
The Macaronesian province: patterns of species richness and endemism of arthropods

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Introduction

Oceanic island ecosystems offer great opportunities for the study of ecology, conservation biogeography and evolution and have for a long time been recognized as natural laboratories for studying evolution owing to their discrete geographical nature and diversity of species and habitats. Indeed, they have been both the inspiration for new theories and the test bed of ideas generated from across the life and environmental sciences (MacArthur & Wilson, 1967; Carlquist, 1974; Williamson, 1981; Gillespie & Roderick, 2002; Gillespie, 2006; Stuessy, 2007; Whittaker & Fernández-Palacios, 2007; Losos & Ricklefs, 2009).

Island biotas are composed of “survivors” of a continuous dynamic interplay between immigration, extinction and speciation (Losos & Ricklefs, 2009), a statement of general relevance to all biological systems, but which on islands in particular produces emergent patterns that are both diagnostic and analytically tractable. Since the seminal work of MacArthur & Wilson (1967) the origin and maintenance of the diversity of species and lineages on isolated islands has been related to many factors, including island area, distance to the nearest species source, habitat diversity, maximum elevation and geological age of the island (see reviews in Hart & Horwitz, 1991; Rosenzweig, 1995; Borges & Brown, 1999; Triantis *et al.* 2003; Whittaker & Fernández-Palacios, 2007; Whittaker *et al.*, 2008).

Macaronesia is a biogeographical province located in the North Atlantic; it consists of five Atlantic volcanic archipelagos, including Cape Verde, Madeira, the Salvages, the Canary Islands and the Azores (Fig. 1) plus some small areas of the Moroccan and Iberian coasts, although its exact definition remains subject to debate (e.g., Vanderpoorten *et al.*, 2007; Kim *et al.*, 2008). The five archipelagos are situated between 15° to 40° N latitude, with distances from the European or African continents varying from 95 to 1,600 km. Geological ages of

individual islands vary from 0.25 million years (My) for Pico (Azores) to 27 My for Selvagens (Geldmacher *et al.*, 2005; Anchochea *et al.*, 2006, Kim *et al.*, 2008; Hoernle & Carracedo, 2009). Within the almost 3,000 km of latitudinal span of the Macaronesian province, a diverse array of climates is present, ranging from sub-Saharan conditions found on parts of the Canaries and the Mediterranean-like climate of Madeira, Salvages and Canary Islands, to the humid Atlantic climate of the Azores in the north and the typically tropical arid conditions of Cape Verde Islands, to the south (see chapter from J. M. Fernández-Palacios, this book).

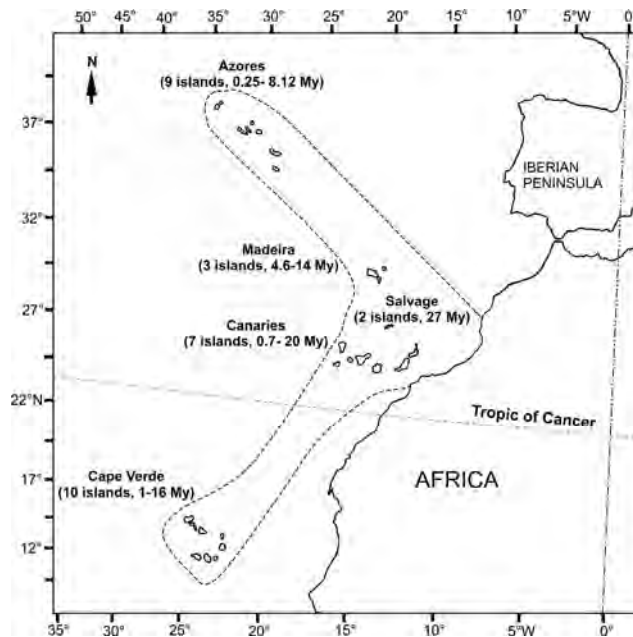


Figure 1. The five Atlantic volcanic archipelagos (the Azores, the Madeiras, the Salvage Islands, the Canary Islands, and the Cape Verde Islands) included in the biogeographic region of Macaronesia (modified from Kim *et al.* 2008).

The region in general, and especially the Canary Islands, differs markedly from the “typical” archipelagos of the Pacific, such as Hawaii and Galapagos, in that most of the islands are relatively close to continental source areas. For example, the easternmost Canary Island, Fuerteventura, is currently less than 100 km from the west coast of Morocco, and has been within 65 km during the sea level minima associated with the most extreme Pleistocene glacial stages (see García-Talavera, 1999; Fig. 2b). The islands also exhibit a comparatively old and broad range of geological ages, from <1 to around 20 My (Fig. 2a). These two features contribute to several unusual patterns of colonization and diversification and to

relatively high levels of genetic variation compared to other oceanic archipelagos. The Madeira and Cape Verde island groups are mainly constituted of “old islands”, in comparison to typical “hotspot islands”, where the maximum age rarely surpasses 10 My, although some can persist as atolls (see Clouard & Bonneville, 2005; Neall & Trewick, 2008). In particular, Porto Santo Island in the Madeiran archipelago has an age of 14 My, while in the Cape Verde archipelago most of the islands (e.g. Sal, Boavista, Santiago) are older than 5 My (Holm *et al.* 2006). By contrast, the Azores is, in general, a young island group (see discussion below), although Santa Maria Island has a maximum age of 8.12 My (see Borges *et al.*, 2009). The Canary Islands are almost double the area of Cape Verde, nearly three times the area of the Azores, and 10 times larger than the Madeiran group (see Table I).

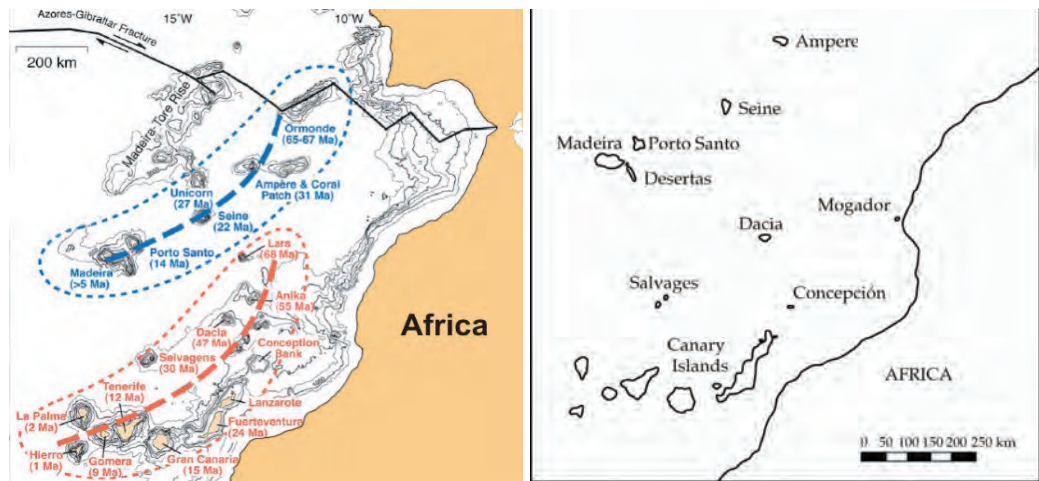


Figure 2. A) The Canaries and Madeira through time (after Hoernle & Carracedo, 2009). B) A reconstruction of Macaronesia islands at the minimum sea-level during the last glacial period (redrawn from García-Talavera, 1999 after Whittaker & Fernández-Palacios, 2007). Ma is millions of years ago. Note that precise age estimates vary between sources as shown by a comparison of Canary Islands ages in Figures 1 and 2.

The Macaronesian arthropod fauna displays a number of characteristics typical of oceanic islands, including a high degree of endemism, ranging from 19% for the Azores (Borges *et al.*, 2005a), to 28% for Madeira (Borges *et al.*, 2008a), 30% for Cape Verde (Arechavaleta *et al.*, 2005) and 45% for the Canary Islands (Izquierdo *et al.*, 2004; see Table I). The preponderance of endemic species has made the Macaronesian islands an outstanding area for studies of evolution and speciation, and arthropods from these islands have been the focus of particularly intensive investigation in the last ten years. Numerous biogeographic analyses of Macaronesian arthropod groups have provided valuable insights into the processes regulating

species richness as well as the relationships among the region's endemics (e.g. Juan *et al.*, 1996; Arnedo & Ribera, 1999; Borges & Brown, 1999; Emerson *et al.*, 1999, 2006; Emerson & Oromí, 2005; Dimitrov *et al.*, 2008; Borges & Hortal, 2009; Hochkirch & Görzig, 2009).

Here we investigate the factors shaping arthropod species richness and patterns of endemism in the Macaronesian archipelagos, considering two levels of analysis: a) individual archipelagos of the Macaronesian region (except Madeira and Salvages due to their limited number of islands), and b) all the islands of the region altogether. We do this following the recently published works of Whittaker *et al.* (2008) and Borges & Hortal (2009), examining data sets for several taxa from the Macaronesian archipelagos.

Table I. Total area for the island systems studied and the respective richness of indigenous, archipelagic endemic and single island endemic species (SIE) of arthropods and beetles. For a full list of data sources, see text.

| Island group | Total area (km ²) | Arthropods | | | Beetles | | |
|--------------|-------------------------------|--------------------|-----------------|------|--------------------|-----------------|-----|
| | | Indigenous species | Endemic species | SIE | Indigenous species | Endemic species | SIE |
| Azores | 2324 | 1373 | 258 | 108 | 210 | 64 | 39 |
| Canaries | 7496 | 6826 | 3079 | 1757 | 1954 | 1250 | 796 |
| Cape Verde | 4020 | 1768 | 473 | 241 | 398 | 140 | 68 |
| Madeira | 824 | 3249 | 979 | 845 | 901 | 416 | 356 |

Whittaker *et al.* (2008; see also Whittaker *et al.*, 2009) introduced the General Dynamic Model of oceanic island biogeography (GDM), a model that explicitly incorporates the geological history of oceanic islands, which exhibit a characteristic “life-cycle” from youth, to maturity, to old age and eventual loss. The life-history (‘ontogeny’) of an island itself, is one of the most important components for describing the interplay of immigration, extinction and speciation in establishing species richness for oceanic islands (Whittaker *et al.*, 2008, 2009; see also Peck, 1990; Borges & Brown, 1999; Stuessy, 2007). Following this rationale, the GDM is based on the premise that the size, topographic complexity, ability to support life, and potentially the likelihood of promoting speciation first increases over time, and then reaches some form of plateau or peak, subsequently to decline as the island erodes and/or subsides back into the sea. This and other contributions can offer the foundation for an expanded theory of island biogeography, unifying ecological and evolutionary biogeography (see Whittaker *et al.*, 2009).

Our main hypotheses here are that: (1) due to its recent history, the Azorean islands would present a positive relationship between richness and both area and island age, as suggested by previous analyses by Borges & Brown (1999) and Borges & Hortal (2009); (2) for the Canary Islands, with a wide range of island ages, a combination of a hump-shaped relationship between richness and age and an increase of richness with area would be the most effective model (see previous analyses by Whittaker *et al.*, 2008); (3) Cape Verde, consisting mainly of “old” islands would present a positive relationship between richness and area but a negative one with geological age; and (4) the descriptive ability of island area should progressively reduce from indigenous species, to archipelagic endemics and to single-island endemics, when all the islands of the region are analysed, as a result of the increased effect of the archipelagic idiosyncrasies.

Data origin

We used the most recent compilation of terrestrial arthropod (Arthropoda) species lists for the five Macaronesian island groups: the Canary Islands (Izquierdo *et al.*, 2004); the Azores (Borges *et al.*, 2005b); Madeira and Salvages considered together (Borges *et al.*, 2008b) and Cape Verde islands (Arechavaleta *et al.*, 2005). Updated databases for the Canary Islands and Cape Verde were kindly provided by José Luis Martín (Centro de Planificación Ambiental, Consejería de Medio Ambiente y Ordenación Territorial del Gobierno de Canarias; <http://www.gobiernodecanarias.org/medioambiente>). The list of the Azorean arthropods is also an updated version, including all the new archipelago endemics described since the publication of the Borges *et al.* (2005b) checklists and many new records for individual islands (see e.g. Borges *et al.*, 2006, 2007; Borges & Wunderlich, 2008; Cardoso *et al.*, 2009). The list of arthropods of the Cape Verde islands is a preliminary list (as indicated in the title of Arechavaleta *et al.*, 2005), and should be considered with caution, due to the lower level of completeness (see also Cardoso *et al.*, 2010).

For each island we counted the number of indigenous species (i.e., archipelagic endemics plus natives), excluding all introduced species. In addition, we compiled and recorded the number and percentage of Single Island Endemics (SIE; i.e., species endemic to each island), (see Table I). We thus described the arthropod diversity and endemism on each island using four different metrics: (i) number of indigenous species; (ii) number of archipelago endemics; (iii) number of single island endemics (nSIE); and (iv) proportion of SIEs (pSIE), calculated as the ratio between single island endemics and indigenous species (nSIE/indigenous species).

The latter two metrics can be regarded as measures of evolutionary dynamics while species richness of indigenous and non-natives species reflect, to a greater degree, shorter time-scale ecological dynamics (see Whittaker *et al.*, 2008, 2009). Given that Coleoptera (beetles) are probably the most studied, and thus best-known, order of the Macaronesian arthropods (see Borges *et al.*, 2005a, 2008a), we also extracted these four diversity indices and conducted all subsequent analyses for this group, too.

Data on the ages of the island complexes were extracted from Borges *et al.* (2009) for the Azores, Geldmacher *et al.* (2005) for the Madeiran group, Carracedo *et al.* (2002) for the Canary Islands, Geldmacher *et al.* (2001) for Salvages, and Holm *et al.* (2006) for the Cape Verde Islands. Estimation of maximum island ages follows these sources but it should be noted that, first, some of these estimates are subject to debate, and that, second, the effective biological age of an island may have a quite variable relationship to the maximum known geological age (see Discussion).

Analyses

We analysed the patterns of diversity and endemism at two different levels, considering (i) the islands within each main island group separately (excluding the Madeira and Salvages due to their small numbers of islands and disparity in size), and (ii) all the islands of the Macaronesian region altogether (32 islands in total; see below). For the two levels of analysis we applied the classical species–area model (SAR; Arrhenius, 1921) in its logarithmic form. We also applied standard multiple linear regressions, which were used to explore the relationships between the different diversity metrics and age, elevation and area. The two smaller islands of Cape Verde (Branco and Raso) were excluded from all the analyses in which the age variable was considered due to the lack of information on their geological ages.

We then evaluated the performance in analyses of these datasets of the different mathematical formulations of the GDM, a model that explicitly incorporates the geological history of islands in a number of variants. Although it is expected that all diversity metrics show a positive relationship with area, the relationship with island age can vary according to the extent of the geological ages involved, from positive, to hump-shaped, or negative (see Fig. 3).

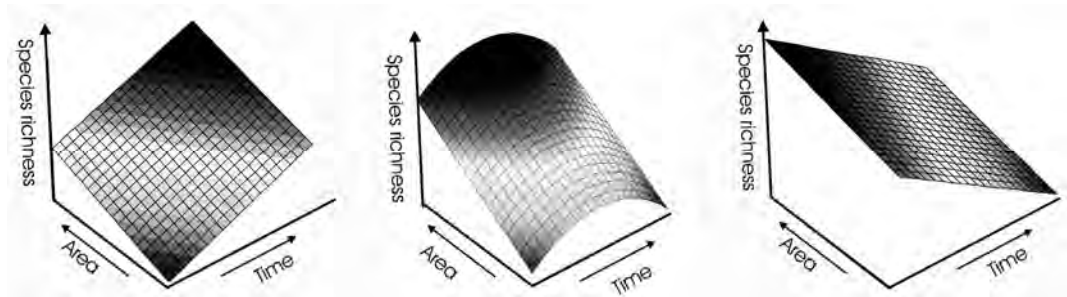


Figure 3. The three different forms of the species–area–time relationship for oceanic island groups predicted within the context of the general dynamic model of oceanic island biogeography (Whittaker *et al.*, 2008, 2009). The first and the third are described by simple log (Area)–Time relationship (AT; with a positive and negative relationship for the first and the third model respectively), and a log (Area) + Time–Time² model (ATT²) for the second.

While a positive relationship should be expected for island groups consisting of relatively young islands (e.g. Azores; Borges & Hortal, 2009), a hump-shaped relationship is predicted by the theory/model when a full range of ages are present, or the relationship might even be negative if all islands of the group are old and declining (see Whittaker *et al.*, 2009), or if required habitats for the group in question decline rapidly (Borges & Hortal, 2009). For example, the number of SIE species of the Azorean cave-adapted arthropods exhibit a negative relationship with island age since in the earlier stages of development of an island, volcanic activity creates a diverse underground environment in the form of pit-caves, lava tubes, and volcanic pits, which offer higher opportunities for speciation. As the level of volcanic activity subsides, the underground environment is progressively reduced and disappears as the island ages, due to erosive processes.

We therefore evaluated four different models for each dataset. Following Whittaker *et al.* (2008; see also Borges & Hortal, 2009), we assessed the performance of: (i) the AT model [diversity metric=log (area) + time], assuming a linear relationship between time and richness, and (ii) the ATT² model [diversity metric=log (area) + time - time²], which assumes that the relationship with the age of the islands is hump-shaped. In addition, we applied a modified version of (area–time) models, where we replaced area with the choros parameter (K), i.e. the result of the multiplication of the island size with the number of habitat types present on the island (see Triantis *et al.*, 2003, 2008b). The (choros–time) models, (iii) KT and (iv) KTT² were applied using the habitat types from Enghoff & Baez (1993) for the Canary Islands (six vegetation zones), Borges (unpubl.) for the Azores (three vegetation types) and Duarte *et al.*

(2008) for Cape Verde (two vegetation types; see also Triantis *et al.*, 2008b). Here is important to note that, although the units used for estimating habitat diversity in each island group are quite similar, caution is needed in inter-archipelagos comparisons. The best model describing each of the four diversity indices was selected within all models considered based on the Akaike Information Criterion (AIC) and the adjusted R^2 values. All statistical analyses were carried out using STATISTICA 6.0.

Correlation and model testing

The explanatory power of area alone was, in general, quite high both for arthropods and beetles separately in all island groups considered, except the Canary Islands, where none of the diversity metrics showed statistically significant relationships with area (see Table II).

Table II. The species–area relationships for indigenous, archipelagic endemic and single island endemic species (SIE), for arthropods and beetles, for the three main groups of the Macaronesian region. SIE are a subset of the archipelagic endemics and they in turn are a subset of indigenous species. For each case the coefficient of determination (R^2), the F-value and the slope of the relationship (z) is presented. In all the cases except those for the Canary Islands the relationship was statistically significant at the $P < 0.05$ level.

| Group | No Islands | Taxon | Indigenous | | | Endemics | | | SIE | | |
|-------------|------------|------------|------------|-------|-------|----------|-------|-------|------|-------|-------|
| | | | z | R^2 | F | z | R^2 | F | Z | R^2 | F |
| Azores | 9 | Arthropods | 0.47 | 0.90 | 60.10 | 0.49 | 0.92 | 83.38 | 0.91 | 0.70 | 16.24 |
| | | Beetles | 0.46 | 0.58 | 9.63 | 0.50 | 0.62 | 11.44 | 0.61 | 0.60 | 10.42 |
| Canaries | 7 | Arthropods | - | - | - | - | - | - | - | - | - |
| | | Beetles | - | - | - | - | - | - | - | - | - |
| Cape Verde | 12 | Arthropods | 0.81 | 0.91 | 96.27 | 0.65 | 0.86 | 62.67 | 0.59 | 0.72 | 25.61 |
| | | Beetles | 0.74 | 0.83 | 48.09 | 0.62 | 0.68 | 21.19 | 0.39 | 0.50 | 9.89 |
| Macaronesia | 32 | Arthropods | 0.71 | 0.72 | 77.06 | 0.68 | 0.65 | 56.05 | 0.71 | 0.45 | 24.73 |
| | | Beetles | 0.68 | 0.60 | 44.72 | 0.67 | 0.45 | 25.76 | 0.54 | 0.30 | 12.91 |

When all the Macaronesian Islands are analyzed altogether, the amount of variability (R^2) explained by area showed a trend of diminishing correlation from indigenous, to archipelagic endemics and then to single island endemics, ranging from 0.70 to 0.45 in the case of arthropods, and from 0.60 to 0.30 in the case of beetles, respectively (see Table II and Fig. 4).

The different GDM formulations showed only slight increases of the explanatory power compared with the simplest area and choros models in the cases of the Azores and Cape Verde Islands, if showing any increase at all. Age is included as a linear predictor of diversity metrics, being positive for Azores and negative for Cape Verde (see Tables III & IV). In contrast, the hump-shaped relationship between diversity metrics and time resulted in the best models for the Canary Islands in all cases, with the KTT² model having the highest explanatory power in each case (Table III; see also Table IV). The slight differences between the correlation coefficient values for the ATT² for the Canarian arthropods between this work and the original analyses of Whittaker *et al.* (2008) are due to minor changes of the species lists used.

Species diversity patterns in Macaronesia

Understanding the causes of variation in species diversity among islands in isolated archipelagos and between archipelagos in a particular biogeographical realm remains a major challenge (see recent discussions in Emerson & Kolm, 2005; Whittaker *et al.*, 2008; Borges & Hortal, 2009). The simplicity of MacArthur & Wilson's (1967) dynamic equilibrium model of island biogeography has resulted in its long-term prevalence as one of the cores of current ecological theory. However, the simplicity of the standard implementation of their model, which is to focus on area (~extinction rate) and isolation (~immigration rate) as the key variables to describe the main processes in island biogeography, has constrained the ability of this model to explain the diversity of patterns shown by island biotas in the large number of remote archipelagos scattered worldwide (Heaney, 2000).

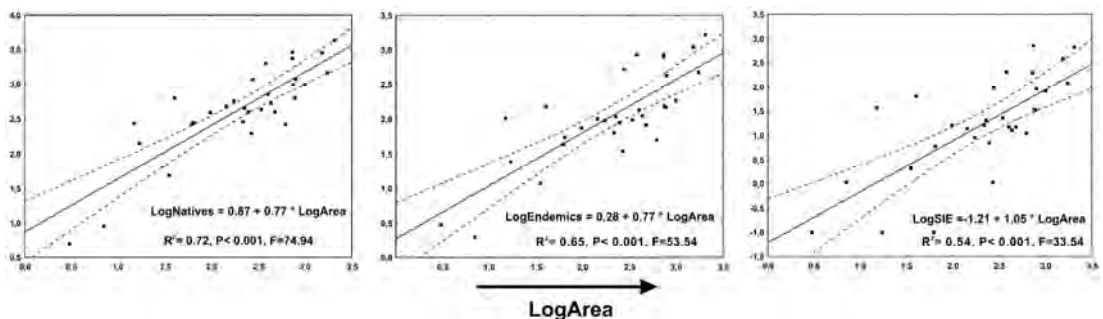


Figure 4. The species–area relationships for the indigenous, endemic and single-island endemic species for the 32 Macaronesian islands included in this study (Area in km²).

A broader theoretical framework, based on MacArthur and Wilson's dynamic equilibrium model of island biogeography is, however, emerging (e.g., Lomolino, 2000; Heaney, 2007; Whittaker & Fernández-Palacios, 2007; Whittaker *et al.*, 2008; Borges & Hortal, 2009; Fattorini, 2009); an improved theory of island biogeography must consider more explicitly the simultaneous influence of speciation, immigration and extinction, as well as the ecological interactions and differences among species in all these features (Whittaker *et al.*, 2009).

Within this context, the different geological histories, regional processes and geographical configurations of the Macaronesian archipelagos and islands make them an exceptional study system to evaluate and expand the existing island biogeography theories, allowing the integration of ecological and evolutionary models of species diversity.

Table III. Best models based on the Akaike Information Criterion (AIC) and the adjusted R^2 values (not shown) for each of the diversity metrics used both for arthropods and beetles for the three main Macaronesian Islands groups. A: Area, K: choros, T: Geological age.

* In these cases, for both the beetles and arthropods overall, island age had a negative on the number of endemic species.

| Island group | Taxon | Indigenous | Endemics | SIE | pSIE |
|--------------|------------|------------------|------------------|------------------|------------------|
| Azores | Arthropods | A | K | AT | KT |
| | Beetles | KT | KT | AT | KT |
| Canaries | Arthropods | KTT ² | KTT ² | KTT ² | KTT ² |
| | Beetles | KTT ² | KTT ² | KTT ² | KTT ² |
| Cape Verde | Arthropods | K | KT* | K | - |
| | Beetles | K | KT* | - | - |

Larger is richer (but not always)

Although the mechanisms through which area determines the number of species that can establish populations on a given territory are still only partly understood, so far area has proved to be the most powerful single explanatory variable of species richness (MacArthur & Wilson, 1967; Rosenzweig, 1995; Whittaker & Fernández-Palacios, 2007, Triantis *et al.*, 2008a). In fact, such explanatory capacity translates from single islands to their whole archipelagos (Santos *et al.*, 2010). This is also apparent in our results, where area has proven to be the best descriptor (if not the only property exerting a statistically significant contribution) for most of the island groups for the diversity metrics used (see Table II).

Although the explanatory capacity of area diminishes from indigenous, to endemic and then to single island endemic species, both for beetles and arthropods overall, our analyses prove it to be an effective macroecological descriptor of island species richness patterns despite the large differences between the 32 islands considered (Table II) and the varying characteristics of the archipelagos. The sequential reduction of R^2 from indigenous to archipelagic endemics and to SIE can be attributed to the more intense effect of the idiosyncrasies of each island (e.g. area, isolation, geological age, within-archipelago island distances) on its evolutionary dynamics. Thus, although the total species carrying capacity of an island can be approximated by its area, for describing the island's capacity in terms of archipelagic or single-island endemic species we have to consider more variables than just area.

Table IV. Model fits for the ATT² and the KTT² models for species richness and two metrics of evolutionary dynamics, namely nSIE, number of single-island endemics; and pSIE, proportion of SIEs. For each model, we provide R^2 values and F-values. † Denotes those cases for which the hump-shaped pattern is not observed. All the models were statistically significant at the $P < 0.05$ level.

| Island group | Taxon | Model | Indigenous | | Endemics | | SIE | | pSIE | |
|--------------|------------|------------------|---------------|----------|---------------|----------|---------------|----------|---------------|----------|
| | | | R^2 | F-values | R^2 | F-values | R^2 | F-values | R^2 | F-values |
| Azores | Arthropods | ATT ² | 0.87 | 50.83 | 0.93 | 123.69 | 0.75 | 11.72 | † 0.80 | 19.23 |
| | | KTT ² | 0.87 | 52.62 | 0.95 | 165.35 | 0.76 | 11.97 | † 0.83 | 22.03 |
| | Beetles | ATT ² | † 0.92 | 91.64 | † 0.89 | 55.76 | † 0.76 | 10.82 | † 0.79 | 19.23 |
| | | KTT ² | † 0.93 | 112.59 | † 0.89 | 57.65 | † 0.75 | 10.32 | † 0.76 | 13.27 |
| Canaries | Arthropods | ATT ² | 0.89 | 35.90 | 0.88 | 31.29 | 0.88 | 16.42 | 0.84 | 67.50 |
| | | KTT ² | 0.98 | 248.60 | 0.97 | 131.41 | 0.96 | 44.92 | 0.88 | 92.33 |
| | Beetles | ATT ² | 0.92 | 74.74 | 0.88 | 31.46 | 0.88 | 16.97 | 0.83 | 30.34 |
| | | KTT ² | 0.99 | 440.89 | 0.95 | 91.77 | 0.96 | 57.32 | 0.91 | 59.36 |
| Cape Verde | Arthropods | ATT ² | 0.67 | 15.67 | 0.68 | 17.52 | 0.53 | 4.97 | 0.22 | 10.97 |
| | | KTT ² | 0.73 | 19.42 | 0.76 | 24.00 | 0.58 | 5.75 | 0.22 | 10.93 |
| | Beetles | ATT ² | 0.60 | 12.31 | 0.56 | 10.60 | 0.36 | 5.95 | 0.11 | 5.00 |
| | | KTT ² | 0.68 | 15.56 | 0.64 | 13.19 | 0.43 | 6.80 | 0.15 | 5.24 |

In general, the addition of a surrogate of niche availability (i.e., available ecological space, see Gillespie, 2006) by means of the choros parameter K , improves the models in comparison with those based solely on area for most of the cases considered (Table III; see also MacArthur & Wilson, 1967; Hart & Horwitz, 1991; Kohn & Walsh, 1994; Triantis *et al.*, 2008b; Hortal *et al.*, 2009). Much attention has traditionally been given to the direct effect of area on species richness through the higher carrying capacity of larger areas, deriving from several effects: (i) larger areas can host larger populations, which in turn have reduced extinction risks (i.e. higher population viability), and (ii) larger areas offer larger “targets” for dispersing individuals (see Whittaker & Fernández-Palacios, 2007). However, area also has indirect effects on species richness through increased habitat diversity, i.e. larger areas are able to host more species due to their higher probability of containing more habitat types (see MacArthur & Wilson, 1967; Connor & McCoy, 1979; Hart & Horwitz, 1991; Triantis *et al.*, 2003). For example, in a recent study of taxa from a variety of island groups (including the Canaries, Azores and Cape Verde islands), Triantis *et al.* (2008b) reported that improved estimations of the surface area of each island through using a digital terrain model instead of planar area were not able to improve model fits, in contrast to the enhanced explanatory capacity of models incorporating simple independent measures of habitat diversity. They concluded that the precise quantification of factors such as climate, habitat diversity and evolutionary history (that may partially co-vary with area) might significantly improve our ability to develop predictive models of how species numbers vary across insular systems.

The general dynamic model of oceanic island biogeography

Within the framework offered by the GDM a number of different mathematical formulations can be developed, relating the area of each island, or other approximations of its carrying capacity, with its geological age (see Fig. 3), in order to explain diversity patterns. The heterogeneity in the processes generating and shaping diversity patterns in the different island groups of Macaronesia is reflected in the fact that no single model outperforms the rest for all datasets analysed (e.g. Borges & Hortal, 2009). Rather, a number of different formulas are selected as the best models for each of the taxonomical groups and/or archipelagos considered (see Tables III & IV). In the Azores, where most of the islands are relatively young (seven out of the nine islands are less than 4My), and in Cape Verde, with most of the islands being relatively old (eight out of 10 are older than 6 My), simple species–area or species–choros models, as well as AT models, are the best in describing the diversity patterns of arthropods and beetles, although their slopes have opposite signs (see Tables III & IV). In

the Canary Islands, which span a wide range of geological ages, the models follow a hump-shaped relationship between species richness and time, consistent with the GDM expectations for such a range of island ages as first proposed by Whittaker *et al.* (2008). As previously hypothesized, in general, species diversity in the Azores is better described by the left panel form of the species–area–time relationship in Figure 3 (see also Borges & Hortal, 2009), while species diversity in Cape Verde is better described by the right panel, with a general decrease with geological age.

Even though a number of different ‘best’ models were selected for the Azores and Cape Verde data sets (see Tables III and IV), in the Canary Islands the KTT² was the best model in all cases. In this archipelago the hump-shaped relationship with time (TT²) is needed to describe diversity patterns, whether in combination with area or the modified area–habitat diversity metric termed the choris (K) parameter. Islands of volcanic origin build up relatively quickly, reaching their maximum area and elevational range in their youth; afterwards their size and relief become increasingly dissected as they erode, gradually subsiding to finally disappear back into the sea, or persist as a low-lying atoll (see Whittaker *et al.*, 2008, 2009). Therefore for most oceanic archipelagos, one of the younger islands, or even the youngest, is the largest one (e.g. Hawaii, Galapagos). The current configuration of the Canaries corresponds reasonably well with the generalised island ontogeny, with islands of intermediate age being the largest and highest ones, compared to the younger and older ones. As a result, both area and, especially, elevation exhibit a hump-shaped relationship with geological age in this archipelago. This can, to a large extent, explain the effectiveness of models describing the diversity of many different Canarian taxa (see Whittaker *et al.*, 2008; see also below).

In contrast, the ATT² model (or the modified KTT²) is largely inadequate for the Azores, which can be explained within the GDM framework as being due to the recent age of the archipelago. Here, most groups of species deviate from the general ATT² form; for the Azores the AT (or the modified KT) model is the most parsimonious (see Table IV), corroborating the results of Borges & Hortal (2009), based on the SIE of beetles and arthropods (see also below). This can be attributed to a number of factors. On the one hand, although the oldest island of the group, Santa Maria, has a maximum geological age of 8.12 My, four of the islands of the group, representing 38% of its total area, are younger than 1 My. This “youthfulness” is a possible explanation of the observed pattern of endemism in the Azores. An additional crucial factor is the geological history of the largest island of the group, São Miguel. This island has a maximum geological age of 4.01 My, but it reached its current

shape just 0.05 My ago, by the formation of a land bridge between an older eastern island that originated 4 My ago and a younger western island that originated 0.55 My. Thus, most of the island is younger than 1 My, increasing the percentage of the archipelagic area that is younger than 1 My to 62% (see Fig.1 in Van Riel *et al.*, 2005). The complex geological history of São Miguel has certainly played an additional role in determining the comparatively low endemism of the Azores. Since just one-fourth of the island is older than 3 My, it is likely that its role as stepping-stone for most species to colonize the central islands from Santa Maria might have been limited due to its reduced area and elevation, compared to its current configuration (e.g. Van Riel *et al.*, 2005). This would in turn have increased the isolation of the central islands, such as Terceira, throughout large periods of time. Moreover, most of Terceira Island is also young, and the recent part was the result of highly destructive eruptions of Plinian and Sub-Plinian type that formed the St. Bárbara Caldeira. This implies that the older stepping-stone to the Central Group of Islands was also only recently available for colonization with its current large area, and that many species went extinct during these episodes of explosive volcanism. All these factors together lead us to hypothesize that some of the new clades originated in Santa Maria have gone extinct during the missing step phase, vanishing for ever. We call this the “*missing step hypothesis*” (see also below).

Geological idiosyncrasies and seamounts

Many remote oceanic islands (e.g. in hotspot archipelagos, fracture zones, etc) are formed by volcanic activity of limited duration. Thus, apart from some well-known exceptions, remote volcanic islands forming over oceanic crust are typically short-lived. All Macaronesian islands share a number of common features, such as being oceanic and of volcanic origin, having formed over oceanic plates, and never having been connected to continental landmasses. However, the mechanisms forming the different islands vary greatly from group to group, resulting in a highly dynamic and complex set of archipelagos. Importantly, none of the Macaronesian archipelagos exhibit the configuration of the simplest hot-spot chains, such as Hawaii. Rather, Cape Verde group is virtually stationary relative to the lithosphere, without plate movement being involved (see Holm *et al.*, 2006), and the Azores arose over three different continental plates, the American, the European and the African, and exhibit complex geological dynamics (see, e.g., Borges *et al.* 2009). The Canary and Madeiran archipelagos are quite different in their current configuration, with the Madeira group being now reduced to a single major island (i.e. Madeira, 755 km²), an old small island that is almost entirely eroded (i.e. Porto Santo, 40 km²), and a few small islets (Geldmacher *et*

al. 2005; see Fig. 2a). In contrast, the distribution of volcanoes within the Canaries does not confirm tightly to the age-dependency posited within the GDM, since individual volcanoes are active for much longer intervals, so that their spatial distribution and age variation are in practice very complex (e.g., Geldmacher *et al.*, 2005). Regardless of these differences between archipelagos, according to Hoernle & Carracedo (2009) the hotspot model can adequately explain the parallel age progressions for the Canary and Madeira volcanic provinces, after considering the rotation of the African Plate (see Fig. 2a).

In addition to the differences in their patterns of emergence from the oceanic crust, the geological complexity of the Macaronesian system is also apparent in the process of island construction. Within an archipelago, islands may differ in the types of volcanism, so that they contain volcanic edifices of very different types, e.g. Hawaiian (i.e., massive lava flows), Strombolian (i.e., explosive), Plinian or Sub-Plinian (i.e., violent eruptions, even within the same island (Carracedo & Tilling, 2003). The prevalence of more destructive types of volcanism can have dramatic effects on the biota of the island, as can the occurrence of renewed volcanism. This latter point is well exemplified in the case of Tenerife, where two or three ageing massifs were joined into a single island by Pleistocene volcanism. In such cases, the maximum age of the island is likely to be at best an imperfect surrogate for the time available for diversification. This is a particularly important feature of the Macaronesian Islands, since most of them (if not all) have suffered repeated volcanic episodes, some of them potentially capable of extinguishing multiple lineages while putting new terrain in place, thus replenishing area and habitat. Consequently, although the maximum age of each of the islands considered here (i.e., their age of emergence from the sea) is more or less agreed upon (although the geology of Cape Verde Islands is least known), it is not always clear which estimate is most appropriate to describe the time available for the establishment, evolution and extinction of lineages and species, particularly when different taxa are considered (see Carracedo & Tilling, 2003; Emerson & Kolm, 2005; Whittaker & Fernández-Palacios, 2007; Whittaker *et al.*, 2008, 2009; Borges & Hortal, 2009).

The relatively recent discovery of a wide array of subsided seamounts throughout the Atlantic (Wessel, 2009), which once formed a large archipelago above sea level, provides additional insight into the potential origins and age of island floras and faunas. Although the possible contribution of these palaeo-islands as sources of diversity has been appreciated in the case of Hawaiian Islands (see for example Givnish *et al.*, 2009 and general discussion in Price & Clague, 2002), in the case of the Macaronesian Islands (see Fig. 2) a general

overview of their contribution is still lacking (but see Yanes *et al.*, 2009 and J.M. Fernández-Palacios this book).

Here we hypothesize that a number of characteristics of the Macaronesian island groups are likely to be strongly related with the existence of these palaeo-islands, currently reduced to seamounts. Namely, three different factors might be contributing to their idiosyncrasies in terms of species richness and endemism (see also the chapter from J.M. Fernández-Palacios, this book):

1) ***Reduced isolation from the closest species source, larger species pools and rescue effects.*** Compare Figures 1 and 2 in terms of the isolation of Madeira and Porto Santo Islands, which are part of an island chain that dates back to 65-67 My. Currently these islands are 630 km from the closest mainland and 450 km from the closest island group, the Canary Islands. However, current seamounts Seine and Ampère were above the sea-level during the last glacial maximum (according to García-Talavera, 1999; see Fig. 2b). Thus, some 15,000 years ago the isolation from the large species pools of either the Iberian Peninsula and/or Morocco was much smaller than the current configuration of the island group, thanks to the role of these seamounts as stepping-stones. This stepping-stone hypothesis may help explaining the exuberant diversity of Madeira (see Borges *et al.*, 2008a), as well as why the Madeiran biota is comparatively more closely related with the Iberian Peninsula than with the biota of the Canary Islands (see Borges *et al.*, 2008a, b).

Apart from reducing the isolation from possible source pools, the existence of these palaeo-islands at some point during the “life” of the current islands of the island groups in Macaronesia increases the number of species that could potentially overcome the sea barrier and colonise them, also reducing the probability of extinction of many species thanks to rescue effects.

2) ***The time for speciation available.*** Perhaps the most important feature in shaping colonization and diversification processes in a chain of oceanic islands is the simultaneous existence above sea-level of at least two large-sized islands, allowing the fauna and flora existing in the older island to colonize the youngest one, i.e. producing a progression rule pattern (see Funk & Wagner, 1995). For example, although the total age of the Hawaiian-Emperor chain goes back to 70 My, there was a long period, at least between 33 My and 29 My, when no large islands existed. Thus, distant colonization was the only possible source of colonizers for the younger islands of the Hawaiian chain that began to emerge between about 29 and 23 My (Clague *et al.*, 2010). Considering the total age of the island chains that the Canaries and the Madeira archipelagos belong to, i.e. more than 60 My, this realisation

increases dramatically the possible persistence of many lineages in the palaeo-archipelagos, and therefore the time available for diversification since colonization from the continent.

3) **Increased adaptability.** Certain clades, such as the beetle genera *Trechus*, *Tarphius* or *Acalles*, show impressively large radiations in the Macaronesia, with large numbers of derived species in most islands/island groups. Based on the patterns of diversification of these groups it is tempting to postulate that oceanic island chains not only operate as an array of stepping stones for colonization processes, but that they could also act as evolutionary filters where the lineages that already colonized a part of the island system accumulate an increasing propensity to radiate in response to ecological opportunities offered as islands appear sequentially. These lineages would gradually dominate the respective ecological space within the island chain. Savolainen *et al.* (2002) noted that one of most interesting and less studied patterns in macroevolution is the potential heritability of cladogenesis, i.e. whether daughter lineages tend to be similar to their ancestors in rates of speciation and/or extinction. However, little direct evidence has been available to assess the occurrence, strength, or generality of this heritability. Studying the most remarkable example of evolutionary radiation, the cichlid fishes of the Great African Lakes, Seehausen (2006, p. 1994) proposed that “the propensity to radiate in response to ecological opportunity is a derived property that accumulated or increased sequentially within the evolutionary history of one lineage among the African cichlids.” and also “Instead of attributing the propensity for intralacustrine speciation to morphological or behavioural innovations, it is tempting to speculate that the propensity is explained by genomic properties that reflect a history of repeated episodes of lacustrine radiation: the propensity to radiate was significantly higher in lineages whose precursors emerged from more ancient adaptive radiations than in other lineages”. The island groups of the Macaronesia, due to their proximity and up to a certain extent similarity, can offer significant insights in the study of such patterns since the behaviour of the same taxon/clade can be studied in the different island groups, allowing us to identify those clades that consistently show unusually high diversification rates.

Concluding remarks

Recent studies have developed a number of new hypotheses to explain the emergent macroecological and macroevolutionary diversity patterns in Macaronesia, relating these patterns to several geographical factors, the particularities of each biological group, or the climatic history of the islands (Kim *et al.*, 2008; Whittaker *et al.*, 2008, 2009; Borges &

Hortal, 2009; Carine & Schaefer, 2010). Recently, Carine & Schaefer (2010) proposed the late Quaternary palaeoclimatic variation as an important factor for the low percentage of SIEs in the Azorean flora, compared with the Canary Islands. According to these authors, the climatic stability of the Azores would not have allowed recent diversification of the Azorean flora. Kim *et al.* (2008) studying the radiations of monophyletic endemic plant lineages across Macaronesia, identified three discrete waves of colonization of Macaronesia islands from the western Mediterranean, offering support to the “colonization window hypothesis” (Carine, 2005), according to which the opportunity for island colonization may have been constrained to one or more distinct periods of time. Such diversity of hypotheses illustrates the difficulty of finding a unique explanation for the patterns of species diversification in the complex and heterogeneous system formed by all Macaronesian archipelagos.

In spite of this, the results of the present work confirm that a combination of area and geological age of the islands is enough to provide a basic explanation for the diversity of endemic arthropods. Also, and importantly, habitat diversity, instead of just area, stands out as one of the main drivers of arthropod diversity and, potentially, diversification in the Macaronesia. The existence of numerous seamounts that have arisen in the past as palaeo-islands, some of them also emerging above sea level during the glaciations, adds a further dimension of complexity to the evolutionary patterns on this region. Understanding the effects of habitat diversity and the potential role of the palaeo-islands in the evolutionary patterns of diverse groups might help in efforts to disentangle the complex history of the Macaronesian biota.

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