CHARACTERISTIC PATTERN OF SPECIES DIVERSITY ON THE CANARY ISLANDS

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Summary: We use an island specific presence/absence data set for the Canary Islands' *Arthropoda, Spermatophyta, Fungi, Lichenes, Bryophyta, Mollusca, Chordata, Pteridophyta, Annelida* and *Nematoda* to assess the relative influence of environmental and historical factors on species distribution and endemism. Species richness and the percentage of island endemic species as well as similarity indices for island comparisons were calculated for all species groups. Hierarchical partitioning is used to identify the independent and joined influence of 21 environmental and historical variables. The pattern of species richness is best explained by island elevation. Elevation reflects a variety of factors that contribute to habitat diversity. A similar pattern is detected for the "percentage of single island endemics" (pSIE), a factor associated with speciation. Variables associated with geographical distance have highest explanatory power for biotical similarity of islands. Various Canary Islands species groups show strong distance-decay within the archipelago. According to our findings, speciation is not necessarily driven by species richness or island age alone. Thus, we conclude that correlations between species richness and pSIE, identified in previous studies, could represent an artefact related to differing degrees of isolation between zonal altitudinal ecosystems. This would lead to an increase of speciation with altitude resulting in higher values for pSIE on high altitude islands.

Zusammenfassung: Für die Kanarischen Inseln wird auf Grundlage eines inselspezifischen Präsenz/Absenz-Datensatzes der Artengruppen *Arthropoda, Spermatophyta, Fungi, Lichenes, Bryophyta, Mollusca, Chordata, Pteridophyta, Annelida* und *Nematoda* die Bedeutung von Umwelt- und historischen Variablen für Artverbreitung und Endemismus analysiert. Artenreichtum, Anteil an Inselendemiten sowie Ähnlichkeit in der Artzusammensetzung (im Vergleich der Inseln) werden inselspezifisch für alle genannten Artengruppen bestimmt. Mittels Hierarchischer Partitionierung wird der gemeinsame und unabhängige Anteil an der durch 21 untersuchte Umwelt- und historische Variablen erklärbaren Varianz ermittelt. Das Muster der Artenvielfalt lässt sich am besten durch die von einer Insel erreichte Höhe über NN erklären. Diese Kenngröße reflektiert eine Vielzahl an Eigenschaften, welche die Vielfalt von Lebensräumen repräsentieren. Ein ähnliches Muster findet man für den Anteil der Inselendemiten, eine Variable, die mit Artbildung assoziiert wird. Variablen, die mit geographischer Distanz im Zusammenhang stehen, weisen den höchsten Zusammenhang mit der biotischen Ähnlichkeit innerhalb des Archipels auf. Eine direkte Abnahme der Ähnlichkeit in der Artzusammensetzung einzelner Inseln mit deren Entfernung („distance-decay") findet sich für mehrere Artengruppen. Unsere Ergebnisse weisen darauf hin, dass Artbildung nicht notwendigerweise alleine von Artenreichtum oder Inselalter abhängig ist. Ein in anderen Studien gefundener Zusammenhang zwischen Artenreichtum und dem Anteil an Inselendemiten kann auch als Artefakt interpretiert werden, welches dadurch entstehen könnte, dass höhenzonale Ökosysteme einzelner Inseln unterschiedlich stark isoliert sind. Als Folge würde es zu einem Anstieg des Anteils an Inselendemiten mit der Höhe kommen. Dies zieht dann für Inseln, die eine größere Höhe erreichen, auch höhere Prozentwerte an Inselendemiten nach sich.

Keywords: Species turn-over, species-area, beta-diversity, alpha-diversity, Macaronesia, distance decay, Atlantic Ocean, island biogeography, speciation

1 Introduction

Ecological and evolutionary processes operate in overlapping spatial and temporal dimensions (Carroll et al. 2007; Fussmann et al. 2007; Kinnison and Hairston 2007). Heaney (2000) demonstrates that migration, extinction, and phylogenesis can be effective within comparable time spans. Therefore, it is difficult to differentiate the most influential processes responsible for the present pattern of spe-

cies distribution. Simplified assumptions in popular biogeographical concepts, like the idea of equilibrium, have been proven to be wrong (see Brown and Lomolino 2000; Whittaker 2000; Heaney 2007; Whittaker and Fernández-Palacios 2007). In contrast to the suggestions made by MacArthur and Wilson (1967), immigration and extinction are not necessarily continuous processes, but can occur in the context of discrete events ("taxon pulses") (Ricklefs and Bermingham 2002; Halas et al. 2005).

The identification of variables that control processes and patterns in ecological systems is of major concern (HEANEY 2007; WHITTAKER et al. 2007). The understanding of ecological processes in isolated regions, such as fragmented landscapes or patchy ecosystems, can profit from the research on island ecosystems (DUARTE et al. 2008). By studying drivers for floristic richness on island ecosystems, various authors contributed to an improved understanding of global patterns of biodiversity (e.g. MORRISON 2002; WILLERSLEV et al. 2002; PRICE 2004; ROOS et al. 2004; MCMASTER 2005; PANITSA et al. 2006; DAPPORTO and DENNIS 2008; DUARTE et al. 2008; HANNUS and VON NUMERS 2008).

The mere area of potential habitats is an important, albeit indirect, physical parameter that can be used to analyse patterns of species distribution (MCMASTER 2005; WHITTAKER and FERNÁNDEZ-PALACIOS 2007). For many archipelagos, a certain correlation of area with species number is documented (e.g. PRICE 2004; ROOS et al. 2004; MCMASTER 2005; DUARTE et al. 2008; HANNUS and VON NUMERS 2008). This linkage was even said to be one of the most powerful "rules" in ecology (LOMOLINO 2000b; TJORVE 2003; TRIANTIS et al. 2003). Nevertheless, the functional background of this pattern is manifold and can hardly be traced precisely due to ecological complexity. Various explanations are under debate. The "habitat diversity hypothesis" (WILLIAMS 1964) assumes that a larger area, due to its supposed spatial heterogeneity, is connected with the conditional probability of hosting more species. According to the "area per se" hypothesis (PRESTON 1960; MACARTHUR and WILSON 1967) larger areas host more species, as the extinction risk of local populations is reduced on larger surfaces. Furthermore, according to the "passive sampling hypothesis" (CONNOR and MCCOY 1979) and the "target area hypotheses" (MACARTHUR and WILSON 1967), the chance of an area to be colonised by locally "new" species increases with its size. The relevance of proximity is highlighted by the "rescue hypothesis" (BROWN and KODRIC-BROWN 1977). It predicts declining populations or species that do not surpass minimum viable population sizes to be maintained when large and viable populations are close by and individuals or diaspores can disperse. This dynamics directly refers to the "source sink theory" for metapopulations introduced by PULLIAM (1988). According to this concept, (large or suitable) habitat patches with population growth beyond their capacity contribute to the maintenance of habitat patches that can not sustain permanent viable populations. For general overviews see TRIANTIS et al. (2003), ROOS et al. (2004), BEIERKUHNLEIN (2007) and WHITTAKER and FERNÁNDEZ-PALACIOS (2007).

Investigating a spectrum of physical and historical factors may reveal the processes behind single explanatory variables such as area. Such an approach has to be designed in a manner that allows assessing whether species richness, despite being correlated with area ("area per se" hypothesis), could be explained by parameters associated with habitat diversity ("habitat diversity hypothesis"). The "passive sampling -", the "target area -", the "rescue hypothesis" and the "source-sink theory" are more associated to an island's isolation from the target species source region. In this case, spatial filters like distance might be more important by reducing the probability of migratory and dispersal success.

HANNUS and VON NUMERS (2008) find both island area and habitat diversity to be correlated with species richness for an island archipelago in south-western Finland. For Mediterranean islands, SCHMITT (1998) identified a linear increase in the number of taxa in ferns and flowering plants with elevation and log (area). Including endemic species can provide information on speciation processes. For the west Italian islands, DAPPORTO and DENNIS (2008) confirm the influence of distance to the nearest landmass source on species assemblage, species richness and endemism.

In this study, we test whether the number of species on an island and the dissimilarity in the species pool of islands are predominantly determined by ecological or spatial factors. The ecological background and the availability and heterogeneity of habitats directly control resource availability and ecological niches. It can be assumed that this is more important for species diversity than spatial or temporal qualities, which are considered in traditional island biogeography (BEIERKUHNLEIN 1998). Habitat conditions are characterized in our study by a set of variables such as soil traits, geology, precipitation, temperature, forest cover, human population, inclination and elevation. A second group of variables was selected with focus on geographical aspects related to an island's isolation (distance to Africa, distance to next island, human induced connectivity, mean distance to the islands in the archipelago). In the following, the first group of variables is referred to as the 'ecological setting' and the second group of variables as the 'spatial setting'. As discussed above, area (active surface) could be associated with both categories. In addition, the historic factors "time" (available for evolution and

immigration) and "age" of the island (existence) are analysed and discussed. These two terms are not necessarily exchangeable.

We hypothesize that species number is predominantly controlled by ecological settings and not by spatial settings (H1). Therefore, physical factors representing habitat diversity should explain more of the variance of the species richness patterns than isolating spatial parameters. Comparable analyses were applied for other archipelagos (e.g. MORRISON 2002; WILLERSLEV et al. 2002; PRICE 2004; ROOS et al. 2004; MCMASTER 2005; PANITSA et al. 2006; DAPPORTO and DENNIS 2008; DUARTE et al. 2008; HANNUS and VON NUMERS 2008). Besides methods applied in these studies, similarity indices for beta diversity are calculated for the Canarian flora and fauna. We test if similarity in species compositions ("differentiation diversity" sensu JURASINSKI et al. 2009) between the islands of the Canary Archipelago is more influenced by environmental isolation (species from a source region do not find suitable habitats) and less by spatial isolation (these species can not reach suitable habitats on the island) (H2). This is the first time, the relationship between distance in environmental parameters and similarity of species composition is investigated on oceanic islands.

2 Study area

The Canary Islands are located near the African coastline between 27° and 29° northern latitude and 14° and 18° western longitude. The archipelago is of volcanic origin and consists of seven main islands larger than 250 km² (from east to west: Lanzarote, Fuerteventura, Gran Canaria, Tenerife, La Gomera, La Palma and El Hierro, see Fig. 1). Five smaller islets (between 1 and 30 km²) are not objects of this study. The oldest basalt shield of the island group in Fuerteventura rose around 20 million years ago over the sea surface. However, the formation of the submarine parts started already 70 to 80 million years ago (ANGUITA et al. 2002; compare Fig. 1). 16 million years ago, the first parts of the subsequent island of Lanzarote emerged ("Femes"). The next islands to appear were Gran Canaria (14 million years), La Gomera (12 million years) and Famara (10 million years). The basalt blocks Teno, Adeje and Anaga rose around 8 million years ago. They fused together to one single island 1.5 million years ago and now form the edges of Tenerife. La Palma and El Hierro emerged rather late, 1.5 and 1.1 million years ago, respectively.
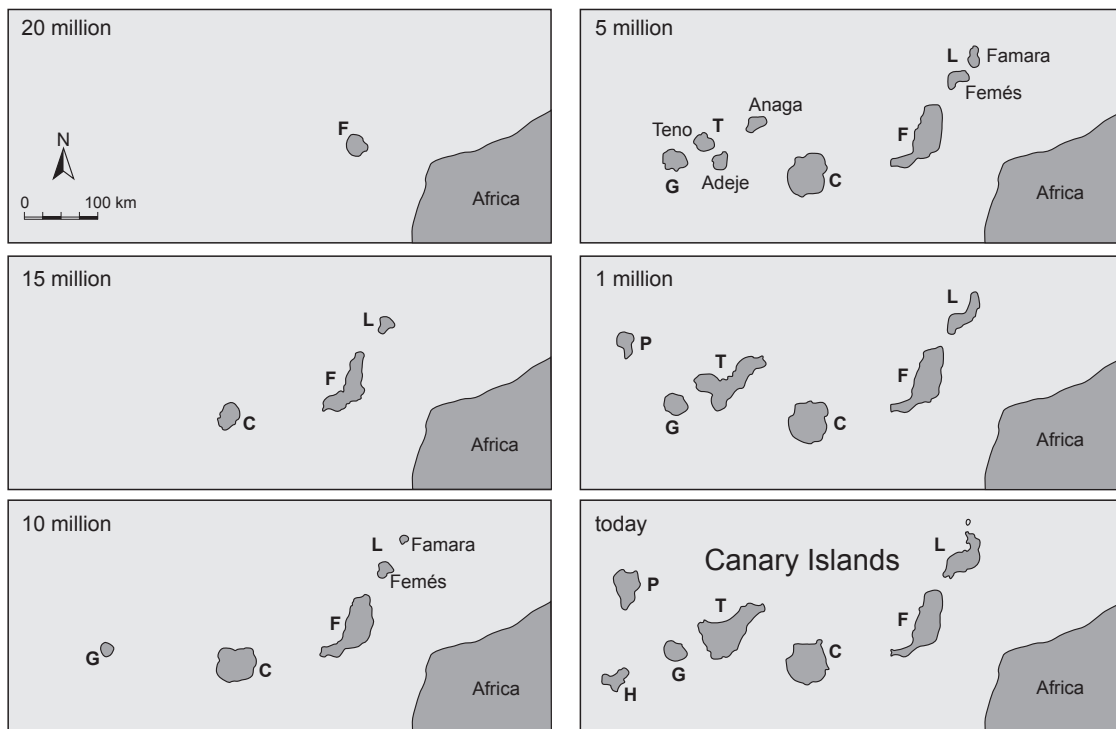

Fig. 1: Volcanic evolution of the Canarian Archipelago: L=Lanzarote, F=Fuerteventura, C=Gran Canaria, T=Tenerife, P=La Palma, G=La Gomera, H=El Hierro (Modified after MARRERO and FRANCISCO-ORTEGA 2002).

The islands have always been separated from the African mainland by a trench which has a recent depth of at least 1,500 m. Sea level changes driven by glacial/interglacial cycles of the Pleistocene were responded by a fluctuating distance to Africa ranging from 60 km (glacial period with low sea-level) to 95 km today (García-Talavera 1999; Fernández-Palacios and Whittaker 2008).

The seven main islands differ noticeable in size, altitude, and age. Tenerife is seven times larger than El Hierro and its highest elevation, El Teide (3,718 m), is by far higher than for instance on Lanzarote (670 m). These topographic differences are reflected by climatic gradients within and between islands. On Tenerife, mean annual temperature at the highest meteorological station (Cañadas-Pico Teide; 3,530m asl) is 3.5 °C, while the lowest station (Anaga-San Andrés; 20 m asl), records 20.6 °C mean annual temperature (Del Arco et al. 2006). Because of the predominant north-eastern trade winds, precipitation varies especially between north-eastern and south-west facing slopes. On Tenerife, the station with the lowest annual precipitation (Guía de Isora-Alcalà Chiquita; 70 m asl) is located on the south-western coast in the rain shadow of El Teide. It only has 47.4 mm of annual precipitation. Highest precipitation is recorded on the Esperanza Ridge (Matanza-Lagunetas; 1,400 m asl) on the north-eastern part of the island with 928 mm of annual precipitation (Del Arco et al. 2006). Despite the indicated spatial variations and regional climate distinctions, in general the Canary Islands are characterised by an even-tempered, subtropical climate that is balanced by the sea, constant trade winds and ocean currents.

3   Methods

This study analyses presence/absence data for *Arthropoda* (7,044 species), *Spermatophyta* (1,962 species), *Fungi* (1,713 species), *Lichenes* (1,262 species), *Bryophyta* (474 species), terrestrial *Mollusca* (240 species), *Chordata* (137 species), *Pteridophyta* (63 species), *Annelida* (61 species) and *Nematoda* (31 species) for the seven Canarian main islands. The data were obtained from Izquierdo et al. (2004). Subspecies were excluded. Altogether the dataset contains 12,997 species of which 3,663 are endemic to the Canary Islands.

In a first survey, species richness and the percentage of island endemic species (pSIE) for the different species groups were analysed. Variables used to describe island characteristics are listed in table 1 and 2.

To identify the amount of total variation explained by ecological, spatial and historic variables, a hierarchical partitioning was conducted. Hierarchical partitioning was developed to estimate the joint and independent contribution of correlated predictor variables. The independent contribution is the part of variance that only one single predictor can explain, while the joint contribution can be explained by more than one predictor. Hierarchical partitioning computes the independent contribution by comparing the goodness-of-fit of all possible models with and without a predictor variable (for more details see Chevan and Sutherland 1991; Mac Nally 2002). The purpose of hierarchical partitioning is not to calculate a predictive model, but to generate a detailed basis for inferring causality in multivariate regression settings (Watson and Peterson 1999). Heikkinen et al. (2005) suggest hierarchical partitioning, as it contributes to a better understanding of predictive variables in ecological studies.

Hierarchical partitioning was conducted using linear regression and R^2 as the goodness-of-fit measure implemented in the package "hier.part" version 1.0-3 (Walsh and Mac Nally 2008) within the statistical program R (R Development Core Team 2008).

As the algorithm is only capable to consider nine variables, the variables with highest explained variance were identified in a preliminary investigation. Hierarchical partitioning was applied on nine coincidentally chosen variables. Then, these variables were weighted according to their explained variance. This procedure was repeated 500 times. Weighting scores for each variable were summed up and those nine variables with the highest cumulative scores were chosen for the final hierarchical partitioning.

As hierarchical partitioning does not provide significance values, a separate linear regression model was calculated for each predictor with the dependent variable (linear regression and R^2 as the goodness-of-fit measure). Significance ($p < 0.05$) was tested using F-test as implemented in function "lm" within the statistical program R.

In a further analysis, the explanatory power for the similarity in species composition was assessed. For the survey of similarity between the Canary Islands, the Simpson Index was chosen. This index is independent of richness (Koleff et al. 2003; Baselga 2007) and is widely used. Similarity indices were calculated by using R-package "simba" version 0.2-5 (Jurasinski 2007).

The geographical distance between the islands and the calculated Euclidean distance of selected

Table 1: References and descriptions for the variables used for the analyses. "Island circumference" as well as "inclination under 20%" (not listed here) were not included in later calculations, as they are strongly correlated with "area 2D" and "inclination", respectively.

Variable name	Description	Reference
Area 2D	Island area in a two dimensional projection	INSTITUTO NACIONAL DE ESTADISTICA (2005)
Area 3D	Three dimensional island area calculated from a digital elevation model.	SRTM-data performed in ENVI 4.0
Elevation	Island elevation	INSTITUTO NACIONAL DE ESTADISTICA (2005)
Time	Represents the time that was available for species immigration and evolution on an island. As suggested by Whittaker et al. (2007, 2008), an age of 8 million years was chosen for Tenerife, as at that time the lava domes that would later form the island exceeded see level. Due to the sterilising volcanic eruption 3.5 million years ago, this time span was chosen for Gran Canaria.	WHITTAKER et al. (2007, 2008)
Island age	The maximum age of the island.	In DEL ARCO et al. (1996) modified with new records reported in WHITTAKER et al. (2007, 2008).
Population	Human population on the island.	INSTITUTO NACIONAL DE ESTADISTICA (2005)
Distance to Africa	The nearest geographical distance to mainland Africa.	Google Earth
Next island	The shortest distance to the next island measured from coast to coast.	Google Earth
Mean distance	The mean of an island's distance to all other islands. This mean island distance is the higher the closer to the edge of the archipelago an island is situated	Google Earth
Connectivity	A measurement for travelling possibilities between the islands. It represents the maximum number of ferry and aerial connections that could be found per day and island.	All available net sources that could be found within a two-hour survey.
Soil	The number of illustrated main classes in the map.	INSTITUTO GEOGRÁFICO NACIONAL (1994)
Geology	The number of illustrated main classes on the geological map.	Geological map assessed from GRAFCAN – Sistema de información territorial, Gobierno de Canarias
Mean precipitation	Mean precipitation on the island.	FERNANDO-PULLÉ (1976)
Max. precipitation	Precipitation of the meteorological station with highest mean precipitation on the island.	Meteorological data were taken from DEL ARCO et al. (1996), DEL ARCO et al. (1999), REYES-BETANCORT et al. (2001), DEL ARCO et al. (2002), DEL ARCO et al. (2006), DEL ARCO et al. (2008) based on RODRÍGUEZ-DELGADO et al. (2005), DEL ARCO et al. (2009), www.climatedata.eu (02/2010) and www.globalbioclimatics.org (02/2010).
Min. precipitation	Precipitation of the meteorological station with lowest mean precipitation on the island.	See "max. precipitation"
Precipitation range	The range between maximal and minimal precipitation	See "max. precipitation"
Max. temperature	Temperature of the meteorological station with highest mean temperature on the island.	See "max. precipitation"
Min. temperature	Temperature of the meteorological station with lowest mean temperature on the island.	See "max. precipitation"
Temperature range	The range between maximal and minimal temperature.	See "max. precipitation"
Forest cover	The percentage of island area that is covered by forest	Forest management plan published by the Canarian ministry (Consejería de Política Territorial y Medio Ambiente Gobierno de Canarias, 2000)
Inclination	Mean inclination of the island calculated from a digital elevation model.	SRTM-data performed in ENVI 4.0

Table 2: Variables used for the analyses.

Variable name	El Hierro	La Palma	La Gomera	Tenerife	Gran Canaria	Fuerte-ventura	Lanzarote
Area 2D [km²]	269	708	370	2034	1560	1660	846
Area 3D [km²]	308	777	413	2127	1645	1675	823
Elevation [m asl]	1501	2423	1487	3718	1949	807	671
Time [million year]	1.1	1.5	12.0	8.0	3.5	16.0	20.0
Island age [million year]	1.1	1.6	12.0	8.0	13.9	16.1	20.0
Population [thousand]	11	86	22	853	807	90	127
Distance to Africa [km]	382	416	333	287	196	96	127
Next island [km]	61	58	27	27	61	11	11
Mean distance [km]	197	184	141	112	140	195	252
Connectivity [number of connections]	13	29	9	76	71	42	34
Soil [number of main types]	3	7	4	7	5	2	3
Geology [number of main types]	9	10	11	27	21	22	11
Mean precipitation [mm]	426	586	410	420	325	147	135
Precipitation range [mm]	718	1123	609	881	842	141	122
Max. precipitation [mm]	827	1295	758	928	987	246	218
Min. precipitation [mm]	109	172	149	47	145	105	96
Temperature range [°C]	9.5	11.7	8.2	18.6	8.9	2.5	3
Max. temperature [°C]	22.2	21.3	20.8	22.1	21.5	20.4	21
Min. temperature [°C]	12.7	9.6	12.6	3.5	12.6	17.9	18
Forest cover [%]	24	45	25	24	10	0	0
Inclination [%]	27	33	39	23	28	13	10
Species richness [-]	2879	5189	4509	9008	5987	2839	2590
Number of Arthropoda [-]	1310	2655	2181	4777	3151	1620	1338
Number of Spermatophyta [-]	619	836	848	1383	1256	701	673
Number of Fungi [-]	206	917	502	1073	477	31	60
Number of Lichenes [-]	287	529	531	878	302	76	165
Number of Bryophyta [-]	189	318	278	408	293	122	109
Number of Mollusca [-]	33	55	62	103	69	30	35
Number of Chordata [-]	63	65	68	104	95	68	62
Number of Pteridophyta [-]	33	41	41	53	47	16	14
Number of Annelida [-]	11	20	21	57	24	6	3
Number of Nematoda [-]	8	9	9	24	9	3	8
Endemic species [-]	757	1128	1181	2228	1509	623	561
pSIE [%]	5	5	7	10	9	5	4

variables (listed in table 1) were implemented as predictive variables for the biogeographical analysis. As explained above, the detection of explanatory power was performed by using hierarchical partitioning.

Significance tests for linear relations between distance matrices have to account for the problem of pseudoreplication. One solution is to apply permutation tests. Here, a Mantel-test was performed

using R-package "ecodist" version 1.1.4 (Goslee and Urban 2007).

Finally, the percentage of single island endemics (pSIE) was investigated in detail. The connection to species diversity and other already mentioned variables were questioned. Analyses were restricted to *Arthropoda* (SIE n=1,534), *Spermatophyta* (SIE n=294), *Fungi* (SIE n=99) and *Mollusca* (SIE n=173). *Lichenes* (SIE n=14), *Bryophyta* (SIE n=4), *Chordata* (SIE n=6), *Pteridophyta* (SIE n=1), *Annelida* (SIE n=0) and *Nematoda* (SIE n=1) were not taken into considerations due to the small number of SIE.

4   Results

Altitude was attributed with the highest explanatory power for species richness (Fig. 2). It explains the largest proportion of variance for most species groups (R^2 between 0.55 and 0.90). Other variables such as the temperature range, the minimum temperature, precipitation range, the human population, the mean distance to the other islands, human connectivity and the number of soil types also have a high explanatory power. Due to the high inter-correlations among these variables, a precise differentiation between them seemed neither possible nor reasonable.

Good predictor variables for pSIE are human population size, mean distance to the other islands, minimum temperature and elevation (Fig. 3).

Similarity in species composition is best reflected by geographical distance, difference in the precipitation parameters and distance to mainland Africa (Fig. 4). Furthermore, the differences in inclination were a good predictor for similarity.

Median values for similarity in species composition vary between 0.9 (for *Annelida*) and 0.4 (*Mollusca*) (Fig. 5). Incomplete records in species groups that are difficult to detect or to determine, such as *Fungi* and *Lichenes*, could be the reason for low values and a high variance of similarity. Different taxa might erroneously be assumed to be identical. Some species are distinct but can not be discriminated visually. Morphological variability may lead to the description of separate species, which are in fact just varieties. Such problems are likely to occur also in *Annelida* and *Nematoda*. However, the high values of variance are probably related rather to the low number of species in these groups. The species group "*Arthropoda*" is rich in species and ecologically very heterogeneous. Hence,

similarity values are close to the overall mean. For *Chordata,* the high similarity of species composition between the islands reflects the large percentage of birds with high migratory ability. Strong distance decay was identified for most species groups (Fig. 6). The explanatory power of the distance-decay relation is best for *Chordata.*

5   Discussion

5.1 Variables correlated with the species richness pattern (H1):

Island elevation was identified to be most suitable for describing species richness patterns on the Canary Islands (Fig. 2). This is consistent with the findings of Fernández-Palacios and Andersson (2000). Elevation summarises a variety of habitat characteristics. Together with predominant wind patterns, elevation is responsible for a manifold mesoclimate. Especially, higher elevations cause pronounced windward and leeward effects. Fernández-Palacios and Andersson (2000) find elevation to be strongly correlated (95%) with habitat diversity on Macaronesian Islands. For the Canary Islands, elevation might substitute area as the variable summarising ecological conditions and carrying capacity. This is consistent with other oceanic island archipelagos (e.g. Hamilton et al. 1963), especially if they are of volcanic origin (like Hawaii; Price 2004). However, a high explanatory power of elevation for area or species richness is not a global phenomenon (Kreft et al. 2008).

An increase of island species diversity with island elevation must not necessarily be caused by habitat diversity. Schoener et al. (2001) show elevation to be a key variable for species survival during catastrophic events (e.g. storm floods, fire). In addition to advantages during short-term events, elevation gradients also facilitate populations persistence and survival during long-term environmental fluctuations such as cold stages.

Besides altitude, variables like "precipitation range", "minimum temperature", "medium distance to other islands" and "number of soil types" are suitable variables to describe the distribution pattern. These variables can be understood as the integral of abiotic conditions on the islands. Elevation represents topography. "Number of soil types", "minimum temperature" and "precipitation range" are defining living conditions for biota. These variables could also be seen to repre-
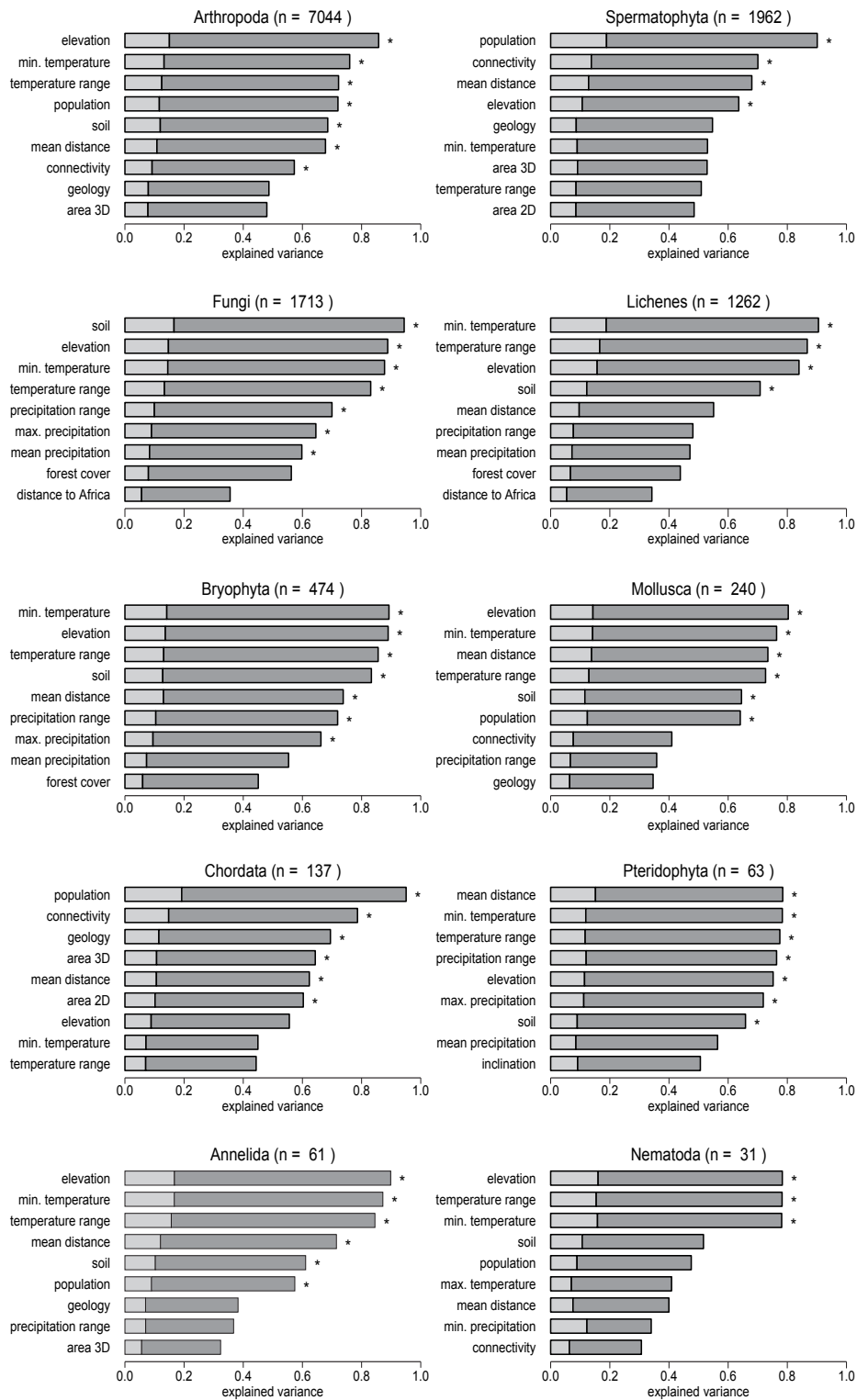
Fig. 2: The number of species analysed by using hierarchical partitioning. Grey parts of the bars illustrate the amount of variance that a variable can explain independently, black parts show the amount of variance that a variable can explain together with other variables. Significance (p < 0.05) is indicated by a star besides the bar.
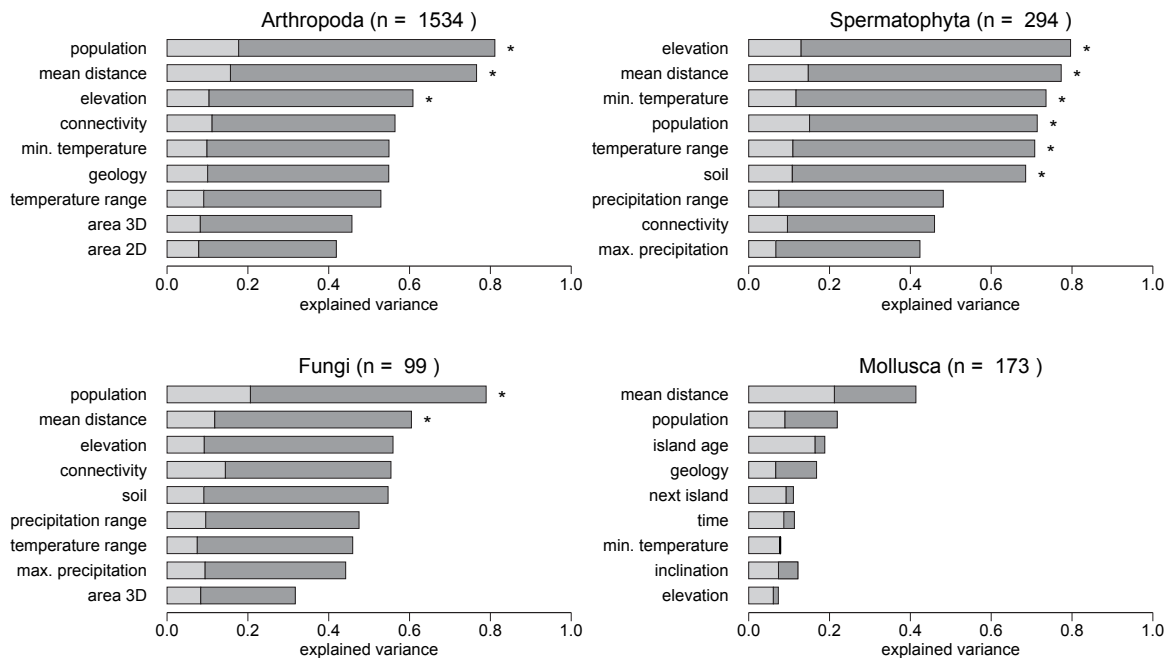
Fig. 3: The percentage of single island endemic species analysed by using hierarchical partitioning. Grey parts of the bars illustrate the amount of variance that a variable can explain independently, black parts show the amount of variance that a variable can explain together with other variables. Significance (p < 0.05) is indicated by a star besides the bar.

sent mechanisms that define the islands' ecological niches and carrying capacity. Consequently, even a higher rate of species immigration will not necessarily result in a much larger number of overall species. Hypothesis 1 could be proved: it is not primarily the recent distance to mainland Africa that influences species abundance on the Canary Islands. Yet the influence of distance cannot be neglected, as indicated by the effects of "mean [island] distance". The identified effect illustrates that islands located in the centre of the archipelago host more species than those at the borders. As two islands with comparably high elevations are located in the centre of the archipelago (Gran Canaria, Tenerife), one could dismiss this effect as a coincidental correlation. However, the pattern we found could also be interpreted as an indication for the importance of species exchange among the islands. This would mean that within archipelagos, immigration from neighbouring islands is more important for species richness than immigration from the mainland. This argumentation would support the results of SANMARTÍN et al. (2008) who applied a Bayesian modelling approach on the Canary Islands and found the inter-island dispersal within the archipelago to be more important for the explanation of diversification within lineages than dispersal between the continent and the islands.

5.2 pSIE as an indicator for speciation:

pSIE was introduced as a indicator for speciation on island archipelagos by EMERSON and KOLM 2005 (see also WHITTAKER et al. 2007). As pSIE and species number show colinearity for the Canary Islands, it is not surprising that again variables correlated with elevation have the highest explanatory power. However, while elevation is among the best variables that explain pSIE, it is not the overall best (compare figure 3). EMERSON and KOLM (2005) identified a correlation between species richness and pSIE for the Canary Islands. They suggested that species richness promotes speciation. In that study, species richness was, besides elevation and area, the most adequate variable for the explanation of patterns in pSIE for *Spermatophyta* and *Arthropoda*. We show that there are more variables representing either ecological or distance related factors that could explain most variance of the pattern. Therefore, the identified linkage between species number and pSIE could be driven by hidden underlying processes. WHITTAKER et al. (2007, 2008) suggest that a higher complexity of an island will enable more colonists to find suitable habitats to establish. This will further on intensify the adaptive radiation of already established species. With time, this will deepen the genetic gap between
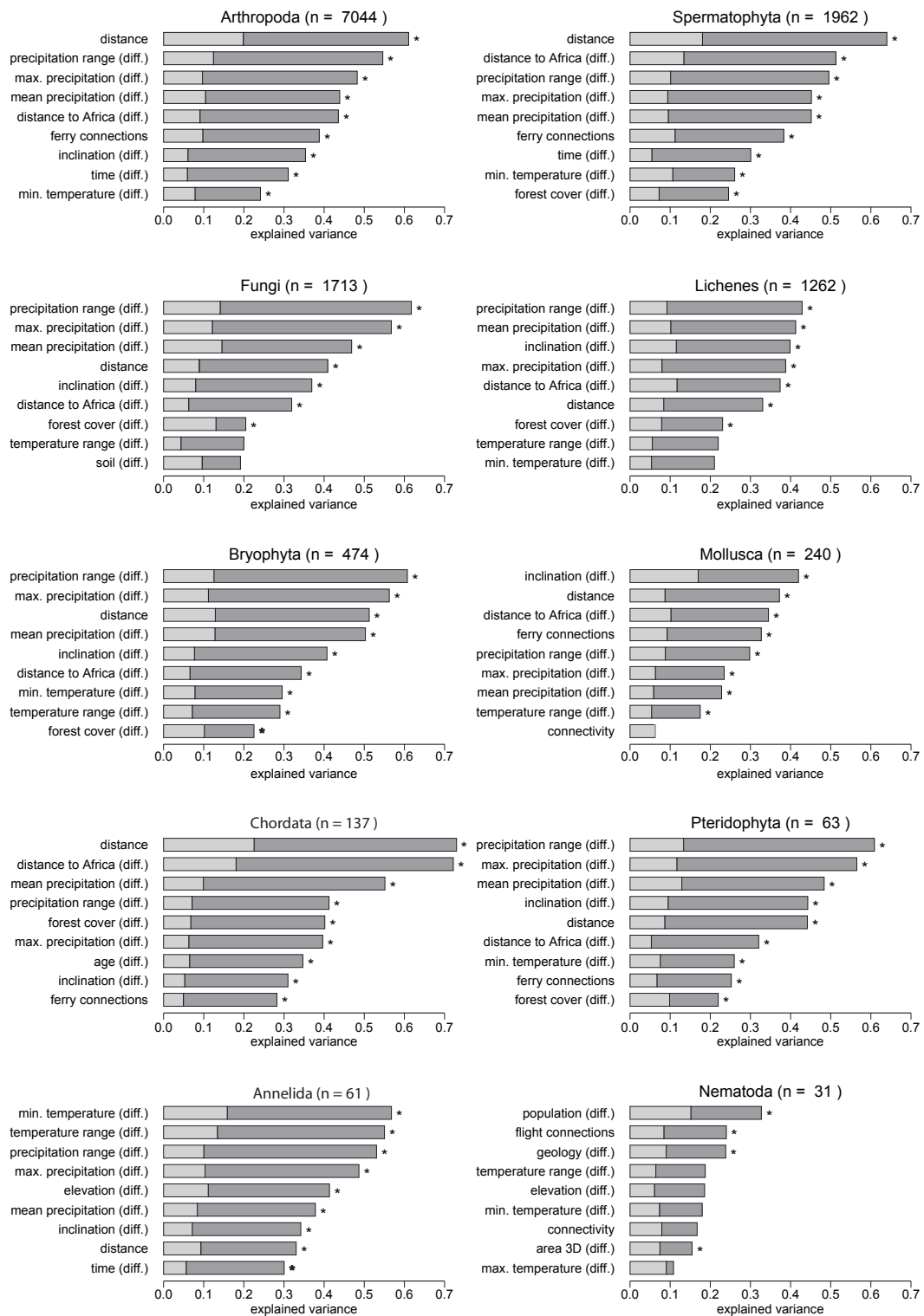
Fig. 4: Beta diversity analysed by using hierarchical partitioning. Grey parts of the bars illustrate the amount of variance that a variable can explain independently, black parts show the amount of variance a variable can explain together with the other variables. Note that the Euclidian distance of the variables listed in table 1 was used for the analyses of similarity. Significance (p < 0.05) is indicated by a star besides the bar. The sum of all single island endemic species of a group on the Canary Islands is indicated in brackets.
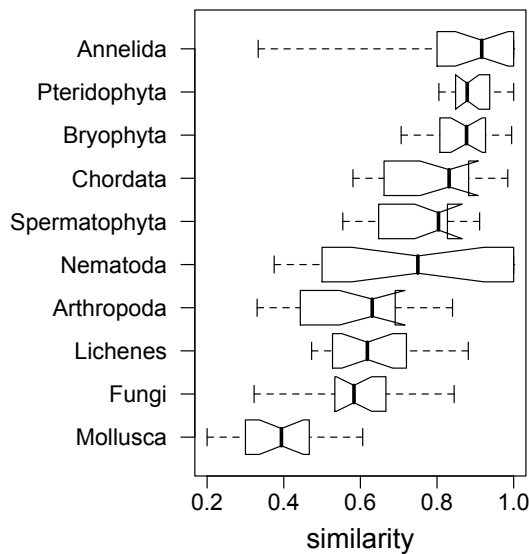
Fig. 5: Similarity values (Simpson Index) for pairs of islands differentiated for species groups. Dark lines in the box-and-whisker plots represent the median values, boxes indicate quartiles and whiskers data extremes.

populations on different islands. It is assumed that speciation is stimulated by the availability of more ecological niches. These are considered to be especially diverse on young and topographically heterogeneous islands. Heaney (2000) points to the fact that immigration and speciation exclude each other to a certain extent. Both are related to distance from a species source region.

These linkages between speciation, ecological complexity (Whittaker et al. 2007, 2008) and the distance to a species' source region (Heaney 2000; Lomolino 2000a), together with the results presented here, suggest an alternative explanation for the correlation between species richness and pSIE. There might be an isolation gradient with altitude within an island. High elevation ecosystems on the mainland (possible source regions) are more probably to be found in the inland, far from to the coastline. Consequently, high elevation ecosystems on islands are farther away from potential species source regions on the mainland than this is the case for low elevation ecosystems. Species that have adapted to high elevation ecosystems have to cross a larger distance and a larger ecological gradient to reach a suitable habitat than low elevation species. The high elevation ecosystems are genetically more isolated (low immigration rate) and will thus have a higher rate of speciation. In the case of the Canary Islands, ecosystems with comparable altitude as El Teide (Tenerife) can again be found in the High Atlas Mountains. In future research,

investigations on species distribution and speciation on oceanic islands should not only focus on island level, but rather also differentiate zonal ecosystems on these islands.

5.3 Similarity in species composition (H2)

On the Canary Islands, similarity in species composition is strongly influenced by geographic distance (falsifying hypothesis 2). The high explanatory power of the distance between the islands and the differences in the distance to mainland Africa for similarity values confirms the rule of "distance-decay" (Nekola and White 1999; Baselga 2007). Contributing mechanisms are the decline in the exchange of organisms, an increasing dissimilarity in abiotic and biotic circumstances and distance itself (Nekola and White 1999).

Hints on the migratory and dispersal ability within species groups can be obtained by using the explanatory power of distance (Fig. 6) together with the median values of similarity in species composition (Fig. 5). Wind dispersal of diaspores between islands may explain the high values in similarity within plants. The slight increase in mean similarity from *Spermatophyta* over *Bryophyta* to *Pteridophyta* indicates increased colonisation success, probably due to the smaller size of spores and thus a larger importance of wind dispersal in the later groups. As nearly all other ways of dispersal are more constrained by distance than wind dispersal, the decrease in explanatory power by distance (Fig. 6) from *Spermatophyta* to *Pteridophyta* supports this hypothesis. However, *Fungi*, which can be dispersed via microscopic spores, were expected to have higher similarity values. One explanation may be the close dependence on a specific environment or host organism (e.g. *Spermatophyta*). Many fungi can only establish themselves if taxa of an other group of organisms are already there. Low median values in similarity for *Mollusca* represent the low dispersal ability of this group. A low explanatory power of the distance-decay relationship could indicate that immigration is more dependent on stochastic events (like birds transporting eggs from one island to the next) than on migration. High similarity values together with a strong distance-decay for *Chordata* might reflect that some species within the group (such as birds) have colonised all islands, while others (such as amphibians) have limited capacity to cross the ocean.
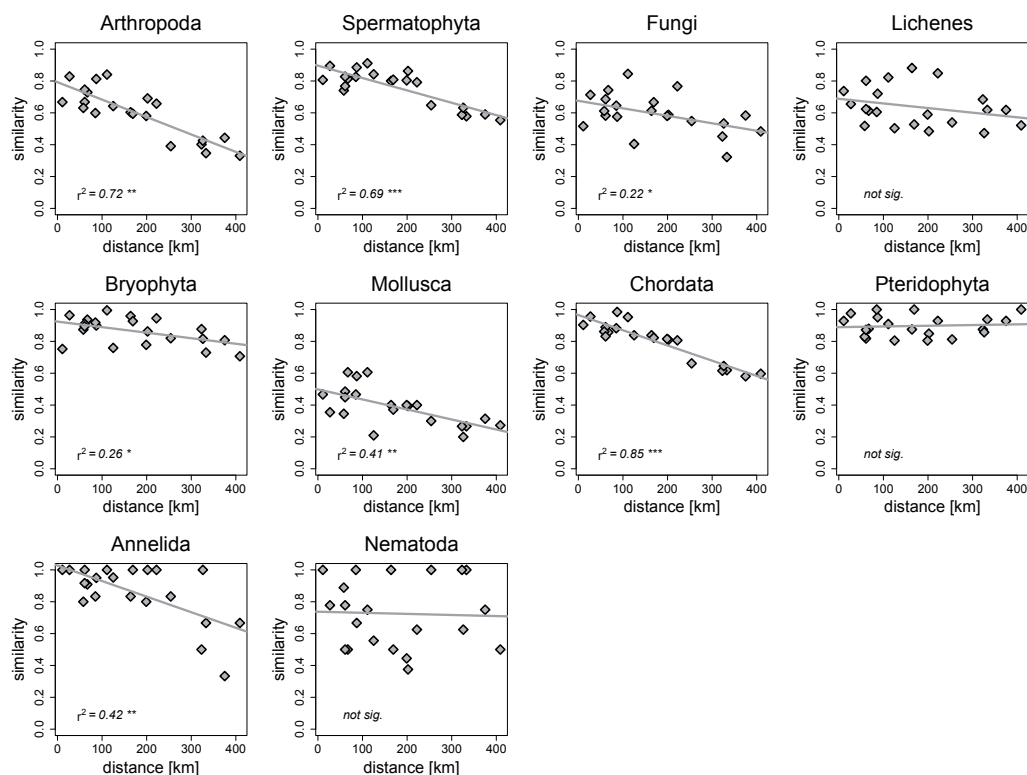
Fig. 6: Relationship between similarity of species composition (Simpson Index) and geographical distance between the islands. Each dot marks one of a total of 21 interinsular relationships.

5.4 Changes in ecological settings

Historic changes in the ecological settings of islands (e.g. pedogenesis, erosion, tectonic activity) and modifications of the distances between them (e.g. temporarily available stepping stones, sea level rise) contribute to the explanation of species distribution and speciation on archipelagos. The apparent problem is the difficulty, if not impossibility, to measure or capture historical conditions. As we can not ignore the importance of time and age, proxies have to be included in analyses. In this paper, island age has been corrected for volcanic events that have sterilised the whole surface of an island. 3.5 million years ago, the island of Gran Canaria was sterilised by the eruption of the Roque Nublo. Only two small hideaways remained after the catastrophe (Francisco-Ortega et al. 1996).

Eustatic sea level fluctuations during the Pleistocene (more than 100 m) alternately doubled and halved the area of the islands from 14,000 km² during the glacial period to 7,500 km² during the interglacial (García-Talavera 1999). During the climax of the last glaciation, the relative elevation of the islands was about 130 m higher than the present

elevation. Fuerteventura and Lanzarote were connected, forming the island of Mahan with a surface of 5,000 km². The distance to the African mainland diminished from today's 100 km to roughly 60 km. In addition, small sea mounds exceeded the sea level as islands and formed "stepping stones" between the Canary Islands, Madeira and the Iberian Peninsula (Whittaker and Fernández-Palacios 2007). This might have promoted species interchange between the islands.

The evolution of island biodiversity does not only reflect the continuous and long-term development of relief and environment. Single short-term events such as volcanic eruptions and large landslides have strong impacts. By eradicating a large percentage of a species island population, such events might contribute to a narrowing of the genetic pool (Moya et al. 2004). A diminishing population can suffer from inbreeding depression. The genetic depletion can lead through a "bottle neck". After this an increasing population size cannot re-establish the previous genetic diversity and ecological range of the surviving species. Due to limitations in access and measurement, extreme events have been neglected in ecology for a long time. In face of climatic changes, there

is increasing attention on disturbances and extremes (JENTSCH and BEIERKUHNLEIN 2008). We expect that this perspective will be even more important when evaluating the future development of island floras and faunas.

6   Conclusions

Our results support a strong contribution of ecological complexity to the pattern of species richness. In contrast to other cases (LOMOLINO 2000b; TJØRVE 2003; TRIANTIS et al. 2003), on the Canary Islands elevation is shown to be a more suitable variable than island area to detect complexity and diversity.

Especially on islands with high elevations, distance from high elevation habitats to comparable sites on other islands or on the mainland might vary strongly. High altitude ecosystems on the continent, which are potential sources for species immigration on islands might be far away from the coast in the inland. In the case of the alpine communities of the Canary Islands, the nearest neighbours are found in the Atlas Mountains in Morocco. The distance an immigrating species has to overcome affects the driving processes of island biodiversity like immigration or speciation. However, distance and mechanisms are linked to the spatial and "ecological" distance between potential habitats and not to the geographic distance between islands and a continent. We therefore suggest to focus further research on the ecosystem scale, rather than the island scale. An appropriate approach is to work with elevation zones or with specific ecological settings.

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