Mediterranean island biogeography: Analysis of fern species distribution in the system of islets around Sicily

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**Mediterranean island biogeography: Analysis of fern species distribution in the system of islets around Sicily**

ANGELO TROIA, FRANCESCO MARIA RAIMONDO, & PIETRO MAZZOLA

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**Abstract**

The aim of this article was to test the way in which geographical factors influence island floras in the Mediterranean basin, using ferns as target organisms, and the islands surrounding Sicily as location. A matrix with presence/absence data concerning fern taxa in the 16 islands studied was compiled. Cluster analysis, principal co-ordinates analysis (PCoA), principal components analysis (PCA) and a Bayesian analysis were performed. For each island, the total number of fern taxa was regressed against three factors: island area, island elevation and isolation. All the analyses pointed to affinities between islands according to their different geological composition, independently from their geographic position. A clear positive island species/area relationship (ISAR) was shown only for the volcanic islands. The island species/(area × elevation) relationship (ISAER), on the contrary, was unsatisfactory. The main features of interest are the following: (1) the clear division of the islands into two groups, volcanic vs. sedimentary; (2) the floristic richness of the volcanic compared to sedimentary islands and (3) the uniqueness of the pteridophyte flora of Pantelleria. This seems to demonstrate that the lower number of taxa in the islands farthest away from the “mainland” (Sicily, Tunisia) is not due to isolation, but due to another factor, probably habitat availability.

**Keywords:** Ferns, pteridophytes, flora, island biogeography, Sicily, islets, Mediterranean, floristic affinity

**Abbreviations:** ISAR, island species/area relationship; ISAER, island species/(area × elevation) relationship; MTR, monolet/trilete ratio

**Introduction**

Although the basic geographical factors, such as isolation, area and landscape heterogeneity, and the way they interact to influence island floras, are well known (e.g. Whittaker & Fernández-Palacios 2007), every group of islands or archipelago has a unique geography that can greatly influence the status of organisms on each island.

The Mediterranean islands are considered conservative systems, well buffered against the effects of climatic and evolutionary changes. Greuter (2001) relates this trait to the “continental islands” (which he calls “chersogenous” islands), i.e. all Mediterranean islands of an appreciable size. Actually, conservative characteristics have also been observed in volcanic “oceanic” islands, as in the case of the paleoenemic *Cytisus aelicus* Guss. in the Aeolian Islands (Conte et al. 1998).

The islands around Sicily (Figure 1), at the centre of the Mediterranean basin, one of the richest biodiversity hotspots of the world, seem predestined to biogeographical studies; due to their considerable variability in size, degree of isolation, geological history and topographic characteristics, they offer an excellent setting for analysing the processes that underlie patterns of species distribution.

Ferns also seem ideal subjects for biogeographical studies. Thus, because of their life-history attributes, they offer an independent test of how broadly biogeographical principles may be applied (Barrington 1993). Three biogeographically distinctive attributes of ferns, compared to the more commonly studied angiosperms and higher vertebrates, are the most prominent (Barrington 1993). First, their
independence from pollen and seed vectors and (partially) from co-evolved herbivores, so that habitat preference – and hence distribution – reflects climate and other abiotic features such as substrate, rather than an intricate combination of climatic and co-evolutionary features. Second, their unique reproductive biology with intergametophytic (and sometimes intragametophytic) selfing as the rule. Third, the prominent role of long-distance dispersal. Finally, the current distribution of the majority of fern species seems to be greatly influenced by dispersal and environmental conditions (Birks 1976; Moreno Saiz & Lobo 2008).

This article presents the first results of a numerical analysis of the data concerning fern species distribution on the small islands around Sicily, with the aim of highlighting affinities between islands and of ascertaining the role of geographic features in determining the distribution of taxa. In particular, we considered the following questions: (1) How does richness vary as a function of area, elevation, isolation and geological substrate? (2) Is it possible, on the basis of fern flora distribution, to differentiate between volcanic/“oceanic” and sedimentary/“continental” islands?

Materials and methods

The islands

With a surface of nearly 26,000 km², Sicily is the largest island in the Mediterranean Sea. Located at the centre of the basin (Figure 1), it is separated from Italy and Tunisia by narrow, but quite deep, sea straits, thus constituting an ideal bridge between Europe and Africa. It is surrounded by a number of archipelagos and isolated islets, which are the subject of this study. For each of these islands, the following data were summarised (Table I): surface area (km²), maximum elevation (m), geological substrate, the shortest over-water distance from the nearest source area (Sicily, Tunisia or other islands, expressed in km), the number of taxa of “ferns” (defined as below) and, when known, the number of total vascular plant species.

As regards the modes of origin of the islands, following the nomenclature proposed by Greuter (2001), all volcanic islands can be considered “thalassogenous” (=“oceanic”), never connected to the mainland, whereas the sedimentary (carbonatic) islands are “chersogenous” (=“continental”), in the past connected (more or less) with other land-masses. The Aeolian Islands differ from the other volcanic islands (Ustica, Linosa and Pantelleria) for the geochemical composition of their rocks, which generally provide acid substrates for the plants; however, the influence of this factor is complex (e.g. in Pantelleria, we found both acidic and basic substrates), and we preferred not to consider it when processing the data. As for the volcanic islands, age was not taken into account in the present data processing because, since their formation, they have shown periodic volcanic activity, usually over an extended period of time, thus making it difficult to attribute a definite age to each island as far as plant life is concerned.

Figure 1. General map of Sicily and adjacent areas, with the location of the 16 islands studied.
The species

We restricted our study to the Monilophytes (*sensu* Cantino et al. 2007), or "ferns" in the strict sense of the word (including Equisetopsida and Psilotopsida, but not Lycopodiophytes).

Compilation of a critical and updated floristic inventory for the islands (Table II) was based on the available bibliography, including floras, partial floristic contributions and taxonomic revisions. In particular, the list of native Sicilian ferns considered in this study follows the work of Giardina et al. (2007), with the inclusion of the genera *Ceterach* and *Phyllitis* into genus *Asplenium* (e.g. Pinter et al. 2002), the exclusion of doubtful taxa (e.g. *Asplenium adiantum-nigrum*, cf. Pichi Sermolli 1990; Marchetti 2004), the addition of new taxa (*Cosentinia vellea* subsp. *bivalens*, *Cheilanthes guan- chica*, in Marchetti 2008), and new data on taxa distribution.

Although several interesting subspecies with distinctive geographical distributions occur in the Sicilian pteridophyte flora, in some cases subspecies were not recorded separately, considering that the inevitable deficiencies in recording could alter processing results. This is the case for *Asplenium ceterach* L. subsp. *mediterraneum* Pinter, Nov. 2002 (=*A. ceterach* subsp. *cyprium* [Viane & Van den heede] Viane, Dec. 2002), a hexaploid subspecies reported only in Sicily and Pantelleria, but probably occurring in other sites; *A. ceterach* L. subsp. *bivalens* (D.E. Mey.) Greuter & Burdet, reported only in Sicily, but probably occurring in other sites; *C. vellea* (Aiton) Tod. subsp. *bivalens* (Reichstein) Rivas Mart. & Salvo, recently reported in Sicily, but probably occurring in Levanzo and other sites.

Taxa that were reported by reliable sources in the past, and which are now locally extinct, were included in the processing (marked with an asterisk in Table II), since they express the latent quality of the location and the recent environmental deterioration due to (direct or indirect) human activities.

Data analysis

As a first stage, a matrix of similarity between all pairs of islands based on their fern floristic composition was computed. Several similarity measures (Euclidean, Hamming, Kulczynski, Jaccard, etc.) were used.

The second stage in the numerical analysis involved the arrangement of the islands into a scheme reflecting, to some degree, the floristic similarities and dissimilarities between them. The results of the cluster analysis of the matrix were represented as conventional dendrograms.

Hierarchical cluster analysis can have several disadvantages; one of these is the distortion inherent in the two-dimensional dendrogram representation of the original similarity matrix. It is, therefore, important to compare the cluster analysis results with those obtained by non-hierarchical methods of data analysis, such as a scaling procedure.

For this reason, principal co-ordinates analysis (PCoA) and principal components analysis (PCA) were used.

Moreover, the patterns of floristic affinities between islands were investigated using the BAPS 5.2
Table II. Presence/absence matrix of fern taxa on the islands examined.

<table>
<thead>
<tr>
<th>Fern Taxon</th>
<th>Alicudi</th>
<th>Filicudi</th>
<th>Salina</th>
<th>Lipari</th>
<th>Vulcano</th>
<th>Stromboli</th>
<th>Ustica</th>
<th>Favignana</th>
<th>Levanzo</th>
<th>Marettimo</th>
<th>Pantelleria</th>
<th>Lampedusa</th>
<th>Linosa</th>
<th>Malta</th>
<th>Gozo</th>
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</thead>
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<td><em>Adiantum capillus-veneris</em> L.</td>
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<td><em>Anogramma leptophylla</em> (L.) Link</td>
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<tr>
<td><em>A. splenium billoti</em> F.W. Schultz (= <em>Asplenium obovatum</em> Viv. subsp. <em>lanceolatum</em> (Fiori) P. Silva)</td>
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<tr>
<td><em>Asplenium obovatum</em> Viv. subsp. obovatum</td>
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<td><em>Asplenium scolopendrium</em> L. subsp. scolopendrium</td>
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<tr>
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<td><em>Athyrium filix-fama</em> (L.) Roth</td>
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<tr>
<td><em>Pteridium aquilinum</em> (L.) Kuhn subsp. <em>aquilinum</em></td>
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<td>11</td>
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<td>18</td>
<td>5</td>
<td>6</td>
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</table>

Note: Taxa that are locally extinct are marked with an asterisk
programme (Bayesian Analysis of Population Structure; Corander et al. 2008), which uses stochastic optimisation (instead of Markov chain Monte Carlo randomisations) to infer the correct model for the data.

We employed the spatial model option in BAPS, using individual islands with known geographical coordinates as the units to be clustered. The rationale of using spatial information is to assign a biologically relevant non-uniform prior distribution over the space of clustering solutions, which expects that underlying clusters are spatially smooth at least to some extent. This increases the power to correctly detect the underlying population structure, and can be used to investigate the population structure also, visually (Corander et al. 2008). In the spatial clustering model, the landscape occupied by the population is divided into a “coloured Voronoi tessellation” (Corander et al. 2008), in which identical colours identify populations with homogeneous floristic composition, whereas different colours represent floristically differentiated populations. Identical colour for particular tessellation cells is inferred through Bayes’ formula using both floristic data and a spatial prior distribution, which is measured as the units to be clustered. The rationale is the lack of homogeneous data about habitat types, we tested another simple relationship, replacing “A” of 25 taxa were recorded on volcanic islands, which were recorded on sedimentary islands, while 24 taxa were recorded on Pantelleria, Linosa, Lampedusa, Gozo, Ustica, Vulcano and Favignana.

Comparison between geographical and floristic distance matrices between islands was done by using the Mantel test (Bonnet & Van de Peer 2002). All the aforementioned analyses were performed using the “PAST” programme, version 1.35 (Hammer et al. 2001), except where indicated otherwise.

Island area, elevation and isolation

For each island, the total number of fern taxa was regressed against three factors suggested to be important in predicting species richness: island area, island elevation and isolation.

The island species/area relationship (ISAR) is one of the classic patterns in ecological geography. For a particular taxon, and within any given region of relatively uniform climate, the ISAR can often be approximated by the power function model: $S = c A^z$ which, with the logarithmic transformations of both axes, becomes: $\log S = \log c + z \log A$ (where $S$ is the number of species of a given taxon on an island, $A$ is the area, and $c$ and $z$ are constants determined empirically from the data, which thus vary from system to system; Whittaker & Fernández-Palacios 2007). In this equation, $z$ describes the slope of the log-log relationship, and $\log c$ describes its intercept. The explanatory power of area for species number variations is variable, with empirical studies demonstrating significant roles for an array of subsidiary variables (cf. Triantis et al. 2008). A modification of the traditional approach was proposed by Triantis et al. (2003) with the so called “choros model”, incorporating habitat diversity within species number modelling for island data sets. In our case, owing to the lack of homogeneous data about habitat types, we tested another simple relationship, replacing “$A$” (area) with “$AE$”, i.e. the product of island Area and Elevation, in order to better estimate not the real surface area of each island but the true resource space available to island species. It is clear, in fact, that although the surface area is the same, a higher island offers more “spaces” than a flatter one.

Island elevation is considered to be one possible measure of habitat and ecological diversity. However, there are no studies showing that a higher maximum altitude equates to more habitat types on these islands. There are practical difficulties in measuring the isolation of a target island because of the existence of other islands (the configuration of which varies through time) which may serve as networks (or “stepping-stones”) for species movements across the sea. So we limited our study, in this case, to the islands whose distance (isolation) from the “mainland” (Sicily or Tunisia) was clear and easily measurable: Pantelleria, Linosa, Lampedusa, Gozo, Ustica, Vulcano and Favignana.

This index, which was developed by Pichi Sermolli et al. (1988) as the “m/t index”, is the ratio between the number of fern species with monolete (bilateral) spores and the number of fern species with trilete (tetrahedral) spores; it has been shown to increase significantly with altitude and latitude (Pausas & Saez 2000). Trilete species are a phylogenetically older group of ferns occurring earlier in the fossil record and evolving mainly in the Tropics, while most monolete species are in phylogenetically derived families, most of which have become adapted to colder environments (Pausas & Saez 2000).

Results

**Floristic richness**

The final data matrix used for the analysis (Table II) consisted of 25 taxa in 16 islands; another matrix (not shown) including Sicily and Tunisia, with 18 areas and 49 taxa (which represent the final number of native moniliphytes in Sicily and adjacent islands), was also used.

Pantelleria is by far the richest island, with 18 taxa, and Levanzo the poorest, with four taxa. Only 14 taxa were recorded on sedimentary islands, while 24 of 25 taxa were recorded on volcanic islands, which...
are, therefore, richer (on average 10.4 vs. 7.0 taxa per island on volcanic and sedimentary islands, respectively). Only one species (*Asplenium sagittatum*) is restricted to sedimentary islands. Eleven taxa are private to volcanic islands (*Asplenium obovatum, Athyrium filix-femina, Cheilanthes maderensis, Cheilanthes tinei, C. guanchica, Dryopteris pallida, Equisetum telmateia, Ophioglossum lusitanicum, Polystichum setiferum, Asplenium billotii* and *Osmunda regalis*), two of them being private to Pantelleria (*C. guanchica* and *A. billotii*), and two others to Vulcano (*E. telmateia* and *O. regalis*). The most widespread taxa are *Anogramma leptophylla* (15 of 16 islands), *Adiantum capillus-veneris* and *Polypodium cambricum* (13 of 16 islands).

The number of fern species today extinct in Lampedusa is remarkable, due to the drastic reduction or destruction of primeval habitats in the past two centuries (Pasta 2001).

Floristic affinities between islands

Cluster analysis, using different similarity measures, resulted in scarcely supported dendrograms; nevertheless, one of them (Figure 2) clearly shows the separate position of Pantelleria island and the (weakly supported) separation between volcanic and sedimentary islands.

PCoA and PCA produced similar results. The results of the PCoA, using the Hamming index, are

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**Figure 2. Dendrogram resulting from the cluster analysis with bootstrap values (Hamming similarity, unweighted pair group method with arithmetic mean (UPGMA), number of bootstrap replicates=1000).** Note: The Hamming distance is used to denote the difference between two binary strings (Hammer et al., 2001). Stars=volcanic islands, Squares=sedimentary islands.
shown in Figure 3. The first axis distinguishes between volcanic (positive co-ordinates) and sedimentary islands (negative co-ordinates); along the second axis, Pantelleria is well isolated in the upper part of the graph, and Vulcano is partially separated from the other volcanic islands in the lower part of the graph.

The Bayesian analysis identified three groups (Figure 4): one includes the sedimentary islands, the second includes the volcanic islands and the third...
includes only Pantelleria. As shown in Figure 4, there is no geographic pattern.

**Island surface area**

Results concerning the ISAR and island species/area (area × elevation) relationship (ISAER) are shown and compared in Table III.

A clear positive ISAR exists only for volcanic islands, but not for sedimentary islands, and not for all islands. The value of $R^2$, however, is only 0.71, and the slope of the regression, or $z$-value, is 0.12, at the lower end of the theoretical norm of 0.13–0.30 for plants in island groups (Triantis et al. 2008).

In this context, ISAER proved not to be a good relationship; even though in the case of “all islands” it had a higher descriptive power than ISAR, low values of $z$ and $R^2$ made it unsatisfactory.

**Island elevation**

In this case also, our results show no relationship between island elevation and the number of fern species (Table III); it is noteworthy that a slightly negative, though not supported, relationship occurred in the Aeolian archipelago.

**Island isolation**

When considering all the selected islands, plotting their distances from other landmasses and the number of fern species, values of $z$ (slope) = −0.02, $R^2$ = 0.07 and $p$ = 0.58 (Figure 5) were obtained. It is clear that this regression explains a very small part of the variation, and that it is not significant.

Regression of geographic distance against floristic similarity considering all the islands (data not shown) shows an expected negative relationship, but with low values of slope and $R^2$. The Mantel test, with an observed correlation of $-0.52$ ($p < 0.0001$), confirms this weak (negative) correlation between geographic distances and floristic (fern) similarities.

**Monolete/trilete ratio**

MTR (Table I) varies from 0.50 (Filicudi, Linosa and Stromboli) to 2.50 (Malta). With the exception of Malta and Ustica, all the islands have values below 2.0, and no clear latitudinal, altitudinal or geological pattern is evident.

**Discussion**

The Mediterranean basin, a biodiversity hotspot of worldwide importance, is remarkable among other temperate zones in terms of its plant species richness and endemism, new species being continuously

<table>
<thead>
<tr>
<th>Island group</th>
<th>N of islands</th>
<th>Elevation range (m a.s.l.)</th>
<th>Geology</th>
<th>ISAR</th>
<th>ISAER</th>
<th>Species/elevation relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>All circumsicilian islands</td>
<td>16</td>
<td>133–962</td>
<td>Volcanic/sedimentary</td>
<td>Z</td>
<td>$R^2$</td>
<td>Z</td>
</tr>
<tr>
<td>Aeolian Archipelago</td>
<td>7</td>
<td>421–962</td>
<td>Volcanic</td>
<td>0.0925</td>
<td>0.34</td>
<td>0.018</td>
</tr>
<tr>
<td>All volcanic islands</td>
<td>10</td>
<td>195–962</td>
<td>Volcanic</td>
<td>0.008</td>
<td>0.018</td>
<td>0.018</td>
</tr>
<tr>
<td>All sedimentary islands</td>
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<td>133–686</td>
<td>Sedimentary</td>
<td>0.0027</td>
<td>0.03</td>
<td>0.009</td>
</tr>
</tbody>
</table>

Note: The model with significant fit is indicated in bold font.
identified and described (e.g. Ernandes et al. 2010). Nevertheless, the Mediterranean does not play a pre-emi-
cent role in terms of pteridophyte diversity and has been considered a secondary centre of diversity for this group of plants (Moreno Saiz & Lobo 2008). In the investigated area, no endemic fern species occurs. Even though the islands around Sicily have been subject to human impact since prehistoric times, they still offer a great variety of geographic, geological and ecological situations (Privitera & Puglisi 2009).

Several features of interest emerge from the results of the present analysis. One is the division of the islands into two groups, volcanic vs. sedimentary (Figures 2–4), and the greater floristic richness of the former compared to the latter group. Interestingly, the division into these two groups affects the biogeographical patterns of species–area relationships (Table III), in such a way that these relationships are more or less significant according to the geology of the islands. It is noteworthy that, since geology includes another important biogeographical factor (i.e. the mode of origin of the islands), as aforementioned, it is also possible to describe this division in terms of thalassogenous (oceanic) vs. chersogenous (continental) islands.

A second feature of floristic interest is the uniqueness of the pteridophyte flora of Pantelleria: here, we find the highest number of taxa (18 of a total of 25 taxa found on all the islands). Even if no endemic species occur, on Pantelleria, we find two private taxa, which are absent on the rest of the islands. The peculiarity of this island is evident also considering the relationships of floristic affinity with the other islands: Figures 2, 3, and more clearly, Figure 4 show the isolated position of the island. Indeed, the reasons for the numerous taxa on Pantelleria are to be found in its great availability of different habitats, not only because of its (relatively) large surface area but also because of its topography and geological diversity (although completely volcanic, the island is formed by different kinds of rocks).

In Figure 5, the position of Pantelleria seems to demonstrate that the lower number of taxa in the farthest islands is not due to isolation, but due to another factor, probably habitat availability. The weak correlation between geographic and floristic distances emerges also from Figure 4 and from other parameters (see “island isolation” in Results).

The results of the ISAER are not encouraging, but can no doubt be more fruitful in other geographical contexts or with other taxonomic groups. Finally, the MTR index turned out to be of little use for this kind of analysis, or at least not on this scale, and/or in this geographical area.
In conclusion, this study confirms that fern species have a high dispersal capability and no tendency to speciation also in the Mediterranean area, and that due to these characteristics, they are excellent subjects for biogeographical analyses of islands. As regards the questions raised in the present study:

(1) Fern richness was found to be correlated with the geological substrate (volcanic islands having more species, Table I), and partially with island area (ISAR, Table III), but not with island elevation (Table III). Isolation appears not to have a priority role. In the present scenario, at the centre of the Mediterranean basin, fern species are not limited by distance, but probably by other factors, such as habitat availability, which appears to be very important for the presence (and conservation) of some rare scattered species.

(2) On the basis of fern flora distribution, it is possible to differentiate between volcanic and sedimentary islands. We have seen that this dichotomy can also be defined as oceanic/continental. However, the results of the present work suggest that, in the Sicilian scenario, geographic distances are not barriers to the great dispersal capacities of the ferns (thereby confirming data from the literature; cf. Wolf et al. 2001). Thus, considering that volcanic islands (never connected with other landmasses) hold more species than the sedimentary islands (which are usually older and closer to other landmasses), it is likely that the difference between the two groups of islands can be attributed to their different geological substrates, and not to their different modes of origin.

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References


