

Climate Change and Elevated Extinction Rates of Reptiles from Mediterranean Islands

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ABSTRACT: Recent climate change has caused the distributions of many species to shift poleward, yet few empirical studies have addressed which species will be vulnerable to longer-term climate changes. To investigate past consequences of climate change, we calculated the population extinction rates of 35 reptile species from 87 Greek land-bridge islands in the Mediterranean that occurred over the past 16,000 years. Population extinction rates were higher for those species that today have more northern distributions. We further found that northern species requiring cool, mesic habitats had less available suitable habitat among islands, implicating loss of suitable habitat in their elevated extinction rates. These extinctions occurred in the context of increasing habitat fragmentation, with islands shrinking and separating as sea levels rose. Thus, the circumstances faced by reptiles on the islands are similar to challenges for numerous species today that must cope with a changing climate while living in an increasingly human-fragmented landscape. Our island-biogeographical approach to investigating historical population extinctions gives insight into the long-term patterns of species responses to climate change.

Keywords: island biogeography, conservation, faunal relaxation, herpetology, Aegean Sea, global warming.

Introduction

The geographic ranges of many species from a wide variety of taxonomic groups have shifted toward the poles over the last several decades of climate change (Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003; Parmesan 2006). Despite this fingerprint of global climate change, inference about climate impacts on populations over the next century is limited on several fronts. First, studies documenting recent range shifts are generally restricted to species for which extensive time-series data are available (Parmesan et al. 1999) or that have experienced rapid shifts

(Shoo et al. 2006). Therefore, documented cases of range shifts are dominated by well-studied and vagile species, such as birds and butterflies (Thomas and Lennon 1999; Wilson et al. 2005; Chamaille-Jammes et al. 2006; but see Hickling et al. 2006; LaSorte and Thompson 2007). Second, most studies of range shifts have focused on range expansion at the leading (poleward) edge of the range (Hampe and Petit 2005; Thomas et al. 2006). Movement of the trailing edge of the range, however, may be more important for species conservation, because this drives the contraction of a species' range; rapid range retraction from the trailing edge coupled with a slow expansion at the leading edge could lead to substantial population declines or even species extinction (Huntley 1999; Franco et al. 2006). Finally, current climate change is occurring simultaneously with human-caused habitat fragmentation (Warren et al. 2001; Travis 2003). Fragmentation will inhibit range shifts not only because it limits poleward range expansion (Honnay et al. 2002) but also because it can increase population extinction rates at the trailing edge (Koprowski et al. 2005). It is unknown which species in habitat fragments (e.g., national parks, relict habitats) will be most susceptible to climate change.

Understanding the responses of biological communities to past climate shifts can help us evaluate the effects of ongoing climate change on current species distributions. We investigated the natural population extinctions of 35 reptile species from 87 land-bridge islands in the northeast Mediterranean Sea that separated from the mainland starting 16,000 years ago at the end of the last ice age. These islands today harbor species communities that are impoverished in comparison to communities in mainland areas of equal sizes, indicating that population extinctions have been common (see "Results"). The environmental changes faced by these 35 species were similar to those that will be experienced by large numbers of species over the next century of climate change, including habitat change and fragmentation. In the eastern Mediterranean,

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the early Holocene (11,000–7000 BP) was a period of wet, mild conditions and extensive forested areas (Caner and Algan 2002; Magny et al. 2002; Mudie et al. 2002; Eastwood et al. 2007), while the period after 6000 BP saw increasing aridity (Eastwood et al. 2007) and reduction in forest cover over most (Rossignol-Strick 1999; Roberts et al. 2001; Geraga et al. 2005) but not all (Bottema and Sarpaki 2003) of the region. Thus, the 35 study species experienced climate change and a concomitant vegetation change. Second, increasing global temperatures over the past 16,000 years led to a 120-m rise in sea level that resulted in the sequential fragmentation of a continuous coastal landscape into land-bridge islands. Hence, the study species experienced a progressive fracturing of continuous populations into ever-smaller island groups, similar to the situation faced by many species today that live in an increasingly human-fragmented landscape.

Here, we first calculate the natural extinction rates of island populations of 35 reptile species using the current presence/absence distribution of each species. Second, we analyze the relationship between these extinction rates and the distributional patterns of the species on the mainland. In particular, we ask whether species that have more northerly ranges are more likely to have higher population extinction rates on the study islands. We would expect this to be the case if more northern species have lower tolerance for the hotter, drier conditions and habitats at the equatorial boundary of their ranges. Thus, we are using the latitudinal range of species on the mainland as a surrogate for climatic preferences or tolerances of species. Finally, we ask how the amount of suitable habitat available for each species influenced extinction rates. This question addresses the importance of climatic effects on the biotic environment for the vulnerability of species to extinction.

Methods

Species selection. We analyzed data from 87 Greek islands. Present-day reptile distributions were collected from the literature (Chondropoulos 1986, 1989) and were supplemented by field surveys by J. Foufopoulos. The present reptile fauna of all Aegean islands consists of 49 species. Of these, we included the 35 species that occurred on at least one of our 87 study islands and for which we could obtain data on population densities and habitat specialization. The 35 species analyzed in this study include 28 species from an earlier study (Foufopoulos and Ives 1999b) and 7 additional species with newly collected distributional information. A listing of the distribution and ecological characteristics of all species is available in a file available in appendix C in the online edition of the *American Naturalist*.

Calculation of extinction rates. We calculated population

extinction rates for each species from the current presence/absence of species on islands that were formerly connected to a larger landmass during the last ice age (Perissoratis and Conispoliatis 2003). To infer the past distribution of reptile species among islands, we divided islands into five archipelagos that were either connected to the mainland (eastern Aegean, Argosaronic, Sporades, and Ionian clusters) or formed a large continuous landmass (Cyclades) during the last glacial maximum. We inferred the sequence and timing of island formation from bathymetric charts and the known rate of sea-level rise since the height of the Wisconsin-Würm glaciation (Pirazzoli 1991; Perissoratis and Conispoliatis 2003). This resulted in five island cladograms whose roots represent the ancestral landmasses and whose tips represent the present-day islands (fig. 1; see also Foufopoulos and Ives 1999a).

We then mapped the patterns of species presence/absence onto these island cladograms under the parsimony assumption that a species occurred on an ancestral island if it occurred on any of its daughter islands that formed as the island fragmented (fig. 1). The assumption that current presence indicates past occurrence and not immigration is based on a wealth of evidence demonstrating that the likelihood of over-water colonizations—whether natural or as the result of anthropogenic activities—is very low (Foufopoulos and Ives 1999b). First, contrasting tropical island regions such as the Caribbean or Melanesia have warm waters and abundant vegetation that can form rafts and enable dispersal (Calsbeek and Smith 2003), but in the Aegean, the relatively cold waters, general absence of floating vegetation, and substantial interisland distances make over-water travel unlikely. Second, if substantial over-water colonization had occurred, one would expect islands closer to either the mainland or other larger islands to harbor more species. However, analyses revealed that there is no such relationship; instead, the number of species on islands was negatively associated with the time at which islands were isolated during the island fragmentation process (Foufopoulos and Ives 1999b). Third, a lack of over-water colonization is reflected in some seemingly idiosyncratic distributions where species have failed to disperse across narrow but deep straits separating islands. Taxonomic analyses based on morphological and molecular criteria resulted in the description of five allopatric *Podarcis* lizard species, more than 25 subspecies of *Podarcis erhardii*, and at least 13 subspecies of *Cyrtopodion kotschy* in the Aegean Sea alone (Mayer and Tiedemann 1980, 1981; Beutler 1981; Gruber 1986; Poulakakis et al. 2005a, 2005b). The distribution patterns of these groups mirror the time of separation of islands rather than geographic proximity, showing lack of substantial gene flow across water straits. Finally, detailed population genetic analyses of the lizard *P. erhardii* demonstrated lack of an isolation-

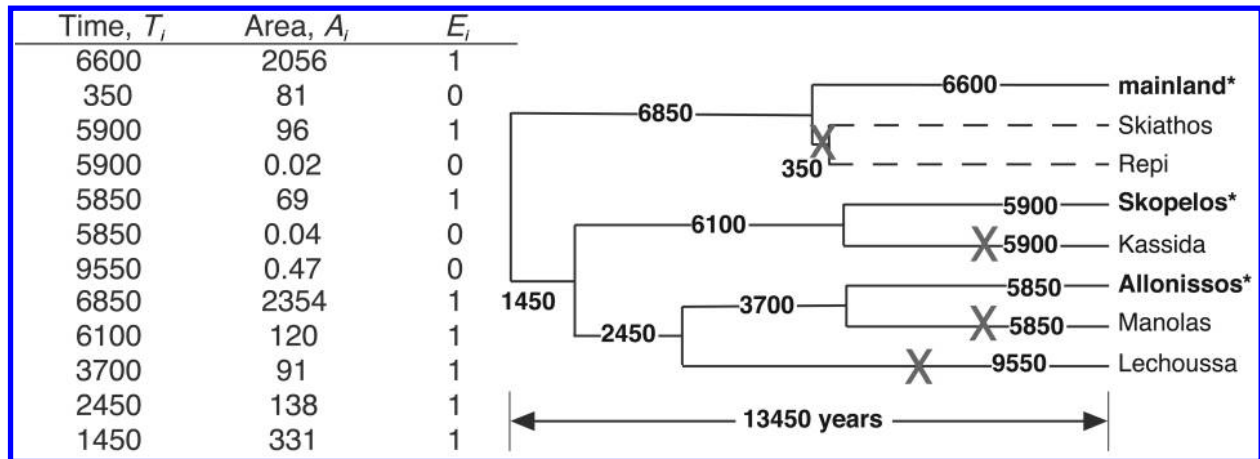


Figure 1: Illustration of the calculation of extinction rates for an example species, the Turkish gecko *Hemidactylus turcicus*, on the Sporades Archipelago. This species survives today on two islands and on the mainland adjacent to the archipelago (*bold text*). The cladogram gives the sequence of island separations over the last 13,450 years as obtained from bathymetric maps, and the times of separation were estimated using the known progression of sea level rise. Extinction events (X) were assigned using a parsimony assumption that minimized the number of extinctions needed to give the observed presence/absence distribution among islands. Extant populations could either persist or become extinct during the period before the next separation event (or present day), and these events E_i (extinction = 0, persistence = 1) are given in the table along with the time periods over which these events occurred. The table includes information not only on the present islands but also on the ancestral islands. These values were used in equation (1) to give extinction rates r . Note that data for the separate islands of Skiathos and Repi (*dashed lines*) are not included, because *H. turcicus* was assumed to have become extinct on the ancestral landmass. Thus, the species never occurred on these islands.

by-distance effect in the genetic structure of the examined populations and a progressive loss of genetic diversity over time. Both of these relationships indicate the absence of significant gene flow in *P. erhardii* even between populations separated by narrow water straits (Poulakakis et al. 2005; Hurston et al. 2009).

To calculate extinction rates, we assumed that the instantaneous rate of extinction of a species is constant between the time of island formation and fragmentation (ancestral islands) or since the time of formation (extant islands). We also assumed that the extinction rate depends on the size of the island. Specifically, for island i the instantaneous extinction rate is $r - a(A_i - \bar{A})$ where r is the overall (average) extinction rate, and a measures the sensitivity of the extinction rate to island area, A_i . For extant islands A_i is the current area of the island, and for ancestral islands A_i is the size of the island immediately before it separated into daughter islands, giving the minimum size of the ancestral island; this assumes that the minimum island area sets the extinction risk. The average area of islands (both past and present) from the archipelagos on which the species occurred, \bar{A} , is subtracted from A_i so that r gives the average extinction rate over all islands, since the average of $(A_i - \bar{A})$ over all islands i is 0. With these assumptions, the probability that a species will become extinct on island i is given by the logistic regression model

$$E_i = e^{-[r - a(A_i - \bar{A})]T_i}, \quad (1)$$

where E_i is the fate (0 = extinction, 1 = persistence) of the species on the current or ancestral island i and T_i is the time between when the island was formed and either when it divided or today. This model produces estimates of extinction rates rather than extinction probabilities, because time T_i is incorporated; preliminary analyses (not presented) showed that time was a significant predictor of population extinctions. In summary, the logistic regression given by equation (1) estimates for each species the mean extinction rate r and the parameter a that represents the sensitivity of extinction rates to island area, with larger values of a corresponding to increased extinction rates on smaller islands. Figure 1 illustrates the information used in the calculations.

In fitting equation (1), rather than use the logit link function normally used in logistic regression (McCullagh and Nelder 1989), instead we used the log-link function, because this easily accommodates the exponential form of equation (1). Logistic regression is known to give biased estimates of the coefficients, and we therefore modified the method of Firth (1993), which incorporates a penalty into the likelihood that is proportional to the determinant of the corresponding information matrix. To obtain confidence intervals for the estimates of extinction rates r and

area-sensitivity coefficient a , we performed bootstrapping. This not only revealed the precision of the estimates but also any residual bias that was not corrected by the modified Firth method. Extinction rates and area sensitivities for all species as well as bootstrapped confidence intervals are presented in supplementary data tables in appendix C.

Our approach involving the reconstruction of the sequence of island separation and species loss gives a more refined picture of extinction rates than would be obtained from the current presence/absence patterns of species among islands alone. For example, if a species is absent from an entire archipelago despite being present on a nearby mainland, we scored these multiple absences as only a single, ancient population extinction event. This guards, at least in part, against incorrectly inflated estimates of extinction rates for species that currently have sparse distributions among islands.

Our estimation of extinction rates assumes that species were originally uniformly distributed across the ancestral landmass, since we assume that absences of species from islands indicate extinctions. The (sub)fossil record from the islands, although far from complete, supports the existence of rich prefragmentation species communities with several documented cases of persistence (fossils from islands where the species still survive) and extinctions (fossils on islands of species that subsequently became extinct; Bachmayer et al. 1975; Schneider 1975; Szyndlar 1991). Nonetheless, to assess the sensitivity of our results to the two underlying assumptions of the estimation of extinction rates—uniform ancestral distributions of species and no colonization between islands—we performed two simulation studies (app. A in the online edition of the *American Naturalist*). In the first, we violated the assumption that species were distributed uniformly throughout the ancestral landmass from which extinctions were calculated by instead supposing that the ancestral species distributions were patchy. Second, we violated the assumption that there was no immigration between islands by incorporating colonization. Even large violations of both assumptions did not change our overall conclusions (app. A). Although both of our original assumptions are supported by considerable evidence, these simulation studies nonetheless make our results more secure.

Extinction rates and species characteristics. We hypothesized that if the current latitudinal distribution of species on the mainland reflects their sensitivity to climatic conditions, then there should be a relationship between the latitudinal range of the 35 species and their extinction rates on Aegean islands. To determine the latitudinal ranges of species, we identified the northern- and southernmost points of each species' current range from published distributional information (Böhme 1981) and museum records. The northern- and southernmost range points were

averaged to give the latitudinal midpoint (LM) of the species' range. Although there are multiple ways of measuring the latitudinal range of species, our approach is simple and incorporates the full range of latitudes at which species are found. We explore alternative measures of species ranges, specifically the northern and southern range limits, and the latitudinal span (northern limit minus southern limit) in appendix B in the online edition of the *American Naturalist*.

We regressed extinction rates on the latitudinal midpoints of ranges. Because the species are phylogenetically related, such regressions run the risk of Type I errors, identifying a statistically significant pattern when in fact there is none (e.g., Martins and Garland 1991). Therefore, we analyzed the data with a regression method that incorporates the species phylogeny. Standard phylogenetic comparative methods assume that the residual variation from the regression can be described by a Brownian motion evolutionary process; this is the assumption of both the independent contrasts (Felsenstein 1985; Garland et al. 1992) and the generalized least squares approaches (Martins and Hansen 1997; Garland and Ives 2000). Rather than make this strict assumption, we instead used the program *Regressionv2.m* from Lavin et al. (2008), in which the strength of phylogenetic signal exhibited by the residuals of the analysis is estimated simultaneously with the regression coefficients. The strength of the phylogenetic signal is given by a parameter d that varies from 0 when residuals are independent to 1 when the phylogenetic correlations among residuals are consistent with Brownian motion evolution. Thus, the parameter d statistically adjudicates between nonphylogenetic regression and regression under a Brownian motion model of evolution. To correct for heteroscedasticity in the residuals, we square root transformed the extinction rates before analyses.

In addition to the latitudinal midpoint of species ranges, we considered two other species traits that were previously shown to be related to extinction rates of reptile populations on Aegean islands—maximum population density and the breadth of habitats used by the species (Foufopoulos and Ives 1999b). To measure population density, species were categorized into four groups according to the maximum density (number per unit area) they achieve on the study islands. We use these maximal estimates as species-specific traits, rather than as an attribute of any one population. Because we are using these estimates as traits that affect extinction rates, we are assuming that maximum densities have not changed appreciably over the course of the Holocene. We used four broad categories of maximum densities because uncertainty in these species traits prevents any finer-scale designations. To obtain a metric of the breadth of habitats used by species, we identified 10 habitat categories that summarize the types of habitats on the

islands (Watson 1964). Our metric of breadth of habitat use is the fraction of these 10 categories used by each species. We performed multiple regression as above, using Regressionv2.m to account for possible phylogenetic signal in the residuals (Lavin et al. 2008).

Extinction rates and suitable habitats. We also performed analyses to determine whether availability of suitable habitat could explain differences in extinction rates. To obtain measures of the amount of suitable habitat remaining on each island for each species, we used ArcGIS to analyze a CORINE 1 : 100,000 land cover database (EEA 2000) that included 71 of the 87 islands in our study. The 44 land-use/land-cover classes in CORINE were collapsed into the 10 habitat categories previously used to estimate breadth of habitat use. Various reptile groups differ broadly in the minimum area of suitable habitat they require to persist. To scale the amount of suitable habitat by the area requirements of a species, we determined the minimum area of suitable habitat on any island that was supporting a species in each order (turtles: 6.25 ha) or suborder (snakes: 2.88 ha, lizards: 0.5 ha). The total area of suitable habitat for each species among all islands was then divided by the minimum area each species required according to their order or suborder. Finally, we scaled these values to range between 0 and 1 by dividing this value for each species by the maximum value obtained among all species, thereby giving a metric of the availability of suitable habitat for each species, SH. Because the resulting values were not normally distributed, we arcsine transformed SH for subsequent analyses. Note that SH is a measure of island characteristics for each species and was scaled according to the habitat requirements for the different groups of species. In contrast, the maximum population density of species and the breadth of habitat use are treated as species traits in the analyses of the next section (see *Extinction rates and species characteristics* in “Results”).

To determine whether the loss of suitable habitat could explain the higher extinction rates of more northern species, we regressed SH against the latitudinal midpoint of species ranges, LM, and we then regressed the extinction rates r against SH. Thus, we addressed whether more northern species have less suitable habitat currently available on the study islands and then whether a lack of availability of suitable habitat could explain higher extinction rates. These analyses were performed using Regressionv2.m (Lavin et al. 2008) to incorporate the possibility of phylogenetic signal.

Potentially confounding factors. We analyzed data to test two general assumptions we used to calculate extinction rates: (i) humans have played a minor role in the extinction or redistribution of species among islands, and (ii) species were broadly distributed among ancestral islands, so that

the current absence of a species from an island implies population extinction.

i) Regarding human impact on the distribution of species, it is possible that humans have played a role in the colonization and extinction of species from islands and therefore that the current distributions reflect human activity rather than natural long-term patterns of climate change and population extinctions. To assess the effect of human habitation, we regressed the number of species per island on whether or not islands were inhabited by humans, including island area in the regression because island area is known to affect the number of species per island. Because we are particularly interested in the extinction rates of northern versus southern reptile species, we also divided the species into a northern group and a southern group, with the northern group having latitudinal midpoints above the midlatitude of the islands, 37.6°N ($N = 22$ species), and the southern group below ($N = 13$). If humans caused the positive relationship between extinction rates and species latitudinal midpoints, then we would expect these regressions to show a larger decrease in the occurrence of species caused by humans for northern species than for southern species. Note that for these analyses the dependent variable is the number of species on islands. Therefore, to determine whether the effect of human habitation on the distribution of species depends on the latitudinal range of species, we have to categorize species as northern or southern and perform separate analyses for both groups.

ii) Regarding homogeneous prefragmentation distribution of species, our calculations of extinction rates (eq. [1]) assume that species were distributed uniformly across the ancestral landmasses of the archipelagos on which they

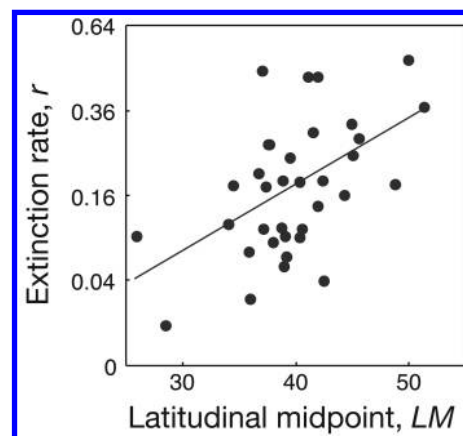


Figure 2: Mean population extinction rates r ($1,000 \text{ year}^{-1}$, square root transformed) versus the latitudinal midpoint (LM; degrees N) of the range of 35 reptile species. The relationship is statistically significant ($P < .002$; table 1).

currently occur. If species were initially patchily distributed, then the sequential fragmentation of islands during the Holocene might not have led to extinctions. Instead, species that do not occur on an island today might not have existed in the same location before fragmentation. This concern is addressed in appendix A using a simulation study. Here we address this issue empirically.

We constructed a species-area curve for the islands and compared this to a species-area curve for the mainland areas adjacent to the islands with species-area data from Chondropoulos (1986, 1989) and field data from J. Foufopoulos. The areas on the mainland occupy low-lying regions near the coast and are topographically and climatically similar to the islands. If this analysis shows that islands have fewer species than mainland areas of the same size, then this would imply a strong role of extinctions in determining the pattern of species occurrences on islands (MacArthur and Wilson 1967). If instead the distribution of species on current islands were determined solely by their former patchy distribution across the ancestral landmass, then there is no reason to expect that the number of species on islands would be lower than on comparably sized areas on the mainland.

Results

Extinction rates r , which give the instantaneous probability that a population becomes extinct on an island of average size, ranged from 0.0095 to 0.47 1,000 years⁻¹ (see app. C). For the 35 species, there were only three whose southern boundary on the mainland was farther north than the southernmost island on which it was scored as being absent in the calculation of extinction rates (see app. C). Therefore, the extinction rates do not simply reflect the northward movement of the southern range limits of species. The area sensitivity parameter a ranged from -0.034 to 0.070 1,000 years⁻¹ per km⁻². All but two species had positive estimates of a , indicating that extinction rates increased on smaller islands; of the two species with negative estimates, one was nonsignificant and the other weakly significant ($.05 > P > .02$).

Extinction rates and species characteristics. Extinction rates r were positively correlated with the latitudinal mid-

Table 1: Phylogenetic regression of square root-transformed extinction rates r (1,000 years⁻¹) on the latitudinal midpoint (LM) of species ranges

Effect	Coefficient	t	P
Intercept	-.205	-1.14	
LM	.0158	3.52	<.002

Note: The estimate of phylogenetic signal in the residuals is $d = 0$, with $N = 35$ and $R^2 = 0.27$. Analyses were performed using Regressionv2.m from Lavin et al. (2008).

Table 2: Phylogenetic regression of square root-transformed extinction rates r (1,000 years⁻¹) on maximal species densities, the breadth habitats used by species, and latitudinal midpoint (LM)

Effect	Coefficient	t	P
Intercept	.201	1.31	
Maximal density	-.0486	-2.52	<.02
Breadth of habitat use	-.0294	-2.94	<.01
LM	.0130	3.81	<.001

Note: The estimate of phylogenetic signal in the residuals is $d = 0$, with $N = 35$ and $R^2 = 0.62$. Analyses were performed using Regressionv2.m from Lavin et al. (2008).

point of species ranges on the mainland (fig. 2; table 1). In the regression the estimate of the strength of phylogenetic signal (parameter d) was 0. This indicates that closely related species were not more likely to have similar extinction rates after the effect of LM was removed.

We also performed multiple regression of extinction rates r against LM and two additional variables known to affect extinction rates, the maximum density achieved by species and their breadth of habitat use (table 2). Both of these additional variables were statistically significant, as was LM, and there was no evidence of phylogenetic signal in the residual variation ($d = 0$). The regression coefficient for LM, 0.013, was only slightly lower than in the regression with LM alone (0.016; table 1), indicating that the additional two variables do not explain the observed relationship between extinction rates and LM.

Extinction rates and suitable habitat. For each species, we calculated the relative amount of suitable habitat available across the study islands. The SH values were negatively related to LM, indicating that more northern species have less suitable habitat available on the islands (fig. 3A; table 3). Furthermore, extinction rates r were negatively related to SH, indicating that species with more available habitat had lower extinction rates (fig. 3B; table 4). This provides one potential explanation for the relationship between extinction rates r and LM (fig. 2): northern species had less available suitable habitat and as a consequence had higher extinction rates.

A multiple regression of r against both LM and SH provides support for this explanation. Even with the inclusion of LM, the coefficient for SH on extinction rates remains statistically significant. However, the coefficient for LM is reduced from 0.016 (table 1) to 0.0089 (table 5), and statistical significance of this relationship was lost. This indicates that, while both LM and SH are related to extinction rates, at least part of the explanation for northern species having higher extinction rates is that they have less available habitat.

Human impact on the distribution of species. The number of reptile species on an island was not statistically related to the presence of humans in a regression analysis

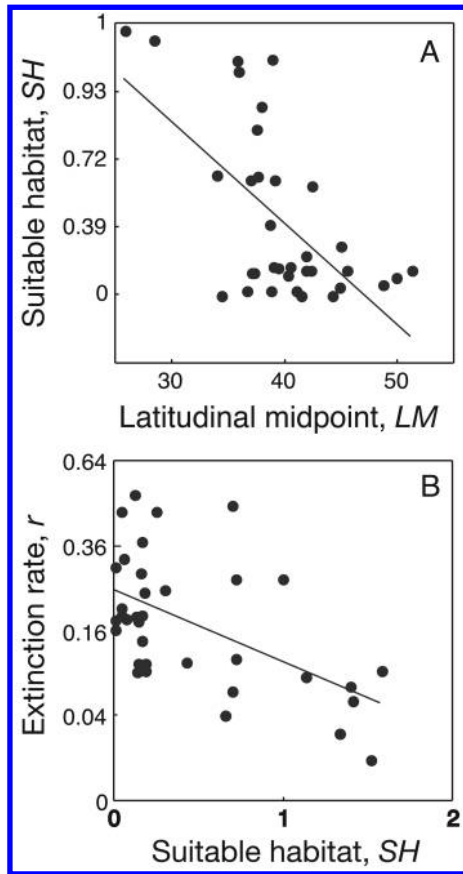


Figure 3: A, Relative availability of suitable habitat (SH, arcsine transformed) versus the latitudinal midpoint of species ranges (LM). The relationship is statistically significant ($P < .001$; table 3). B, Mean population extinction rates r (1,000 year⁻¹, square root transformed) versus SH (arcsine transformed). The relationship is statistically significant ($P < .001$; table 4).

that accounted for the effects of island area (humans: $t = -0.175$, $P = .861$; area: $t = 10.427$, $P < .001$; total model: $R^2 = 0.809$, $N = 87$). These results suggest it is unlikely that the presence of humans has strongly impacted extinction or colonization by reptile species. We performed a similar analysis on the subsets of 22 northern (LM above the midlatitude of the islands) and 13 southern species (northern species: $t = -0.317$, $P = .752$; southern species: $t = -0.106$, $P = .916$). Because subsets of northern and southern species showed no effect of human presence, it is unlikely that human presence was responsible for the higher extinction rates of northern species (fig. 2).

Species-area relationships on islands and mainland. Species-area curves for the islands and the mainland showed lower numbers of species on islands than on comparably sized areas on the mainland (fig. 4). This suggests that, similar to other land-bridge islands or habitat frag-

ments (Wilcox 1978; Newmark 1987; Newmark 1991; Burkey 1995), the reptile communities in the Aegean underwent relaxation following isolation from the mainland. As the steepness of the island slope indicates, the population extinctions underlying this relaxation process were most pronounced on smaller islands. This is consistent with our calculations of area sensitivity a in the extinction rates, for which the preponderance of negative species-specific values indicates higher extinction rates on smaller islands. The apparently strong effect of extinction in the island species-area curve relative to that from the mainland indicates that the pattern of species occurrences on islands that we used to calculate extinction rates cannot be attributed to an initially patchy distribution of species across the ancestral landmass.

Discussion

We found that island populations of more-northern reptile species had higher extinction rates r (fig. 2; table 1). This is consistent with the expectation that species from northern climates were impacted more severely by climate change on the study islands during the Holocene (Geraga et al. 2005; Eastwood et al. 2007; Fuchs 2007). While investigating possible explanations for this pattern, we also accounted for two species characteristics known to affect extinction rates: the maximum population density of a species (Pimm et al. 1988; Purvis et al. 2000) and the breadth of habitat types used by the species (Rossignol-Strick 1999; Owens and Bennett 2000). Our goal was to determine whether these two species characteristics underlie the observed relationship between extinction rates and the midpoint of species' latitudinal ranges. For example, more northern species might be species that naturally occur at lower population densities, and the resulting smaller populations might be more prone to extinction. However, including these two species traits did not reduce the strength of the relationship between latitudinal range midpoints and mean extinction rates (table 2).

Higher population extinction rates of northern species

Table 3: Phylogenetic regression of the arcsine-transformed metric of suitable habitat available on islands and the latitudinal midpoint (LM) of species ranges

Effect	Coefficient	t	P
Intercept	2.38	4.85	
LM	-.0479	-3.90	<.001

Note: The estimate of phylogenetic signal in the residuals is $d = 0.13$, with $N = 35$ and $R^2 = 0.32$. At this small value of d , the estimates for the coefficients and t values are within 1% of those obtained under standard (nonphylogenetic) regression. Analyses were performed using *Regression2.m* from Lavin et al. (2008).

Table 4: Phylogenetic regression of square root-transformed extinction rates r (1,000 years⁻¹) on arcsine-transformed suitable habitat (SH)

Effect	Coefficient	<i>t</i>	<i>P</i>
Intercept	.498	16.5	
SH	-.171	-3.78	<.001

Note: The estimate of phylogenetic signal in the residuals is $d = 0$, with $N = 35$ and $R^2 = 0.30$. Analyses were performed using Regressionv2.m from Lavin et al. (2008).

could be due to direct effects of climate (e.g., temperature) or indirect effects through changes in the biotic environment such as shifts in plant communities. Although it is not possible to completely disentangle direct and indirect effects, circumstantial evidence suggests that higher extinction rates of northern species resulted at least in part from the disproportionate loss of cooler, mesic habitats (e.g., deciduous and coniferous forest). The amount of suitable habitat for each species was negatively related to the latitudinal midpoint of species ranges. Furthermore, extinction rates r were negatively related to SH. Reduced area of suitable habitat could lead to extinction by making some islands unsuitable or by restricting the suitable area of islands, which thereby reduces population sizes and makes them more prone to extinction. Whereas conditions were cool and moist at the beginning of the Holocene, when most of the islands became separated, the region has since experienced increasing aridity (Caner and Algan 2002; Magny et al. 2002; Mudie et al. 2002; Eastwood et al. 2007) and a general decrease in forest cover (Rossignol-Strick 1999; Roberts et al. 2001; but see Bottema and Sarpaki 2003; Geraga et al. 2005). Consequently, the paleoclimatic record, though incomplete, suggests that in the northeast Mediterranean Basin conditions have become increasingly unsuitable for taxa with cool or mesic habitat preferences.

Humans caused significant changes in vegetation cover after 6000 BP (Fuchs 2007) on 40 (46%) of the study islands that have been inhabited. Nevertheless, in field observations (J. Foufopoulos, unpublished data) we found that human presence had surprisingly little effect on reptile communities, with all resident species widely distributed throughout anthropogenically modified habitats and no clear differences between areas with and without human habitation. Indeed, in our statistical analyses, after correcting for island area, the presence of humans had no effect on the number of reptile species on islands, either for all species combined or for subsets of northern and southern species. Our data indicate that while human activities have had effects on the vegetation cover of the islands in the region (Grove and Rackham 2003), this did not translate into observable changes in the local reptile communities, possibly because the gradual expansion of

nonintensive agricultural practices allowed local taxa to adapt to an anthropogenically modified landscape.

Our calculations of population extinction rates presuppose that all species were distributed throughout the proto-archipelagos of the Aegean Sea. Indirect evidence for the widespread distribution of reptiles across the prefragmentation landscapes comes from the palynological record. It indicates that during the earliest Holocene, conditions were cool and relatively dry, similar to what is typical of present-day northern latitudes where these species are widespread today (Digerfeldt et al. 2007). Therefore, in the past northern species likely had broad geographical distributions within this island region. Also, all of the northern species currently occur on islands spread throughout the broader geographic area (Valakos et al. 2008), often close to sea level, again pointing toward a widespread distribution on the prefragmentation landscapes.

In summary, our results suggest that species from cooler, mesic regions were more susceptible to extinction from our study islands, and their elevated susceptibility was caused at least in part by the loss of suitable habitats. What lessons do these results hold for current climate change? Because the southern range limits of almost all our study species on the mainland lay south of the southernmost island on which they became extinct, the extinctions from islands do not simply represent a retraction of the southern range limit that matches the nearby mainland. Instead, island extinctions occurred north of the present southern range limit on the mainland. Thus, range retraction in the fragmented, island landscape is a sporadic, nonuniform process, with extinctions occurring especially on small islands as a mosaic within the equatorial edge of a species range. This represents an interaction of the climate change and fragmentation processes, with more extensive fragmentation (smaller islands) leading to higher extinction rates that are further exacerbated for species that are sensitive to climatic changes. From this example in the Aegean, we would expect to see the effects of climate change on species in a fragmented landscape as inflated extinction rates on the equatorial edge of species' ranges before there

Table 5: Phylogenetic regression of square root-transformed extinction rates r (1,000 years⁻¹) on arcsine-transformed suitable habitat (SH) and latitudinal midpoint (LM)

Effect	Coefficient	<i>t</i>	<i>P</i>
Intercept	.118	.505	
SH	-.141	-2.03	<.05
LM	.0089	1.64	<.2

Note: The estimate of phylogenetic signal in the residuals is $d = 0$, with $N = 35$ and $R^2 = 0.36$. Analyses were performed using Regressionv2.m from Lavin et al. (2008).

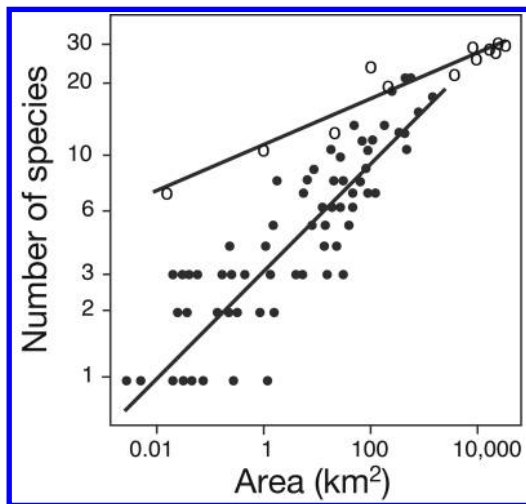


Figure 4: Species-area curves giving the number of species on 87 islands (solid circles) and areas on the mainland (open circles). Islands, in particular small ones, have experienced substantial loss of species in comparison to the mainland. On the mainland, larger sites are prefectures and smaller sites are locations of detailed field surveys. See Valakos et al. (2008).

is range retraction. These extinctions could give a warning sign of full-blown range contraction.

Although the extinctions of reptiles on islands in the Aegean over the last 10,000 years were unlikely to have been caused by human activities, the patterns of habitat change that precipitated them share many similarities with present-day anthropogenic climate change and habitat fragmentation. Human activities tend to first destroy flat, lowland habitats that are amenable to agriculture and development. As a result, many natural habitats survive today only as small habitat islands confined to mountainous regions that are surrounded by a “sea” of low domesticated land. Such upland areas tend to be topographically diverse, as are the islands in the Aegean. Similarly, the matrix surrounding habitat islands in many human-dominated landscapes is hostile to slowly dispersing terrestrial organisms such as reptiles, presenting obstacles that might be almost as impenetrable as the cold waters of the Aegean Sea. This fragmentation presents a threat in its own right and is also a major challenge for species whose distributions are shifting poleward as the climate warms.

The scenario of population extinctions suggested by our analyses allows integration of several independently observed patterns. As the climate warms, species ranges are expected to contract from their equatorial boundary (Huntley 1999; Franco et al. 2006). Loss of suitable habitat is the primary cause of extinction risk for species throughout the world (Groombridge 1992) and for Mediterranean herptiles in particular (Cox et al. 2006). And fragmentation

is well known to increase population extinction rates, as fragmentation creates small populations and isolates them from the possibility of recolonization (Newmark 1987). Together these components represent a complex of processes that will likely play out over centuries, rather than decades. While there have been numerous documented cases of rapid, contemporary changes in species ranges (Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003; Parmesan 2006), these may represent only that subset of species susceptible to rapid and direct effects of climate change. In contrast, the extinction process of reptiles from Aegean islands has progressed through millennia, and the indirect effect of climate change through habitat loss appears to play a major role. Our results suggest that in the coming centuries, fragmentation will exacerbate the effects of a warming climate, leading to differential extinctions of those species that are habitat specialists and/or that naturally occur at low densities. Unfortunately, documenting slow or delayed effects of contemporary climate change on species ranges and population extinction will be difficult. Therefore, patterns of past population extinctions, while not mimicking precisely the patterns we expect over the coming centuries, may nonetheless give insights into the types of processes that will drive changes in species populations in the future.

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