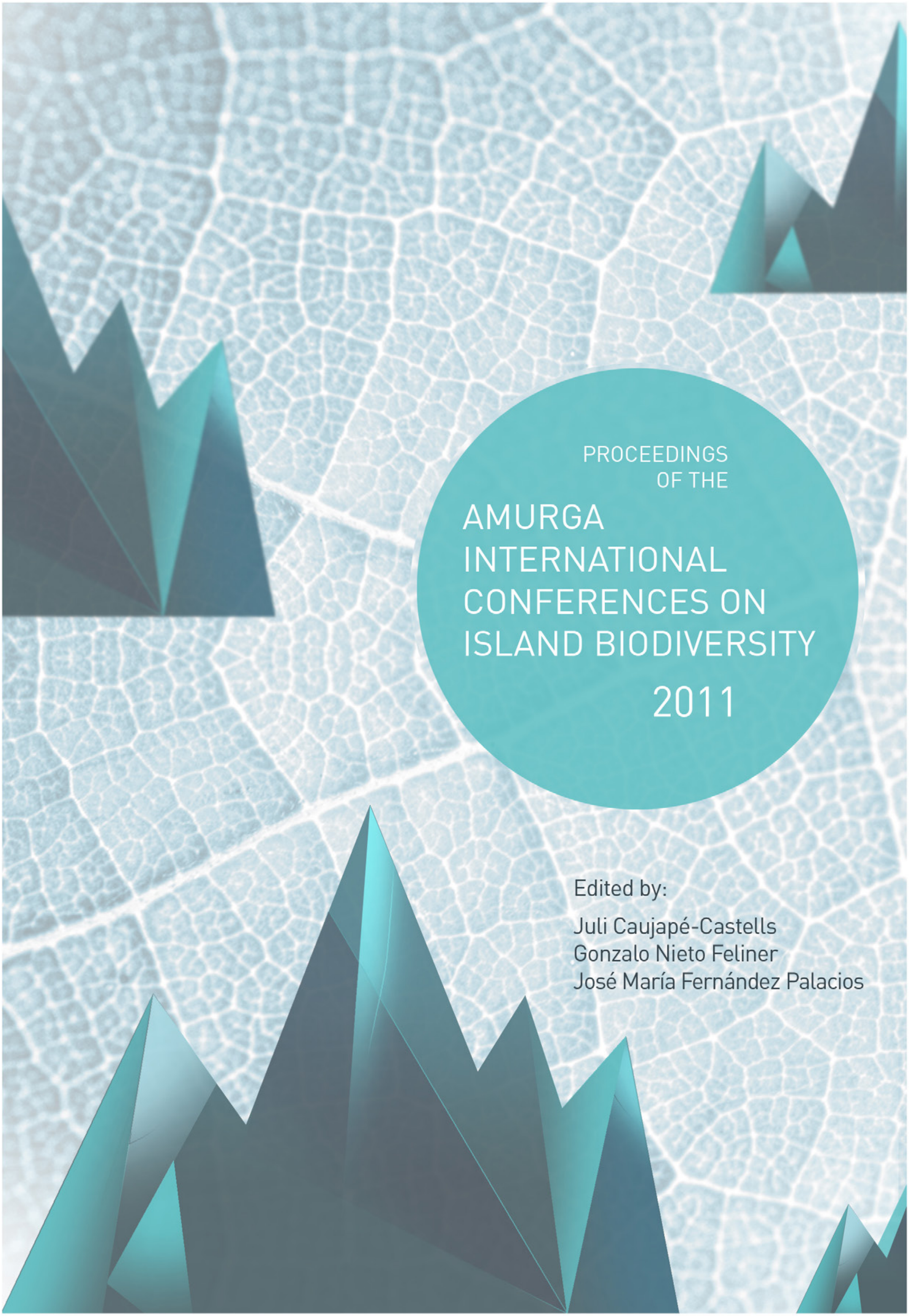

PROCEEDINGS OF THE AMURGA INTERNATIONAL CONFERENCES ON ISLAND BIODIVERSITY 2011

Edited by:
Juli Caujapé-Castells
Gonzalo Nieto Feliner
José María Fernández Palacios

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SUMMARY

1. Island Biogeography

2. Genetic Diversity and Ecology In The Canaries

3. Evolutionary Processes

4. Plant Life Out of Macaronesia

5. Macaronesian Floras

A comparison of bryophyte diversity in the Macaronesian Islands. Island versus habitat approach

González-Mancebo, J.M.[1], R. Gabriel[2], R. Otto[3], M. Sim-Sim[4], L. Luís[4,5], C. Sérgio[4], V. Garzón- Machado[1], Aranda, S. C[2], J. Capelo6 & A. Vanderpoorten[7].

[1]Department of Botany.
University of La laguna.
La Laguna, Tenerife (Canary Islands). Spain.
jglezm@ull.es

[2] Dep. Biogeografía y Cambio Global. Museo Nacional de Ciencias Naturales. c/ José Gutiérrez Abascal 2. 28006, Madrid

[3]Department of Ecology.
University of La Laguna.
La laguna, Tenerife (Canary Islands). Spain.

[4] Universidade de Lisboa, Faculdade de Ciências de Lisboa, DBV, Centro de Biologia Ambiental, C2, Campo Grande, 1749-016 Lisboa, Portugal and Museu Nacional de História Natural, Jardim Botânico/CBA, Rua da Escola Politécnica, nº 58, 1250-102 Lisboa, Portugal

[5] Instituto Piaget. Campus Universitário de Santo André, Apartado 38, 7500-999 Vila Nova de Santo André.

[6] Instituto Nacional de Recursos Biológicos, IP, Unidade de Silvicultura e Produtos Florestais Quinta do Marquês, 2780-159 Oeiras-Portugal.

[7]Institute of Botany, University of Liège, B22 Sart Tilman, 4000 Liège, Belgium.

Introduction

Macaronesia has been recognized as a biogeographic region comprising the Azores, Madeira, Canary Islands (Engler, 1978) and Cape Verde Islands (e.g. Dansereau, 1961), from more than a century (Whittaker & Fernández Palacios, 2007). Despite the fact that there is considerable variation in abiotic conditions across these archipelagos, the Macaronesian concept has been widely accepted (e.g. Médail and Quézel, 1997), although some authors reject the wide concept of Macaronesia, excluding the Cape Verde islands for both, vascular plants (eg. Lobin 1982) and cryptogams (Vanderpoorten *et al.*, 2007). In addition, the Macaronesian concept may be different depending on the group of organisms. For instance, the relictualism theory of Macaronesia shows more consistency for ferns and liverworts than for mosses (Vanderpoorten *et al.*, 2007).

Nicolás *et al.* (1989) presented a study of relationships of the vascular floras within the Macaronesian region and highlighted the similarities between the Canarian and Madeiran floras and the distinctiveness of both the Azorean and Cape Verdean floras. These authors showed a close correlation between variation in floristic similarity and latitude, altitude and distance to the mainland. González-Mancebo *et al.* (2008a), shows that mosses respond to major environmental factors in a more complex way than liverworts. Sim-Sim *et al.* (2010a) by means of a cluster analysis revealed the affinities in the bryoflora composition of the driest islands of Madeira, namely Selvagens, Desertas and Porto Santo, and found a close proximity between Fuerteventura and Lanzarote in Canary Islands and the Selvagens bryoflora. The different patterns of richness and diversity for both liverworts and mosses of Madeira were due to the habitats' variability and environmental conditions of the different islands of Madeira Archipelago. Vanderpoorten *et al.* (2007), using parsimony and Bayesian analyses of floristic data sets, revealed for mosses the Canary Islands as sister to North Africa, while both liverwort and pteridophyte analyses suggested an Azorean-Madeiran-Canarian clade (hereafter Macaronesia s.s.). According to these authors, dynamic interchange of taxa with neighboring continental areas rather than relictualism best explains the relationships of the Cape Verde cryptogamic flora and the Canary Island moss flora.

Factors influencing these differences have also been included in studies on richness analyses; in fact, most factors that rule/condition inter-island similarity (area, altitude, age, geographical isolation) also explain richness pattern on islands (Rosenzweig, 1995; Whittaker & Fernández Palacios, 2007). In this context, biodiversity in the Macaronesian islands has been mostly related to age, area, isolation and habitat diversity (or its surrogate, maximum altitude) (Nicolás et al, 1989; Pereira *et al.*, 2007; Borges & Hortal, 2009). For bryophytes, González-Mancebo *et al.* (2008a) pointed out that altitude and island age are the most important factors influencing bryophyte richness in the Canary Islands.

Habitat diversity is a key factor explaining species richness (e.g. Kreft *et al.*, 2008) and similarity between islands (Nicolás *et al.*, 2008; González-Mancebo *et al.*, 2008; Borges *et al.*, 2011). Scientists have identified, beside the factor time, two major mechanisms of species accumulation (immigration and speciation) on islands, the increase of area and of habitat diversity, usually due to increase in altitude (Losos & Schluter 2000, Triantis *et al.*, 2003). A simple mathematical model that unifies these two dominant explanatory variables was used by Triantis *et al.* (2003). However, few authors have developed more direct approaches to address the habitat effect on diversity (Buckley 1982, 1985; Deshaye & Morriset, 1988; Domínguez *et al.*, 2010; Zobel *et al.*, 2011). In this context, habitats from individual islands have rarely been compared between islands, within or between biogeographic regions.

In this paper, we present a comparison of richness patterns and floristic similarity for bryophytes in the five most important altitudinal habitat types in the Macaronesian islands. We evaluate the importance of different factors discussed in the literature in predicting species diversity applying the traditional island approach and within the framework of the new habitat approach, including area, isolation, climatic factors, geological age and human influence. From the analysis of patterns of bryophyte species distribution for selected habitats across islands and archipelagos, we specifically test the hypothesis that (i) floristic similarity is primarily determined by climatic factors, but not by geographical distance due to high dispersal ability in this species group and (ii) bryophyte richness is best predicted by area, but not by geological age of the habitat due to very low endemicity or speciation rate and high colonization rate.

Methods

Data collection

Information on species distribution and frequency on each archipelago was recorded from a complete literature survey for the Macaronesian islands (Macaronesia s.s.) as well as herbarium data from AZU (Azores), LISU, S, MADS, MADJ and MADM and TFC-Bry.

Habitat data

The three Macaronesian archipelagos considered are very different with respect to climatic conditions with bioclimatic belts varying from a temperate hyperoceanic (Itc 470-120) and mediterranean oceanic (Itc 480-420) in the Azores; from temperate hyperoceanic (410-170) to mediterranean xeric oceanic (510-430) and mediterranean pluvi-seasonal oceanic (520-350) in Madeira and from mediterranean pluvi-seasonal oceanic (550-120 to mediterranean xeric oceanic (560-400) and Mediterranean desertic oceanic (570-490) in the Canaries (Rivas-Martínez, 2009). We assigned bryophyte species to major and minor habitat types (caves, human disturbed, water habitats, recent lava flows) that latter were grouped in different bioclimatic belts following altitudinal gradients: lowlands, mesic areas, humid and hyper-humid mountain belts, and high mountain belt. Major habitat types were distinguished following Dias (1996) for the Azores, Mesquita *et al.* (in preparation) and Capelo *et al.* (2004, 2007) for Madeira and Del Arco *et al.* (2010) for the Canary Islands. Disturbed areas at each habitat were generally not separated. However, open areas in the humid or hyperhumid mountain belt (where laurel forests were destroyed or natural open areas) were specifically distinguished because they represent a very different type of habitat for bryophytes with a very distinct floristic composition, at least in the Canary Islands (González-Mancebo *et al.*, 2008b). Additionally, in the Canary Islands, pine forest was distinguished from those areas situated above the timberline, in the Supramediterranean and Oromediterranean belts.

Variables

Geological, geographical and habitat variables (see table 1) were compiled from Forjaz (2004) DROTRH (2008) and Del Arco et al (2006b), using digital maps. Climatic data, such as precipitation and temperature, were largely obtained from Azevedo (2003) and Forjaz (2004) for the Azores, PRAM (2002) for Madeira and Del Arco et al (1999, 2002; 2006a, 2009; Reyes-Betancort (2001) for the Canaries. In Madeira, climatic data were originally gathered from the National Institute of Meteorology for the period between 1961 – 1990. For Desertas, the data was obtained from "WORLDCLIM" (www.worldclim.com). The population density data was calculated from Forjaz (2004) for the Azores, from Instituto Canario de Estadística (ISTAC), censos 2001 for the Canaries and "Instituto Nacional de Estatística. Direcção Regional de Estatística da Madeira - Censos 2001 for Madeira.

Habitats	**LOWLAND**			**MESIC**			**LAUREL FOREST**			**PINE FOREST**	**HIGH MOUNTAIN**		
Archipelagos	Azores	Madeira	Canaries	Azores	Madeira	Canaries	Azores	Madeira	Canaries	Canaries	Azores	Madeira	Canaries
Potential area (km2)	*16,35*	*72,35*	*592,87*	*131,71*	*85,30*	*138,13*	*79,90*	*192,35*	*144,45*	*288,79*	*35,00*	*96,90*	*91,64*
Current veg. area (km2)	*9,32*	*12,72*	*127,16*	*0,00*	*26,63*	*23,08*	*6,38*	*77,50*	*52,46*	*159,43*	*35,00*	*48,35*	*91,31*
%Veg Conserv	*67,28*	*26,54*	*29,73*	*0,00*	*26,98*	*18,97*	*6,79*	*20,20*	*34,41*	*56,19*	*100,00*	*49,94*	*90,00*

Habitats	LOWLAND			MESIC			LAUREL FOREST			PINE FOREST	HIGH MOUNTAIN		
Archipelagos	Azores	Madeira	Canaries	Azores	Madeira	Canaries	Azores	Madeira	Canaries	Canaries	Azores	Madeira	Canaries
Min Altitude (m)	*0,00*	*0,00*	*0,00*	*8,89*	*233,33*	*228,57*	*371,89*	*350,00*	*491,67*	*825,00*	*1200,00*	*1450,00*	*1916,67*
Max Altitude (m)	*350,00*	*333,33*	*421,43*	*717,22*	*560,00*	*788,71*	*851,67*	*1010,00*	*1371,50*	*1862,50*	*2351,00*	*1861,00*	*2683,00*
Mean Altitude (m)	*175,00*	*166,67*	*210,71*	*367,50*	*513,33*	*622,93*	*797,72*	*855,00*	*1177,42*	*1756,25*	*2275,50*	*2380,50*	*3258,17*
Nºhabitants/ km2	*1009,98*	*407,74*	*340,68*	*23,99*	*74,05*	*363,61*	*0,00*	*32,19*	*277,86*	*73,74*	*0,00*	*0,00*	*0,00*
Min, Age (m.y.)	*0,56*	*5,10*	*0,44*	*0,59*	*5,27*	*0,44*	*1,16*	*8,25*	*4,40*	*0,78*	*0,24*	*1,50*	*1,30*
Max, Age (m.y.)	*2,52*	*7,83*	*13,11*	*2,15*	*7,67*	*13,11*	*1,20*	*9,75*	*9,72*	*7,20*	*0,30*	*3,00*	*3,10*
Mean Temp. (°C)	*18,69*	*18,50*	*20,29*	*16,05*	*17,67*	*17,43*	*13,86*	*14,75*	*15,17*	*12,70*	*8,50*	*9,50*	*8,87*
Annual Prec. (mm)	*1376,06*	*516,67*	*350,00*	*1939,56*	*626,67*	*488,57*	*2893,42*	*1195,00*	*850,00*	*825,00*	*5100,00*	*2500,00*	*530,00*
Dist,Mainland (km)	*1853,33*	*662,67*	*268,57*	*1853,33*	*662,67*	*268,57*	*1853,33*	*674,00*	*291,33*	*326,00*	*1860,00*	*668,00*	*305,33*
Dist, nearest habitat (km)	*34,89*	*46,00*	*36,41*	*34,89*	*46,00*	*36,41*	*67,00*	*243,50*	*77,50*	*92,00*	*1241,00*	*430,00*	*122,33*

Table 1. Relation of the mean values among islands of each archipelago for the most important variables considered at each habitat.

Data analysis

Floristic similarity was analysed using multivariate statistical techniques. We applied Detrended Correspondence Analysis (DCA, Hill & Gauch 1980) to evaluate floristic similarities within and across archipelagos, islands and habitat types. To explore correlations between floristic gradients and environmental variables, we applied Canonical Correspondence Analysis (CCA) as implemented by CANOCO (ter Braak & Smilauer, 1998). TWINSPAN (Hill 1979) was selected as a hierarchical classification method.

Total bryophyte richness, hepatic and moss richness was modelled applying generalized linear models (GLM; McCullagh and Nelder 1989; Dobson 1990). AIC (Akaike information criteria) with forward stepwise selection was used to obtain the optimal set of predictor variables, choosing the lowest AIC value for every possible combination of explanatory variables, starting with the explanatory variable with the best fit. The fit of the model was tested by the log-likelihood statistics. Distributions of residuals as well as potential problems of over-dispersion were analysed.

Before running GLMs, we applied a Principal Component Analysis (PCA) to explore relationships among explanatory variables. In order to avoid multicollinearity and eliminate redundant information, we used the first two components of the PCA constructed from the island characteristics matrix directly as explanatory variables in the GLM. In case of the habitat approach, we selected the best explanatory variables to enter in the GLM analysis, by eliminating those variables that were highly correlated with each other and the first two PCA components. The following variables were retained: mean annual precipitation, mean annual temperature, habitat area, mean geological age, distance to nearest habitat and population density. Variables were log transformed if distribution across islands was skewed. GLMs can also detect non-linear relationships, if quadratic terms are included (Zuur *et al.* 2007), therefore we included quadratic terms of mean annual temperature and geological age in all models, since we expected possible non-linear relationships for these variables.

Results

General aspects

In all three northern Macaronesian archipelagos we found a total of 725 species (501 mosses and 224 liverworts (including hornworts)). The bryophyte species diversity of the three archipelagos was very similar with 451 (Azores), 461 (Madeira) and 485 species (Canary Islands). The same holds true for the two groups of hepatics and mosses, although there seems to be a slight tendency of increase of hepatics (161, 158 and 147, respectively) and decrease of mosses (290, 303 and 338, respectively) with latitude, corresponding to a precipitation gradient. Species number per island and habitat is given in Table 2. Comparisons of habitat richness between archipelagos (table 2) showed a similar altitudinal pattern of richness for the Azores and the Canary Islands. Richness is increasing from lowland areas to open areas and laurel forest in the most humid mountain belt on each archipelago. However, lower levels of richness are recorded for the laurel forest compared to open areas in the Canaries. In the Azores an opposite pattern occurs in this bioclimatic belt. The laurel forest of Madeira shows the highest species richness; whereas the open areas have the lowest species number. Also, the mesic habitats of this archipelago revealed a higher richness for both liverworts and mosses.

	Corvo	Flores	Faial	Pico	Graciosa	Sao jorge	Terceira	Sao Miguel	Santa María
T	*168*	*259*	*254*	*266*	*123*	*236*	*348*	*333*	*199*
M	*102*	*154*	*152*	*149*	*76*	*132*	*204*	*215*	*129*
L	*66*	*105*	*102*	*117*	*47*	*104*	*144*	*118*	*70*
	AZORES								

	Lowland	*Mesic*	*Open*	*Laurel forest*	*High mountain*
T	*139*	*219*	*238*	*256*	*143*
M	*93*	*137*	*132*	*141*	*80*
L	*46*	*82*	*106*	*115*	*63*

<table>
<tr><th></th><th>Madeira</th><th>Porto Santo</th><th>Desertas</th><th>Hierro</th><th>Palma</th><th>Gomera</th><th>Tenerife</th><th>Gran Canaria</th><th>Fuertevent.</th><th>Lanzarote</th></tr>
<tr><td>T</td><td>523</td><td>128</td><td>95</td><td>194</td><td>345</td><td>292</td><td>434</td><td>305</td><td>131</td><td>113</td></tr>
<tr><td>M</td><td>343</td><td>57</td><td>60</td><td>135</td><td>245</td><td>193</td><td>300</td><td>223</td><td>93</td><td>88</td></tr>
<tr><td>L</td><td>180</td><td>71</td><td>35</td><td>59</td><td>100</td><td>99</td><td>134</td><td>82</td><td>38</td><td>25</td></tr>
<tr><td></td><td colspan="5">MADEIRA</td><td colspan="6">CANARIES</td></tr>
<tr><td></td><td>Lowland</td><td>Mesic</td><td>Open</td><td>Laurel forest</td><td>High mount.</td><td>Lowland</td><td>Mesic</td><td>Open</td><td>Laurel forest</td><td>Pine forest</td><td>High mountain</td></tr>
<tr><td>T</td><td>124</td><td>231</td><td>182</td><td>301</td><td>56</td><td>113</td><td>173</td><td>249</td><td>205</td><td>180</td><td>140</td></tr>
<tr><td>M</td><td>90</td><td>163</td><td>118</td><td>165</td><td>54</td><td>78</td><td>117</td><td>182</td><td>117</td><td>146</td><td>126</td></tr>
<tr><td>L</td><td>90</td><td>163</td><td>118</td><td>165</td><td>54</td><td>35</td><td>56</td><td>67</td><td>88</td><td>34</td><td>14</td></tr>
</table>

Table 2. Species number by island and type of habitat distinguished at each archipelago. T (total species number), M (mosses), L (liverworths). Open (areas included in the potential area of the laurel forest, including both, natural areas (rock communities) and disturbed areas where the laurel forest was destroyed).

Most of the species are able to occupy more than one type of habitat in Macaronesia, since only 29% were exclusive for one habitat type, half of them belonging to the laurel forest, the rest of them divided equally into the other four habitat types. Out of these habitat specialists, only seven species were found in all three archipelagos. One hundred and twenty species were observed in two habitat types and 73 species were real generalists appearing in all five habitat types and mostly in all three archipelagos.The proportion of species exclusive to the laurel forest was lowest for the Azores (29%), followed by the Canaries (67%) and Madeira islands (89%).

Floristic similarity (see figures 1, 2 and 3, TWINSPAN and CCA analyses for island-unit and habitat-unit models are not shown in this summary).

The macroecological analyses presented here reveal the particularities of the Macaronesian archipelagos and main relationship among them. When islands data were used with ordination analyses (CA, CCA) and cluster analysis, Azores and Canary islands were clearly differentiated; while drier islands in Madeira archipelago showed a close relationship with drier Canary Islands such as Lanzarote and Fuerteventura. However, island data represent an extremely oversimplification of the relationship between islands, which leads to a strong affect of the geographical position of the island. When islands and habitats were considered the inter-archipelago distances were reduced. In fact, floristic distances between habitats of the same island can be higher than distances between the same habitat types of different archipelagos. The habitat-unit model allows us to see how geographical distances are less important than environmental conditions for wide-dispersal groups like bryophytes.

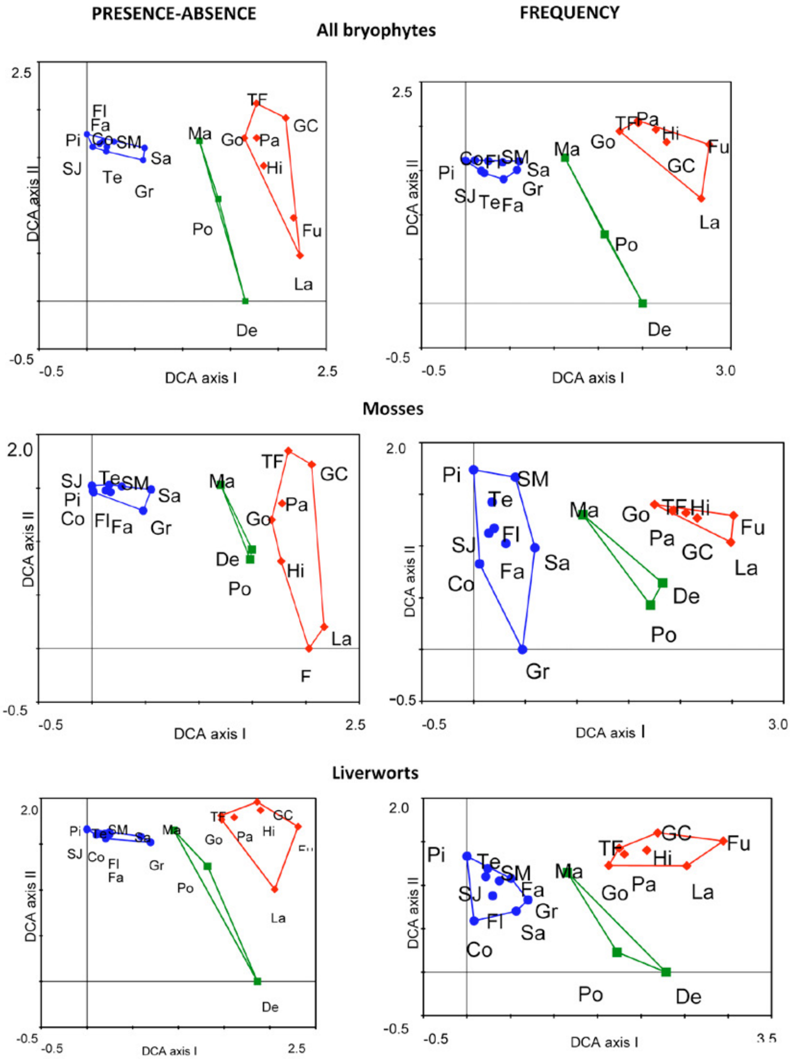

Figure 1. Detrended Correspondence Analysis with presence-absence data (Left) and Frequency (right) of all islands and total bryophyte species (above), mosses (middle) and liverworts (down). For presence-absence data Total species (eigenvalues axis 1,2: 0.363, 0.095, total inertia: 1.563; cumulative percentage variance for the first two axes 29,3), mosses (eigenvalues: 0.334, 0.080, total inertia:1.263; cumulative percentage variance for the first two axes 28,3) and liverworts (eigenvalues axis 1,2: 0.334, 0.080, total inertia: 1.263; cumulative percentage variance for the first two axes 32.8). For frequency data Total species (eigenvalues axis 1,2: 0.435, 0.100, total inertia: 1.763; cumulative percentage variance for the first two axes 30,3), mosses (eigenvalues: 0.396, 0.109, total inertia:1.537; cumulative percentage variance for the first two axes 32,9) and liverworts (eigenvalues axis 1,2: 0.440, 0.103, total inertia: 1.816; cumulative percentage variance for the first two axes 29,9).

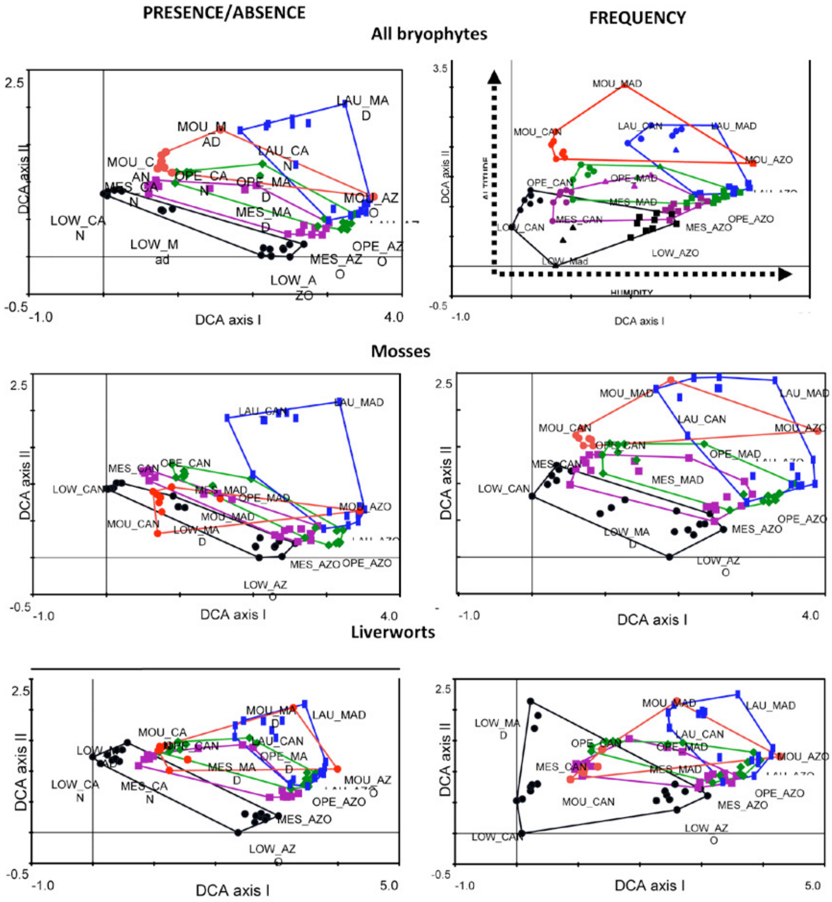

Figure 2. Detrended Correspondence Analysis with presence-absence data (Left) and Frequency (right)

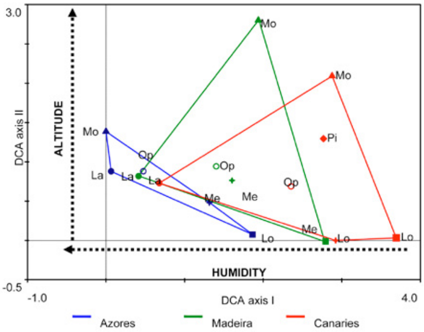

Figure 3. Detrended Correspondence Analysis with frequency data of open habitats and laurel forest habitats of humid and hyper-humid bioclimatic belts. For all bryophytes (eigenvalues axis 1,2: 0.566, 0.280, total inertia: 2.674; cumulative percentage variance for the first two axes 31.6).

Two types of inter-island similarity relations may be observed between all these northern Macaronesian islands. The first one is related to precipitation, which in these islands seems to mostly reflect inter-island similarity of the laurel forest ecosystem. The second one is related with the temperature gradient and the capacity of bryophytes to persist in microhabitats where a suitable microenvironment persists, demonstrating a much higher altitudinal and latitudinal distribution gradient for most of the species.

Richness (see table 3)

The overwhelming majority of studies on species diversity pattern in island biogeography applied the classical island approach, i.e. used the whole island as the sample unit and identified factors like area, isolation, geological age and habitat diversity (or its surrogate, maximum altitude) as best predictors for richness in different species groups (Rosenzweig 1995, Losos & Schluter 2000, Whittaker & Fernández Palacios, 2007). This has the advantage that many islands and even archipelagos can simultaneously be compared since environmental data for whole islands are easily available. But this approach has, at least when applied to many oceanic archipelagos, the disadvantage that some ecological factors are strongly correlated at the island level. When analyzing bryophyte richness in Macaronesia with the classical island approach we are confronted with the same problem. In contrast, when applying the habitat-unit-model to the bryophyte diversity of the northern Atlantic islands, we separate altitudinal habitat types, i.e. we split the altitude gradient and disentangle, at least partially, habitat diversity from island area. Including all fragments of all habitat types of each island and archipelago in the statistical model, we were able to identify habitat area and climatic variables (mean annual precipitation and temperature) as very good predictors of total bryophyte richness.

Model	Variable	Estimate	Wald-stat.	P	AIC	P	Dev. expl. (%)
ALL HAB	**Precipitation (log)**	**0,744**	**166,9**	**< 0.0001**	*798,4*	*< 0.0001*	*70,2*
	Temperature	*0,647*	*144,1*	*< 0.0001*			
	*Temp * Temp*	*-0,022*	*143,5*	*< 0.0001*			
	Habitat Area (log)	*0,195*	*73,3*	*< 0.0001*			
LOW	**Precipitation (log)**	**0,896**	**15,5**	**< 0.0001**	*42,6*	*< 0.0001*	*64,5*
	Habitat Area (log)	*0,239*	*7,0*	*0,008*			
MESIC	**Precipitation (log)**	**0,565**	**33,1**	**< 0.0001**	*149,5*	*< 0.0001*	*64,6*
	Habitat Area (log)	*0,242*	*14,5*	*0,000*			
OPEN	**Precipitation (log)**	**0,805**	**55,4**	**< 0.0001**	*127,5*	*< 0.0001*	*83,6*
	Habitat Area (log)	*0,089*	*4,2*	*0,040*			
LAUREL	**Precipitation (log)**	**0,815**	**62,1**	**< 0.0001**	*152,0*	*< 0.0001*	*70,1*
	Habitat Area (log)	*0,220*	*28,4*	*< 0.0001*			
MOUNT	**Habitat Distance (log)**	**0,992**	**40,5**	**< 0.0001**	*38,6*	*< 0.0001*	*66,0*
	Habitat Area (log)	*0,424*	*12,9*	*< 0.0001*			

Model	Variable	Estimate	Wald-stat.	P	AIC	P	Dev. expl. (%)
ALL HAB	**Habitat Area (log)**	**0,304**	**313,6061**	**< 0.0001**	*887,1*	*< 0.0001*	*62,50*
	Temperature	*0,207*	*50,7411*	*< 0.0001*			
	*Temp * Temp*	*-0,009*	*80,9688*	*< 0.0001*			
LOW	**Habitat Area (log)**	**0,315**	**24,04500**	**< 0.0001**	*149,0*	*< 0.0001*	*45,3*
	Precipitation (log)	*0,703*	*20,57964*	*< 0.0001*			
MESIC	**Habitat Area (log)**	**0,465**	**60,27610**	**< 0.0001**	*14,4*	*< 0.0001*	*70,9*
	Temperature	*-2,005*	*8,55560*	*0,003*			
	*Temp * Temp*	*0,059*	*8,55140*	*0,003*			
OPEN	**Habitat Area (log)**	**0,405**	**145,2425**	**< 0.0001**	*-4,3*	*< 0.0001*	*81,6*
	Precipitation (log)	*-0,345*	*16,4894*	*< 0.0001*			
LAUREL	**Habitat Area (log)**	**0,489**	**167,930**	**< 0.0001**	*149,5*	*< 0.0001*	*82,7*
	Population density (log)	*-0,164*	*39,784*	*< 0.0001*			
MOUNT	**Habitat Area (log)**	**0,241**	**16,133**	**< 0.0001**	*66,9*	*< 0.0001*	*70,3*

Table 3. Results of generalized linear models (GLMs), showing the best set of explanatory variables explaining richness of hepatics (Upper) and mosses (down) as response variable, using AIC best set selection and Poisson distribution with log-link function. Temperature and geological age were introduced both as a linear and as quadratic terms. (Dev. expl. = deviance explained by the model).

If we consider a step further and analyze habitat types separately and, in consequence, reduce the variation of climatic variables in the whole data set, then habitat area is by far the best predictor for overall bryophyte richness, followed by precipitation or temperature. When separating liverworts from mosses, we obtained further new insights in the richness pattern, since liverworts, as we mentioned before, are much more sensible to variation in mean annual precipitation than mosses, and this could be detected in all habitat types. That means that the latitudinal precipitation gradient affects especially liverworts and that the differences between the more arid Canary Islands and Madeira are more important for liverworts richness than the differences between Madeira and the Azores, in spite of the longer geographical distance.

Human disturbance, despite to high degree of landscape transformation on these archipelagos, shows only a weak negative effect on bryophyte richness within the laurel forest ecosystem (see table 3 mosses). Therefore, this habitat seems to be the most sensitive to destruction and fragmentation.

Habitat age, ie. historical factors, were not important (table not shown) in explaining richness pattern, which can be again attributed to the high dispersal abilities and high colonization rates of this species group.

Conclusions

Inter-islands similarity and richness pattern are better described with the habitat-unit-model than by the islands-unit model. The habitat approach allows us to see how the floristic distances vary between islands depending on the type of habitat, and the factors that influence both species distribution and richness.

Using frequency instead presence/absence data represents a great improvement for data interpretation in the habitat-unit-model; while the island-unit-model only offers an adequate approach when the compared islands are more homogeneous, as occurs in the Azores. Azores show the highest similarities of bryophyte compositions among different habitats. This is notable when disturbed (open) and preserved laurel forest areas were compared, which means that, especially for liverworts in the laurel forests, human disturbance has a stronger impact on species composition for drier regions, such as on the Canary Islands where precipitation conditions within this type of forest are limiting for bryophyte richness. The highest diversity and richness was found in the preserved laurel forest area of Madeira, where the distinct tree species strongly shape the liverworts and mosses composition and distribution (Sim-Sim *et al.* 2011).

The bryophyte flora of Macaronesia is heterogeneous when whole islands are considered. The habitats approach shows that this heterogeneity might be primarily interpreted as the differences between oceanic and Mediterranean habitats. Oceanic habitats, mostly represented by laurel forests, are the most similar and probably also the most differentiated from the surrounding mainland areas. In consequence, they are the best to define the Macaronesian concept for the phylogenetic groups of mosses and liverworts. Drier habitats, here represented by the Mediterranean bioclimatic belts, show higher ecological and floristic dissimilarities between islands and archipelagos, which presumably might be also related to a more effective species interchange with the surrounding mainland areas. Some functional groups of mosses are more tolerant to aridity and consequently show closer relationship with mainland areas at the same latitudinal level. The island-unit-model does not allow us to distinguish these differences in similarity and gives us an overestimation of the differences between mosses and liverworts distribution within Macaronesia.

In short, applying the habitat-unit-model we reduce environmental, mostly climatic variation in the data set by splitting the altitudinal gradient and analyzing habitat types separately, which enables us to evaluate and interpret better bryophyte richness and similarity pattern. As already was confirmed in other studies, the species-area relationship holds also true at the habitat level but depending on species groups. We can confirm this habitat area effect here for the first time for an entire biogeographical region, despite the considerable variation in environmental factors across these three Atlantic archipelagos. Nevertheless, we argue that we cannot detect here the area *per se* effect since there is still a lot of environmental variation within habitat types at the island or archipelago level. There is even a certain environmental variation within a specific habitat type on each single island and this variation will increase with habitat area.

The use of bryophytes, a group with high dispersal capacity and a high representation of both restricted and widely distributed species, at both altitudinal and latitudinal levels, is confirmed in this work as a very adequate approach to analyze and infer phytogeographic affinities.

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References

Azevedo, E. B. 2003. Projecto CLIMAAT - Clima e Meteorologia dos Arquipélagos Atlânticos. PIC Interreg_IIIB - Mac 2.3/A3. Accessed in January 2011 from http://www.climaat.angra.uac.pt/.

Borges, P.A.V. & Hortal, J. (2009) Time, area and isolation: Factors driving the diversification of Azorean arthropods. *Journal of Biogeography,* 36, 178-191.

Borges, P. A., Cardoso, P., Cunha R., Gabriel, R., Gonçalves V., Hortal J., Frias Martins, A., Melo, I., Rodrigues, P.,. Santos, A. M. C, Silva, L., Triantis, K. A., Vieira, P. & Vieira, V. (2011). Macroecological patterns of species distribution, composition and richness of the Azorean terrestrial biota. *Ecologi@,* 1: 22-35.

Buckley, R. 1982. The habitat-unit model on island biogeography. *Journal of biogeography* 9: 339-344.

Buckley, R. 1985. Buckley, R.C. (1985) Distinguishing the effects of area and habitat types on island plant species richness by separating floristic elements and substrate types and controlling for island isolation. *Journal of Biogeography,* 12, 527–535.

Capelo, J., Menezes de Sequeira, M., Jardim, R. & Costa, J.C. 2004. Guia da excursão geobotânica dos V encontros alfa 2004 à Ilha da madeira. In: J.A. Capelo (ed). A paisagem vegetal da Ilha da Madeira. *Quercetea,* 6: 5-45.

Capelo, J., Menezes de Sequeira, M., Jardim, R. & Mesquita, S. 2007. Biologia e importância das florestas nas Ilhas. Madeira. In: J. Silva, (coordenador editorial). *Açores e Madeira. A floresta das Ilhas.* Público. Lisboa: 81-134.

Dansereau, P. 1961. Etudes macaronésiennes I: Géographie des Cryptogames vasculaires. *Agronomica Lusitanica,* 23: 151-181.

Del Arco MJ, Acebes JR, Pe´rez-de-Paz PL, Marrero MC (1999) Bioclimatology and climatophilous vegetation of Hierro (part 2) and La Palma (Canary Islands). *Phytocoenologia* 29(2):253–290

Del Arco MJ, Salas M, Acebes JR, Marrero MC, Reyes-Betancort JA, Pérez-de-Paz PL (2002) Bioclimatology and climatophilous vegetation of Gran Canaria (Canary Islands). *Ann Bot Fenn* 39:15–41

Del Arco MJ, Pérez-de-Paz PL, Acebes JR, González-Mancebo JM, Reyes-Betancort JA, Bermejo JA, de Armas S, González-González R (2006a) Bioclimatology and climatophilous vegetation of Tenerife (Canary Islands). *Ann Bot Fenn,* 43(3):167–192.

Del Arco MJ, Wildpret W, Pérez-de-Paz PL, Rodríguez-Delgado O, Acebes JR, García-Gallo A, Martín VE, Reyes-Betancort JA, Salas M, Bermejo JA, González R, Cabrera MV, García S (2006b) Mapa de Vegetación de Canarias. GRAFCAN, Santa Cruz de Tenerife

Del Arco MJ, Rodrıíguez-Delgado O, Acebes JR, García-Gallo A, Pe´rez-de-Paz PL, González-Mancebo JM, González-González R, Garzón V (2009) Bioclimatology and climatophilous vegetation of Gomera (Canary Islands). *Annales Botanici Fennici,* 46:161–191.

Del Arco, M., González-González, R. Garzón-Machado, V. & Pizarro-Hernández, B. 2010. Actual and potential natural vegetation on the Canary Islands and its conservation status. *Biodiversity and Conservation,* (2010) 19:3089–3140.

Deshaye, J. and Morisset, P. 1988. Floristic richness, area and habitat diversity in hemiarctic archipelago. J. Biogeogr. 15: 747-757.

Dias, E. 1996. Vegetãçao natural dos Azores. *Ecologia e sintaxonomia das florestas naturais 302 p.* PhD Thesis. Universidade dos Açores, Angra do Heroísmo.

Dias, E., Mendes, C., Melo, C., Pereira, D. & Elias, R. 2005. Azores central islands. Vegetation and flora field guide. *Quercetea,* 7: 123-173.

Domínguez Lozano, F., Price, J., Otto, R. & Fernández Palacios, J.M. 2010. Using taxonomic and phylogenetic evenness to compare diversification in two Island Floras. *Perspectives in Plant Ecology, Evolution and Systematics,*12: 93–106.

DROTRH 2008. Carta de ocupação do solo da região Autónoma dos Açores - Projecto SUEMAC. Secretaria Regional do Ambiente, Direcção Regional do Ordenamento do Território e dos Recursos Hídricos. Ponta Delgada.

Engler, A. 1879. Versuch einer Eintwicklungsgeschichte, insbesondere der Florengebiete seit der Tertiärperiode. I. Die extra-tropischen Gebiete der nördlischen Hemisphäre. W. 857 Engelmann, Leipzig.

Forjaz, V. H. (coord.) (2004). *Atlas básico dos Açores*. Observatório Vulcanológico e Geotérmico dos Açores. Ponta Delgada.

Gonzalez-Mancebo, J. M., Romaguera, F., Ros, R. M., Patino, J. & Werner, O. 2008a. Bryophyte flora of the Canary Islands: an updated compilation of the species list with an analysis of distribution patterns in the context of the Macaronesian Region. *Cryptogamie Bryologie,* 29: 315-357.

González-Mancebo, J.M., Losada-Lima, A., Patiño, J., Leal, J., 2008b. Los briófitos del Parque Nacional de Garajonay. In: Beltrán, E. (Ed.), Hongos, líquenes y briófitos del Parque Nacional de Garajonay. Organismo Autónomo de Parques Nacionales, Madrid, pp. 565-775.

Kreft, H. Jetz, W., Mutke, J., Kier, G. & Barthlott, W. 2008. Global diversity of island floras from a macroecological perspective. *Ecology Letters,* 11 (2): 116–127.

Lobin, W. 1982. Untersuchung über Flora, Vegetation und biogeographishce Beziehungen der Kapverdischen Inseln. *Courier Forschungsinstitut Senckenberg,* 53.

Médail, F., and P. Quézel. 1997. Hot-spots analysis for conservation of plant biodiversity in the Mediterranean basin. *Annals of the Missouri Botanical Garden,* 84: 112–127.

Mesquita S., Capelo J, & Sequeira M., Evolução dos hotsposts de biodiversidade na ilha da Madeira entre 1988 3 2007 em relação com alterações no uso do solo. Análise preliminar do impacte dos incêndios de 2010. (*in preparation*).

Mesquita S., Sequeira M., & Capelo J. Floristical biodiversity hotspots and nature conservation areas in Madeira, Portugal. (*in preparation*).

Nicolás J.P., Fernández Palacios J.M., Ferrer, F.J. & Nieto E., 1989. Inter-islands floristic similarities in the Macaronesian region. *Vegetatio,* 84: 117-125.

Pram. 2002. Plano regional da Água. Caracterização e diagnóstico da situação actual. Investimentos e Gestão da Água, Funchal.

Reyes-Betancort JA, Wildpret W, León-Arencibia MC (2001). The vegetation of Lanzarote (Canary Islands). *Phytocoenologia,* 31(2):185–247.

Rivas-Martínez, S. 2009. *Ensayo geobotánico global de la Macaronesia.* Instituto de Estudios canarios. La Laguna pp. 255-296.

Rosenzweig, M.L. (1995) *Species diversity in space and time.* Cambridge Univ. Press.

Sim-Sim M., Fontinha S., Luís L., Martins S., Lobo C., Stech M. & W. Frey. 2010a. The Selvagens Islands bryoflora and its relation with other islands of the Madeira and Canary Islands Archipelagos. *Nova Hedwigia,* 138: 185-197.

Sim-Sim M., Bergamini, A. Luís L., Fontinha S., Martins S., Lobo C. & W. Stech. 2011. Epiphytic bryophyte diversity on Madeira Island: Effects of tree species on bryophyte species richness and composition. *The Bryologist,* 114(1):142-154. 2011. In press.

Triantis, K.A., M. Mylonas, K. Lika and K. Vardinogiannis. 2003. A model for species area-habitat relationship. *Journal of Biogeography,* 30: 19-27

Vanderpoorten, A., Rumsey, F. J. & Carine, M. A. (2007). Does Macaronesia exist? Conflicting signals in the bryophyte and pteridophyte floras. *American Journal of Botany* **94**, 625–639.

Vanderpoorten, A., Gradstein, R.S., Carine, M.A. & Devos, N. 2009. The ghosts of Gondwana and Laurasia in modern liverwort distributions. *Biological Reviews,* 85: 471–487.

Whittaker, R.J. & Fernández Palacios, J.M. (2007) *Island biogeography,* 2nd edn. Oxford University Press, Oxford.

Zobel, M., Otto, R., Laanisto, L., Naranjo-Cigala, A., Pärtel, & M. Fernández Palacios, J.M. 2011. The formation of species pools: historical habitat abundance affects current diversity. *Global Ecology and Biogeography,* 20(2): 251-259.