



Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.de/ppees

Research article

Additive partitioning as a tool for investigating the flora diversity in oceanic archipelagos

Alessandro Chiarucci^{a,*}, Giovanni Bacaro^a, José Ramón Arévalo^b,
Juan Domingo Delgado^c, José María Fernández-Palacios^b

^a BIOCONNET, Biodiversity and Conservation Network, Department of Environmental Science “G. Sarfatti”, University of Siena, Via P.A. Mattioli 4, 53100 Siena, Italy

^b Department of Ecology, La Laguna University, La Laguna, 38206 Tenerife, Spain

^c Department of Physical, Chemical and Natural Systems, Pablo de Olavide University, E-41013 Sevilla, Spain

ARTICLE INFO

Article history:

Received 24 January 2009

Received in revised form

4 January 2010

Accepted 5 January 2010

Keywords:

Additive partitioning

Biodiversity

Pteridophytes

Island biogeography

Species diversity

Spermatophytes

ABSTRACT

This paper introduces the integration of additive partitioning with species–area relationships to island biogeography in order to address the question “How are the pteridophyte and spermatophyte native and endemic flora of different oceanic archipelagos partitioned across islands?”.

Species richness data of all endemic species and all native species of pteridophytes and spermatophytes were obtained for the Azores, Canaries and Cape Verde in the Atlantic Ocean and Galápagos, Hawaii and Marquesas in the Pacific Ocean. Additive partitioning of species diversity was used to quantify how much of the total diversity of an oceanic archipelago flora (γ -diversity) is due to (i) the mean species richness of the flora of each island (α -diversity), (ii) the variability in species richness of the floras across islands ($\beta_{\text{Nestedness}}$) and (iii) the complementarity in species composition of the floras of different islands ($\beta_{\text{Replacement}}$). The analysis was separately performed for the native and endemic pteridophyte and spermatophyte floras.

The diversity partitioning of the six archipelagos showed large differences in how the flora of each archipelago is partitioned among the α , $\beta_{\text{Nestedness}}$ and $\beta_{\text{Replacement}}$ components, for pteridophytes and spermatophytes and for all endemic species and all native species. The α -diversity was more important for all native species than for endemic species and more important for pteridophytes than for spermatophytes, with the Azores showing outstanding high values of α -diversity. The $\beta_{\text{Nestedness}}$ was higher for pteridophytes than for spermatophytes and higher for endemic species than for all native species in both pteridophytes and spermatophytes. The values of $\beta_{\text{Replacement}}$ suggested that: (i) the spermatophyte native flora is more differentiated across islands than the pteridophyte native flora and (ii) the pteridophyte endemic flora and, especially, the spermatophyte endemic flora are more differentiated across islands than the corresponding native flora. An outstanding value of $\beta_{\text{Replacement}}$ for endemic and all native spermatophytes was found in Hawaii, confirming the biogeographical island differentiation in this archipelago.

© 2010 Rübél Foundation, ETH Zürich. Published by Elsevier GmbH. All rights reserved.

Introduction

After Wallace (1881) oceanic archipelagos are defined as groups of islands with an exclusive volcanic origin that have never been connected to continents. Volcanic islands are subject to erosion and subsidence, and after a variable existence their emerged mass can disappear or be replaced by atolls. Their native biotas are composed of species that arrived via long-distance dispersal or evolved through *in situ* speciation and are characterised by species poverty and disharmony, in comparison to the nearby continental ones (Whittaker and Fernández-Palacios,

2007; Whittaker et al., 2008). Because of the colonization difficulties, speciation processes are particularly important in these ecosystems and result in high percentages of endemic taxa (Carlquist, 1974; Williamson, 1981; Kier et al., 2009). These endemic taxa can be exclusive to a single island (Single Island Endemics, SIEs hereafter) or shared by some or all of the islands of an archipelago (Multiple Island Endemics, MIEs). Similarly, the non-endemic native species can be present on a single island (Single Island Natives, SINS) or spread across several islands within an archipelago (Multiple Island Natives, MINs). These features make the biota of each island and archipelago a unique product of ecological and evolutionary factors (Wagner and Funk, 1995; Grant and Grant, 2008). Catastrophic events such as volcanic eruptions, landslides and tsunamis can destroy part or all of the island biotas, making terrain available for new processes

* Corresponding author: Tel.: +39 0577 232872; fax: +39 0577 232896.
E-mail address: chiarucci@unisi.it (A. Chiarucci).

of colonization, succession and evolution (Thornton, 2007; Whittaker and Fernández-Palacios, 2007).

Despite oceanic archipelagos share several biogeographical and ecological characteristics, they differ in features such as number of islands, island distribution, area, age, isolation, altitudinal ranges and climate (Whittaker and Fernández-Palacios, 2007). They are natural experiments, in which the biotas have been shaped by a specific combination of ecological and evolutionary processes. Species diversity patterns in these ecosystems have been widely investigated, for native, endemic and also alien species, within a single archipelago (Wagner and Funk, 1995; Price and Clague, 2002; Willerslev et al., 2002; Price, 2004; Price and Elliott-Fisk, 2004; Duarte et al., 2008; Kueffer et al., 2010) or across different archipelagos (e.g. Triantis et al., 2008a, 2008b; Whittaker et al., 2008), but with the focus constantly at the island scale.

Plants are well studied *taxa* in many oceanic archipelagos but, despite the availability of species richness data, few global tests have been performed on the flora diversity at the archipelago scale (Hobohm, 2000; Kreft et al., 2008). Kreft et al. (2008) observed that the global patterns of plant species richness on islands is poorly documented, while Kier et al. (2009) showed that islands have a number of endemics largely exceeding that of continents, but scarce emphasis was given to the floristic patterns at the entire-archipelago scale. As pteridophytes and spermatophytes differ in dispersal abilities they are expected to show non-concordant responses to the biogeographical and ecological factors in oceanic archipelagos (Whittaker and Fernández-Palacios, 2007).

The partitioning of species diversity across the islands of an archipelago in species-rich *taxa* is poorly known, and few data exist to permit across-archipelagos comparisons. Partitioning of species diversity can be performed by different approaches, the most attractive being additive partitioning (Lande, 1996; Wagner et al., 2000). Unlike the classic multiplicative method of Whittaker (1960, 1972), in additive partitioning the total species richness of a system (γ -diversity) is obtained by summing the mean α -diversity and the β -diversity:

$$\gamma = \bar{\alpha} + \beta. \quad (1)$$

This approach is attractive, since all the components of species diversity (α -, β - and γ -diversity) are measured with the same unit, that is simply species richness.

Additive partitioning of species diversity was recently applied for the testing of biogeographical or ecological questions (e.g. Wagner et al., 2000; Crist et al., 2003; Chiarucci et al., 2008), but it has not yet been applied to island biogeography. In addition, the proposal by Crist and Veech (2006) for combining additive partitioning with species–area curves is very attractive for island biogeography studies. In fact, this approach also permits to quantify how much of the β -diversity is due to the differences in flora size across units, as the islands of an archipelago, and how much is due to the differences in species composition across them.

The aim of this paper is to introduce the integration of additive partitioning with species–area relationships to island biogeography island biogeography, by answering to the following question: *How are the native and endemic pteridophyte and spermatophyte flora of different oceanic archipelagos partitioned across islands?* The archipelagos with data for testing this question were Azores, Canaries and Cape Verde in the Atlantic Ocean and Galápagos, Hawaii and Marquesas in the Pacific Ocean.

Study areas

The six previously indicated archipelagos (Fig. 1 and Table 1) are shortly described here.

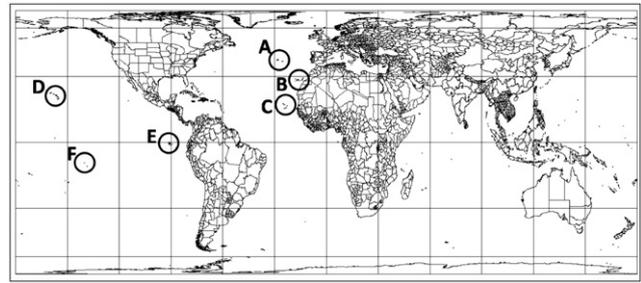


Fig. 1. Geographic location of the six investigated archipelagos. A: Azores; B: Canaries; C: Cape Verde; D: Hawaii; E: Galápagos; F: Marquesas.

Azores

The Azorean archipelago is located in the Northern Atlantic Ocean and formed by 9 islands belonging to three clusters: Eastern (Santa María and Sao Miguel), Central (Terceira, Graciosa, Sao Jorge, Pico and Faial) and Western (Flores and Corvo). Located on both sides of the Central Atlantic Submarine Ridge, the western and eastern extremes of the archipelago are actually drifting away from each other (França et al., 2003). During the last glaciation, Faial and Pico made a single landmass and some submarine banks emerged forming stepping-stones, enhancing the intra-archipelago dispersal (França et al., 2003). Thanks to the Gulf Stream, Azores possess wet and mild climate. In general they are an ecologically homogeneous system, with a fair proportion of endemic plants (ca. 33% Carine and Schaefer, 2010).

Canaries

The Canary archipelago is formed by 11 islands and islets that share biotic affinities with the Mediterranean region. Despite its age (20 My), all the islands, except La Gomera, are volcanically active. The Pleistocene glaciations have reiteratively doubled and halved the archipelago area, with consequences such as the fusion of Lanzarote, Fuerteventura and their satellite islets (Lobos, La Graciosa, Alegranza and Montaña Clara) into a single landmass (Mahan), the emersion of several seamounts (Amanay, Dacia, Conception) and the reduction of the distance to the African mainland (García Talavera, 1999). Affected by a Mediterranean-type climate, the Canaries exhibit an outstanding ecosystem diversity, ranging from the hot, dry semi-desert vegetation of the coastal lowlands, through the thermophilous woodlands, the laurel forest zone, pine forest to the summit scrub. This ecosystem diversity, its long history and a persistent isolation have enabled the existence of a very important endemic flora, comprising 680 different plant taxa (Reyes-Betancort et al., 2008).

Cape Verde

The Cape Verde archipelago comprises 12 volcanic islands and islets divided into two well-defined groups, the windward (Santo Antao, Sao Vicente, Santa Luzia, Branco, Razo, Sao Nicolau, Boavista and Sal) and the leeward (Maio, Sao Thiago, Fogo and Brava) chains. During the glaciations the windward islands (except Boavista and Sal) joined reiteratively into a single landmass (Kämmer, 1982). The archipelago is frequently affected by the Saharan dust-carrying winds as well as by the tropical monsoons, which result in a dry, summer-rain, climate. Its species-poor native flora has both Macaronesian and tropical affinities, with a low to moderate endemism level (Brochmann et al., 1997; Arechavaleta et al., 2005).

Table 1
Selected geographical and biological features of the six investigated archipelagos.

	Azores	Canaries	Cape Verde	Galápagos	Hawaii	Marquesas
No islands > 1 km ²	9	11	12	17	8	9
Total area (km ²)	2764	7445	4033	7876	16,759	1049
Maximum elevation (m)	2351 (Pico)	3718 (Tenerife)	2835 (Fogo)	1707 (Isabela)	4205 (Hawaii)	1230 (Ua Pou)
Continental isolation (km)	1369 (Sao Miguel)	97 (Fuerteventura)	571 (Boavista)	927 (San Cristóbal)	3675 (Hawaii)	4737 (Hatutaa)
Mean intra-archipelago isolation (km)	220.0	196.5	140.8	140.1	168.8	146.5
Latitude (deg)	37–40N	27–29N	15–17N	1N–1S	19–23N	7–11S
Age (My)	8 (Sta. María)	20 ^a (Fuerteventura)	16 (Sal)	3.3 ^a (Española)	5.1 ^a (Niihau)	7 (Eiao)
Last volcanic eruption	1957 (Faial)	1971 (La Palma)	1995 (Fogo)	2008 (Isabela)	2008 (Hawaii)	Pleistocene (?)
Pteridophyte ANS	48	50	33	110	161	102
Pteridophyte AES	7	3	1	5	119	31
Spermatophyte ANS	164	1204	209	439	1003	229
Spermatophyte AES	61	582	65	141	905	130

^a Age of the oldest emerged island, which does not preclude the existence in the archipelago of older, today-submerged islands. Various sources: ANS: All Native Species; AES: All Endemic Species.

Galápagos

Located in the East Pacific Ocean, this archipelago was formed by the activity of a hot spot that has been active for more than the age of the present oldest island (Española, 3.3 My). This implies that islands at the eastern extreme of the archipelago have previously existed and have since been submerged (Werner et al., 1999). During the glacial age, the large western-central islands (Fernandina, Isabela, Santa Cruz and the islets between them) seem to have formed a single large island (Geist et al., in press), whereas the major volcanoes of Isabela seem to have been separated by water or barren lava fields throughout their existence, so the island is functionally six separate islands (Willerslev et al., 2002). For a tropical location, the Galápagos Islands possess a rather poor flora, even if rich in endemisms. This is considered to be caused by the persistent volcanic activity on the young islands (Isabela, Fernandina, Santiago, Pinta and Marchena) and the dry climate. However, the trade winds that dominate January–June create orographic drizzle or rain on the south side of the islands, so that all islands higher than 500 m have some mesic to hydric vegetation.

Hawaii

The Hawaiian archipelago is made by 8 islands located in the middle of the Pacific Ocean. Although the oldest extant island (Niihau) is just 5.1 My old, the origin of the archipelago dates back to almost 70 My ago. During this time interval this hot spot has formed the islands that today constitute the reefs, shoals and atolls of the Hawaiian leeward chain (Price and Clague, 2002). During the Pleistocene sea-level minima Maui, Molokai, Lanai and Kahoolawe formed a single, large island named Maui Nui (Price and Elliott-Fisk, 2004). The influence of the NE trade winds, coupled with the high elevation of the islands (Hawaii and Maui peaks surpass 3000 m) creates steep climatic gradients, both in elevation and exposition, resulting in an array of ecosystems ranging from the arid scrubs at the leeward coasts, through dry, mesic and wet forests, to alpine summit scrubs. Furthermore, the outstanding isolation of Hawaii has given rise to a biota relatively poor in species but almost exclusively endemic (Price, 2004).

The Marquesas

The Marquesas archipelago, located in the Eastern Pacific Ocean, is made by 9 main islands, belonging to two entities: the northern (Eiao, Hatutaa, Nuku Hiva, Ua Pou and Ua Huka) and the

southern (Tahuata, Moho Tani, Fatu Hiva and Hiva Oa) groups. All islands are moderately high volcanic islands with extremely rugged terrain and not surrounded by protective fringing reefs (Clouard and Bonneville, 2005). Although the islands lie within the tropics, they are the first major break in the prevailing easterly winds spawned from the extraordinarily dry air masses above the Humboldt Current. The islands are thus subjected to frequent drought conditions, with only the higher, cloud encompassed islands having reliable precipitation (from 1000 to over 2800 mm per year). These conditions determines an homogeneous system characterized by an impoverished native flora (ca. 360 species), although with an important (42%) endemic element (Florence and Lorence, 1997).

Methods

Data collection

Data about the native pteridophyte and spermatophyte flora of each island and archipelago (only the species-level *taxa* were included in the data) were obtained from Borges et al. (2005) for the Azores, Kunkel (1980) for the Canaries (the checklist by Izquierdo et al. 2004 was not used, since it lacks data for the islets Alegranza, Montaña Clara, La Graciosa and Lobos); Arechavaleta et al. (2005) for the Cape Verde; Lawesson et al. (1987) for the Galápagos; Price (2004) for the Hawaiian islands; and *The Flora of Marquesas webpage* (2008) by the Smithsonian Institution for the Marquesas. Only islands larger than 1 km² were included in the analyses, as the smaller islets usually lacked good quality data. The islands included in the analyses, with the indication of their number of SIEs, MIEs, SINS, MINs and All Native Species (ANS), for both pteridophytes and spermatophytes are reported in Appendix 1.

Data analyses

For each archipelago, the mean α -diversity was defined as the mean species richness per island i (\bar{S}_i). Similarly, the γ -diversity was defined as the total species richness of the archipelago. For each archipelago, the total β -diversity (β_{Total}) was then calculated by subtracting the mean α -diversity (\bar{S}_i) from the γ -diversity, which is the same of using the following equation:

$$\beta_{\text{Total}} = \frac{1}{N} \sum_{i=1}^N \gamma - S_i \quad (2)$$

where S_i is the species richness of the island i , γ is the total species richness of the archipelago and N is the number of islands of the

archipelago. Accordingly, the total β -diversity of an archipelago (β_{Total}) represents the average number of species of the archipelago flora that is missing from each island.

Then, two different components of β -diversity were quantified by using a modification of the method of Crist and Veech (2006). They proposed to calculate the different components of β -diversity based on differences in area size across units (e.g. the islands of an archipelago). However, in oceanic islands, area alone can be distorting, because of the volcanic activity and other factors. As an example, consider Big Island in the Hawaiian archipelago, which is larger than the sum of all other Hawaiian islands, but its flora is less rich than those of Maui, Oahu and Kauai (which are 5.5–7.3 times smaller), simply because most of the area in Big Island is made by recent lava barren. To cope with this, some authors used a modified measure of area, defined as the area not covered by recent lava (Willerslev et al., 2002). Here, the size of the flora (species richness) of each island i (S_i) was used as an indirect variable expressing the effect of island area but also age, isolation, habitat diversity and other factors.

The first component of β -diversity ($\beta_{\text{Nestedness}}$) quantified the degree of nestedness of the flora, i.e. the differences in species richness across islands due to the “thinning” of the flora in each island from the flora of the richest one. The second β -diversity component ($\beta_{\text{Replacement}}$) measured the differences in species composition among the flora of the islands within an archipelago, and it is a measure of the compositional differences across islands. To do this, let S_{max} be the number of species present in the most species rich island; it is then possible to estimate $\beta_{\text{Nestedness}}$, by substituting S_{max} into Eq. (2):

$$\beta_{\text{Nestedness}} = \frac{1}{N} \sum_{i=1}^N S_{\text{max}} - S_i \quad (3)$$

where S_i is the observed species richness on each island i and N is the number of islands. In this way, $\beta_{\text{Nestedness}}$ quantifies the mean deviation between the species richness of the most species rich island and the species richness of each island. In an archipelago with a perfectly nested flora, the flora of the most species-rich island (S_{max}) corresponds to the flora of the whole archipelago (γ -diversity), while each other island only has a subset of this species pool; consequently, in this case, the total β -diversity is only due to the differences in the size of the island floras ($\beta_{\text{Nestedness}} = \beta$). In reality, the islands of an archipelago also differ in species composition and, consequently, the flora of the most species-rich island (S_{max}) is less rich in species than the flora of the whole archipelago (γ). As a consequence, the total species richness of the archipelago is given by the sum of the mean island flora (α), the differences in the island floras due to nestedness ($\beta_{\text{Nestedness}}$) and those due to differences in species composition ($\beta_{\text{Replacement}}$), as given below:

$$\gamma = \alpha + \beta_{\text{Nestedness}} + \beta_{\text{Replacement}} \quad (4)$$

Then, the value of $\beta_{\text{Replacement}}$ can be calculated by subtracting the $\beta_{\text{Nestedness}}$ from the total β -diversity.

Following this approach, the α , $\beta_{\text{Nestedness}}$ and $\beta_{\text{Replacement}}$ components of the species richness of each archipelago were calculated for ANS (calculated as SIEs+MIEs+SINs+MINs) and all endemic species (AES, calculated as SIEs+MIEs) of both pteridophytes and spermatophytes. To make the value comparable, the values of α , $\beta_{\text{Nestedness}}$ and $\beta_{\text{Replacement}}$ were then expressed as percentage of the γ -diversity for that *taxon* (pteridophytes and spermatophytes) and chorological group (ANS and AES) within each archipelago.

Given the low number of archipelagos used for this investigation it was not possible to apply rigorous statistical tests for assessing differences. A measure of the differences in the

partitioning of species richness across archipelagos was estimated according to the following procedure. For each *taxon* and chorological group, each archipelago was defined as a point in a three-dimensional space, with axes defined by the proportion of α , $\beta_{\text{Nestedness}}$ and $\beta_{\text{Replacement}}$ components of species richness, so that the differences in species richness did not have any effect. To measure the difference in the partitioning of species diversity, the distance between each pair of archipelagos was calculated as Euclidean Distance.

Results

The diversity partitioning of the six archipelagos (Fig. 2), showed huge differences in how the total archipelago species richness is partitioned in the α , $\beta_{\text{Nestedness}}$ and $\beta_{\text{Replacement}}$ components for the two *taxa* (pteridophytes and spermatophytes) and the two chorological groups (ANS and AES). The α -diversity accounted on average for 43.8% of the pteridophyte ANS, and for 40.4% of the spermatophytes ANS, but it varied largely across archipelagos. The Azores showed consistently the highest relative value of α -diversity for all the cases studied, while the lowest value was showed by Galápagos for pteridophyte and spermatophyte ANS and by the Canaries for pteridophyte and spermatophyte AES. In general, the α -diversity was less important for AES than for ANS (Fig. 2), with this pattern being consistent across pteridophytes and spermatophytes for all the archipelagos except Galápagos.

The $\beta_{\text{Nestedness}}$ component of species diversity also varied considerably across the six archipelagos and the four groups of plants considered, averaging 39.2% for the pteridophyte ANS and 27.6% for spermatophyte ANS. This component of species diversity was consistently higher for AES than for ANS, for all the archipelagos and the two chorological groups, except spermatophytes at Galápagos.

Thus, the two components of species diversity linked to the flora size of each island and its variation (α and $\beta_{\text{Nestedness}}$) showed contrasting responses for ANS and AES in pteridophytes and spermatophytes: in pteridophyte, the AES showed a lower importance of α -diversity and a higher importance of $\beta_{\text{Nestedness}}$ than the ANS, while an opposite pattern was shown in spermatophytes.

The $\beta_{\text{Replacement}}$ component of species diversity, measuring the compositional differences across the islands within an archipelago, showed the largest differences between pteridophytes and spermatophytes, with spermatophytes having almost double the values of $\beta_{\text{Replacement}}$ than pteridophytes (for both ANS and AES) and AES showed slightly larger values than ANS. This indicated that: (i) within an archipelago, the flora of spermatophyte ANS is more differentiated across islands than the flora of pteridophyte ANS and (ii) within an archipelago the flora of pteridophyte AES and, especially, the flora of spermatophyte AES is more differentiated across islands than the corresponding flora of ANS. This pattern had some exceptions: for the flora of pteridophyte AES, Cape Verde and Galápagos had zero values of $\beta_{\text{Replacement}}$, because all their endemic species were MIEs (i.e. shared by different islands), and there is consequently no replacement. For spermatophytes, Azores and, in a smaller measure, Cape Verde had a lower $\beta_{\text{Replacement}}$ for AES than for ANS, indicating that their endemic flora is largely shared by different islands.

When the α , $\beta_{\text{Nestedness}}$ and $\beta_{\text{Replacement}}$ diversity partitioning are compared across archipelagos (Table 2) the following observations emerge: (i) the six archipelagos are more differentiated for pteridophytes than for spermatophytes (the mean distance across archipelago was 34.2 and 28.4 for pteridophyte and spermatophyte ANS, respectively; 42.5 and

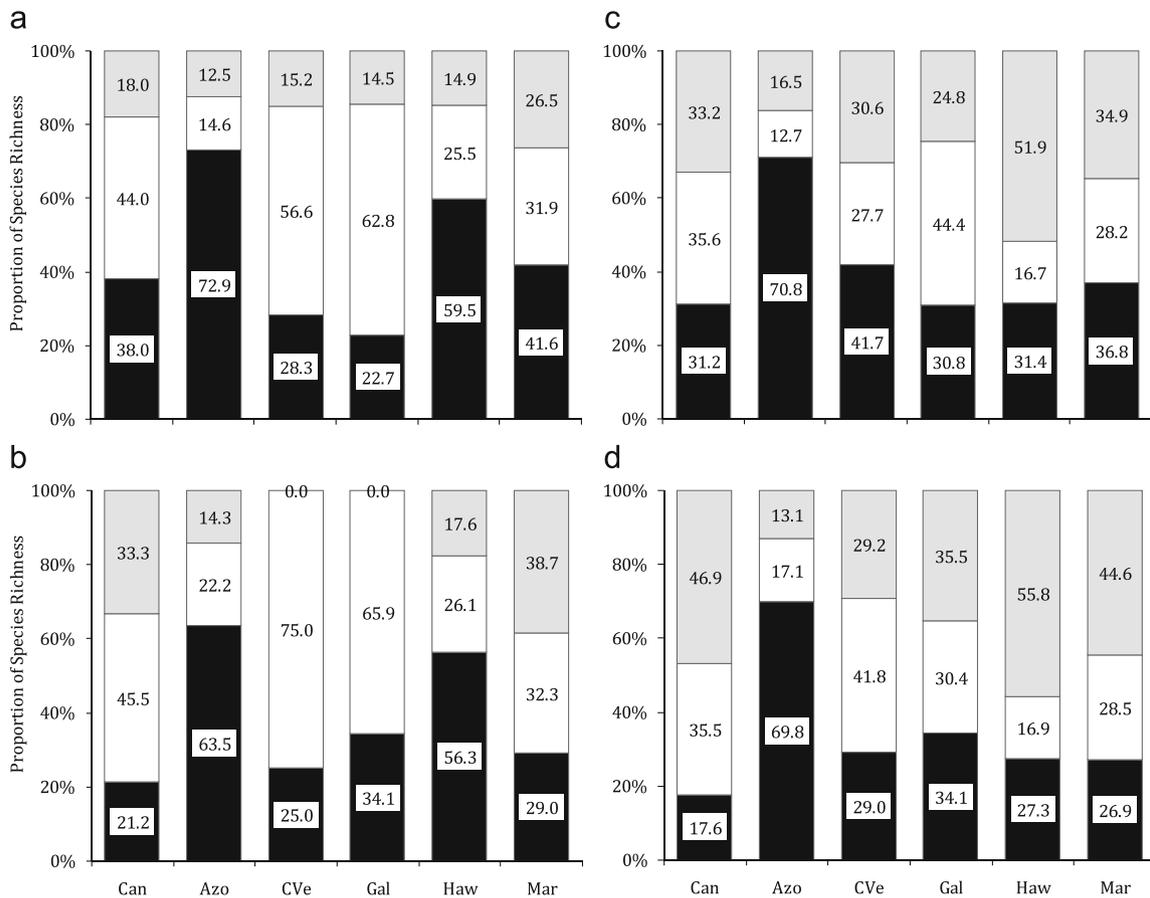


Fig. 2. Summary of the additive partitioning of species richness (black for the α -, white for the $\beta_{\text{Nestedness}}$ - and grey for the $\beta_{\text{Replacement}}$ - components of species diversity) for the six investigated archipelagos: (a) Pteridophyte ANS (All Native Species); (b) Pteridophyte AES (All Endemic Species), (c) Spermatophyte ANS and (d) Spermatophyte AES.

31.7 for pteridophyte and spermatophyte AES, respectively); (ii) the six archipelagos are more different for the flora of AES than for that of ANS (the mean distance across archipelagos was 34.2 and 42.5 for pteridophyte ANS and AES, respectively; 28.4 and 31.7 for spermatophyte ANS and AES, respectively). For pteridophyte ANS, Azores shows the most different partitioning pattern with respect to the other archipelagos (mean distance 46.6, Table 2), while Canaries shows the most similar one (mean distance 26.1, Table 2); for pteridophyte AES, Cape Verde shows the most different partitioning pattern with respect to the other archipelagos (mean distance 48.6, Table 2), while Hawaii shows the most similar one (mean distance 39.3, Table 2). For spermatophytes, Azores is the archipelago with the most different partitioning of species richness for ANS and for AES (mean distance 46.2 and 54.8, respectively, Table 2), and this is clearly due to its extremely high value of its α -diversity. The other archipelagos show more compact distances, with Marquesas showing the least distant partitioning compared to the other five archipelagos for both ANS and AES (mean distance 19.8 and 22.9, respectively, Table 2).

Discussion

To our knowledge, this is the first attempt to use the integration of additive partitioning of species diversity (Lande, 1996; Wagner et al., 2000) with species–area relationships, proposed by Crist and Veech (2006), to analyse the diversity of the native flora in oceanic archipelagos, a classic issue in island biogeography. This approach was adopted to address questions as

how the ecological heterogeneity and distance-decay affect total species richness of birds within landscapes and ecoregions (Veech and Crist, 2007) or how the different size and ecological similarity of nature reserves contribute to the total plant species richness within a region (Chiarucci et al., 2008). Here, this approach was used to quantify how much of the total flora of a oceanic archipelago (γ -diversity) is due to (i) the mean species richness of the flora of each island (α -diversity), (ii) the variability in species richness of the island floras measurable in terms of flora nestedness ($\beta_{\text{Nestedness}}$) and (iii) the complementarity in species composition of island floras ($\beta_{\text{Replacement}}$), in pteridophytes and spermatophytes and for both all native and endemic species. The results showed consistent patterns in the three diversity components of species richness (α , $\beta_{\text{Nestedness}}$ and $\beta_{\text{Replacement}}$). The pteridophyte flora of each archipelago, for both all native and endemic species, is largely related to the size of the island floras and its variability (α and $\beta_{\text{Nestedness}}$), whereas the spermatophyte flora is more dependent on the compositional differences across the islands which form the archipelago ($\beta_{\text{Replacement}}$). The results are consistent with the different ecological requirements and dispersal abilities of pteridophytes and spermatophytes. Given also the fact that data from complete floristic survey – and not from samples (as in Veech and Crist, 2007 or Chiarucci et al., 2008) – were here used, this analysis provided a complete picture of the diversity partitioning of the flora of each archipelago (Crist and Veech, 2006) by means of simple and intuitive components of diversity, as α , $\beta_{\text{Nestedness}}$ and $\beta_{\text{Replacement}}$.

The additive partitioning of species richness provided some general patterns, but also evidenced which archipelagos have a

Table 2

Differences between each pair of archipelagos measured as Euclidean Distance on a three-dimensional space, with axes defined as the proportion of α , $\beta_{\text{Nestedness}}$ and $\beta_{\text{Replacement}}$ components of species richness, for pteridophyte ANS (All Native Species), pteridophyte AES (All Endemic Species), spermatophyte ANS and spermatophyte AES. Note that the similarity matrices are symmetric and all the values (not only the basic semimatrix) are given to facilitate comparisons. The mean distance of each archipelago to the other five is also indicated in the rightmost column (*Mean Distance*). Archipelago abbreviations are as follows: Can: Canaries; Azo: Azores; CVe: Cape Verde; Gal: Galapagos; Haw: Hawaii; Mar: Marquesas.

	Can	Azo	CVe	Gal	Haw	Mar	Mean distance
<i>Pteridophyte ANS</i>							
Can		46.0	16.1	24.5	28.5	15.2	26.1
Azo	46.0		61.3	69.7	17.5	38.4	46.6
CVe	16.1	61.3		8.4	44.0	30.2	32.0
Gal	24.5	69.7	8.4		52.4	38.1	38.6
Haw	28.5	17.5	44.0	52.4		22.3	32.9
Mar	15.2	38.4	30.2	38.1	22.3		28.8
<i>Pteridophyte AES</i>							
Can		51.9	44.7	41.2	43.1	16.3	39.4
Azo	51.9		66.9	54.5	8.8	43.4	45.1
CVe	44.7	66.9		12.9	60.7	57.8	48.6
Gal	41.2	54.5	12.9		48.9	51.5	41.8
Haw	43.1	8.8	60.7	48.9		35.0	39.3
Mar	16.3	43.4	57.8	51.5	35.0		40.8
<i>Spermatophyte ANS</i>							
Can		48.7	13.4	12.1	26.6	9.4	22.1
Azo	48.7		35.7	51.7	53.2	41.7	46.2
CVe	13.4	35.7		20.7	26.1	6.5	20.5
Gal	12.1	51.7	20.7		38.8	19.9	28.6
Haw	26.6	53.2	26.1	38.8		21.3	33.2
Mar	9.4	41.7	6.5	19.9	21.3		19.8
<i>Spermatophyte AES</i>							
Can		64.8	22.0	20.8	22.8	11.9	28.5
Azo	64.8		50.3	44.1	60.2	54.4	54.8
CVe	22.0	50.3		14.0	36.4	20.5	28.6
Gal	20.8	44.1	14.0		25.4	11.8	23.2
Haw	22.8	60.2	36.4	25.4		16.1	32.2
Mar	11.9	54.4	20.5	11.8	16.1		22.9

different partitioning of the flora. The most deviating data was the importance of the α -diversity for all the species groups in the Azores and – to some extent – of the pteridophytes in Hawaii. In these cases the total species richness of the archipelago flora was largely due to the mean species richness of each island and thus the different islands were largely redundant in their species composition. This was especially true for Azores, which showed the highest α -diversity values (60–75% for all the cases). Carine and Schaefer (2010) studied the endemic spermatophyte flora of Azores and found that most of these species are found in the majority of islands, a pattern contrasting with those from other archipelagos, in which the majority of endemic spermatophytes is present only in one or few islands. Our results mirrored this study for all native spermatophytes and for both endemic and all native pteridophytes. Within the investigated oceanic archipelagos, Azores stand apart because they are located at the highest latitude (35–40°North) and have the poorest flora (Borges et al., 2005; Table 1). Here each island hosts a huge proportion of the total archipelago flora: the three largest islands, Sao Miguel, Pico and Terceira, host 137, 135 and 131 spermatophyte species, respectively, corresponding to 80% or more of the archipelago flora, and the smallest island, Corvo, is only 0.73% of the archipelago area but hosts 56% of its native spermatophyte flora (Appendix 1). Azorean pteridophytes show similar data. The similar elevation (five of nine islands are in the range 900–1100 m) and latitude are likely to be the causes of the Azorean floristic homogeneity. These factors reduce the habitat

differentiation: only two islands bear exclusive habitats (Santa Maria, the driest, and Pico, the highest), while the others have different facets of humid-to-wet laurel forest (Dias et al., 2007). The scarcity of endemic species in the Azores flora, lead to the recognition of the “Azores diversity enigma”, interpreted as a consequence of the lack of abrupt climatic transitions in the late Quaternary (Carine and Schaefer, in press).

With the exception of the all native species of pteridophytes of Galápagos, the lowest value of the α -component was shown by the Canaries. Thus, the flora of the Canary archipelago is minimally due to the mean size of the flora of each island. Here, the important geographical (the eastern arid, low, old, and proximal islands versus the western, humid, high, young and distal islands) and ecological heterogeneity across islands interacted with a complex geological and climate history (Fernández-Palacios and Whittaker, 2008). This history includes the sterilization of Gran Canaria, the junction of Teno-Adeje and Anaga palaeo-islands to constitute Tenerife, the reiterative fusion of Lanzarote and Fuerteventura, the collapse of significant portions of Tenerife, La Palma and El Hierro, and the emergence of islets as Alegranza, Montaña Clara, La Graciosa and Lobos in the last 50 ky (Fernández-Palacios and Whittaker, 2008). Within this complex biogeographical frame, the easy colonization of the eastern islands by Mediterranean and North African species contrasts with the difficult colonization of the western islands, where *in situ* speciation of the rare colonist lineages is faster than immigration (Whittaker et al., 2008), providing a very heterogeneous species composition across islands.

The $\beta_{\text{Nestedness}}$ component quantifies how the differences in flora size across islands influence the total flora of an archipelago. While the α -component measures the importance of the mean species richness of the island flora in contributing to the archipelago flora, the $\beta_{\text{Nestedness}}$ identify the importance of its variations across islands. These two measures are somehow, but not fully complementary (Crist and Veech, 2006), as demonstrated by the following data. The lowest values of $\beta_{\text{Nestedness}}$ were observed in the Azores, since their islands scarcely differed in species richness, while the second lowest value of $\beta_{\text{Nestedness}}$ was observed in Hawaii for all the groups, except for spermatophyte ANS (in which it was the absolutely lowest). However, in Azores, the low $\beta_{\text{Nestedness}}$ combines with the highest α -diversity values, while in Hawaii the low $\beta_{\text{Nestedness}}$ combines with low value of spermatophyte α -diversity, indicating that the Hawaiian spermatophyte flora is scarcely dependent on both the size and variability of the island floras. In fact, Hawaii is known to have a highly differentiated flora in the different islands (Price, 2004), as also demonstrated by the high $\beta_{\text{Replacement}}$ values (see below).

The $\beta_{\text{Replacement}}$ is certainly the most attractive diversity component for interpreting the biogeographical history of archipelagos, because it synthesises the compositional differences (Crist and Veech, 2006; Chiarucci et al., 2008) across islands and, thus, the evolutionary and ecological processes that shaped the flora. Hawaii show outstanding values of the $\beta_{\text{Replacement}}$ component, for both all native and endemic spermatophytes, and this is due to the extremely high proportion of SIEs and SINs, the largest of any archipelago (> 50% of the archipelago flora). The driving forces for the diversity components of the Hawaiian archipelago are very similar to that of the Canaries, with regards to the ecological and climate aspects, but with a very important difference: the inaccessibility of the Hawaiian islands to colonizers. This is to say that the native non-endemic element is extremely reduced in Hawaii (Price, 2004), and its flora was built up with a lower number of colonization events. This fact has given rise to the existence of significant differences in the phylogenetic structure across *taxa* and habitats among Hawaii and the Canaries (Domínguez Lozano et al., 2010).

To generalize the potentiality of additive partitioning of species diversity (Lande, 1996; Wagner et al., 2000; Veech et al., 2002; Crist et al., 2003) in island biogeography we demonstrated that: (1) the additive components of species diversity differed in pteridophytes and spermatophytes and (2) these additive components differently contributed to the species richness of all native and endemic species. These two findings reflect the different dispersal abilities and evolutionary capacities of pteridophytes and spermatophytes. The contribution of $\beta_{\text{Nestedness}}$ to the richness of the flora of an archipelago was higher for pteridophytes, than that for spermatophytes, while the contribution of $\beta_{\text{Replacement}}$ was higher for spermatophytes than for pteridophytes and the endemic flora was more differentiated across islands (higher $\beta_{\text{Replacement}}$) for spermatophytes than for pteridophytes. The higher importance of $\beta_{\text{Nestedness}}$ for pteridophytes indicated that, for this *taxon*, the flora of each island is largely formed by a subset of species that make up the archipelago flora, with less evolutionary or ecological differentiation across islands. This reflects the high sensitivity of pteridophytes species richness to the increment of island area and, as a consequence, to the diversity in climatic conditions (Aldasoro et al., 2004), and contrasts with the major role of colonisations and speciation events for spermatophytes. Highly dispersive *taxa* such as pteridophytes, tend to be represented by the same species in all suitable habitats, with the differences across islands largely due to the island area or other factors that affect the size of the flora more than its composition, as measured by the $\beta_{\text{Nestedness}}$ component. This is not the case for *taxa* with a much lower dispersal capacity as spermatophytes, for which intra-insular or inter-insular vicariance play a major role both from the evolutionary and ecological points of view (Wagner and Funk, 1995). In fact the endemic component is not very important in pteridophytes, as 6% in the Canarian flora (Izquierdo et al., 2004) or 5% in the Galápagos one (Lawesson et al., 1987); in the archipelagos with an important endemic component of pteridophytes, as Hawaii (74%; Price, 2004) or Marquesas (30%; The Flora of Marquesas webpage, 2008), it is largely made by MIEs and, thus, does not differentiate

the flora. The differences across islands are simply due to the variation in the flora size.

To conclude, the behaviour of the components of species diversity here explored showed the existence of strong differences in the diversity patterns of pteridophytes and spermatophytes and, within each *taxon*, between endemic and all native species. As demonstrated here, additive partitioning of species diversity may provide useful, and easy-to-interpret, data for investigating the within-archipelago pattern of species diversity and quantify contrasting cases, such as that of Azores. In the future, once species richness data could be made available per habitat type, this approach could be useful to weigh the importance of island area and habitat heterogeneity in determining the total species richness of archipelagos, a key topic of present-day island biogeography (Triantis et al., 2003, 2005).

Acknowledgements

This work was made possible thanks to a LLP/Erasmus/Ts Mobility (20–26 April 2008) and a Study Leave supported by the University of La Laguna (09 June–09 August 2009), both given to the first author (AC) for permanence at the University of La Laguna, Tenerife, Spain. We thank two anonymous referees and Christoph Küffer for comments and suggestion on a previous version of the manuscript, and Romaney Pinnock for a linguistic check of the text.

Appendix 1

Number of Single Island Endemics (SIEs), Multiple Island Endemics (MIEs), Single Island Native (SINs), Multiple Island Natives (MINs) and All Native Species (ANS) for both pteridophyte and spermatophyte species in each island larger than 1 km² in the Canaries, Azores, Cape Verde, Galápagos, Hawaii and Marquesas (Sources in main text). Islands are listed according to their area within each archipelago (see Table A1).

Table A1

Island name	Pteridophytes					Spermatophytes				
	SIEs	MIEs	SINs	MINs	ANS	SIEs	MIEs	SINs	MINs	ANS
Sao Miguel	0	4	0	34	38	1	49	3	84	137
Pico	0	5	4	33	42	1	52	1	81	135
Terceira	1	5	0	35	41	0	46	1	84	131
Sao Jorge	0	4	0	31	35	0	50	0	71	121
Faial	0	5	0	35	40	0	48	0	78	126
Flores	0	6	0	36	42	0	49	0	74	123
Santa Maria	0	3	0	25	28	1	31	1	75	108
Graciosa	0	3	0	15	18	0	18	0	54	72
Corvo	0	4	0	27	31	0	37	0	55	92
Azores	1	6	4	37	48	3	58	6	97	164
Tenerife	0	1	2	38	41	135	174	7	488	804
Fuerteventura	0	0	0	14	14	13	56	9	328	406
Gran Canaria	1	1	0	38	40	102	124	5	514	745
Lanzarote	0	0	0	12	12	12	54	7	309	382
La Palma	1	1	1	36	39	40	111	0	350	501
La Gomera	0	1	1	37	39	47	115	0	356	518
El Hierro	0	1	0	23	24	17	90	2	293	402
La Graciosa	0	0	0	0	0	0	12	0	104	116
Alegranza	0	0	0	0	0	0	4	0	77	81
Lobos	0	0	0	0	0	1	12	0	100	113
Mña. Clara	0	0	0	0	0	0	6	0	56	62

Table A1 (continued)

Island name	Pteridophytes					Spermatophytes				
	SIEs	MIEs	SINs	MINs	ANS	SIEs	MIEs	SINs	MINs	ANS
Canaries	2	1	4	43	50	367	215	30	593	1204
Sao Thiago	0	0	0	14	14	1	26	3	105	135
Santo Antao	0	1	4	23	28	4	42	7	92	145
Boavista	0	0	1	1	2	0	9	2	79	90
Fogo	0	0	3	20	23	4	17	0	81	102
Sao Nicolau	0	1	0	19	20	4	23	2	79	108
Maió	0	0	0	1	1	0	8	0	71	79
San Vicente	0	1	0	10	11	0	28	0	83	111
Sal	0	0	0	0	0	0	11	2	59	72
Brava	0	0	0	12	12	0	15	0	61	76
Santa Luzia	0	0	0	1	1	0	11	0	35	46
Raso	0	0	0	0	0	0	12	0	31	43
Branco	0	0	0	0	0	0	11	0	27	38
Cape Verde	0	1	8	24	33	13	52	16	128	209
Big Island	0	89	0	41	130	81	216	1	81	379
Maui	3	95	1	38	137	75	310	3	86	474
Oahu	5	86	0	39	130	133	225	1	83	442
Kauai	11	87	0	38	136	193	207	3	79	482
Lanai	0	73	0	34	107	11	167	0	57	235
Molakai	0	82	0	36	118	31	245	0	78	354
Niihau	0	2	0	2	4	2	37	0	27	66
Kahoolawe	0	3	0	2	5	2	41	0	43	86
Hawaii	19	100	1	41	161	528	377	8	90	1003
Isabela	0	5	11	78	94	6	85	6	229	326
Santa Cruz	0	5	4	75	84	9	82	6	233	330
Fernandina	0	1	0	34	35	0	74	0	92	166
Santiago	0	5	3	49	57	5	70	4	164	243
San Cristóbal	0	4	3	51	58	6	81	8	146	241
Floreana	0	1	1	26	28	8	66	5	150	229
Marchena	0	1	0	5	6	0	26	1	24	51
Pinta	0	2	2	40	44	0	59	1	71	131
Española	0	1	0	0	1	1	35	1	72	109
Baltra	0	0	0	0	0	0	19	0	37	56
Santa Fe	0	1	0	1	2	0	34	0	37	71
Pinzón	0	2	0	10	12	1	41	0	645	105
Genovesa	0	0	0	0	0	0	29	0	28	57
Rábida	0	1	0	1	2	0	41	0	49	90
Wolf	0	0	0	1	1	0	18	0	13	31
Darwin	0	0	0	0	0	0	8	0	7	15
Seymour	0	0	0	0	0	0	14	0	35	49
Galápagos	0	5	24	81	110	36	105	32	407	439
Nuku Hiva	2	12	6	55	75	28	44	8	69	149
Hiva Oa	3	16	3	53	75	14	46	3	65	128
Ua Pou	0	13	1	48	62	4	30	2	57	93
Fatu Hiva	0	11	0	38	49	11	37	1	59	108
Ua Huka	3	10	1	45	59	4	28	1	55	88
Tahuata	1	10	0	38	49	7	39	1	57	104
Eiao	0	0	1	4	5	0	9	0	25	34
Moho Tani	0	0	0	6	6	0	8	0	25	33
Hatutaa	0	0	0	2	2	0	6	1	15	22
Marquesas	9	22	12	59	102	68	62	17	85	229

References

- Aldasoro, J.J., Cabezas, F., Aedo, C., 2004. Diversity and distribution of pteridophytes in sub-Saharan Africa, Madagascar and some islands of the South Atlantic. *J. Biogeogr.* 31, 1579–1604.
- Arechavaleta, M., Zurita, N., Marrero, M.C., Martín, J.L., 2005. Lista preliminar de especies silvestres de Cabo Verde (hongos, plantas y animales silvestres). Consejería de Medio Ambiente y Ordenación Territorial, Gobierno de Canarias.
- Borges, P.A.V., Cunha, R., Gabriel, R., Martins, A.F., Silva, L., Vieira, V., 2005. A list of terrestrial fauna (Mollusca and Arthropoda) and flora (Bryophyta, Pteridophyta and Spermatophyta) from the Azores. Direcção Regional do Ambiente/Universidade dos Açores.
- Brochmann, C., Rustan, O.H., Lobin, W., Kilian, N., 1997. The endemic vascular plants of the Cape Verde Islands. *W. Africa. Sommerfeltia* 24, 1–356.
- Carine, M.A., Schaefer, H., 2010. The Azores diversity enigma: why are there so few Azorean endemic flowering plants and why are they so widespread? *J. Biogeogr.* 37, 77–89.
- Carlquist, S., 1974. *Island Biology*. New York. Columbia University Press.
- Chiarucci, A., Bacaro, G., Rocchini, D., 2008. Quantifying plant species diversity in a Natura 2000 network: old ideas and new proposals. *Biol. Cons.* 141, 2608–2618.
- Clouard, V., Bonneville, A., 2005. Ages of seamounts, islands and plateaus on the Pacific Plate. In: Foulger, G.R., Natland, J.H., Presnall, D., Anderson, D.I. (Eds.), *Plates, Plumes and Paradigms*. Geological Society of America Special Paper, Boulder, CO, pp. 71–90.

- Crist, T.O., Veech, J.A., 2006. Additive partitioning of rarefaction curves and species-area relationships: unifying alpha-, beta- and gamma-diversity with sample size and habitat area. *Ecol. Lett.* 9, 923–932.
- Crist, T.O., Veech, J.A., Gering, J.C., Summerville, K.S., 2003. Partitioning species diversity across landscapes and regions: a hierarchical analysis of α , β , and γ diversity. *Am. Nat.* 162, 734–743.
- Dias, E., Elias, R.B., Melo, C., Mendes, C., 2007. *Biologia y ecología das florestas das ilhas. Açores*. In: Silva Sande, J. (Ed.), *Açores y Madeira. A floresta das ilhas*. Fundación Luso americana, Diário Público, Lisboa, pp. 51–80.
- Domínguez Lozano, F., Price, J., Otto, R., Fernández-Palacios, J.M., 2010. Using taxonomic and phylogenetic evenness to compare diversification in two island floras. *Persp. Pl. Ecol. Evol. Syst.* 12, 93–106.
- Duarte, M.C., Rego, F., Romeiras, M.M., Moreira, I., 2008. Plant species richness in the Cape Verde Islands—eco-geographical determinants. *Biodiv. Cons.* 17, 453–466.
- Fernández-Palacios, J.M., Whittaker, R.J., 2008. The Canaries. An important biogeographical meeting place. *J. Biogeogr.* 35, 379–387.
- Flora of Marquesas webpage < <http://ravenel.si.edu/botany/pacificislandbiodiversity/marquesasflora/query.cfm> >. Visited in May 2008.
- Florence, J., Lorence, D.H., 1997. Introduction to the flora and vegetation of Marquesas islands. *Allertonia* 7, 226–237.
- França, Z., Cruz, J.V., Nunes, J.C., Forjaz, V.H., 2003. Geologia dos Açores: Uma perspectiva actual. *Rev. Açoreana* 10, 1–140.
- García Talavera, F., 1999. La Macaronesia. Consideraciones geológicas, biogeográficas y paleoecológicas. In: Fernández-Palacios, J.M., Bacallado, J.J., Belmonte, J.A. (Eds.), *Ecología y cultura en Canarias*, Organismo Autónomo de Museos. Cabildo Insular de Tenerife, pp. 39–63.
- Geist, D., Snell, H., Snell, H., Goddard, C., Kurz, M., in press. Paleogeography of the Galapagos: Islands and Biogeographical Implications.
- Grant, P.R., Grant, B.R., 2008. *How and Why Species Multiply*. Princeton University Press, Princeton.
- Hobohm, C., 2000. Plant species diversity and endemism on islands and archipelagos, with special reference to the Macaronesian Islands. *Flora* 195, 9–24.
- Izquierdo, I., Martín, J.L., Zurita, N., Arechavaleta, M., 2004. Lista de especies silvestres de Canarias (hongos, plantas y animales terrestres). Consejería de Medio Ambiente y Ordenación Territorial, Gobierno de Canarias; Santa Cruz de Tenerife.
- Kämmer, F., 1982. Beiträge zur einer kritischen Interpretation der rezenten und fossilen Gefäßpflanzenflora und Wirbeltierfauna der Azoren, des Madeira-Archipels, der Ilhas Selvagens, der Kanarischen Inseln und der Kapverdischen Inseln, mit einem Ausblick auf Probleme des Artenschwundes in Makaronesien. Self Edition; Freiburg im Breisgau.
- Kier, G., Kreft, H., Lee, T.M., Jetz, W., Ibsch, P.L., Nowicki, C., Mutke, J., Barthlott, W., 2009. A global assessment of endemism and species richness across island and mainland regions. *Proc. Natl. Acad. Sci.* 106, 9322–9327.
- Kreft, H., Jetz, W., Mutke, J., Kier, G., Barthlott, W., 2008. Global diversity of island floras from a macroecological perspective. *Ecol. Lett.* 11, 116–127.
- Kueffer, C., Daehler, C.C., Torres-Santana, C.W., Lavergne, C., Meyer, J.-Y., Otto, R., Silva, L., 2010. A global comparison of plant invasions on oceanic islands. *Perspect. Pl. Ecol. Evol. Systematics*, in press, doi:10.1016/j.ppees.2009.06.002.
- Kunkel, G., 1980. *Die Kanarischen Inseln und ihre Pflanzenwelt*. Gustav Fischer Verlag, Stuttgart–New York.
- Lande, R., 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76, 5–13.
- Lawesson, J., Adersen, H., Bentley, P., 1987. An updated and annotated check list of the vascular plants of the Galápagos Islands. Reports from the Botanical Institute, University of Aarhus 16, 1–74.
- Price, J.P., 2004. Floristic biogeography of the Hawaiian Islands: influences of area, environment and paleogeography. *J. Biogeogr.* 31, 487–500.
- Price, J.P., Clague, D.A., 2002. How old is the Hawaiian biota? Geology and phylogeny suggest recent divergence. *Proc. R. Soc. B–Biol. Sci.* 269, 2429–2435.
- Price, J.P., Elliott-Fisk, 2004. Topographic history of the Maui Nui complex, Hawai'i, and its implications for biogeography. *Pac. Sci.* 58, 27–45.
- Reyes-Betancort, J.A., Santos-Guerra, A., Guma, I.R., Humphries, C.J., Carine, M.A., 2008. Diversity, rarity and the evolution of the Canary Islands endemic flora. *Anales Jardín Botánico de Madrid* 65, 25–45.
- Thornton, I., 2007. *Island Colonization. The Origin and Development of Island Communities*. Cambridge University Press, Cambridge.
- Triantis, K.A., Mylonas, M., Lika, K., Vardinoyannis, K., 2003. A model for the species-area-habitat relationship. *J. Biogeogr.* 30, 19–27.
- Triantis, K.A., Mylonas, M., Weiser, M.D., Lika, K., Vardinoyannis, K., 2005. Species richness, environmental heterogeneity and area: a case study based on land snails in Skyros archipelago (Aegean Sea, Greece). *J. Biogeogr.* 32, 1727–1735.
- Triantis, K.A., Mylonas, M., Whittaker, R.J., 2008a. Evolutionary species-area curves as revealed by single-island endemics: insights for the interprovincial species-area curves. *Ecography* 31, 401–407.
- Triantis, K.A., Nogués-Bravo, D., Hortal, J., Borges, P.A.V., Adersen, H., Fernández-Palacios, J.M., Araújo, M.B., Whittaker, R.J., 2008b. Measurements of area and the (island) species-area relationship: new directions for an old pattern. *Oikos* 117, 1555–1559.
- Veech, J.A., Crist, T.O., 2007. Habitat and climate heterogeneity maintain beta-diversity of birds among landscapes within ecoregions. *Glob. Ecol. Biogeogr.* 16, 650–656.
- Veech, J.A., Summerville, K.S., Crist, T.O., Gering, J.C., 2002. The additive partitioning of species diversity: recent revival of an old idea. *Oikos* 99, 3–9.
- Wagner, H.H., Wildi, O., Ewald, K.C., 2000. Additive partitioning of plant species diversity in an agricultural mosaic landscape. *Landscape Ecol.* 15, 219–227.
- Wagner, W.L., Funk, V.A., 1995. *Hawaiian Biogeography. Evolution on a Hot Spot Archipelago*. Smithsonian, Washington, DC.
- Wallace, A.R., 1881. *Island Life*. Prometheus Books, New York (reprinted edition of 1998).
- Werner, R., Hoernle, K., van den Bogaard, P., Ranero, C., von Huene, R., 1999. Drowned 14-m.y.-old Galapagos archipelago off the coast of Costa Rica: implications for tectonic and evolutionary models. *Geology* 27, 499–502.
- Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* 30, 279–338.
- Whittaker, R.H., 1972. Evolution and measurement of species diversity. *Taxon* 21, 213–251.
- Whittaker, R.J., Fernández-Palacios, J.M., 2007. *Island Biogeography, Ecology, Evolution and Conservation* 2nd Ed. Oxford University Press, Oxford.
- Whittaker, R.J., Triantis, K.A., Ladle, R.J., 2008. A general dynamic theory of oceanic island biogeography. *J. Biogeogr.* 35, 977–994.
- Willerslev, E., Hansen, A.J., Nielsen, K.K., Adersen, H., 2002. Number of endemic and native plant species in the Galápagos Archipelago in relation to geographical parameters. *Ecography* 25, 109–119.
- Williamson, M., 1981. *Island Populations*. Oxford University Press, Oxford.