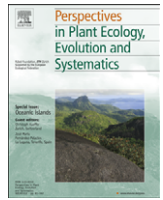




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Research article

Using taxonomic and phylogenetic evenness to compare diversification in two Island Floras

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ABSTRACT

This study compares the phylogenetic structure in the Canary Islands and Hawaii by means of the distributions of the species number for plant families (Taxonomic evenness) and lineages (Phylogenetic evenness) across archipelagos and across habitats in both archipelagos using the Gini coefficient. We then investigate phylogenies to identify particular habitats contributing to such differences using Taxonomic distinctness (AvTD) and its variation (VarTD).

Our results show that the distribution of species number among Hawaiian lineages is much more uneven than the Canary Islands. In contrast, Hawaii produces a more even distribution of species number by family than the Canary Islands. This may be due to the Hawaiian Flora being derived from considerably fewer colonists than the Canarian Flora as a result of its much greater degree of isolation. At the same time, Hawaii is represented by the same number of families as the Canary Islands. This may stem from Hawaii's flora being derived from a greater range of source areas despite its isolation. Finally, there is much more diversification spread across a larger number of lineages in Hawaii. The higher degree of Hawaiian diversification may be due to a greater range of habitats, more diverse and phylogenetically distinct floristic sources, and low initial species diversity resulting from extreme isolation.

Two Canarian habitats (Rock communities and Thermophilous habitats) and one Hawaiian habitat (Wet communities) contribute to the differences in phylogenetic structure between the two archipelagos. These habitats exhibit disproportionate levels of unevenness and may represent centres of diversification. We propose a combination of two habitat properties, high receptivity and low stability, to explain these results.

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Introduction

Island biogeography has proven a useful arena to test hypotheses of the relative contributions of ecological (MacArthur and Wilson, 1963, 1967) and evolutionary (Losos and Schluter, 2000) processes to basic patterns in species richness. Because oceanic island biotas are entirely derived from long distance dispersal (Fosberg, 1948; Carlquist, 1974; Cowie and Holland, 2006), autochthonous evolution has produced high degrees of endemism strongly related to the ecological and historical properties of species. For example, plant species richness on individual islands is a complex function of both ecological attributes and geologic history in the Hawaiian Islands (Price, 2004) and Canary Islands (Fernández-Palacios and Andersson, 2000), two of the best studied island groups. In fact, these two

archipelagos share enough physical attributes that comparison of biological processes within them may promote reciprocal corroboration. On the other hand, notable differences in the physical landscapes and biogeographical setting may elucidate how taxa respond evolutionarily to different circumstances. A mounting body of study has pursued such comparison by assembling comparable data sets for the two archipelagos. For example, Carlquist (1974) recognized the surprising degree of evolutionary convergence related to similar physical environments of the two island groups. More recently, Emerson and Kolm (2005) stimulated considerable interest by asserting that the endemic proportions of each archipelago indicated different rates of evolution, while Gruner et al. (2008) refuted this by invoking a null model based on several data sets for the two islands. Whittaker et al. (2007, 2008) have drawn from these islands in particular in synthesizing a general model of long-term community assembly for islands, and very recently Chiarucci et al. (2010) have used data from these archipelagos, among others, to disentangle the additive partitioning pattern of their floras. One drawback to

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these studies, however, is that species are considered individually rather than as part of any taxonomic, phylogenetic, or ecological units, and where phylogenetic groups are considered they are rarified into “typical” island lineages. Moreover, the potential for a small number of groups to disproportionately influence overall patterns has not been thoroughly addressed.

Species numbers are not distributed randomly among taxonomic groups, and exhibit persistent patterns whereby some taxa became richer in species than others (Willis and Yule, 1922). This overall pattern has received several theoretical and experimental approaches (Dial and Marzluff, 1989; Latham and Ricklefs, 1993; Fenner et al., 1997; Scotland and Sanderson, 2004). Recently, the bias in species distribution across taxonomies has been quantified and employed as a measure of the evenness of the taxonomic groups, such as species among families (Webb and Pitman, 2002; Domínguez Lozano and Schwartz, 2005a). Similarly, phylogenetic groups of plants are now generally recognized as expressing a wide range of clade size and diversification rate (Sanderson and Donoghue, 1994). The Hawaiian flora (Price and Wagner, 2004) and Avian fauna (Fleischer and McIntosh, 2001) both exhibit strongly skewed distributions of the size of colonist lineages (clades of species derived from a given colonist from outside the archipelago), with a large number of monospecific lineages and a small number of species-rich lineages. The Canarian flora similarly exhibits a pattern whereby a small number of highly diverse colonist lineages have given rise to a large proportion of the endemic flora (Santos, 2001). Although it is clear that both groups of islands exhibit this pattern of unevenness in their floras, there is no exact quantification, nor general explanations, of such a pattern for oceanic islands.

This study compares the distributions of the size of taxonomic groups (plant families) and phylogenetic groups (descendants of putative colonization events) in each archipelago. Our primary aims are: (1) to compare phylogenetic structure in the Canarian and Hawaiian floras, analyzing the bias in size distribution of both plant families (Taxonomic unevenness) and colonist lineages (Phylogenetic unevenness) of plants in each archipelago, and (2) to identify the relative contributions of important groups to species composition. Our quantification of differences in the distribution of species richness among colonist lineages groups may elucidate differences in the diversification processes in the two archipelagos beyond that which has been done using less phylogenetically explicit means.

Habitat diversity is a key factor explaining species numbers on islands (Welter-Schultes and Williams, 1999; Cody, 2006; Kreft et al., 2008). We therefore examine phylogeny unevenness with respect to major community types in both islands sets to explore how environmental heterogeneity may shape any taxonomic or phylogenetic bias of the floras. This constitutes an in-depth assessment of ecological processes that may drive adaptive radiation.

We use three measures for our comparison to take into account phylogenetic weight, Gini coefficient (Gini, 1912) and Taxonomic distinctness and its variation (Clarke and Warwick, 1998, 2001). The indices employed provide accurate ways to quantify biases and identify differences among ranked or branched systems.

Study area

The most significant similarities between the two archipelagos are their geologic and climatic settings. Both island groups emerged *de novo* from the sea as volcanic mountaintops and have never been connected to a continental landmass (Coello et al., 1992; Clague, 1996). The sequential propagation of

volcanoes produced two archipelagos with comparably sized and spaced islands (Fig. 1). Not only do they share similar mountainous volcanic topography, but both archipelagos achieve considerable altitude (with 4205 m for Mauna Kea on Hawaii, and 3718 m for El Teide on Tenerife) making them the two highest volcanic archipelagos in the world. The topography and regional climate systems of these two archipelagos generate a wide range of environments, in terms of both temperature and moisture regimes (Giambelluca and Schroeder, 1998; Marzol, 2001). They experience comparable climates, both have a strong maritime influence and pronounced wet and dry aspects according to prevalent moisture-bearing trade winds. More importantly, islands of different age encompass a range of environments, and thus these two important factors vary independently permitting their influences to be decoupled (Price, 2004).

Despite these similarities, however, there are important differences between the two groups. Most notably, the Canary Islands, at about 95 km from the coast of North Africa, are much less isolated than the Hawaiian Islands, at nearly 3700 km from the nearest continental landmass. Furthermore, the isolation of the Canary Islands has been even less (ca. 60 km) during the Quaternary sea level maxima (García Talavera, 1999). This difference is mitigated somewhat by the fact that the moderately moist climate of the Canary Islands is quite different from the arid climate of the nearby African mainland, and is more similar to the Mediterranean region considerably further away (Marzol, 2001). In addition, the Canary Islands are somewhat close to other comparable island groups, the Madeiras, Cape Verde, and the Azores, whereas the Hawaiian Islands are 4000 km from the nearest comparable islands, the Marquesas. The wettest regions of Canary Islands receive approximately 1000 mm of precipitation per year (Marzol, 2001, although some stations in La Palma have recorded 1500 mm), much less than the extremely wet rainforest environments of the Hawaiian Islands, which receive in excess of 10,000 mm annual precipitation (Giambelluca and Schroeder, 1998); however the addition of significant fog input in the Canary Islands (Marzol, 2008) may mitigate this difference somewhat. Another key difference is that, while both groups include very young islands with active volcanoes, the oldest of the Canary Islands, (Fuerteventura, 21 My) is considerably older than any of the main Hawaiian Islands. However there are now-eroded islands in the Hawaiian archipelago that are much older (ca. 30 million years) that are considered to have contributed, in a limited way, to the present biota (Price and Clague, 2002). Differences notwithstanding, these archipelagos exhibit remarkably similar physical conditions that support similar biotic patterns.

Biologically, the archipelagos also mirror one another. Both archipelagos support floras derived entirely from over water dispersal, although distances and source areas differ. The Hawaiian flora is derived from colonists from throughout the Pacific Basin, although there is a prevalence of stepping stone dispersal across the South Pacific (Fosberg, 1948), an assertion largely supported by recent phylogenetic work (J. Price and W.L. Wagner, unpub. data). The Canarian flora, on the other hand, has its origins in nearby North Africa and especially the Mediterranean region, although many taxa represent a “relictual” flora apparently related to fossil taxa from the Tertiary period from these source areas (Takhtajan, 1969; Sunding, 1970; Bramwell, 1976; Santos, 2001; Vargas 2007). Overall the vascular floras of the two island groups are highly comparable. The Hawaiian flora contains just over 1000 native angiosperm species (Wagner et al., 1999) and 161 fern species (Palmer, 2003), for a total flora of 1164 species of which 88% are endemic. The Canary Islands harbor about 951 native angiosperms, 43 ferns and six gymnosperms for a total flora of 998 (somewhat less than previous estimates) of which 51% are endemic (Acebes et al., 2001). Most importantly

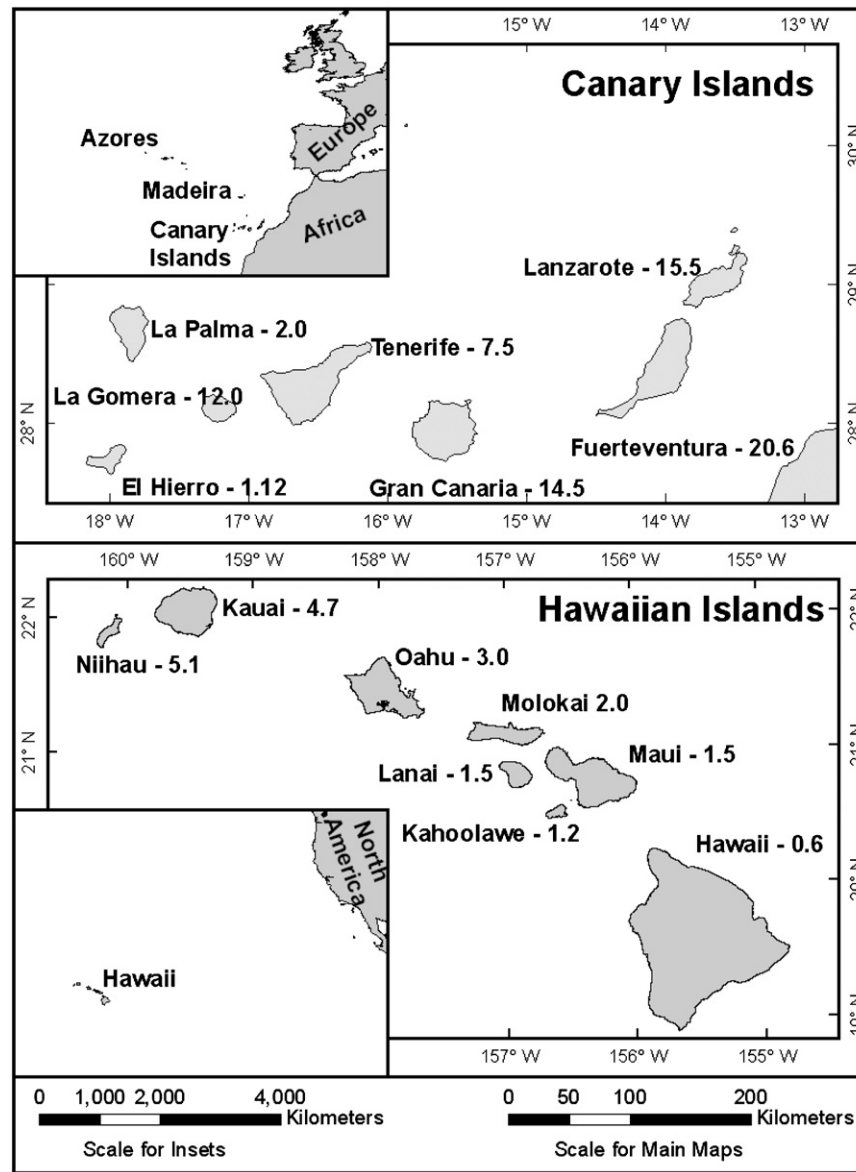


Fig. 1. Geographic location, composition and isolation of both island systems: Canary Islands (above) and Hawai'i (below).

both archipelagos have experienced spectacular adaptive radiations that, along with other colonist lineages, have been the subject of numerous phylogenetic studies. Sakai et al. (1995) and Price and Wagner (2004) have summarized these for the Hawaiian flora, while Reyes-Betancort et al. (2008) have summarized the major colonist lineages for the endemic Canarian flora. In both cases, a small number of highly diverse radiations suggest strongly skewed distributions of species richness in colonist lineages.

Methods

Phylogenetic data

We collated taxonomic and habitat preference data for all native species in both archipelagos. For the Hawaiian Islands, we used an updated version of the database created by Price (2004). This has accounted for newly published taxonomic changes and new location data from various sources. It also now includes native pteridophytes based on the taxonomy of Palmer (2003) and

with habitat data based on herbarium specimen databases at Bishop Museum in Honolulu, the US National Herbarium in Washington, D.C., and the National Tropical Botanical Garden Herbarium on Kauai. For the Canary Islands, species names and chorological status follow Acebes et al. (2001). In both cases a wealth of phylogenetic data and supplemental studies permits the floras to be divided into groups of species derived from each given colonization event. For the Hawaiian Islands, we used the database developed by Price and Wagner (2004), again updated to include pteridophytes (Palmer, 2003). This database builds on previous studies (Fosberg, 1948; Carlquist, 1974; Sakai et al., 1995; Wagner et al., 1999), as well as incorporating numerous phylogenetic studies (see Table A1 in Appendix). Our present treatment recognizes a total of 367 colonization events, including 243 that resulted in endemic species and 111 that resulted in multiple species.

We followed a systematic approach to parsing the Canarian flora into colonist lineages. First, numerous multi-species lineages have been verified through phylogenetic studies (summarized in Appendix Table A2). These account for 321 species (32.1% of the flora). Second, 30 single-species lineages (3% of the flora) are

defined by various phylogenetic studies, many of these being studies that defined multiple colonists for a given genus within the archipelago. Another 3 pairs of species in the genera *Dracaena* (Dracaenaceae), *Euphorbia* (Euphorbiaceae), and *Myrica* (Myricaceae) each bear a strong affinity and so we assign them to three two-species lineages accounting for another 6 species (0.6% of the flora). An important contribution comes from recent work by Reyes-Betancort et al. (2008), who identify a number of lineages consisting of multiple endemic species (see Table A3, Appendix). Together, these account for another 115 species (11.5% of the flora). They also recognize another 49 lineages (4.9% of the flora) with a single endemic species; most of these are single endemic representatives of a given non-endemic genus, although in a few cases they are in genera that also contain a non-endemic native species. Another nine species (1% of the flora) constitute monotypic endemic genera with no close relatives in the Canary Islands, which we interpret as having been derived from individual colonization events. 418 non-endemic species (41.8% of the flora) represent essentially widespread taxa that probably colonized the Canary Islands separately from outside; we therefore interpret these to be monospecific lineages within the archipelago. The remaining 49 species are in genera that contain both endemic and native non-endemic species; while Reyes-Betancort et al. (2008) account for relationships among endemic species, it is not clear whether some of these may share a lineage with non-endemic species in the same genus. We therefore take the conservative approach in assuming that they are not related and that the remaining species constitute their own single-species lineages. The opposite assumption (that non-endemic and endemic species have sister relationships within the Canary Islands) would mean that there are 49 fewer single-species lineages, and a modestly higher number of relatively small lineages. The difference in the analysis using lumped or split lineage distributions is noticeably minor (results not shown) because it involves relatively small numbers of species and putative lineages. Using the information and assumptions stated, we estimate that the Canarian flora is derived from a total of 599 colonization events, including 158 that resulted in endemic species, and 67 lineages that resulted in multiple endemics (a full lineages designation is provided in Table S1 in supplement material). Hawaiian and Canary Islands primary data are available from the corresponding author on request.

Habitat data – Hawaiian Islands

We assigned Hawaiian plant species to major community types following Price (2004). This draws from the classification developed by Jacobi (1989) and Cuddihy and Stone (1990), recognizing three moisture zones, as well as subalpine/alpine communities (>2000 m asl.) and coastal areas. Here we subdivide some vegetation types treated by Price (2004) and additionally consider lava flows.

Arid shrubland

Very low elevations on the leeward (Southwestern) sides of all of the islands receive very low amount of precipitation (<500 mm/y) and support arid shrubland typically dominated by *Dodonaea viscosa* (Sapindaceae) (Cuddihy and Stone, 1990). Here, mean annual temperature is about 23–24 °C.

Lowland dry forest

Leeward areas at lower elevations receiving precipitation 500–1200 mm/y that support dry forests (Cuddihy and Stone, 1990) are often dominated by a variety of woody species including *Diospyros sandwicensis* (Ebenaceae) and *Erythrina sandwicensis*

(Fabaceae). These communities have been severely reduced and degraded by human activity. Mean annual temperatures range from about 15 to 24 °C.

Mesic zone

Communities receiving intermediate amounts of precipitation (1200–2500 mm/y) constitute the Mesic zone (Cuddihy and Stone, 1990). These are the most species-rich Hawaiian communities (Price, 2004), often dominated by a mixture of *Acacia koa* (Fabaceae) and *Metrosideros polymorpha* (Myrtaceae). Mean annual temperatures range from about 11 to 24 °C.

Montane dry forest and shrubland

At intermediate elevations (1000–2000 m asl.) on the leeward sides of Maui and Hawaii only, there are unique montane dry communities dominated by *Acacia koa* (Fabaceae) and *Sopohora chrysophylla* (Fabaceae) (Cuddihy and Stone, 1990). Mean annual temperatures range from about 11 to 15 °C.

Wet zone

The wettest areas (>2500 mm/y) occur on the windward (Northeastern) sides of the major islands, and support a varied vegetation of forests, shrublands, and bogs (Cuddihy and Stone, 1990). These are often dominated by *Metrosideros polymorpha* (Myrtaceae), *Cibotium* tree ferns (Dicksoniaceae), and the matted fern *Dicranopteris linearis* (Gleicheniaceae). Mean annual temperatures range from about 11 to 23 °C.

Subalpine/Alpine communities

Above about 2000 m asl., freezing occurs frequently and conditions are generally dry, supporting shrublands and forests that attenuate into alpine desert above 3000 m asl. (Cuddihy and Stone, 1990). Mean annual temperatures range from about 11 °C down to as low as 3 °C on the highest summits. Important components include *Leptecophylla tameiameiae* (Ericaceae), *Dodonaea viscosa* (Sapindaceae), and *Sopohora chrysophylla* (Fabaceae).

Coastal vegetation

Despite encompassing a wide range of precipitation, coastal areas generally share features of salt spray, wind, and poor soil development (beaches and cliffs) (Cuddihy and Stone, 1990).

Lava flows

On the Island of Hawaii and to a lesser degree Maui, recent lava flows are undergoing primary succession and support unique pioneer communities (Cuddihy and Stone, 1990). These include a sparse vegetation of *Metrosideros polymorpha* (Myrtaceae), ferns, and lichens.

Habitat data – Canary Islands

We assigned native species to at least one of the major zonal or azonal ecosystems of the Canarian Archipelago following habitat definition provided by Rivas Martínez et al. (1993), and Schoenfelder and Schoenfelder (2005).

Information about distribution of species with respect to ecosystem was compiled using all available publications and field data.

Coastal sub-desert scrub

The coastal sub-desert scrub is an open shrub vegetation adapted to the subtropical semi-arid climate of the coastal region, dominated by stem succulents of the genus *Euphorbia* and leaf succulents or sclerophyllous shrubs that grow up to 2–3 m tall. It is located between 0 and 300 m asl. at windward slope and up to

700 m asl. at leeward slope. Precipitation is low (0–250 mm/year) and average temperature is high (> 20 °C).

Thermophilous woodlands

Thermophilous woodlands grow above the coastal scrub between 200/300 and 600 m asl. at windward slope and between 400 and 800 m asl. at leeward slope. The climate is semi-arid with annual precipitation 200–500 mm and average temperature 15–19 °C, depending on exposition and elevation. Many species, belonging to genera such as *Juniperus*, *Pistacia*, *Olea*, *Jasminum*, *Helianthemum* have a Mediterranean origin. This ecosystem has almost disappeared due to the human impact.

Laurel forest

These forests are formed by evergreen tree species belonging to genera such as *Laurus*, *Apollonias*, *Persea*, *Ilex*, *Prunus*, and covered in the past large areas between 600 and 1200 m asl. on the north and east sides of higher islands. Due to trade wind regime climate is humid (max. 1000 mm/y) and mean annual temperatures varies between 13 and 18 °C.

Pine forest

The endemic tree species *Pinus canariensis* dominates completely this ecosystem that is distributed above the laurel forest at windward slope and above the thermophilous woodland at leeward slope and forms the upper timber line at about 2000–2200 m asl. on this archipelago.

Summit scrub

This vegetation type, restricted to Tenerife and La Palma, the two highest islands, is distributed above the timber line and formed by shrub species such as *Spartocytisus supranubius* or *Pteropetalus lasiospermus*, adapted to low temperature in winter and warm and dry conditions in summer. Precipitation reaches 400 mm/year and mean annual temperatures vary between 10 and 5 °C.

Rock communities and disturbed places

In addition to the five zonal ecosystems we distinguished two habitat types that are not conditioned by climate, but by substrate and topography or by human activities. Rock communities are very common in all zonal ecosystems, due to abrupt topography, consequence of volcanic history and erosion. Many annual and perennial herb species considered native are abundant in disturbed places, including abandoned fields, ruderal places, road edges etc. Since it is often difficult to assign these species to zonal ecosystems, due to the lack of information about the altitudinal distribution, we decided to separate them as a distinct habitat.

Analysis

We quantified differences in the distribution of species richness among taxonomic and phylogenetic groups and across habitats for both archipelagos. We use three indexes based on the summation over the difference or distance of species pairs in a particular flora.

The first index, known as the Gini coefficient, summarizes the relative mean difference of the difference of species richness between every possible pair of whichever taxonomic group (usually genera or families) related to the mean group size in the flora (Damgaard and Weiner, 2000; Gini, 1912).

It is defined by:

$$GC = \frac{\sum_{i=1}^n \sum_{j=1}^n |x_i - x_j|}{2n^2\mu}$$

where n is the number of families present; μ the average sp. number by family; x_i the sps. number of family i ; x_j the sps. number of family j .

The Gini index (hereafter GC) works extraordinary well as a summary statistic for ranked systems, it describes inequality among groups in a very elegant way and it is independent of sample distribution (how species are shared among families or lineages). This means that it is very useful to detect differences in unevenness among large groups, such as flora families or lineages. Here, it was used to show differences between the taxonomic structure of the Canary Islands and Hawai'i. It ranges between 0 and 1: values close to 0 indicate a very equal distribution (all families or lineages have a similar number of species or size), values close to 1 indicate families or lineages with a highly uneven distribution (a few large families and many small families). However its drawback is that it is sensitive to sample size, specifically when we deal with sample sizes below 150. This is the case for the floras of some habitats, where species richness falls below 100 species.

A second index, the Average Taxonomic distinctness (AvTD), describes the average taxonomic distance of all the species in a flora considering different weights or distinctness according to the path length of the taxonomy of all the species pairs (Clarke and Warwick, 1998). So it calculates (Clarke and Warwick, 2001):

$$\Delta^+ = \frac{\sum \sum_{i \neq j} \omega_{ij}}{s(s-1)}$$

where Δ^+ is the Average Taxonomic distinctness (or AvTD); s the number of species present; ω_{ij} the distinctness weight between species i and species j . We adopted the simplest form of ω_{ij} with equal step-lengths between two successive taxonomic levels (Magurran, 2004; Mérigot et al., 2007).

Finally, a third index is based on the calculation of the variance of the taxonomic diversity index (Δ^+ or VarTD):

$$\Delta^+ = \frac{\sum \sum_{i \neq j} \omega_{ij}^2}{s(s-1)} - \Delta^2$$

Taxonomic diversity index (AvTD) also known as Taxonomic distinctness, and VarTD or variation of Taxonomic distinctness have two properties that make them suitable for the habitat analysis. First, they are independent of sample size, which means they do not produce biased results for species poor habitats. In addition, both consider not just one level (species among families) but whole taxonomic relationships in the flora (species among lineages and lineages among families). So, AvTD shows which habitats exhibit higher Taxonomic distinctness or differences in the phylogenetic clade. Taxonomic distinctness values close to 100 indicate floras, in our case habitats, of high originality, i.e. floras with a fairly large number of families and lineages related to total species richness (i.e. long branches predominate in the general clade). Values close to 0 identify just the opposite: floras with fewer families and lineages in relation with their total species richness, so floras with short branch lengths. AvTD, as GC, also relies on average distances and it is robust to sample size, but it does not discriminate well among floras with similar species richness but a very dissimilar number of upper nodes of the taxonomy (i.e. lineages and families). This could be a problem for some habitats with very similar species, lineages and family numbers but very different relations among them. To overcome this problem Clarke and Warwick (2001) proposed the use of VarTD: high values denote higher imbalance in taxonomic structure with not only few families but also unbalanced distribution of lineages and species.

As differences in sample size in both islands sets may pose a problem, we compared species assemblages using rarefaction (Simberloff, 1972; Gotelli and Graves, 1996), in order to produce

floras with equal sample size. Thus the Hawaiian flora was rarefied to Canary Islands sample size. We did not use analytical methods to provide statistical significance of our indexes (Brewer and Williamson, 1994); instead we computed confidence limits from bootstrapped floras. In our view, bootstrapping techniques have two main advantages over analytical methods: they are less computationally intensive and they allow a better understanding of the underlying distributions. In fact, bootstrapping has proven useful in providing accurate estimators of GC indexes (see Dixon, 1993).

If species distribution among different habitats is similar to species distribution of the total pools of islands, then evenness among habitats does not differ from evenness of the total pool of species in both groups of islands. This implies that the evenness of random subsamples of species from the total pools do not differ from the evenness of any habitat subset (Gotelli and Graves, 1996, Stark et al., 2006). To test this null hypothesis, we generated several random subsamples (from 50, 60, 70 up to 550 species for Canary Islands and again from 50, 60, etc. up to 800 species for Hawai'i) from the whole species pools as a null model. Then, we calculated Phylogenetic evenness and its confidence intervals for 5000 random draws of each species subsets for each archipelago. Statistically significant confidence intervals were set as the 97.5 and 2.5 percentiles of the generated distributions (Dixon, 1993).

Species were classified according to habitat preferences, and some species were placed in more than one single environment, especially for the Hawaiian species. Therefore habitat species richness does not sum up to the total species pool in either island group's sets (see Table 1). We then produced null models for AvTD calculations derived from random samples from the total species pools from both archipelagos, and AvTD habitat values were compared with those derived from null models.

Finally, we are aware that the use of different classification systems, APG II or classical systems such as Cronquist, may render some differences in AvTD and VarTD interpretations. We decided to perform the analysis up to the family level instead of using the whole phylogenetic tree in order to overcome this problem, particularly because many deeper relationships within the angiosperms remain unresolved.

Table 1
Numbers of families (*F*), lineages (*L*), genera (*G*) and species (*S*) within each archipelago and habitat. "Total" rows show total figures for Canary Islands and Hawai'i. ΣS denotes sums of all species in selected habitats for both, Canary Islands and Hawai'i. See text for details.

Habitats		<i>F</i>	<i>L</i>	<i>G</i>	<i>S</i>
Canary Islands	Total	105	599	364	998
	Coastal scrub	51	206	348	348
	Laurel forest	65	147	124	222
	Rock communities	26	79	69	208
	Thermophilus	45	96	89	213
	Pine forest	33	75	68	129
	Summit scrub	21	43	42	53
	Disturbed places	57	325	183	333
	ΣS				1506
	Hawai'i	Total	105	367	270
Coast		50	112	96	154
Arid		31	57	53	84
LowlandDry		58	122	110	225
MontaneDry		49	84	77	122
Mesic		92	282	224	742
Wet		88	257	192	760
Subalp-Alp		38	65	59	90
Lava		47	79	73	91
ΣS					2268

Results

Taxonomic evenness between the Canarian and Hawaiian Floras

Hawaii shows a more even distribution of species richness by family than the Canary Islands. With bootstrapping, the Hawaiian flora has a rarefied Gini coefficient (GC) of 0.67 ± 0.01 . The Canarian flora has a GC of 0.71, indicating a statistically more heterogeneous distribution of species number among families. Looking at the species by family accumulation curve (Fig. 2a and Table A4 in Appendix), the largest Hawaiian families do not exhibit large differences in species richness (around 69 species difference between the largest, Campanulaceae, and the eighth largest family, Cyperaceae, in the rarefied sample). However the eight largest Canarian families exhibit strong differences (140 species difference between the largest, Asteraceae, and the eighth largest, Boraginaceae). The largest families in each flora contribute differently to the overall species pools: Asteraceae accounts for 17% of the total species number in the Canarian flora but Campanulaceae only about 11% for the total species number in the Hawaiian flora.

Results on lineage unevenness show a different pattern (Fig. 2b). Hawaii has a consistently more unbalanced lineage structure than the Canary Islands. The Hawaiian flora has a rarefied lineage Gini coefficient of 0.59 ± 0.01 , whereas Canary Islands obtain a significantly lower GC of 0.38. Species accumulate in Hawaiian lineages in an extraordinarily uneven manner: the largest 20% of the lineages accumulate 70% of the total species. By comparison, in the Canary Islands the largest 20% lineages contain approximately 50% of the total species. The difference between the first and 30th largest lineages in the rarefied Hawaiian Flora is 102.02 species, whereas the same value for the Canary Islands is 47 (see Table A5 in Appendix). The largest lineage in rarefied Hawaii is Lobelioidae with 108.02 species on average. The clade "Aeonium+" with 51 species is the largest of the Canarian lineages. Gini coefficient values for lineages summarize this trend.

Two underlying quantities account for the difference in family GC and lineage GC values. First, there are many more lineages in Canary Islands (599 lineages) than in Hawaii (just 367, see Table 1). However, there is no difference in family number between the Canary Islands and Hawaii (both floras have 105 families). Moreover, not only does Hawaii possess fewer lineages but the difference in species number among largest lineages is larger than the difference among the largest families. Thus, the four largest lineages in Hawaii contain almost twice as many species as the four largest Canaries lineages. Unlike lineages, figures for the family structure are similar, being that family sizes are more homogeneous in both floras.

Differences in Phylogenetic evenness among habitat types

AvTD and VarTD values showed clear differences among habitats (Table 2). We used a null model derived from the total floras and we contrasted average Taxonomic distinctness (AvTD) for each habitat assemblage in both archipelagos (Fig. 3). Rock communities and Thermophilous woodlands appear as the most significant outliers in the Canary Islands set. Rock habitat has an especially low distinctness in phylogeny distribution (AvTD value of 93.29, Table 2). A lower AvTD indicates a relatively short averaged branch length, in other words few families and lineages per species totals, and Rock communities are in fact among the poorest Canarian habitats in a number of families. In addition, it also exhibits a large VarTD (328.66, see Table 2) indicating an uneven distribution of the taxa along the phylogeny. About 50% of all the species in this habitat type are contained in just two

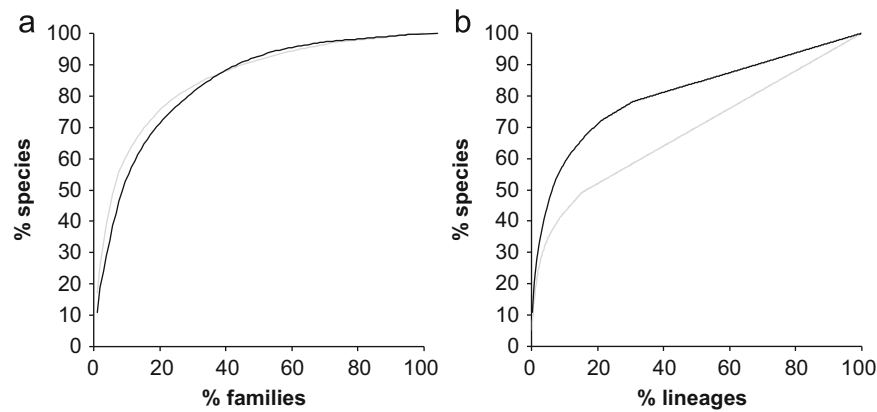


Fig. 2. Percentage of cumulative species richness for all species by family (a) and by lineages (b) among the Canarian and Hawaiian flora. Grey line: Canary Islands, Black line: Hawaii.

Table 2

Average Taxonomic distinctness (AvTD) and its variation value (VarTD) for all habitats in both archipelagos. Results are sorted by habitat name.

	Habitats	AvTD	VarTD
Canary Islands	Coastal scrub	97.34	161.4
	Laurel forest	98.22	79.86
	Rock communities	93.29	328.7
	Thermophilus	96.15	170.3
	Pine forest	97.1	120.8
	Summit scrub	97.27	103
	Disturbed places	97.34	81.86
	Hawai'i	Coast	98.13
Arid		97.63	111.7
LowlandDry		98.15	82.6
MontaneDry		98.48	69.65
Mesic		98.38	87.89
Wet		97.55	141.7
Subalp-Alp		97.96	93.77
Lava		99.07	37.67

families (Crassulaceae with 52 species and Asteraceae with 50 species); one single lineage, *Aeonium*+ accumulates 50 species in the Crassulaceae, and two more, *Sonchus* and *Cheirolophus*, add 20 species in the Asteraceae. Thermophilous woodlands behave similarly, although values are less extreme (see Fig. 3a and Table 2). The fact that a large proportion of species is shared between these two habitats may explain this similarity. In conclusion, these habitats represent floras with low deep distinctions (a shortage of families and lineages) and a very unbalanced species distribution, perhaps representing great opportunities for radiation but only for a limited number of lineages.

There are other Canarian habitats that differ statistically from the null model (see open circles in Fig. 3a), but they contribute only minor changes to the general pattern. However the effect of Laurel forest habitat is more interesting in that it is the only habitat with AvTD values greater than the null model, although within its confidence limits. It has a large proportion on long branches (families and lineages) related to its species numbers. This means it has the most original and balanced distribution of family and lineage sizes. The floristic structure of the Laurel forest consists of families with very similar numbers of lineages and species and relatively equal sizes on each group.

Hawaiian habitats are more phylogenetically distinct than the Canary Islands, although, fewer outliers depart from the null model (see Fig. 3b). Wet and Mesic habitats produce the most

contrasted AvTD values, and these contain significant portions of the total Hawaii flora (see Table 1). Their AvTD values fall beyond confidence limits and their effect on the overall pattern is major because they are both on the far end of the sample size axis (see Fig. 3b). Wet habitat has a lower AvTD (97.54) than expected and a large VarTD. This means a tree with a large proportion of small branches related to long branches, (similar situation to Rock, and Thermophilous communities in the Canary Islands). Thus, some families accumulate species in a disproportionately high share (i.e. the largest families, Campanulaceae, Gesneriaceae and Rutaceae sum up to 204 species in 7 lineages). On the other hand, Mesic has a larger AvTD than expected (98.38) and a low VarTD. This value resembles that of Canarian Laurel forest, indicating a more even distribution of species among lineages and lineages among families. Mesic habitats contain slightly fewer species than Wet habitats but the largest numbers of families and lineages in Hawaii (92 and 282 respectively, Table 1). In addition, a relatively low VarTD indicates a more homogeneous share of taxonomic groups along the phylogenetic structure. For example, the three largest families, Campanulaceae, Asteraceae and Rubiaceae, contain 161 species and 21 lineages.

Lava environments are also outside the confidence limits of the model. It has more large branches than expected according to its total species size. Thus, in spite of its small sample size, just 7.8% of the total species, it contains as much as 44.8% of the total families in Hawaii. In addition, it exhibits a fairly balanced distribution of species in both families and lineages (low VarTD).

Discussion

Taxonomic and Phylogenetic evenness between the Canary Islands and Hawai'i Floras

Why do species distribute so differently across families and lineages in the two island groups? To answer this, it is necessary to rectify the differences in the number of colonization events, related to isolation from mainland, with the similarities in the numbers of families represented, related to source floras, and the numbers of species generated through diversification.

The Hawaiian Flora is derived from considerably fewer colonists than the Canarian Flora (367 versus 599, respectively). Assuming that both island groups offer similar degrees of hospitability to immigrants (and therefore similar rates of colonization success), this is almost certainly due to the much greater degree of isolation (ca. 37 times larger) exhibited by the

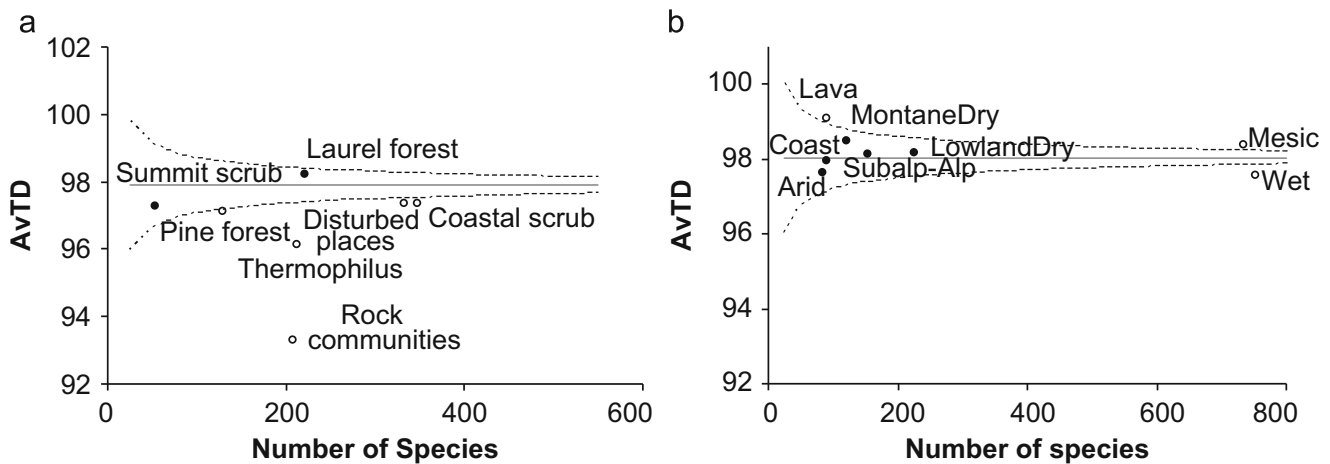


Fig. 3. Solid line: Null model values of the Average Taxonomic distinctness index for Canary Islands (a) and Hawaii (b). Dashed lines: 95% confident interval for the model. Abscissa: species number per habitat. Open circles: habitat with AvTD statistically different from null model AvTD. Solid circles: habitats with non-significant differences in AVTD values.

Hawaiian Islands. So there are fewer lineages spread among the same number of major taxa (families) in Hawaii.

Nonetheless, Hawaii is represented by the same number of families (105) as the Canary Islands. This may stem from a difference in the number of source areas that have contributed to the two floras. The Canary Islands have received colonists mainly from a single continental source region, the Mediterranean, and to a lesser degree from Africa (Santos, 2001) representing not only a limited pool of plant families but a rather uneven source, in that the Mediterranean flora includes disproportionate numbers of species in some families (see Domínguez Lozano and Schwartz, 2005b). In contrast, Hawaii, although extremely isolated, has received colonists from several highly distant and disparate source regions, including Australia, the Indo-Malayan region, the Neotropics, and even temperate North America (Fosberg, 1948; J.P. Price and W.L. Wagner, unpubl. data), representing a large pool of families for potential colonists. While the filter of isolation reduced this diverse pool to a modest subset, it nonetheless encompasses novel combinations of taxa that do not co-occur elsewhere, producing a more even distribution of species across families.

Diversification of lineages

The most significant contribution to the overall process, however, is diversification. By almost any measure, Hawaii has fostered more diversification than the Canary Islands. As the high lineage GC value indicates, the largest lineages in the Canary Islands contain considerably fewer species than those in Hawaii, and many more lineages in Hawaii experience large diversifications (see Table A5 in Appendix). There are many more speciation events spread across a larger number of lineages in Hawaii, whereas a purely random distribution of large lineages would favor the Canary Islands, since they have been colonized more than half again as many times as Hawaii. There are several potential factors contributing to diversification patterns in Hawaii. First of all, Hawaii includes more islands with more topographically distinct mountains, which may favor intra- and inter-island isolation and allopatric speciation. It represents as well a wider range of climatic habitats than the Canaries, including a greater range in elevation, temperatures and precipitation, and therefore may provide greater opportunities for ecological specialization and adaptive radiation.

The pattern suggests that island age may not be very important, since the Canary Islands are on average much older

than the present main Hawaiian Islands. The Hawaiian flora does contain lineages that pre-date the present high islands and began diversifying on now-vanished islands to the northwest (Givnish et al., 2009; Yi et al., 2004), however the bulk of lineages in the Hawaiian Islands are no older than the island of Kauai, about 5 million years, including many species-rich plant lineages (Price and Clague, 2002). The Canary Islands similarly include surprisingly young and diverse lineages (Kim et al., 1996; Böhle et al., 1996; Baldwin et al., 1998; Kim et al., 2008).

One possible explanation for the presence of large, monophyletic lineages in these island groups is the concept of niche pre-emption (Silvertown, 2004), whereby a colonizing taxon diversifies, increasing competition for niche space, and thus prevents the colonization of closely related taxa. Herben et al. (2005) counter that subsequent related colonists may be subsumed into a diversifying clade through hybridization, however Silvertown et al. (2005) maintain that the potential for occasional hybridization still constitutes the failure of a new clade to establish, and therefore that hybridization does not provide an alternative to niche pre-emption.

Both the Hawaiian and Canary Islands floras experience adaptive radiation (speciation between habitats) and non-adaptive radiation (speciation between islands or within islands), the former due to selective pressures and the latter due to genetic drift. In Hawai'i both forms of radiation are common (Price & Wagner, 2004), whereas in the Canary Islands inter-island speciation is the major source of radiation, with little subdivision among habitats (Francisco-Ortega et al., 1996; Allan et al., 2004).

Species radiations relate to dispersal abilities in several ways. In Hawai'i there are species-rich lineages with dispersal limitation. Price and Wagner (2004) found that the number of species in endemic clades correlated negatively with the average range size of constituent species, with diverse clades containing numerous restricted taxa. Also taking into account inter-island dispersal events within large radiations (Funk and Wagner, 1995), we conclude that many groups diversify as a function of limited dispersal between islands, which promotes isolation and divergence. Such taxa, with only a modest ability to disperse between adjacent islands, can be interpreted as having a much lower frequency of long distance dispersal from source areas to islands. Therefore, diversification and infrequent colonization may both stem from limited dispersal ability. In the Canary Islands, because of its proximity to mainland and flora sources, we can expect two dispersal limitation modes. Moderately dispersal-limited taxa may colonize easily but will not be able to maintain gene flow

from the continent. Natural selection, perhaps resulting in adaptive radiation, may permit niche pre-emption to maintain monophyly (examples are *Argyranthemum* or *Echium* among others lineages). More severely dispersal-limited taxa, that nonetheless manage to colonize islands, may have limitations that restrict them to certain habitats, such as canyon cliffs. Those taxa may experience radiation, although driven by genetic drift rather than natural selection, and will remain within habitats similar to those of the source species. The result is that closely related species occupy the same narrow habitat type in scattered locations (microspecies or neoendemic species), often with only a handful of small populations (e.g. *Cheirolophus*, *Limonium*, *Pericallis*, *Helianthemum*, *Cistus*, etc.). In conclusion, in Hawaii large monophyletic groups may result from variation in ecological characteristics among taxa, particularly dispersal ability. In the Canary Islands, monophyly may not relate to niche pre-emption exclusively but may also stem from diversification of very dispersal-limited taxa. Moreover, in some lineages such as *Sonchus* and perhaps *Aeonium* clades, these two may coexist.

Another proposed contributor to diversification is species diversity itself, whereby a high density of species on an island contributes to fragmented populations of a given species that are then more likely to diverge (Emerson and Kolm, 2005). However after comparing the two archipelagos, our data do not support this hypothesis. Individual islands in the Canary Islands have similar species numbers to islands of comparable size in Hawaii. For example, compare the two most species-rich islands in the Canary Islands, Tenerife (626 vascular plant species) and Gran Canaria (533) to the two most species rich islands in Hawaii, Kauai (615) and Oahu (571) (Price, 2004; J.P. Price and W.L. Wagner, unpubl. data). The areas of these islands are fairly comparable (ranging from 1400 to 2000 km²) such that species densities are similar. Nonetheless there has clearly been far more diversification in Hawaii, with Kauai supporting over 200 single island endemic plant species (Price, 2004), much more than any single island in the Canary Islands. Furthermore, the numbers of colonist lineages represented on Tenerife (450) and Gran Canaria (416) compared with Kauai (312) and Oahu (312), suggest a greater number of colonizing species on individual Canary Islands and therefore an initially higher species density. In either case, the diversity-driven-diversification hypothesis makes no distinction among the behavior of different clades, whereas our analysis indicates that clades diversify to very different degrees within each archipelago. We therefore propose that the Hawaiian Islands provide a greater amount of open niche space, as a function of both the sparseness of initial colonists and the greater range of climatic habitats, and that this in turn provides a greater opportunity for radiation for certain taxa.

Differences in Phylogenetic evenness among habitat types

We have identified three habitats with the largest differences in phylogenetic structure and where radiation has been extensive: Rock communities and Thermophilous woodlands in the Canary Islands, and Wet habitats in Hawaii. Two features of these habitats may contribute to the shape of phylogeny structures: historical fragmentation and receptivity to new immigrants. Fragmentation of habitat may promote isolation processes through paleogeographic history. Rock habitats are naturally fragmented in the Canary Islands, and Thermophilous communities would have experienced range contractions and expansions during the Quaternary as a function of climate change (Del Arco, 2006). In fact, the Canarian Thermophilous woodland is a relatively young ecosystem, having formed with onset of Mediterranean climate in the region, which occurred only 2.5 My ago (Blondel and Aaronson, 2005). Several

tree species belonging to these woodlands (*Juniperus turbinata*, *Pistacia atlantica*, *P. lentiscus*, *Phillyrea angustifolia*) are native non-endemic elements, suggestive of recent colonization from Mediterranean climate regions of the mainland. Wet habitats in Hawai'i have potentially also undergone fragmentation through paleoclimatic history, with cooler drier conditions predominant during glacial periods (Hotchkiss and Juvik, 1999).

Another inherent quality of these habitats is their capacity to receive colonists. Habitats that are similar to species-rich communities in source areas have a potentially larger pool of potential colonists. For example, Rock communities sustain the highest rare species concentrations in Iberia (see for example Domínguez Lozano and Schwartz, 2005b) and the Anti-Atlas mountains of Morocco (Médail and Quézel, 1999). Diversification may therefore be favored in those island habitats similar to mainland habitats characterized by high rates of diversification, in agreement with the species pool hypothesis governing local species richness (Taylor et al., 1990; Zobel and Pärtel, 2008), whereby local species richness derives from the species pool at the regional scale. Island and mainland habitats would share basal phylogeny branches (species rich families) although will not necessarily experience radiation in the same tip taxa (i.e lineages). In addition to Rock communities, we also identify Thermophilous woodlands in the Canary Islands, and Wet habitats in Hawai'i as habitats with high levels of receptivity as a function of similarity to species-rich source areas.

Other habitats may differ in either fragmentation history or receptivity, representing an opposite trend. For example, Laurel forests are considered the most ancient habitats in the Canary Islands, and include relict ("leftover") species previously occurring on nearby continents under different climatic conditions in the past (Takhtajan, 1969; Santos, 2001). This forest may therefore be poorly receptive to species coming from nearby continental habitats. In addition, species from the mainland may not be adapted to the levels of light competition and allelopathy typical of Laurel forest. We also assert that this habitat has been comparatively stable (rather than periodically fragmented) over its long history: it is located in a core position at middle elevations (and therefore may be buffered from temperature changes associated with Pleistocene climatic cycles) and may not have contracted significantly during Pleistocene climatic cycles as other habitats in the Canary Islands (Báez et al., 2001). Therefore, high stability and low receptivity, may explain the high concentration of basal taxa (families) and relatively low speciation rates evident in Laurel Forest. In Hawaii, however, relictualism is not a general condition of any particular habitat, due to the greater isolation. The high AvTD value recorded for Mesic habitat may be due to its intermediate moisture, which hosts a combination of Dry and especially Wet habitat lineages, disproportionately increasing the number of families and lineages. One of the highest AvTD values (Fig. 3b) is that of Montane dry habitat, which is also a very good example of low receptivity habitat, which includes some families and lineages not common in the main source floras of Hawaii. The phylogeny of Lava habitats, with deep branching (high AvTD) and even structure (low VarTD) represents an extreme situation: Lava flows are extremely recent habitats and subject to rapid alteration, and they offer few possibilities for speciation (low VarTD). Nonetheless, they exist across a diverse array of climates, supporting a variety of tolerant colonizers from disparate source areas and therefore exhibiting some deep phylogenetic branches (high AvTD).

A conceptual model for phylogeny organization

Based on these habitat differences we can illustrate a more general framework useful for understanding community phylo-

geny structures (*sensu* Webb et al., 2002), especially those of island floras. This conceptual outline derives from examining a combination of both Phylogenetic distinctness and evenness, and it can be visualized in Fig. 4:

Type I produces an unbalanced, uneven, and a fairly indistinct phylogenetic structure. Rock communities and Thermophilous woodlands in the Canary Islands and Wet habitats in Hawaii most solidly represent this type.

Type II is characterized by an unbalanced but distinct structure. This means a subflora with a high proportion of families and lineages related to species total and uneven distribution of taxa. No subflora in our work fits this type, although there may be floras elsewhere that do.

Type III or relictual shielded floras represent an even and a distinct phylogenetic structure. These are floras with high originality and low diversification. In our work, Laurel forests, and to some extent Mesic habitats fit this type. Type III floras may be good indicators of relictualism related to old and species poor lineages, although these habitats are also able to produce some recent taxa as well (Trusty et al., 2005).

Type IV floras are characterized by an even structure but low level of distinctness. These floras are among the poorest both in basal and tip taxa because they experience no diversification and they contain few families and lineages related to species totals. Strictly speaking no flora on both archipelagos exhibits these conditions, although summit floras in both archipelagos come closest to this concept. They are characterized by low overall species richness and also poor lineage and family numbers (see Table 1). In this case, species derive from preadapted species of similar ecosystems from the mainland or by vertical colonization from lower vegetation belts, therefore overall endemism seems to be rather high, and some of the most striking and well-known examples occur here (silverswords and *Echium*). We may call this flora type a depauperate flora.

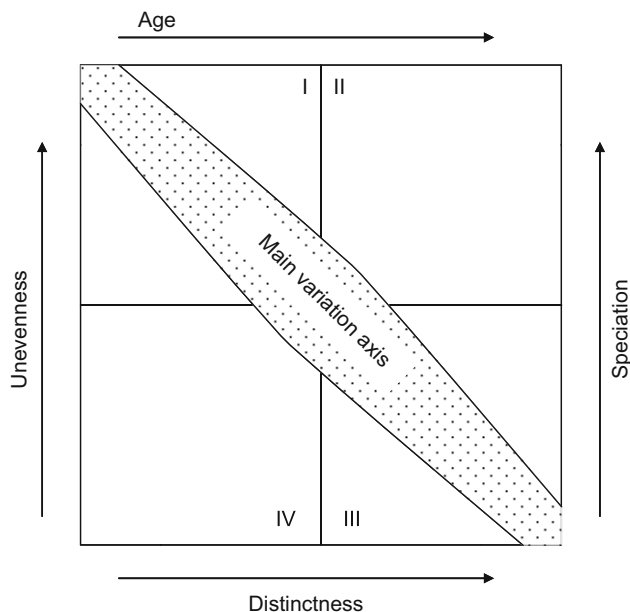


Fig. 4. Relationship between habitats properties (age and speciation) and phylogenies structure expressed by unevenness (VarTD) and distinctness (AVTD). As age (or stability) of the habitat increases, so does distinctness of the flora that it contains. Particularly old and stable habitats are defined by a very original, highly distinct flora. In the same way, as speciation increases, unevenness of the flora will increase as well, and species will accumulate in small number of families. Habitat receptivity and stability regulate the relationship between unevenness and distinctness of a particular flora (see text for details), and we therefore propose four community phylogeny types (I–IV), although VarTD and AVTD values will fall within the shaded region for the majority of floras.

These four types of phylogenies result from a combination of two factors. Receptivity is one of them, meaning the availability of preadapted species from neighboring floras will contribute to shape phylogenies in the same manner that they will contribute to local species richness (Taylor et al., 1990). Stability of host habitats related to the frequency of pulses of fragmentation and isolation following speciation (Kim et al., 2008) is the second. These two factors contribute to differences in colonization and extinction rates and ultimately to phylogeny organization. We propose a post factum hypothesis in accordance to this framework (Fig. 4): high rates of colonization success, derived from a high receptivity for source floras, followed by fragmentation and isolation pulses would produce uneven phylogenies (Type I). On the other hand, highly original and even phylogenies are expected, provided that long histories of stability and low receptivity rates become dominant (Type III). Most habitats in our analysis fall along a continuum between the extremes of types I and III. Although this overall framework may seem an oversimplification of real situations, where exceptions exist (Lava environments in Hawaii), these postulates may help us to identify particular locations with different community phylogenies and speciation modes.

In summary, differences in the phylogenetic structures among both archipelagos could be explained by differences in diversification rates, isolation and availability of source floras. In addition, differences may be further dissected in portions of each total flora (i.e. habitats). Thus, there are particular habitats (or islands inside islands) where most of the unevenness occurs and where diversification rules. These habitats house a large portion of neoendemic species produced in the most diverse lineages.

Acknowledgments

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Appendix

See Tables A1–A5 for details.

Table A1

Groups of Hawaiian plant species divided into lineages based on published studies. In some cases, the original colonist diversified into many species constituting multiple genera. Together, these diversifying groups comprise a large portion of the species diversity in the archipelago. Species included in these studies represent over half of all endemic species.

Group: Genera (Family)	Number of species in multi-species lineages	Reference
<i>Brighamia</i> , <i>Cyanea</i> , <i>Clermontia</i> , <i>Delissea</i> , <i>Lobelia</i> , <i>Trematolobelia</i> (Campanulaceae)	125	Givnish et al. (2009)
<i>Cyrtandra</i> (Gesneriaceae)	58	Cronk et al. (2005)
<i>Haplostachys</i> , <i>Phyllostegia</i> , <i>Stenogyne</i> (Lamiaceae)	57	Lindqvist and Albert (2002)
<i>Melicope</i> , <i>Platydesma</i> (Rutaceae)	52	Harbaugh et al. (2008)
<i>Scheidea</i> (Caryophyllaceae)	32	Nepokroeff et al. (2005)

Table A1 (continued)

Group: Genera (Family)	Number of species in multi-species lineages	Reference
<i>Argyroxiphium</i> , <i>Dubautia</i> , <i>Wilkesia</i> (Asteraceae)	30	Baldwin and Sanderson (1998)
<i>Hedyotis</i> (Rubiaceae)	20	Motley (2003)
<i>Bidens</i> (Asteraceae)	19	Ganders et al. (2000)
<i>Labordia</i>	16	Motley and Carr (1998)
<i>Psychotria</i>	11	Nepokroeff et al. (2003)
<i>Tetramolopium</i> (Asteraceae)	11	Lowrey (1995)
<i>Pittosporum</i>	10	Gemmill et al. (2002)
<i>Munroidendron</i> , <i>Reynoldsia</i> , <i>Tetraplasandra</i> (Araliaceae)	9	Costello and Motley (2001)
<i>Silene</i> (Caryophyllaceae)	7	Eggers et al. (2007)
<i>Scaevola</i> (Goodeniaceae)	6	Howarth et al. (2003)
<i>Viola</i>	6	Ballard and Sytsma (2000)
<i>Metrosideros</i>	5	Wright et al. (2001)
<i>Geranium</i>	5	Pax et al. (1997)
<i>Korthalsella</i>	5	Molvray et al., (1999)
<i>Kokia</i>	4	Seelanan et al. (1997)
<i>Hesperomannia</i>	3	Kim et al. (1996)
<i>Vaccineum</i>	3	Powell and Kron (2002)
Total	494	

Table A2

Groups of Canarian plant species divided into lineages based on published studies. In some cases, the original colonist diversified into many species constituting multiple genera. Together, these diversifying groups comprise a large portion of the species diversity in the archipelago. Species included in these studies represent over half of all endemic species.

Group: Genera (Family)	Number of species in multi-species lineages	References
<i>Aeonium</i> , <i>Aichryson</i> , <i>Greenovia</i> , <i>Monanthes</i> (Crassulaceae)	51	Mort et al. (2002)
<i>Babcockia</i> , <i>Lactucosonchus</i> , <i>Sonchus</i> , <i>Sventenia</i> , <i>Taekholmia</i> (Asteraceae)	30	Kim et al. (1996)
<i>Echium</i> (Boraginaceae)	23	Böhle et al. (1996)
<i>Sideritis</i> (Lamiaceae)	22	Barber et al. (2000)
<i>Argyranthemum</i> (Asteraceae)	19	Francisco-Ortega et al. (1996)
<i>Lotus</i> (Fabaceae)	19	Allan et al. (2004)
<i>Limonium</i> (Plumbaginaceae)	15	Lledo et al. (2005)
<i>Micromeria</i> (Lamiaceae)	15	Meimberg et al. (2006)
<i>Cheirolophus</i> (Asteraceae)	14	Susanna et al. (1999)-
<i>Pericallis</i> (Asteraceae)	12	Swenson and Manns (2003)
<i>Crambe</i> (Brassicaceae)	10	Francisco-Ortega et al. (2002)

Table A2 (continued)

Group: Genera (Family)	Number of species in multi-species lineages	References
<i>Tolpis</i> (Asteraceae)	8	Moore et al. (2002)
<i>Euphorbia</i> (Euphorbiaceae)	8	Molero et al. (2002)
<i>Convolvulus</i> (Convolvulaceae)	7,3	Carine et al. (2004)
<i>Bencomia</i> , <i>Dendriopoterium</i> , <i>Marcetella</i> (Rosaceae)	7	Helfgott et al. (2000)
<i>Descurainia</i> (Brassicaceae)	7	Goodson et al. (2006)
<i>Bystropogon</i> (Lamiaceae)	5	Trusty et al. (2005)
<i>Gonospermum</i> , <i>Lugoa</i> , <i>Tanacetum</i> (Asteraceae)	7	Francisco-Ortega et al. (2001a)
<i>Teline</i> , <i>Adenocarpus</i> (Fabaceae)	5,4,3	Percy and Cronk (2002)
<i>Plantago</i> (Plantaginaceae)	4	Ronsted et al. (2002)
<i>Kickxia</i> (Scrophulariaceae)	3	Gebrehiwet (2000)
<i>Ferula</i> (Apiaceae)	3	Kurzyna-Mtynik et al. (2008)
<i>Cistus</i> (Cistaceae)	3	Batista et al. (2001)
<i>Isoplexis</i> (Scrophulariaceae)	3	Brauchler et al. (2004)
<i>Tinguarra</i> (Apiaceae)	3	Downie et al. (2000)
<i>Schizogyne</i> , <i>Allagopappus</i> , <i>Pulicaria</i> , <i>Vieraea</i>	2	Francisco-Ortega et al. (2001b)
<i>Asteriscus</i> (Asteraceae)	2	Goertzen et al. (2002)
<i>Ceropegia</i> (Asclepiadaceae)	2	Meve and Liede-Schumann (2007)
<i>Bupleurum</i> (Apiaceae)	2	Neves and Watson (2004)
Total	321	

Table A3

Lineages identified by Reyes-Betancort et al. (2008) consisting of multiple endemic species.

Genus	Family
<i>Asparagus</i>	Convallariaceae
<i>Carduus</i>	Asteraceae
<i>Carlina</i>	Asteraceae
<i>Dorycnium</i>	Fabaceae
<i>Globularia</i>	Globulariaceae
<i>Helianthemum</i>	Cistaceae
<i>Helichrysum</i>	Asteraceae
<i>Herniaria</i>	Caryophyllaceae
<i>Hypericum</i>	Hypericaceae
<i>Kunkiella</i>	Santalaceae
<i>Lavandula</i>	Lamiaceae
<i>Minuartia</i>	Caryophyllaceae
<i>Ononis</i>	Fabaceae
<i>Onopordon</i>	Asteraceae
<i>Parolinia</i>	Brassicaceae
<i>Pimpinella</i>	Apiaceae
<i>Polycarpha</i>	Caryophyllaceae
<i>Pterocephalus</i>	Dipsicaceae
<i>Reichardia</i>	Asteraceae
<i>Rhamnus</i>	Rhamnaceae
<i>Ruta</i>	Rutaceae
<i>Salvia</i>	Lamiaceae
<i>Scilla</i>	Hyacinthaceae

Table A3 (continued)

Genus	Family
<i>Scrophularia</i>	Scrophulariaceae
<i>Semele</i>	Convallariaceae
<i>Senecio</i>	Asteraceae
<i>Silene</i>	Caryophyllaceae
<i>Solanum</i>	Solanaeae
<i>Spartocytisus</i>	Fabaceae
<i>Vicia</i>	Fabaceae
<i>Viola</i>	Violaceae
<i>Voluntaria</i>	Asteraceae

Table A4

Family ranking of species richness for the 8th largest families. Hawaiian flora has been rarefied. Av: Mean of the rarefaction. Var: Variance of the rarefaction.

Rank	Canary Islands		Hawaii		
	Family	Sp #	0	Av	Var
1	Asteraceae	171	Campanulaceae	108.02	13.19
2	Poaceae	87	Asteraceae	80.52	10.0
3	Fabaceae	75	Lamiaceae	51.47	6.65
4	Crassulaceae	55	Gesneriaceae	49.67	7.05
5	Lamiaceae	55	Rutaceae	48.1	6.43
6	Caryophyllaceae	42	Rubiaceae	46.99	6.83
7	Brassicaceae	41	Poaceae	39.42	5.34
8	Boraginaceae	31	Cyperaceae	38.47	5.15
1–8		140		69.54	8.04

Table A5

Lineage ranking of species richness for the 30th largest lineages in both floras. Hawaiian flora has been rarefied. Av: Mean of the rarefaction. Var: Variance of the rarefaction.

Lineage size Ranking	Canary Islands		Hawaii		
	Lineage	Sp #	0	Av	Var
1	Aeonium+	51	Lobelioidae	108.03	13.79
2	Sonchus+	30	Hap/Phy/Sten	48.86	6.68
3	<i>Echium</i>	23	Melicope	44.56	6.42
4	<i>Sideritis</i>	22	Schiedea	27.44	3.81
5	<i>Argyranthemum</i>	19	Madiinae	25.72	3.72
6	<i>Lotus</i>	19	Gesneriaceae.3	25.72	3.66
7	<i>Micromeria</i>	15	Pritchardia	18.03	2.54
8	<i>Limonium1</i>	15	Hedyotis	18.02	2.61
9	<i>Cheirolophus</i>	14	Myrsine	17.12	2.43
10	<i>Pericallis</i>	12	Bidens	16.29	2.3
11	<i>Crambe</i>	10	Peperomia.4	14.56	2.03
12	<i>Helianthemum1</i>	9	Labordia	13.74	1.88
13	<i>Polycarpaea</i>	9	Chamaesyce	13.7	1.97
14	<i>Tolpis</i>	8	Gesneriaceae.1	12.83	1.83
15	<i>Euphorbia1</i>	8	Melanthera	12	1.65
16	<i>Convolvulus1</i>	7	Sicyos	11.15	1.57
17	<i>Gonospermae</i>	7	Gesneriaceae.2	11.14	1.55
18	<i>Silene1</i>	7	Lysimachia.1	11.12	1.62
19	<i>Bencomia+</i>	7	Wikstroemia	10.32	1.47
20	<i>Descurainia</i>	7	Coprosma.1	10.27	1.44
21	<i>Bystropogon</i>	5	Psychotria	9.45	1.33
22	<i>Teline1</i>	5	Pittosporum	9.43	1.36
23	<i>Asparagus1</i>	5	Tetramolopium	9.43	1.34
24	<i>Carlina</i>	5	Panicum.1	9.4	1.32
25	<i>Vicia1</i>	5	Eragrostis	7.73	1.07
26	<i>Parolinia</i>	5	Adenophorus	7.73	1.07
27	<i>Pteroccephalus</i>	4	Tet/Mun/Rey	7.69	1.11
28	<i>Pimpinella</i>	4	Scaevola.1	6.87	0.96
29	<i>Kunkelella</i>	4	Viola	6.02	0.83
30	<i>Teline2</i>	4	Hibiscadelphus	6	0.86
1–30 Difference	0	47	0	102.02	12.93

Appendix B. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ppees.2009.12.001.

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