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Author(s): Simone Fattorini

Source: Journal of Herpetology, 44(2):242-252. 2010.
Published By: The Society for the Study of Amphibians and Reptiles
DOI: 10.1670/09-046.1
URL: http://www.bioone.org/doi/full/10.1670/09-046.1

Journal of Herpetology, Vol. 44, No. 2, pp. 242–252, 2010

Influence of Recent Geography and Paleogeography on the Structure of Reptile Communities in a Land-Bridge Archipelago

SIMONE FATTORINI

Water Ecology Team, Department of Biotechnology and Biosciences, University of Milano Bicocca, Piazza della Scienza 2, I-20126, Milan, Italy; E-mail: simone_fattorini@virgilio.it

ABSTRACT.—**The herpetofauna of the Tuscan Islands (Central Italy) is well known and represents an ideal subject to understand the role of current and historical factors responsible for biogeographical patterns in a complex archipelago. Multidimensional Scaling, cluster analyses, species-area relationships, Mantel tests and co-occurrence statistics were used to investigate the influence of current geography and Pleistocene connections with the mainland on the structure of insular communities. Although reptile colonization likely occurred via land bridges for islands that were connected to the mainland in the Pleistocene, a long time relaxation (species extinction by island habitat loss after disconnection and new colonization by over sea dispersal or human-assisted introductions) equilibrated the faunas according to island area. Biogeographical similarities among islands increased for islands located farther from Corsica and Tuscany, thus suggesting that, for remote islands, interisland faunal exchanges occurred more frequently than mainland-island colonization. Also, a possible influence of Pleistocene geography emerged more clearly when populations suspected to be introduced by man were removed. Co-occurrence analyses indicated a nonrandom distribution influenced by island area and distance, suggesting that the time elapsed since post-Pleistocene disconnection may have reshaped biogeographical similarities by an increase in competition resulting from reduction in island areas and introduction of certain species. From a conservation viewpoint, the land-bridge distribution of organisms with poor mobility should be carefully considered in conservation biogeography, because depletion of island populations cannot be balanced by new immigrations from the mainland, whereas introduction of nonnative species may have a negative impact on the original fauna.**

The biogeography of the Tuscan Islands (Fig. 1) has long been studied to highlight the major ecological and historical factors that are potentially responsible for present day distributional patterns, making this archipelago one of the best investigated in the Mediterranean Basin (e.g., Baroni Urbani, 1971; Società Italiana di Biogeografia, 1974; Piantelli et al., 1990; Fattorini, 2009a).

Because of their location between the Corsardian plate (Corsica plus Sardinia) and Tuscany region (Central Italy), the Tuscan Islands are expected to show transitional faunas, and this has already been well demonstrated for several groups (Fattorini, 2009a). The common opinion is that paleogeography is a key factor in determining the distribution of plants and animals on these islands, which have been regarded as a classical example of land-bridge islands (see references in Mariotti, 1990; Dapporto and Cini, 2007). According to this view, islands that were connected to Tuscany during Pleistocene glacial maxima are characterized by a preponderance of species that reached the Tuscan Islands from the Italian mainland, whereas islands closer to Corsardinia (but which were isolated during Pleistocene glacial maxima) exhibit a larger proportion of species distributed in Corsica and Sardinia but absent from Tuscany. In fact, recent studies demonstrated that, at least in animals with high mobility (such as chrysidid hymenopterans and butterflies), a transitional pattern can be simply explained by current geography alone (Fattorini, 2009a).

Although for oceanic islands (i.e., islands never connected to the mainland) a general model has been recently proposed that takes into account island evolution through time (Whittaker et al., 2008; Fattorini, 2009b), there is no comprehensive theory on the evolution of land-bridge islands. According to the model postulated by Fattorini (2009a) for the Tuscan Islands, land-bridge islands were largely colonized (and possibly saturated) by different groups during the Pleistocene sea regressions, and then there have been extensive extinctions as a result of area and, hence, habitat loss. However, although mobile animals were able to currently colonize virtually all islands, mostly erasing the historical signal and resulting in a negative correlation of species richness and distance, even small distances preclude less mobile groups such as tenebrionid coleopterans from colonizing an island regularly, such that no correlation between species richness and distance appears in these insects (Fattorini, 2009c). Thus, the role of dispersal should be

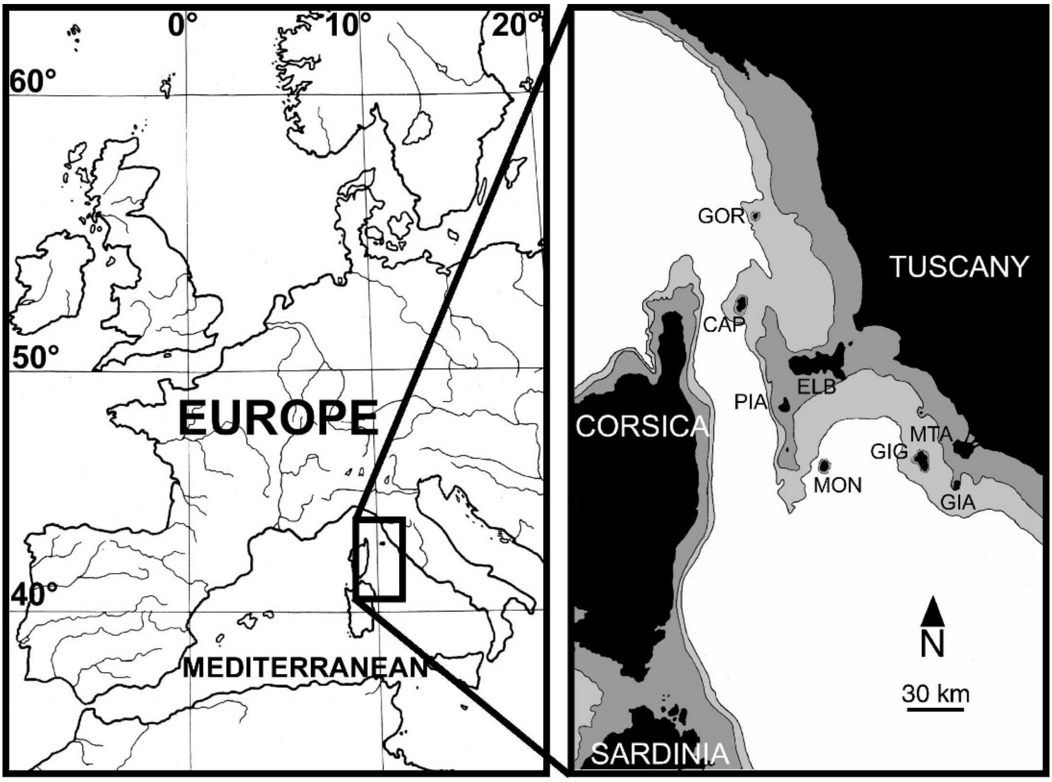

FIG. 1. The Tuscan Archipelago and its relative position in the Mediterranean. Present day land (black) and extent of land mass during the last (Pleistocene) glacial maximum (dark grey) are indicated. Depth contours are also shown for 200 m (light grey). CAP: Capraia, ELB: Elba, GIA: Giannutri, GIG: Giglio, GOR: Gorgona, MON: Montecristo, MTA: Mt. Argentario, PIA: Pianosa.

accurately considered for understanding the evolution of archipelagos that include land-bridge islands. Compared with other groups, reptiles are relatively less mobile; thus, their island faunas tend to be usually relictual (e.g., Foufopoulos and Ives, 1999). Therefore, the reptiles of the Tuscan Islands may represent an excellent model to investigate the role of current and historical factors in determining biogeographical patterns in a composite archipelago, which includes both land-bridge and oceanic islands.

The herpetofauna of the Tuscan Islands has been investigated by naturalists for more than a century, and all of these islands are faunistically well known (Balletto, 2005; Vanni and Nistri, 2006). However, there is no detailed study aimed to understand the role of current and historical factors responsible for biogeographical patterns. An analysis of the relative importance of current and historical factors is particularly compelling because of the conservation concern of these islands, which are included in the Tuscan Archipelago National Park. The recent development of conservation biogeography (Whittaker et al., 2005) stresses the importance of considering biogeographical information in assessing conservation priorities. Thus, the understanding of the processes underlying reptile biogeographical patterns in the Tuscan Islands may serve as a case study to address some general problems of biological conservation in land-bridge archipelagos.

The aims of this paper were as follows: (1) to investigate the biogeographical relationships of reptile faunas of the Tuscan Islands; (2) to determine the relative importance of current (Recent) and historical (Pleistocene) geography in determining such patterns; (3) to assess the mechanisms that may explain the role of Recent and Pleistocene factors; and (4) to discuss some implications for biodiversity conservation.

MATERIALS AND METHODS

Data Sources.—The study islands included Capraia, Gorgona, Montecristo, Elba, Pianosa, Giglio, Giannutri, and the fossil-island of Mt. Argentario (Dapporto and Cini, 2007; Fig. 1).

Table 1. Reptile distribution in the Tuscan Archipelago. Presence/absence indicated by 1/0.

	Gorgona	Capraia	Elba	Pianosa	Giglio	Montecristo	Giannutri	Mt. Argentario
Tarantola mauritanica	1	1	1	1	1	0	1	1
Hemidactylus turcicus	1	1	1	1	1	1	1	1
Euleptes europaea	0	1	1	1	1	1	1	1
Lacerta bilineata	0	0	1	0	0	0	0	1
Podarcis sicula	0	1	1	1	1	1	1	1
Podarcis muralis	1	0	1	1	0	0	0	1
Chacides chalcides	0	0	1	0	0	0	0	1
Hierophis viridiflavus	1	1	1	1	1	1	1	1
Coronella austriaca	0	0	1	0	0	0	0	0
Zamenis longissimus	0	0	1	0	0	0	0	1
Elaphe quattorilineata	0	0	0	0	0	0	0	1
Natrix natrix	0	0	1	0	0	0	0	1
Vipera aspis francisciredi	0	0	1	0	0	0	0	1
Vipera aspis hugyi	0	0	0	0	0	1	0	0

Distributional data are taken from Fattorini (2009a; Table 1). Field research was performed on Giglio and Giannutri in August 2008.

The turtle *Testudo hermanni* was excluded as it has been introduced into the Tuscan Archipelago by humans (Vanni and Nistri, 2006). The occurrence of *Vipera aspis* on Montecristo is also problematic (Zuffi and Bonnet, 1999). In fact, the taxonomic status of Italian populations of vipers is disputed. Recently, Zuffi (2002) proposed to consider *Vipera aspis francisciredi* synonymous with the typical form and *Vipera aspis hugyi* as a good species. However, this interpretation has been criticized (Filippi, 2003), and *V. a. francisciredi* is retained as valid (Sindaco et al., 2006). Recent molecular investigations showed a paraphyletic status of *V. a. hugyi*, which has been interpreted as a result of an introgressive hybridization and capture of *francisciredi*-like lineages in the *hugyi* mitochondrial genome (Barabanera et al., 2009). The population of Montecristo has been initially classified as an endemic subspecies (*Vipera aspis montecristi*). However, successive analyses based on morphological characters, and genetic data revealed that this population has to be referred to the subspecies *hugyi*, which lives in southern Italy (for details, see Barbanera et al., 2009). This contrasts with the distribution of *V. aspis* in central Italy, because Tuscan populations, as well as those of Elba and Mt. Argentario, belong to the subspecies *francisciredi*. At present, it is controversial whether Montecristo vipers are native (and established by unlikely overseas dispersion from southern Italy) or introduced from southern Italy (Zuffi and Bonnet, 1999; Barbanera et al., 2009).

For both *Podarcis sicula* and *Podarcis muralis* a number of taxa endemic to single islands of the Tuscan Archipelago have been described, including *Podarcis muralis beccarii* (Port'Ercole islet, Mt. Argentario SE), *Podarcis muralis colosii* (Elba, Portoferraio islet, Palmaiola, Scoglio della Paolina, fossil islands of Massoncello and Punta Ala), *Podarcis muralis insulanica* (Pianosa and La Scarpa islet), *Podarcis muralis marcuccii* (Argentarola islet, Mt. Argentario W), *Podarcis muralis muellerlorenzi* (La Scola), *Podarcis muralis paulinii* (Mt. Argentario), *Podarcis muralis vinciguerrai* (Gorgona), *Podarcis sicula calabresiae* (Montecristo), *Podarcis sicula caporiaccoi* (Capraia and La Peraiola islet), *Podarcis sicula cerbolensis* (Cerboli), *Podarcis sicula roberti* (Formica Grande di Grosseto), and *Podarcis sicula tyrrhenica* (Giglio, Giannutri). Most authors tend to consider all these taxa synonymous with the typical form (Sindaco et al., 2006), and I have refrained from attribution of insular populations to subspecies. In fact, low values of genetic variability in specimens of *P. sicula* from Montecristo and Elba have suggested the possibility that populations on these islands were founded by a small number of individuals originating from episodes of human transportation (Capula, 1994). However, low genetic variability is everywhere expected in island populations, which are inherently less numerous than mainland populations, especially if they originated from few individuals (as expected also in case of natural overseas dispersal) or if they underwent bottlenecks (as expected if island populations underwent demographic drops, such as by habitat loss). The native status of the geckos *Tarentola mauritanica* and *Hemidactylus turcicus*, two anthropophylous species cited from all of the studied islands, is also questioned (Harris et al., 2004; Carranza and Arnold, 2006). Based on the absence of fossils of *H. turcicus* in the Mediterranean region and the recency of recorded arrivals in many parts of the New World, Carranza and Arnold (2006) considered the occurrence of this species around most of the Mediterranean (excluding the Middle East) as recent and anthropogenic.

Harris et al. (2004) found that a single haplotype characterizes populations of *T. mauritanica* across Spain, Portugal, Italy, Menorca, Crete, and Tunisia, raising the possibility of an anthropogenic introduction followed by rapid population expansion throughout southern Europe. Moreover, although repeatedly reported in literature also from Montecristo Island, *T. mauritanica* has not been found on this island during recent studies (M. A. L. Zuffi, pers. comm.); thus, its actual occurrence on this island is doubtful, and I have omitted it from this island in all analyses. Finally, the snake *Zamenis longissimus* has been recently found on the island of Elba, but it is really uncertain whether it is native or introduced to the island (Vaccaro and Turrisi, 2007).

Because of the uncertain origin of some populations, in this study I performed two sets of analyses. A first set of analyses was conducted considering all populations as native (i.e., including all records of *T. mauritanica*, *H. turcicus*, *P. sicula*, *Z. longissimus*, and *V. aspis*). This represented the most ''conservative'' scenario. A second set of analyses was performed according to the ''worst'' wilderness scenario (i.e., excluding *V. aspis* from Montecristo, *T. mauritanica* and *H. turcicus* from all islands, *P. sicula* from all islands except Mt. Argentario, and *Z. longissimus* from Elba).

Recent and Pleistocene data about island isolation and areas are the same as in Fattorini (2009a; for details about calculations, see that paper). Here Pleistocene always indicates Pleistocene glacial maxima.

Influence of Recent and Pleistocene Factors on Species Richness.—Species richness was correlated with Recent and Pleistocene factors (namely, area and isolation; Dapporto and Cini, 2007; Dapporto et al., 2007). Because of the occurrences of several tied values, I applied the gamma statistic G to test levels of associations.

According to Dapporto et al. (2007), if paleogeography determined species richness in the Tuscan Archipelago, one should also expect that Pianosa (which in the Pleistocene was connected to Elba and Tuscany) should have a greater richness compared with all other islands (except Elba). In fact, the hypothesis is not well formulated, because the Pleistocene richness of Pianosa is expected to have decreased because the island was disconnected and reduced in size. Thus, if paleogeography favored island colonization and species accumulation, and its influence is superior to (i.e., not still erased by) current factors, Pianosa is not expected to have a larger number of species than other islands but a larger number of species than predicted by its current area (Fattorini, 2009a). To obtain the expected number of species for Pianosa, I modeled a species-area relationship (SAR) using a power function ($S = CA^z$, where S is the number of species, A is area, and C and z are fitting parameters) with a nonlinear fitting procedure (Quasi Newton algorithm; Fattorini, 2006c). If colonization occurred via land-bridge connections, Pianosa, as well as the other islands connected to Tuscany, are expected to have more species than predicted by the model (i.e., positive residuals; Fattorini, 2006b) as a consequence of larger area and greater accessibility during the Pleistocene. Calculations were done using STATISTICA software (vers. 6, StatSoft, Inc., Tulsa, OK, available from www.statsoft.com).

Biogeographical Relationships among Islands.—Cluster analyses of biogeographical similarities have been proposed as a tool to investigate the influence of current and historical factors in species distributions (e.g., Graham et al., 2005; Guerrero et al., 2005; Dapporto et al., 2007), whereas Dapporto and Cini (2007) used an ordination technique (Multidimensional Scaling).

In fact, biogeographical relationships hardly can be contrived in a dendrogram if areas did not originate by dichotomous splits; therefore, ordination techniques usually are preferred (Fattorini, 2002a; Fattorini and Fowles, 2005). However, interpretation of results from ordination analyses is more arbitrary because there is generally no obvious way to find groups of objects in a space. This is critical particularly when there are few points (as for the Tuscan Archipelago), and different arrangements can be subjectively recognized by the researcher. In such a case, a dendrogram may provide a more objective, albeit crude, way to define relationships. For these reasons, I have applied both techniques here. Non-Metric Multidimensional Scaling (NMDS) was applied to obtain a representation of multiple interisland relationships, whereas a cluster analysis was conducted to ''force'' islands into hierarchical arrangements that may serve as testable hypotheses. If current geography is the dominant factor, species assemblages are expected to be random samples mostly regulated by island area and distance (Fattorini, 2007b); therefore, islands are expected to cluster in a chained dendrogram reflecting species richness. By contrast, under the influence of historical factors, islands are expected to cluster according to relationships that are largely independent from current species richness. In particular, for the Tuscan Islands, we expect to find the small islands of Montecristo and Gorgona to cluster close to Elba (the largest island), all being close to the mainland in the Pleistocene.

In this study, biogeographical similarities among islands based on species presence/absence were calculated using Kulczynski 2 coefficient (for a discussion about the use of this coefficient in biogeographical analyses, see Hausdorf and Hennig, 2005). Similarity values were then converted to dissimilarities and clustered with the UPGMA amalgamation rule, which is considered the clustering strategy that minimizes the distortion of the original data matrix (Shi, 1993; McGarigal et al., 2000); therefore, it is favored particularly in biogeographical studies in a variety of contexts (e.g., Fattorini, 2002a; Graham, et al., 2005; Guerrero et al., 2005; Smith and Bermingham, 2005).

Kulczynski 2 dissimilarities were also used for a NMDS analysis. The NMDS attempts to arrange ''objects'' (islands) in a space with a particular number of dimensions to reproduce the observed distances. The NMDS does not have to try to reproduce the dissimilarities but only their order. I used an ordinal algorithm for which the order of the distances in the representation space must correspond to the order of the corresponding dissimilarities, but if there are two dissimilarities of the same rank, then there are no restrictions on the corresponding distances. The NMDS iteratively moves objects around in the space defined by the requested number of dimensions searching for the configuration that minimizes lack-of-fit (i.e., which minimizes the distortion between the original distances among objects and the new distance in the new n-dimensional space). As a criterion of goodness-of-fit to build an optimal representation, I used the raw stress (the smaller the stress value, the better is the fit of the reproduced distance matrix to the observed distance matrix). In each analysis, the algorithm was repeated from 100 randomly generated configurations with 1,000 iterations and the convergence criterion was set at 0.00001. Calculations were done using XLSTAT 7.5.2 software (Addinsoft, available from www.xlstat.com).

Influence of Recent and Pleistocene Factors on Biogeographical Patterns.—To study the influence of current and historical factors on biogeographical patterns I applied Mantel tests between matrices of biogeographical distances (i.e., Kulczynski 2 dissimilarities) among islands and the following matrices of island characteristics: (1) Recent interisland isolation; (2) Pleistocene interisland isolation; (3) Recent isolation from Corsica and Tuscany; (4) Pleistocene isolation from Corsica and Tuscany. Recent and Pleistocene interisland isolations were measured as minimal sums of distances across the sea between islands, whereas Recent and Pleistocene isolations from Corsica and Tuscany were measured as Euclidean distances between islands based on the minimal sums of distances across the sea from Tuscany and Corsica-Sardinia (for details, see Fattorini, 2009a). In Mantel tests, the null hypothesis H_0 is that the distances in a dependent matrix A (e.g., a matrix of biogeographical dissimilarities between islands) are independent of those between the same objects in the independent matrix B (e.g., a matrix of geographical distances between the same islands). Although the use of Mantel tests has been questioned because it is difficult to express overall geographical and historical relationships among areas by simply using geographical distances or a dissimilarity coefficient (Fattorini, 2006a), more complex approaches appeared not appropriate for the Tuscan Islands because of the small number of islands and variables involved. I applied Mantel tests using the Pearson correlation coefficient (r). For each test, probability values were calculated using the exact number of permutations. For each correlation, probability values were assessed using one-tailed tests with $P < 0.05$. Calculations were done using XLSTAT 7.5.2 software (Addinsoft, available from www.xlstat.com).

Although many tests were done, in accordance with the suggestions of Moran (2003), I did not apply the Bonferroni correction but focused on P-values and consistence of results.

Species Interactions.—To study whether species interactions play a key role in structuring species assemblages on islands, I tested possible nonrandom distributions of species among islands by co-occurrence analysis. Special patterns of co-occurrence are indicative of either mutual exclusion or positive species associations, with the former commonly interpreted as a result of competitive exclusion (Gotelli and Ellison, 2002).

For this approach, I used the Ecosim7 software (N. J. Gotelli and E. L. Entsminger, available from http://homepages.together.net/~gentsmin/ecosim.htm). I considered two indices of co-occurrence: the number of checkerboards (Checker index) and the C-score. The number of checkerboards is defined as the number of species pairs in the matrix that form perfect checkerboards and never co-occur. In a competitively structured community, the observed number of checkerboard species pairs should be significantly larger than expected by chance. The C-score measures the tendency for species to not occur together. The larger the C-score, the less the average co-occurrence among species pairs. If a community is structured by competition, we would expect the C-score to be large relative to a randomly assembled community. To generate random matrixes, I applied the Sim9 algorithm, which uses fixed row and column sums (those of the original matrix) and which is recommended for these two indexes because it is less prone to Type I errors. For both indices, 5,000 null matrices were produced using the sequential swap algorithm. To explicitly include the effect of area and isolation, I incorporated as weights the ratio ''island area / island distance'' (with distance of Mt. Argentario set at 0.1). The underlying null model is an ''area-distance based random sampling'' model, in which islands represent ''targets'' of different areas placed at different distances, and species represent ''darts'' that are tossed randomly at the set of different targets. If islands passively intercept individual colonists of different species, each island behaves as a target, and its chances of getting hit are directly proportional to its area and inversely to its distance from the mainland source.

RESULTS

Influence of Recent and Pleistocene Factors on Species Richness.—Reptile species richness was positively correlated with Recent island area ($G = 0.714$, $P = 0.032$) and Pleistocene island area ($G = 0.889$, $P = 0.016$), and negatively with Recent isolation ($G = -0.714$, $P = 0.032$), Pleistocene isolation ($G = -1.000$, $P = 0.008$), and Pleistocene distance to Tuscany ($G = -1.000$, $P = 0.008$). When possibly introduced species were omitted, significant correlations were found with Pleistocene area ($G = 0.867$, $P = 0.034$), Pleistocene isolation ($G = -1.000$, $P = 0.033$), Pleistocene distance to Tuscany ($G = -1.000$, $P = 0.033$), as well as with Recent isolation ($G = -0.778$, $P = 0.031$) and Recent distance to Tuscany ($G = -1.000$, $P = 0.037$).

To take into account a possible bias in species richness for the fossil island of Mt. Argentario, which is currently connected with the mainland, the last analysis was repeated omitting Mt. Argentario singletons. In this case, species richness resulted correlated with Pleistocene area ($G = 1.000$, $P = 0.014$), Pleistocene isolation ($G = -1.000$, $P = 0.033$), and Pleistocene distance to Tuscany ($G = -1.000$, $P = 0.033$).

Using a power function to model SARs, Recent island area explained a good proportion of variance ($S = 3.049A^{0.263}$, $R^2 = 0.766$). Analysis of residuals showed that all residuals were low, with Pianosa having a residual of about 0.37. When Pleistocene area is used, the SAR was less adequately fitted ($S = 1.1916A^{0.242}$, $R^2 = 0.566$).

When possibly introduced species were omitted, Recent island area still explained a relatively good proportion of variance ($S = 1.200A^{0.376}$, $R^2 = 0.620$). Residuals were generally low, with Pianosa having a residual of 0.12. When Pleistocene area is used, the SAR was poorly fitted ($S = 0.483\text{A}^{0.388}$, $R^2 = 0.472$).

Biogeographical Relationships among Islands.—The two matrices resulting from the different treatment of possibly introduced populations gave partially similar results (Fig. 2A, B). Cluster analysis under different treatments for doubtfully native occurrences grouped islands in accordance with their position in the NMDS, and the resulting patterns may be simply explained by species richness (Fig. 2C, D). However, the NMDS plot obtained omitting doubtfully native occurrences indicates a paleogeographical trend along Axis 1 for land-bridge islands (Pianosa, Elba and Mt. Argentario).

Influence of Recent and Pleistocene Factors on Biogeographical Patterns.—Reptile island dissimilarities calculated omitting possibly introduced taxa were negatively correlated with recent distances to Corsardinia and Tuscany ($r = -0.365$, $P = 0.035$), whereas no significant correlation was found when all occurrences were considered.

Species Interactions.—Using all occurrences and including the area : distance ratio as a probability constraint, the observed C-score (0.374) was significantly higher than the value expected by chance (0.074 [± 0.065 SD]), suggesting a negative pattern of species co-occurrence (P [Observed ≥ Expected] = 0.001). Under the same conditions, the total number of checkerboards (10) was also significantly higher (P [Observed ≥ Expected] = 0.001) than the value expected by chance (0.412 [± 1.240 SD]). When possibly introduced populations were omitted, neither the C-index nor the number of checkerboard pairs was significantly different from the values expected by chance.

DISCUSSION

A positive SAR is an obvious result because species richness tends to increase at larger areas (Fattorini, 2007a). A significant SAR may result from both current immigration/extinction processes (as postulated by dynamic models based on current geography and ecology) and historical processes consisting of island saturation during land-bridge connections with the mainland followed by extensive extinctions when the islands were disconnected and their area and habitats were consequentially reduced (faunal relaxation after saturation) (Fattorini, 2007b). If current immigration is a key factor in determining species richness on islands, a negative correlation with current isolation is expected (Fattorini, 2002b). For the reptiles of the Tuscan Islands, species richness was actually correlated with current isolation but even tightly with

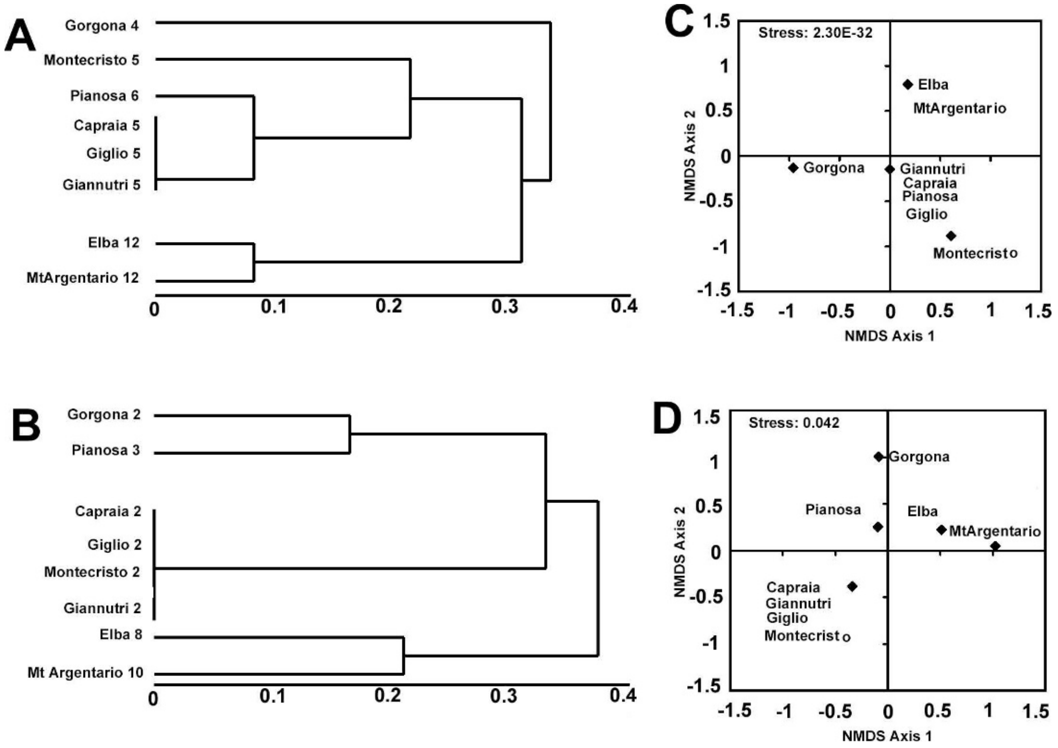

FIG. 2. Cluster analyses (A and B) and Non-Metric Multidimensional Scaling (NMDS) plots (C and D) based on Kulczynski 2 dissimilarities, showing patterns of reptile biogeographical relationships among the Tuscan Islands, assuming all populations as native (A and C) and removing all occurrences suspected to be recent introductions (B and D). Numbers after island names indicate species richness.

Pleistocene isolation. However, Pianosa does not show a large residual, as expected if paleogeography still determines species richness. This suggests that relaxation operated for a time sufficient to equilibrate the faunas, as evidenced by the high proportion of variance explained by the power function model. Hence, although reptile colonization likely occurred via land bridges for islands that were connected to the mainland in the Pleistocene, a long time relaxation equilibrated the faunas according to island area, leading to a significant relationship of species richness with current island area and isolation. In fact, when species occurrences suspected to be caused by human introductions were omitted, correlations increased, thus supporting a Pleistocene colonization followed by human-aided colonization. In particular, a negative correlation with Pleistocene distance to Tuscany (coupled with the lack of correlation with distance to Corsardinia) indicates that colonization occurred from Tuscany.

Current biogeographical similarity patterns do not fit either Pleistocene or Recent geography but simply reflect gradients in species richness. This suggests a random colonization and does strongly contrast with biogeographical patterns found in other groups, such as tenebrionid coleopterans, chrysidid hymenopterans, and butterflies, which have transitional faunas, with several species that colonized various islands from Corsardinia (Fattorini, 2009a).

In fact, in other animal groups, such as tenebrionids, chrysidids, and butterflies, it was possible to distinguish between Sardo-Corsican species (i.e., species occurring in both Corsardinia and the Tuscan Archipelago but not in Tuscany) and the Tuscan species (i.e., species occurring in both Tuscany and the Tuscan Archipelago but not in Corsardinia). For reptiles, there are no Sardo-Corsican species; thus, it is obvious that biogeographical similarities do not show a twofold colonization process.

Also, Mantel tests indicated that, rather surprisingly, biogeographical similarities among islands increased for islands located farther from Corsica and Tuscany. This result can be explained by assuming that, for remote islands, interisland faunal exchanges (favored by stepping-stone dispersal or interisland land-bridge connections) occurred more frequently than mainland-island colonization.

Thus, it appears that Pleistocene geography had an important role in determining island colonization (as shown by strong influence of Pleistocene geography on species richness), possibly superior to current immigration (as shown by the inverse correlation between biogeographical patterns and distance from Tuscany and Corsardinia) but that relaxation after saturation led the system to a virtually complete equilibration (as shown by the excellent fit of the SAR for the data set including possibly nonnative populations and the influence of species richness in determining island similarities), which mostly erased the Pleistocene influence. Now, the question is which mechanisms regulated the relaxation process.

Co-occurrence analyses using all occurrences indicated mutually exclusive distributions of reptile species, whereas a random pattern of co-occurrence was found omitting possibly introduced populations. These results suggest that the time elapsed since post-Pleistocene disconnection may have reshaped biogeographical similarities by an increase in competition, likely because of reduction in island areas. The model postulated here is that land-bridge islands were largely colonized (and possibly saturated) by reptiles during the Pleistocene island connections with the mainland and that there have been extensive extinctions drawn by competition when islands were disconnected as a result of area and, hence, habitat loss. However, this process of faunal impoverishment was contrasted by man, who imported accidentally (or not, as in the case of tortoises), sometimes successfully, sometimes not, many taxa, and this immigration was sometimes enough to balance depletion of island populations.

The nonrandom distribution of organisms with poor mobility should be carefully considered in conservation biogeography, because local species extinction is not easily compensated by present immigration (Fattorini, 2008a). Island populations of species with high dispersal power can be at least partially reconstituted by new immigrants from adjacent source areas. By contrast, depletion of island populations of reptiles, which have relatively low dispersal power, is hardly balanced by new immigrations from mainland populations, whereas human-assisted introduction may represent an additional serious threat for native species. At present, the most important influence of man on the Tuscan Islands is represented by tourism and associated threats. All islands are included in the Tuscan Archipelago National Park (although not the entire territory of Capraia, Giglio, and Elba is under protection). Accesses to Montecristo, Gorgona, and Pianosa are strictly regulated. However, other islands are subject to high tourism pressures, notably Elba and Giglio, which are leading tourist destinations. A serious consequence of mass tourism (and partly also of the so-called ecotourism) is the rapid degradation of fragile natural habitats, which are becoming more and more attractive to tourists just because of their increasing rarity. This led to high tourism pressure also on the island of Giannutri. Although most of the footways on this island are currently forbidden, this is not known by most tourists, who reach the island by ferry-boats and concentrate in the few accessible places. However, field research revealed that, in spite of the high tourist pressure on these islands, *Podarcis* populations of Giglio and Giannutri are characterized by very confident animals that frequently came near the researcher, thus suggesting that they are not severely disturbed by man. Also, on the island of Giglio, we were able to detect the occurrence of *Hierophis viridiflavus* (Campese, road to Vado dell'Allume), as well as a number of *P. sicula* (most of the island) and *Euleptes europaea* (Cannelle) (60% of species richness), in few hours of research. This suggests that populations are likely numerous, although literature data are usually relatively scarce and old (no detailed records of *E. europaea* were reported after 1982) (Balletto, 2005).

The influence of man on the reptiles of the Tuscan Archipelago in the past was particularly complex. Human activity probably affected the natural turnover of species assemblages by increasing extinction rates in the most anthropized islands and introducing some species, thus contributing to conceal the influence of historical factors on the current composition of island faunas. For example, the occurrence of *T. hermanni* on the islands of Elba, Capraia, Montecristo, and Pianosa is caused by introductions by man. The occurrence on Montecristo of *V. a. hugyi*, which is distributed in south Italy, instead of *V. a. francisciredi*, which occurs in Tuscany (as well as in other regions of northern and central Italy) is still puzzling. First, it is questioned whether vipers are present as the result of long-distance dispersal (e.g., by floating objects) or historical introduction by man. According to Barbanera et al. (2009), vipers were introduced in ancient times, when these snakes were thrown as weapons during attack to vessels coming from Africa and Sardinia to pirate the rich Etruscan towns. They were protected as commercial partners by Greeks, who established a military base on Montecristo Island. *Vipera aspis hugyi* specimens, carried by the ancient militia from *Magna Graecia* during centuries VIII to III BC could have originated the Montecristo population (Barbanera et al, 2009). Also, Zuffi and Bonnet

FIG. 3. *Euleptes europaea* under *Eucalyptus* bark on the Giglio Island.

(1999) put forth the hypothesis that competition molded the current distribution of the two subspecies. If in the past the two taxa had been in close proximity in southern Tuscany, a possible colonization from coastal populations would have been possible and *francisciredi* could have successively pushed *hugyi* southward.

Indeed, it is possible that a recent establishment of *V. aspis* in Montecristo and *P. sicula*, *T. mauritanica*, and *H. turcicus* in several islands contributed to the final structuring of reptile communities by increased competition. *Podarcis sicula* is known to be a superior competitor with respect to other native lizards (Capula, 1992); thus, it could be responsible for the absence of *P. muralis* from various islands. Lack of nonrandom patterns of species co-occurrence obtained when this species was omitted in tandem with *T. mauritanica* and *H. turcicus* from all islands, *V. aspis* from Montecristo, and *Z. longissimus* from Elba supports this hypothesis. However, especially for *P. sicula*, which occurs on the adjacent mainland with populations genetically close to those of the sampled islands (Capula, 1992), natural colonization cannot be excluded in favor of human introductions. Similarly, the recent colonization of the geckos *T. mauritanica* and *H. turcicus*, possibly introduced by humans, could have been responsible for the current absence of *E. europaea* from Gorgona. In continental France, *E. europaea* seems present only in places at higher altitude where *T. mauritanica* and *H. turcicus* are absent (Renet et al., 2008). It might be postulated that *E. europaea* was originally present on Gorgona and that it disappeared on this very small and rather flat island because of competition with *T. mauritanica* and *H. turcicus*.

Finally, the occurrence of *Z. longissimus* on Elba has been long disputed. The species was not found after a first record in 1954, which was considered very doubtful, until 2002 (Vaccaro and Turrisi, 2007). Rarity of *Z. longissimus* on Elba has been attributed to habitat degradation and loss (in particular, reduction of oak forests), but it cannot be excluded that the species has been imported (Vaccaro and Turrisi, 2007). Lack of records of this snake for a long time may also suggest repeated introductions.

The continued influence of mankind on the Tuscan Islands shaped so profoundly the natural environment that unnatural habitats may be also of conservation value for reptiles, such as old constructions that offer shelter for various species. This is also the case of *Eucalyptus* trees that have been frequently planted as ornamental plants. Eucalypts shed their bark regularly. If the outer part of the bark is completely shed but not completely detached from the trunk (a condition found in a great number of eucalypt species), the shedding process provides suitable resting places for a number of animals (Fattorini, 2008b). A survey on the Island of Giglio in summer 2008 revealed that these trees now play an important role in reptile conservation providing refuge for *E. europaea*, which finds shelter under their bark (Fig. 3). Thus, although conservation and restoration plans usually include the extirpation of introduced plants and removal of human-made habitats, before this happens it should be necessary to evaluate the implications on conservation of animals that appear to rely on older established exotics or other anthropogenic habitats.

Acknowledgments.—I wish to express my gratitude to my wife Federica for her assistance in the field, to L. Dapporto for continued discussions on the biogeography of the Tuscan Islands, and to T. M. Doan, R. Sindaco, A. Venchi, and M. A. L. Zuffi for critical comments on a first draft of this paper.

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Accepted: 22 October 2009.