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Analysing the importance of stepping-stone islands in maintaining structural connectivity and endemicity

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We analysed the species–area relationship and structural connectivity among islands of La Maddalena Archipelago (Italy), a numerous group of small islands very close to Sardinia. We related species richness (amphibians and reptiles) to several environmental factors (area; number of unique habitats; topographical variables; and distances of each island to Sardinia, to the nearest island and to the nearest large island) using generalized additive models and connectivity analysis by graph theory and the software Conefor 2.6. Using each method, we performed several comparisons: considering all species; excluding species with a high exchange rate ('in transit'); including only autochthonous species; and including species present on large islands. We also excluded, in turn, all amphibians; all Scincidae; all Gekkonidae; all Lacertidae; all Colubridae; and one species in turn. Except in the case of species present on large islands, all models selected the same variables: ruggedness standard deviation, area, number of unique habitats, and mean and maximal elevation. When excluding Sardinia, the highest connectivity value corresponded to the largest islands. Species richness is related to island complexity (habitat diversity and topographical complexity) and not simply to area. Network connectivity is dominated by the internal connectivity of the largest islands, but small islands are essential to maintain the network connectivity and endemicity.

ADDITIONAL KEYWORDS: Conefor – connectivity analyses – generalized additive model – herpetofauna – islands – Mediterranean.

INTRODUCTION

The species richness of an island is determined by immigration and extinction rates, which are a function of the distance to a source of colonists from the mainland or other islands (MacArthur & Wilson, 1967); therefore, more isolated islands have a lower probability of receiving immigrants than less isolated islands, in consequence increasing the extinction rate. Hence, a population suffering a massive extinction event on an isolated island will recover with more difficulty owing to the low immigration rate. The number of species that an island can receive (immigration) and lose (extinction) is affected by island size. Small islands, supporting small populations, are more prone to lose species than larger ones, especially if population fluctuations increase with time. This relationship is indirect and depends mainly on the complexity of the islands. In general, larger islands have a more complex topography (with numerous microclimates, habitats and soil types), and thus can host more species. At the same time, larger habitats reduce the probability of extinction as a result of chance events.

In many studies, the factors that drive species richness on islands have been analysed by considering different groups of flora and fauna (Russell, Clout & McArdle, 2004; Okie & Brown, 2009; Triantis & Sfenthourakis, 2012). The fumigation of the mangrove islands of the Florida Keys to clear the arthropod communities showed that islands closer to the mainland recovered their original species richness faster (Simberloff & Wilson, 1969). In general, species richness does not depend exclusively on island size, but the relationship is additive to

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*Corresponding author. E-mail: neftali.sillero@gmail.com climate and isolation variables (Kalmar & Currie, 2006). Although nowadays the accuracy in measuring the surface of an island is greater, a better relationship is not achieved by considering island size alone (Triantis *et al.*, 2008); better results are obtained when variables such as habitat heterogeneity are added. Other variables can be the distance to the continent, degree of isolation (distance to the nearest island and/or mainland), island age, initial plant and animal composition, ocean currents and, of course, human activity. In fact, the species composition of many islands has been modified by humans, for instance by the introduction of new species. This has happened on many Mediterranean islands (Corti *et al.*, 1999a, b; Ficetola, Thuiller & Padoa-Shioppa, 2009; Stuckas *et al.*, 2011), where conservation measures are essential because these islands host many endemic species (Corti *et al.*, 1999a, b).

The study case we describe here deals with a group of numerous small islands belonging to the La Maddalena Archipelago near the large island of Sardinia, Italy. The Archipelago hosts 17 species: three amphibians and 14 reptiles (Table 1). Our objective was twofold: we aimed to test the species–area relationship and to analyse connectivity among islands. Specifically, we wanted to analyse whether area or other environmental factors are driving the species richness of amphibians and reptiles in the La Maddalena system and to identify the islands that promote migration within the system. We tested the relationship of species richness with several environmental factors through generalized additive models (GAMs) and connectivity analysis using graph theory and the software Conefor 2.6.

MATERIAL AND METHODS

Study area

La Maddalena Archipelago (Sardinia, Italy), situated in the Strait of Bonifacio, between Corsica and northeast Sardinia, comprises seven main islands (La Maddalena, Caprera, Spargi, Santo Stefano, Santa Maria, Budelli and Razzoli; with surfaces ranging from 1.673 to 20.116 km^2) and > 50 islets and rocks. The current arrangement of the Archipelago can be traced back to the last glacial maximum, ~18 000 years ago, and to the subsequent eustatic changes in sea level. The islands belonging to La Maddalena Archipelago derive from the Sardinian–Corsican Massif fragmentation, which occurred during the Miocene, with the separation of the two main islands and the origin of the Strait of Bonifacio (Cesaraccio, 1990).

The hydrographic network of the Archipelago is extremely reduced and mainly dependent on rainfall. Watercourses, with torrential regimes (and artificial basins), are present on La Maddalena and Caprera islands; small coastal wetlands are also present on some of the biggest islands. Average annual precipitation ranges between 600 and 700 mm, and the average annual temperature is ~17 °C; dominant and rough winds blow from the west (Bocchieri 1992).

For further information about geological and botanical features of the Archipelago see, for example, Bocchieri (1992), Biondi & Bagella (2005) and Ulzega (1996).

Table 1. List of amphibian and reptile species occurring on La Maddalena islands (Sardinia, Italy)

Type	Family	Species
Amphibians	Discoglossidae	*Discoglossus sardus* Tschudi in Otth, 1837
	Bufonidae	*Bufo balearicus* Boettger, 1880
	Hylidae	*Hyla sarda* (De Betta, 1857)
Reptiles	Emydidae	*Emys orbicularis* (Linnaeus, 1758)
	Testudinidae	*Testudo hermanni* Gmelin, 1789
	Testudinidae	*Testudo marginata* Schoepff, 1792
	Gekkonidae	*Euleptes europaea* (Gené, 1839)
	Gekkonidae	*Hemidactylus turcicus* (Linnaeus, 1758)
	Gekkonidae	*Tarentola mauritanica* (Linnaeus, 1758)
	Lacertidae	*Algyroides fitzingeri* (Wiegmann, 1834)
	Lacertidae	*Archaeolacerta bedriagae* (Camerano, 1885)
	Lacertidae	*Podarcis siculus* (Rafinesque, 1810)
	Lacertidae	*Podarcis tiliguerta* (Gmelin, 1789)
	Scincidae	*Chalcides chalcides* (Linnaeus, 1758)
	Scincidae	*Chalcides ocellatus* (Forskål, 1775)
	Colubridae	*Hierophis viridiflavus* (Lacépède, 1789)
	Colubridae	*Natrix maura* (Linnaeus, 1758)

Sampling methods

Sampling surveys on 51 islands, islets and rocks were carried out mainly in spring and late summer in 2011, 2012 and 2014. We aimed at: (1) updating the checklist of reptile species on those islands for which previous data were available; and (2) gathering data on the presence of species on those islets for which no data were available. The updated information on the herpetofauna of the Archipelago after the surveys performed in 2011–2012 is reported by Corti *et al.* (2014). In 2014, the surveys confirmed the results obtained in 2011–2012 on 12 islands and islets. We used the visual encounter survey technique (Crump & Scott, 1994), along transects or during free search (also looking under rocks and vegetation and inside rock crevices), depending on environmental features. The smallest islets and the rocks were searched entirely, whereas on bigger islands we performed multiple surveys in different habitats. To identify the presence of some species, such as *Euleptes europaea* (Gené, 1839), which is particularly elusive and with mainly nocturnal habits, we searched and identified faecal pellets, typically deposited on rocks and inside crevices. We also performed nocturnal surveys on some islands.

We also considered bibliographical data derived from investigations carried out in the 1980s (Lanza, 1983a, b; Cesaraccio & Lanza, 1984; Lanza, Cesaraccio & Malenotti, 1984; Borri *et al.*, 1988) and summarized by Poggesi *et al.* (1996) and Corti, Lo Cascio & Razzetti (2006). Corti *et al.* (2014) reported an update of information on the herpetofauna of the Archipelago.

Environmental data

We considered only those environmental data with enough variability in the Archipelago. Therefore, we excluded climatic variables because all the islands have a similar climate, owing to their small size. We used the following environmental variables to characterize the islands of the Archipelago: area (calculated using GIS layers provided by the La Maddalena Archipelago National Park); islands' centroids (x and y coordinates); number of unique habitats (calculated using the CORINE dataset from the European Environmental Agency); topographical variables (obtained from the ASTER Global Digital Elevation Model: mean, maximum and SD of elevation, and mean, maximum and SD of ruggedness index). In addition to these variables, we calculated the distance of each island to Sardinia, to the nearest island and to the nearest big island (La Maddalena, Caprera, Spargi, Santo Stefano, Santa Maria, Budelli and Razzoli islands; Fig. 1). All procedures were performed with the software QGIS 2.18.

Statistical analysis

We analysed the relationships among the species richness, environmental and distance variables of islands using three different methods: Spearman's correlation, GAMs and connectivity analysis. Each method was performed through several comparisons: considering all species (Table 1); excluding species 'in transit' (those species with a high exchange rate), namely *Chalcides ocellatus*, *Podarcis siculus* and *Hierophis viridiflavus*; including only autochthonous/endemic Sauria species (from less to more complex habitats: *E. europaea*, *Podarcis tiliguerta*, *Archaeolacerta bedriagae* and *Algyroides fitzingeri*); and including species present on island types A (size ≤ 10 000 m^2), B (size ≤ 100 000 m^2) and C (size ≤ 1 000 000 m^2) following Poggesi *et al.* (1996). La Maddalena Islands were classified into five categories depending on size, from A (smallest area) to E (largest area) (Poggesi *et al.*, 1996). In addition to these comparisons, we excluded, in turn, all amphibians (*Discoglossus sardus*, *Bufo balearicus* and *Hyla sarda*); all Scincidae (*Chalcides chalcides* and *C. ocellatus*); all Gekkonidae (*E. europaea*, *Hemidactylus turcicus* and *Tarentola mauritanica*); the four Lacertidae (*A. fitzingeri*, *A. bedriagae*, *Podarcis siculus* and *P. tiliguerta*); all Colubridae (*H. viridiflavus* and *Natrix maura*); and the following species in turn: *Hyla sarda*, *E. europaea*, *Tarentola mauritanica*, *C. ocellatus*, *H. viridiflavus*, *Podarcis siculus* and *P. tiliguerta*. When excluding one species in turn we did not consider the following species owing to their very low sample size: *Discoglossus sardus* (2), *Bufo balearicus* (2), *A. fitzingeri* (3), *A. bedriagae* (3), *C. chalcides* (1), *Hemidactylus turcicus* (3), *Natrix maura* (3) and *Testudo marginata* (2). *Emys orbicularis* and *Testudo hermanni* were not sighted during fieldwork surveys. These analyses provided information on different connectivity patterns attributable to taxonomical or guild groups; species groups are not equally affected by the same variables (Russell *et al.*, 2004; Kalmar & Currie, 2006; Triantis *et al.*, 2008; Okie & Brown, 2009; Triantis & Sfenthourakis, 2012).

For each comparison, we measured the importance of each environmental variable to the species richness by non-parametric Spearman's correlation. We wanted to know whether correlation values for each variable changed along the comparisons. We used non-parametric GAM to analyse the relationship of species richness with the environmental variables, after rejecting normality. The GAM is a generalized linear model in which the linear predictor depends in a linear manner on unknown smooth functions of some predictor variables, and interest focuses on inference about these smooth functions. The model relates a univariate response variable, Y, to some predictor variables, X_i. An exponential family distribution is specified for

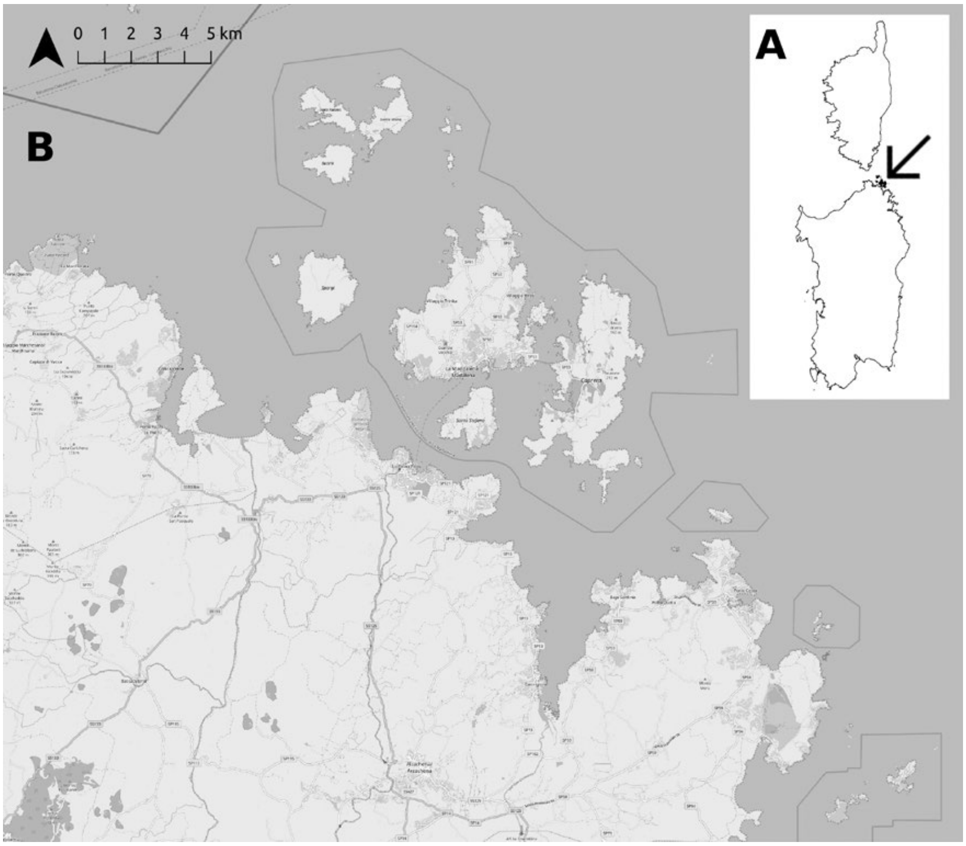


Figure 1. A, location (Sardinia, Italy). B, map of La Maddalena Archipelago.

Y (in this case, Poisson distributions because variable Y is species richness) along with a link function, g (for example, the identity or log functions), relating the expected value of Y to the predictor variables. Generalized additive model analyses were performed with a stepwise process. The correlation matrix and GAM analysis were performed using R software.

CONNECTIVITY ANALYSIS

Graph theory is the study of 'graphs', mathematical structures composed of nodes (or vertices) and links (lines or edges) in order to model pairwise relationships between objects (Saura & Torné, 2009). Nodes are characterized by an attribute (e.g. area, habitat suitability) and links by Euclidean or environmental distance. Therefore, graph theory considers functional connectivity by using dispersal distances and the behavioural response of individuals or species to the physical structure of the landscape, and not only the spatial arrangement of the habitat (structural connectivity or topology). A graph may be undirected, meaning that there is no distinction between the two vertices associated with each edge, or its edges may be directed from one vertex to another.

We performed a connectivity analysis using the freeware Conefor 2.7.1 by command line (Saura & Torné, 2012) and the authors' recommended probability connectivity (PC) index (Saura & Pascual-Hortal, 2007). Conefor works exclusively with symmetrical relationships, thus without distinction on the connecting direction. We considered the islands as nodes (the elements hosting suitable habitats where species can establish populations) and the sea among islands as links (without suitable habitats and thus species populations). Therefore, species dispersion occurs among nodes through links. We characterized nodes (islands) with area size and links (sea) with the Euclidean distance among islands. We performed the analysis two times, including and excluding Sardinia, in order to understand connectivity patterns inside La Maddalena Archipelago. This approach classifies the islands as connected or not, with regard to a distance threshold (i.e. dispersal capacity of the animals), which has to be defined previously. Information about dispersal ability of the Italian amphibians and reptiles is limited, and almost non-existent about sea dispersal events. In the case of studies about dispersion in terrestrial environments in Central Europe, dispersal distance is very variable among species (Kovar *et al.*, 2009). Thus, we established several thresholds from 500 to 9000 m with increments of 500 m. For each distance threshold, we calculated the overall value of connectivity of the entire network and used this value as a reference for the following steps. Subsequently, we applied a jackknife analysis, removing one island at the time from the analysis and recalculating the overall value of connectivity for the study area. The more the removed islands lowered the overall value, the greater was its importance for the connectivity of the landscape. We used the difference between the overall value for the entire network of islands and the same value for the Archipelago missing one of the islands. The higher the value of dPC, the higher the importance of the deleted node (island):

$$\mathrm{dPC} = \mathrm{PC}_{\text{entire network}} - \mathrm{PC}_{\text{network node } x}$$

The importance values of the PC index can be partitioned in three different fractions (intra, flux and connector) considering how a particular element, k (node or link), contributes to the overall connectivity (Saura & Rubio, 2010):

$$\mathrm{dPC}_k = \mathrm{dPCintra}_k + \mathrm{dPCflux}_k + \mathrm{dPCconnector}_k$$

The $\mathrm{dPCintra}_k$ is the intra-patch connectivity contribution of the patch k, i.e. the internal connectivity of the patch k, dependent on the available habitat area (or any other patch attribute). Links do not contribute to this fraction, as they contain no habitat. Therefore, $\mathrm{dPCintra}_k$ does not depend on patch k connectivity to other patches or dispersal distance of the focal species; $\mathrm{dPCintra}_k$ is the same whenever patch k is completely isolated or not. The $\mathrm{dPCflux}_k$ is the flux of dispersion, starting or ending on patch k, to all the rest of connected patches. The $\mathrm{dPCflux}_k$ depends on the patch attribute (e.g. area) and on the patch position within the network. Thus, the higher the patch attribute, the higher the flux value. As in the previous fraction $\mathrm{dPCintra}_k$, links do not contribute through this fraction because they contain no habitat and, consequently, there is no flux within links. The $\mathrm{dPCflux}_k$ measures dispersion through patch k but not its importance in maintaining connectivity among patches. This is measured by $\mathrm{dPCconnector}_k$, i.e. the contribution of patch or link k (as a connecting element or a stepping stone) to the connectivity among patches. Therefore, $\mathrm{dPCconnector}_k$ depends only on the topological position of patch or link k in the network and not on patch attribute (e.g. area). In conclusion, dPC of patch k will be higher or lower depending on its attribute and topological position within the network. When patch k is completely isolated, it will contribute to dPC_k through $\mathrm{dPCintra}_k$. When patch k is connected to other patches, it will contribute to dPC_k through $\mathrm{dPCintra}_k$ and $\mathrm{dPCflux}_k$, but also through $\mathrm{dPCconnector}_k$, depending on its topological position. Thus, we analysed the contribution of these three fractions to the overall connectivity (dPC) for each island of La Maddalena Archipelago.

In addition to the PC index, we used also the betweenness centrality (BC) index, which measures the frequency with which a patch falls between other pairs of patches in the network (Saura & Rubio, 2010). The BC index is calculated by finding the shortest paths between every pair of patches in the network and then counting the number of times those paths cross each node (Saura & Rubio, 2010).

RESULTS

SPECIES RICHNESS AND COMPOSITION

Seventeen species are present on the islands of La Maddalena Archipelago: three amphibians and 14 reptiles (Table 1). The islands with the highest number of species are La Maddalena Island (17) and Caprera Island (16; Supporting Information, Table S1; Fig. 1). The most common species are *E. europaea* and *P. tiliguerta*. There are 11 islands with no species, and 17 with one or two species (Supporting Information, Table S1; Fig. 1).

CORRELATIONS

Almost all correlations among species richness and the environmental variables showed the same pattern (Table 2); the most correlated variables were the number of unique habitats, as well as maximal and SD elevation. There were three exceptions: the comparison without species 'in transit'; with only autochthonous species; and with species present on islands of type A, B and C. In the first case, the most important variable was the number of unique habitats, followed by area and maximal elevation; in the second case, the most important variables were mean and SD elevation; and in the third case, the most important variables were the number of unique habitats and the area.

GENERALIZED ADDITIVE MODELS

The pattern in the GAM results was also similar among comparisons. Except in the case of species present on islands of type A, B and C, all models selected the same variables (Table 3): SD of ruggedness, area, number of unique habitats, and mean and maximal elevation. The model for the number of autochthonous species selected only three (SD of ruggedness, area and number of unique habitats) of these five variables, but only SD of ruggedness was significant. For

Table 2. Spearman correlation results among species richness and environmental variables per species group comparison: including all species; excluding all amphibians (*Discoglossus sardus*, *Bufo balearicus* and *Hyla sarda*); excluding all Scincidae (*Chalcides chalcides* and *Chalcides ocellatus*); excluding all Gekkonidae (*Euleptes europaea*, *Hemidactylus turcicus* and *Tarentola mauritanica*); excluding all Lacertidae (*Algyroides fitzingeri*, *Archaeolacerta bedriagae*, *Podarcis siculus* and *Podarcis tiliguerta*); excluding all Colubridae (*Hierophis viridiflavus* and *Natrix maura*); excluding one species in turn; excluding species 'in transit' (*C. ocellatus*, *P. siculus* and *H. viridiflavus*); including only autochthonous species (*E. europaea*, *P. tiliguerta*, *A. bedriagae* and *A. fitzingeri*); and including species with presence in island types A, B and C (smallest islands)

Comparison	Number of unique habitats	Maximal elevation	SD of elevation	Mean elevation	Area	Maximal ruggedness	Mean ruggedness	SD of ruggedness	*X*	*Y*	Distance to islands	Distance to big island	Distance to Sardinia
All species	**0.91**	**0.85**	**0.85**	0.83	0.80	0.75	0.65	0.63	−0.04	−0.02	−0.09	−0.13	−0.35
No Amphibians	**0.90**	**0.83**	**0.83**	0.81	0.78	0.75	0.65	0.63	−0.01	−0.04	−0.10	−0.11	−0.36
No Scincidae	**0.91**	**0.85**	**0.85**	0.83	0.80	0.74	0.63	0.61	−0.06	0.01	−0.10	−0.16	−0.34
No Gekkonidae	**0.92**	**0.87**	**0.86**	0.85	0.82	0.77	0.66	0.63	−0.02	−0.03	−0.10	−0.12	−0.36
No Lacertidae	**0.93**	**0.86**	**0.86**	0.83	0.83	0.75	0.64	0.62	−0.03	−0.02	−0.08	−0.11	−0.35
No Colubridae	**0.91**	**0.85**	**0.84**	0.83	0.80	0.74	0.64	0.60	−0.04	−0.02	−0.08	−0.14	−0.37
No species 'in transit'	**0.94**	**0.86**	0.85	0.83	**0.87**	0.72	0.58	0.54	−0.09	0.04	−0.07	−0.17	−0.33
Autochthonous species	0.68	0.68	**0.69**	**0.70**	0.53	0.64	0.61	0.59	−0.06	−0.02	−0.06	−0.14	−0.33
Islands A, B, C	**0.75**	0.29	0.30	0.32	**0.65**	0.30	0.33	0.35	0.20	−0.20	−0.07	0.07	−0.21
No *D. sardus*	**0.90**	**0.84**	**0.84**	0.82	0.78	0.75	0.65	0.62	−0.03	−0.02	−0.10	−0.12	−0.35
No *B. balearicus*	**0.91**	**0.85**	**0.85**	0.83	0.81	0.75	0.65	0.62	−0.02	−0.03	−0.09	−0.12	−0.37
No *H. sarda*	**0.91**	**0.85**	**0.85**	0.83	0.80	0.76	0.66	0.63	−0.03	−0.02	−0.09	−0.12	−0.35
No *T. hermanni*	**0.91**	**0.85**	**0.85**	0.84	0.79	0.76	0.66	0.63	−0.04	−0.02	−0.09	−0.12	−0.35
No *T. marginata*	**0.91**	**0.85**	**0.85**	0.84	0.79	0.75	0.66	0.63	−0.03	−0.02	−0.09	−0.12	−0.36
No *E. europaea*	**0.93**	**0.87**	**0.86**	0.85	0.82	0.76	0.65	0.62	−0.04	−0.01	−0.10	−0.13	−0.35
No *H. turcicus*	**0.91**	**0.85**	**0.85**	0.84	0.79	0.76	0.66	0.63	−0.04	−0.02	−0.09	−0.12	−0.35
No *T. mauritanica*	**0.92**	**0.85**	**0.85**	0.83	0.81	0.75	0.65	0.63	−0.02	−0.03	−0.09	−0.12	−0.36
No *A. fitzingeri*	**0.91**	**0.84**	**0.84**	0.82	0.80	0.75	0.65	0.62	−0.03	−0.02	−0.10	−0.12	−0.35
No *A. bedriagae*	**0.92**	**0.85**	**0.85**	0.83	0.81	0.75	0.65	0.62	−0.02	−0.03	−0.09	−0.12	−0.36
No *P. siculus*	**0.90**	**0.85**	**0.85**	0.84	0.79	0.76	0.66	0.63	−0.04	−0.01	−0.09	−0.12	−0.35
No *P. tiliguerta*	**0.93**	**0.87**	**0.87**	0.85	0.83	0.76	0.65	0.61	−0.05	0.00	−0.08	−0.13	−0.34
No *C. ocellatus*	**0.92**	**0.86**	**0.85**	0.83	0.82	0.75	0.63	0.60	−0.07	0.02	−0.09	−0.15	−0.33
No *H. viridiflavus*	**0.92**	**0.85**	**0.85**	0.83	0.82	0.74	0.63	0.59	−0.04	−0.02	−0.08	−0.14	−0.37

Bold numbers indicate the variables (two or three when tied) with the highest correlation values.

Table 3. Generalized additive model results *P*-values among species richness and environmental variables per species group comparison: including all species; excluding all amphibians (*Discoglossus sardus*, *Bufo balearicus* and *Hyla sarda*); excluding all Scincidae (*Chalcides chalcides* and *Chalcides ocellatus*); excluding all Gekkonidae (*Euleptes europaea*, *Hemidactylus turcicus* and *Tarentola mauritanica*); excluding all Lacertidae (*Algyroides fitzingeri*, *Archaeolacerta bedriagae*, *Podarcis siculus* and *Podarcis tiliguerta*); excluding all Colubridae (*Hierophis viridiflavus* and *Natrix maura*); excluding one species in turn; excluding species 'in transit' (*C. ocellatus*, *P. siculus* and *H. viridiflavus*); including only autochthonous species (*E. europaea*, *P. tiliguerta*, *A. bedriagae* and *A. fitzingeri*); and including species with presence on island types A, B and C (smallest islands)

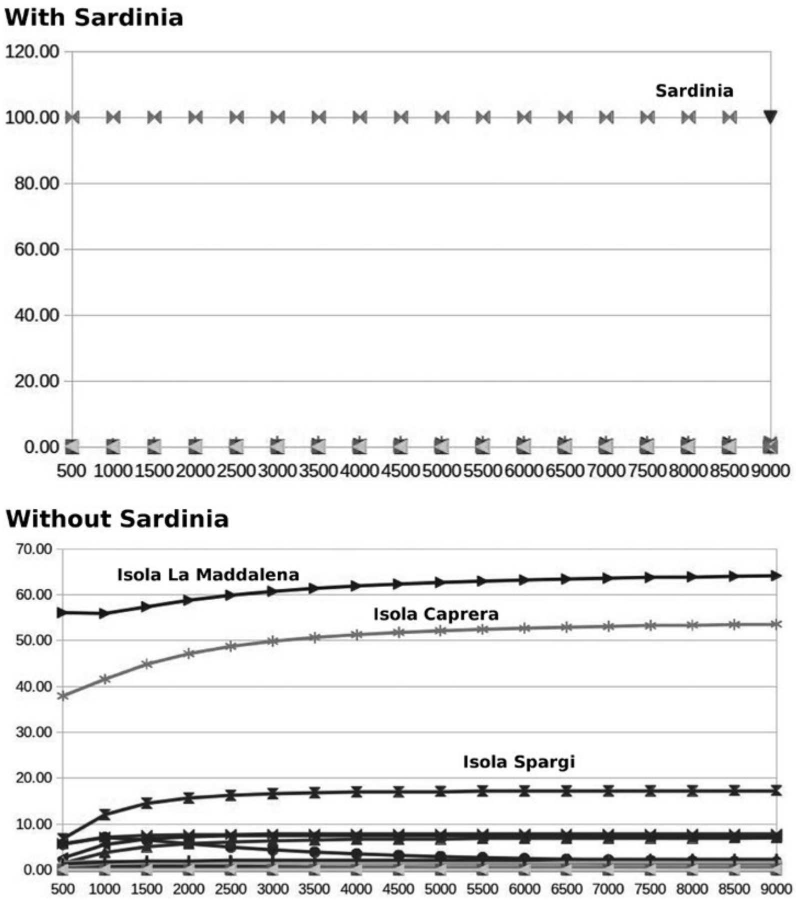
Comparison	SD of ruggedness	Area	Number of unique habitats	Maximum elevation	Mean elevation
All species	0.0001	0.0001	0.0001	0.8527	0.0002
No amphibians	0.0001	0.0001	0.0001	0.5039	0.0018
No Scincidae	0.0001	0.0001	0.0001	0.8800	0.0001
No Gekkonidae	0.0001	0.0001	0.0001	0.6296	0.0003
No Lacertidae	0.0001	0.0001	0.0001	0.6752	0.0001
No Colubridae	0.0001	0.0001	0.0001	0.8200	0.0001
No species 'in transit'	0.0001	0.0001	0.0001	0.4600	0.0001
Autochthonous species	0.0001	0.0517	0.0049	–	–
No *D. sardus*	0.0001	0.0001	0.0001	0.6924	0.0002
No *B. balearicus*	0.0001	0.0001	0.0001	0.8314	0.0005
No *H. sarda*	0.0001	0.0001	0.0001	0.6993	0.0004
No *T. hermanni*	0.0001	0.0001	0.0001	0.8681	0.0003
No *T. marginata*	0.0001	0.0001	0.0001	0.9334	0.0002
No *E. europaea*	0.0001	0.0001	0.0001	0.7400	0.0001
No *H. turcicus*	0.0001	0.0001	0.0001	0.8681	0.0003
No *T. mauritanica*	0.0001	0.0001	0.0001	0.6988	0.0005
No *A. fitzingeri*	0.0001	0.0001	0.0001	0.6389	0.0004
No *A. bedriagae*	0.0001	0.0001	0.0001	0.7547	0.0007
No *P. siculus*	0.0001	0.0001	0.0001	0.9594	0.0002
No *P. tiliguerta*	0.0001	0.0001	0.0001	0.9200	0.0001
No *C. ocellatus*	0.0001	0.0001	0.0001	0.9931	0.0001
No *H. viridiflavus*	0.0001	0.0001	0.0001	0.8800	0.0001
	SD of ruggedness	Area	Maximum elevation	Mean elevation	Maximum ruggedness
Islands A, B, C	0.0018	0.0001	0.0139	0.1330	0.0627

No variables related to distances to islands were selected in any model.

the species of island types A, B and C, the selected variables were the maximum and SD of ruggedness, area, and mean and maximal elevation (Table 3). The most important variables were SD of ruggedness, area and number of unique habitats, whereas mean and maximal elevation were not significant in the last step of GAM analyses, even in the case of species in island types A, B and C.

CONNECTIVITY ANALYSIS

Sardinia obtained the highest dPC value of the network when included in the analysis, with values close to 100% of possible maximum (Fig 2). When Sardinia was excluded from the analysis, the picture changed completely, and the highest dPC value corresponded to La Maddalena Island, followed by Caprera and Spargi islands (Fig. 2). Decomposition of dPC fractions for the entire Archipelago including Sardinia (Fig. 3) showed that connectivity was absolutely dominated by dPCintra, i.e. the internal connectivity of each island. When excluding Sardinia (Fig. 3), dPCintra was important until the distance threshold of 1000 m, and thereafter dPCflux (i.e. connectivity through islands) was the dominating fraction. In addition, from 1000 m on, dPCconnector (i.e. the contribution of each island to the connectivity among islands) decreased continuously. When analysing the dPC fractions for the islands (including Sardinia) with the highest contributions (Fig. 4), Sardinia contributed to dPCintra and dPCflux, whereas Caprera Island contributed to dPCconnector. When excluding Sardinia (Fig. 4),


With Sardinia

Without Sardinia

Figure 2. Conefor jackknife analysis of the connectivity index difference (dPC) between the overall value for the entire network of islands and the same value missing one of the islands. The dPC total values are represented by the entire network (with and without Sardinia) for each distance threshold considered (from 500 to 9000 m in increments of 500 m).

La Maddalena Island contributed to dPCintra and dPCflux; meanwhile, Scoglio 2 a Sud dell'Isolotto dei Paduleddi Settentrionale contributed to dPCconnector. In both cases (with and without Sardinia), trends of dPC fractions of islands with the highest contributions were similar to dPC fractions of the entire Archipelago (Fig. 4).

Regarding the BC index, Spargiotto Islet was the most important island when including Sardinia, and Scoglio 2 a Sud dell'Isolotto dei Paduleddi Settentrionale when excluding Sardinia.

DISCUSSION

Univariate and multivariate analyses identified the number of unique habitats and mean elevation, respectively, as the most important factors to explain the species richness across different species groups.

CORRELATIONS

Regarding species richness, island area showed a high correlation value in most of the comparisons performed. However, area was not the most important factor. The variables that were most highly correlated (and had high values) were the number of unique habitats, maximal elevation and SD of elevation. Only in the analyses excluding species 'in transit' and when including species present on islands of type A and B, C, area appeared as the second most important variable. Therefore, species richness is mainly influenced by the number of unique habitats, when considered independently from other factors. This relationship does not change among species groups, except for the number of autochthonous/endemic Saurian species. Indeed, the analysis excluding species 'in transit' presented the highest correlation value for the number of unique habitats (0.94), whereas the analyses including autochthonous/endemic Saurian species (0.68) and species present on islands of types A, B and C (0.75)

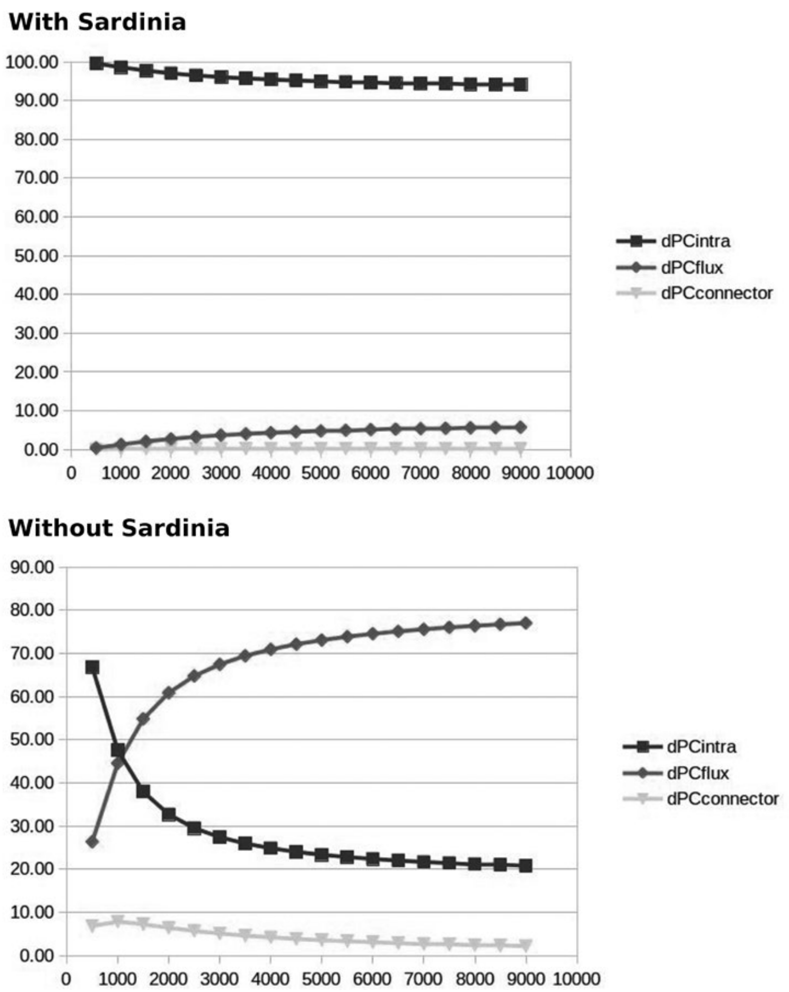


Figure 3. Partitioning of the importance values of dPC index into three fractions (dPCintra + cPCflux + dPCconnector) for the entire network (with and without Sardinia), represented as a percentage of the dPC total values (i.e. dPC values 100%). See main text for details.

yielded the lowest values (Table 2). The rest of the comparisons showed values between 0.91 and 0.93. Species 'in transit' and small islands (types A, B and C) are the elements that contribute to maintain the network connectivity and endemicity of the Archipelago as stepping stones (see connectivity analyses).

GENERALIZED ADDITIVE MODELS

The multivariate analyses performed by the GAMs showed slightly different results (Table 3). All comparisons selected the same variables, although the most important ones were the SD of ruggedness, area, number of unique habitats, and mean elevation. Maximal elevation was not significant in all models. The model for the number of autochthonous species selected only three variables (SD of ruggedness, area and number of unique habitats), but only SD of ruggedness was significant. However, even when the model for number of species present on islands of types A, B and C selected different variables (maximum and SD of ruggedness, area, and mean and maximal elevation), SD of ruggedness continued to represent the most important variable.

Other studies showed that area is not the only factor determining species richness (Triantis & Sfenthourakis, 2012); elevation, habitat diversity, climate and isolation are also of great importance (Russell *et al.*, 2004; Kalmar & Currie, 2006; Triantis *et al.*, 2008; Okie & Brown, 2009). However, better models can be obtained when including human-related variables (Ficetola & Padoa-Schioppa, 2009). All these variables are related to the complexity of islands (Triantis *et al.*, 2003, 2005). 'Simple' islands, with low elevation gradient and low habitat diversity, can host very few species. Thus, bigger islands, which are in general characterized by higher elevation and, consequently,

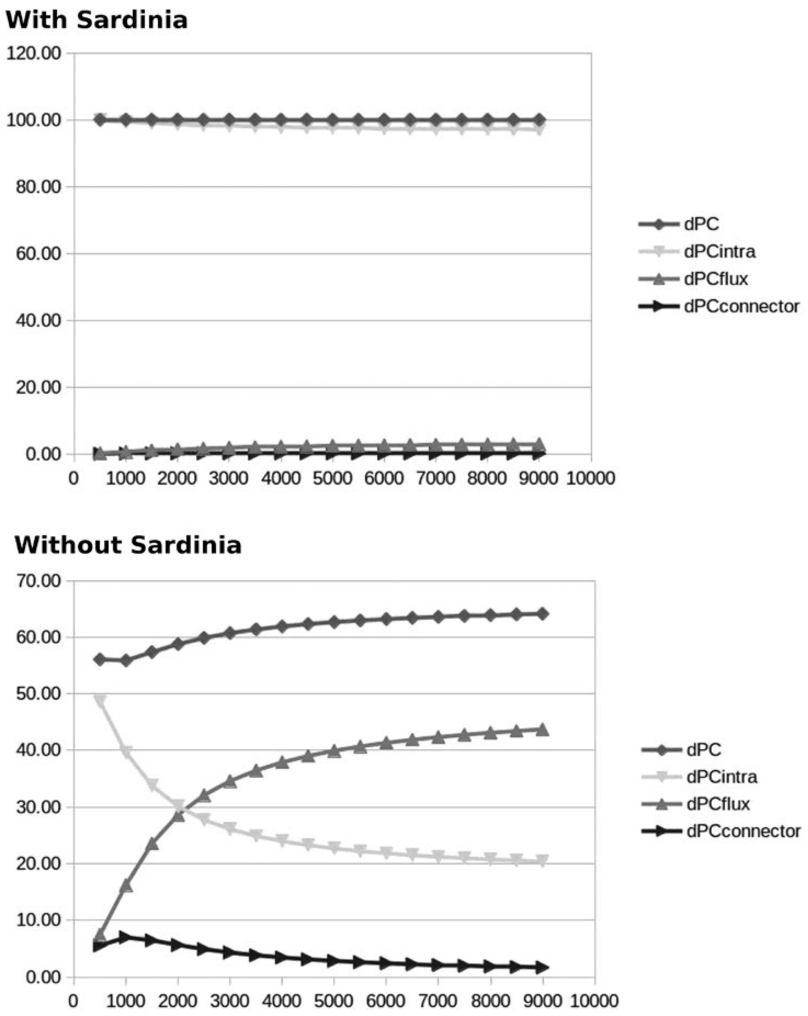


Figure 4. Partitioning of the importance values of dPC index into three fractions (dPCintra + cPCflux + dPCconnector) of the node with maximal values (with and without Sardinia). When including Sardinia, Sardinia had maximal values of dPCintra and dPCflux, and Caprera Island of dPCconnector. When excluding Sardinia, La Maddalena Island had maximal values of dPCintra and dPCflux, and Scoglio 2 a Sud dell'Isolotto dei Paduleddi Settentrionale of dPCconnector.

are topographically more complex, are therefore able to host a greater diversity of habitats and a greater species diversity (Triantis & Sfenthourakis, 2012).

CONNECTIVITY ANALYSES

The connectivity analyses presented an obvious result. Sardinia obtained the highest connectivity value, close to the possible maximum. The network connectivity was dominated by the internal connectivity of Sardinia and by Caprera Island, but of much less importance. The very large size of Sardinia in comparison to the islands of the La Maddalena Archipelago hid a more informative picture. Sardinia was the main source of all species of the system. Therefore, when excluding Sardinia from the analyses, La Maddalena, Caprera and Spargi islands emerged as the islands contributing the most to the global connectivity of the network. Connectivity fractions depended on distance. Internal and flux connectivity showed opposite patterns: patch characteristics lost influence when distance increased, being more important than the dispersal capacity of the network. From a certain distance threshold, the characteristics of the islands became less important, and the dispersal capacities of the species became the main factor that explained the connectivity of the whole network. As a result, the contribution of each island to the connectivity among islands decreased continuously with distance. However, the most 'central' islands in terms of connectivity were not the largest ones. Small islands were very important stepping stones in order to maintain the general connectivity and number of endemisms of the network. Despite being small islands, they hosted endemic species (e.g. *E. europaea*, *P. tiliguerta*).

Conefor results corroborated the correlation and GAM analyses, as connectivity depended on the largest islands. Islands with higher connectivity should receive more species and should have greater species richness (Visconti & Elkin, 2009). In fact, islands with species 'in transit' obtained the highest correlation value with habitat diversity. Likewise, small islands (types A, B and C) presented different correlation and GAM results, related to a lower connectivity capacity.

To our knowledge, this is the first time that Conefor has been used to analyse the connectivity of an island group. Conefor has been used successfully to analyse the connectivity among amphibian ponds (Ribeiro *et al.*, 2011), forests (Saura *et al.*, 2011), and in the process of colonization of newly burnt areas by birds (Zozaya, Brotons & Saura, 2012). Other studies used similar approaches to analyse connectivity among lizard populations (Rödder *et al.*, 2016).

Together with the novelty on the methods presented in this work, our sampling was complete and exhaustive. This is of great relevance because these groups of terrestrial vertebrates are characterized by secretive behaviour. To our knowledge, few studies have used amphibians and reptiles as models to analyse island biogeography and connectivity (e.g. Thornton *et al.*, 2002; Barrett, Wait & Anderson, 2003; Ficetola *et al.*, 2014).

FINAL REMARKS

The present study presents some limitations: (1) the total number of species richness per island is low; (2) islands with similar low species richness can have different species composition and different natural history; and (3) islands are inhabited by species with different dispersal capacity (for most species, the dispersal capacity is unknown). However, all these limitations do not hamper to obtain robust results, because the study system comprises numerous islands of different sizes and characteristics. In fact, there are several islands with very small size and no species, creating a gradient from islands with many species to islands without species. Moreover, although the total number of species is seemingly low, we have to take into account, as already mentioned above, that we are dealing with non-flying terrestrial vertebrates. Our results confirmed that species richness is driven by variables related to island complexity and not simply to area. Habitat diversity and topographical complexity (elevation and ruggedness) provide more information than simply area. The most interesting result of the present work is the role played by small islands, which are essential to maintain the network connectivity and endemicity of the Archipelago.

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