**Island fragmentation by sea level rise and global warming drive prehistoric extinctions in Mediterranean island reptiles**

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**Statement of Authorship**

All authors contributed equally in the analysis, method, interpretation of results and discussions on its wider significance. SK led the analysis and interpretation of results; the work and underlying ideas were conceived and led by JF, the workflow was developed by KFR, JDG, EEvL and LHMD.

**Data accessibility statement**

Should the manuscript be accepted, the data supporting the results will be archived in an appropriate public repository (Dryad, Figshare or Hal) and the DOI will be included in the data accessibility statement.

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**ABSTRACT**

We assess how reptile population extinctions on Mediterranean islands has been influenced since the Last Glacial Maximum (LGM) by the interacting effects of island area, timing of fragmentation, changing climate, and topography. By using geophysical models of sea-level rise we produce island-fragmentation cladograms which depict the sequence and timing by which 80 islands and 52 paleo-islands in the Aegean and Ionian seas progressively became separated from paleo-landmasses. These cladograms are used to reconstruct the progressive sequence of local reptile population extinctions. We found that population extinctions rise linearly with increased duration of isolation and that extinctions correlate negatively with (paleo-) island area. In addition, extinctions are positively associated with higher summer temperatures implicating heat stress, as well as with higher island topographic roughness, which may be an indication of diminished resource availability. These conclusions point forward to understanding, predicting, and eventually preventing future species extinctions due to climatic change.

**INTRODUCTION**

Habitat fragmentation and reduction, alone or in combination with global warming, is increasingly recognized as perhaps the most important driver of species extinction particularly in insular species, raising the urgency to better understand this typically drawn-out process better (Sohdi et al. 2004; Prugh et al. 2008; Ceballos et al. 2015; Halley et al. 2016; Steinbauer et al. 2016). Especially in the coastal realm or archipelagic settings the added effects of sea level rise leading to habitat loss (coastal squeeze) and habitat fragmentation increases species threat levels (Mazaris et al. 2009; Machinski et al. 2011; Bellard et al. 2013; 2014). However, most studies focusing on long-term population extinctions in fragmented landscapes, whether in true islands or habitat patches, have been of limited scope, being temporally confined to the last century (Newmark 1995, Halley et al. 2016; Fahrig 2017). While broader-scope paleontological studies have aimed to understand similar species extinctions over longer time-scales, the relatively coarse quality of paleontological data has limited our insights into the causes and processes of population paleo-extinctions (Barnosky et al. 2011). Here we take advantage of a natural long-term fragmentation process that occurred when, following the end of the last ice age, planetary warming and accompanying rising sea levels led to the separation of numerous Mediterranean land-bridge islands from the nearby mainland (Fig. 1a, Simaiakis et al. 2017; Hammoud et al. 2021), ultimately resulting in the extinction of resident reptile populations. Global average temperatures have increased by six degrees Celsius since the Last Glacial Maximum (LGM, 24-20 ky ago), and global average sea levels have risen more than 130 m (Lambeck et al. 2014; Tierney et al. 2020). The large scale coastal landscape transformation that occurred during that period provides an excellent opportunity to investigate how long-term climate change caused species extinctions (Diamond 1975; 1984; Mayer and Diamond 2001; Foufopoulos and Ives 1999). Because such extinctions could have resulted by combined directly altered thermal/hydric conditions, and/or indirectly through landscape inundation (coastal squeeze) and the progressive breakup of continuous coastal landscapes into isolated land-bridge islands, it is important to understand how these factors act as proximate drivers to population loss (Foufopoulos et al. 2011; Simaiakis et al. 2017). It is well known that while immediately after habitat fragmentation communities have a full complement of species and with passing time, these taxa progressively die out (Diamond 1972, 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 over time through a process of progressive community relaxation (MacArthur and Wilson 1967; Brown 1971; Wilcox 1978). Although such community relaxation has been documented, and its importance for conservation recognized, it is still not understood which factors beyond habitat size affect its speed and extent (Halley et al. 2016).

The Aegean and Ionian Sea archipelagos in the northeastern Mediterranean encompass more than 3,000 islands of various sizes and habitats, making them ideal study subjects (Trichas and Legakis 1987). They are particularly well suited for island biogeography studies because they contain numerous 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 because their sex determination is temperature-dependent, large climatic shifts can put reptile populations at risk of demographic collapse (Gibbons et al. 2000). Both present-day and historical climate features may be important for determining species distributions (Simaiakis et al. 2017; Hammoud et al. 2021). Furthermore, modern and late-Pleistocene precipitation and temperature patterns 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). Present-day climatic predictors like temperature, precipitation, and climatic variability help explain the distributions of lizards in Mediterranean-type habitats (Sillero and Carratero 2013; Rodder and Shulte 2010, Silva-Rocha et al. 2015; Carneiro et al. 2017). In addition, landscape heterogeneity and topography have been shown to influence both presence and abundance of several reptile species (Fischer et al. 2005; McElhinny et al. 2006; Brown et al. 2011) by providing thermal refugia that allow them to survive otherwise detrimental climatic changes (Hannah et al. 2014; Pontes-da-Silva et al. 2018; Senczuk et al. 2019).

At present, the interactive effects of paleo-climate and landscapes on population persistence over the millennia remain poorly understood. Recent studies have found that paleo-geographic landscape configurations have shaped modern island species distributions (Weigelt et al. 2016; Simaiakis et al. 2017; Hammoud et al. 2021). While the importance of island area, distance from the mainland, and (for land-bridge islands) time since isolation from the mainland on island biodiversity has been well established (MacArthur and Wilson 1967; Wilcox 1978), other factors such as rate of change, topography, and paleoclimate have been implied but not well documented (Burkey 1995; Diamond 1972; Halley et al. 2016; but see Steinbauer et al. 2016; 2018). In this study, we use modeled reconstructions of climate (Fordham et al. 2017; Brown et al. 2018) and a paleo-coastline model (De Groeve et al. 2022) on Mediterranean islands going back to the LGM, in conjunction with island fragmentation cladograms, to assess how local extinctions of reptile populations are influenced by past and present day physiographic and climatic factors. Although studies such as these have shown that present day climate and landscape features are important in explaining reptile distributions today, this is the first study to our knowledge to show how these factors in conjunction, shape extinctions of island taxa over a multi-thousand year time-scale. Because past climate change and habitat fragmentation are similar stressors to the ones present-day wildlife species face, study of past extinctions can help us understand the process of modern species loss and serve as a model to understand the long-term implications of anthropogenic landscape change on wildlife.

This study focuses on the Aegean and Ionian Seas (Greece), part of a global biodiversity hotspot (Myers 2000). Located in a mountainous, rocky, and semi-arid region, the islands belong to the Mediterranean vegetation biome, and are covered by a patchwork of maquis, heaths, coniferous forests, and occasional coastal wetlands. Humans have inhabited the region for millennia, and have had an extensive influence on the landscape and ecology (Blondel 2006; Grove and Rackham 2003). The region harbors a diverse herpetofauna, comprised of taxa of European, Asian, and African origins (Valakos et al. 2008). The study islands belong to five distinct archipelagoes, here termed “island groups”, each encompassing islands that were once connected with each other and / or the continent (Fig. 1a).

In this vicariant approach we assume that all islands in a group started with the same continental fauna and any differences in present-day species communities are due to different local extinctions on each island (see Text Box 1; Fig. 1b). This approach, which reconstructs the period and location of each extinction, ultimately allows one to determine the number of aggregate extinctions on each island. Because the timing, as well as the associated climatic and landscape circumstances of these extinctions are known, we can analyze the relative contributions of these factors to the overall island species loss.

Underlying the analysis of the drivers of island reptile population extinctions is the accurate reconstruction of past island fragmentation processes. For this, we utilize an advanced geophysical sea level rise simulation model (De Groeve et al. 2022) that includes spatially explicit crustal uplift and subsidence rates in addition to eustatic sea level changes to model the precise timings of fragmentation of paleo-islands due to land bridge drowning (c.f. Lambeck 1995; 1996). Based on the calculated timings of island fragmentations (see Fig. 1b), we present as a first result the island fragmentation trees, recreating the sequence of island splitting for the five island groups (Text box 1). As a second result, we use these trees to reconstruct a series of local extinctions of reptile populations on these islands. The aggregate number of local extinctions on each (paleo)island is then used as a dependent variable in the last part of this study.

As our third result we report on the factors that are associated with the observed extinction patterns. More specifically, we first evaluate the relative contributions of two known factors, island area and duration of isolation on species extinctions (MacArthur and Wilson 1967; Wilcox 1978). Given the profound climatic changes occurring at the time, we further assess also the role of climatic parameters influencing extinction rates. Furthermore, we investigate the role of topographic heterogeneity, which can affect the diversity of microclimates and therefore the existence of thermal refugia, on reptile extinction rates. Ultimately, we hypothesize that local reptile extinctions are not random but have been driven by the interacting effects of area loss, changing temperature and precipitation, and topographic change. Through linear regression analysis, we aim to assess whether local extinctions are shaped by past fragmentation predictors, past and present topographic states of the islands, as well as past and present bio-climatic conditions on the islands. We therefore build a historical and environmental model to test and quantify the relative importance of these extrinsic factors in explaining island population extinctions.

**MATERIALS AND METHODS**

To investigate the relation between extinctions with island configurations and environmental drivers, several steps needed to be performed to prepare data for a robust statistical analysis. The complete workflow has been summarized in Figure 2. In short, (1) we reconstruct the paleo landscape of each island in the five island group, (2) we manually reconstruct island fragmentation trees, (3) we manually reconstruct local species extinctions for each island, (4) we associated a broad range of environmental variables which are potential drivers of extinction, (5) exploratory statistics is used to retain the most explanatory drivers (6) AIC model selection procedure allows to identify the best model retaining the variables that best explain species extinction.

**land-bridge island groups and species selection**

We used a set of 80 present-day land-bridge islands in the NE Mediterranean Basin for which high quality herpetofaunal data were available. The islands belong to five island groups that form major archipelagos in the Aegean Sea, and each group is characterized by a common fragmentation history (see Foufopoulos and Ives 1999). Each group separated in the past from the nearby continental mainland, with the exception of the Cyclades which are all located on the shelf of a large, continent-like paleo-landmass (Cycladia, 10,750 km2) that underwent a similar fragmentation process as the other island clusters (Fig. 1; Simaiakis et al. 2017). These islands contained a total of 44 reptile taxa (Supplementary Data S2), representing the majority of the reptile species pool in the region: the Ionian (25 species), the Sporades (16 species), the Cyclades (17 species), the Argo-Saronic (26 species), and the East Aegean archipelago (42 species).

**Island fragmentation trees and local extinctions**

To obtain our predictors for the analysis (Step 1, Fig. 2) we first modeled the island configuration change over time of Greece following the workflow proposed by Norder et al. (2018), using a bathymetry corrected for uplift and subduction rates combined with a geophysical spatial-explicit sea level model (De Groeve et al., 2022). The latter model allows to account for local sea level fluctuations when reconstruction paleo island shapes and sizes (See Supplementary data S1a for a detailed description). The resulting dataset consists out of paleo and present-day island polygons of Greece covering a period of 21,500 years at time steps of 500 years.

Visualisation in GIS allows to further identify and explore the timing of fragmentation resulting into the present-day set of 80 land-bridge islands (step 2). The moment in time (ky BP) that island fragments became isolated due to the drowning of the land bridges, was termed as the “Timing of isolation (Tiso)” in ky BP (Fig. 1b). Also we assess for each present-day island and paleo-island how long it did retain its island status before the present (for existing islands) or before eventually fragmenting further (for paleo-islands). This measure of time over which observed extinctions occurred is termed “Duration of isolation (ΔTiso)” in ky (Fig 1b; Supplementary Data S2). On top of the 80 present-day islands, examination of the island fragmentation history allowed to identify an additional set of 52 (intermediate) paleo islands, resulting in a total set of 132 islands, across the five island groups. Using both variables Tiso and ΔTiso we manually constructed a chronology of island fragmentation over time for each island group (step 3a). The result is an island fragmentation tree, for each island group, whereby the root node represent the mother paleo(is)land of an island group, the internal nodes represent an intermediate paleoisland at Tiso, the length of the branches represent the duration of the isolation, ΔTiso, and the leaves the present-day islands (see text box 1). Each internal tree node (e.g. , intermediate paleoisland) was given a unique readable name for ease of analysis (See supplementary Data S2 for the island fragmentation trees for each of the five respective island groups).

As a fourth step (Fig. 2) we reconstructed the percentage and absolute number of local species extinctions that may have occurred on each modern and paleo-island based on present-day occurrences of each reptile species and the assumed ancestral mainland community (Supplementary Data S2). The aggregated number of local extinctions is the dependent variable for further statistical analysis.

**Environmental predictors of local extinctions**

After obtaining island fragmentation trees and the number of local extinctions, various environmental factors influencing local species extinctions were derived for each island (Supplementary Data S1b; Fig. 2: step 3b). All environmental predictors were aggregated to the island level and are thus represented by a single value (e.g. mean, standard deviation, sum).

First, we calculated the area of each island as an important predictor for local species extinctions. The island area was further used to calculate two predictors of area change, both in absolute and relative terms (percentages): total area contraction (original area minus final area) and rate of contraction (total area contraction divided by ΔTiso). The original area is measured as the surface area of the first island fragment that formed after drowning of the land bridge that connected the island with the continent.

Topographic predictors were derived from the bathymetric model through spatial intersection with the islands and included 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 aspect between 315o and 45o), and proportion of south-facing slopes (number of cells with aspect between 135o and 225o. For two islands topographic variables could not be derived. Bioclimatic predictors included mean temperature of the warmest quarter (MTWQ) and mean annual precipitation and were derived from PaleoClim, a series of global climate raster reconstructions that include bioclimatic predictors for each of seven major climate periods going back to the LGM (see Brown et al. 2018; Fordham et al. 2017). For each climatic period we calculated the mean of each climatic predictor over all pixels intersecting an island (see Supplementary Data S2).

As a last factor we also gathered data on modern human population levels from the 2011 Greek census (Hellenic Statistical Authority 2011; Supplementary data S2). Spatial data handling and geoprocessing was done mostly in ARCGIS Pro 2.9.

**Statistical Analysis**

As final step 5 (Fig. 2) we first conducted an exploratory analysis performing standard univariate OLS regressions of the local extinctions against each predictor listed in Table 1. Based on these results, we created a set of nested generalized linear models to predict local extinctions, using ΔTiso and log(Area) as core-predictors in each model and the most promising variables (based on the explorative analysis) as potential additional predictors. A negative binomial error distribution appeared to be suitable in these models with over-dispersed count data as response predictor (Walker 2018). We selected the model which corresponded the best with the observations using the Akaike Information Criterion (AIC). Finally, we standardized each predictor in this model using a z-transformation to assess the relative influence of each parameter in explaining extinctions through their standardized beta coefficients (β). All statistical analyses were done within the R version 4.1.3 programming environment (R Core Team, 2016; Supplementary Data S2).

**Results**

**Island fragmentation trees and local extinctions**

As a first result we produced the island fragmentation trees reconstructed for the five island groups compellingly describe the island fragmentation history (Fig. 3a; see Supplementary Data S2). Most islands across island groups were fragmented and reduced in area between 14 ky and 6 ky BP due to rapid sea level rise in the Northgrippian, Greenlandian and Dryas stadials. During this island fragmentation process, 52 paleo-islands came into existence that later split into the present-day 80 islands. More generically, trees show that most present-day islands were formed before 6000 years ago, with only eight islands forming less than 2000 years ago. The Cyclades fragmented into the largest group of islands (30) and the Ionian into the smallest (8). Contraction of the original insular areas were severe, often amounting to >80%, and up to >99%. As a second result we determined the aggregate number of extinctions that occurred on each paleo- or modern island (Supplementary Data S2). On average over all islands 7 extinctions occurred per island, with a maximum of 24 on Arkios which is part of the East Aegean island group. We observed extinction rates for present-day islands that vary between 10 and 90% (Fig 3b). A generic pattern is that most extinctions occurred on the smallest island fragments and those islands that fragmented earliest. For the Sporades for example (Fig. 3c), the average number of extinctions is 8, but most extinctions occurred on the smallest fragments e.g. Arkos and Tsougria (> 80%; 14 and 15 respectively) or on the larger islands Kyra Panagia and Gioura (> 80% extinctions) that split off earliest from the mainland, 21,5 ky ago. Islands that split off more recent and remained larger fragments, the least extinctions occurred. On the other hand the larger islands of Skiatos and Skopolos split off relatively recent 5000 year ago and only 1, respectively 4, extinctions occurred.

**Statistical Analysis**

The results of the univariate OLS regression are summarized in Table 1 and showed that ΔTiso was positively associated with extinctions with the highest R2 value for the predictors we considered (R2 = 0.36; Fig. 4a). It was followed by area, which was negatively associated (R2 = 0.20; Fig. 4b), and percentage of area loss with a positive association (R2 = 0.16; Table 1). Concerning topographic effects on local extinctions, we found that topographic roughness was weakly correlated with local extinctions and the rest of the parameters were not significantly correlated. In regard to the bioclimatic parameters, both MTWQ, and mean annual precipitation were positively associated with local extinctions, with MTWQ yielding the highest R2 value (R2 **=** 0.23; Table 1; Fig. 4c).

From a set of eight candidate univariate OLS regression models containing the most important predictors resulting from the univariate explorative analysis, the best model (ΔAIC = 0; Table 2) shows that the Log(Area) had the largest effect size, with a negative relationship to number of extinctions (β = -0.73), followed by positive effect parameters for ΔTiso (β = 0.64), mean temperature of the warmest quarter (β = 0.42), original precipitation (β = 0.19), and average roughness (β = 0.14) (Fig. 4d).

**DISCUSSION**

Our final model 8 (Table 2) shows that island reptile extinctions are associated – in order of diminishing importance – negatively with island area, and positively with duration of isolation (ΔTiso), mean temperature of the warmest quarter (MTWQ), original (pre-fragmentation) precipitation (OP), and average topographic roughness (AR). In the univariate analyses, duration-of-isolation was the best single predictor of extinctions, while in the standardized multivariate model, the largest effect size was for Log(Area) and the second largest was for ΔTiso. Although it has long been established that extinction rates are negatively associated with island area and positively associated with duration of isolation (MacArthur and Wilson 1967; Wilcox 1978), extinction studies have focused on “ecological time”, that is relatively short timescales, in which speciation can be ignored, with only rare empirical attempts to test the theories using longer millennia time scales to assess the role of “evolutionary time” (Diamond 1972; Heaney 2000; Whittaker et al. 200; Jackson and Sax 2009). As such, the 21,500 year period considered in this novel approach here, represents a significant extension of regular conservation biogeography studies, which typically focus on temporal scales close to a human lifespan (e.g. Pimm et al. 1993; Newmark 1995). Hence, our results confirm existing theory and demonstrate for the first time that local extinctions are influenced by area and isolation legacy effects that operate at epoch-level temporal scales as well.

One of our most robust results shows that number of extinctions decreases with increase in surviving island area (Fig. 4b); this confirms multiple earlier studies that have shown that availability of large habitat areas robustly buffers against extinction. In the case of the Aegean reptiles the minimum size for islands without extinctions would be in the order of > 2000 km2 (Supplementary Data S2).

The population extirpations observed in our system are typical for the ‘extinction debt’ experienced by communities found on land-bridge islands, which is “paid” through the process of community relaxation, i.e. progressive species loss (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 almost linear rate over time (ca 1 per 1000 year) as shown by a simple regression model with R2 = 0.35, p = 1.83e-14), while an exponential model has a lower fit (R2 = 0.31, 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 here, fragments kept shrinking post-fragmentation, and conditions became progressively more dry and hostile, apparently preventing extinction rates from decelerating over time, indicating the species community is still in disequilibrium (e.g. Heaney et al. 2013; Fernandéz-Pálacios et al. 2016).

The mean temperature of the warmest quarter was the third most important associate of extinctions (model 8), and the second strongest relationship in our univariate analysis (Fig. 4c). Despite the general understanding of reptiles as thermophilic organisms, increased summer temperatures can have a negative effect on reptile life histories and can promote extinctions (Sinervo et al. 2010; Garcia-Porta et al. 2019). Higher incubation temperatures have been associated with reduced size and movement ability in lizards (Brana and Ji 2000; Kubisch et al. 2016), as well as genome instability, reduced embryo survival, growth rate and decreased population growth (Van Damme et al. 1992; Meiri et al. 2012; Jara et al. 2013; Kearney 2013; Dupoué et al. 2017). 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, Jensen et al. 2017). Higher temperatures are also associated with lower vegetation cover, and many reptile taxa require a certain degree of structural vegetation complexity for survival (Keppel et al. 2017; Foufopoulos et al. 2011). Our results suggest that elevated summer temperatures have likely resulted in past Aegean species extinctions and raise the concerns about the impacts of future warming on resident Mediterranean species communities.

Both annual precipitation and original precipitation were positively associated with extinctions in univariate analysis (Supplementary Data S2). They were the only parameters which showed a significant association with extinctions after controlling for Log(Area) and ΔTiso. Our best multivariate model also included original precipitation, which had a significant positive relationship with extinctions. In the final model 8, precipitation was the fourth largest contributor, showing a weaker effect than Log(Area), ΔTiso, or temperature, but a stronger effect than topographic roughness. The positive association of original precipitation with extinction may be actually attributed to landscape 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 more likely 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). Senior et al. (2021) argues that higher precipitation often is 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 human population sizes, as well as densities, on present-day islands and found no significant relationship regardless of whether or not we controlled for area and time.

The average topographic roughness parameter had a significant positive association with extinctions in a univariate analysis, but was no longer significant after controlling for Log(Area) and ΔTiso. It emerged as significant positively associated with extinctions in our final model 8; however, it had the weakest effect. Most studies investigating the effects of physiography and landscape characteristics find a beneficial effect of topographic heterogeneity on species persistence (Gonçalves et al. 2016). Instead, we found that fewer species survived on islands with high topographic roughness. However, islands with high roughness scores, such as Gioura 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 herptile communities. 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). 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. We did not identify any effect of an island’s predominant slope aspect on extinctions contrasting with .prior research on the influence of slope aspect on microclimatic conditions and resource availability (Miller and Poole 1980; Pavlicek et al. 2003; Li et al. 2011). The lack of evidence for an effect of total area loss on extinctions was unexpected, considering that the species-area relationship 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 loss in area occurred on very large islands, where even substantial losses of land area may not result in extinctions. This seems indicated by the negative trendline between area and local extinction intersecting the area at 3500 km2 and first extinctions appearing on areas smaller than 2000 km2 (Supplementary Data S2).

**CONCLUSION**

Overall, our results suggest that the largest environmental drivers of island reptile extinctions since the LGM are unavailability of sufficiently large island area, together with extended periods of isolation from the mainland, as well as increasingly hot summer temperatures. Wetter, lusher areas that likely harbored more diverse faunas at the LGM have lost more species than areas that were drier. We find no evidence for an influence of dominant slope aspect and little for an effect of rate of area contraction on extinctions at this time scale. Our findings suggest that the Mediterranean reptile communities, having partially evolved in cooler and moister conditions, may be particularly vulnerable to global warming and the associated desiccation at the hot edge of their distributions. Over the next several centuries, the combination of accelerating sea level rise, which is expected to reduce island area and productive coastal lowland habitats further (Levermann et al. 2013)– and rising warm-season temperatures, will likely induce further species loss, unless mitigating actions are taken (Sinervo et al. 2010; Wiens 2016; Steinbauer et al. 2018; Garcia-Porta et al. 2019). The approach outlined here provides a well-needed workflow to assess millennium time scale effects of isolation and fragmentation on local extinctions and assessment of extinction debt states of current insular species pools (cf. Jackson and Sax 2009). Moreover the approach may also facilitate studies on how long term natural baseline rates of habitat loss and temperature increase affected genepools and genetic vitality of insular populations. 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, and especially consider that faunas on islands are still in the process of paying their extinction debts.

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**Supporting Information**

The data and scripts that support the findings of this study are available in Figshare at: **https://doi.org/**

**79.v1./TO BE IMPLEMENTED**

**Supplementary Data S1a: Method paleo-ecoastline raster generation**

In order to produce the paleo-coastline rasters we used 53 rasters showing relative sea level positions since 26 ky ago representing time step of 500 years. These rasters were produced by combining a geophysical simulation program SELEN4 (Spada and Melini, 2019) with a geological vertical motion grid. The geophysical simulation computes relative sea level changes based on mass exchanges between seas and land-locked ice. The simulation includes modelling the global effects of gravitational fields of ice sheets on seawater, deformation of the Earth’s mantle-crust system by melt water and ice sheets loading, and also includes the rotation of the earth. Details of the model are outlined in (De Groeve et al. 2022). We modified the geophysical model by including the vertical motions of geological processes (long-term uplift and subsidence) generated by plate tectonic forces prevailing over the Mediterranean. This ensured that we obtained accurate drowning times of land-bridges that were flooded by marine transgression. In order to improve paleo-depth accuracy we used an updated bathymetric model of the Aegean Basin by combining a satellite sensor generated Digital Elevation Model (DEM) with a harmonized bathymetric model based on various marine surveys. We combined both models to obtain a smooth bathymetric model including both topography information above and below sea level. To obtain such a model we merged both datasets in Google Earth Engine and used the focal mean to fill gaps at island boundaries. The Digital Elevation Model over Europe (EU-DEM, 25 m x 25 m) was developed through the GMES RDA project, it is a Digital Surface Model (DSM) representing the first surface as illuminated by the sensors. The emodnet bathymetric model (115 m x 115 m), which is a harmonized European bathymetric model combining various resources. The EU-DEM dataset is a realization of the Copernicus programme, managed by the European Commission, DG Enterprise and Industry.

For all island entities generated by our model we produced the area and altitude of the islands. In addition we used the Terrain function of the Terra Spatial Data Analysis R Package to obtain all topographic metrics analysed in this paper: 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 aspect between 315o and 45o), and proportion of south-facing slopes (number of cells with aspect between 135o and 225o).

**Supplementary Data S1b: Data table of all used predictors**

**Table S1.** *Data table showing all used predictors with a short explanation of their meaning and sources. Because we calculated both mean annual precipitation and original precipitation, these two showed a high degree of multicollinearity (VIF > 10); we retained original precipitation to investigate the hypothesis that number of local extinctions is determined in part by pre-isolation precipitation conditions.*

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Predictor** | **n** | **Calculation/description** | **Source** | **Acro-**  **nym** |
| Area | 132 | Island area (km2) in historic coastline rasters | GMES RDA 2021; EMODnet 2021; GEBCO | **Area** |
| Original area | 132 | Area (km2) of each island’s mother island at its last time-step before fragmentation | GMES RDA 2021; EMODnet 2021; GEBCO | -- |
| **Fragmentation** | | | | |
| Total area loss | 132 | Original area – Area (km2, %) | GMES RDA 2021; EMODnet 2021; GEBCO | -- |
| Average area loss rate | 132 | Total area loss ÷ Duration of isolation | GMES RDA 2021; EMODnet 2021; GEBCO | -- |
| Duration of isolation | 132 | 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 | **ΔTiso** |
| **Topography** | | | | |
| Average roughness | 121 | Mean of each raster cell’s largest difference in altitude from its neighboring cells | GMES RDA 2021; EMODnet 2021; GEBCO | **AR** |
| Proportion of north-facing slopes | 121 | Proportion of grid cells contained in an island with aspect *a* such that 315o < *a* < 45o, i.e. aspect within 45o of true North | GMES RDA 2021; EMODnet 2021; GEBCO | -- |
| Proportion of south-facing slopes | 121 | Proportion of grid cells contained in an island with an aspect *a* such that 135o < *a* < 225o, i.e. aspect within 45o of true South | GMES RDA 2021; EMODnet 2021; GEBCO | -- |
| **Climate** | | | | |
| Mean temperature of the warmest quarter | 132 | Mean temperature (Co\*10) of the warmest 3 month period of the year | PaleoClim (Brown et al. 2018; Fordham et al. 2017) | **MTWQ** |
| Final annual precipitation | 132 | 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 before fragmentation for paleo-islands) | PaleoClim (Brown et al. 2018; Fordham et al. 2017) | -- |
| Original annual precipitation | 132 | 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) | **OP** |
| **Other** | | | | |
| Human population | 80 | Population according to the 2011 Greek census | Hellenic Statistical Authority, 2011 | -- |
| Population density | 80 | Human population ÷ Area (km2) | Hellenic Statistical Authority, 2011 | -- |

**Supplementary Data S2: Reproduction package for Kalb et al. (2023)**

This reproduction package contains the zipped data and code to reproduce the results presented in Kalb et al. (2023).

**Directory structure:**

**data** directory where datasets are saved

* **species\_presence\_absence.xls**: source data to derive species extinctions
* **island\_fragmentation\_cladograms.docx**
* plot extinctions vs. area.
* **all\_data.csv**: present day and past island variables used as input for the statistical analysis
* **all\_data\_polygons.gpkg**: present day and past island polygons and associated variables used as input for the statistical analysis
* **rasters\_paleoclim**: directory with mean precipitation and MTWQ rasters (tiff) per period (present, 4500 BP, 8500 BP, 12000 BP, 13000 BP, 15000 BP, 17000 BP, LGM)

**code** directory with statistical analysis scripts

* **analysis.Rmd**: R-markdown file of statistical analysis
* **analysis.html**: html rendered version of statistical analysis

**Usage**

Click the Rproj file in the root directory to open the project in Rstudio. From within Rstudio, navigate to analysis.Rmd and click the file to add it to the editor.