isolated populations, supporting the hypothesis that there is no significant gene flow for reptiles among these islands (Hurston et al. 2009). Secondly, according to the theory of island biogeography (MacArthur and Wilson 1967), if recolonization is occurring, islands closer to the mainland and to other islands should have higher species richness; instead, prior studies have shown that no statistically significant difference exists in island species richness based on distance to the nearest neighboring landmass (Foufopoulos and Ives 1999). Finally, although research has established that terrestrial reptiles are capable of floating between islands for many hours (Schoener and Schoener 1984), they require vegetation mats to do so (Heatwole and Levins 1973); there is no indication that such mats would have developed in the Aegean sea given its high aridity and limited scrub vegetation.

### ***Climatic variables***

We obtained climatic information from the publicly available dataset PaleoClim (Brown et al. 2018; Fordham et al. 2017), a series of global climate reconstructions that include TIFF files of bioclimatic variables for each of seven major climate periods going back to the LGM: the Meghalayan (0.3-4.2 kybp); the Northgrippian (4.2-8.3 kybp); the Greenlandian (8.3-11.7 kybp); the Younger Dryas (11.7-12.9 kybp); the Bolling-Allerod (12.9-14.7 kybp); the Heinrich Stadial (14.7-17.0 kybp); and the Last Glacial Maximum (21.5 kybp) (Cohen et al. 2020). For each interstadial period we calculated the mean of each climatic variable over all pixels intersecting each island.

We selected a set of bioclimatic variables based on previous studies to assess the influence of temperature and precipitation on these island population extinctions. As our metric of temperature, we chose Mean Temperature of the Warmest Quarter (MTWQ) based on our hypothesis, backed up by prior research, that reptile life histories are affected by high summer temperatures (e.g. Janzen 1994; Megia-Palma et al. 2020). For a metric of precipitation, we calculated mean annual precipitation based on its frequent use in ecological studies (e.g. Araujo et al. 2008; Senior et al. 2021). As with the physiography variables, each variable was recorded for the latest time period of an island's existence. However, we also gathered data on what we term "Original Precipitation" (OP), calculated for an island as the mean annual precipitation of its mother island at the last time-step before fragmentation. We included this variable in order to test the hypothesis that post-isolation extinctions are related to pre-isolation precipitation. In addition, in exploring the drivers of the relationship between precipitation and extinctions, we also gathered data on modern human population levels from the 2011 Greek census (Hellenic Statistical Authority 2011). A complete list of variables used, along with their sources and methods of calculation, can be found in Appendix C.

## *Statistical Analysis*

We first conducted an exploratory analysis performing standard univariate OLS regressions of each variable against the number of reconstructed extinction events (“extinctions”) that occurred during the period of existence of each present day or paleo-island. We then tested each variable against extinctions that were corrected for time-since-isolation and natural log-transformed area by running a bivariate regression of extinctions against these two variables, and then testing each other variable against the residuals of this regression.

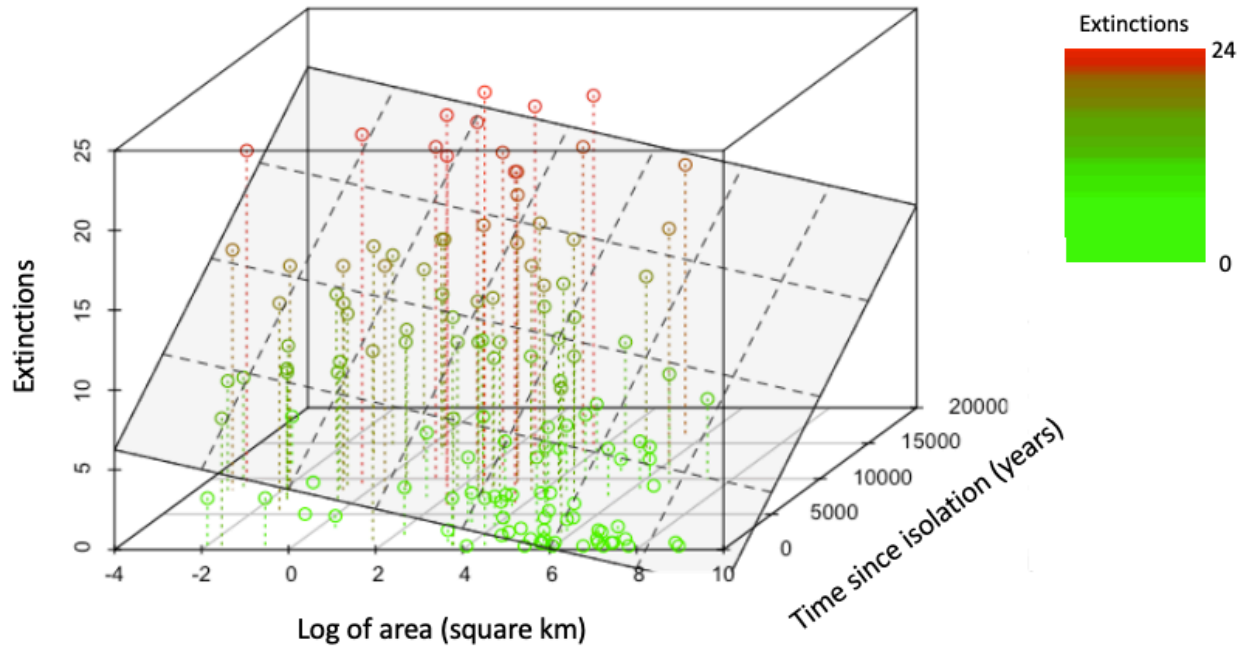
We then assessed the interacting effects of these factors in driving extinctions by building a multivariate model. We used a negative binomial generalized linear model because our dependent variable (number of extinctions) is count data and is overdispersed (Ch. 20, Walker 2018).

Well-established island biogeography theory indicates that extinctions are dependent on island area and time-since-isolation (MacArthur and Wilson 1967; Wilcox 1978). As such, we used these two variables in all models and tested the hypothesis that extinctions are caused by the interacting effects of these two variables along with temperature, precipitation, and topographic heterogeneity. Because we calculated both mean annual precipitation and original precipitation, these two showed a high degree of multicollinearity ( $VIF > 10$ ); we decided to include original precipitation in order to test the hypothesis that island population extinctions are driven in part by pre-isolation precipitation conditions. We selected variables to include in our final model using the Akaike Information Criterion (AIC) (Table 1). Finally, we standardized each variable in this model using a standard z-score normalization to shed light on the relative influence of each variable in explaining extinctions by examining their standardized beta coefficients ( $\beta$ ).

## **Results**

### *Exploratory Analysis*

Our exploratory analysis involving univariate OLS regression of each variable against reconstructed extinctions indicated that area and time-since-isolation showed strong associations with extinctions on the temporal scale we consider (Fig 5). The relationships for area ( $\beta = -1.0766$ ,  $p = 4.9e^{-8}$ ,  $R^2 = 0.198$ ), and time-since-isolation ( $\beta = 0.0009031$ ,  $p = 1.8e^{-14}$ ,  $R^2 = 0.357$ ) were the strongest and most significant in our univariate tests.



**Figure 5.** Extinctions are strongly associated with log-transformed area of an island as well as an island's time since isolation from a paleo-landmass. Grey polygon represents best-fit regression plane.

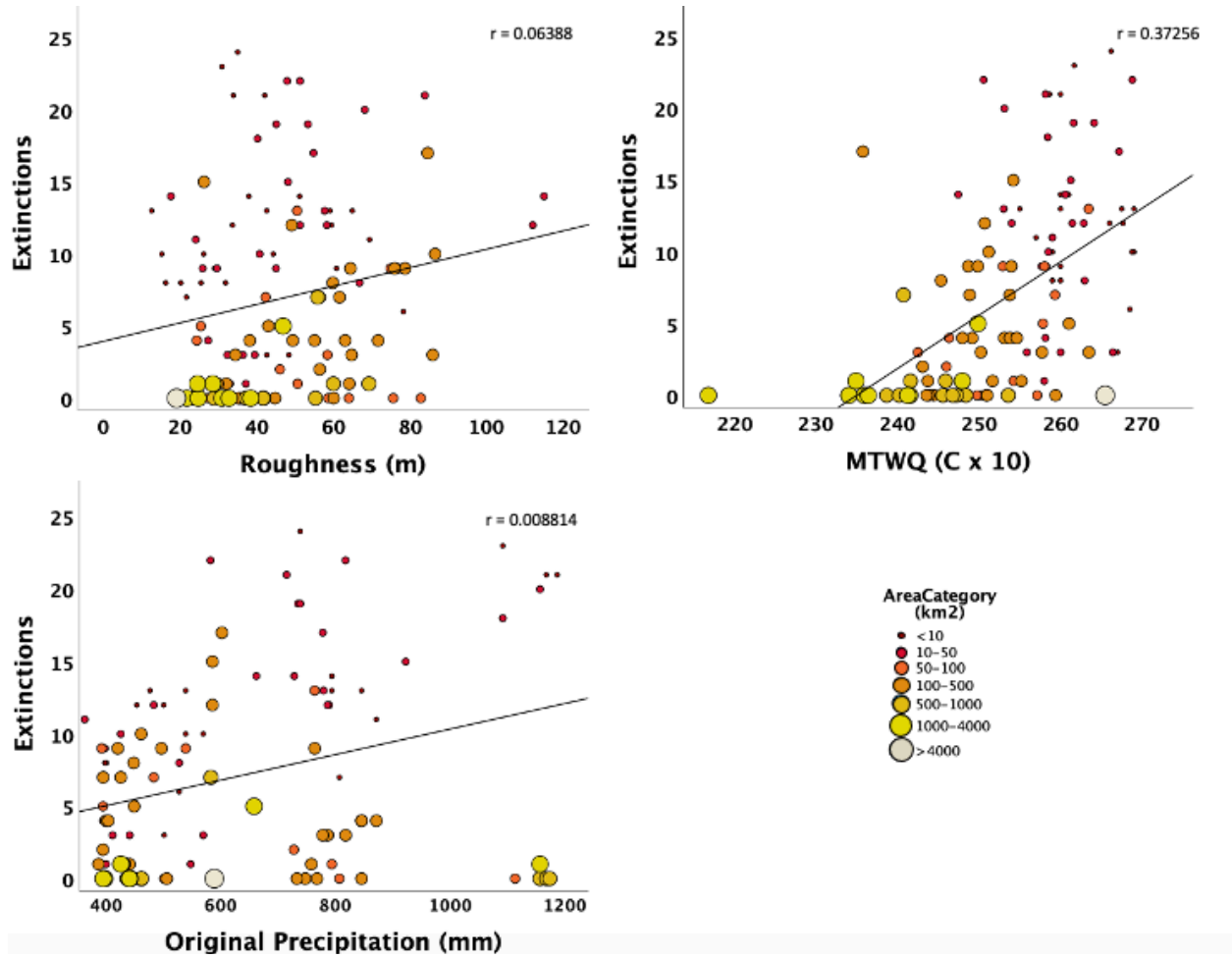
We found that mean temperature of the warmest quarter ( $\beta = 0.3637$ ,  $p = 5.66e^{-9}$ ,  $R^2 = 0.229$ ), average roughness ( $\beta = 0.06388$ ,  $p = 0.0347$ ,  $R^2 = 0.03695$ ), original precipitation ( $\beta = 0.010738$ ,  $p = 9.79e^{-6}$ ,  $R^2 = 0.1391$ ) and final precipitation ( $\beta = 0.009892$ ,  $p = 3.22e^{-5}$ ,  $R^2 = 0.124$ ) were significantly associated with extinctions in simple univariate regressions (Fig. 6). We found no significant relationship for proportion of north or south facing slopes, nor for area reduction.

Because island biogeography theory predicts that area and time-since isolation are the largest controlling factors on island species communities (MacArthur and Wilson 1967; Wilcox 1978), and we confirmed a significant relationship in our data, we then controlled each other variable for these. After controlling for area and time-since-isolation, only two variables showed a significant ( $p < 0.05$ ) univariate association with extinctions: final annual precipitation ( $\beta = 0.009811$ ,  $R^2 = 0.204$ ,  $p = 2.9e^{-8}$ ), and original annual precipitation ( $\beta = 0.00971$ ,  $R^2 = 0.19$ ,  $p = 9.5e^{-8}$ ).

### **Multivariate Analysis**

To test the effects of multiple variables simultaneously in explaining extinctions, we compared a number of nested models. Because of the broad support for the effects of time-since-isolation and area on extinction rates, we included these variables in the default baseline model. We then tested the effects of adding our selected metrics of precipitation (OP), temperature (MTWQ), and topography (AR). We present the univariate associations of each of these variables with extinctions (Fig. 6):





**Figure 6:** Univariate relationships of Average Roughness (AR), Mean Temperature of the Warmest Quarter (MTWQ), and Original Precipitation (OP) against extinctions.  $r$  = regression coefficient.

All nested models were compared according to their AIC values and are shown below. Our final model supports the hypothesis that reptile extinctions on Mediterranean islands are driven by the interacting effects of area, time-since-isolation, summer temperature, pre-fragmentation precipitation, and topographic roughness.

**Table 1:** Nested model series.  $\Delta AIC$  = difference in AIC value from the final selected model. Akaike weight  $w$  calculated as  $w_i = \exp\left(-\frac{\Delta_i}{2}\right) / \sum_{i=1}^M \exp\left(-\frac{\Delta_i}{2}\right)$  (Turkheimer et al. 2003).

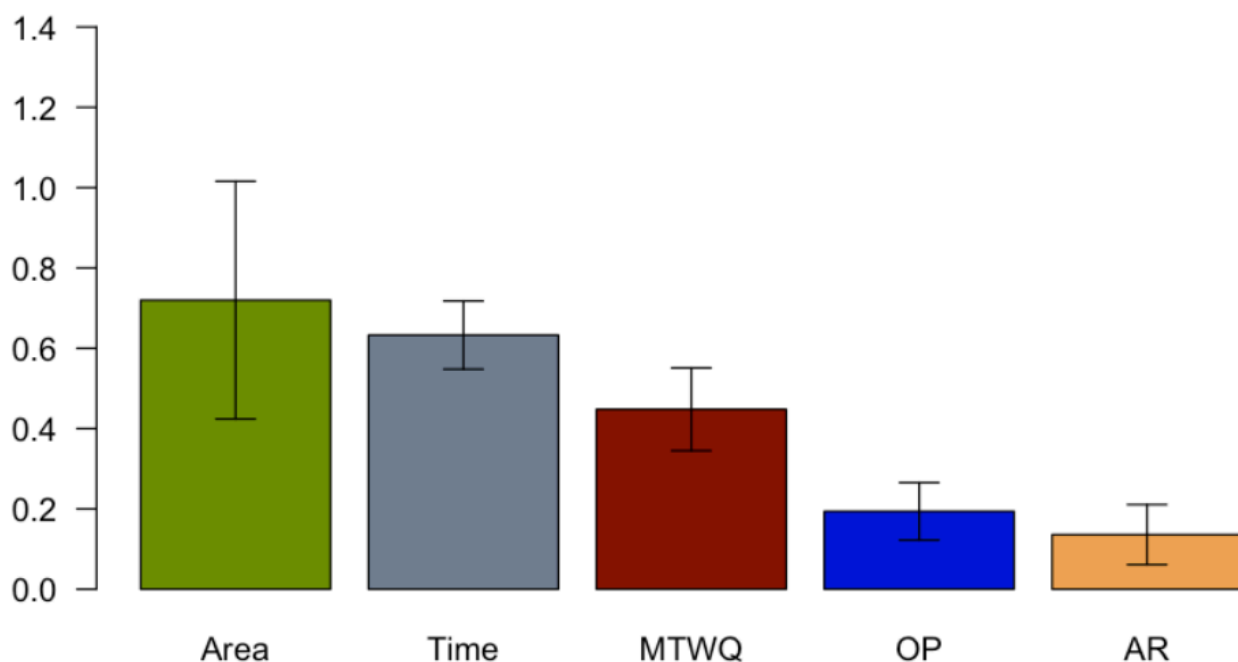
Model structure	Model No.	AIC	$\Delta AIC$	Akaike weight
Extinctions ~ Area + Time-since-isolation (base model)	1	652.74	+25.27	$2.903e^{-6}$
Extinctions ~ Area + Time-since-isolation + MTWQ	2	641.30	+13.83	0.000885

Extinctions ~ Area + Time-since-isolation + OP	3	641.93	+14.46	0.000646
Extinctions ~ Area + Time-since-isolation + AR	4	647.51	+20.04	3.969e <sup>-5</sup>
Extinctions ~ Area + Time-since-isolation + AR + OP	5	642.02	+14.55	0.000618
Extinctions ~ Area + Time-since-isolation + MTWQ + OP	6	633.78	+6.31	0.038028
Extinctions ~ Area + Time-since-isolation + MTWQ + AR	7	632.62	+5.15	0.067918
<b>Extinctions ~ Area + Time-since-isolation + MTWQ + Average roughness + Original precipitation</b>	<b>8</b>	<b>627.47</b>	<b>0</b>	<b>0.891862</b>

The final model (8) revealed a negative relationship between extinctions and area ( $\beta = -0.102$ ,  $p = 0.006563$ ), and positive relationships between extinctions and time-since-isolation ( $\beta = 1.382e^{-4}$ ,  $p = 4.83e^{-13}$ ), original precipitation ( $\beta = 0.005249$ ,  $p = 0.0008961$ ), mean temperature of the warmest quarter ( $\beta = 0.04357$ ,  $p = 0.000165$ ), and average roughness, ( $\beta = 0.01037$ ,  $p = 0.005466$ ).

To obtain an understanding of the relative contributions of different variables in explaining extinctions, we z-score normalized the variables in our final model (Fig. 8). Following standardization, it emerged that area had the largest effect, ( $\beta = -0.71983$ ) followed by time-since-isolation ( $\beta = 0.63280$ ), and smaller effect sizes for mean temperature of the warmest quarter ( $\beta = 0.44793$ ), original precipitation ( $\beta = 0.19390$ ), and average roughness ( $\beta = 0.13592$ ).

## Standardized Beta Coefficients (Absolute Value)



**Figure 7:** Standardized  $\beta$  coefficients (absolute value) of all variables in the final model; Time = time-since-isolation, MTWQ = mean temperature of the warmest quarter, OP = original precipitation, AR = average roughness.

### Discussion

Our final model shows that island reptile extinctions are negatively associated with island area, and positively associated with time-since-isolation, mean temperature of the warmest quarter (MTWQ), original (pre-fragmentation) precipitation (OP), and average topographic roughness (AR). The model displays that area has the largest effect on extinctions, followed by time-since-isolation, and MTWQ, OP, and AR all have smaller effect sizes.

### *The temporal scale of island biogeography theory*

The strongest evidence from our analyses points to an effect of island area and time elapsed since isolation on island reptile extinctions. In univariate analysis, time-since-isolation was the best single predictor of extinctions and area was the second best, whereas in our standardized multivariate model, the largest effect size was for area and the second largest was for time-since-isolation. Although it has long been established in island biogeography that extinction rates are negatively associated with island area and positively associated with time-since-isolation (MacArthur and Wilson 1967; Wilcox 1978) studies of island biogeography theory have largely focused on “ecological time”, that is relatively short timescales, often on the scale of a human lifespan, on which speciation can be ignored, with some attempts to extend the theory to “evolutionary time” (e.g. Whittaker, Triantis, and Ladle 2008), i.e. time scales large enough to consider speciation within the taxon of interest (Lomolino and Brown 2009). While

not quite reaching speciation-relevant timescales (Ricklefs, Losos, and Townsend 2007), the 21,500 year period considered here represents a significant extension of typical conservation biogeography studies, which focus on temporal scales close to a human lifespan (e.g. Pimm et al. 1993; Newmark 1995). As such, our results suggest that the area and isolation effects typically considered in island biogeography theory also operate at epoch-level temporal scales.

The population extirpations observed in our system are typical for the extinction debt experienced by communities found on land-bridge islands, and which is “paid” through a process of community relaxation (Diamond 1972; Halley et al. 2016). Past research has indicated that this relaxation occurs at an exponentially decaying rate, with extinctions happening rapidly early on and then slowing down over time (e.g. Wilcox 1978). In contrast, we find that extinctions proceed at an unabated linear rate over time as evidenced by the fact the extinctions against time relationship was better fitted to a linear ( $R^2 = 0.3547$ ,  $p = 1.83e^{-14}$ ) than to an exponential model ( $R^2 = 0.3057$ ,  $p = 3.12e^{-12}$ ). This result is best explained by the fact that past biogeography studies typically investigate community responses in fragments of stable size and conditions (e.g. Newark 1995, Halley et al. 2016). Instead, on our land-bridge islands, conditions post-separation continued to deteriorate as sea-level continued rising and ambient conditions became increasingly warmer.

These findings raise questions about the community relaxation process and how researchers can predict changes in biodiversity over long periods. Over the next several centuries we will see sea levels rise significantly, reducing island area further (Levermann et al. 2013), and assumably inducing further species loss. An important question that future studies could consider is whether these island communities are currently at equilibrium, and if so, whether the area loss we are likely to see as anthropogenic climate change progresses will lead to another wave of community relaxation. We did not extend our analysis to the level of prediction, but future studies could consider the important question of how long the community relaxation process takes to complete.

### *The thermal environment as a driver of extinction*

Our findings also suggest that high summer temperatures are an important part of the Mediterranean reptile extinction process. In the final model, the third most important driver of extinctions, after area and time-since-isolation, was the mean temperature of the warmest quarter. It is important however to not interpret any temperature effects too narrowly; lower temperatures are related to other important landscape traits such as high vegetation cover (Keppel et al. 2017) and are associated with moisture retention, all of which have been shown to be important aspects of species survival in arid landscapes (Foufopoulos et al. 2011).

Nonetheless, this line of evidence is consistent with much current research which has found that high temperatures can have, either directly or indirectly, a negative effect on reptile life histories. This body of research provides some suggestions as to possible mechanisms behind the pattern we show. For example, higher incubation temperatures have been associated with reduced size and movement ability in lizards (Brana and Ji 2000), as well as reduced embryo survival and growth rate (Van Damme et al. 1992). High temperatures are also known to influence reptile sex determination, raising the possibility that temperature increase could put reptile populations at risk of demographic collapse (Janzen et al. 1994). Beyond the direct effects of temperature on reptile life histories, higher temperatures are also associated with lower

vegetation cover, and many reptile taxa rely on a certain degree of structural vegetation complexity (Keppel et al. 2017; Foufopoulos et al. 2011).

Our results not only confirm that high temperatures are part of the reptile extinction process, but also suggest that over long time periods consistent warming may be a very important factor in driving reptile extinctions on islands. In the age of anthropogenic climate change, these findings support the idea that conservation managers should focus attention on island reptiles, which may be more vulnerable to warming-related population declines than previously thought.

### ***Pre-isolation climate***

Both annual precipitation (the precipitation of an island at its latest point in existence) and original precipitation (the precipitation of an island at its earliest point in existence) were positively associated with extinctions in univariate analysis. They were the only variables which showed a significant association with extinctions after controlling for area and time-since-isolation. Our best multivariate model also included original precipitation, which had a significant positive relationship with extinctions. In the final standardized model, precipitation was the fourth largest contributor, showing a weaker effect than area, time-since-isolation, or temperature, but a stronger effect than topographic roughness.

The positive association of early precipitation with extinction is likely not causative, and may be attributed to two factors: spatial patterns of diversity, and the identity of the species going extinct. Higher precipitation is associated today with islands that are larger, more mountainous, and closer to the mainland, all factors that are known to independently facilitate higher reptile diversity. As a result, mesic islands at the LGM harbored more diverse herpetofaunas and thus simply had more species to lose. Furthermore, the taxa that occur on such mesic islands tend to be more moisture-dependent, heat-intolerant temperate species such as wetland snakes and terrapins. Because these species are known to have small, patchy distributions, they are particularly sensitive to both habitat fragmentation and warming, and are the first to go extinct on land-bridge islands (Foufopoulos et al. 2011).

We are aware of one prior study which found a similar relationship (Senior et al. 2021), in which the authors suggest that the pattern is actually driven by human developments; higher precipitation is often associated with higher primary productivity, which tends to foster higher human populations and thus higher levels of potentially ecologically detrimental human activities. We tested the association between extinctions and present day human population sizes, as well as densities, and found no significant relationship regardless of whether or not we controlled for area and time. However, this analysis did not include the extinctions or human populations on paleo-islands, and future studies may be able to incorporate data on historic human population numbers to shed more light on the role of human population size on past extinctions.

### ***Physiography and landscape change***

Physiographic characteristics have long been assumed to be important determinants of population persistence (Foufopoulos et al. 2011). Based on prior studies that found a role for various metrics of landscape heterogeneity, we investigated whether average topographic roughness played a role in island population extinctions. This variable was significantly positively associated with extinctions in univariate analysis, but was no longer significant after

controlling extinctions for area and time-since-isolation. It emerged as significant in our final model; while it had the weakest effect in our standardized model, we found that island average roughness was positively associated with species extinctions. Most studies investigating the effects of physiography and landscape characteristics find a beneficial effect of topographic heterogeneity on species persistence. Instead, we found that fewer species survived on islands with high topographic roughness, a perhaps counter-intuitive result. However, it is noteworthy that average roughness for an island is calculated as the mean of the highest inter-pixel difference in altitude for each pixel in an island. Consequently, islands with high roughness scores, such as Gioura (see Fig. 1C), and Telendos, tend to be steep, rocky, and barren, without the diversity of lush, productive microhabitats found in flat landscapes, and which can facilitate the persistence of diverse herpetile communities. As a result, the relationship between island roughness and reptile extinctions could be interpreted as evidence of the importance of productive habitats that can support strong reptile populations.

It should be noted that average roughness, unlike some other metrics of landscape heterogeneity, does not take into account heterogeneity in vegetation or soil. Vegetation is likely one of the most important environmental factors affecting reptile population dynamics (Brown et al. 2011; Pontes-da-Silva et al. 2018). In the Mediterranean Basin in particular, present-day persistence of many temperate zone taxa is tied to the continued presence of cool, humid habitats such as forests and wetlands (Foufopoulos et al. 2011). However, although some pollen studies and niche models have attempted to reconstruct the vegetative environments of the Aegean borderlands (Kotthoff et al. 2008; Sadori et al. 2013), the relatively arid conditions of the archipelagoes are not amenable to the formation of bogs and lakebeds, the primary sources of palynological stratigraphy. As a result, to our knowledge no study has yet reconstructed paleo-vegetation of Aegean islands, a gap preventing us from including and testing vegetation information for paleo-islands in this study. Should this information become available, it would allow future studies to shed more light on the relationship between reptile extinctions and landscape by testing the role of past vegetation characteristics.

Also important were the physiographic factors for which we did not find a significant association with extinctions. Prior research has documented an influence of slope aspect on microclimatic conditions and resource availability (Miller and Poole 1980; Pavlicek et al. 2003; Li et al. 2011), with significant effects on vegetation distributions (Sternberg and Shoshany 2001). In contrast, we did not identify any effect of an island's predominant slope aspect on extinctions.

Similarly unexpected was the lack of an effect for area reduction, considering the species-area relationship which dictates that larger area losses should lead to more population extinctions. One possible explanation comes from the power-function pattern of the fundamental species-area relationship in ecology. Much of the observed reduction in area occurred on very large islands, where even substantial losses of land area are likely to result in only minor drops in species richness, hence making any effect of area reduction on extinction dynamics easier to miss. This in turn could explain the seemingly contradictory result that we see a highly significant relationship between extinctions and island area, but no relationship between extinctions and amount or rate of area loss.

A broader explanation, however, is that the effects of landscape and landscape change may operate on a different temporal scale than the one considered in this paper. The research that has considered the relationship between physiography and reptile distributions has largely been focused on present-day conditions. Future studies may consider the question of whether

physiography, and especially rate of area loss, are in fact important drivers of extinction, but on different time scales from the 21,500 years considered here.

## **Conclusions**

Overall, our results suggest that the largest extrinsic drivers of island reptile extinctions since the LGM are lack of island area and extended periods of isolation from the mainland, along with a hot summer temperatures. Wetter, more lush areas that likely harbored more diverse faunas at the LGM have lost more species than areas that were drier. We also find that islands with high topographic roughness have experienced more extinctions, likely because they are unproductive and do not offer high quality habitats. Also important to understanding the patterns we demonstrated are the variables that were not related to the number of extinctions: we find no evidence for an influence of dominant slope aspect or area shrinkage on extinctions at this time scale. Our findings suggest that the particular Mediterranean reptile communities having partially evolved in cooler, more moist conditions may be particularly vulnerable to global warming and the associated desiccation. Overall, this study suggests that conservation managers need to prioritize the preservation of mesic, cool habitats and focus on the heat intolerant taxa occurring there, as they are likely to be most affected by climate change.

**Appendix A: Species Considered in this Study**

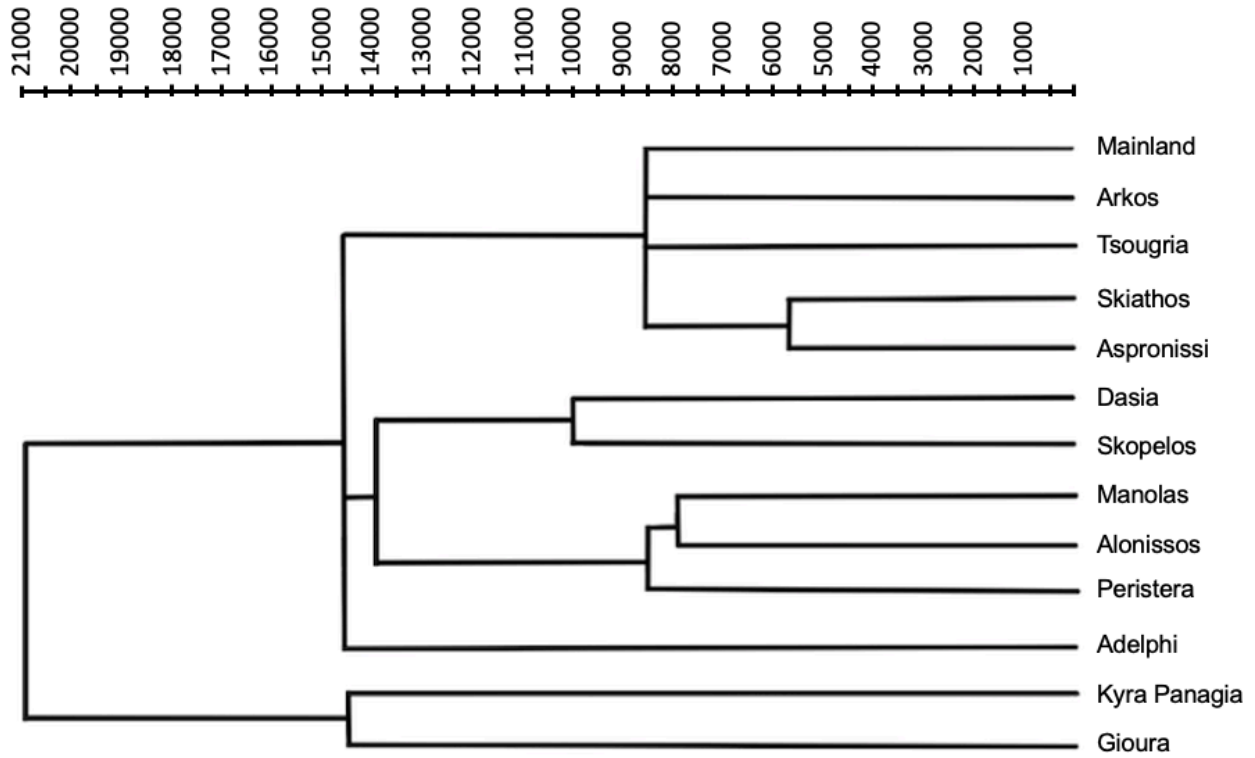
<b>Cyclades</b>	<b>Sporades</b>	<b>Argo-Saronic Gulf</b>	<b>East Aegean</b>	<b>Ionian</b>
<i>Mauremys rivulata</i>	<i>Mauremys rivulata</i>	<i>Mauremys rivulata</i>	<i>Mauremys rivulata</i>	<i>Mauremys rivulata</i>
<i>Testudo marginata</i>	<i>Testudo marginata</i>	<i>Emys orbic</i>	<i>Emys orbic</i>	<i>Emys orbic</i>
<i>Mediodactylus spp.</i>	<i>Mediodactylus spp.</i>	<i>Testudo hermannii</i>	<i>Testudo graeca</i>	<i>Testudo hermannii</i>
<i>Lacerta trilineata</i>	<i>Lacerta trilineata</i>	<i>Testudo marginata</i>	<i>Mediodactylus spp.</i>	<i>Mediodactylus spp.</i>
<i>Podarcis erhardii</i>	<i>Podarcis erhardii</i>	<i>Pseudopus spp.</i>	<i>Chamaeleo spp.</i>	<i>Pseudopus spp.</i>
<i>Ablepharus kitaibeli</i>	<i>Ablepharus kitaibeli</i>	<i>Mediodactylus spp.</i>	<i>Blanus spp.</i>	<i>Anguis fragilis</i>
<i>Xerotyphlops vermicularis</i>	<i>Lacerta viridis</i>	<i>Algyroides moreoticus</i>	<i>Lacerta trilineata</i>	<i>Algyroides nigropunctatus</i>
<i>Eryx jaculus</i>	<i>Pseudopus spp.</i>	<i>Anguis fragilis</i>	<i>Pseudopus spp.</i>	<i>Eryx jaculus</i>
<i>Dolichophis caspius</i>	<i>Dolichophis caspius</i>	<i>Lacerta trilineata</i>	<i>Anatololacerta spp.</i>	<i>Algyroides moreoticus</i>
<i>Platyceph najadum</i>	<i>Platyceph najadum</i>	<i>Ablepharus kitaibeli</i>	<i>Ophisops spp.</i>	<i>Lacerta trilineata</i>
<i>Elaphe quatrolineata</i>	<i>Elaphe quatrolineata</i>	<i>Podarcis pelepones</i>	<i>Ablepharus spp.</i>	<i>Lacerta viridis</i>
<i>Zamenis situla</i>	<i>Zamenis situla</i>	<i>Podarcis erhardii</i>	<i>Heremites auratus</i>	<i>Podarcis ionicus</i>
<i>Telescopus fallax</i>	<i>Telescopus fallax</i>	<i>Lacerta viridis</i>	<i>Xerotyphlops spp.</i>	<i>Ablepharus kitaibeli</i>
<i>Natrix natrix</i>	<i>Natrix natrix</i>	<i>Ophiomorus punctatis</i>	<i>Eryx spp.</i>	<i>Xerotyphlops vermicularis</i>
<i>Natrix tesselata</i>	<i>Malpolon insignitus</i>	<i>Xerotophlops vermicularis</i>	<i>Dolichophis caspius</i>	<i>Dolichophis caspius</i>
<i>Vipera ammodytes</i>	<i>Vipera ammodytes</i>	<i>Eryx jaculus</i>	<i>Platyceph najadum</i>	<i>Hierophis gemonensis</i>
<i>Macrovipera lebentina</i>		<i>Hierophis gemonensis</i>	<i>Hemorrhoids nummifer</i>	<i>Platyceph najadum</i>
		<i>Dolichophis caspius</i>	<i>Eirenis spp.</i>	<i>Elaphe quatrolineata</i>
		<i>Platyceph najadum</i>	<i>Dolichophis jugularis</i>	<i>Zamenis situla</i>
		<i>Elaphe quatrolineata</i>	<i>Zamenis situla</i>	<i>Elaphe longissima</i>
		<i>Zamenis situla</i>	<i>Malpolon spp.</i>	<i>Malpolon insignitus</i>



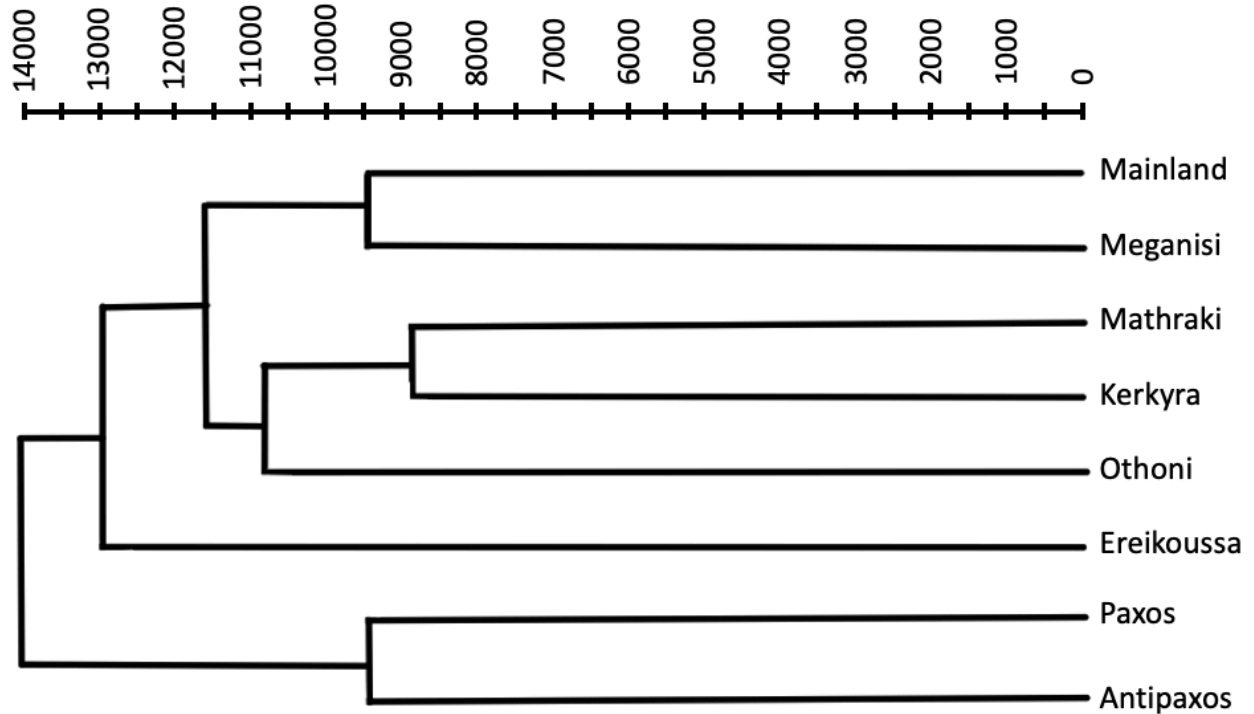
		<i>Malpolon insignitus</i>	<i>Telescopus fallax</i>	<i>Telescopus fallax</i>
		<i>Telescopus fallax</i>	<i>Natrix natrix</i>	<i>Natrix natrix</i>
		<i>Natrix natrix</i>	<i>Natrix tessellata</i>	<i>Natrix tessellata</i>
		<i>Natrix tessellata</i>	<i>Montivipera xanthina</i>	<i>Vipera ammodytes</i>
		<i>Vipera ammodytes</i>	<i>Testudo marginata</i>	
			<i>Lacerta viridis</i>	
			<i>Podarcis erhardii</i>	
			<i>Coronella austriaca</i>	
			<i>Elaphe longissima</i>	
			<i>Elaphe sauromates</i>	
			<i>Vipera ammodytes</i>	
			<i>Podarcis tauricus</i>	

**Appendix B: Island fragmentation cladograms for each archipelago considered**

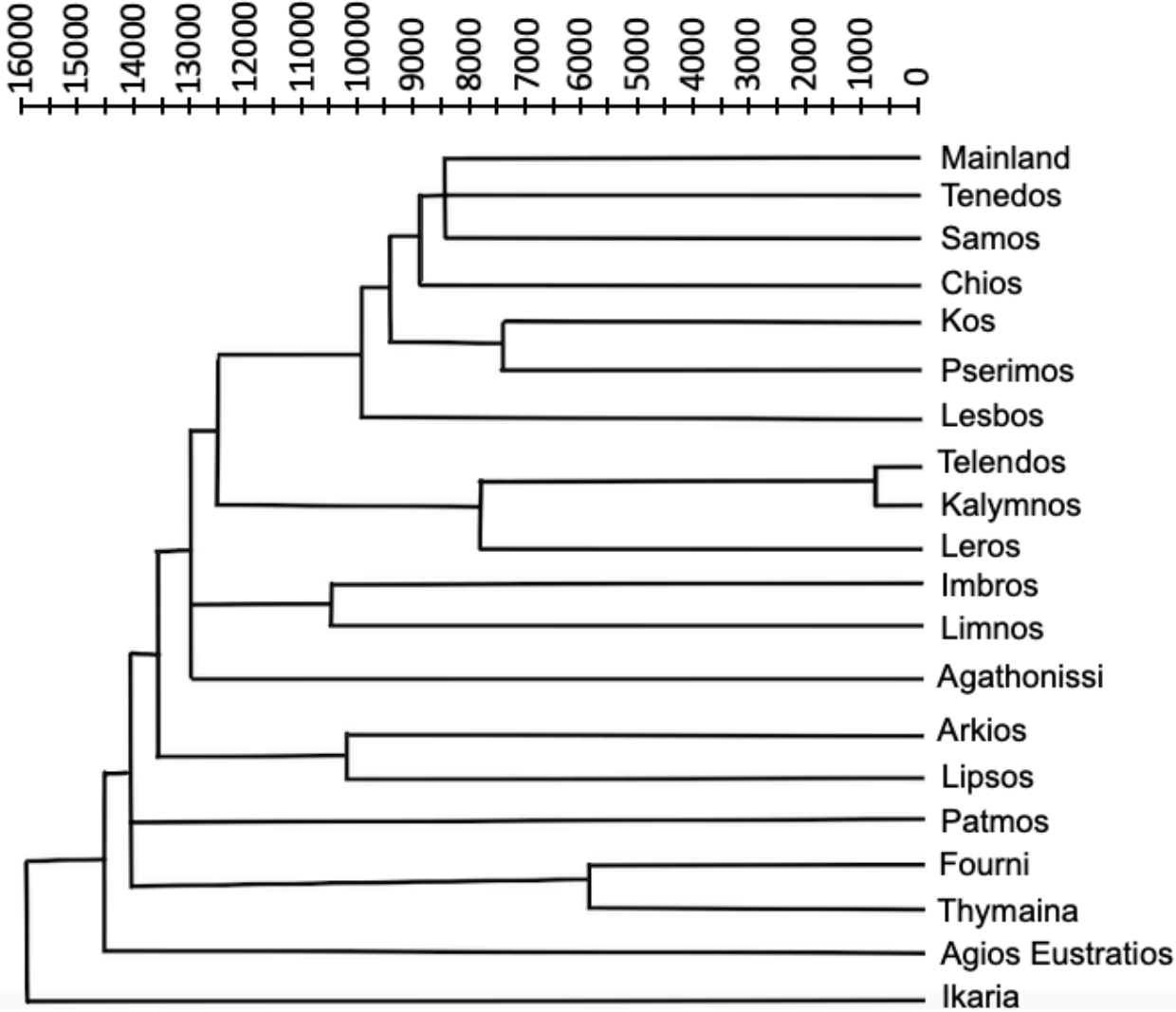
*The Sporades*



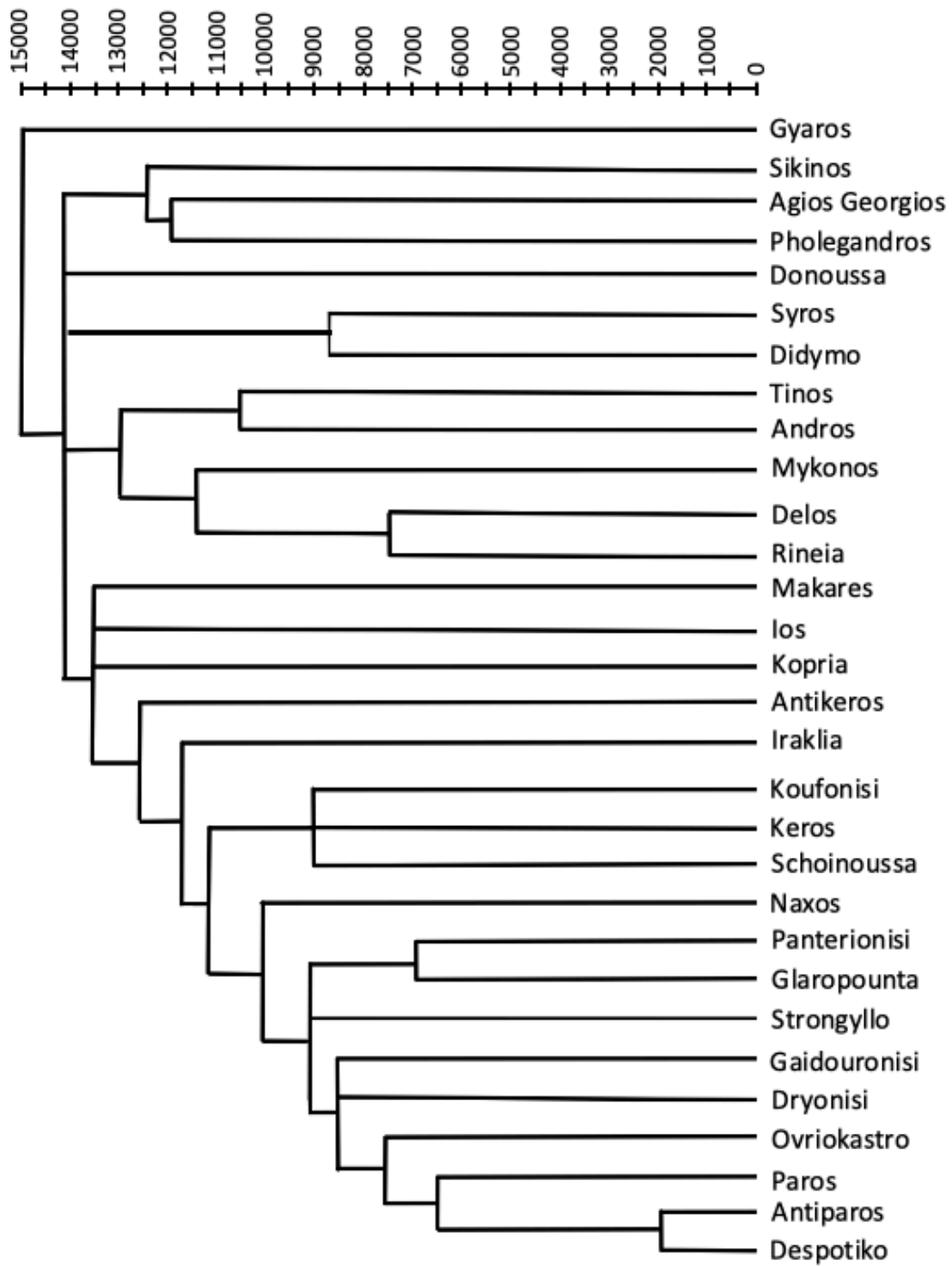
*The Ionians*



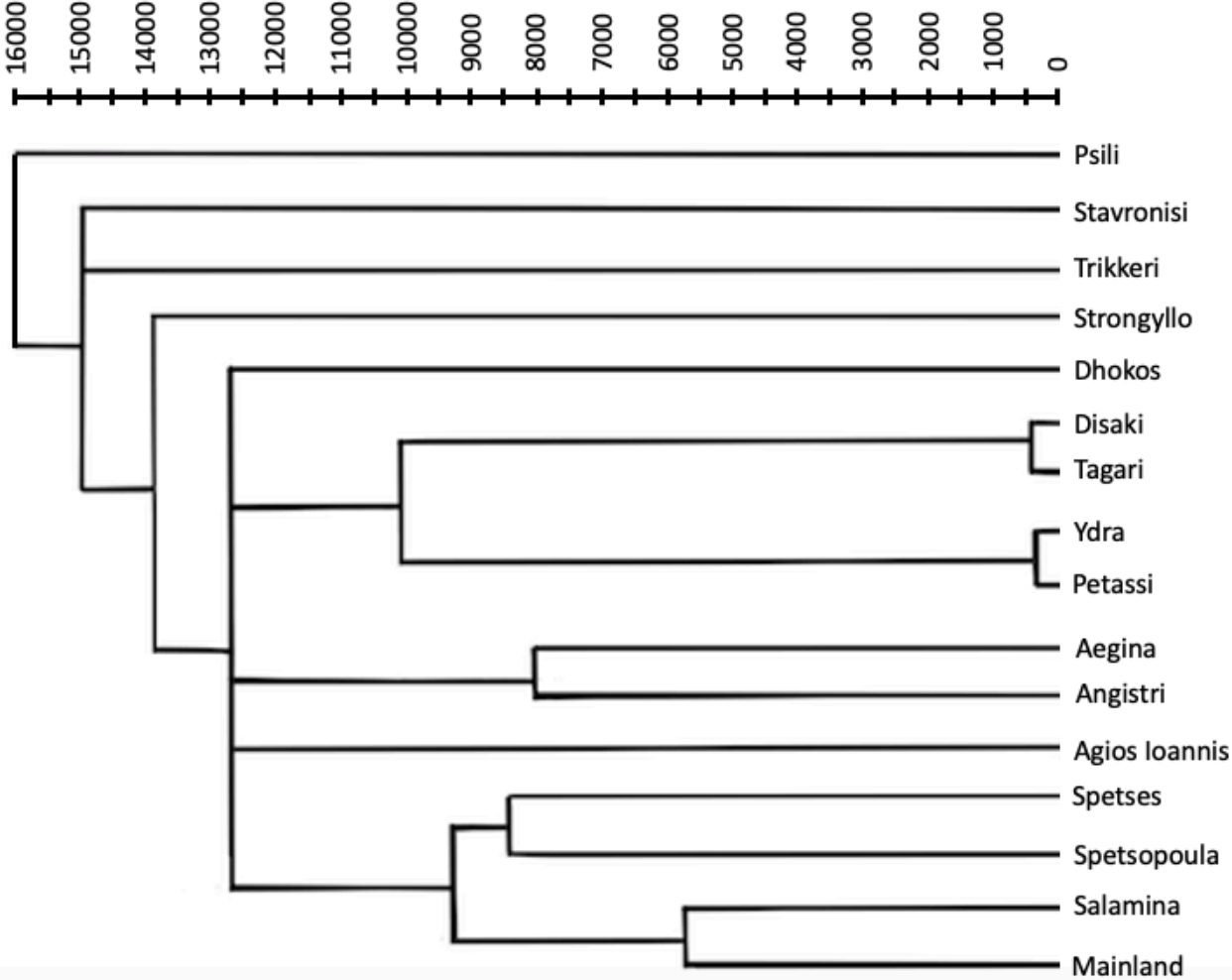
*The East Aegean*



*The Cyclades*



*The Argo-Saronics*



### Appendix C: Complete list of variables assessed

<b>Physiographic</b>			
<b>Variable</b>	<b>Calculation/description</b>	<b>Source</b>	<b>Model acronym *</b>
Area	Island area (km <sup>2</sup> ) in historic coastline rasters	GMES RDA 2021; EMODnet 2021; GEBCO	<b>Area</b>
Average roughness	Mean of each raster cell's largest difference in altitude from its neighboring cells	GMES RDA 2021; EMODnet 2021; GEBCO	<b>AR</b>
Proportion of north-facing slopes	Proportion of grid cells contained in an island with aspect $a$ such that $315^\circ < a < 45^\circ$ , i.e. aspect within $45^\circ$ of true North	GMES RDA 2021; EMODnet 2021; GEBCO	--
Proportion of south-facing slopes	Proportion of grid cells contained in an island with an aspect $a$ such that $135^\circ < a < 225^\circ$ , i.e. aspect within $45^\circ$ of true South	GMES RDA 2021; EMODnet 2021; GEBCO	--
Original area	Area (km <sup>2</sup> ) of each island's mother island at its last time-step before fragmentation	GMES RDA 2021; EMODnet 2021; GEBCO	--
Total shrinkage	Original area – Area	GMES RDA 2021; EMODnet 2021; GEBCO	--
Average shrinkage	Total shrinkage ÷ time-since-isolation	GMES RDA 2021; EMODnet 2021; GEBCO	--
<b>Climate</b>			
Mean temperature of the warmest quarter	Mean temperature (C°*10) of the warmest 3 month period of the year	PaleoClim (Brown et al. 2018; Fordham et al. 2017)	<b>MTWQ</b>
Final annual precipitation	Total precipitation (mm) over a year, calculated for the latest possible time-step of an island's existence (i.e. present-day for present day islands, final time-step	PaleoClim (Brown et al. 2018; Fordham et al. 2017)	--

	before fragmentation for paleo-islands)		
Original annual precipitation	Total precipitation (mm) over a year, calculated for the final time-step in existence of each island's mother island	PaleoClim (Brown et al. 2018; Fordham et al. 2017)	<b>OP</b>
<b>Other</b>			
Time-since-isolation	Amount of time (years), at a resolution of 500 year time steps, between and island's isolation from its mother island until its fragmentation into daughter islands, or until the present day	GMES RDA 2021; EMODnet 2021; GEBCO	<b>Time</b>
Human population	Population according to the 2011 Greek census	Hellenic Statistical Authority, 2011	--
Population density	Human population ÷ area (km <sup>2</sup> )	Hellenic Statistical Authority, 2011	--

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