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# BIOGEOGRAPHIC COMPARISONS OF PLANT DISTRIBUTION ON OCEANIC ISLANDS

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# Summary

**1** Oceanic islands are excellent model systems to study biogeography, ecology, evolution and conservation. Thanks to the isolation of many islands, they exhibit special patterns of biodiversity, such as lower species diversity, high endemism and disharmony. Important processes in the assembly of these communities are immigration, extinction (increasingly through human agency), and adaptive radiation. These processes help explain why island plant species exhibit, albeit to different degrees, a common set – or syndrome – of traits, including reduced dispersal ability, low competitive ability, and characteristic breeding systems. The overall aim of this PhD thesis was to improve our understanding of biodiversity patterns on oceanic islands, including the role of humans as dispersal agents for changing island biogeography.

**2** The 'island disharmony' hypothesis states that species on islands are more unequally distributed among higher taxa (genera or families) than on continents. To investigate this hypothesis, I assembled a global data set of the floristic composition of both oceanic islands and, for comparison, of continental regions. Taxonomic disharmony varied strongly with size of the flora, island floras being more disharmonic than expected from random assembly from the global flora, but not more disharmonic than continental ones. Indeed, smaller island floras tend to be particularly diverse phylogenetically, underlining their importance for global biodiversity.

**3** The same data were used to investigate the role of three possible factors – species richness, niche pre-emption, and predisposition of families (including their dispersibility) – as drivers of adaptive radiation on islands. Species richness and other factors (isolation from nearest continent, island type, maximal elevation, number of islands, and latitude) were shown to influence speciation rates on islands. I conclude that rapid speciation is possible in all plant families, but arriving on an island soon after its formation increases the likelihood that this actually occurs. Because there is a strong element of chance in which families reach an island first, the relative abundance of plant families varies greatly among islands.

**4** In a field study, I measured plant functional traits in the subalpine flora of Tenerife, a subtropical island in the Canary islands (Macaronesia), and related these to important dimensions of plant adaptation (competition, growth strategy, phenology, plant-nutrient relations, and plant-water relations). I found high functional diversity, especially within genera that were not specialized to high elevation habitat, while species from specialized and putatively pre-adapted species showed a narrower range of traits more typical of the habitat (e.g. low leaf area and specific leaf area). It appears that adaptive radiations from herbaceous species have been able to fill a broad range of niches within this subalpine habitat, but that the niche of larger woody plants is occupied by species from high elevation genera.

**5** To investigate the role of humans as new dispersal agents for island biogeography, I made the following trait comparisons for European plants: (a) species introduced to the Hawaiian archipelago (Pacific ocean) *versus* species that were not introduced, and (b) species that became invasive *versus* species that did not become invasive. My results show that traits conferring success during the introduction phase were partly different from those important in the invasion phase. While the majority of species introduced to Hawaii were mostly from fertile, anthropogenic habitats, the species that went on to become invasive came from a broad range of habitats. Climate matching played an important role in the first stage, with species from warm lowland areas and evergreen species being overrepresented among introduced species, while edaphic factors became more significant in the invasion phase. I conclude that correlative studies of the traits of invasive species (‘invasiveness’) will only produce reliable results if they take account of which species are actually introduced to an area.

**6** As well as providing new insights into island biogeography, the work described here challenges several fundamental assumptions of island biogeography, especially regarding the relative importance of immigration and *in situ* speciation. The data highlight the often high phylogenetic and functional diversity of island floras, underscoring their importance for global biodiversity. My results also show the great potential of using global datasets to disentangle the factors determining patterns of biodiversity on islands. Further studies based on more comprehensive and diverse datasets hold much promise for advancing island biogeography and ecology more generally.

# Zusammenfassung

**1** Ozeanische Inseln sind ausgezeichnete Untersuchungsgebiete für die Biogeografie, Ökologie, Evolutionsbiologie, und Naturschutzbiologie. Wegen ihrer oft grossen Isolation, beherbergen Inseln eine spezielle Biodiversität, welche sich durch tiefe Artenvielfalt, hohen Endemismusgrad, und taxonomische Disharmonie auszeichnet. Wichtige Prozesse, welche die Biodiversität auf Inseln prägen, sind Immigration, Aussterben (zunehmend auch durch den Einfluss des Menschen), und adaptive Radiation. Diese Prozesse helfen zu erklären, weshalb Pflanzen auf Inseln zum Teil durch ähnliche Eigenschaften charakterisiert sind: reduzierte Fähigkeit zur Ausbreitung, tiefe Konkurrenzkraft, und charakteristische Reproduktionsbiologie. Das Ziel dieser Dissertation war es, ein besseres Verständnis von Biodiversität auf Inseln zu erlangen, inklusive der Rolle des Menschen als Verbreiter von Arten für die Insel-Biogeografie.

**2** Die 'Insel-Disharmonie'-Hypothese besagt, dass Arten auf Inseln ungleicher zwischen Gattungen und Familien verteilt sind als auf Kontinenten. Um diese Hypothese zu untersuchen, habe ich einen globalen floristischen Datensatz von Inseln und kontinentalen Gebieten erstellt. Es zeigte sich, dass die taxonomische Disharmonie stark von der Grösse einer Flora abhängt. Inselfloren sind disharmonischer als durch zufällige Auswahl von Arten von Kontinenten zu erwarten wäre, aber sie sind nicht disharmonischer als vergleichbare kontinentale Floren. Vielmehr sind kleine Inselfloren phylogenetisch besonders vielfältig, was ihre grosse Bedeutung für die globale Biodiversität zusätzlich unterstreicht.

**3** Der gleiche Datensatz wurde verwendet, um die Beeinflussung von adaptiver Radiation durch drei Einflussfaktoren – Artenvielfalt, unbesetzte Nischen, und die Prädisposition von Pflanzenfamilien (und insbesondere deren Ausbreitungsfähigkeit) – zu untersuchen. Es zeigte sich, dass Artenvielfalt wie auch andere Faktoren (Isolation von Kontinenten, Inseltyp, maximale Höhe der Insel, Anzahl von Inseln im Archipel, und Breitengrad) die Artenbildung auf Inseln beeinflussen. Schnelle Artenbildung scheint in allen Pflanzenfamilien möglich zu sein, aber ein früher Zeitpunkt der Besiedelung nach der Formierung einer Insel beeinflusst die Artenbildungsrate in einer Pflanzenfamilie. Weil der Besiedlungszeitpunkt stark vom Zufall abhängt, variiert die relative Häufigkeit von Pflanzenfamilien stark zwischen

verschiedenen Inseln.

**4** In einer Feldstudie habe ich verschiedene funktionelle Eigenschaften der subalpinen Flora auf Teneriffa, einer subtropischen Insel der Kanarischen Inseln (Makaronesien), gemessen, welche mit wichtigen Dimensionen der ökologischen Anpassung von Pflanzen (Konkurrenzverhalten, Wachstumsstrategie, Phänologie, Pflanzen-Boden-Interaktionen, und Wasserhaushalt) verbunden sind. Ich habe eine hohe funktionelle Diversität dokumentiert, insbesondere bei denjenigen Gattungen, welche sich nicht für ein Leben in der subalpinen Klimazone spezialisiert haben, während mutmasslich an dieses Habitat spezielle angepasste Gattungen eine kleinere Breite an funktionellen Eigenschaften zeigten, welche für das Habitat besonders typisch sind (zum Beispiel kleine Blattfläche und spezifische Blattfläche [‘specific leaf area’]). Es scheint, dass Krautpflanzen durch adaptive Radiation eine grosse Breite an Nischen in diesem subalpinen Habitat besetzen konnten, aber nicht die Nische der grösseren Gehölzpflanzen, welche durch subalpine Gattungen besetzt ist.

**5** Um die Rolle des Menschen als neuer Verbreiter von Pflanzen für die Insel-Biogeografie zu untersuchen, habe ich folgende Vergleiche von Eigenschaften der Pflanzen Westeuropas gemacht: (a) Arten, welche im Hawaiianischen Archipel (Pazifischer Ozean) eingeführt wurden oder nicht, und (b) Arten, welche in Hawaii invasiv wurden oder nicht. Meine Analyse zeigt, dass Eigenschaften, welche den Erfolg von Arten bei der Einfuhr fördern zum Teil andere sind, als diejenigen, welche den Invasionserfolg begünstigen. Während die Mehrzahl der in Hawaii eingeführten Arten an nährstoffreiche, anthropogene Standorte angepasst ist, wurden Arten von vielen verschiedenen Standorten invasiv. Während die Voranpassung an ein Hawaiianisches Klima eine wichtige Rolle für die erfolgreiche Einfuhr und Etablierung spielte – die meisten eingeführten Arten waren Tieflandarten und immergrüne Arten waren übervertreten, war in der Invasionsphase die Anpassung an Bodenbedingungen besonders wichtig. Eine wichtige Schlussfolgerung dieser Analyse ist, dass korrelative Studien von Eigenschaften invasiver Arten (‘invasiveness’) nur verlässliche Resultate liefert, wenn einbezogen wird, welche Arten in ein neues Gebiet eingeführt wurden und welche nicht.

**6** Durch diese Dissertation wurden ein erweitertes Verständnis von wichtigen Prozessen der Insel-Biogeografie erarbeiten; zum Teil sind diese Einsichten von fundamentaler Bedeutung. Insbesondere zeigte sich, dass die Bedeutung der Isolation überschätzt und die *in situ* Artbildung unterschätzt wird. Die Studie zeigt auch, dass Inselfloren häufig sowohl eine hohe phylogenetische wie auch funktionelle Diversität aufweisen, was die hohe Bedeutung von Inseln für die globale Biodiversität zusätzlich unterstreicht. Meine Analyse illustriert das grosse Potenzial von globalen Datensätzen, um die relative Bedeutung von verschiedenen Mechanismen für die Artenbildung auf Inseln besser zu verstehen. Weitergehende Studien mit umfassenderen Datensätzen dürften daher von grossem Wert für die Inselbiogeografie und allgemeiner die ökologische Forschung sein.

# General Introduction

Loss of biodiversity is considered one of the major societal challenges of our time (Heywood 1995, Millennium Ecosystem Assessment 2005). It is predicted that over the coming decades a large proportion of global biodiversity will be lost due to human impacts unless immediate and major conservation actions are taken (Millennium Ecosystem Assessment 2005, Ehrlich and Pringle 2008, Caujapé-Castells et al. 2010, Kueffer and Kaiser-Bunbury 2013). Such biodiversity loss might be particularly problematic because of its importance for ecosystem functioning, stability, and provisioning of essential services to society (Naeem et al. 1994, Tilman and Downing 1994, Chapin et al. 2000, Loreau et al. 2002). A necessary basis for any action to save the Earth’s biodiversity is a thorough understanding of what biodiversity is, where it is found, and how it is formed (Rosenzweig 1995, Loreau et al. 2001, Sodhi and Ehrlich 2011).

These questions have interested biogeographers and evolutionary biologists for centuries. Over time a rich understanding of biodiversity has developed that acknowledges its different dimensions (Rosenzweig 1995, Purvis and Hector 2000, Sodhi and Ehrlich 2011). Species diversity constitutes an important aspect of biodiversity, but also diversity at lower and higher hierarchical levels must be considered: the diversity of genes, populations, and higher taxonomic groups such as genera or families (nowadays often termed phylogenetic diversity) (Webb et al. 2002, Cadotte et al. 2009). Biodiversity also includes ecological aspects such as the diversity of ecological specializations and interactions among species (functional diversity) (Walker 1992, Petchey and Gaston 2002, Lavorel et al. 2007, Cadotte et al. 2009). A general feature of biodiversity is its very uneven distribution in space, time, and across the tree of life. Some geographic areas are very species-rich while others are species-poor (Myers et al. 2000). Such spatial heterogeneity can be found at different spatial scales: between habitats, between biomes, and between geographic regions (Rosenzweig 1995, Sodhi and Ehrlich 2011). Similarly, while some phylogenetic lineages, families or genera are very species-rich, others are species-poor (Scotland and Sanderson 2004). And possibly most important for society, while some groups of species encompass a large functional diversity, others might be taxonomically diverse but functionally uniform (e.g. Prinzing et al. 2008).

## Biodiversity pattern on oceanic islands

Due to very high levels of endemism, oceanic islands in a broad sense – i.e. islands occurring in one of the world's oceans – contribute very substantially to global biodiversity. Thus, as much as one quarter of the world's plants may occur exclusively on islands (Kreft et al. 2008), with many island species being confined to one island or one island group (Carlquist et al. 1965, Carlquist 1974, Whittaker and Fernández-Palacios 2007, Kier et al. 2009). But islands are also hotspots of species extinctions, partly due to particularly high levels of alien species invasions and habitat destruction (Whittaker and Fernández-Palacios 2007, Caujapé-Castells et al. 2010, Sodhi and Ehrlich 2011).

Since Charles Darwin (1859) and Alfred Russell Wallace (1880) developed modern evolutionary theory, studies on islands have greatly contributed to our understanding of biodiversity and its conservation. For example, islands inspired fundamental work in evolutionary biology (Grant 1998, Grant and Grant 2008, Losos and Ricklefs 2009), biogeography (MacArthur and Wilson 1967, Losos and Ricklefs 2010), and conservation biology (reviewed in Hansen 2010, Kaiser-Bunbury et al. 2010, Kueffer and Kaiser-Bunbury 2013). As study systems, islands are globally distributed, spatially well defined, replicated, and variable in area, topography, geology, climate, degree of isolation, native species diversity, and history (Whittaker and Fernández-Palacios 2007, Gillespie and Clague 2009, Kueffer 2012).

Of particular importance to island research has been MacArthur and Wilson's dynamic equilibrium model of island biogeography (MacArthur and Wilson 1967). This interprets the level of biodiversity on an island as reflecting the balance between processes of immigration and extinction, both of which are influenced by the isolation and area of an island. This theoretical framework acknowledges the great importance of immigration through long-distance dispersal for the assembly of island biotas; which is expected to lead to biotas that are skewed towards some taxonomic groups that are particularly well adapted to long-distance dispersal ('island disharmony') (Carlquist 1974).

However, island biogeography theory neglects the role of evolutionary and ecological processes in shaping the biodiversity after immigration has occurred. As impressively illustrated by dramatic examples of adaptive radiation events on many islands, *in situ* speciation is of great importance to the formation of island biodiversity (Gillespie 2004, Gillespie 2009, Losos and Ricklefs 2009, Losos and Mahler 2010). And some of the most conclusive research on the role of ecological interactions in evolution – including coevolution and character displacement through competitive interactions – comes from oceanic islands (Grant 1998, Grant and Grant 2008). Only recently extended models of island biogeography have been proposed that better account for evolutionary and ecological processes (Lomolino 2000, Whittaker et al. 2008, Losos and Ricklefs 2010, Rosindell and Phillimore 2011). With the increasing availability of data on species presences and their functional traits from many islands worldwide, it becomes now possible to test such refined models empirically (Emerson and Gillespie 2008).

Through developments at the intersection of biogeography, functional ecology, community ecology, and evolutionary biology, islands are once again moving to the forefront of ecological and evolutionary research (Kueffer and Fernandez-Palacios 2010). For instance, a central question in community ecology is what allows species to co-exist (Webb et al. 2002, Levine and HilleRisLambers 2009). By studying patterns of taxonomic, phylogenetic and functional diversity on islands it will be possible to better understand the relative importance of stochastic processes, environmental filtering processes, and biotic interactions for community assembly. If the species co-occurring are functionally more similar than expected from null models based on random assembly processes, it would suggest that environmental filtering and/or dispersal limitation matter (Webb et al. 2002, Silvertown et al. 2006). On the other hand, a lower than expected functional similarity between co-occurring species would be a predicted consequence of the competitive exclusion of functionally similar species, and would contradict neutral theory (Hubbell 2001).

However, our knowledge about the functional diversity of island biodiversity remains limited. It is often assumed that island species are characterized by a common set or syndrome of traits such as woodiness of herbaceous plants, loss of dispersibility, low competitive ability and growth rates, or high rate of selfing (Carlquist 1974, Barrett et al. 1996, Givnish 1998, Leigh et al. 2007, Whittaker and Fernández-Palacios 2007). If true, this would mean that functional diversity of island plants is low, with traits of different species largely converging.

But research on islands has also documented some of the best examples where evolution of new species is linked to ecological divergence, especially when adaptive radiations produce species-rich lineages that come to occupy many habitats or microhabitats (Losos and Ricklefs 2009). Such adaptation to different habitats would be expected to lead to a diversification of functional traits, although few studies have attempted to study the evolution of plant traits during adaptive radiations (but see Montgomery and Givnish 2008, Dunbar‑Co et al. 2009, Santiago and Kim 2009).

Recent advances in research on plant functional traits open up new possibilities for studying the functional diversity of island floras. Standard protocols have been defined for determining key plant traits (Cornelissen et al. 2003, Kattge et al. 2011), and the ecological significance of many traits are increasingly well understood (Westoby et al. 2002, Wright et al. 2004, Lavorel et al. 2007). So far, however, these approaches have rarely been applied to island biota, and then only at a small scale.

## The human dimension of island biogeography

Humans transform island ecosystems in many ways, and they also affect island biodiversity by changing dispersal pathways to islands and connectivity among islands and between islands and continents (Denslow et al. 2009, Kueffer et al. 2010, Kueffer 2013, Traveset et al. 2014). Humans as a new dispersal agent seem set to fundamentally change island biogeography and the biodiversity on islands. This will partly happen because some species introduced by humans (so-called alien or non-native species) become invasive and can threaten native biodiversity (Reaser et al. 2007, Caujapé-Castells et al. 2010, Kueffer et al. 2010). But more generally, humans add many new alien species to islands and thereby change the taxonomic, phylogenetic, and functional diversity and size of island biota. First studies have documented emerging novel biodiversity patterns, but a more mechanistic understanding of how alien species are distributed on islands remains largely missing (Sax and Gaines 2008, Traveset et al. 2014).

## Outline of the thesis

In this thesis, floristic information compiled from databases with information on the taxonomy and distribution of alien and native plant species from up to 118 island or island groups (and several 100 continental areas for comparison) was used to identify general determinants of island plant diversity on oceanic islands at a global scale. Chapters 1 and 2 present meta-analyses focused on the phylogenetic diversity of island floras. These secondary data analyses were complemented by a field-based empirical study of the functional diversity of the flora of subalpine summit scrub habitat on Tenerife in the Canary islands (chapter 3). A final fourth chapter investigated emerging human-shaped island biogeography patterns through a case study of those species in the alien flora of the Hawaiian archipelago (Pacific island) that are of European origin.

In chapter 1 *A global-scale analysis of taxonomic disharmony of island floras* we tested the generality of island disharmony by assembling complete native species lists for 23 flowering plant families from 118 islands or island groups (and 252 geographic regions on continents for comparison) worldwide and tested different hypotheses about how island characteristics might affect taxonomic disharmony. We found that all disharmonic measures in our study varied strongly with size of flora, and islands were more disharmonic both at a family and genus level than expected from random assembly from the global flora. But the same deviation from null model predictions was also found for continental floras. Thus, we conclude that islands floras are not more disharmonic than continental ones; indeed, smaller island floras tend to be phylogenetically particularly diverse, underlining their importance for global biodiversity.

In chapter 2 *The macroecology of adaptive radiations on oceanic islands w*e used the same data as in chapter 1 to investigate the role of three possible factors – species richness, niche pre-emption, and predisposition of families (including their dispersibility) – as drivers of adaptive radiation on islands. We found evidence for an important role of species richness but also other factors (isolation from nearest continent, island type, maximal elevation, number of islands, and latitude) for speciation rates on islands. Our results suggest that rapid speciation is possible in all plant families, but that arriving on an island soon after its formation increases the likelihood that this actually occurs. Moreover, because there is a strong element of chance in which families reach an island first, the relative abundance of plant families varies greatly among islands.

In chapter 3 *Functional diversity of summit scrub vegetation on Tenerife Island (Canary Islands, Spain),* we investigated the plant functional diversity of subalpine summit scrub habitat on a subtropical island, Tenerife (Canary islands, Macaronesia). We measured traits related to important dimensions of plant adaptation, including competition, growth strategy, phenology, plant-nutrient relations, and plant-water relations. High functional diversity was found especially within genera that were not specialized to high elevation habitat, while species from specialized and putatively pre-adapted species showed a narrower range of traits more typical of the habitat (e.g. low leaf area and specific leaf area). It appears that adaptive radiations from herbaceous species have been able to fill a broad range of niches within this subalpine habitat, but that the niche of larger woody plants is occupied by species from high elevation genera. The high functional diversity recorded in this subalpine flora, which has apparently arisen through high phylogenetic diversity and adaptive radiations within phylogenetic lineages, contradicts the idea that island floras are ecologically depauperate.

In chapter 4 *Human species selection explains plant invasions in the Hawaiian islands* we compared the characteristics of species of European origin (all species that occur as natives in Switzerland) that were introduced to and became invasive in the Hawaiian archipelago (Pacific ocean). The aim of this study was to understand which plant traits contribute to the success of alien plants at two stages of the invasion process - introduction and invasion. We show that partly different traits characterize successful species at the two stages. While the majority of species introduced to Hawaii are from very fertile and man-made habitat, species with diverse habitat affinities showed a high potential to become invasive once introduced. Climate matching played an important role in the first stage with species from warm lowland areas and evergreen species being overrepresented among introduced species on subtropical Hawaiian islands. In the invasion phase, soil factors became a more important filter. We conclude that correlative studies of the traits of invasive species (‘invasiveness’) only produce reliable results if they take account of which species are actually introduced to an island.

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# Chapter 1

# A global analysis of the taxonomic disharmony of island floras

## Abstract

Research on oceanic islands has contributed considerably to our understanding of the phylogenetic structure of biotic communities and regional biota. One important idea arising from this research is the ‘island disharmony hypothesis’, which postulates that species are more unevenly distributed among higher taxa on islands than continents. Our objective was to test the generality of this hypothesis using a global dataset of island and continental floras.

We assembled complete native species lists for 23 flowering plant families from 118 islands or island groups and 252 geographic regions on continents worldwide. Using these data, we generated null models to test whether island patterns deviate from continental patterns. We used five types of measure to describe disharmony: (1) numbers of families (F) or genera (G) present on an island, (2) species-to-family or species-to-genus ratios (S/F, S/G), (3) Gini coefficients, (4) the proportion of species in the largest genera or families (dominance), and (5) the proportion of monospecific genera or families (disparity). In addition, we used multiple regressions to investigate how taxonomic disharmony might be affected by various geographical and ecological attributes of islands. All analyses were performed at both the generic level (the distribution of species among genera) and the family level (the distribution of species among families). Results were cross-validated with complete flowering plant species lists for 32 island groups.

We found that island floras tend to be more disharmonic both at the family and generic levels than would be expected from a null model based upon the random assembly of species, with the level of disharmony increasing according to the size of the flora. However, continental floras also deviated from the null model predictions in a similar fashion. Multivariate analyses revealed that species richness was the strongest predictor of taxonomic disharmony for all disharmony measures, while there were no significant effects of isolation. Besides species richness, latitude and in some cases area, elevation and endemism affected the distribution of species across genera and families.

To explain our findings we propose that the main driver of species diversity on islands varies depending on flora size, with colonization leading to the accumulation of a broad range of taxa in small floras, while *in situ* radiation by a few taxa causes increasing disharmony in larger floras. The fact that similar phylogenetic patterns can be detected in continental floras suggests that dispersal limitation may be less important on islands than previously thought, while *in situ* radiations may be equally important in continental regions than on oceanic islands. Thus, islands floras are not more disharmonic than continental ones; indeed, smaller island floras tend to be phylogenetically very diverse, underlining their importance for global biodiversity.

## Introduction

Research on oceanic islands has contributed greatly to our understanding of how biodiversity is formed and distributed (Carlquist 1965, Whittaker and Fernández-Palacios 2007, Gillespie and Clague 2009). For example, observations on islands were crucial for the development of Charles Darwin's (1859) ideas on evolution, and later for the understanding of evolution in action (Grant and Grant 2008); and (McArthur and Wilson 1967) theory of island biogeography is by far the most widely discussed theory in the field of biogeography (Losos and Ricklefs 2010).

One reason for the attractiveness of islands as a model system is that they are globally distributed and isolated geographic spaces characterized by comparable conditions, which allows observations to be replicated at a regional or planetary scale. Most of these larger-scale comparative studies of biodiversity have concerned the numbers of species on islands, while more detailed studies of species richness have been restricted to single islands/archipelagos or compared only few island groups (Kueffer and Fernandez-Palacios 2010). With the growing availability of comprehensive taxonomic information from many islands worldwide, however, it becomes feasible to investigate aspects of diversity in addition to total species richness (Emerson and Gillespie 2008).

Understanding how species diversity is distributed phylogenetically is an important topic linking biogeography (McArthur and Wilson 1967, Cook 1969), macroevolution (Emerson and Kolm 2005, Maruvka et al. 2013) and community ecology (Enquist et al. 2002, Emerson and Gillespie 2008). It has long been considered that a common feature of the biodiversity of islands is a strong phylogenetic clustering of species, with most higher-level taxonomic groups (genera or families) being species poor, while a few are very species rich. In fact, this is a general pattern across all forms of life, not only on islands but also on continents (Willis and Yule 1922, Jarvinen 1982, Dial and Marzluff 1989, Fenner et al. 1997, Enquist et al. 2002), but is assumed to be more pronounced on islands (Carlquist 1965, McArthur and

Wilson 1967).

A number of factors have been proposed to explain why the biotas of islands should have a different phylogenetic structure than continents. First, only species with the adaptations necessary for long-distance dispersal (including establishment after arrival and often in coastal and lowland habitat) can reach and establish on remote islands, and species characterised by high dispersability and particular habitat affinities or ecological plasticity tend to be phylogenetically clustered (Carlquist 1965, 1966, Simberloff 1970, Gillespie and Roderick 2002). This idea forms the basis of the classical ‘island disharmony’ hypothesis first formulated by Joseph Hooker in 1866 (Williamson 1984), which predicts that only a subset of the higher-level taxa present on continents will be represented on islands. Island disharmony should therefore increase with increasing isolation of an island from continental source areas. Second, due to their small area, habitat diversity on islands is lower than in comparable biogeographic units on continents (Whittaker and Fernández-Palacios 2007). Since closely related species tend to have similar ecological requirements, island species are more likely to be phylogenetically clustered than expected by chance (Simberloff 1970, Webb et al. 2002, Emerson and Gillespie 2008).

Contrary to these two factors, however, both of which would tend to cause phylogenetic clustering, it has been argued that a low habitat diversity could make island biota more harmonic than in continental areas, i.e. species should be distributed evenly across higher taxa, especially genera (Grant 1966, Simberloff 1970). The reason for this is that competitive interactions would prevent closely related species from coexisting in a restricted, homogeneous environment (Elton 1946). Indeed, the relative importance of habitat filtering (second proposition) and competitive exclusion (third proposition) in determining the phylogenetic structure of biotic communities is a topic of great current interest in ecology and biogeography (e.g. Webb et al. 2002, Silvertown et al. 2006, Emerson and Gillespie 2008).

Low habitat diversity might also reduce opportunities for geographic or environmental isolation as a basis for allopatric speciation (Losos and Ricklefs 2009), and therefore hinder adaptive radiations. However, prolific adaptive radiation from a few colonizing species has often been observed on islands and often contributes substantially to total species richness on islands (Gillespie and Roderick 2002, Whittaker and Fernández-Palacios 2007, Losos and Ricklefs 2009). The importance of this *in situ* speciation relative to colonization is expected to increase with island isolation (Emerson and Gillespie 2008). Since *in situ* radiation is often associated with a few taxa, however, it is likely to cause increasing disharmony in the flora. Indeed, it has been proposed that species richness within higher-level taxa is itself a driver of speciation (Emerson and Kolm 2005).

Despite the general importance of skewed taxonomic distributions for understanding biodiversity patterns and macroevolution, there has to our knowledge never been a large-scale analysis of taxonomic disharmony across many islands worldwide. In this study we used taxonomic information from over 100 islands or island groups (and several 100 geographic regions on continents for comparison) to investigate phylogenetic patterns among flowering plants. To characterise these patterns we used five types of metric: (i) numbers of families (F) and genera (G), (ii) species-to-family and species-to-genus ratios (S/F, S/G), (iii) Gini coefficients, based upon the distribution of species within higher-level taxa, (iv) dominance, as represented by the proportion of species in the largest families or genera, and (v) disparity, as represented by the proportion of monospecific families or genera. Using these metrics, we investigated whether island floras differ in their phylogenetic structure from continental floras, and from null models generated by assembling plant species randomly from the global dataset.

To investigate how taxonomic disharmony is influenced by different geographical and ecological attributes of islands, we tested the following specific hypotheses:

(1) *Species richness:* A relationship between the disharmony of an island flora and flora size can be expected through random assembly from continental source floras alone due to the taxonomic structure of continental floras (Simberloff 1970). Two alternative hypotheses about

how post-dispersal process might modulate this relationship between flora size and disharmony can be formulated. It might be expected that large floras are more harmonic than small floras because niche complementarity tends to favour speciation in species-poorer genera or families. Alternatively, it has been proposed that species diversity within a taxonomic group can drive further speciation (Emerson and Kolm 2005), and therefore large floras might be characterised by few very species-rich genera or families formed through adaptive radiation.

(2) *Isolation:* more isolated islands are likely to have a more disharmonic flora because of a more pronounced dispersal filter, especially at higher taxonomic levels (families) (Carlquist 1965, 1966). And this initial disharmony might be accentuated on isolated islands if *in situ* speciation is relatively more important than dispersal assembly, especially at lower taxonomic level (species within genera).

(3) *Area and elevation*: larger and/or higher islands have higher habitat diversity (Kreft et al. 2008). This could lead either to an increase or decrease in taxonomic harmony (see above), especially at lower taxonomic levels (genera).

(4) *Endemism*: If adaptive radiation is important in shaping the taxonomic structure of island floras, we would expect to find disharmony reflected in the level of endemism, since the proportion of endemic species in the flora is a measure of *in situ* speciation (Emerson and Kolm 2005). We would also expect this proportion to be higher on isolated, large and old islands (Emerson and Gillespie 2008, Whittaker et al. 2008).

(5) *Latitude*: We would expect a more disharmonic taxonomic pattern towards high latitudes (Cook 1969, Krug et al. 2007), because the number of phylogenetic lineages decreases towards higher latitudes and therefore a flora of a certain size would be composed of fewer genera and families.

# Method

## Species lists

### *Global dataset*

We derived the ‘global dataset’ for 21 flowering plant families from lists of native species in the Kew World Checklist of selected plant families (WCSP, 2013), supplemented with data for Asteraceae from the Global Compositae Checklist (Flann, 2009) and for Leguminosae from the ILDIS World Database of Legumes (Roskov *et al*., 2005). We restricted the analysis to 23 families (Appendix 1) for reasons of data quality (we included only data from families for which review of the data was completed) and global comparability (all selected families have a global distribution and are represented on islands in all major oceanic regions). However, we checked how well the data for 23 families reflected variation in the total floras of islands, using data for 32 island groups for which we had complete species lists. We found the number of species in the 23 focal families was highly correlated with the total number of flowering plant species on these island groups ($R^2 = 0.997$).

Species lists were generated for most botanical countries as defined by level 3 of the World Geographical Scheme for Recording Plant Distributions of Biodiversity Information Standards (TDWG) (Brummitt *et al*., 2001; hereafter ‘TDWG level 3’). This resulted in a sample of 118 island datasets, with islands being defined as landmasses smaller than Australia surrounded by an ocean, and 242 species lists for continental regions for comparison (Figure 1). We included all native (indigenous or endemic species) species but did not differentiate between subspecies.

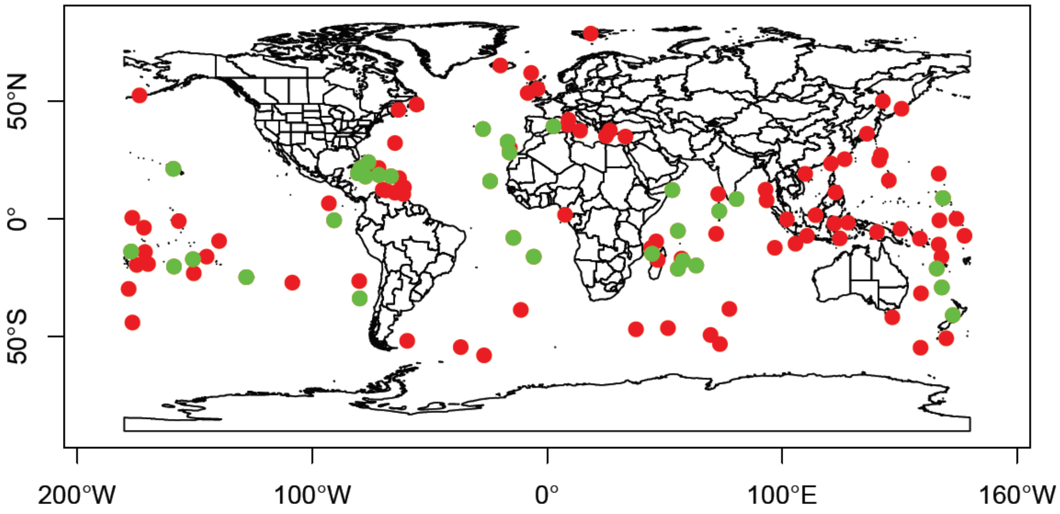

**Figure 1:** Geographical location of 118 islands or island groups (indicated by red dots) and 242 continental regions (areas delineated on map) included in the study. 32 islands for which independent floristic data was used for comparison are indicated in green ('focal islands'). For more information see Appendix 2.

The resulting dataset includes 164'711 species from 360 botanical countries, of which 47'546 species are native to one of the 118 islands. For a full list of regions included in the analyses (and an explanation of some minor adaptations of TDWG level 3 definitions of botanical countries) see Appendix 2. As expected from well-known species-area relationships, the log-transformed species richness of the 23 focal families across all 360 botanical countries was well predicted by the long-transformed area ($R^2$ = 0.60***, z = 0.38, c = 7.46 for all regions, and $R^2$ = 0.63***, z = 0.49, c = 3.06 for islands only), further supporting the validity of our data.

### *Cross-validation with complete country-level species lists*

For cross-validation of the global dataset we compiled lists of all flowering plant families on 32 islands (‘focal islands’, see Appendix 3) using the most up-to-date taxonomic treatments available. We used these local data to cross-validate the global dataset by comparing different metrics of disharmony (see below for definitions) in two different ways at both the generic and family levels. First, for 32 focal islands for which data were available, we compared the disharmony metrics across 23 families obtained using the global and local datasets. This comparison was used to test whether differences in data quality between the global and local sources might have affected our analyses. Second, we compared disharmony measures for the 23 focal families and all families present on the 32 focal islands. To avoid problems from differing numbers of species, we used rarefaction to make the two datasets comparable, i.e. from the flora including all families randomly the number of species represented in the 23 focal families was selected for 10’000 runs and then geometric mean values of disharmony measures were calculated. Because no major differences between datasets were found in either of the two analyses (Appendix 4), all analyses presented in this study are based on the global dataset. However, we present all disharmony measures and regression analyses for the 32 focal islands – both for the 23 focal families and all flowering plant families – in Appendix 3.

## Characteristics of islands and botanical regions

We investigated the relationships between taxonomic disharmony and eight attributes describing the islands: area, elevation range (from lowest to highest elevation, which is the same as maximal elevation for islands), isolation (from nearest continent), latitude, number of islands, island type (oceanic, continental, atoll, mixed), and endemism and species richness for the 23 focal families (Appendix 2). For comparison between islands and continents, we also compiled data for area, elevation range, latitude, endemism and species richness for the 23 families for all continental botanical countries.

We calculated the area of islands in ArcGIS using TDWG level 3 ArcView shapefiles (http://www.kew.org/science-research-data/kew-in-depth/gis/resources-and publications/data/tdwg/index.htm, accessed on June 1th, 2013). We extracted the minimum and maximum elevations for all TDWG level 3 polygons from the 30 arc-seconds altitude grid data provided by WorldClim (http://www.worldclim.org/, accessed on June 6th, 2013). Isolation was defined as the closest distance between the coastline of the island of the archipelago nearest to a continent and the coastline of this continent and was extracted from Weigelt and Kreft (Weigelt and Kreft 2013) where available, or else it was determined with ArcGIS based on TDWG level 3 maps. For latitude, we used the absolute value of the latitude of the centroid of the island group or botanic country. Island types were classified as ‘continental’ (either on continental landmass or continental fragments such as Seychelles), ‘volcanic’ or ‘atoll’, using Gillespie (2009) as the main source, and in a few cases the UNEP island directory (http://islands.unep.ch/isldir.htm, accessed on April 1th, 2013). A category of ‘mixed’ was used for island groups such as Fiji that include several different island types. We used three categories to represent the number of islands: A (1-2 islands), B (2-10 islands), C (> 10 islands) by including islands with an area greater than 1 km$^2$. For species richness and endemism, we used the total number of species in the 23 focal families, and the proportion of endemic species in this total. To analyse the correlation among these 8 island attributes we used pairwise Pearson correlation coefficients. In particular, area was significantly positively correlated with elevation and decreased with increasing isolation, i.e. larger islands tend to be higher and less isolated (Appendix 5).

## Data analyses

We calculated five measures of taxonomic inequality (disharmony; below) which we used to investigate the following: (i) correlations among measures; (ii) differences between island floras, continental floras, and the null-model (generated) floras; and (iii) whether island characteristics predict differences in disharmony between islands. We described the taxonomic structures in terms of both the distribution of species among families (‘family level’) and the distribution of species among genera (‘generic level’).

### *Measures of disharmony*

The five types of metric used to characterise the taxonomic structure and disharmony of floras were:

(i) numbers of families (out of the 23 studied; F) and genera (G) present on an island.

(ii) species-to-family ratio (S/F) and (ii) species-to-genus ratio (S/G). These ratios are widely used in biogeography (e.g. Simberloff 1970, Jarvinen 1982, Gotelli and Colwell 2001, Krug et al. 2007); they describe how many families or genera are represented in a flora with a certain species richness, and are therefore closely related to F or G. However, they do not necessarily reflect the skewedness of taxonomic distributions, since the same values could in principle be obtained with both even and uneven distributions of species across genera or family.

(iii) The Gini coefficient, based upon the distribution of species within families and genera. This index is widely used in economics to describe the skewedness of wealth distribution, but has also been applied in macroecology (Damgaard and Weiner 2000) and biodiversity studies (Lozano et al. 2010). It is calculated as the deviation of an observed cumulative distribution curve from a line that represents equal distribution. The Gini coefficient varies from 0 (perfect equality, i.e. observed cumulative distribution curve is a line; in other words every group – such as a genus or family – includes the same number of elements – such as species) to 1 (maximal skewedness, i.e. one genus or family includes all species). The Gini coefficient can be interpreted as a ‘‘relative mean difference,’’ i.e., the mean of the difference between every possible pair of groups (families or genera), divided by the mean size (number of species) (Damgaard and Weiner 2000).

(iv) Dominance index. This index characterises the contribution of the most species-rich genera/families to disharmony. Sometimes the most species-rich family (or genus) is used to calculated dominance (e.g. Scotland and Sanderson 2004). Here we defined dominant families / genera as those with a species number of at least twice the median of the other families / genera in a particular flora. We calculated dominance as the ratio of species that are in a dominant genera or families divided by the total species richness. It gives an indication of the importance of very species-rich groups, e.g. those that experienced adaptive radiation, for total species richness.

(v) Disparity index. This was defined as the proportion of monospecific genera or families (i.e. those with only one species) to the total number of genera or families. It gives an indication of the number of genera or families that colonised only once and did not speciate (since the last extinction event).

### *Null model simulations*

To test whether the floras of islands and continental regions differ in composition from random assemblages of plant species we performed null-model simulations. This was done by randomly selecting a specified number of plant species from a source flora and calculating the various disharmony metrics for this sample. By repeating the process 10,000 times, we could obtain the geometric means and the 97.5 and 2.5 percentile confidence intervals for the various metrics, and compare these values with those for a flora of the same size. We used three different source floras: the 23 focal families from (1) the global flora, (2) the subtropical and tropical flora, and (3) a separate regional flora for each island derived from the nearest continents, but no significant differences were found between these null models and therefore the global species pool was used for all analyses (Appendix 6). Null model simulations were performed in R (R Development Core Team 2012).

### *Regression analyses*

To understand the differences in disharmony among geographic regions, we run different multivariate regression analyses with glm in R (R Development Core Team 2012). We performed these analyses both at a generic and family level and for all five disharmony measures separately. S/F ratios and F were log-transformed before analysis. Among explanatory variables, we log-transformed species richness and area and used absolute values for latitude. Model selection based on AIC was used to select the most parsimonious model. We run two separate analyses with the complete and island dataset, respectively:

(1) With the complete dataset (both islands and continental regions) we used island/continent, area, elevation, latitude, and species richness to (i) test whether disharmony on islands differs from continental floras, (ii) investigate the effect of flora size on disharmony, and (iii) explore the effect of some of the most important biogeographical determinants of species richness (area, elevation as a proxy of habitat diversity, and latitude) on disharmony.

(2) For the island datasets, we also included isolation, endemism, island type, and number of islands to (i) test whether more isolated islands are more disharmonic than less isolated ones, and (ii) investigate the effect of different island characteristics on disharmony. Endemism was included as a proxy for speciation, while island type and number of islands were included because they are both known to affect speciation processes on islands (Losos and Ricklefs 2009).

# Results

## *Relationships between different measures of disharmony*

Correlations amongst the parameters used to describe the various floras were similar at a family and generic level (Figure 2 and Appendix 7). As expected, the ratios of total species numbers to numbers of families (S/F) and genera (S/G) were correlated with the values for F and G, although relatively weakly in the case of G. The relationships between S/F and S/G and the Gini coefficient were non-linear, with the Gini coefficient levelling off at c. 0.6 while values S/F and S/G continued to increase. Dominance was highly correlated with Gini but less so with S/F and S/G ratios (or F and G). At a family level, dominance ranged between 40-90%, independently of F. At a genus level, G and dominance varied widely and independently, except that low dominance was never found in combination with high G. At a family level, disparity was related to S/F but not to Gini, while at a family level there was a strong correlation between disparity and Gini.

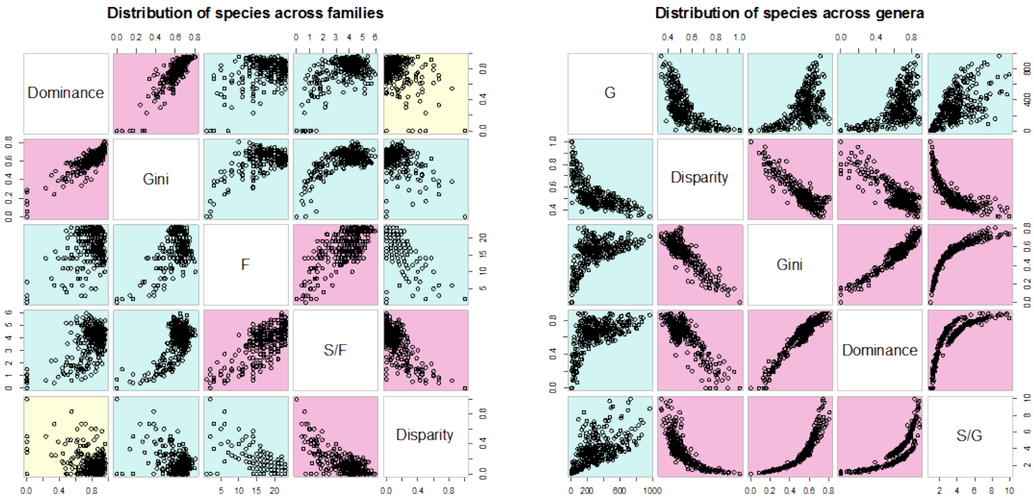

**Figure 2:** Correlations between different measures of disharmony: number of present families (F, out of a total of 23 families) or genera (G), species-to-family (S/F) viz. species-to-genus (S/G) ratio, Gini coefficients, dominance, disparity. The analyses are based on data from 118 islands and 242 continental areas. Colors indicate strength of correlations with highest correlations closest to the diagonal indicated by red color (correlation coefficients ≥ 0.7), followed by turquoise (0.4 ≤ correlation coefficients < 0.7), and yellow (correlation coefficients < 0.4). The left panel shows data for family level and the right one for generic level. For more information see Appendix 7.

### *The relationship between disharmony and size of flora*

All measures of taxonomic distribution varied strongly with the size of a flora (Figure 3 and 4), with large floras tending to be more disharmonic than small ones both at a family and generic level. Thus, large floras included on average more species per family, had a higher Gini coefficient, more species concentrated in the species-richest groups (dominance), and fewer monospecific families and genera (disparity). At a family level, patterns in Gini, dominance and disparity were driven by a very rapid accumulation of families (Figure 3), with F increasing rapidly in very small floras and then levelling off; thereafter species were added to existing families, which increased the S/F ratio. Once all families are present, at a flora size of some 200 species (for the 23 families studied), only S/F changes further with flora size, while Gini, dominance, and disparity remain relatively constant. Thus, while in small floras most species are in different families, and there are very few if any families that are substantially more species-rich than others, in large floras monospecific families are the exception and some families contribute very substantially to the overall species richness (Figure 3). At a generic level, patterns are similar but more gradual, and monospecific genera remain frequent (Figure 4), accounting for some 40% of genera even in the largest floras. Interestingly, both Gini coefficients – at c. 0.6 – and dominance – at c. 80-90% - level off at about the same values at both family and generic levels.

Comparisons with null model simulations indicated that relationships between disharmony measures and flora size follow some patterns predicted by the random assembly of species from the global flora (Figure 3 & 4). However, there were also important differences, which were consistent at both family and generic level: thus, island floras had lower values of F and G than simulated floras of the same size, Gini-coefficients and dominance values were higher and – especially at a generic level – disparity values were lower. These findings indicate that species on islands were distributed among fewer families and genera, and were more concentrated in particular families or genera, with monotypic families or genera being less frequent than in the global flora as a whole.

Several authors have shown that the relationship between G or F and flora size can be described by a power law (Willis and Yule 1922, Enquist et al. 2002). We found a strong fit for a regression between log (G) or log (F) and log (flora size) ($R^2$: 0.694 – 0.999, $P < 0.001$, see Appendix 8). However, a power law overestimates G or F at very large flora sizes (Appendix 8). The exponents of the power law function ranged for G between 0.715-0.973 and for F between 0.189-0.636 depending on model assumptions (Appendix 8).

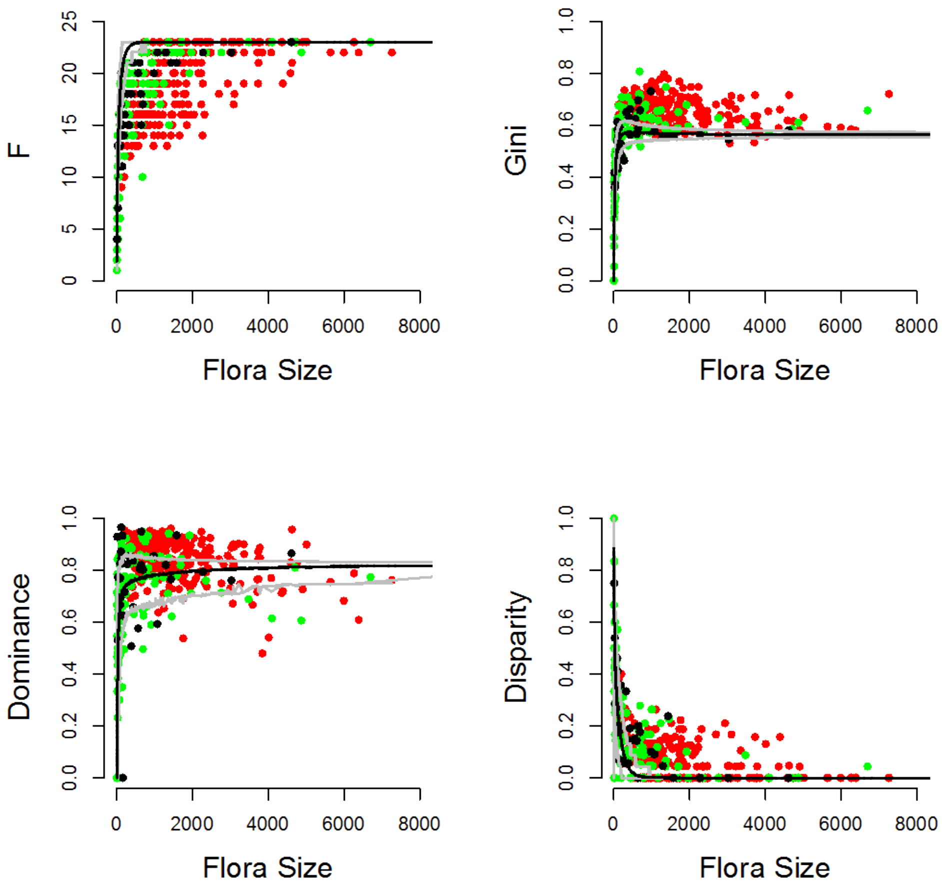

**Figure 3:** Different measures of taxonomic disharmony as a function of size of flora (total species number in 23 focal families) at a family level. Data is shown for islands (green dots), continental areas (red dots), 32 focal islands (total species number in 23 focal families, black dots), and simulated data generated through random sampling from the global flora (black line: geometric mean; grey lines: 95% of simulations).

### *Are islands more disharmonic than continents?*

The same analyses performed for continental floras showed that these were also more disharmonic than would be expected through random assembly from the global flora (Fig 3 &

4). Thus, like the island floras, these also had lower values of F and G, and higher Gini coefficients and dominance values than the null models predicted.

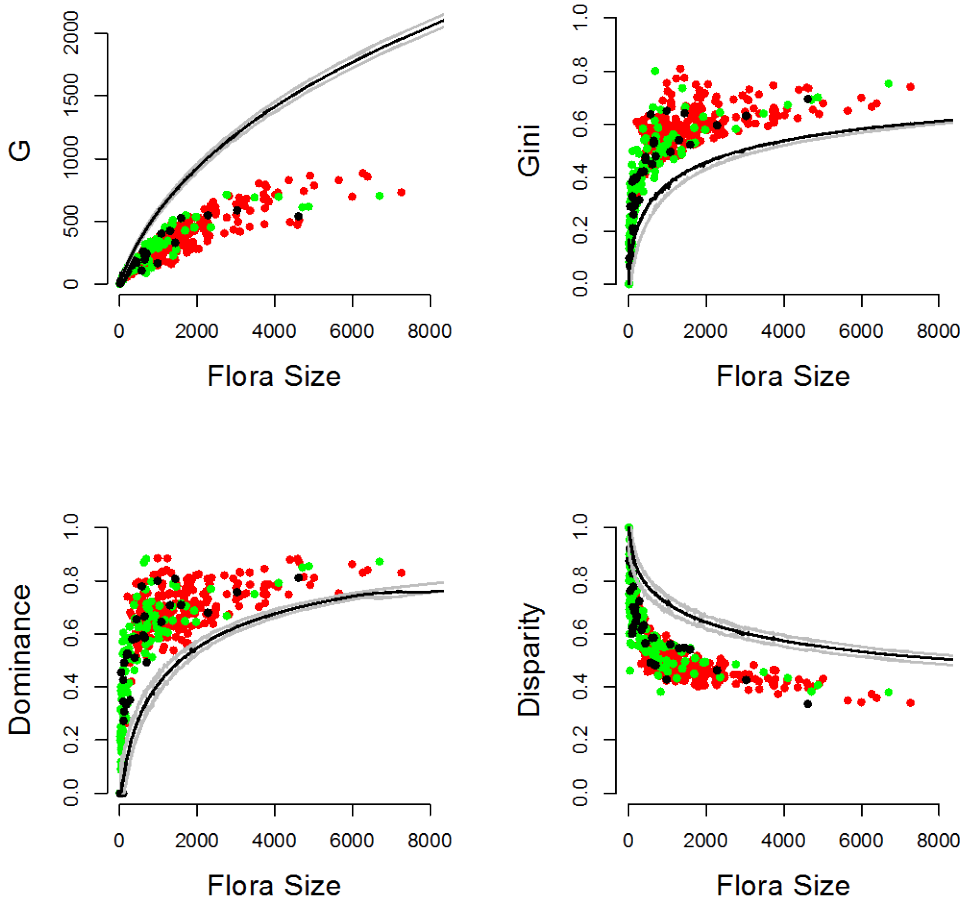

**Figure 4:** Different measures of taxonomic disharmony as a function of size of flora (total species number in 23 focal families) at a generic level. Data is shown for islands (green), continental areas (red), and 32 focal islands (total species number in 23 focal families, black) and simulated data generated through random sampling from the global flora (black line: geometric mean; grey lines: 95% of simulations).

To test whether islands differ in the degree of disharmony from continental regions, we performed multiple regression analyses using a combined dataset (islands and continents) containing several important biogeographical factors (island/continent, area, elevation, latitude, and species richness both at a family level and generic level; Table 1 & 2). Species richness was the strongest predictor of taxonomic disharmony for all disharmony measures, both for island flora and continental flora, followed by area and latitude: floras with larger areas and at high latitudes were more disharmonic both at generic and family levels. After accounting for these three significant factors, we found no other significant differences for any measure of disharmony between islands and continents at a family level. At a generic level, however, we also found lower dominance and higher disparity in island compared with continental floras (Table 2).

**Table 1:** Multivariate regression models with different measures of disharmony as dependent variable and different island characteristics as predictors. The analysis was performed for island floras and the combined data (islands and continents) at a family level. F: number of families, S: number of species, S/F: species-to-family ratio. The natural logarithm was used for log-transformations. Significance: ***P < 0.001; **P < 0.01; *P < 0.1.

| Island floras | | Combined data | |
|---|---|---|---|
| Retained terms | Parameters | Retained terms | Parameters |
| **F** | $R^2 = 0.92$ | **F** | $R^2 = 0.92$ |
| Log(S) | 0.90*** | Log(S) | 0.83*** |
| Log(S)$^2$ | -0.06*** | Log(S)$^2$ | -0.05*** |
| abs(Latitude) | -0.008*** | Log(Area) | -0.02*** |
| | | abs(Latitude) | -0.01*** |
| | | | |
| **S/F** | $R^2 = 0.98$ | **S/F** | $R^2 = 0.99$ |
| Log(S) | 0.10*** | Log(S) | 0.17*** |
| Log(S)$^2$ | 0.06*** | Log(S)$^2$ | 0.05*** |
| abs(Latitude) | 0.01*** | Log(Area) | 0.02*** |
| | | abs(Latitude) | 0.01*** |
| | | | |
| **Gini** | $R^2 = 0.80$ | **Gini** | $R^2 = 0.80$ |
| Log(S) | 0.20*** | Log(S) | 0.22*** |
| Log(S)$^2$ | -0.014*** | Log(S)$^2$ | -0.02*** |
| Endemism | -0.08* | abs(Latitude) | 0.01*** |
| | | Island/Continent | -0.03*** |
| | | | |
| **Dominance** | $R^2 = 0.60$ | **Dominance** | $R^2 = 0.65$ |
| Log(S) | 0.30*** | Log(S) | 0.31*** |
| Log(S)$^2$ | -0.03*** | Log(S)$^2$ | -0.02*** |
| Log(Area) | 0.003*** | Log(Area) | 0.01*** |
| | | | |
| **Disparity** | $R^2 = 0.46$ | **Disparity** | $R^2 = 0.53$ |
| Log(S) | -0.07*** | Log(S) | -0.11*** |
| | | | 0.004 |

### *Why do some island floras have more skewed taxonomic distributions than others?*

We investigated the factors influencing the level of disharmony on islands using multiple regression. At both the generic and family levels, and for all disharmony measures, species richness was the strongest predictor. Size of the flora explained between 81% (Gini-coefficient) and 90% (S/F) of variation at a family level, and between 82% (Gini-coefficient) and 92% (S/G) of variation at a generic level. The second most important predictor was latitude; with floras at high latitudes being more disharmonic both at a generic and family level than those at lower latitudes. No significant effect of isolation from nearest continent was found on any disharmony measures and at both taxonomic levels. Island type and number of islands also never had a significant effect. The factors area, elevation range and endemism varied in their influence according to the taxonomic level of analysis. At a family level, Gini was positively correlated with elevation, and dominance with island area, while endemism had no significant effect upon any measure. At a generic level, endemism was significantly related to all measures of disharmony, positively for Gini, S/G and dominance and negatively for G and disparity.

**Table 2:** Multivariate regression models with different measures of disharmony as dependent variable and different island characteristics as predictors. The analysis was performed for island floras and the combined data (islands and continents) at a generic level. G: number of genera, S: number of species, S/G: species-to-genus ratio. The natural logarithm was used for log-transformations. Significance: ***P < 0.001; **P < 0.01; *P < 0.1.

| Island floras | | Combined data | |
|---|---|---|---|
| Retained terms | Parameters | Retained terms | Parameters |
| **G** | $R^2 = 0.99$ | **G** | $R^2 = 0.98$ |
| Log(S) | 0.86*** | Log(S) | 1.10*** |
| $\text{Log}(S)^2$ | -0.005*** | $\text{Log}(S)^2$ | 0.04*** |
| abs(Latitude) | -0.008*** | abs(Latitude) | 0.01*** |
| Endemism | -0.50*** | | |
| | | | |
| **S/G** | $R^2 = 0.90$ | **S/G** | $R^2 = 0.91$ |
| $\text{Log}(S)^2$ | 0.02*** | Log(S) | -0.10*** |
| Log(Area) | 0.004*** | $\text{Log}(S)^2$ | 0.04*** |
| abs(Latitude) | 0.005*** | abs(Latitude) | 0.01*** |
| Endemism | 0.51*** | | |
| | | | |
| **Gini** | $R^2 = 0.91$ | **Gini** | $R^2 = 0.91$ |
| Log(S) | 0.10*** | Log(S) | 0.08*** |
| $\text{Log}(S)^2$ | -0.005** | Log(Area) | 0.008*** |
| Log(Area) | 0.02*** | abs(Latitude) | 0.003*** |
| abs(Latitude) | 0.002*** | | |
| Endemism | 0.12*** | | |
| | | | |
| **Dominance** | $R^2 = 0.89$ | **Dominance** | $R^2 = 0.87$ |
| Log(S) | 0.16*** | Log(S) | 0.15*** |
| $\text{Log}(S)^2$ | -0.01*** | $\text{Log}(S)^2$ | -0.005*** |
| Log(Area) | 0.04*** | Log(Area) | 0.02*** |
| Endemism | 0.12* | abs(Latitude) | 0.002*** |
| | | Island/Continent | 0.05*** |
| | | | |
| **Disparity** | $R^2 = 0.76$ | **Disparity** | $R^2 = 0.84$ |

| | | | |
|---|---|---|---|
| $Log(S)^2$ | -0.006*** | Log(S) | -0.005*** |
| abs(Latitude) | -0.002*** | abs(Latitude) | -0.002*** |
| Endemism | -0.11** | Island/Continent | 0.03** |

### *Why do some island floras have more skewed taxonomic distributions than others?*

We investigated the factors influencing the level of disharmony on islands using multiple regression. At both the generic and family levels, and for all disharmony measures, species richness was the strongest predictor. Size of the flora explained between 81% (Gini-coefficient) and 90% (S/F) of variation at a family level, and between 82% (Gini-coefficient) and 92% (S/G) of variation at a generic level. The second most important predictor was latitude; with floras at high latitudes being more disharmonic both at a generic and family level than those at lower latitudes. No significant effect of isolation from nearest continent was found on any disharmony measures and at both taxonomic levels. Island type and number of islands also never had a significant effect. The factors area, elevation range and endemism varied in their influence according to the taxonomic level of analysis. At a family level, Gini was positively correlated with elevation, and dominance with island area, while endemism had no significant effect upon any measure. At a generic level, endemism was significantly related to all measures of disharmony, positively for Gini, S/G and dominance and negatively for G and disparity.

## Discussion

In a classic paper, Willis and Yule (1922) showed that the distribution of species among higher taxonomic groups (genera or families) is highly skewed, with most species being concentrated in relatively few taxa. Since then, the reasons for such uneven taxonomic distributions have been widely discussed (e.g. Hairston 1965, Dial and Marzluff 1989, Scotland and Sanderson 2004). However, the work presented here represents the most comprehensive study of the factors influencing floristic disharmony on islands.

In assembling our global dataset, we took several precautions to minimise errors associate with variable data quality. First, we used the global standardized database hosted by Kew Botanic Gardens (WCSP, 2013) to minimize the risk of our results being affected by nomenclatural problems. Second, we focused on 23 families that have been particularly well-studied. Third, we cross-validated our global data with recent floristic lists from 32 islands or island archipelagos, and obtained good correspondence between the two datasets. Finally, although our dataset also covered all continents, we focused on island floras because islands represent due to their geographic isolation independent samples of regional biotas; and taxonomic patterns on islands have been particularly intensively discussed under the heading of “island disharmony” in the past (Carlquist 1965, 1966, McArthur and Wilson 1967, Simberloff 1970, Whittaker and Fernández-Palacios 2007).

### *How does the size of a flora affect taxonomic disharmony?*

As theory predicts, all measures of taxonomic structure and disharmony were strongly influenced by the size of a flora (Simberloff 1970, Gotelli and Colwell 2001, Enquist et al. 2002, Reed and Hughes 2002). In small floras, there was a very steep relationship between species richness and number of higher-level taxa, which levelled off in larger floras. For example, in floras of < 50 species (in the 23 families studied) almost every species was from a different genus, and almost every second species from a different family (Fig 3 & 4). In contrast, in floras with > 3000 species, the number of genera was almost independent of flora size, both for the global dataset (for 23 families) and for the 32 focal islands (including all families; Appendix 8).

The analyses for the ratios species-to-genus and species-to-family confirm that these scale with species richness, and that observed floras have higher ratios than those generated through null model simulations (e.g. Simberloff 1970, Gotelli and Colwell 2001). However, while these ratios are highly correlated with other aspects of the taxonomic structure of floras at small flora size, they represent patterns in large floras poorly (Fig 2), which limits their usefulness for biodiversity analyses. In particular, estimates of species richness based on genus or family number – often used in an applied context (e.g. Gaston and Williams 1993) – are unreliable in large floras where species richness varies independently of genus or family diversity.

The relationship between genus or family size and species richness has been described by a power law (Willis and Yule 1922, Enquist et al. 2002, Reed and Hughes 2002). However, a power law function did not adequately capture the patterns in our data, but overestimated number of genera or families in large floras (Appendix 8). As we discuss below, a possible explanation for this pattern is that the processes important for driving species diversity on islands shift as the flora grows larger. Interestingly, the exponents of power functions for the island floras were lower – indicating a high level phylogenetic clustering – than those reported by Enquist et al. (2002), who used a similar approach to investigate the phylogenetic structure of local tree communities across several biogeographical zones (even after constraining our data to floras of less than 300 species like in Enquist et al. 2002). One possible reason for this difference is that their data were collected at the community scale, and competitive interactions amongst species may have reduced the degree phylogenetic clustering (e.g. Webb et al. 2002, Silvertown et al. 2006, Emerson and Gillespie 2008).

### *Comparisons with null models*

Our data on dominance and Gini-coefficients hint at a possible explanation for the phylogenetic clustering of island floras compared to randomly assembled floras. Both of these values are substantially higher in observed than simulated floras, which is evidence that a higher than expected proportion of species are concentrated in a few taxa. The most plausible explanation is that speciation on islands occurs mainly in species-rich genera and families. In this respect, the patterns at a generic level are particularly revealing, since the emergence of new genera and multiple colonization from the same genus are both events that occur very rarely (for Canary Islands and Hawaii, Lozano et al. 2010).

This interpretation is supported by the many well-known examples of adaptive radiation on islands (Carlquist 1965, Gillespie and Roderick 2002, Whittaker and Fernández-Palacios 2007, Losos and Ricklefs 2009), and is consistent with the idea that species richness can drive speciation (Emerson and Kolm 2005). Indeed, on some islands the proportion of the flora belonging to a few species-rich genera and families may exceed 80% (Fig. 3 & 4).

### *Which factors explain taxonomic disharmony?*

It has long been debated whether species are clustered in fewer genera and families on islands compared to continents (Elton 1946, Carlquist 1965, 1966, Grant 1966, McArthur and Wilson 1967, Simberloff 1970, Williamson 1984, Whittaker and Fernández-Palacios 2007). In particular, it has been hypothesised that there should be fewer genera and families given a certain flora size on islands than continents (Carlquist 1965, 1966); although it has also been argued that competition in small and ecologically homogeneous islands should lead to a phylogenetic over-dispersion of species across higher taxa (Elton 1946, Grant 1966). Once differences in flora size had been taken into account, we found little evidence for any difference in the taxonomic structure of island floras compared to those of the mainland (Fig 3 & 4). The only exceptions were minor differences in dominance and disparity at the generic level, with islands having slightly lower dominance and higher disparity values (Table 1).

There was also no evidence that isolation affects disharmony (Table 1), with islands several 1000 km away from the nearest continent being no different from islands a few 100 km away. Thus, the geographical attributes of islands seem to have much less influence upon the phylogenetic structure of floras than had previously been supposed. In particular, dispersal limitation seems to play a relatively minor role for the overall taxonomic structure of island biotas, at least for flowering plants. Even very small island floras of some 30 species already harbour about two thirds of the 23 families we studied (Fig. 3), and this is also the case for very isolated islands such the Society or Hawaiian islands. The data from the 32 focal islands with complete floras confirm this pattern: the Society islands for instance are 5400 km from the nearest continent but include over 100 flowering plant families.

Two other factors - latitude and the area of islands – also had some influence upon disharmony. As other authors have shown, we found that the number of genera and families declined with latitude on both islands and continents (Cook 1969, Krug et al. 2007), while disharmony increased. Lastly, we found that area (or in one case elevation) of an island was positively related to species-to-genus and species-to-family ratios, Gini coefficients and dominance (both at a generic and family level), although these effects were weak (Table 1). This seems to indicate that higher habitat diversity (correlated with area / elevation) allows for more diverse species-rich genera and families, either because habitat diversity facilitates allopatric speciation (Losos and Ricklefs 2009) and/or attenuates competitive exclusion of closely related species (Elton 1946, Grant 1966).

## Conclusions

We documented very general patterns of how phylogenetic diversity of regional floras – as described by the distribution of species across genera and families – varies with flora size. Our results strongly suggest that the main driver of species richness shifts from colonization in small floras to *in situ* adaptive radiation in larger floras. Whereas small floras are formed by a rapid accumulation of different genera and families, additional richness in large floras is mostly associated with *in situ* speciation concentrated within a few genera and families; which increases disharmony. Unexpectedly, the observed patterns did not differ greatly between islands and continents, which suggests that dispersal limitation has less influence upon the phylogenetic structure of island biota than previously thought, while adaptive radiation may be equally important on continents. Thus, islands floras are not necessarily more disharmonic than continental ones. Indeed, smaller island floras tend to be phylogenetically very diverse, which provides another argument for protecting them.

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# Supporting Information

**Appendix 1: Plant families:** Plant families included in the study. Data sources are: Asteraceae (Global Compositae Checklist: http://compositae.landcareresearch.co.nz/), Fabaceae (ILDIS World Database of Legumes: http://www.ildis.org/), all other families (Kew World Checklist of Selected Plant Families: http://apps.kew.org/wcsp/home.do).

For comparison, number of species and genera in the global flora are also presented from the Plant List (http://www.theplantlist.org/).

| **Family** | **Number of species (and genera), Plant List** | **Number of species (and genera), this study** |
|---|---|---|
| *Amaryllidaceae* | 2164 (79) | 2242 (86) |
| *Apocynaceae* | 5031 (402) | 1788 (175) |
| *Araceae* | 3174 (113) | 3366 (137) |
| *Araliaceae* | 1505 (46) | 1441 (45) |
| *Arecaceae* | 2466 (187) | 2567 (195) |
| *Asparagaceae* | 3632 (143) | 2944 (131) |
| *Asteraceae* | 23000 (1620) | 23046 (1368) |
| *Begoniaceae* | 1529 (2) | 1586 (2) |
| *Campanulaceae* | 2374 (88) | 2366 (89) |
| *Cyperaceae* | 5732 (113) | 5822 (139) |
| *Euphorbiaceae* | 6511 (229) | 6563 (267) |
| *Fabaceae* | 19400 (730) | 14232 (657) |
| *Iridaceae* | 2182 (80) | 2270 (73) |
| *Lamiaceae* | 7852 (250) | 7858 (267) |
| *Myrtaceae* | 5774 (144) | 5932 (161) |
| *Orchidaceae* | 27135 (925) | 27806 (902) |
| *Pandanaceae* | 1048 (4) | 996 (4) |
| *Phyllanthaceae* | 2099 (58) | 2126 (92) |
| *Poaceae* | 11461 (777) | 9758 (744) |
| *Rubiaceae* | 13548 (617) | 13565 (603) |
| *Sapotaceae* | 1271 (58) | 1339 (71) |
| *Verbenaceae* | 1071 (34) | 973 (39) |
| *Zingiberaceae* | 1548 (50) | 1649 (58) |

**<u>Appendix 2: Botanical areas:</u>** Islands and continental areas included in the analyses. The list corresponds to all TDWG ('World Geographical Scheme for Recording Plant Distributions of Biodiversity Information Standards') 'level 3' botanical countries except for some minor adaptations: 1) a number of areas were excluded: Antarctic and Greenland (ice cover), Caroline Island, Mexican Pacific Island, South China Sea and Tokelau-Manihiki (geographically too widely distributed groups of islands), Marcus I. and Bouvet I. (no species records). 2) Norfolk Island was separated into two islands: Norfolk (NRK) and Lord Howe (LH). 3) Dominican Republic and Haiti were combined into Hispaniola, and New Zealand North and New Zealand South into New Zealand.

| **Abbr.** | **Island** | **Continental/ Island** | **Area (km$^2$)** | **Elevation range (m)** | **Isolation (km)** | **Latitude** | **Number of Islands** | **Island Type** | **Species Richness (of 23 families)** | **Endemism (of 23 families)** |
|---|---|---|---|---|---|---|---|---|---|---|
| AFG | Afghanistan | Continent | 641921.21 | 6347 | NA | 34.94 | NA | NA | 2232 | 0.21 |
| ALA | Alabama | Continent | 134424.81 | 689 | NA | 32.03 | NA | NA | 1292 | 0.00 |
| ASK | Alaska | Continent | 1497892.95 | 6098 | NA | 59.81 | NA | NA | 517 | 0.02 |
| ALB | Albania | Continent | 28676.35 | 2462 | NA | 41.09 | NA | NA | 1667 | 0.01 |
| ABT | Alberta | Continent | 663485.79 | 3346 | NA | 52.74 | NA | NA | 603 | 0.00 |
| ALD | Aldabra | Island | 183.07 | 11 | 626.20 | -9.47 | A | Atoll | 88 | 0.18 |
| ALU | Aleutian Is. | Island | 12624.53 | 1972 | 32.00 | 52.56 | C | Volcanic | 78 | 0.00 |
| ALG | Algeria | Continent | 2317502.79 | 2700 | NA | 31.42 | NA | NA | 1779 | 0.04 |
| ALT | Altay | Continent | 263328.87 | 4113 | NA | 51.65 | NA | NA | 971 | 0.02 |
| ASP | Amsterdam-St.Paul Is | Island | 72.00 | 821 | 3370.50 | -38.17 | A | Volcanic | 9 | 0.44 |
| AMU | Amur | Continent | 361578.67 | 2286 | NA | 53.39 | NA | NA | 520 | 0.01 |
| AND | Andaman Is. | Island | 5935.85 | 718 | 293.00 | 12.49 | B | Mix | 656 | 0.11 |
| ANG | Angola | Continent | 1240507.83 | 2542 | NA | -11.76 | NA | NA | 3025 | 0.16 |
| ATP | Antipodean Is. | Island | 860.96 | 583 | 2662.95 | -50.65 | A | Volcanic | 70 | 0.06 |

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|---|---|---|---|---|---|---|---|---|---|---|
| AGE | Argentina Northeast | Continent | 1122740.84 | 2672 | NA | -32.09 | NA | NA | 1935 | 0.07 |
| AGW | Argentina Northwest | Continent | 873300.09 | 6685 | NA | -30.08 | NA | NA | 1753 | 0.14 |
| AGS | Argentina South | Continent | 785015.40 | 4658 | NA | -45.56 | NA | NA | 675 | 0.10 |
| ARI | Arizona | Continent | 294228.88 | 3684 | NA | 34.48 | NA | NA | 1615 | 0.03 |
| ARK | Arkansas | Continent | 137545.63 | 814 | NA | 34.85 | NA | NA | 1024 | 0.00 |
| ARU | Aruba | Island | 206.40 | 129 | 27.04 | 12.52 | A | Volcanic | 88 | 0.02 |
| ASC | Ascension | Island | 98.42 | 768 | 1536.58 | -7.94 | A | Volcanic | 14 | 0.29 |
| ASS | Assam | Continent | 171289.61 | 3302 | NA | 24.84 | NA | NA | 2409 | 0.07 |
| AUT | Austria | Continent | 84132.93 | 3439 | NA | 47.62 | NA | NA | 1960 | 0.02 |
| AZO | Azores | Island | 2102.12 | 2259 | 1370.04 | 38.27 | B | Volcanic | 246 | 0.07 |
| BAH | Bahamas | Island | 12812.50 | 51 | 150.00 | 24.19 | C | Atoll | 378 | 0.15 |
| BAL | Baleares | Island | 5101.61 | 1212 | 88.00 | 39.41 | B | Continental | 833 | 0.05 |
| BLT | Baltic States | Continent | 189207.67 | 290 | NA | 56.97 | NA | NA | 1102 | 0.03 |
| BAN | Bangladesh | Continent | 138820.43 | 936 | NA | 23.06 | NA | NA | 1338 | 0.01 |
| BLR | Belarus | Continent | 207723.12 | 338 | NA | 53.44 | NA | NA | 915 | 0.00 |
| BGM | Belgium | Continent | 33224.35 | 692 | NA | 50.71 | NA | NA | 1108 | 0.00 |
| BLZ | Belize | Continent | 22141.49 | 1072 | NA | 17.49 | NA | NA | 1445 | 0.01 |
| BEN | Benin | Continent | 116173.07 | 667 | NA | 9.55 | NA | NA | 1011 | 0.01 |
| BER | Bermuda | Island | 40.25 | 43 | 1056.04 | 32.32 | A | Atoll | 64 | 0.03 |
| BIS | Bismarck Archipelago | Island | 48922.83 | 2153 | 760.72 | -4.15 | B | Volcanic | 705 | 0.22 |
| BOL | Bolivia | Continent | 1086526.14 | 6253 | NA | -16.02 | NA | NA | 3708 | 0.24 |
| BOR | Borneo | Island | 740169.23 | 3920 | 510.30 | 1.68 | A | Continental | 4874 | 0.55 |
| BOT | Botswana | Continent | 578326.36 | 975 | NA | -22.68 | NA | NA | 1095 | 0.01 |
| BZN | Brazil North | Continent | 3832660.70 | 2521 | NA | -2.94 | NA | NA | 3845 | 0.17 |

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|---|---|---|---|---|---|---|---|---|---|---|
| BZE | Brazil Northeast | Continent | 1544347.53 | 1876 | NA | -8.50 | NA | NA | 3061 | 0.30 |
| BZS | Brazil South | Continent | 564661.96 | 1768 | NA | -28.05 | NA | NA | 3362 | 0.21 |
| BZL | Brazil Southeast | Continent | 924175.89 | 2703 | NA | -20.34 | NA | NA | 5994 | 0.43 |
| BZC | Brazil West-Central | Continent | 1608040.53 | 1548 | NA | -16.14 | NA | NA | 2762 | 0.18 |
| BRC | British Columbia | Continent | 946776.24 | 3577 | NA | 52.26 | NA | NA | 815 | 0.00 |
| BUL | Bulgaria | Continent | 111006.43 | 2738 | NA | 42.81 | NA | NA | 1890 | 0.02 |
| BKN | Burkina | Continent | 272332.00 | 566 | NA | 11.91 | NA | NA | 813 | 0.00 |
| BUR | Burundi | Continent | 27181.49 | 2092 | NA | -3.13 | NA | NA | 1459 | 0.02 |
| BRY | Buryatiya | Continent | 352355.15 | 2900 | NA | 53.25 | NA | NA | 523 | 0.02 |
| CAB | Cabinda | Continent | 6981.70 | 838 | NA | -4.93 | NA | NA | 367 | 0.05 |
| CAL | California | Continent | 407748.23 | 4239 | NA | 36.13 | NA | NA | 2229 | 0.14 |
| CBD | Cambodia | Continent | 182007.41 | 1740 | NA | 12.44 | NA | NA | 1246 | 0.05 |
| CMN | Cameroon | Continent | 464799.01 | 3902 | NA | 6.64 | NA | NA | 3261 | 0.11 |
| CNY | Canary Is. | Island | 7521.19 | 3450 | 96.54 | 28.29 | B | Volcanic | 696 | 0.20 |
| CPP | Cape Provinces | Continent | 661493.54 | 2946 | NA | -30.66 | NA | NA | 4585 | 0.51 |
| CVI | Cape Verde | Island | 3525.22 | 2517 | 570.69 | 16.12 | B | Volcanic | 234 | 0.11 |
| CPV | Caprivi Strip | Continent | 20091.20 | 167 | NA | -17.94 | NA | NA | 188 | 0.00 |
| CAY | Cayman Is. | Island | 306.41 | 42 | 491.73 | 19.51 | A | Atoll | 166 | 0.07 |
| CAF | Central African Repu | Continent | 618574.22 | 1033 | NA | 6.23 | NA | NA | 1643 | 0.03 |
| CPI | Central American Pac | Island | 31.82 | 2 | 490.98 | 6.71 | A | Atoll | 32 | 0.25 |
| RUC | Central European Rus | Continent | 852832.67 | 367 | NA | 54.73 | NA | NA | 951 | 0.00 |
| CHA | Chad | Continent | 1271863.79 | 3241 | NA | 12.17 | NA | NA | 931 | 0.02 |
| CGS | Chagos Archipelago | Island | 104.45 | 10 | 1590.00 | -6.26 | B | Atoll | 9 | 0.00 |

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|---|---|---|---|---|---|---|---|---|---|---|
| CTM | Chatham Is. | Island | 705.40 | 285 | 2800.00 | -43.93 | A | Volcanic | 97 | 0.10 |
| CLC | Chile Central | Continent | 186455.30 | 6071 | NA | -34.83 | NA | NA | 943 | 0.30 |
| CLN | Chile North | Continent | 259595.38 | 6669 | NA | -23.68 | NA | NA | 435 | 0.12 |
| CLS | Chile South | Continent | 299467.43 | 3826 | NA | -49.40 | NA | NA | 426 | 0.07 |
| CHN | China North-Central | Continent | 1110306.18 | 5514 | NA | 37.28 | NA | NA | 1816 | 0.08 |
| CHC | China South-Central | Continent | 1307943.27 | 6243 | NA | 28.66 | NA | NA | 6261 | 0.31 |
| CHS | China Southeast | Continent | 1425192.76 | 2220 | NA | 27.31 | NA | NA | 3745 | 0.22 |
| CTA | Chita | Continent | 431835.07 | 2532 | NA | 53.41 | NA | NA | 488 | 0.01 |
| XMS | Christmas I. | Island | 123.98 | 317 | 953.00 | -10.45 | A | Atoll | 59 | 0.10 |
| CKI | Cocos (Keeling) Is. | Island | 28.74 | 15 | 1624.94 | -12.18 | A | Atoll | 26 | 0.00 |
| CLM | Colombia | Continent | 1135623.58 | 5452 | NA | 4.53 | NA | NA | 8480 | 0.32 |
| COL | Colorado | Continent | 270183.18 | 3302 | NA | 38.37 | NA | NA | 1198 | 0.01 |
| COM | Comoros | Island | 2173.54 | 2322 | 295.00 | -12.24 | B | Volcanic | 327 | 0.25 |
| CON | Congo | Continent | 344043.36 | 911 | NA | -1.17 | NA | NA | 1719 | 0.02 |
| CNT | Connecticut | Continent | 12843.47 | 687 | NA | 41.42 | NA | NA | 723 | 0.00 |
| COO | Cook Is. | Island | 201.04 | 402 | 4741.41 | -20.14 | B | Mix | 100 | 0.19 |
| COR | Corse | Island | 8782.86 | 2404 | 82.38 | 42.17 | A | Continental | 1144 | 0.01 |
| COS | Costa Rica | Continent | 51063.82 | 3732 | NA | 9.63 | NA | NA | 4078 | 0.18 |
| CRZ | Crozet Is. | Island | 353.58 | 892 | 2411.44 | -46.30 | B | Volcanic | 5 | 0.00 |
| CUB | Cuba | Island | 109977.02 | 1748 | 197.36 | 21.71 | A | Continental | 2353 | 0.53 |
| CYP | Cyprus | Island | 9258.51 | 1879 | 68.63 | 35.06 | A | Continental | 808 | 0.06 |
| CZE | Czechoslovakia | Continent | 127687.64 | 2347 | NA | 49.32 | NA | NA | 1765 | 0.01 |
| DEL | Delaware | Continent | 5069.51 | 136 | NA | 39.17 | NA | NA | 673 | 0.00 |
| DEN | Denmark | Continent | 42959.61 | 164 | NA | 55.83 | NA | NA | 1001 | 0.00 |

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|---|---|---|---|---|---|---|---|---|---|---|
| DSV | Desventurados Is. | Island | 6.00 | 330 | 893.29 | -26.30 | A | Volcanic | 6 | 0.17 |
| WDC | District of Columbia | Continent | 159.99 | 122 | NA | 38.89 | NA | NA | 484 | 0.00 |
| DJI | Djibouti | Continent | 21434.22 | 1840 | NA | 11.73 | NA | NA | 265 | 0.01 |
| EAI | East Aegean Is. | Island | 5596.34 | 1407 | 4.74 | 37.71 | C | Continental | 1004 | 0.03 |
| RUE | East European Russia | Continent | 735790.31 | 1588 | NA | 55.43 | NA | NA | 705 | 0.01 |
| EHM | East Himalaya | Continent | 132216.89 | 6858 | NA | 27.78 | NA | NA | 2822 | 0.07 |
| EAS | Easter Is. | Island | 189.00 | 467 | 3512.74 | -26.98 | A | Volcanic | 19 | 0.16 |
| ECU | Ecuador | Continent | 247904.63 | 6169 | NA | -1.69 | NA | NA | 7262 | 0.40 |
| EGY | Egypt | Continent | 926271.78 | 1929 | NA | 28.54 | NA | NA | 803 | 0.02 |
| ELS | El Salvador | Continent | 20585.16 | 2309 | NA | 13.77 | NA | NA | 1231 | 0.01 |
| EQG | Equatorial Guinea | Continent | 24894.03 | 1212 | NA | 1.55 | NA | NA | 642 | 0.02 |
| ERI | Eritrea | Continent | 121035.15 | 2955 | NA | 14.90 | NA | NA | 603 | 0.02 |
| ETH | Ethiopia | Continent | 1127530.04 | 4459 | NA | 9.49 | NA | NA | 2466 | 0.12 |
| FAL | Falkland Is. | Island | 11751.17 | 698 | 498.42 | -51.71 | A | Continental | 48 | 0.00 |
| FIJ | Fiji | Island | 19318.75 | 1197 | 2607.96 | -17.65 | C | Mix | 692 | 0.52 |
| FIN | Finland | Continent | 335929.59 | 1299 | NA | 63.64 | NA | NA | 1327 | 0.00 |
| FLA | Florida | Continent | 146581.84 | 108 | NA | 27.94 | NA | NA | 1529 | 0.06 |
| FOR | Foroyar | Island | 1599.57 | 881 | 327.00 | 62.10 | B | Continental | 207 | 0.00 |
| FRA | France | Continent | 539595.03 | 3907 | NA | 46.68 | NA | NA | 3106 | 0.05 |
| OFS | Free State | Continent | 129991.37 | 2112 | NA | -28.52 | NA | NA | 806 | 0.00 |
| FRG | French Guiana | Continent | 83625.65 | 819 | NA | 3.78 | NA | NA | 1754 | 0.05 |
| GAB | Gabon | Continent | 260691.97 | 1011 | NA | -0.95 | NA | NA | 2232 | 0.09 |
| GAL | Galapagos | Island | 7940.45 | 1685 | 927.69 | -0.50 | B | Volcanic | 146 | 0.34 |
| GAM | Gambia | Continent | 10715.64 | 58 | NA | 13.46 | NA | NA | 416 | 0.00 |

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|---|---|---|---|---|---|---|---|---|---|---|
| GEO | Georgia | Continent | 152470.21 | 1452 | NA | 32.23 | NA | NA | 1380 | 0.00 |
| GER | Germany | Continent | 357574.66 | 2679 | NA | 52.18 | NA | NA | 2038 | 0.01 |
| GHA | Ghana | Continent | 239032.52 | 882 | NA | 7.63 | NA | NA | 1668 | 0.01 |
| GIL | Gilbert Is. | Island | 448.91 | 12 | 3460.00 | 0.15 | C | Mix | 41 | 0.02 |
| GRB | Great Britain | Island | 231139.79 | 1293 | 30.00 | 55.34 | A | Continental | 1377 | 0.01 |
| GRC | Greece | Continent | 117547.72 | 2728 | NA | 38.60 | NA | NA | 2315 | 0.14 |
| GUA | Guatemala | Continent | 108992.42 | 4157 | NA | 15.30 | NA | NA | 3075 | 0.08 |
| GUI | Guinea | Continent | 245061.75 | 1578 | NA | 10.26 | NA | NA | 1448 | 0.03 |
| GNB | Guinea-Bissau | Continent | 33969.22 | 272 | NA | 11.65 | NA | NA | 727 | 0.00 |
| GGI | Gulf of Guinea Is. | Island | 3193.12 | 2867 | 35.75 | 1.82 | B | Volcanic | 775 | 0.14 |
| GST | Gulf States | Continent | 82411.04 | 1800 | NA | 24.98 | NA | NA | 302 | 0.01 |
| GUY | Guyana | Continent | 210679.85 | 2302 | NA | 4.87 | NA | NA | 2348 | 0.07 |
| CHH | Hainan | Island | 34026.08 | 1724 | 18.40 | 19.23 | A | Continental | 1367 | 0.13 |
| HAW | Hawaii | Island | 16871.77 | 4176 | 569.94 | 21.37 | A | Volcanic | 619 | 0.79 |
| HMD | Heard-McDonald Is. | Island | 402.62 | 2686 | 1500.00 | -53.08 | A | Volcanic | 2 | 0.00 |
| HIS | Hispaniola | Island | 75678.61 | 2967 | 4334.33 | 18.79 | A | Continental | 1686 | 0.30 |
| HON | Honduras | Continent | 112160.45 | 2752 | NA | 14.63 | NA | NA | 2371 | 0.03 |
| HBI | Howland-Baker Is. | Island | 4.92 | 5 | 3629.56 | 0.56 | B | Atoll | 3 | 0.33 |
| HUN | Hungary | Continent | 92988.74 | 978 | NA | 47.29 | NA | NA | 1435 | 0.01 |
| ICE | Iceland | Island | 102951.03 | 2005 | 971.83 | 65.28 | A | Volcanic | 678 | 0.00 |
| IDA | Idaho | Continent | 216450.67 | 3356 | NA | 45.26 | NA | NA | 929 | 0.01 |
| ILL | Illinois | Continent | 150173.83 | 310 | NA | 39.27 | NA | NA | 986 | 0.00 |
| IND | India | Continent | 2669437.16 | 2625 | NA | 21.52 | NA | NA | 3784 | 0.32 |
| INI | Indiana | Continent | 94754.01 | 280 | NA | 38.69 | NA | NA | 901 | 0.00 |

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|---|---|---|---|---|---|---|---|---|---|---|
| CHI | Inner Mongolia | Continent | 1202874.04 | 3361 | NA | 43.85 | NA | NA | 909 | 0.03 |
| IOW | Iowa | Continent | 145268.55 | 356 | NA | 42.13 | NA | NA | 721 | 0.00 |
| IRN | Iran | Continent | 1623445.19 | 5415 | NA | 32.72 | NA | NA | 3727 | 0.31 |
| IRQ | Iraq | Continent | 436280.87 | 3501 | NA | 34.32 | NA | NA | 1515 | 0.03 |
| IRE | Ireland | Island | 83999.78 | 909 | 400.00 | 53.59 | A | Continental | 666 | 0.00 |
| IRK | Irkutsk | Continent | 773705.68 | 2641 | NA | 58.32 | NA | NA | 704 | 0.01 |
| ITA | Italy | Continent | 250764.37 | 4498 | NA | 43.10 | NA | NA | 2931 | 0.05 |
| IVO | Ivory Coast | Continent | 321361.58 | 1345 | NA | 7.41 | NA | NA | 1847 | 0.02 |
| JAM | Jamaica | Island | 11038.59 | 2097 | 622.57 | 18.11 | A | Mix | 1026 | 0.31 |
| JAP | Japan | Island | 370584.27 | 3671 | 130.37 | 36.27 | A | Volcanic | 1920 | 0.18 |
| JAW | Jawa | Island | 130751.35 | 3455 | 823.88 | -7.09 | A | Volcanic | 2760 | 0.17 |
| JNF | Juan Fernandez Is. | Island | 151.65 | 505 | 601.63 | -33.68 | A | Volcanic | 62 | 0.47 |
| KAM | Kamchatka | Continent | 464214.66 | 4734 | NA | 59.46 | NA | NA | 345 | 0.03 |
| KAN | Kansas | Continent | 211983.19 | 1003 | NA | 38.90 | NA | NA | 859 | 0.00 |
| KAZ | Kazakhstan | Continent | 2723396.15 | 5983 | NA | 48.63 | NA | NA | 2262 | 0.10 |
| KZN | Kazan-retto | Island | 41.14 | 405 | 1570.00 | 25.04 | A | Volcanic | 48 | 0.08 |
| KTY | Kentucky | Continent | 104142.62 | 1221 | NA | 37.81 | NA | NA | 864 | 0.00 |
| KEN | Kenya | Continent | 581883.21 | 4725 | NA | 0.62 | NA | NA | 3082 | 0.07 |
| KEG | Kerguelen | Island | 7464.08 | 1791 | 1800.00 | -49.23 | A | Volcanic | 6 | 0.17 |
| KER | Kermadec Is. | Island | 50.06 | 392 | 2760.80 | -29.66 | A | Volcanic | 32 | 0.19 |
| KHA | Khabarovsk | Continent | 822718.45 | 2738 | NA | 54.54 | NA | NA | 568 | 0.01 |
| KGZ | Kirgizstan | Continent | 199585.06 | 6281 | NA | 41.09 | NA | NA | 1703 | 0.12 |
| KOR | Korea | Continent | 220273.37 | 2632 | NA | 37.34 | NA | NA | 1105 | 0.08 |
| KRA | Krasnoyarsk | Continent | 2388967.37 | 2832 | NA | 71.09 | NA | NA | 554 | 0.03 |

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|---|---|---|---|---|---|---|---|---|---|---|
| KRI | Kriti | Island | 8611.81 | 2336 | 93.30 | 35.33 | A | Continental | 1000 | 0.10 |
| KRY | Krym | Continent | 25627.44 | 1503 | NA | 45.45 | NA | NA | 1217 | 0.04 |
| KUR | Kuril Is. | Island | 10653.71 | 2153 | 11.12 | 46.88 | C | Volcanic | 396 | 0.05 |
| KUW | Kuwait | Continent | 16812.05 | 291 | NA | 29.53 | NA | NA | 125 | 0.00 |
| NAT | KwaZulu-Natal | Continent | 92726.63 | 3305 | NA | -28.97 | NA | NA | 1879 | 0.07 |
| LAB | Labrador | Continent | 287357.09 | 1572 | NA | 55.70 | NA | NA | 278 | 0.00 |
| LDV | Laccadive Is. | Island | 60.51 | 17 | 240.00 | 10.66 | C | Atoll | 36 | 0.00 |
| LAO | Laos | Continent | 229921.99 | 2776 | NA | 18.54 | NA | NA | 1753 | 0.06 |
| LBS | Lebanon-Syria | Continent | 198184.03 | 3007 | NA | 35.20 | NA | NA | 1763 | 0.05 |
| LEE | Leeward Is. | Island | 3415.55 | 1336 | 656.26 | 17.40 | C | Volcanic | 687 | 0.03 |
| LES | Lesotho | Continent | 30539.15 | 2037 | NA | -29.50 | NA | NA | 674 | 0.01 |
| LSI | Lesser Sunda Is. | Island | 105148.47 | 3339 | 700.00 | -8.19 | C | Continental | 1162 | 0.12 |
| LBR | Liberia | Continent | 96025.91 | 1265 | NA | 6.60 | NA | NA | 1056 | 0.03 |
| LBY | Libya | Continent | 1617602.65 | 2284 | NA | 30.04 | NA | NA | 875 | 0.04 |
| LIN | Line Is. | Island | 619.51 | 7 | 5238.66 | -0.84 | C | Atoll | 19 | 0.11 |
| LH | Lord Howe I. | Island | 14.55 | 260 | 570.361 | -31.55 | A | Volcanic | 96 | 0.45 |
| LOU | Louisiana | Continent | 119130.58 | 155 | NA | 30.31 | NA | NA | 1148 | 0.00 |
| MAQ | Macquarie Is. | Island | 128.29 | 328 | 1947.99 | -54.63 | A | Volcanic | 15 | 0.20 |
| MDG | Madagascar | Island | 592995.18 | 2744 | 415.03 | -17.36 | A | Continental | 4708 | 0.77 |
| MDR | Madeira | Island | 825.12 | 1755 | 641.17 | 32.86 | A | Volcanic | 328 | 0.12 |
| MAG | Magadan | Continent | 1179715.53 | 2262 | NA | 64.84 | NA | NA | 318 | 0.03 |
| MAI | Maine | Continent | 84027.46 | 1474 | NA | 44.76 | NA | NA | 701 | 0.00 |
| MLW | Malawi | Continent | 118524.53 | 2802 | NA | -12.90 | NA | NA | 2485 | 0.04 |
| MLY | Malaya | Continent | 132152.15 | 2058 | NA | 4.13 | NA | NA | 4012 | 0.24 |

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|---|---|---|---|---|---|---|---|---|---|---|
| MDV | Maldives | Island | 140.46 | 7 | 426.00 | 3.41 | C | Atoll | 41 | 0.00 |
| MLI | Mali | Continent | 1252272.57 | 1027 | NA | 14.23 | NA | NA | 961 | 0.01 |
| MOL | Maluku | Island | 59736.00 | 2854 | 811.88 | -1.52 | C | Continental | 1351 | 0.24 |
| CHM | Manchuria | Continent | 790256.88 | 2576 | NA | 46.18 | NA | NA | 1013 | 0.04 |
| MAN | Manitoba | Continent | 650499.33 | 823 | NA | 56.16 | NA | NA | 566 | 0.00 |
| MRN | Marianas | Island | 1192.59 | 774 | 2297.99 | 16.47 | C | Atoll | 206 | 0.20 |
| MPE | Marion-Prince Edward Is. | Island | 338.06 | 1161 | 1715.55 | -46.81 | A | Volcanic | 5 | 0.20 |
| MRQ | Marquesas | Island | 1086.53 | 1103 | 4762.02 | -9.29 | B | Volcanic | 114 | 0.56 |
| MRS | Marshall Is. | Island | 129.28 | 14 | 3265.07 | 8.93 | C | Atoll | 45 | 0.00 |
| MRY | Maryland | Continent | 25586.94 | 1004 | NA | 38.79 | NA | NA | 905 | 0.00 |
| MAS | Massachusetts | Continent | 21052.77 | 981 | NA | 41.97 | NA | NA | 823 | 0.00 |
| MTN | Mauritania | Continent | 1038464.98 | 892 | NA | 18.39 | NA | NA | 403 | 0.00 |
| MAU | Mauritius | Island | 2055.72 | 714 | 1745.58 | -16.77 | A | Volcanic | 482 | 0.29 |
| MXC | Mexico Central | Continent | 66276.11 | 5420 | NA | 19.31 | NA | NA | 1943 | 0.06 |
| MXG | Mexico Gulf | Continent | 71169.32 | 4786 | NA | 19.94 | NA | NA | 2022 | 0.05 |
| MXE | Mexico Northeast | Continent | 871043.49 | 3643 | NA | 23.94 | NA | NA | 3004 | 0.16 |
| MXN | Mexico Northwest | Continent | 382803.28 | 2838 | NA | 27.02 | NA | NA | 1666 | 0.13 |
| MXT | Mexico Southeast | Continent | 236552.07 | 3744 | NA | 18.86 | NA | NA | 2999 | 0.07 |
| MXS | Mexico Southwest | Continent | 329131.11 | 3998 | NA | 19.40 | NA | NA | 3741 | 0.22 |
| MIC | Michigan | Continent | 250766.26 | 441 | NA | 44.87 | NA | NA | 844 | 0.00 |
| MIN | Minnesota | Continent | 224991.51 | 494 | NA | 46.72 | NA | NA | 768 | 0.00 |
| MSI | Mississippi | Continent | 124059.74 | 214 | NA | 32.37 | NA | NA | 1096 | 0.00 |
| MSO | Missouri | Continent | 180416.14 | 486 | NA | 38.13 | NA | NA | 1025 | 0.00 |

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|---|---|---|---|---|---|---|---|---|---|---|
| MON | Mongolia | Continent | 1562956.54 | 3673 | NA | 48.24 | NA | NA | 1467 | 0.04 |
| MNT | Montana | Continent | 381000.52 | 3196 | NA | 46.13 | NA | NA | 914 | 0.00 |
| MOR | Morocco | Continent | 403295.31 | 4016 | NA | 32.03 | NA | NA | 2153 | 0.13 |
| MOZ | Mozambique | Continent | 786426.41 | 2277 | NA | -17.41 | NA | NA | 2348 | 0.05 |
| MCI | Mozambique Channel I | Island | 14.97 | 9 | 280.00 | -14.71 | A | Mix | 34 | 0.12 |
| MYA | Myanmar | Continent | 668128.21 | 5530 | NA | 18.07 | NA | NA | 3587 | 0.11 |
| NAM | Namibia | Continent | 804652.58 | 2458 | NA | -23.33 | NA | NA | 1491 | 0.13 |
| NNS | Nansei-shoto | Island | 2107.96 | 443 | 421.32 | 25.45 | B | Volcanic | 675 | 0.06 |
| NRU | Nauru | Island | 28.92 | 37 | 2857.12 | -0.53 | A | Atoll | 11 | 0.00 |
| NEB | Nebraska | Continent | 200155.61 | 1378 | NA | 41.61 | NA | NA | 715 | 0.00 |
| NEP | Nepal | Continent | 147199.06 | 6933 | NA | 28.17 | NA | NA | 2189 | 0.05 |
| NET | Netherlands | Continent | 35786.19 | 300 | NA | 52.19 | NA | NA | 1085 | 0.00 |
| NLA | Netherlands Antilles | Island | 792.22 | 188 | 80.00 | 12.19 | A | Volcanic | 156 | 0.03 |
| NEV | Nevada | Continent | 286612.06 | 3701 | NA | 38.34 | NA | NA | 1101 | 0.02 |
| NBR | New Brunswick | Continent | 72842.16 | 769 | NA | 46.50 | NA | NA | 442 | 0.00 |
| NWC | New Caledonia | Island | 19231.12 | 1504 | 1267.67 | -21.00 | B | Mix | 1453 | 0.77 |
| NWG | New Guinea | Island | 816427.27 | 4613 | 150.28 | -5.51 | A | Continental | 6698 | 0.70 |
| NWH | New Hampshire | Continent | 24202.01 | 1839 | NA | 43.96 | NA | NA | 620 | 0.00 |
| NWJ | New Jersey | Continent | 19835.85 | 508 | NA | 39.99 | NA | NA | 866 | 0.00 |
| NWM | New Mexico | Continent | 315095.94 | 3013 | NA | 34.23 | NA | NA | 1540 | 0.01 |
| NSW | New South Wales | Continent | 804762.03 | 2159 | NA | -32.48 | NA | NA | 3049 | 0.20 |
| NWY | New York | Continent | 137029.75 | 1484 | NA | 41.95 | NA | NA | 981 | 0.00 |
| NZ | New Zealand | Island | 267535.47 | 2943 | 1647.87 | -40.82 | A | Mix | 820 | 0.30 |

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|---|---|---|---|---|---|---|---|---|---|---|
| NFL | Newfoundland | Island | 112135.05 | 832 | 17.29 | 48.70 | A | Continental | 364 | 0.00 |
| NIC | Nicaragua | Continent | 128124.06 | 1754 | NA | 12.86 | NA | NA | 2339 | 0.02 |
| NCB | Nicobar Is. | Island | 1865.90 | 520 | 1300.00 | 7.99 | B | Mix | 380 | 0.09 |
| NGR | Niger | Continent | 1182011.38 | 1780 | NA | 15.29 | NA | NA | 547 | 0.00 |
| NGA | Nigeria | Continent | 908617.06 | 2381 | NA | 8.11 | NA | NA | 2465 | 0.02 |
| NUE | Niue | Island | 252.73 | 84 | 3840.00 | -19.06 | A | Atoll | 85 | 0.01 |
| NFK | Norfolk Is. | Island | 34.60 | 256 | 570.36 | -29.03 | A | Volcanic | 133 | 0.18 |
| NCA | North Carolina | Continent | 128191.23 | 1961 | NA | 35.37 | NA | NA | 1302 | 0.00 |
| NCS | North Caucasus | Continent | 253444.28 | 5488 | NA | 44.50 | NA | NA | 1728 | 0.07 |
| NDA | North Dakota | Continent | 182557.97 | 811 | NA | 47.10 | NA | NA | 528 | 0.00 |
| RUN | North European Russi | Continent | 1363303.53 | 1676 | NA | 65.49 | NA | NA | 980 | 0.04 |
| TVL | Northern Provinces | Continent | 335731.20 | 2176 | NA | -25.65 | NA | NA | 1928 | 0.10 |
| NTA | Northern Territory | Continent | 1348765.94 | 1327 | NA | -13.56 | NA | NA | 1791 | 0.18 |
| RUW | Northwest European R | Continent | 195195.18 | 303 | NA | 58.81 | NA | NA | 873 | 0.00 |
| NWT | Northwest Territorie | Continent | 1342568.46 | 2710 | NA | 71.71 | NA | NA | 363 | 0.00 |
| NOR | Norway | Continent | 321797.19 | 2292 | NA | 65.93 | NA | NA | 1224 | 0.00 |
| NSC | Nova Scotia | Continent | 55339.58 | 530 | NA | 45.22 | NA | NA | 416 | 0.00 |
| NUN | Nunavut | Continent | 2079791.01 | 2416 | NA | 70.20 | NA | NA | 200 | 0.01 |
| OGA | Ogasawara-shoto | Island | 76.54 | 374 | 1830.00 | 27.20 | B | Volcanic | 135 | 0.25 |
| OHI | Ohio | Continent | 116422.94 | 320 | NA | 39.37 | NA | NA | 862 | 0.00 |
| OKL | Oklahoma | Continent | 181138.68 | 1419 | NA | 34.94 | NA | NA | 1127 | 0.00 |
| OMA | Oman | Continent | 308800.35 | 2883 | NA | 21.86 | NA | NA | 485 | 0.05 |
| ONT | Ontario | Continent | 1076076.16 | 668 | NA | 49.69 | NA | NA | 871 | 0.00 |

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|---|---|---|---|---|---|---|---|---|---|---|
| ORE | Oregon | Continent | 251331.77 | 3169 | NA | 44.46 | NA | NA | 1206 | 0.02 |
| PAK | Pakistan | Continent | 795103.22 | 6836 | NA | 29.42 | NA | NA | 1762 | 0.04 |
| PAL | Palestine | Continent | 116178.39 | 1712 | NA | 31.94 | NA | NA | 1384 | 0.04 |
| PAN | Panama | Continent | 74530.64 | 3312 | NA | 8.39 | NA | NA | 3714 | 0.18 |
| PAR | Paraguay | Continent | 398816.88 | 725 | NA | -24.39 | NA | NA | 2087 | 0.09 |
| PEN | Pennsylvania | Continent | 119338.29 | 975 | NA | 40.94 | NA | NA | 912 | 0.00 |
| PER | Peru | Continent | 1290870.41 | 6547 | NA | -8.25 | NA | NA | 6386 | 0.31 |
| PHI | Philippines | Island | 294705.82 | 2804 | 944.17 | 11.33 | B | Volcanic | 4098 | 0.56 |
| PHX | Phoenix Is. | Island | 90.67 | 8 | 4374.49 | -3.64 | B | Atoll | 6 | 0.00 |
| PIT | Pitcairn Is. | Island | 53.64 | 191 | 5252.13 | -24.66 | A | Mix | 34 | 0.26 |
| POL | Poland | Continent | 311695.59 | 2220 | NA | 51.94 | NA | NA | 1730 | 0.00 |
| POR | Portugal | Continent | 88595.79 | 1960 | NA | 39.70 | NA | NA | 1358 | 0.03 |
| PRM | Primorye | Continent | 164936.79 | 1803 | NA | 45.28 | NA | NA | 753 | 0.04 |
| PEI | Prince Edward I. | Island | 5994.82 | 140 | 15.00 | 46.40 | A | Volcanic | 258 | 0.00 |
| PUE | Puerto Rico | Island | 9245.97 | 1239 | 702.02 | 18.20 | A | Continental | 942 | 0.10 |
| CHQ | Qinghai | Continent | 734155.14 | 4953 | NA | 35.45 | NA | NA | 761 | 0.07 |
| QUE | Quebec | Continent | 1513230.30 | 1454 | NA | 54.53 | NA | NA | 777 | 0.02 |
| QLD | Queensland | Continent | 1728796.25 | 1550 | NA | -19.75 | NA | NA | 3777 | 0.29 |
| REU | Reunion | Island | 2645.02 | 2930 | 1664.74 | -21.10 | A | Mix | 471 | 0.34 |
| RHO | Rhode I. | Continent | 2727.33 | 246 | NA | 41.60 | NA | NA | 564 | 0.00 |
| ROD | Rodrigues | Island | 116.49 | 346 | 2450.57 | -19.71 | A | Volcanic | 93 | 0.20 |
| ROM | Romania | Continent | 237375.26 | 2481 | NA | 45.62 | NA | NA | 1821 | 0.02 |
| RWA | Rwanda | Continent | 25142.85 | 3158 | NA | -2.11 | NA | NA | 1246 | 0.02 |
| SAK | Sakhalin | Island | 75450.80 | 1415 | 7.50 | 50.12 | A | Continental | 439 | 0.06 |
| SAM | Samoa | Island | 3172.18 | 1787 | 3918.01 | -13.98 | B | Volcanic | 353 | 0.30 |

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|---|---|---|---|---|---|---|---|---|---|---|
| SCZ | Santa Cruz Is. | Island | 851.75 | 753 | 2040.00 | -10.81 | B | Volcanic | 88 | 0.03 |
| SAR | Sardegna | Island | 24136.94 | 1812 | 184.26 | 40.00 | A | Continental | 968 | 0.04 |
| SAS | Saskatchewan | Continent | 651973.39 | 1180 | NA | 53.60 | NA | NA | 518 | 0.00 |
| SAU | Saudi Arabia | Continent | 1954760.72 | 2961 | NA | 23.30 | NA | NA | 876 | 0.03 |
| SEL | Selvagens | Island | 1.86 | 0 | 374.00 | 30.14 | A | Volcanic | 37 | 0.05 |
| SEN | Senegal | Continent | 196061.56 | 514 | NA | 13.91 | NA | NA | 1074 | 0.01 |
| SEY | Seychelles | Island | 328.50 | 757 | 640.00 | -4.99 | B | Continental | 207 | 0.18 |
| SIC | Sicilia | Island | 26047.95 | 3237 | 3.11 | 37.60 | A | Continental | 1239 | 0.05 |
| SIE | Sierra Leone | Continent | 72497.81 | 1675 | NA | 8.40 | NA | NA | 1390 | 0.02 |
| SIN | Sinai | Continent | 56690.01 | 2494 | NA | 29.94 | NA | NA | 526 | 0.02 |
| SCI | Society Is. | Island | 1529.71 | 1707 | 5884.29 | -17.04 | B | Mix | 237 | 0.48 |
| SOC | Socotra | Island | 3904.11 | 1439 | 232.73 | 12.36 | A | Continental | 280 | 0.34 |
| SOL | Solomon Is. | Island | 36875.41 | 2641 | 1625.00 | -8.28 | C | Volcanic | 909 | 0.23 |
| SOM | Somalia | Continent | 636286.83 | 2434 | NA | 7.83 | NA | NA | 1289 | 0.23 |
| SOA | South Australia | Continent | 983621.43 | 1375 | NA | -33.98 | NA | NA | 1537 | 0.13 |
| SCA | South Carolina | Continent | 80530.12 | 1010 | NA | 33.24 | NA | NA | 1211 | 0.00 |
| SDA | South Dakota | Continent | 198701.29 | 1892 | NA | 44.00 | NA | NA | 667 | 0.00 |
| RUS | South European Russi | Continent | 437005.81 | 371 | NA | 48.98 | NA | NA | 916 | 0.01 |
| SGE | South Georgia | Island | 3614.53 | 2758 | 1755.00 | -54.39 | A | Continental | 7 | 0.00 |
| SSA | South Sandwich Is. | Island | 279.08 | 1327 | 2322.00 | -57.88 | B | Volcanic | 2 | 0.00 |
| SWC | Southwest Caribbean | Continent | 355.67 | 295 | NA | 14.69 | NA | NA | 82 | 0.01 |
| SPA | Spain | Continent | 494020.72 | 3353 | NA | 40.57 | NA | NA | 3352 | 0.13 |
| SRL | Sri Lanka | Island | 66288.49 | 2406 | 53.82 | 8.54 | A | Continental | 1583 | 0.22 |

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|---|---|---|---|---|---|---|---|---|---|---|
| STH | St.Helena | Island | 133.03 | 718 | 1858.34 | -15.97 | A | Volcanic | 30 | 0.37 |
| SUD | Sudan | Continent | 2502428.17 | 3063 | NA | 11.61 | NA | NA | 1603 | 0.02 |
| SUL | Sulawesi | Island | 186001.80 | 3306 | 1090.62 | -1.92 | A | Mix | 1968 | 0.33 |
| SUM | Sumatera | Island | 470941.94 | 3605 | 65.09 | -0.13 | A | Continental | 3477 | 0.29 |
| SUR | Suriname | Continent | 145018.16 | 1111 | NA | 4.19 | NA | NA | 1735 | 0.03 |
| SVA | Svalbard | Island | 63032.49 | 2103 | 670.00 | 78.82 | A | Continental | 91 | 0.00 |
| SWZ | Swaziland | Continent | 17121.80 | 1747 | NA | -26.58 | NA | NA | 1143 | 0.02 |
| SWE | Sweden | Continent | 446397.56 | 1955 | NA | 61.16 | NA | NA | 1430 | 0.00 |
| SWI | Switzerland | Continent | 41507.46 | 4071 | NA | 46.81 | NA | NA | 1827 | 0.01 |
| TZK | Tadzhikistan | Continent | 142387.02 | 6660 | NA | 38.90 | NA | NA | 1849 | 0.23 |
| TAI | Taiwan | Island | 36163.74 | 3741 | 136.14 | 23.62 | A | Continental | 1705 | 0.18 |
| TAN | Tanzania | Continent | 941389.81 | 5768 | NA | -7.10 | NA | NA | 5008 | 0.16 |
| TAS | Tasmania | Island | 68502.12 | 1551 | 199.08 | -41.70 | A | Continental | 755 | 0.21 |
| TEN | Tennessee | Continent | 108936.98 | 1860 | NA | 35.79 | NA | NA | 1020 | 0.00 |
| TEX | Texas | Continent | 684964.51 | 2549 | NA | 29.95 | NA | NA | 2272 | 0.05 |
| THA | Thailand | Continent | 512815.29 | 2552 | NA | 12.71 | NA | NA | 4907 | 0.17 |
| CHT | Tibet | Continent | 1133790.84 | 6416 | NA | 31.54 | NA | NA | 2080 | 0.11 |
| TOG | Togo | Continent | 57125.83 | 941 | NA | 8.68 | NA | NA | 1137 | 0.01 |
| TON | Tonga | Island | 776.17 | 730 | 3393.29 | -19.44 | B | Mix | 198 | 0.06 |
| TCS | Transcaucasus | Continent | 185533.07 | 4769 | NA | 41.01 | NA | NA | 3087 | 0.11 |
| TRT | Trinidad-Tobago | Island | 5029.53 | 849 | 14.56 | 10.64 | A | Mix | 788 | 0.04 |
| TDC | Tristan da Cunha | Island | 170.94 | 1961 | 2770.36 | -38.57 | A | Volcanic | 31 | 0.61 |
| TUA | Tuamotu | Island | 288.23 | 86 | 5637.59 | -15.95 | C | Atoll | 45 | 0.16 |
| TUB | Tubuai Is. | Island | 98.86 | 343 | 5521.39 | -23.03 | B | Volcanic | 87 | 0.32 |

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|---|---|---|---|---|---|---|---|---|---|---|
| TUN | Tunisia | Continent | 155383.48 | 1444 | NA | 34.83 | NA | NA | 1113 | 0.01 |
| TUR | Turkey | Continent | 756176.32 | 4972 | NA | 38.79 | NA | NA | 4384 | 0.18 |
| TUE | Turkey-in-Europe | Continent | 23839.57 | 921 | NA | 41.08 | NA | NA | 1221 | 0.01 |
| TKM | Turkmenistan | Continent | 471714.24 | 2791 | NA | 39.51 | NA | NA | 1130 | 0.11 |
| TCI | Turks-Caicos Is. | Island | 420.14 | 25 | 895.00 | 21.73 | B | Atoll | 26 | 0.08 |
| TVA | Tuva | Continent | 169686.80 | 3341 | NA | 51.53 | NA | NA | 483 | 0.02 |
| TUV | Tuvalu | Island | 52.81 | 14 | 3190.00 | -7.08 | B | Atoll | 13 | 0.00 |
| UGA | Uganda | Continent | 242065.66 | 4077 | NA | 1.47 | NA | NA | 2369 | 0.01 |
| UKR | Ukraine | Continent | 605803.88 | 1968 | NA | 48.57 | NA | NA | 1774 | 0.03 |
| URU | Uruguay | Continent | 177842.59 | 458 | NA | -32.66 | NA | NA | 1097 | 0.07 |
| UTA | Utah | Continent | 219874.99 | 3342 | NA | 38.61 | NA | NA | 1231 | 0.03 |
| UZB | Uzbekistan | Continent | 446622.45 | 4316 | NA | 40.76 | NA | NA | 1660 | 0.08 |
| VAN | Vanuatu | Island | 12697.74 | 1698 | 1722.00 | -15.98 | C | Mix | 450 | 0.20 |
| VEN | Venezuela | Continent | 910220.31 | 4783 | NA | 7.66 | NA | NA | 5642 | 0.19 |
| VNA | Venezuelan Antilles | Island | 1401.40 | 801 | 10.00 | 11.23 | B | Mix | 220 | 0.01 |
| VER | Vermont | Continent | 24701.35 | 1196 | NA | 43.96 | NA | NA | 647 | 0.00 |
| VIC | Victoria | Continent | 227725.76 | 1907 | NA | -37.26 | NA | NA | 1834 | 0.10 |
| VIE | Vietnam | Continent | 325521.76 | 3004 | NA | 15.99 | NA | NA | 4354 | 0.21 |
| VRG | Virginia | Continent | 103919.20 | 1654 | NA | 37.64 | NA | NA | 1131 | 0.00 |
| WAK | Wake I. | Island | 19.53 | 5 | 4250.00 | 19.30 | A | Atoll | 5 | 0.00 |
| WAL | Wallis-Futuna Is. | Island | 166.35 | 383 | 3142.68 | -13.75 | A | Volcanic | 110 | 0.00 |
| WAS | Washington | Continent | 174437.68 | 4351 | NA | 47.46 | NA | NA | 964 | 0.02 |
| WHM | West Himalaya | Continent | 293725.75 | 6811 | NA | 33.58 | NA | NA | 2232 | 0.04 |
| WSB | West Siberia | Continent | 2564673.50 | 2141 | NA | 69.26 | NA | NA | 1089 | 0.01 |

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|---|---|---|---|---|---|---|---|---|---|---|
| WVA | West Virginia | Continent | 62521.13 | 1381 | NA | 38.70 | NA | NA | 717 | 0.00 |
| WAU | Western Australia | Continent | 2527726.87 | 1198 | NA | -22.94 | NA | NA | 4626 | 0.59 |
| WSA | Western Sahara | Continent | 268991.40 | 614 | NA | 24.24 | NA | NA | 141 | 0.01 |
| WIN | Windward Is. | Island | 3803.37 | 1314 | 137.42 | 13.50 | B | Volcanic | 671 | 0.06 |
| WIS | Wisconsin | Continent | 169707.82 | 403 | NA | 44.74 | NA | NA | 783 | 0.00 |
| WYO | Wyoming | Continent | 254381.29 | 3088 | NA | 44.00 | NA | NA | 968 | 0.01 |
| CHX | Xinjiang | Continent | 1631779.14 | 6999 | NA | 40.99 | NA | NA | 1476 | 0.07 |
| YAK | Yakutskiya | Continent | 3069765.15 | 2821 | NA | 68.52 | NA | NA | 570 | 0.06 |
| YEM | Yemen | Continent | 419969.87 | 3534 | NA | 14.48 | NA | NA | 784 | 0.06 |
| YUG | Yugoslavia | Continent | 255539.99 | 2623 | NA | 44.09 | NA | NA | 2698 | 0.04 |
| YUK | Yukon | Continent | 485330.17 | 5799 | NA | 64.84 | NA | NA | 398 | 0.00 |
| ZAI | Zaire | Continent | 2326813.33 | 4739 | NA | -3.71 | NA | NA | 4746 | 0.15 |
| ZAM | Zambia | Continent | 751901.56 | 1960 | NA | -12.58 | NA | NA | 3218 | 0.07 |
| ZIM | Zimbabwe | Continent | 389855.85 | 2366 | NA | -18.99 | NA | NA | 2451 | 0.04 |

**<u>Appendix 3: Focal islands:</u>** Local floristic data sources used for the 32 focal island groups.

| Island | Abbr. | Reference |
|---|---|---|
| Marquesas | MRQ | Wagner, W. L., D. R. Herbst, and D. H. Lorence 2005. Flora of the Marquesas Islands Website. http://botany.si.edu/pacificislandbiodiversity/marquesasflora/index.htm. Accessed August 2011. |
| Ascension | ASC | Ashmole, P. and M. Ashmole 2000. St Helena and Ascension Island: a natural history. Oswestry: Nelson. |
| Azores | AZO | José Maria Fernandez-Palacios (unpublished data) |
| Bahamas | BAH | Acevedo-Rodríguez, P. and M.T. Strong. 2007. Catalogue of the seed plants of the West Indies Website. http://persoon.si.edu/antilles/westindies/index.htm. Accessed March 2013. |
| Balearic | BAL | Anna Traveset (unpublished data) |
| Cayman | CAY | Acevedo-Rodríguez, P. and M.T. Strong. 2007. Catalogue of the seed plants of the West Indies Website. http://persoon.si.edu/antilles/westindies/index.htm. Accessed March 2013. |
| Canary | CNY | José Maria Fernandez-Palacios (unpublished data) |
| Cook | COO | Cook Islands Natural Heritage Trust, 2007. Cook Islands Biodiversity Database. http://cookislands.bishopmuseum.org/search.asp. Accessed August 2011. |
| Cuba | CUB | Acevedo-Rodríguez, P. and M.T. Strong. 2007. Catalogue of the seed plants of the West Indies Website. http://persoon.si.edu/antilles/westindies/index.htm. Accessed March 2013. |
| Cape Verde | CVI | José Maria Fernandez-Palacios (unpublished data) |
| Fiji | FIJ | Heads M. 2006. Seed plants of Fiji: an ecological analysis. Biological Journal of the Linnean Society 89: 407–431. |
| Galapagos | GAL | Jaramillo, P. et al. 2011. CDF Checklist of Galapagos Flowering Plants: http://www.darwinfoundation.org/datazone/checklists/vascular-plants/magnoliophyta/. Accessed November 2011. |
| Hawaii | HAI | Wagner ,W.L. et al. 2005. Flora of the Hawaiian Islands Website. http://botany.si.edu/pacificislandbiodiversity/hawaiianflora/. Accessed August 2011. |
| Hispaniola | HIS | Acevedo-Rodríguez, P. and M.T. Strong. 2007. Catalogue of the seed plants of the West Indies Website. http://persoon.si.edu/antilles/westindies/index.htm. Accessed March 2013. |
| Jamaica | JAM | Acevedo-Rodríguez, P. and M.T. Strong. 2007. Catalogue of the seed plants of the West Indies Website. http://persoon.si.edu/antilles/westindies/index.htm. Accessed March 2013. |
| Juan Fernandez Is. | JNF | Bernardello G., G.J. Anderson, T.F. Stuessy, D.J. Crawford 2001. A survey of floral traits, breeding systems, floral visitors, and pollination systems of the angiosperms of the Juan Fernández Islands (Chile). Botanical Review 67: 255–308. |
| Mauritius | MAU | Claudia Baider (unpublished data) |
| Madagascar | MDG | Madagascar Catalogue, 2012. Catalogue of the Vascular Plants of Madagascar. Missouri Botanical Garden, St. Louis, U.S.A. and Missouri Botanical Garden, Madagascar Research and Conservation Program, Antananarivo, Madagascar. Available at: http://www.efloras.org/madagascar. Accessed: November 2012. |
| Madeira | MDR | José Maria Fernandez-Palacios (unpublished data) |
| Norfolk | NFK | Flora of Australia Online: Norfolk and Lord Howe Islands is. Australian Biological Resources Study, Canberra. Viewed 27 November 2011. http://www.environment.gov.au/biodiversity/abrs/online-resources/flora/49/index.html. Accessed: November 2012. |
| New Caledonia | NWC | Our Knowledge of the Flora of New Caledonia: Endemism and Diversity in Relation to Vegetation Types and Substrates. Ph. Morat. Biodiversity Letters. Vol. 1, No. 3/4, New Caledonia: A Case Study in Biodiversity (May - Jul., 1993), pp. 72-81 |
| New Zealand | NZ | de Lange P.J., J.W.D. Sawyer, and J.R. Rolfe. 2010. New Zealand indigenous vascular plant checklist. Wellington, New Zealand Plant Conservation Network. |
| Pitcairn | PIT | Florence, J., S. Waldren, and A.J. Chepstow-Lusty 1995. The flora of the Pitcairn Islands: |

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| | | a review. In: The Pitcairn Islands: biogeography, ecology and prehistory, ed. by T.G. Benton & T. Spencer. London, Academic Press. |
| Puerto Rico | PUE | Acevedo-Rodríguez, P. and M.T. Strong. 2007. Catalogue of the seed plants of the West Indies Website. http://persoon.si.edu/antilles/westindies/index.htm. Accessed April 2013. |
| Réunion | REU | Cononservatoire Botanique National de. 2010. Accessible through http://flore.cbnm.org. Accessed November 2011. |
| Rodrigues | ROD | Strahm, W.A. 1989. Plant Red Data Book for Rodrigues. Königstein: Koeltz Scientific Books. |
| Society | SCI | Florence, J., H. Chevillotte, C. Ollier, and J.Y. Meyer. 2007. Base de données botaniques Nadeaud de l'Herbier de la Polynésie française (PAP). Published on the internet; http://www.herbier-tahiti.pf. Accessed June 2011. |
| Seychelles | SEY | Robertson, S. A. 1989. Flowering Plants of Seychelles. Kew: Royal Botanic Gardens. Friedmann, F. 1994. Flore des Seychelles: Dicotylédones. Paris: Ostrom. |
| Socotra | SOC | Mies, B.A. 2001. Flora und Vegetationsökologie der Insel Soqotra. Essener Ökologische Schriften, 15. Westarp-Wiss: Hohenwarsleben. |
| Sri Lanka | SRI | Senaratna, L.K. 2001. A Check List of the Flowering Plants of Sri Lanka, National Science Foundation of Sri Lanka, Colombo. An Annotated Checklist of the Orchids of Sri Lanka. Samantha Suranjan Fernando and Paul Ormerod. |
| St. Helena | STH | Ashmole, P. and M. Ashmole. 2000. St Helena and Ascension Island: a natural history. Oswestry: Nelson. |
| Wallis-Futuna Is. | WAL | Morat, Ph. and J.M. Veillon. 1985. Contribution à la connaissance de la végétation et de la flore de Wallis & Futuna. Adansonia 3: 259-329. |

## Appendix 4: Local validation:

Data from 32 focal islands with complete flowering plant lists ('local') was used for cross-validation. We present disharmony measures at a family level for different datasets in Table 1, and correlations between datasets in Table 2 and Figure 1; and at a generic level in Table 3 (and correlations between datasets in Table 4 and Figure 2).

**Table 1:** Disharmony measures at a family level for the 23 focal islands from the global species list (main dataset for this study, 'Global', '23'), and analyses based on local dataset (data from 32 focal islands with complete flowering plant lists, 'local') for comparison. Local analyses were done for the 23 focal families and for all families using rarefaction ('All', see main text for explanation).

| **Dataset** | **No. Families** | **Island** | **Abbr.** | **No. Species** | **Disharmony measures** | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | **F** | **S/F** | **Gini** | **Dominance** | **Disparity** |
| Global | 23 | Ascension | ASC | 14 | 5 | 2.80 | 0.40 | 0.79 | 0.60 |
| Global | 23 | Azores | AZO | 246 | 16 | 15.38 | 0.64 | 0.92 | 0.31 |
| Global | 23 | Bahamas | BAH | 378 | 19 | 19.89 | 0.52 | 0.74 | 0.11 |
| Global | 23 | Balearic | BAL | 833 | 18 | 46.28 | 0.68 | 0.81 | 0.17 |
| Global | 23 | Cayman Is. | CAY | 166 | 18 | 9.22 | 0.47 | 0.66 | 0.06 |
| Global | 23 | Canary Is. | CNY | 696 | 18 | 38.67 | 0.71 | 0.92 | 0.28 |
| Global | 23 | Cook Is. | COO | 100 | 16 | 6.25 | 0.53 | 0.74 | 0.25 |
| Global | 23 | Cuba | CUB | 2353 | 22 | 106.95 | 0.57 | 0.76 | 0.00 |
| Global | 23 | Cape Verde | CVI | 234 | 16 | 14.63 | 0.67 | 0.92 | 0.25 |
| Global | 23 | Fiji | FIJ | 692 | 20 | 34.60 | 0.58 | 0.50 | 0.15 |
| Global | 23 | Galapagos | GAL | 146 | 16 | 9.13 | 0.49 | 0.35 | 0.25 |
| Global | 23 | Hawaii | HAW | 619 | 20 | 30.95 | 0.64 | 0.86 | 0.10 |
| Global | 23 | Hispaniola | HIS | 1686 | 22 | 76.64 | 0.59 | 0.82 | 0.00 |
| Global | 23 | Jamaica | JAM | 1026 | 22 | 46.64 | 0.58 | 0.77 | 0.05 |
| Global | 23 | Juan Fernandez Is. | JNF | 62 | 12 | 5.17 | 0.55 | 0.85 | 0.50 |
| Global | 23 | Mauritius | MAU | 482 | 21 | 22.95 | 0.56 | 0.77 | 0.10 |
| Global | 23 | Madagascar | MDG | 4708 | 23 | 204.70 | 0.59 | 0.81 | 0.00 |
| Global | 23 | Madeira | MDR | 328 | 16 | 20.50 | 0.63 | 0.82 | 0.25 |
| Global | 23 | Marquesas | MRQ | 114 | 16 | 7.13 | 0.54 | 0.75 | 0.13 |
| Global | 23 | Norfolk Is. | NFK | 133 | 15 | 8.87 | 0.67 | 0.89 | 0.27 |
| Global | 23 | New Caledonia | NWC | 1453 | 22 | 66.05 | 0.58 | 0.62 | 0.23 |
| Global | 23 | New Zealand | NZ | 820 | 19 | 43.16 | 0.67 | 0.93 | 0.21 |
| Global | 23 | Pitcairn Is. | PIT | 34 | 14 | 2.43 | 0.39 | 0.38 | 0.43 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Global | 23 | Puerto Rico | PUE | 942 | 21 | 44.86 | 0.57 | 0.85 | 0.05 |
| Global | 23 | Reunion | REU | 471 | 20 | 23.55 | 0.68 | 0.83 | 0.10 |
| Global | 23 | Rodrigues | ROD | 93 | 19 | 4.89 | 0.57 | 0.67 | 0.26 |
| Global | 23 | Society Is. | SCI | 237 | 17 | 13.94 | 0.48 | 0.71 | 0.06 |
| Global | 23 | Seychelles | SEY | 207 | 21 | 9.86 | 0.63 | 0.78 | 0.19 |
| Global | 23 | Socotra | SOC | 280 | 19 | 14.74 | 0.67 | 0.88 | 0.16 |
| Global | 23 | Sri Lanka | SRL | 1583 | 22 | 71.95 | 0.58 | 0.78 | 0.00 |
| Global | 23 | St. Helena | STH | 30 | 6 | 5.00 | 0.42 | 0.43 | 0.17 |
| Global | 23 | Wallis-Futuna Is. | WAL | 110 | 15 | 7.33 | 0.56 | 0.65 | 0.27 |

| **Dataset** | **No. Families** | **Island** | **Abbr.** | **No. Species** | **Disharmony measures** | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | **F** | **S/F** | **Gini** | **Dominance** | **Disparity** |
| Local | 23 | Ascension | ASC | 9 | 4 | 2.25 | 0.42 | 0.93 | 0.75 |
| Local | 23 | Azores | AZO | 87 | 11 | 7.91 | 0.54 | 0.67 | 0.27 |
| Local | 23 | Bahamas | BAH | 606 | 21 | 28.86 | 0.57 | 0.80 | 0.14 |
| Local | 23 | Balearic | BAL | 689 | 17 | 40.53 | 0.66 | 0.80 | 0.18 |
| Local | 23 | Cayman Is. | CAY | 273 | 18 | 15.17 | 0.46 | 0.82 | 0.06 |
| Local | 23 | Canary Is. | CNY | 644 | 15 | 42.93 | 0.70 | 0.95 | 0.20 |
| Local | 23 | Cook Is. | COO | 88 | 16 | 5.50 | 0.45 | 0.77 | 0.19 |
| Local | 23 | Cuba | CUB | 3027 | 22 | 137.59 | 0.55 | 0.76 | 0.00 |
| Local | 23 | Cape Verde | CVI | 147 | 11 | 13.36 | 0.59 | 0.93 | 0.18 |
| Local | 23 | Fiji | FIJ | 640 | 18 | 35.56 | 0.59 | 0.82 | 0.00 |
| Local | 23 | Galapagos | GAL | 184 | 14 | 13.14 | 0.53 | 0.63 | 0.36 |
| Local | 23 | Hawaii | HAW | 564 | 20 | 28.20 | 0.62 | 0.58 | 0.15 |
| Local | 23 | Hispaniola | HIS | 2275 | 22 | 103.41 | 0.56 | 0.79 | 0.00 |
| Local | 23 | Jamaica | JAM | 1295 | 22 | 58.86 | 0.56 | 0.82 | 0.05 |
| Local | 23 | Juan Fernandez Is. | JNF | 89 | 13 | 6.85 | 0.61 | 0.83 | 0.46 |
| Local | 23 | Mauritius | MAU | 434 | 21 | 20.67 | 0.56 | 0.66 | 0.14 |
| Local | 23 | Madagascar | MDG | 4610 | 23 | 200.43 | 0.58 | 0.87 | 0.00 |
| Local | 23 | Madeira | MDR | 328 | 15 | 21.87 | 0.65 | 0.85 | 0.33 |
| Local | 23 | Marquesas | MRQ | 114 | 14 | 8.14 | 0.50 | 0.87 | 0.07 |
| Local | 23 | Norfolk Is. | NFK | 117 | 17 | 6.88 | 0.43 | 0.97 | 0.18 |
| Local | 23 | New Caledonia | NWC | 1432 | 21 | 68.19 | 0.56 | 0.76 | 0.24 |
| Local | 23 | New Zealand | NZ | 977 | 20 | 48.85 | 0.73 | 0.85 | 0.10 |
| Local | 23 | Pitcairn Is. | PIT | 27 | 13 | 2.08 | 0.36 | 0.53 | 0.54 |
| Local | 23 | Puerto Rico | PUE | 1073 | 22 | 48.77 | 0.58 | 0.59 | 0.09 |
| Local | 23 | Reunion | REU | 430 | 21 | 20.48 | 0.66 | 0.84 | 0.19 |
| Local | 23 | Rodrigues | ROD | 118 | 20 | 5.90 | 0.56 | 0.85 | 0.20 |
| Local | 23 | Society Is. | SCI | 207 | 16 | 12.94 | 0.48 | 0.72 | 0.06 |
| Local | 23 | Seychelles | SEY | 99 | 17 | 5.82 | 0.58 | 0.69 | 0.41 |
| Local | 23 | Socotra | SOC | 386 | 18 | 21.44 | 0.63 | 0.51 | 0.06 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Local | 23 | Sri Lanka | SRL | 1581 | 21 | 75.29 | 0.56 | 0.94 | 0.00 |
| Local | 23 | St. Helena | STH | 33 | 7 | 4.71 | 0.37 | 0.77 | 0.29 |
| Local | 23 | Wallis-Futuna Is. | WAL | 162 | 15 | 10.80 | 0.49 | 0.00 | 0.07 |
| Local | All | Ascension | ASC | 14 | 9 | 1.56 | 0.32 | 0.80 | 0.89 |
| Local | All | Azores | AZO | 209 | 54 | 3.87 | 0.53 | 0.43 | 0.41 |
| Local | All | Bahamas | BAH | 1042 | 120 | 8.68 | 0.69 | 0.60 | 0.33 |
| Local | All | Balearic | BAL | 1471 | 107 | 13.75 | 0.71 | 0.81 | 0.23 |
| Local | All | Cayman Is. | CAY | 537 | 97 | 5.54 | 0.60 | 0.73 | 0.32 |
| Local | All | Canary Is. | CNY | 1337 | 93 | 14.38 | 0.73 | 0.86 | 0.25 |
| Local | All | Cook Is. | COO | 188 | 68 | 2.76 | 0.46 | 0.68 | 0.46 |
| Local | All | Cuba | CUB | 5474 | 175 | 31.28 | 0.75 | 0.51 | 0.15 |
| Local | All | Cape Verde | CVI | 274 | 60 | 4.57 | 0.62 | 0.86 | 0.45 |
| Local | All | Fiji | FIJ | 1304 | 138 | 9.45 | 0.70 | 0.89 | 0.36 |
| Local | All | Galapagos | GAL | 388 | 75 | 5.17 | 0.61 | 0.87 | 0.43 |
| Local | All | Hawaii | HAW | 1043 | 82 | 12.72 | 0.70 | 0.77 | 0.33 |
| Local | All | Hispaniola | HIS | 4353 | 174 | 25.02 | 0.74 | 0.87 | 0.16 |
| Local | All | Jamaica | JAM | 2455 | 164 | 14.97 | 0.73 | 0.89 | 0.24 |
| Local | All | Juan Fernandez Is. | JNF | 155 | 41 | 3.78 | 0.55 | 0.86 | 0.41 |
| Local | All | Mauritius | MAU | 704 | 115 | 6.12 | 0.67 | 0.67 | 0.42 |
| Local | All | Madagascar | MDG | 9668 | 200 | 48.34 | 0.75 | 0.60 | 0.17 |
| Local | All | Madeira | MDR | 674 | 82 | 8.22 | 0.67 | 0.91 | 0.34 |
| Local | All | Marquesas | MRQ | 222 | 58 | 3.83 | 0.52 | 0.81 | 0.36 |
| Local | All | Norfolk Is. | NFK | 254 | 81 | 3.14 | 0.46 | 0.89 | 0.35 |
| Local | All | New Caledonia | NWC | 3045 | 162 | 18.80 | 0.71 | 0.80 | 0.21 |
| Local | All | New Zealand | NZ | 2018 | 119 | 16.96 | 0.76 | 0.87 | 0.27 |
| Local | All | Pitcairn Is. | PIT | 76 | 47 | 1.62 | 0.28 | 0.53 | 0.64 |
| Local | All | Puerto Rico | PUE | 2051 | 157 | 13.06 | 0.71 | 0.37 | 0.22 |
| Local | All | Reunion | REU | 675 | 107 | 6.31 | 0.70 | 0.83 | 0.41 |
| Local | All | Rodrigues | ROD | 201 | 62 | 3.24 | 0.54 | 0.78 | 0.47 |
| Local | All | Society Is. | SCI | 567 | 101 | 5.61 | 0.57 | 0.68 | 0.29 |
| Local | All | Seychelles | SEY | 195 | 73 | 2.67 | 0.52 | 0.53 | 0.62 |
| Local | All | Socotra | SOC | 814 | 100 | 8.14 | 0.66 | 0.77 | 0.31 |
| Local | All | Sri Lanka | SRL | 3057 | 195 | 15.68 | 0.72 | 0.79 | 0.20 |
| Local | All | St. Helena | STH | 56 | 23 | 2.43 | 0.44 | 0.88 | 0.57 |
| Local | All | Wallis-Futuna Is. | WAL | 310 | 74 | 4.19 | 0.59 | 0.63 | 0.42 |

**Table 2:** Correlation analysis between disharmony measures at a family level generated based on different datasets: ‘Global 23’: global data for 23 focal families (main dataset of study); ‘Local 23’: data for 23 focal families from local floristic sources from 32 focal islands; ‘Local All’: data for all flowering plants from 32 focal islands using rarefaction.

| Pearson Correlation | F | S/F | Gini | Disparity | Dominance |
|---|---|---|---|---|---|
| Global 23 vs. Local 23 | 0.92*** | 0.98*** | 0.79*** | 0.86*** | 0.65*** |
| Local 23 vs. Local All | 0.85*** | 0.99*** | 0.77*** | 0.82*** | 0.51*** |

**Figure 1:** Data for different disharmony measures at a family level (F: number of families, S/F: species-to-family ratio) for three data sources (see legend of Table 2 for abbreviations). Red dots: 'Global 23', green dots: 'Local All'.

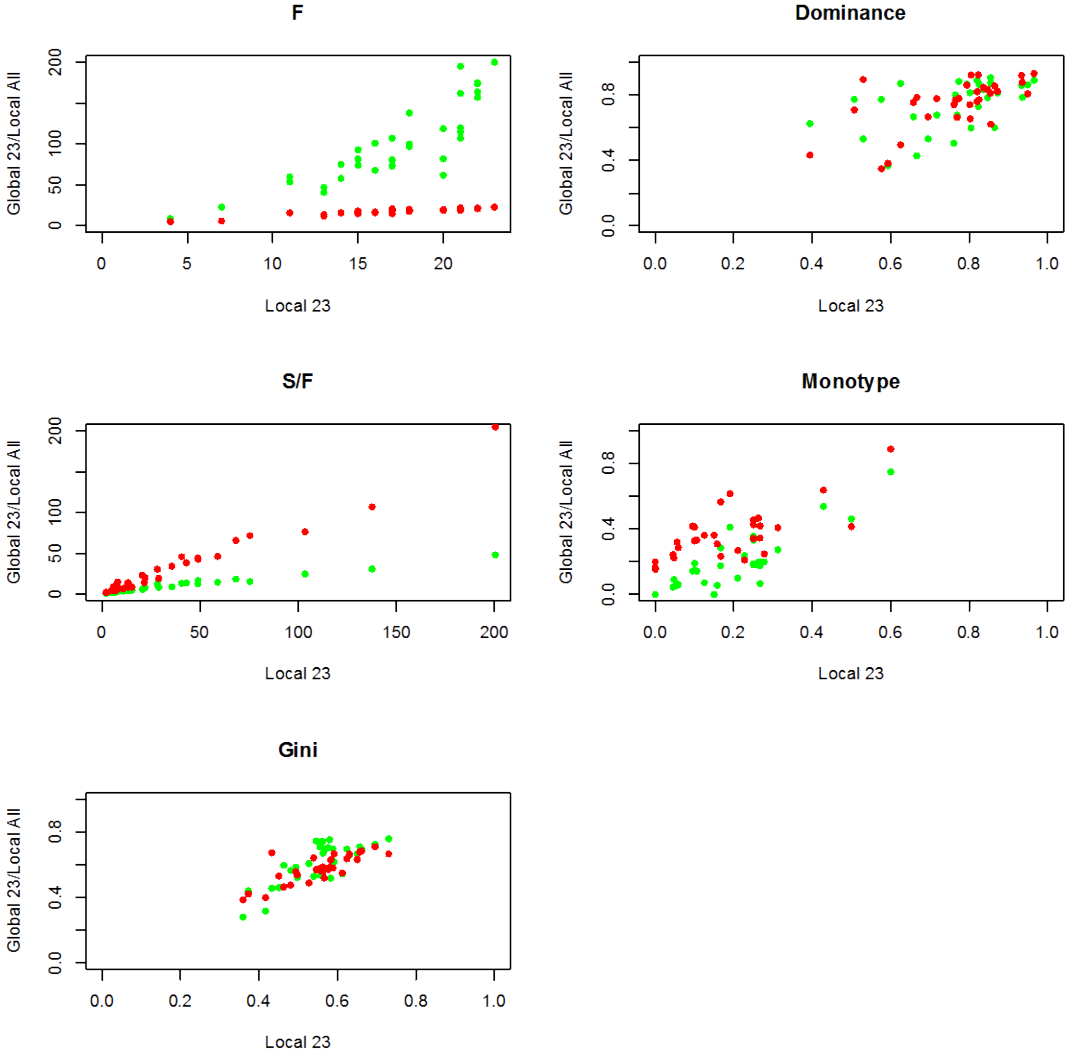


**Table 3:** Disharmony measures at a generic level for the 23 focal islands from the global species list (main dataset for this study, ‘Global’, ‘23’), and analyses based on local dataset (data from 32 focal islands with complete flowering plant lists, ‘local’) for comparison. Local analyses were done for the 23 focal families and for all families using rarefaction (‘All’, see main text for explanation).

| **Dataset** | **No. Families** | **Island** | **Abbr.** | **No. Species** | **Disharmony measures** | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | G | S/G | Gini | Dominance | Disparity |
| Global | 23 | Ascension | ASC | 14 | 11 | 1.27 | 0.18 | 0.21 | 0.82 |
| Global | 23 | Azores | AZO | 246 | 114 | 2.16 | 0.42 | 0.57 | 0.61 |
| Global | 23 | Bahamas | BAH | 378 | 180 | 2.10 | 0.45 | 0.50 | 0.67 |
| Global | 23 | Balearic | BAL | 833 | 285 | 2.92 | 0.50 | 0.51 | 0.47 |
| Global | 23 | Cayman Is. | CAY | 166 | 114 | 1.46 | 0.28 | 0.28 | 0.80 |
| Global | 23 | Canary Is. | CNY | 696 | 232 | 3.00 | 0.54 | 0.70 | 0.54 |
| Global | 23 | Cook Is. | COO | 100 | 74 | 1.35 | 0.23 | 0.19 | 0.82 |
| Global | 23 | Cuba | CUB | 2353 | 453 | 5.19 | 0.65 | 0.77 | 0.44 |
| Global | 23 | Cape Verde | CVI | 234 | 128 | 1.83 | 0.37 | 0.41 | 0.65 |
| Global | 23 | Fiji | FIJ | 692 | 226 | 3.06 | 0.55 | 0.71 | 0.55 |
| Global | 23 | Galapagos | GAL | 146 | 79 | 1.85 | 0.38 | 0.46 | 0.70 |
| Global | 23 | Hawaii | HAW | 619 | 111 | 5.58 | 0.67 | 0.87 | 0.52 |
| Global | 23 | Hispaniola | HIS | 1686 | 429 | 3.93 | 0.59 | 0.65 | 0.45 |
| Global | 23 | Jamaica | JAM | 1026 | 342 | 3.00 | 0.54 | 0.71 | 0.56 |
| Global | 23 | Juan Fernandez Is. | JNF | 62 | 40 | 1.55 | 0.29 | 0.31 | 0.73 |
| Global | 23 | Mauritius | MAU | 482 | 191 | 2.52 | 0.47 | 0.62 | 0.54 |
| Global | 23 | Madagascar | MDG | 4708 | 614 | 7.67 | 0.69 | 0.85 | 0.38 |
| Global | 23 | Madeira | MDR | 328 | 169 | 1.94 | 0.37 | 0.52 | 0.62 |
| Global | 23 | Marquesas | MRQ | 114 | 57 | 2.00 | 0.41 | 0.54 | 0.68 |
| Global | 23 | Norfolk Is. | NFK | 133 | 90 | 1.48 | 0.25 | 0.30 | 0.70 |
| Global | 23 | New Caledonia | NWC | 1453 | 276 | 5.26 | 0.67 | 0.78 | 0.50 |
| Global | 23 | New Zealand | NZ | 820 | 131 | 6.26 | 0.66 | 0.80 | 0.38 |
| Global | 23 | Pitcairn Is. | PIT | 34 | 27 | 1.26 | 0.18 | 0.12 | 0.81 |
| Global | 23 | Puerto Rico | PUE | 942 | 359 | 2.62 | 0.49 | 0.64 | 0.55 |
| Global | 23 | Reunion | REU | 471 | 177 | 2.66 | 0.51 | 0.64 | 0.57 |
| Global | 23 | Rodrigues | ROD | 93 | 76 | 1.22 | 0.15 | 0.06 | 0.80 |
| Global | 23 | Society Is. | SCI | 237 | 111 | 2.14 | 0.43 | 0.54 | 0.63 |
| Global | 23 | Seychelles | SEY | 207 | 135 | 1.53 | 0.30 | 0.34 | 0.76 |
| Global | 23 | Socotra | SOC | 280 | 133 | 2.11 | 0.40 | 0.53 | 0.58 |
| Global | 23 | Sri Lanka | SRL | 1583 | 525 | 3.02 | 0.53 | 0.71 | 0.55 |
| Global | 23 | St. Helena | STH | 30 | 18 | 1.67 | 0.31 | 0.40 | 0.67 |
| Global | 23 | Wallis-Futuna Is. | WAL | 110 | 71 | 1.55 | 0.29 | 0.35 | 0.73 |

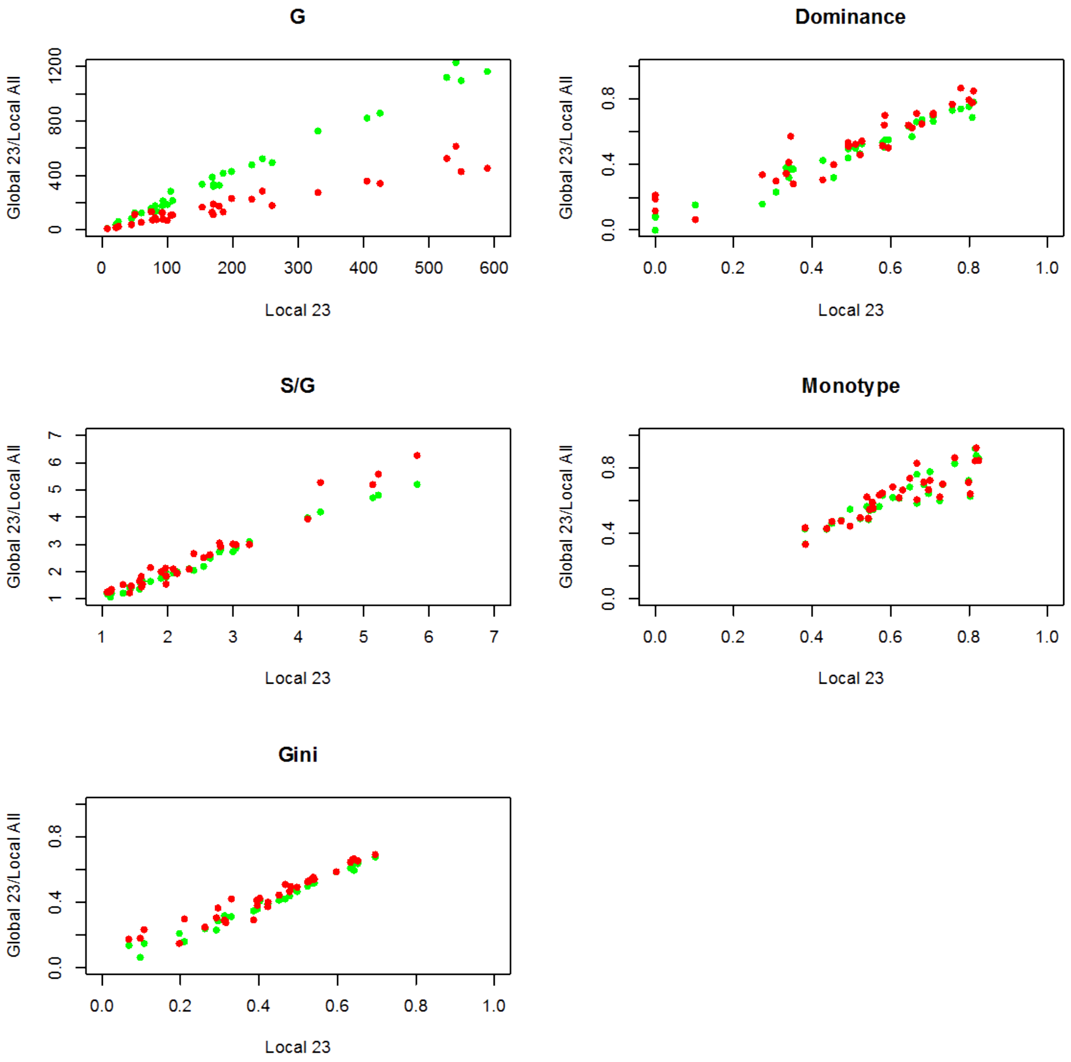
| Dataset | No. Families | Island | Abbr. | No. Species | Disharmony measures | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | G | S/G | Gini | Dominance | Disparity |
| Local | 23 | Ascension | ASC | 9 | 8 | 1.13 | 0.10 | 0.00 | 0.88 |
| Local | 23 | Azores | AZO | 87 | 50 | 1.74 | 0.33 | 0.34 | 0.62 |
| Local | 23 | Bahamas | BAH | 606 | 260 | 2.33 | 0.45 | 0.59 | 0.58 |
| Local | 23 | Balearic | BAL | 689 | 245 | 2.81 | 0.48 | 0.49 | 0.48 |
| Local | 23 | Cayman Is. | CAY | 273 | 170 | 1.61 | 0.32 | 0.35 | 0.72 |
| Local | 23 | Canary Is. | CNY | 644 | 198 | 3.25 | 0.53 | 0.59 | 0.48 |
| Local | 23 | Cook Is. | COO | 88 | 77 | 1.14 | 0.11 | 0.00 | 0.86 |
| Local | 23 | Cuba | CUB | 3027 | 589 | 5.14 | 0.63 | 0.76 | 0.43 |
| Local | 23 | Cape Verde | CVI | 147 | 92 | 1.60 | 0.30 | 0.34 | 0.68 |
| Local | 23 | Fiji | FIJ | 640 | 229 | 2.79 | 0.54 | 0.67 | 0.59 |
| Local | 23 | Galapagos | GAL | 184 | 93 | 1.98 | 0.40 | 0.52 | 0.65 |
| Local | 23 | Hawaii | HAW | 564 | 108 | 5.22 | 0.64 | 0.78 | 0.49 |
| Local | 23 | Hispaniola | HIS | 2275 | 549 | 4.14 | 0.60 | 0.68 | 0.46 |
| Local | 23 | Jamaica | JAM | 1295 | 425 | 3.05 | 0.54 | 0.71 | 0.55 |
| Local | 23 | Juan Fernandez Is. | JNF | 89 | 45 | 1.98 | 0.39 | 0.43 | 0.60 |
| Local | 23 | Mauritius | MAU | 434 | 170 | 2.55 | 0.48 | 0.65 | 0.56 |
| Local | 23 | Madagascar | MDG | 4610 | 541 | 8.52 | 0.70 | 0.81 | 0.34 |
| Local | 23 | Madeira | MDR | 328 | 153 | 2.14 | 0.42 | 0.58 | 0.61 |
| Local | 23 | Marquesas | MRQ | 114 | 60 | 1.90 | 0.39 | 0.49 | 0.70 |
| Local | 23 | Norfolk Is. | NFK | 117 | 81 | 1.44 | 0.26 | 0.31 | 0.78 |
| Local | 23 | New Caledonia | NWC | 1432 | 330 | 4.34 | 0.64 | 0.81 | 0.55 |
| Local | 23 | New Zealand | NZ | 977 | 168 | 5.82 | 0.65 | 0.80 | 0.43 |
| Local | 23 | Pitcairn Is. | PIT | 27 | 25 | 1.08 | 0.07 | 0.00 | 0.92 |
| Local | 23 | Puerto Rico | PUE | 1073 | 405 | 2.65 | 0.50 | 0.64 | 0.56 |
| Local | 23 | Reunion | REU | 430 | 179 | 2.40 | 0.47 | 0.58 | 0.56 |
| Local | 23 | Rodrigues | ROD | 118 | 83 | 1.42 | 0.20 | 0.10 | 0.63 |
| Local | 23 | Society Is. | SCI | 207 | 105 | 1.97 | 0.40 | 0.53 | 0.67 |
| Local | 23 | Seychelles | SEY | 99 | 75 | 1.32 | 0.21 | 0.27 | 0.83 |
| Local | 23 | Socotra | SOC | 386 | 185 | 2.09 | 0.42 | 0.51 | 0.63 |
| Local | 23 | Sri Lanka | SRL | 1581 | 527 | 3.00 | 0.52 | 0.71 | 0.54 |
| Local | 23 | St. Helena | STH | 33 | 21 | 1.57 | 0.29 | 0.45 | 0.76 |
| Local | 23 | Wallis-Futuna Is. | WAL | 162 | 100 | 1.62 | 0.31 | 0.33 | 0.70 |
| Local | All | Ascension | ASC | 14 | 13 | 1.08 | 0.07 | 0.00 | 0.92 |
| Local | All | Azores | AZO | 209 | 127 | 1.65 | 0.31 | 0.37 | 0.69 |
| Local | All | Bahamas | BAH | 1042 | 494 | 2.11 | 0.41 | 0.55 | 0.61 |
| Local | All | Balearic | BAL | 1471 | 523 | 2.81 | 0.48 | 0.50 | 0.48 |
| Local | All | Cayman Is. | CAY | 537 | 336 | 1.60 | 0.31 | 0.37 | 0.71 |
| Local | All | Canary Is. | CNY | 1337 | 430 | 3.11 | 0.51 | 0.55 | 0.49 |
| Local | All | Cook Is. | COO | 188 | 156 | 1.21 | 0.15 | 0.09 | 0.85 |
| Local | All | Cuba | CUB | 5474 | 1162 | 4.71 | 0.61 | 0.73 | 0.43 |
| Local | All | Cape Verde | CVI | 274 | 179 | 1.53 | 0.29 | 0.32 | 0.74 |
| Local | All | Fiji | FIJ | 1302 | 478 | 2.72 | 0.52 | 0.66 | 0.59 |
| Local | All | Galapagos | GAL | 388 | 214 | 1.81 | 0.36 | 0.47 | 0.67 |
| Local | All | Hawaii | HAW | 1043 | 217 | 4.81 | 0.63 | 0.74 | 0.50 |
| Local | All | Hispaniola | HIS | 4353 | 1095 | 3.98 | 0.59 | 0.67 | 0.47 |
| Local | All | Jamaica | JAM | 2455 | 857 | 2.86 | 0.52 | 0.69 | 0.55 |
| Local | All | Juan Fernandez Is. | JNF | 155 | 85 | 1.82 | 0.35 | 0.43 | 0.62 |
| Local | All | Mauritius | MAU | 704 | 321 | 2.19 | 0.44 | 0.57 | 0.62 |
| Local | All | Madagascar | MDG | 9668 | 1227 | 7.88 | 0.68 | 0.78 | 0.33 |
| Local | All | Madeira | MDR | 674 | 336 | 2.01 | 0.39 | 0.53 | 0.62 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Local | All | Marquesas | MRQ | 222 | 126 | 1.76 | 0.36 | 0.44 | 0.71 |
| Local | All | Norfolk Is. | NFK | 254 | 178 | 1.43 | 0.24 | 0.23 | 0.72 |
| Local | All | New Caledonia | NWC | 3045 | 726 | 4.19 | 0.60 | 0.69 | 0.44 |
| Local | All | New Zealand | NZ | 2018 | 388 | 5.20 | 0.64 | 0.75 | 0.44 |
| Local | All | Pitcairn Is. | PIT | 76 | 64 | 1.19 | 0.14 | 0.08 | 0.84 |
| Local | All | Puerto Rico | PUE | 2051 | 821 | 2.50 | 0.47 | 0.63 | 0.55 |
| Local | All | Reunion | REU | 675 | 329 | 2.05 | 0.42 | 0.51 | 0.64 |
| Local | All | Rodrigues | ROD | 201 | 140 | 1.44 | 0.21 | 0.15 | 0.64 |
| Local | All | Society Is. | SCI | 567 | 284 | 2.00 | 0.41 | 0.53 | 0.67 |
| Local | All | Seychelles | SEY | 195 | 160 | 1.22 | 0.16 | 0.16 | 0.86 |
| Local | All | Socotra | SOC | 814 | 417 | 1.95 | 0.39 | 0.50 | 0.65 |
| Local | All | Sri Lanka | SRL | 3057 | 1119 | 2.73 | 0.50 | 0.66 | 0.55 |
| Local | All | St. Helena | STH | 56 | 41 | 1.37 | 0.23 | 0.32 | 0.83 |
| Local | All | Wallis-Futuna Is. | WAL | 310 | 188 | 1.65 | 0.32 | 0.38 | 0.70 |

**Table 4:** Correlation analysis between disharmony measures at a generic level generated based on different datasets: ‘Global 23’: global data for 23 focal families (main dataset of study); ‘Local 23’: data for 23 focal families from local floristic sources from 32 focal islands; ‘Local All’: data for all flowering plants from 32 focal islands using rarefaction.

| Pearson Correlation | G | S/G | Gini | Disparity | Dominance |
|---|---|---|---|---|---|
| Global 23 vs.Local.23 | 0.96*** | 0.98*** | 0.96*** | 0.90*** | 0.94*** |
| Local 23 vs. Local All | 0.99*** | 0.99*** | 0.99*** | 0.97*** | 0.98*** |

**Figure 2:** Data for different disharmony measures at a generic level (G: number of genera, S/G: species-to-genus ratio) for three data sources (see legend of Table 4 for abbreviations). Red dots: ‘Global 23’, green dots: ‘Local All’.

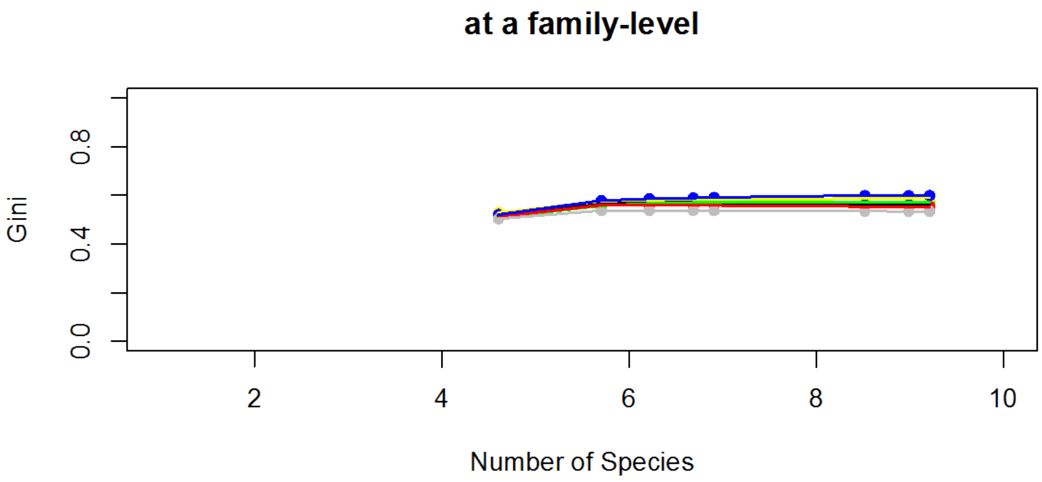


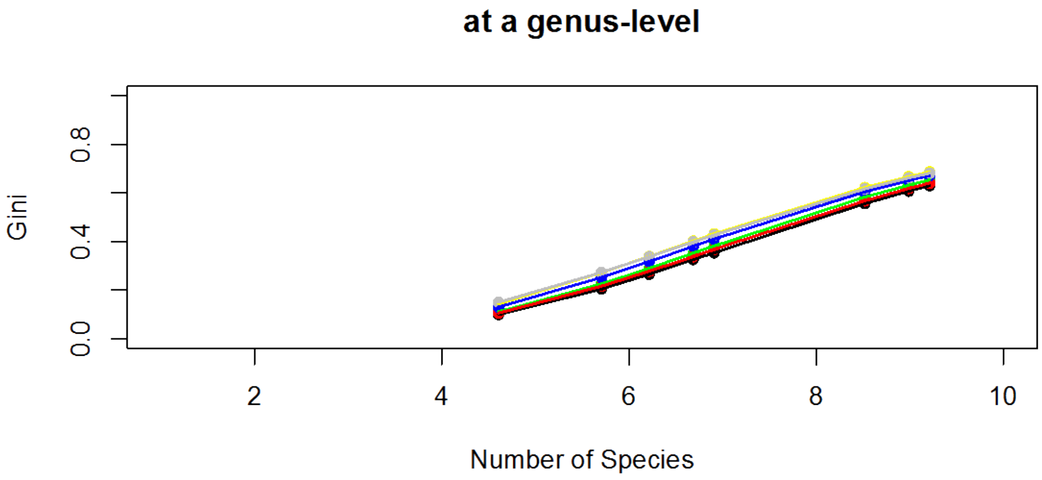
**Appendix 5: Correlations botanical countries:** Pearson correlation coefficients between different characteristics for all botanical countries (252 continental areas and 118 island areas, upper table) and only islands (lower table). Area and latitude are natural logarithm-transformed.

| **Islands and continents** | Log (Area) | Elevation Range | Abs (Latitude) | Endemism | Species Richness |
|---|---|---|---|---|---|
| Log (Area) | 1 | | | | |
| Elevation Range | 0.36 | 1 | | | |
| Latitude | 0.13 | 0.11 | 1 | | |
| Endemism | 0.08 | 0.17 | -0.44 | 1 | |
| Species Richness | 0.40 | 0.55 | -0.05 | 0.37 | 1 |

| **Islands** | Log (Area) | Elevation Range | Isolation | Abs (Latitude) | Endemism | Species Richness |
|---|---|---|---|---|---|---|
| Log (Area) | 1 | | | | | |
| Elevation Range | 0.79 | 1 | | | | |
| Isolation | -0.50 | -0.44 | 1 | | | |
| Latitude | 0.05 | 0.00 | -0.16 | 1 | | |
| Endemism | 0.25 | 0.37 | 0.09 | -0.29 | 1 | |
| Species Richness | 0.73 | 0.68 | -0.36 | -0.27 | 0.48 | 1 |

**<u>Appendix 6: Different null model species pools:</u>** Gini coefficients calculated for different flora sizes (x-axis) and different floras generated through random assembly from different species pools (always including 23 focal families): global flora (black), latitude (35°N-35°S) (red), Atlantic ocean region (green), Caribbean Sea region (yellow), Pacific ocean region (blue), Western Indian ocean region (grey). The flora size on the x-axis is natural logarithm-transformed.





**Appendix 7: Correlations between disharmony measures:** Pearson correlation coefficients among five disharmony measures: species-to-family (S/F) or species-to-genus (S/G) ratio, number of families (F) or genera (G), Gini coefficient (Gini), disparity, and dominance at a family level (upper table) and a generic level (lower table). S/F is natural logarithm-transformed.

| **Family level** | Log (S/F) | F | Gini | Disparity | Dominance |
|---|---|---|---|---|---|
| Log (S/F) | 1 | | | | |
| F | 0.78 | 1 | | | |
| Gini | 0.61 | 0.55 | 1 | | |
| Disparity | -0.73 | -0.60 | -0.44 | 1 | |
| Dominance | 0.50 | 0.48 | 0.88 | -0.35 | 1 |

| **Generic level** | S/G | G | Gini | Disparity | Dominance |
|---|---|---|---|---|---|
| S/G | 1 | | | | |
| G | 0.65 | 1 | | | |
| Gini | 0.81 | 0.54 | 1 | | |
| Disparity | -0.72 | -0.56 | -0.82 | 1 | |
| Dominance | 0.71 | 0.54 | 0.94 | -0.77 | 1 |

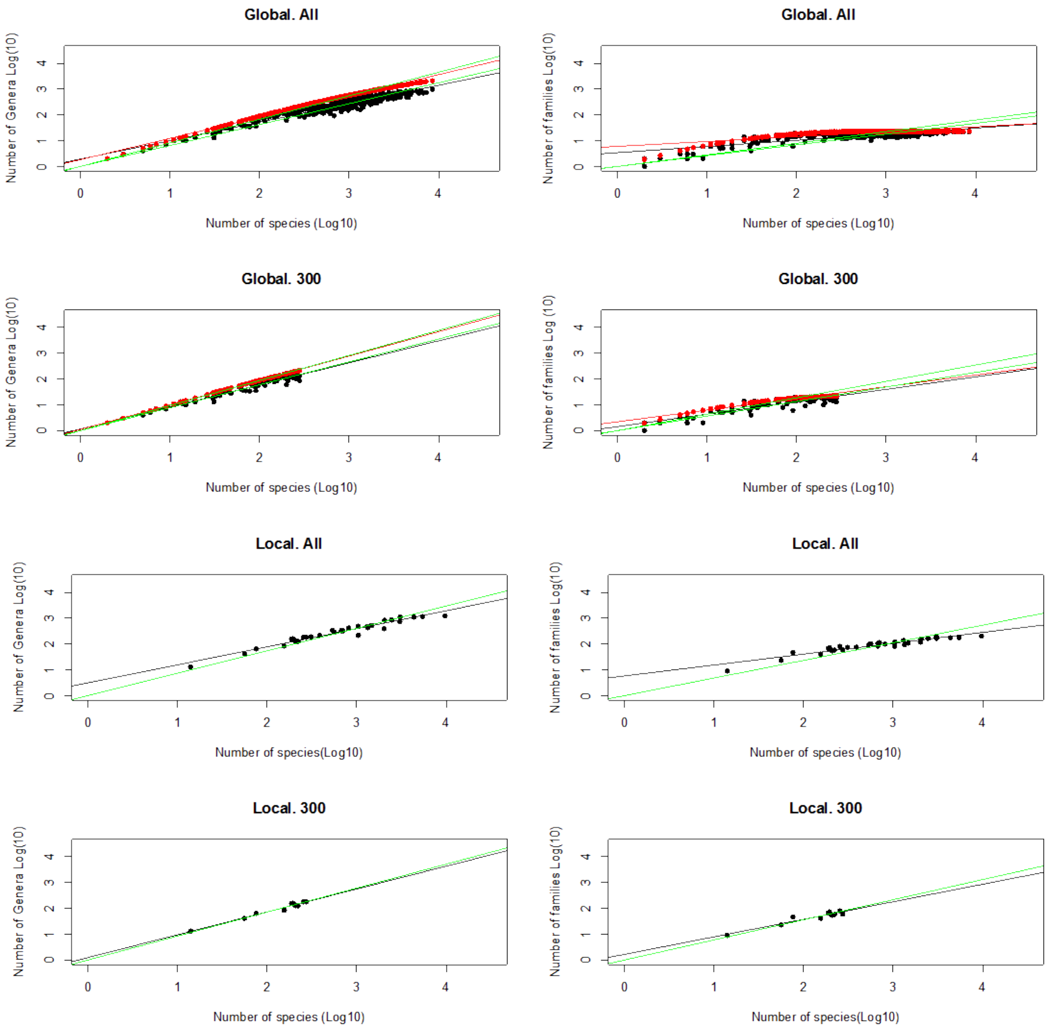
## Appendix 8: Power model:

**Table 1:** Parameters of power law functions fitted between the logarithm of the number of species and the logarithm of the number of genera (upper table) or families (lower table). Models were fitted for different datasets ('Global': 23 focal families for all 360 botanical countries; 'Local': all families for 32 focal islands), both for observed and null-model simulated data, and including either all botanical countries or only those with a flora size of less than 300 species, and setting the intercept either to zero or not.

| **Genus-level** | | | | | | |
|---|---|---|---|---|---|---|
| **Data source** | **Data** | **Max. Flora size** | **Intercept** | **Exponent** | **Standard error** | **$R^2$, P** |
| Global | Observed | All | Non-Zero | 0.72 | 0.01 | 0.96*** |
| Global | Simulated | All | Non-Zero | 0.82 | 0.00 | 0.99*** |
| Global | Observed | All | Zero | 0.81 | 0.00 | 0.99*** |
| Global | Simulated | All | Zero | 0.91 | 0.00 | 0.99*** |
| Global | Observed | 300 | Non-Zero | 0.85 | 0.02 | 0.97*** |
| Global | Simulated | 300 | Non-Zero | 0.95 | 0.00 | 0.99*** |
| Global | Observed | 300 | Zero | 0.89 | 0.01 | 0.99*** |
| Global | Simulated | 300 | Zero | 0.97 | 0.00 | 0.99*** |
| Local | Observed | All | Non-Zero | 0.70 | 0.03 | 0.95*** |
| Local | Observed | All | Zero | 0.87 | 0.01 | 0.99*** |
| Local | Observed | <300 | Non-Zero | 0.89 | 0.05 | 0.97*** |
| Local | Observed | 300 | Zero | 0.93 | 0.01 | 0.99*** |

| **Family-level** | | | | | | |
|---|---|---|---|---|---|---|
| **Data source** | **Data** | **Max. Flora size** | **Intercept** | **Exponent** | **Standard error** | **$R^2$, P** |
| Global | Observed | All | Non-Zero | 0.24 | 0.01 | 0.69*** |
| Global | Simulated | All | Non-Zero | 0.19 | 0.01 | 0.68*** |
| Global | Observed | All | Zero | 0.42 | 0.00 | 0.98*** |
| Global | Simulated | All | Zero | 0.45 | 0.00 | 0.99*** |
| Global | Observed | 300 | Non-Zero | 0.48 | 0.03 | 0.81*** |
| Global | Simulated | 300 | Non-Zero | 0.45 | 0.01 | 0.94*** |
| Global | Observed | 300 | Zero | 0.57 | 0.01 | 0.98*** |
| Global | Simulated | 300 | Zero | 0.64 | 0.01 | 0.99*** |
| Local | Observed | All | Non-Zero | 0.42 | 0.03 | 0.88*** |
| Local | Observed | All | Zero | 0.68 | 0.01 | 0.99*** |
| Local | Observed | 300 | Non-Zero | 0.68 | 0.07 | 0.89*** |
| Local | Observed | 300 | Zero | 0.78 | 0.01 | 0.99*** |

**Figure 1:** Figures of power law functions fitted between the logarithm of the number of species and the logarithm of the number of genera (left column) or families (right column). For the explanation of different datasets (Global vs. Local) and different flora size (All vs. 300) see legend of Table 1. Observed data are indicated by black dots and fitted lines by black lines. Simulated data are indicated by red dots and fitted lines by red lines. Green lines present fitted lines with intercept set to zero.



# Chapter 2

# The macroecology of adaptive radiations on oceanic islands

## Abstract

A central question of evolutionary biology is what drives adaptive radiation on islands. We investigated the role of three possible factors - species richness, niche pre-emption, and predisposition of families (including their dispersibility) – by analyzing complete native species lists for 23 flowering plant families from 118 islands or island groups. We found a positive relationship between endemism (as a proxy of speciation rate) and species richness per island. However, other factors (isolation from nearest continent, island type, maximal elevation, number of islands, and latitude) were also important in explaining differences in endemism. Our results for the role of niche pre-emption were inconclusive, but suggest that spectacular speciation can occur within families containing many genera (which might be considered a constraining factor). Finally, our results suggest that rapid speciation is possible in all plant families, but that arriving on an island soon after its formation strongly influences whether this actually occurs.

Our analyses support the classical idea that plant life on islands is dominated by families containing plants that are readily dispersed (Carlquist 1965). However, there is a strong element of chance in which families reach an island first, which explains why the relative abundance of plant families varies so much among islands.

## Introduction

Islands have attracted the interest of evolutionary biologists and biogeographers since the 19th century, and were an essential inspiration for the development of the theory of evolution by Charles Darwin (Darwin 1859) and Alfred Russell Wallace (Wallace 1902). Because of the high levels of endemism, islands also make an important contribution to global biodiversity (Myers et al. 2000). Indeed, it has been estimated that up to one quarter of global plant diversity is endemic to islands (Kreft et al. 2008).

One process that has led to such high levels of endemism is adaptive radiation, which in the more spectacular cases has produced numerous species from one or a few colonizing species (Gillespie 2004, Whittaker and Fernández-Palacios 2007, Gillespie 2009, Losos and Ricklefs 2009, Losos and Mahler 2010). As a consequence of such speciation events, a high proportion of the plant species on many islands is concentrated in a few species-rich genera and families (Chapter 1). What triggers and drives adaptive radiations on islands, however, remains poorly understood, though several ideas have been proposed.

One of these is that the initial species assemblage in some way triggers self- organized feedbacks that lead to adaptive radiation and increasing species richness. Thus, species richness becomes a driver for further speciation (Sepkoski Jr 1978, Emerson and Kolm 2005), with areas or species groups of high diversity (e.g. through higher immigration rates of new species) exhibiting greater diversification rates. One possible mechanism for this is that species diversity increases the strength of ecological interactions such as competition and predation, thereby strengthening selection for ecological divergence and ultimately speciation (e.g. Losos and Mahler 2010). Another is that average population sizes decrease as more species are packed into a limited space, which increases the possibility for speciation through genetic drift (Hubbell 2001). Finally, biodiversity adds structural complexity to ecosystems, which may provide new niche space for more species (Tokeshi 2009).

Emerson and Kolm (2005) tested this ‘diversity-driven speciation’ hypothesis using data from two archipelagos – Hawaii and Canary islands – by analyzing the relationship between total species richness and the proportion of endemic species (i.e. single island endemism). They found a positive relationship between endemism and species richness and interpreted this as support for the hypothesis. Others authors have criticized this conclusion, however, pointing out that a positive relationship between endemism and species richness can be expected from ‘null model’ assumptions without needing any effect of species richness on speciation (Witt and Maliakal-Witt 2007, Gruner et al. 2008, Chen and He 2009). Alternatively, rather than reflecting a causal link between species richness and endemism, the apparent relationship could arise if both parameters are influenced by hidden variables such as island age or area (Cadena et al. 2005, Pereira et al. 2007, Whittaker et al. 2007).

A second idea to explain the uneven distribution of adaptive radiation is that it only occurs where there are empty niches that allow for ecological release (e.g. Losos and Ricklefs 2009, Losos and Mahler 2010). Both the emergence of new genera and multiple colonisations from the same genus are both rare events on islands (for Canary Islands and Hawaii, Lozano et al. 2010). It can thus be assumed that the number of genera in a family is mostly the result of colonization events, while the number of species per genus is mostly the result of *in situ* speciation. Given that species from the same family tend to occupy similar niches, we can expect a negative relationship between the number of genera and the number of species in the species-richest genera (indicative of rapid *in situ* speciation) in any particular family. The more genera of a family present on an island (through multiple colonization events in the same family), the less niche space will be available for *in situ* speciation; or – *vice versa* – the more species are already present through *in situ* speciation the more difficult it will be for new species (especially from the same family) to establish on an island (Silvertown et al. 2005). The assumption of such a negative correlation between colonization and *in situ* speciation motivates the idea of ‘radiation zones’ at the periphery of a species’ dispersal range (McArthur and Wilson 1967, Diamond 1977).

A third possibility to explain observed patterns of adaptive radiation is that there are inherent differences among families in speciation rates (e.g. Gillespie 2009). Islands are particularly convenient for addressing this question, enabling us to investigate whether some families have consistently higher speciation rates than others, and what characterizes them. This is because the same families have colonized islands throughout the world, so that they can be treated as a huge natural experiment.

We assembled complete lists native plant species belonging to 23 families on 118 islands or island groups. We used these data to investigate the ‘diversity-driven speciation’ hypothesis by analyzing the relationship between endemism and species richness across > 100 island groups worldwide. Being based on a much larger data set than was available to Emerson and Kolm (2005), our analysis avoided the problem of migration between island replicates, and allowed us to consider the possible effects of hidden variables. We also tested the hypothesis that adaptive radiations are more important in families with a higher propensity to reach islands (either through higher dispersibility or a larger global species pool) because they tend to reach islands earlier after island formation when less niche space is occupied (and they have more time for speciation). We compared the relative contribution of different families to the native and endemic species pools of different islands to investigate whether consistently the same families dominate island floras, and whether dominant families are those that have the highest probability to reach islands (measured as the proportion of islands occupied by a particular family).

## Method

### *Floristic data*

We derived lists of native and endemic species for 21 flowering plant families from the Kew World Checklist of selected plant families (WCSP, 2013), supplemented with data for Asteraceae from the Global Compositae Checklist (Flann, 2009) and for Leguminosae from the ILDIS World Database of Legumes (Roskov *et al*., 2005). We restricted the analysis to 23 families (Appendix 1 in Chapter 1) for reasons of data quality (we included only data from families for which review of the data was completed) and global comparability (all selected families have a global distribution and are represented on islands in all major oceanic regions). However, we checked how well the data for 23 families reflected variation in the total floras of islands using data for 32 island groups for which we had complete species lists. We found the number of species in the 23 focal families was highly correlated with the total number of flowering plant species number on these island groups ($R^2 = 0.997$). Further information on the floristic data used for the analyses can be found in Chapter 1.

### *Data analyses*

To investigate the relationship between species richness and speciation, we fitted multivariate regressions between the proportion of endemic species (arcsin-square-root transformed) and species richness (natural-logarithm transformed) (Emerson and Kolm 2005). The analyses included the following geographical characteristics of the islands: area, maximal elevation, isolation (from nearest continent), latitude, number of islands (three categories: A (1-2 islands), B (2-10 islands), C (> 10 islands) by including islands with an area greater than 1 km$^2$), and island type (oceanic, continental, atoll, mixed) (see Chapter 1 for more information). Area was natural-logarithm transformed. For species richness and area we included second order polynomials in the complete analysis, though these were never retained in the final models. We also fitted univariate regressions between the proportion of endemic species (arcsin-square-root transformed) and species richness (natural-logarithm transformed) across present families (up to 23) within each of 118 islands (yielding 118 different regresions), and related the slope-coefficients, R-squares and P-values of the regressions to island characteristics (same as above) (Appendix 1).

To test the effect of the number of genera on speciation, we compared the relationship between number of genera and number of species in dominant genera (defined as those with a species number of at least twice the median of the other genera) per family and island (yielding 14*118 data points). This analysis was restricted to the 14 families that had at least 15 genera on at least one island. We also compared the observed data with values generated through null models simulations. This was done by randomly selecting a specified number of plant species from the global species pool of a particular family and calculating number of genera and number of species in dominant genera for this sample. By repeating the process 10,000 times, we could obtain the geometric means and the 97.5 and 2.5 percentile confidence intervals.

We ranked families by the number of species on each island, and used these values to characterize the species richness on the various islands (i.e. the most species-rich island for a particular family receives rank 1, etc.). We then related the median rank across islands of each family to the prevalence of families on islands (for which we used the number of islands where a particular family was recorded out of 118 islands). We also explored the link between the prevalence of families on islands and their global species richness. In a second step we calculated for each family the median rank and prevalence (i.e. proportion of islands present) separately for islands of three isolation classes (close: < 250 km, medium: 250-2300 km, far: > 2300 km). We then fitted linear regressions across the values from the three isolation classes both for prevalence and rank (yielding two regressions per family). Finally, we calculated the correlation between slope-coefficients from the rank and prevalence regressions across the 23 families to investigate whether change of prevalence and of rank with isolation were related.

## Results

### *Relationship between endemism and species richness*

We found positive relationships between endemism and species richness per island (Fig. 1), both for 23 plant families on 118 islands (global dataset) and for all families 32 focal islands (Fig 1). Species richness explained about 12% of variation in endemism when the intercept of the regression was not constrained to zero, and 68.7% when the intercept was zero. In a multivariate regression, isolation from nearest continent, island type, maximal elevation, number of islands, and latitude were maintained as significant terms in the final model. When the multivariate model was constrained to zero, they explained together only an additional 10.6% of total variation. When the model was not constrained to zero, 24.7% was explained by island characteristics compared to 12.7% by species richness (Table 1). Endemism increased with isolation and maximal elevation, and decreased with latitude; it was higher on volcanic islands, and lower on archipelagoes with more than 10 islands.

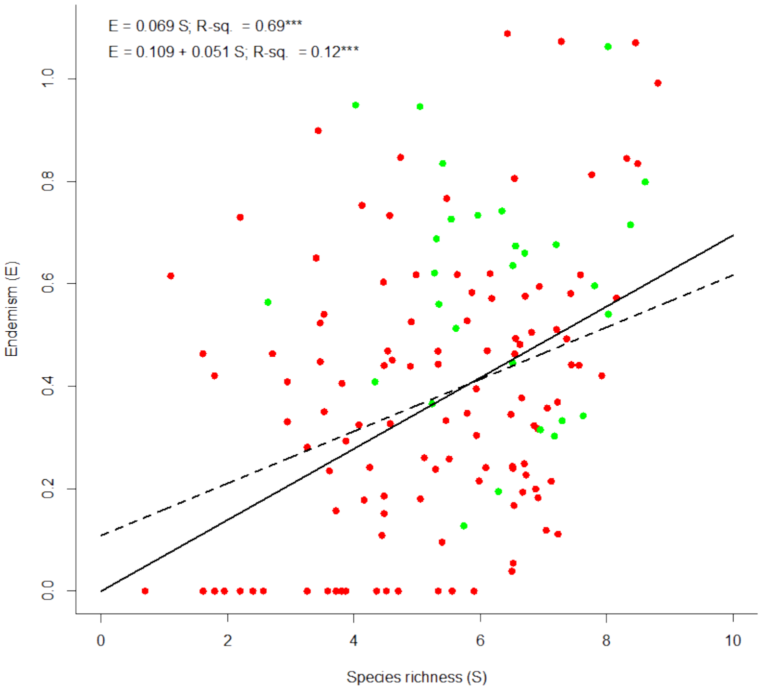


**Figure 1**: The relationship species richness (natural logarithm-transformed) and the proportion of endemic species (‘endemism’, arcsine-square-root-transformed) per island. Data is shown for 118 island groups (‘global data’ covering 23 families, red dots), and complete floras from 32 island groups (green dots). Linear regressions were fitted to global data with intercept either constrained to zero (solid line) or not (dashed line).

**Table 1:** Multivariate regression models with endemism as dependent variable and different island characteristics as predictors. The analysis was performed for 118 island floras. Endemism was arcsine-square-root-transformed and the natural logarithm was used for log-transformations. Intercept of regression model was set either to zero or not. Significance: ***: P < 0.001; **: P < 0.01; *: P < 0.1.

| **Intercept** | **Predictor** | | **Estimate** | **Sum-Square** |
|---|---|---|---|---|
| Constrained to zero<br>($R^2$ = 0.78***) | Log (S) | | 0.04* | 17.01 |
| | Isolation | | 5.08E-05** | 0.83 |
| | Elevation | | 6.07E-05* | 0.47 |
| | abs (Latitude) | | -5.27E-03*** | 0.42 |
| | Number of islands | | | 0.42 |
| | | A (1-2 islands) | 0.08 | |
| | | B (2-10 islands) | -0.02 | |
| | | C (> 10 islands) | -0.06 | |
| | Island Type | | | 0.49 |
| | | Continental | 0.05 | |
| | | Mix | 0.14* | |
| | | Volcanic | 0.17* | |
| | Residuals | | | 5.06 |
| | | | | |
| Not constrained to zero<br>($R^2$ = 0.33***) | Intercept | | 0.03 | |
| | Log (S) | | 0.04* | 1.10 |
| | Log (Area)$^2$ | | -2.02E-04 | 4E-03 |
| | Isolation | | 4.56E-05** | 0.72 |
| | Elevation | | 6.53E-05* | 0.64 |
| | abs (Latitude) | | -4.67E-03** | 0.33 |
| | Island type | | | 0.44 |
| | | Continental | 0.09 | |
| | | Mix | 0.15* | |
| | | Volcanic | 0.19* | |
| | Residuals | | | 5.39 |

### *Relationship between number of genera and number of species in dominate genera*

We found the predicted negative relationship between number of genera and number of species in dominant genera per family (Fig. 2). However, we obtained a similar relationship using a null model based upon the same numbers of species randomly selected from the global species pool. Nevertheless, when observed data deviated from the null model expectation it was almost always in the direction of more species in dominant genera (given a certain number of genera) (Fig. 2).

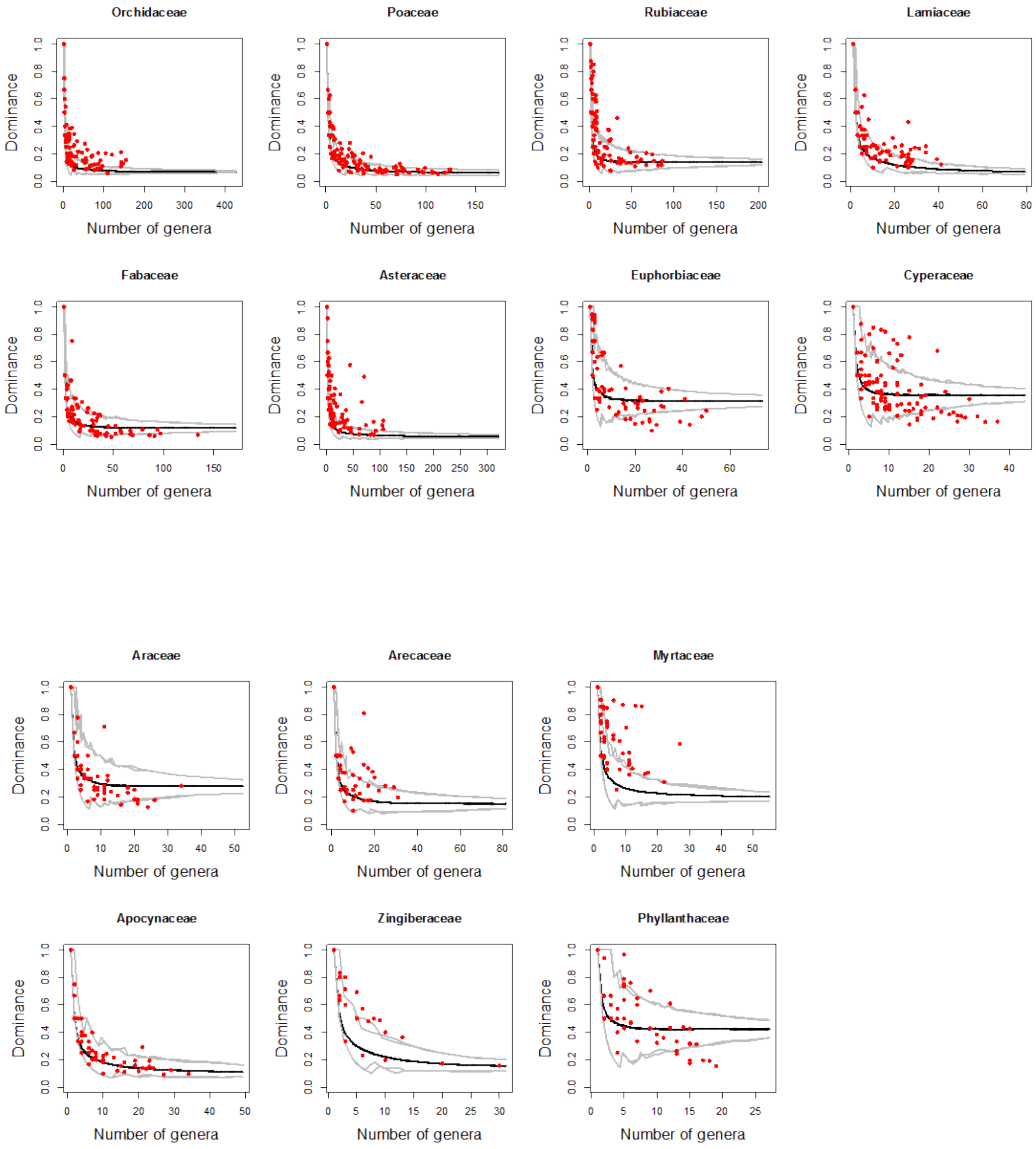


**Figure 2:** The relationship between number of genera and dominance (here measured as proportion of species in species-richest genus) for 14 families with at least 15 genera on at least one island. The graphs show observed data (red dots) and simulated data generated through random sampling from the global species pool of the particular family (black line: mean; grey lines: 95% of simulations).

### *Predisposition of certain families to adaptive radiation*

In general, the same few families were prominent in most island floras (Poaceae, Cyperaceae, Orchidaceae, Rubiaceae), with the remainder of the 23 families contributing little or nothing to overall species richness (Fig. 3). However, individual islands varied greatly in this respect, and each of the 23 families was among the most species rich on some islands (Table 2). With the exception of the Poaceae, which exhibited low endemism, these patterns were similar though less distinct when only endemic species were considered (Fig. 3).

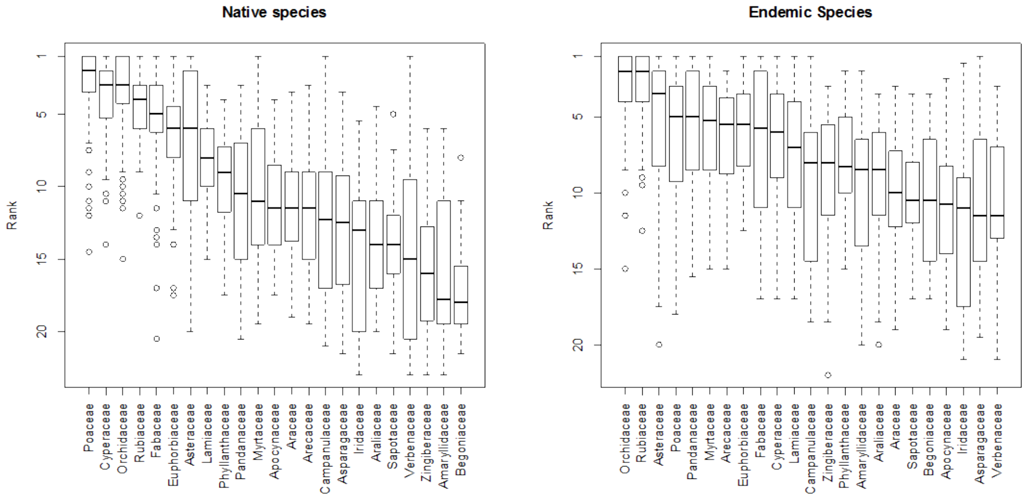


**Figure 3:** Box-and-whisker plots (black lines indicate median) of the rank in species richness of 23 families on 118 islands, whereby rank 1 is assigned to the largest family (among the 23 studied ones) on an island and 23 to the smallest one. An intermediate value is used when more than one family have the same rank, e.g. 7.5 for two families with rank 7. The left figure shows data for all native species and the right figure for endemic species only.

**Table 2:** Species richness of studied families on islands. The table shows for the 23 studied families the total number of species in the family on the 118 studied islands, the number of islands where the family is dominant (i.e. where the species richness is at least twice the median of the other families) and present (in brackets), and maximal number of species on any island with island name in brackets.

| Family | Total species number | Islands (dominant, total) | Max. number on an island |
|---|---|---|---|
| ***Amaryllidaceae*** | 201 | 4 [62] | 48 [East Aegean Is.] |
| ***Apocynaceae*** | 679 | 19 [81] | 106 [Borneo] |
| ***Araceae*** | 876 | 18 [87] | 303 [Borneo] |
| ***Araliaceae*** | 654 | 6 [76] | 116 [New Guinea] |
| ***Arecaceae*** | 1477 | 20 [65] | 310 [Borneo] |
| ***Asparagaceae*** | 421 | 9 [71] | 57 [Japan] |
| ***Asteraceae*** | 4056 | 62 [93] | 784 [Great Britain] |
| ***Begoniaceae*** | 570 | 2 [32] | 113 [Borneo] |
| ***Campanulaceae*** | 457 | 9 [72] | 143 [Hawaii] |
| ***Cyperaceae*** | 2067 | 97 [112] | 392 [Japan] |
| ***Euphorbiaceae*** | 2101 | 65 [98] | 449 [Madagascar] |
| ***Fabaceae*** | 2504 | 71 [91] | 553 [Madagascar] |
| ***Iridaceae*** | 131 | 0 [47] | 23 [East Aegean Is.] |
| ***Lamiaceae*** | 1620 | 47 [94] | 254 [Madagascar] |
| ***Myrtaceae*** | 1982 | 31 [76] | 324 [New Guinea] |
| ***Orchidaceae*** | 10389 | 77 [92] | 2841 [New Guinea] |
| ***Pandanaceae*** | 860 | 15 [54] | 203 [New Guinea] |
| ***Phyllanthaceae*** | 1173 | 33 [71] | 204 [Borneo] |
| ***Poaceae*** | 2812 | 101 [116] | 458 [Madagascar] |
| ***Rubiaceae*** | 5530 | 86 [109] | 783 [New Guinea] |
| ***Sapotaceae*** | 659 | 1 [62] | 123 [Borneo] |
| ***Verbenaceae*** | 142 | 12 [53] | 57 [Cuba] |
| ***Zingiberaceae*** | 815 | 4 [36] | 238 [Borneo] |

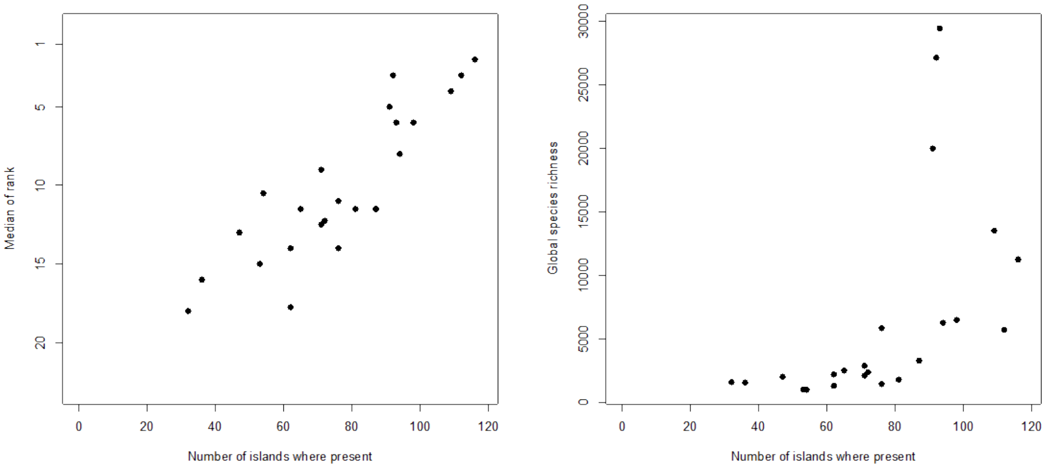
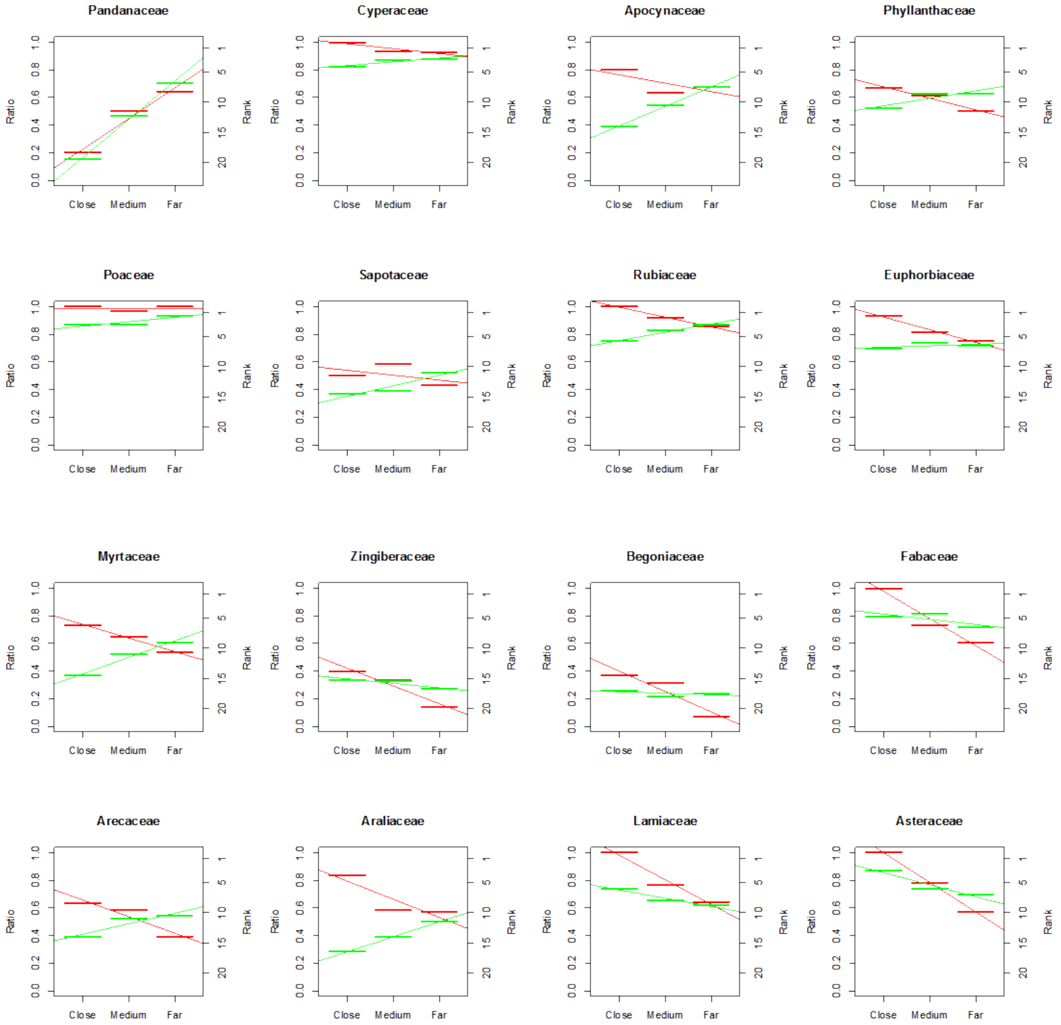
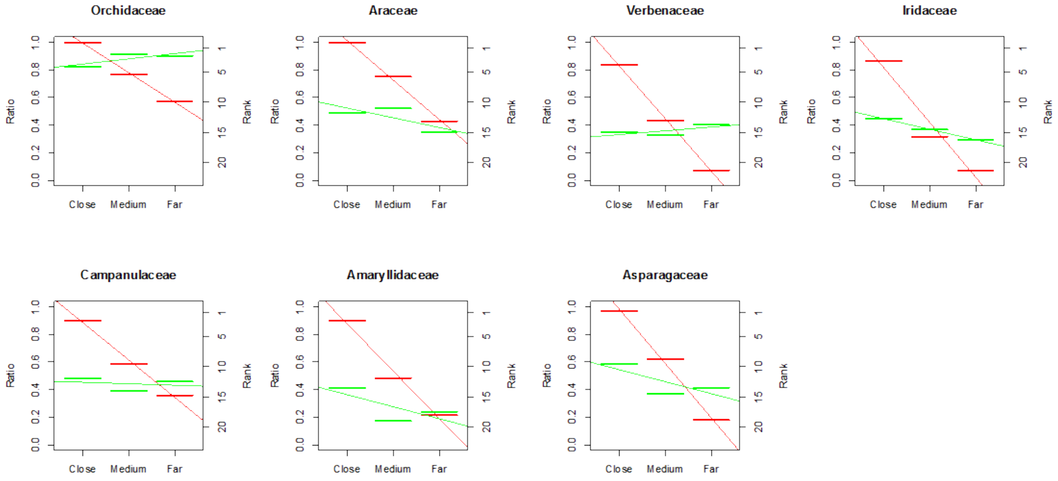


**Figure 4:** The relationship between prevalence of families on islands (measured as number of islands among 118 where a family is present) and the median rank of the family on the islands where present (see Fig. 3 for more information). The right figure shows the relationship between the global species richness and prevalence on islands of each of the 23 families.

The most prevalent families (i.e. those recorded most consistently on islands) were also the most species rich on islands, though not necessarily the most species-rich in the global species pool (Fig. 4). The effect of isolation on prevalence and relative abundance on an island (measured as rank) varied among families (Fig. 5). Prevalence generally decreased with isolation, with this effect being strongest in poorly dispersed families (e.g. Iridaceae, Verbenaceae; Fig. 5), and weaker in families that can be considered very well-dispersed (e.g. Cyperaceae, Poaceae); and for the Pandanaceae prevalence actually increased with isolation. The slope-coefficients of the regressions of the prevalence and relative abundance (rank) data across the three isolation classes were highly correlated (Pearson correlation coefficient: -0.76***). Well-dispersed families tended to become more important in terms of rank on more isolated islands, while the rank of poorly-dispersed families tended to decrease with isolation.

**Figure 5:** The prevalence (proportion of islands where present) and rank (of abundance) of 23 families on 118 islands that were separated into three classes based on isolation from nearest continent (close: <250 km; medium: 250 – 2300 km; far: > 2300 km). Bold horizontal lines show values for each of the three isolation classes (median values for rank). Thin lines show linear regressions across these values. Red color stands for prevalence (left-sided y-axis) and green color for the rank (right-sided y-axis).





## Discussion

Our results revealed that most plant species on oceanic islands (80-90%) belong in a few particularly species-rich genera or families, while 40-80% genera are monospecific (Chapter 1). Since the presence of a particular genus on an island is in most cases due to a single species becoming established (for Canary Islands and Hawaii, Lozano et al. 2010), this difference between species-rich and species-poor taxonomic groups must reflect differences among genera in *in situ* speciation rates. Our study was designed to investigate why some genera and families have apparently speciated more vigorously than others.

### *Does species richness drive speciation?*

Emerson and Kolm (2005) reported a positive relationship between species richness on islands and the proportion of endemic species, which they regarded as a proxy for speciation rates. They argued that this result was evidence that the rate of speciation was directly affected species richness within a taxon (diversity-driven speciation hypothesis). However, because their dataset was restricted to two archipelagos, the endemism patterns they reported could have been influenced by relatively frequent species exchange among the islands of each archipelago and by spatial autocorrelation. We replicated their analyses with a much larger and more comprehensive dataset from 118 island groups that were mostly isolated from each other. Like Emerson and Kolm (2005), we found a positive relationship between species richness and endemism (Fig. 1, Table 1) and we found the same relationship among families within islands (Appendix 1); thus, at an island-scale endemism is generally higher in species-rich than in species-poor families. However, in a multivariate regression (without constraining the intercept to zero), species richness accounted for only one third of explained variation (12.7% of total variation), with the remainder being explained for by isolation from nearest continent, island type, maximal elevation, number of islands in the island group, and latitude. Thus, while species richness may be one driver of speciation, it is not the only one, and perhaps not even the most important (Cadena et al. 2005, Pereira et al. 2007, Whittaker et al. 2007, Witt and Maliakal-Witt 2007, Gruner et al. 2008, Chen and He 2009).

In a previous analysis, it was shown that with increasing size of a flora, *in situ* speciation (leading to endemic species) becomes relatively important than species immigration as a source of new species (Chapter 1). When we compared species-to-genus and species-to-family ratios in dominant genera and families (i.e. those with a species number of at least twice the median of the other genera or families) with those in all other families, we found that these ratios increased rapidly with flora size in the largest genera and families, while they remained almost constant in the others (Fig. 6). Although the distinction between taxa showing frequent and infrequent speciation increases with flora size, we cannot determine from our data whether this is because of feedbacks upon speciation in the more species-rich groups.

As expected, endemism increased with isolation from nearest continent (McArthur and Wilson 1967) and with maximal elevation (Steinbauer et al. 2012), and decreased with latitude (Jablonski et al. 2006). It was also higher on volcanic islands than on continental islands and atolls (Whittaker and Fernández-Palacios 2007). However, endemism was lower on archipelagos with many islands than on isolated islands and smaller archipelagos. This was unexpected, since it is often assumed that allopatric speciation is more likely to occur on archipelagos providing an optimal degree of genetic isolation to emerging species (Whittaker et al. 2008, Gillespie 2009). One possible explanation is that island-rich archipelagos include many low-lying atolls with few endemic species. Alternatively, it might be that anagenetic speciation – whereby a single island endemic species evolves from a progenitor – plays an important for endemism on single-island island groups (Stuessy et al. 2006).

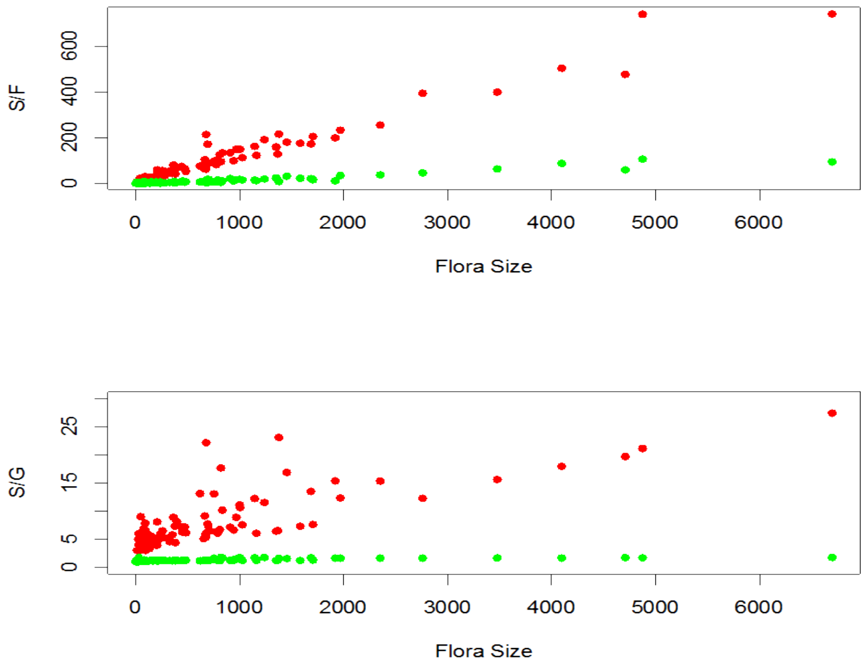


**Figure 6:** The accumulation of species in the species-richest families or genera with increasing flora size. The upper figure presents the species-to-family ratio (S/F) at a family-level and the lower figure present species-to-genus (S/G) at a genus-level. Red dots show data for dominant families or genera (i.e. those with at least twice the species number of the median of all families or genera) and green dots for non-dominant families or genera.

### *Are there indications for a limitation of adaptive radiation through niche pre-emption?*

Although we found a negative relationship between number of genera and species richness in dominant genera of the same family, as predicted, we obtained a similar relationship using species lists randomly assembled from the global species pool. Interestingly, however, when patterns deviated from the null model expectation, they did so mostly through higher dominance (species numbers in dominant genera) given a certain number of genera, indicating that there is not a strict limiting relationship between colonization of new genera and *in situ* speciation in the same family.

### *Are some families predisposed for adaptive radiation?*

Some families, including Poaceaeae, Fabaceae, Asteraceae, Pandanaceae, Campanulaceae and Verbenaceae, show a greater tendency than others to become species-rich on islands (Table 2). However, islands vary greatly in which families actually are the most species rich, and each of the 23 families we studied was among the most species-rich families on some islands (Table 2). Thus, chance appears to be an important factor determining which taxa dominate on particular islands (Gillespie 2009).

In our data, the predisposition of a family to adaptive radiation was strongly related to its prevalence on islands, suggesting that high species richness in some families is related to a greater than average ability to reach and establish on islands. This link between prevalence and species richness can be explained in various ways. First, it could simply be a result of more species from well-dispersed families reaching islands. Second, well-dispersed families are also more likely to reach an island soon after its formation and therefore profit from ecological release and empty niche opportunities; indeed, such an effect of immigration history has also been demonstrated in experimental microcosms (Fukami et al. 2007). Finally, being among the first plants to reach an island also means that the taxon has more time to radiate than later arrivals (Whittaker and Fernández-Palacios 2007, Whittaker et al. 2008, Gillespie 2009, Losos and Ricklefs 2009, Losos and Mahler 2010).

## Conclusions

Classical thinking about the assembly of island floras has been largely deterministic, with biogeographers arguing that plant life on islands is dominated by certain families because they contain species that are readily dispersed (Carlquist 1965). Without contradicting this idea, our results highlight the role of chance by showing that all plant families can potentially speciate vigorously on islands. Whether this actually happens in a particular case depends largely upon the family (or rather, a plant in that family) reaching the island before the most important niches have been occupied by other taxa. In general, the families that arrive soonest will go on to make up a major proportion of the plant diversity on that island. Thus, we can understand why the relative abundances of plant families varies so much among islands, with different taxa dominating on different islands.

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## Supporting Information

**Appendix 1:** Parameters of linear regressions between species richness and endemism (proportion of endemic species) per family across families present on each of 118 islands (Table 1). On most islands endemism is higher in species-rich than species-poor families (i.e. slope-coefficient > 0). Regressions for most islands are significant (P < 0.05) but variation explained is relatively small (R-sq.), especially for islands with less species and/ or plant families (Table 2). We also tested whether the differences in slope (slope-coefficient), variation explained (R-sq.), and significance (P) could be explained by differences in island characteristics (see Appendix 2, Chapter 1) with multivariate regressions (Table 2).

**Table 1:**

| **Island** | **Slope-coefficient** | **R-sq.** | **P** | **Area** | **Maximal elevation** | **Species richness** | **Number families** |
|---|---|---|---|---|---|---|---|
| Aldabra | 0.20 | 0.25 | 0.04 | 183.07 | 11 | 88 | 16 |
| Aleutian Is. | 0.00 | NaN | NaN | 12624.53 | 1972 | 78 | 11 |
| Amsterdam-St.Paul Is | 0.39 | 0.57 | 0.45 | 72.00 | 821 | 9 | 2 |
| Andaman Is. | 0.09 | 0.60 | 0.00 | 5935.85 | 718 | 656 | 22 |
| Antipodean Is. | 0.04 | 0.28 | 0.14 | 860.96 | 583 | 70 | 8 |
| Aruba | 0.03 | 0.06 | 0.36 | 206.40 | 129 | 88 | 14 |
| Ascension | 0.19 | 0.04 | 0.71 | 98.42 | 768 | 14 | 5 |
| Azores | 0.07 | 0.10 | 0.22 | 2102.12 | 2259 | 246 | 16 |
| Bahamas | 0.10 | 0.52 | 0.00 | 12812.50 | 51 | 378 | 19 |
| Baleares | 0.07 | 0.55 | 0.00 | 5101.61 | 1212 | 833 | 18 |
| Bermuda | 0.02 | 0.01 | 0.78 | 40.25 | 43 | 64 | 14 |
| Bismarck Archipelago | 0.12 | 0.62 | 0.00 | 48922.83 | 2153 | 705 | 20 |
| Borneo | 0.15 | 0.71 | 0.00 | 740169.23 | 3920 | 4874 | 22 |
| Canary Is. | 0.12 | 0.38 | 0.01 | 7521.19 | 3450 | 696 | 18 |
| Cape Verde | 0.10 | 0.08 | 0.28 | 3525.22 | 2517 | 234 | 16 |
| Cayman Is. | 0.08 | 0.33 | 0.01 | 306.41 | 42 | 166 | 18 |
| Central American Pac | 0.32 | 0.36 | 0.09 | 31.82 | 2 | 32 | 8 |
| Chagos Archipelago | 0.00 | NaN | NaN | 104.45 | 10 | 9 | 6 |
| Chatham Is. | 0.10 | 0.13 | 0.18 | 705.40 | 285 | 97 | 14 |
| Christmas I. | 0.09 | 0.04 | 0.42 | 123.98 | 317 | 59 | 16 |
| Cocos (Keeling) Is. | 0.00 | NaN | NaN | 28.74 | 15 | 26 | 10 |

|  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
| Comoros | 0.17 | 0.24 | 0.02 | 2173.54 | 2322 | 327 | 20 |
| Cook Is. | 0.15 | 0.13 | 0.15 | 201.04 | 402 | 100 | 16 |
| Corse | 0.03 | 0.44 | 0.00 | 8782.86 | 2404 | 1144 | 17 |
| Crozet Is. | 0.00 | NaN | NaN | 353.58 | 892 | 5 | 3 |
| Cuba | 0.18 | 0.86 | 0.00 | 109977.02 | 1748 | 2353 | 22 |
| Cyprus | 0.07 | 0.55 | 0.00 | 9258.51 | 1879 | 808 | 18 |
| Desventurados Is. | 0.23 | 0.20 | 0.70 | 6.00 | 330 | 6 | 2 |
| East Aegean Is. | 0.04 | 0.45 | 0.00 | 5596.34 | 1407 | 1004 | 19 |
| Easter Is. | 0.13 | 0.05 | 0.67 | 189.00 | 467 | 19 | 5 |
| Falkland Is. | 0.00 | NaN | NaN | 11751.17 | 698 | 48 | 10 |
| Fiji | 0.22 | 0.65 | 0.00 | 19318.75 | 1197 | 692 | 20 |
| Foroyar | 0.00 | NaN | NaN | 1599.57 | 881 | 207 | 12 |
| Galapagos | 0.22 | 0.31 | 0.02 | 7940.45 | 1685 | 146 | 16 |
| Gilbert Is. | 0.03 | 0.03 | 0.61 | 448.91 | 12 | 41 | 11 |
| Great Britain | 0.02 | 0.29 | 0.03 | 231139.79 | 1293 | 1377 | 15 |
| Gulf of Guinea Is. | 0.09 | 0.66 | 0.00 | 3193.12 | 2867 | 775 | 23 |
| Hainan | 0.09 | 0.61 | 0.00 | 34026.08 | 1724 | 1367 | 23 |
| Hawaii | 0.35 | 0.65 | 0.00 | 16871.77 | 4176 | 619 | 20 |
| Heard-McDonald Is. | 0.00 | NaN | NaN | 402.62 | 2686 | 2 | 1 |
| Hispaniola | 0.12 | 0.72 | 0.00 | 75678.61 | 2967 | 1686 | 22 |
| Howland-Baker Is. | 0.00 | 0.00 | 1.00 | 4.92 | 5 | 3 | 2 |
| Iceland | 0.01 | 0.07 | 0.45 | 102951.03 | 2005 | 678 | 10 |
| Ireland | 0.00 | 0.11 | 0.21 | 83999.78 | 909 | 666 | 15 |
| Jamaica | 0.15 | 0.64 | 0.00 | 11038.59 | 2097 | 1026 | 22 |
| Japan | 0.11 | 0.69 | 0.00 | 370584.27 | 3671 | 1920 | 20 |
| Jawa | 0.09 | 0.62 | 0.00 | 130751.35 | 3455 | 2760 | 22 |
| Juan Fernandez Is. | 0.36 | 0.19 | 0.14 | 151.65 | 505 | 62 | 12 |
| Kazan-retto | 0.11 | 0.08 | 0.39 | 41.14 | 405 | 48 | 11 |
| Kerguelen | 0.38 | 1.00 | 0.00 | 7464.08 | 1791 | 6 | 3 |
| Kermadec Is. | 0.21 | 0.07 | 0.41 | 50.06 | 392 | 32 | 11 |
| Kriti | 0.08 | 0.55 | 0.00 | 8611.81 | 2336 | 1000 | 19 |
| Kuril Is. | 0.05 | 0.40 | 0.01 | 10653.71 | 2153 | 396 | 14 |
| Laccadive Is. | 0.00 | NaN | NaN | 60.51 | 17 | 36 | 8 |
| Leeward Is. | 0.04 | 0.36 | 0.01 | 3415.55 | 1336 | 687 | 19 |
| Lesser Sunda Is. | 0.09 | 0.48 | 0.00 | 105148.47 | 3339 | 1162 | 22 |
| Line Is. | 0.14 | 0.16 | 0.32 | 619.51 | 7 | 19 | 7 |
| Lord Howe I. | 0.40 | 0.45 | 0.00 | 14.55 | 260 | 96 | 17 |
| Macquarie Is. | 0.30 | 0.21 | 0.36 | 128.29 | 328 | 15 | 5 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Madagascar | 0.23 | 0.82 | 0.00 | 592995.18 | 2744 | 4708 | 23 |
| Madeira | 0.10 | 0.15 | 0.12 | 825.12 | 1755 | 328 | 16 |
| Maldives | 0.00 | NaN | NaN | 140.46 | 7 | 41 | 11 |
| Maluku | 0.11 | 0.48 | 0.00 | 59736.00 | 2854 | 1351 | 22 |
| Marianas | 0.18 | 0.29 | 0.02 | 1192.59 | 774 | 206 | 18 |
| Marion-Prince Edward Is. | 0.57 | 0.50 | 0.29 | 338.06 | 1161 | 5 | 3 |
| Marquesas | 0.37 | 0.48 | 0.00 | 1086.53 | 1103 | 114 | 16 |
| Marshall Is. | 0.00 | NaN | NaN | 129.28 | 14 | 45 | 11 |
| Mauritius | 0.19 | 0.54 | 0.00 | 2055.72 | 714 | 482 | 21 |
| Mozambique Channel I | 0.12 | 0.23 | 0.12 | 14.97 | 9 | 34 | 11 |
| Nansei-shoto | 0.07 | 0.42 | 0.00 | 2107.96 | 443 | 675 | 22 |
| Nauru | 0.00 | NaN | NaN | 28.92 | 37 | 11 | 6 |
| Netherlands Antilles | 0.05 | 0.21 | 0.09 | 792.22 | 188 | 156 | 14 |
| New Caledonia | 0.24 | 0.78 | 0.00 | 19231.12 | 1504 | 1453 | 22 |
| New Guinea | 0.17 | 0.77 | 0.00 | 816427.27 | 4613 | 6698 | 23 |
| New Zealand | 0.16 | 0.64 | 0.00 | 267535.47 | 2943 | 820 | 19 |
| Newfoundland | 0.00 | NaN | NaN | 112135.05 | 832 | 364 | 15 |
| Nicobar Is. | 0.08 | 0.26 | 0.02 | 1865.90 | 520 | 380 | 21 |
| Niue | 0.02 | 0.03 | 0.54 | 252.73 | 84 | 85 | 14 |
| Norfolk Is. | 0.22 | 0.13 | 0.17 | 34.60 | 256 | 133 | 15 |
| Ogasawara-shoto | 0.22 | 0.17 | 0.07 | 76.54 | 374 | 135 | 19 |
| Philippines | 0.16 | 0.79 | 0.00 | 294705.82 | 2804 | 4098 | 23 |
| Phoenix Is. | 0.00 | NaN | NaN | 90.67 | 8 | 6 | 3 |
| Pitcairn Is. | 0.38 | 0.21 | 0.08 | 53.64 | 191 | 34 | 14 |
| Prince Edward I. | 0.00 | NaN | NaN | 5994.82 | 140 | 258 | 14 |
| Puerto Rico | 0.08 | 0.24 | 0.02 | 9245.97 | 1239 | 942 | 21 |
| Reunion | 0.19 | 0.58 | 0.00 | 2645.02 | 2930 | 471 | 20 |
| Rodrigues | 0.20 | 0.12 | 0.13 | 116.49 | 346 | 93 | 19 |
| Sakhalin | 0.05 | 0.58 | 0.00 | 75450.80 | 1415 | 439 | 14 |
| Samoa | 0.18 | 0.58 | 0.00 | 3172.18 | 1787 | 353 | 19 |
| Santa Cruz Is. | 0.05 | 0.15 | 0.14 | 851.75 | 753 | 88 | 15 |
| Sardegna | 0.04 | 0.41 | 0.00 | 24136.94 | 1812 | 968 | 18 |
| Selvagens | 0.08 | 0.11 | 0.39 | 1.86 | 0 | 37 | 8 |
| Seychelles | 0.20 | 0.20 | 0.04 | 328.50 | 757 | 207 | 21 |
| Sicilia | 0.05 | 0.55 | 0.00 | 26047.95 | 3237 | 1239 | 19 |
| Society Is. | 0.29 | 0.62 | 0.00 | 1529.71 | 1707 | 237 | 17 |
| Socotra | 0.20 | 0.39 | 0.00 | 3904.11 | 1439 | 280 | 19 |
| Solomon Is. | 0.14 | 0.55 | 0.00 | 36875.41 | 2641 | 909 | 21 |

|  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
| South Georgia | 0.00 | NaN | NaN | 3614.53 | 2758 | 7 | 3 |
| South Sandwich Is. | 0.00 |  | NaN | 279.0845103 | 1327 | 2 | 2 |
| Sri Lanka | 0.12 | 0.65 | 0.00 | 66288.49 | 2406 | 1583 | 22 |
| St.Helena | 0.36 | 0.27 | 0.23 | 133.03 | 718 | 30 | 6 |
| Sulawesi | 0.12 | 0.65 | 0.00 | 186001.80 | 3306 | 1968 | 22 |
| Sumatera | 0.10 | 0.50 | 0.00 | 470941.94 | 3605 | 3477 | 23 |
| Svalbard | 0.00 | NaN | NaN | 63032.49 | 2103 | 91 | 6 |
| Taiwan | 0.12 | 0.61 | 0.00 | 36163.74 | 3741 | 1705 | 23 |
| Tasmania | 0.12 | 0.42 | 0.00 | 68502.12 | 1551 | 755 | 17 |
| Tonga | 0.06 | 0.26 | 0.03 | 776.17 | 730 | 198 | 17 |
| Trinidad-Tobago | 0.04 | 0.31 | 0.01 | 5029.53 | 849 | 788 | 22 |
| Tristan da Cunha | 0.38 | 0.81 | 0.04 | 170.94 | 1961 | 31 | 4 |
| Tuamotu | 0.20 | 0.28 | 0.04 | 288.23 | 86 | 45 | 14 |
| Tubuai Is. | 0.24 | 0.47 | 0.00 | 98.86 | 343 | 87 | 14 |
| Turks-Caicos Is. | 0.18 | 0.22 | 0.08 | 420.14 | 25 | 26 | 14 |
| Tuvalu | 0.00 | NaN | NaN | 52.81 | 14 | 13 | 7 |
| Vanuatu | 0.16 | 0.62 | 0.00 | 12697.74 | 1698 | 450 | 19 |
| Venezuelan Antilles | 0.02 | 0.13 | 0.10 | 1401.40 | 801 | 220 | 21 |
| Wake I. | 0.00 | NaN | NaN | 19.53 | 5 | 5 | 3 |
| Wallis-Futuna Is. | 0.00 | NaN | NaN | 166.35 | 383 | 110 | 15 |
| Windward Is. | 0.07 | 0.37 | 0.00 | 3803.37 | 1314 | 671 | 22 |

**Table 2:**

| Dependent variables | Predictors | Parameters |
|---|---|---|
| **Slope-coefficient** | | $R^2 = 0.27$*** |
| | Log (S) | -0.048 *** |
| | Elevation | 3.8E-05** |
| | | |
| **$R^2$** | | $R^2 = 0.52$*** |
| | Number of Families | 0.01 * |
| | Log (Area) | 0.06 *** |
| | | |
| **P** | | $R^2 = 0.57$*** |
| | Number of Families | -0.02 *** |
| | Log (Area) | -0.13 *** |
| | (Log (Area)^2 | 0.007 *** |

# Chapter 3

# Functional diversity of summit scrub vegetation on Tenerife Island (Canary Islands, Spain)

## Abstract

We investigated plant functional diversity within the native subalpine flora of a subtropical island, Tenerife (Canary islands, Macaronesia). We measured traits related to important dimensions of plant adaptation, including competition (especially plant height), growth strategy (esp. specific leaf area, SLA), phenology (flowering period), plant-nutrient relations (leaf nutrient content, C/N ratio, and stable nitrogen isotope ratio, δ15N), and plant-water relations (leaf area, and stable carbon isotope ratio, δ13C).

Values for SLA, LWC, leaf area, and leaf nutrient content were mainly low, as might be expected for plants in a harsh, nutrient-poor environment, but variation among species was high. Species were broadly differentiated into those with thin leaves with low content of structural tissue (high SLA and LWC), large leaf area, and low δ13C (indicative of low water use efficiency), and those with opposing traits. Nutrient uptake strategies – as indicated by differences in δ15N – varied widely among species (including those from the same families such as Fabaceae), with these traits varying to some extent independently of those associated with water use. High functional diversity was found especially within genera that were not specialized to high elevation habitat, while species from specialized and putatively pre-adapted species showed a narrower range of traits more typical of the habitat (e.g. low leaf area and SLA). It appears that adaptive radiations from herbaceous species have been able to fill a broad range of niches within the subalpine, but that the niche of larger woody plants has been occupied by species from high elevation genera. The high functional diversity recorded in this subalpine flora, which has apparently arisen through high phylogenetic diversity and adaptive radiations within phylogenetic lineages, contradicts the idea that island floras are always ecologically depauperate.

## Introduction

Oceanic islands are famous for their high species diversity (Myers et al. 2000, Kreft et al. 2008, Kier et al. 2009, Caujapé-Castells et al. 2010), but less is known about the functional diversity of their biota. It is often assumed that island plants are characterized by a common set or syndrome of traits such as woodiness of herbaceous plants, loss of dispersibility, low competitive ability and growth rates, or high rate of selfing (Carlquist 1974, Barrett et al. 1996, Givnish 1998, Leigh et al. 2007, Whittaker and Fernández-Palacios 2007). If true, this would imply low functional diversity, with traits of different species largely converging. Indeed, there are indications that alien plants sometimes profit from empty niches due to the absence on some islands of traits such as nitrogen-fixation or high resource-use efficiency (Vitousek 1990, Funk and Vitousek 2007), specialized fruits (Kueffer et al. 2009), or a fast growth strategy and associated traits such as high photosynthetic capacity (Pattison et al. 1998, Baruch and Goldstein 1999, Kueffer et al. 2008, Schumacher et al. 2009). But research on islands has also documented some of the best examples of ecological divergence, either when competitive interactions among species have led to character displacement (Grant 1998) or when adaptive radiations produced species-rich lineages that now occupy contrasting habitats or microhabitats (Losos and Ricklefs 2009). Such adaptation to different habitat would be expected to lead to a diversification of functional traits, although few studies have investigated the evolution of plant traits during adaptive radiation (but see Montgomery and Givnish 2008, Dunbar- Co et al. 2009, Santiago and Kim 2009).

Recent research concerning plant functional traits has opened new possibilities for studying the functional diversity of island floras. Standard protocols have been defined for determining key plant traits (Cornelissen et al. 2003a, Kattge et al. 2011, Perez-Harguindeguy et al. 2013), and the ecological significance of many traits are now better understood (Westoby et al. 2002, Wright et al. 2004, Lavorel et al. 2007). It has been suggested that the range of plant functional adaptations is largely defined by three independent dimensions related to dispersibility (esp. seed mass), competition (esp. plant height), and resource use (esp. specific leaf area, SLA) (Westoby et al. 2002). In particular, it has been shown that leaf traits such as SLA, leaf nutrient contents, and leaf longevity are correlated along a trait-spectrum from fast growing to slow growing species (Wright et al. 2004). Besides these growth-related traits, another important dimension of ecological differentiation in plants is the timing of reproductive events – phenology – that allows plants to occupy different reproductive niches (e.g. Grubb 1977, Godoy and Levine 2014).

In this study, we investigated the plant functional diversity of subalpine summit scrub habitat on a subtropical island, Tenerife (Canary islands, Macaronesia). High elevation habitat might be of particular interest for studying the relationship between taxonomic and functional plant diversity on islands for a number of reasons. It is characterized by harsh environmental conditions that expose plant traits to strong selective pressure, endemism is often particularly high in this habitat, and most species are from different phylogenetic lineages resulting in high phylogenetic diversity (Domínguez Lozano et al. 2010, Steinbauer et al. 2012). We were interested in three questions:

- First, do the same dimensions of plant adaptation account for plant functional diversity on islands as on continents? In particular, what is the relative importance of the leaf economics spectrum, measured in terms of SLA and foliar nitrogen concentration (Wright et al. 2004)?
- Second, how functionally diverse is the flora? Is the trait spectrum restricted to narrow ranges, in line with the expectation of reduced functional diversity on islands (e.g. Kueffer et al. 2009), or not? Are there differences in variability among traits?
- Third, do species reaching high-elevation habitats through adaptive radiation exhibit different combinations of traits from habitat specialists that belong to genera confined to this habitat? According to the taxon cycle model proposed by Wilson (1961), species colonize islands at low elevations and thereafter reach geographically and ecologically distant habitat – such as high elevation habitat – through evolutionary expansion across habitats. Alternatively, colonizing species might have established from the beginning at high elevation and some of them might have profited from pre-adaptation to a mountain environment.

## Methods

### *Study area*

This study was performed on Tenerife, the largest and highest volcanic island of the Canary islands archipelago, which is situated c. 100 km off the Northwest coast of Africa in the North Atlantic Ocean (Fig. 1). Tenerife, which is of volcanic origin, reaches 3718 m asl. at the peak of the Teide and occupies a total area of 2039 $km^2$. It is a true oceanic island, having never been connected to a continent (Fernández-Palacios et al. 2014). Summit scrub vegetation is in the Canary Islands also represented on La Palma reaching 2425 m asl. at Taburiente (Fernández-Palacios et al. 2014).

The climate of Tenerife is Mediterranean and is strongly influenced by the prevailing trade winds, which create a steep humidity gradient from the humid northeast to the more arid southwest (Fernández-Palacios 2011). Low elevation vegetation is composed of Euphorbia-dominated scrub, followed by elevation belts of different forest communities (dry sclerophyllous woodlands, laurel forest, and pine forest) and shrub-dominated subalpine vegetation above the treeline (summit scrub) (Fernández-Palacios 1992). Summit scrub vegetation is located between c. 1800 and 2300 m asl. and is characterized by a harsh climate, i.e. low temperatures, high radiation, strong winds, drought and a short flowering season. Plant material was sampled from the summit scrub vegetation and the ecotone with pine forest in Teide National Park (28°15’N, 16° 36’W) at 1755 to 2360 m asl.

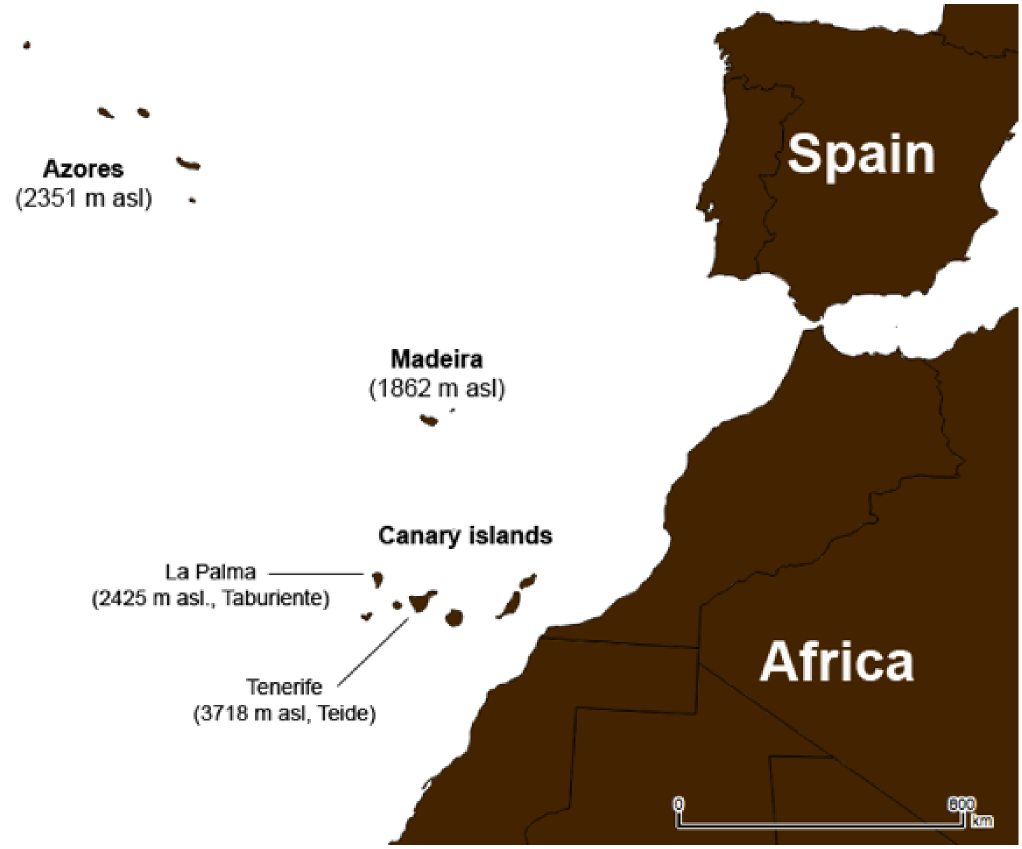

**Figure 1:** The Macaronesian region with the study area situated in the summit scrub vegetation (1800 - 2300 m asl.) on Tenerife island. The highest elevation is given for the two islands in the Canary islands with summit scrub vegetation (Tenerife with the highest peak Teide, and La Palma with Taburiente) and for the other Macaronesian island groups represented on the map.

### *Field collection of plant material*

All plant samples were collected in the field during the growing season from May to June 2012 from a total of 33 native summit scrub species (Appendix 1). We sampled most woody native species of the habitat (chamaephytes, shrubs, trees), excluding herbaceous species.

We aimed to collect replicate leaf samples per species from 10 different locations, but this was only possible for the 14 most abundant species (Appendix 2). For most other species, samples were collected from at least 3 different locations, and for some rare species plant material could only be collected from an *in situ* rare plant living collection at El Portillo Botanical Garden situated within the natural landscape of Teide National Park (Appendix 2). An individual sample consisted in general of measures taken from one randomly selected, healthy adult plant, but in a few cases it was necessary to use several nearby individuals to obtain enough material.

### *Measurements of plant traits*

We measured plant traits that are known to correlate with the main dimensions of plant adaptation, including competition (especially plant height), growth strategy (esp. specific leaf area), phenology (flowering period), plant-nutrient relationship (nutrient content, C/N ratio, and stable nitrogen isotope ratio), and plant-water relationship (leaf area, and stable carbon isotope ratio). For most measurements of plant functional traits we followed protocols outlined in Cornelissen et al. (2003b).

Chlorophyll content was measured using a SPAD-502 chlorophyll meter (Konica Minolta, Tokyo, Japan) on 10 leaves per sampled individual in the field. The chlorophyll meter measures red light absorbance in arbitrary “SPAD units” that correlate closely with leaf chlorophyll content. For each data point, the 3 measurements per leaf blade (avoiding the midrib) were averaged. We then collected twigs growing in sunny situations and bearing young, fully expanded, undamaged leaves. Depending on leaf size, a minimum of 20 adult leaves or 3 grams of dry material were collected per sample and sealed in a polythene bag. The material was subsequently oven-dried at 80 °C for 48 h and reweighed to determine dry mass. Leaf area was calculated from scans using Image-J software (Rueden and Eliceiri 2007). Specific leaf area (SLA) was calculated as the leaf area ($mm^2$) per unit of dry leaf mass (mg). The leaf blades and petioles were separately scanned and weighed (fresh weight), so that values of SLA both with and without petioles could be determined. We did not find any significant difference between these two SLA measures, so only SLA with petiole was included in the analysis. For the leafless plant, *Spartocytisus supranubius*, the top 2 cm of a young twig was sampled and treated as leaf, and then the same procedure was followed as for true leaves. Leaf water content (LWC) was calculated as (fresh mass-dry mass)/ fresh mass.

Dried leaf material was ground for C, N and stable isotope analysis. Dry leaves were milled to a fine powder, and 3 – 5 mg samples were used to determine carbon and nitrogen isotope ratios (δ13C and δ15N, respectively) and the concentrations. These analyses were made using a Flash EA 1112 series elemental analyzer (Thermo Italy, Rhodano, Italy) coupled to a Finnigan MAT DeltaplusXP isotope ratio mass spectrometer (Finnigan MAT, Bremen, Germany) via a six-port valve and a ConFlo III (Werner et al. 1999) . Leaf nitrogen concentration (LNC) is the total amount of nitrogen per unit of dry leaf mass (in mg/g). In addition to these trait measurements, information on taxonomy, habitat distribution, plant height, and flowering period were compiled from the literature (Schönfelder 2012).

### *Data analysis*

We used a restricted maximum likelihood (REML) approach based on the lmer function in R to perform nested analysis of variance. This allowed us to partition the total explained variance among taxonomic levels (individuals, species, families). All other analyses were performed with arithmetic means per species. Correlations among leaf traits were analyzed with Pearson's correlation coefficients. The relationships among plant height, flowering length and 7 leaf traits were analyzed with a principal component analysis. Species were classified into two groups based on whether they belonged to a genus that on Tenerife is confined to pine forest or summit scrub (high elevation specialist, S) or includes species occurring in other habitats (generalist, G). We then used one-way anova to test whether plant traits differed systematically between the two groups. All statistical analyses were carried out using R.

## Result

### *Variability of plant traits*

All plant traits varied widely among species (Fig 2). Most species were low-statured woody chamaephytes or small shrubs of 0.5 m to 1.5 m height, but tall shrubs and tree species were also represented. Leaf sizes tended to be small, which is expected in sun- / UV-radiation-exposed, dry and/or cold environments like summit scrub in Tenerife (Cornelissen et al. 2003a). But especially the leaves of the rosette-forming *Echium* species were large (> 2500 mm$^2$). SLA values tended to be very low, but variation was large. Values for some species were among the lowest reported in the literature (< 6 mm$^2$ mg$^{-1}$). These included not only ‘special cases’, such as the leafless *Spartocytisus supranubius* and the needle-bearing *Pinus canariensis*, but also species with ‘true’ leaves such as *Echium wildpretii*, *Helianthemum juliae*, or *Senecio palmensis*. The thinnest leaves were found for several Asteraceae species (> 16 mm$^2$ mg$^{-1}$), which also had the highest chlorophyll contents (Fig. 3). Nitrogen contents were mainly very low (and C/N ratios were correspondingly high), which could be expected on these nitrogen-poor young volcanic soils; however, some species – especially from the Fabaceae and Brassicaceae and two non-endemic species – had relatively nitrogen-rich leaves. δ15N varied widely but was only weakly related to LNC (Fig. 2 and Appendix 3). For this trait, we found high variation among individuals (Fig. 4), perhaps because of site differences in soil δ15N ratios (Craine et al. 2009). Interestingly, variation in this trait was also high among species from the same family, in particular for species of Fabaceae (-2.0‰ to 1.2 ‰). More generally, differences between species might be related to the importance and type of mycorrhizal symbiosis that can substantially lower δ15N (Craine et al. 2009). As expected, the highest values for δ13C were for the two Crassulaceae species (-23.6 ‰, -22.0‰), and were in the range indicative of facultative CAM metabolism (Perez-Harguindeguy et al. 2013). The other species had values typical of C3 photosynthesis (-25 ‰, to -30‰). The flowering period was well-defined for most species and restricted to a few months. While most of the variation for plant height, leaf area, and carbon isotope ratio was found at a family-level, variation for SLA, chlorophyll content, and nitrogen-related traits was mostly found at a species-level (Fig. 4).

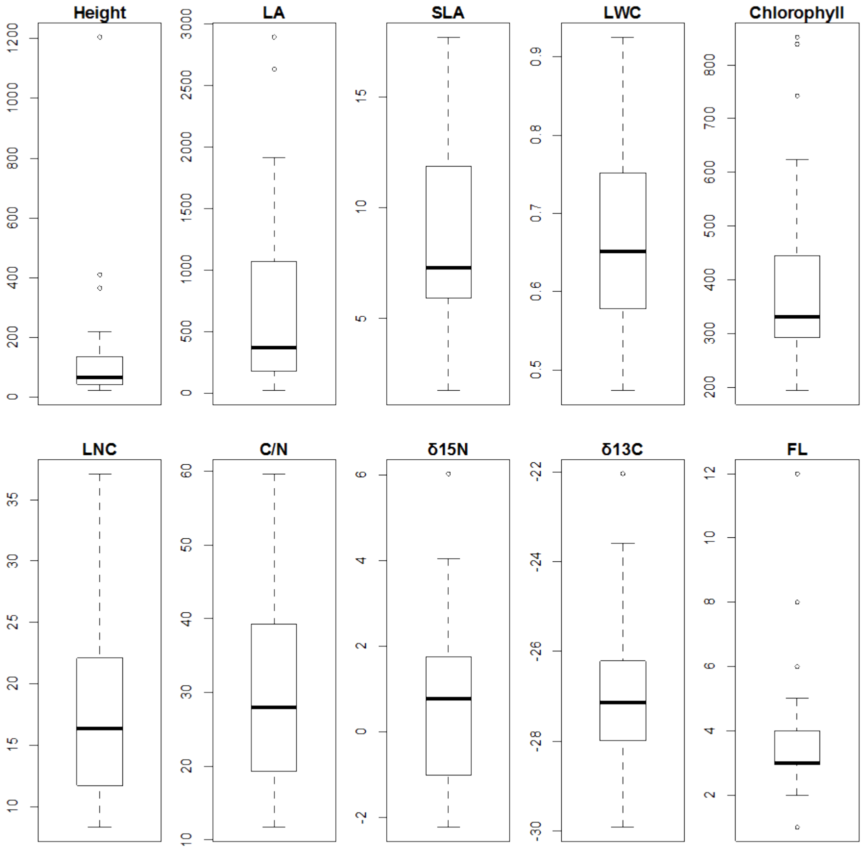

**Figure 2:** Median values and variation (box: 25% and 75% percentiles, whiskers: 1.5-times the interquartile range of the data) of plant height, flowering length (FL) and eight leaf traits for 33 woody species (chamaephytes, shrubs, and trees) of summit scrub habitat on Tenerife (Canary islands): plant height (cm); leaf area (LA, $mm^2$); specific leaf area (SLA, $mm^2/mg$); leaf water content (%, LWC); mass-based chlorophyll content (Chlorophyll, SPAD units), mass-based leaf nitrogen content (LNC, mg/g); carbon to nitrogen content ratio (C/N); stable carbon isotope ratio (δ13C, ‰); stable nitrogen isotope ratio (δ15N, ‰); and flowering length (month). The complete data is shown in Appendix 1.

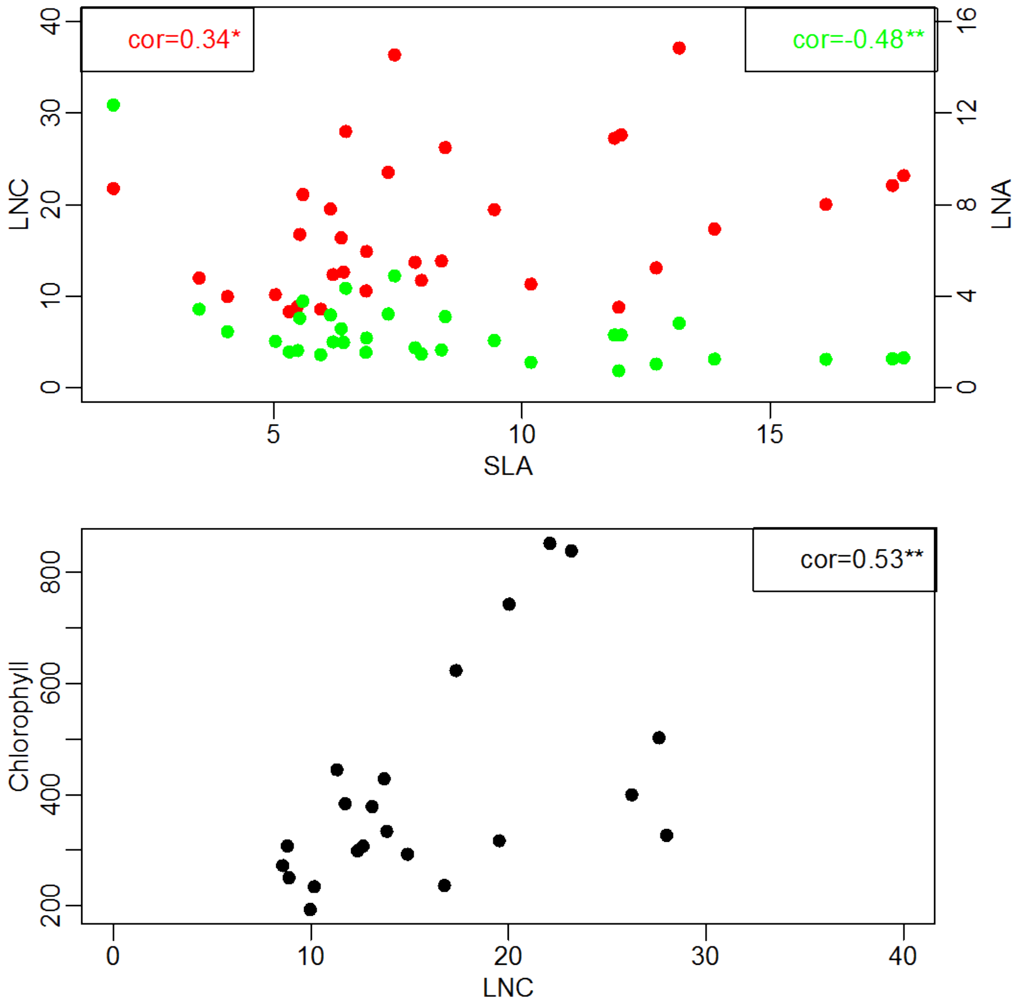

**Figure 3:** The upper panel shows the relationship between specific leaf area (SLA) and leaf nitrogen content per mass (LNC, mg/g, red dots) and per area (LNA, mg/mm$^2$, green dots). The lower panel shows the relationship between LNC and mass-based chlorophyll content (chlorophyll, SPAD units). The four species with the highest chlorophyll values are *Andryala pinnatifida*, *Tolpis lagopoda*, *Tolpis webbii*, and *Nepeta teydea*.

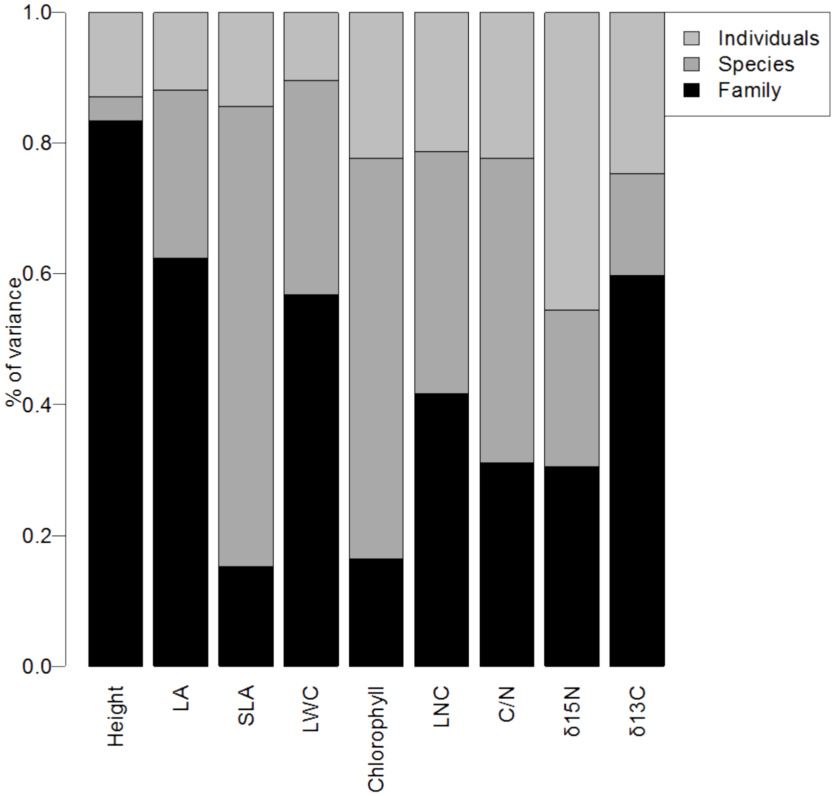

**Figure 4:** Partitioning of the total explained variance among three taxonomic levels (individuals, species, families) for those traits for which the necessary data was available. See Figure 1 for abbreviations.

### *Correlations among leaf traits*

Figure 5 shows the results of a principal component analysis based upon 9 plant traits and 33 plant species. The chlorophyll measurements were excluded from this analysis because of missing values for some species, but chlorophyll and nitrogen content correlated rather well (Fig. 3). The first two axes of the PCA explained 32% and 19.5% of the observed variability, respectively, accounting for a total of 51.5% of the variability (Fig 5). For the first axis, C/N had the highest factor loading of 0.51, followed by specific leaf area (SLA) and leaf nitrogen concentration (LNC) with loadings of 0.47 and 0.46, respectively. For the second axis, leaf water content (LWC) and C/N contributed negatively, with factor loadings of -0.51 and -0.38, respectively, and leaf nitrogen concentration (LNC) and height contributed positively, with loadings of 0.50 and 0.42, respectively. SLA correlated only weakly with leaf nitrogen content, especially when it was calculated 'per unit mass' rather than 'per unit area' (Fig. 3).

Overall, the PCA analysis revealed two major axes. In the lower left corner are tall species with thick and small leaves while in the upper right corner are low-statured species with thin and larger leaves. The second dimension from the upper left to the lower right corner differentiates between species with nitrogen-poor versus nitrogen-rich leaves. The PCA analysis generally grouped species of the same family together (Fig. 5).

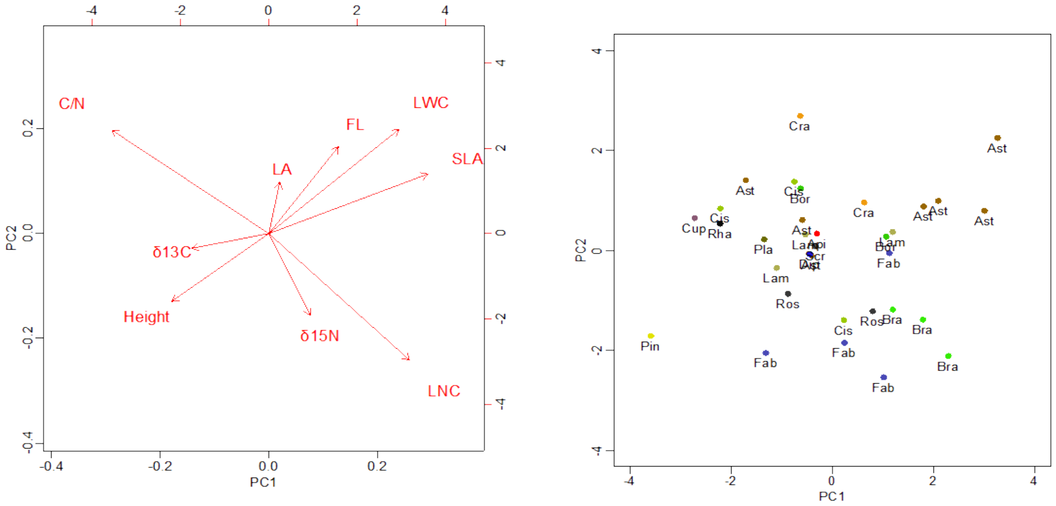

**Figure 5:** Principal-component analysis of 9 plant traits of the 33 study species. See Figure 1 for abbreviations. *Api (Apiaceae), Ast (Asteraceae), Bor (Boraginaceae), Bra (Brassicaceae), Cis (Cistaceae), Cra (Crassulaceae), Cup (Cupressaceae), Dip (Dipsacaceae), Fab (Fabaceae), Lam (Lamiaceae), Pin (Pinaceae), Pla (Plantaginaceae), Rha (Rhamnaceae), Ros (Rosaceae), Scr (Scrophulariaceae).*

### *High elevation generalist versus specialist genera*

Genera restricted to high elevation habitat (‘specialists’) separated from those that also occurred in other habitats (‘generalists’) along the first PCA axis. This reflected the fact that specialists were mostly tall species with small and thick leaves, while generalists had contrary traits. In contrast, there were no differences between the two groups in nitrogen-related traits (Fig 6).

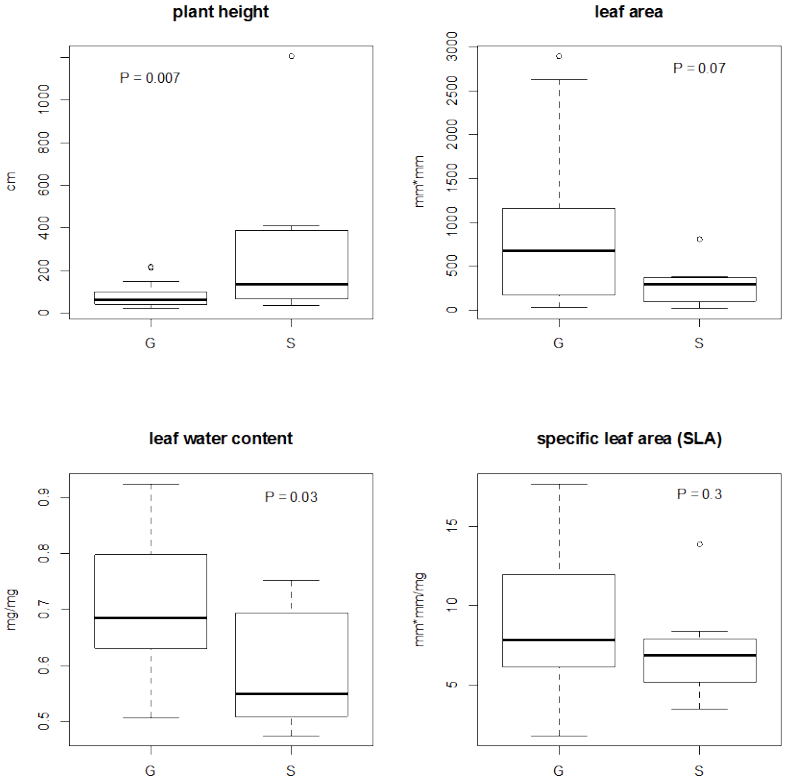

**Figure 6:** plant height, leaf area (LA), leaf water content (LWC) and specific leaf area (SLA) for species that belong either to a genus that occurs on Tenerife exclusively in pine forest or summit scrub (high elevation specialist, S) or with species occurring in more habitats (generalist, G). For other traits in Figure 1 there was no significant difference between the two groups (P = 0.4-0.9).

## Discussion

The plant traits investigated have been shown in other studies to be related to important dimensions of plant adaptation, namely competition (especially plant height), growth strategy (esp. specific leaf area), phenology (flowering period), plant-nutrient relations (nutrient content, C/N ratio, and stable nitrogen isotope ratio), and plant-water relations (leaf area, and stable carbon isotope ratio). We were interested in whether the same patterns of variation also apply to the flora of subalpine summit scrub vegetation on the subtropical island Tenerife (Canary islands, Macaronesia). In particular, we wanted to know how diverse was plant functional diversity in this island flora, and whether species resulting from adaptive radiation differed functionally from those in genera that occurred only at high elevation.

### *Two conflicting dimensions of plant adaptation*

Contrary to expectation (Westoby et al. 2002, Wright et al. 2004), specific leaf area (SLA) and leaf water content (LWC) correlated only weakly with leaf nitrogen content and leaf carbon to nitrogen content ratio (C/N) (Appendix 3 and Fig. 3). It appears that SLA was more a reflection of climatic conditions than of nutrient relations. Thus, species were differentiated into those with thin leaves with low content of structural tissue (high SLA and LWC), large leaf area and a low carbon isotope ratio – indicative of low water use efficiency over a leaf's lifetime (e.g. Lambers et al. 2008) – and those with the opposite traits. Interestingly, small, thick leaves that represent adaptation against environmental harshness (water stress, cold temperature, and/or sunlight- or UV-exposure) (e.g. Cornelissen et al. 2003a) were mostly found in tall shrubs and trees, while some of the smaller plants had leaves that were less protected. One possible explanation is that plants of low stature profited from a more benign microclimate close to the ground and therefore experienced less selection to invest in leaf protection. Some of the species with high SLA – especially several Asteraceae species – were also rich in nitrogen and chlorophyll, but in other species nitrogen-related traits varied independently of SLA (Fig. 4). Indeed, the six Fabaceae and Brassicaceae with particularly nitrogen-rich leaves expressed a broad variation in SLA (1.8 – 13.2 $mm^2/mg$). Thus, we documented a partial decoupling of SLA-related traits from traits related to nitrogen use. Besides the proposed conflicting dimensions of plant adaptation – adaptation to environmental harshness and different resource-use strategies –, the wide range in δ15N values indicates that species differed widely in their strategies for nutrient uptake. It appears that fixation does not play an equally important role in the nitrogen economy of all legumes, and that other processes such as mycorrhizal uptake may also be significant for some species.

### *High functional diversity through high phylogenetic diversity*

As might be expected in a harsh, nutrient-poor environment, values for SLA, LWC, leaf area, and leaf nutrient content were skewed towards the lower ranges found in the global woody flora (compare Cornelissen et al. 2003a, Wright et al. 2004, Kueffer et al. 2008, Kattge et al. 2011), though variation among species was nevertheless very large for all traits (Fig. 2). SLA for instance varied between 1.8 and 17.7 $mm^2$/mg, which is comparable to the variation between 2.7 and 16.2 $mm^2$/mg found among native and invasive woody species in Seychelles (Kueffer et al. 2008).

Such high diversity was in particular found among species from genera that were not specialized to high elevation habitats, while species from specialized and putatively pre-adapted species showed narrower ranges of traits more typical of the habitat (e.g. low leaf area and SLA). It appears that adaptive radiations from mainly herbaceous species were able to fill many niches, but not those of large shrubs and trees, which are taken by pre-adapted species from genera that occur only at high elevation.

The high functional diversity we recorded can partly be related to a high phylogenetic diversity of the flora, reflected in the fact that the species we studied mainly belonged to different genera. Indeed, species of the same family usually grouped together in the principal component analysis (Fig. 5), indicating a high phylogenetic conservatism of functional traits (see also Fig. 4). But there were also indications that traits have diverged (Fig. 4) as species in some families have adapted to a high elevation environment (Fig. 5). For instance, species such as *Echium wildpretii*, *Helianthemum juliae*, or *Senecio palmensis* from large and originally herbaceous genera with relatively thin leaves had very low SLA. The high variation of δ15N values between species from the same family indicates that in particular evolution of nutrient uptake strategies might be worth further investigation.

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# Supporting Information

**Appendix 1:** Characteristics and mean measurement values for the 33 woody summit scrub species from Tenerife (Canary islands) included in the study. Data is shown for: plant height, leaf area (LA), specific leaf area (leaf area per leaf mass, SLA), leaf water content ((fresh-dry leaf weight) to fresh leaf weight, LWC), mass-based chlorophyll content (Chlorophyll, SPAD units), mass-based leaf nitrogen (LNC), carbon to nitrogen content ratio (C/N), stable carbon isotope ratio (δ13C), stable nitrogen isotope ratio (δ15N), flowering length (FL), and life form (LF). The last column classifies the genus of the species as high elevation specialist (S) if all native species of the genus on Tenerife occur only in pine forest or summit scrub; if the genus of the species occurs in more habitats it is classified as a generalist (G). All species are endemic to Tenerife, expect for *Bituminaria bituminosa* and *Rosa canina* (marked by an asterisk).

| Species | Abbr. | Family | Height [cm] | LA [mm$^2$] | SLA [mm$^2$/mg] | LWC [%] | Chlorophyll | LNC [mg/g] | C/N | δ15N [‰] | δ13C [‰] | FL [month] | LF | Specialist |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Adenocarpus viscosus* | Ad.vi | Fabaceae | 161.70 | 18.62 | 7.43 | 0.57 | NA | 36.37 | 13.72 | 0.90 | -26.87 | 3 | Shrub | S |
| *Aeonium smithii* | Ae.sm | Crassulaceae | 22.00 | 327.49 | 12.70 | 0.93 | 378.30 | 13.10 | 31.53 | 2.81 | -22.04 | 4 | Chamaephyte | G |
| *Aeonium spathulatum* | Ae.sp | Crassulaceae | 33.80 | 142.18 | 11.95 | 0.92 | 307.57 | 8.80 | 54.67 | -2.23 | -23.59 | 4 | Chamaephyte | G |
| *Andryala pinnatifida* | An.pi | Asteraceae | 60.60 | 952.60 | 17.47 | 0.82 | 851.91 | 22.10 | 19.99 | -0.84 | -28.58 | 12 | Chamaephyte | G |
| *Argyranthemum tenerifae* | Ar.te | Asteraceae | 36.90 | 311.83 | 9.44 | 0.80 | NA | 19.47 | 22.62 | 0.89 | -29.27 | 8 | Shrub | G |
| *Bencomia exstipulata* | Be.ex | Rosaceae | 136.50 | 1726.46 | 5.52 | 0.58 | 236.52 | 16.75 | 27.91 | 2.18 | -25.48 | 2 | Shrub | G |
| *Bituminaria bituminosa** | Bi.bi | Fabaceae | 61.90 | 1038.16 | 8.45 | 0.70 | 399.84 | 26.24 | 17.12 | -1.95 | -27.11 | 5 | Chamaephyte | G |
| *Carlina xeranthemoides* | Ca.xe | Asteraceae | 66.00 | 174.90 | 6.35 | 0.65 | NA | 16.37 | 26.57 | -1.48 | -26.87 | 3 | Shrub | G |
| *Chamaecytisus proliferus* | Ch.pr | Fabaceae | 410.30 | 371.58 | 6.44 | 0.53 | 326.78 | 28.00 | 17.41 | 1.24 | -27.36 | 6 | Tree | S |
| *Cheirolophus teydis* | Ch.te | Asteraceae | 99.70 | 249.20 | 7.97 | 0.68 | 383.87 | 11.73 | 39.20 | -0.22 | -27.98 | 3 | Shrub | G |
| *Cistus osbaeckiaefolius* | Ci.os | Cistaceae | 87.40 | 739.69 | 5.47 | 0.53 | 250.30 | 8.89 | 51.89 | -1.71 | -26.96 | 3 | Shrub | G |
| *Cistus symphytifolius* | Ci.sy | Cistaceae | 142.17 | 1910.22 | 6.19 | 0.62 | 298.59 | 12.35 | 39.17 | -1.66 | -28.08 | 6 | Shrub | G |
| *Descurainia bourgeauana* | De.bo | Brassicaceae | 66.70 | 61.58 | 13.16 | 0.65 | NA | 37.12 | 11.71 | 2.15 | -26.93 | 3 | Shrub | G |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Descurainia lemsii* | De.le | Brassicaceae | 43.20 | 127.06 | 11.86 | 0.69 | NA | 27.26 | 15.96 | 3.21 | -27.65 | 3 | Shrub | G |
| *Echium auberianum* | Ec.au | Boraginaceae | 27.33 | 2631.54 | 6.14 | 0.81 | 317.17 | 19.53 | 19.33 | 1.66 | -28.19 | 3 | Chamaephyte | G |
| *Echium wildpretii* | Ec.wi | Boraginaceae | 148.90 | 2893.46 | 4.06 | 0.78 | 193.30 | 9.96 | 36.89 | 1.55 | -27.30 | 4 | Chamaephyte | G |
| *Erysimum Scoparium* | Er.sc | Brassicaceae | 55.78 | 179.00 | 7.30 | 0.75 | NA | 23.53 | 16.98 | 4.04 | -26.66 | 4 | Chamaephyte | S |
| *Helianthemum juliae* | He.ju | Cistaceae | 42.50 | 55.86 | 5.58 | 0.63 | NA | 21.11 | 20.54 | 1.93 | -28.21 | 2 | Chamaephyte | G |
| *Juniperus wedrus* | Ju.ce | Cupressaceae | 365.20 | 19.22 | 5.31 | 0.51 | NA | 8.31 | 59.67 | 0.17 | -26.01 | 6 | Tree | S |
| *Nepeta Teydea* | Ne.te | Lamiaceae | 36.60 | 343.10 | 13.88 | 0.71 | 623.19 | 17.34 | 26.17 | 0.93 | -27.73 | 4 | Chamaephyte | S |
| *Pimpinella wumbrae* | Pi.cu | Apiaceae | 36.80 | 1253.21 | 6.86 | 0.69 | 292.72 | 14.89 | 28.70 | -1.01 | -27.20 | 2 | Chamaephyte | G |
| *Pinus canariensis* | Pi.ca | Pinaceae | 1205.60 | 246.52 | 3.49 | 0.51 | NA | 11.99 | 40.45 | -0.32 | -25.88 | 3 | Tree | S |
| *Plantago webbii* | Pl.we | Plantaginaceae | 55.40 | 26.27 | 6.85 | 0.65 | NA | 10.58 | 44.38 | 0.90 | -26.06 | 2 | Chamaephyte | G |
| *Pterocephalus Lasiospermus* | Pt.la | Dipsacaceae | 79.00 | 376.23 | 8.37 | 0.68 | 334.10 | 13.84 | 36.09 | 3.22 | -24.88 | 4 | Shrub | S |
| *Rhamnus integrifolia* | Rh.in | Rhamnaceae | 110.00 | 807.62 | 5.02 | 0.47 | 234.34 | 10.17 | 48.32 | -2.19 | -27.52 | 3 | Shrub | S |
| *Rosa canina** | Ro.ca | Rosaceae | 218.33 | 1689.56 | 12.00 | 0.65 | 502.40 | 27.62 | 17.27 | 0.30 | -25.61 | 1 | Shrub | G |
| *Scrophularia glabrata* | Sc.gl | Scrophulariaceae | 63.30 | 678.26 | 10.18 | 0.72 | 444.91 | 11.31 | 48.62 | 6.03 | -27.14 | 2 | Chamaephyte | G |
| *Senecio palmensis* | Se.pa | Asteraceae | 60.00 | 235.27 | 5.94 | 0.63 | 272.36 | 8.57 | 57.62 | -1.01 | -28.01 | 4 | Chamaephyte | G |
| *Sideritis ericocephala* | Si.er | Lamiaceae | 32.80 | 1068.80 | 6.40 | 0.52 | 307.31 | 12.64 | 37.18 | 1.74 | -27.51 | 2 | Shrub | G |
| *Sideritis oroteneriffae* | Si.or | Lamiaceae | 76.00 | 1158.74 | 7.84 | 0.63 | 428.60 | 13.71 | 33.38 | 0.02 | -26.95 | 3 | Shrub | G |
| *Spartocytisus supranubius* | Sp.su | Fabaceae | 212.30 | 55.65 | 1.76 | 0.51 | NA | 21.77 | 23.89 | 0.65 | -26.21 | 2 | Shrub | G |
| *Tolpis lagopoda* | To.la | Asteraceae | 44.00 | 1079.86 | 17.69 | 0.85 | 838.73 | 23.18 | 19.21 | 0.77 | -29.91 | 4 | Chamaephyte | G |
| *Tolpis webbii* | To.we | Asteraceae | 101.00 | 502.06 | 16.12 | 0.83 | 742.60 | 20.03 | 21.69 | -2.16 | -29.91 | 3 | Chamaephyte | G |

**<u>Appendix 2:</u>** Number of samples (different individuals) and sampling sites per species for the collection of data in the field. The abundance in the habitat is indicated by three categories: very frequent, frequent, and rare.

| **Species name** | **Abbr.** | **Abundance** | **Number of Samples** | **Number of Sites** |
|---|---|---|---|---|
| *Adenocarpus viscosus* | Ad.vi | Very frequent | 10 | 10 |
| *Argyranthemum tenerifae* | Ar.te | Very frequent | 10 | 10 |
| *Carlina xeranthemoides* | Ca.xe | Very frequent | 10 | 10 |
| *Chamaecytisus proliferus* | Ch.te | Very frequent | 10 | 10 |
| *Cheirolophus teydis* | Ch.te | Very frequent | 10 | 10 |
| *Descurainia bourgeauana* | De.bo | Very frequent | 10 | 10 |
| *Echium wildpretii* | Ec.wi | Very frequent | 10 | 10 |
| *Erysimum scoparium* | Er.sc | Very frequent | 10 | 10 |
| *Nepeta teydea* | Ne.te | Very frequent | 10 | 10 |
| *Pimpinella cumbrae* | Pi.cu | Very frequent | 10 | 10 |
| *Pinus canariensis* | Pi.ca | Very frequent | 10 | 10 |
| *Pterocephalus lasiospermus* | Pt.la | Very frequent | 10 | 10 |
| *Scrophularia glabrata* | Sc.gl | Very frequent | 10 | 10 |
| *Spartocytisus supranubius* | Sp.su | Very frequent | 10 | 10 |
| *Bituminaria bituminosa* | Bi.bi | Frequent | 10 | 7 |
| *Senecio palmensis* | Se.pa | Frequent | 10 | 6 |
| *Cistus symphytifolius* | Ci.sy | Frequent | 6 | 6 |
| *Tolpis lagopoda* | To.la | Frequent | 6 | 6 |
| *Echium auberianum* | Ec.au | Frequent | 6 | 3 |
| *Aeonium spathulatum* | Ae.sp | Frequent | 5 | 5 |
| *Andryala pinnatifida* | An.pi | Frequent | 5 | 5 |
| *Descurainia lemsii* | De.le | Frequent | 5 | 5 |
| *Plantago webbii* | Pl.we | Frequent | 5 | 5 |
| *Sideritis ericocephala* | Si.er | Frequent | 5 | 5 |
| *Sideritis oroteneriffae* | Si.or | Frequent | 5 | 5 |
| *Juniperus cedrus* | Ju.ce | Frequent | 5 | 3 |
| *Rhamnus integrifolia* | Rh.in | Frequent | 3 | 3 |
| *Rosa canina* | Ro.ca | Frequent | 3 | 3 |
| *Aeonium smithii* | Ae.sm | Frequent | 3 | 3 |
| *Tolpis webbii* | To.we | Frequent | 3 | 3 |
| *Bencomia exstipulata* | Be.ex | Rare | 10 | 1 |
| *Cistus osbaeckiaefolius* | Ci.os | Rare | 10 | 1 |
| *Helianthemum juliae* | He.ju | Rare | 2 | 1 |

**Appendix 3:** Coefficients and significant values of Pearson correlations among different traits (see Appendix 1 for abbreviations and more information). Significant values are in bold (P<0.1*; P<0.05** ; P<0.001***).

| | Height | LA | SLA | LWC | Chlorophyll | LNC | LNA | C/N | δ15N | δ13C | FL |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Height** | 1 | | | | | | | | | | |
| **LA** | -0.11 | 1 | | | | | | | | | |
| **SLA** | **-0.34*** | -0.10 | 1 | | | | | | | | |
| **LWC** | **-0.43**** | 0.16 | **0.68***** | 1 | | | | | | | |
| **Chlorophyll** | -0.16 | -0.21 | **0.93***** | **-0.47**** | 1 | | | | | | |
| **LNC** | -0.06 | -0.13 | 0.**34*** | 0.03 | **0.53**** | 1 | | | | | |
| **LNA** | 0.22 | -0.12 | **-0.48**** | **-0.41**** | **-0.38*** | **0.37*** | 1 | | | | |
| **C/N** | 0.13 | -0.07 | **-0.35**** | -0.21 | **-0.52**** | **-0.88***** | **-0.34*** | 1 | | | |
| **δ15N** | -0.11 | -0.05 | 0.03 | 0.11 | -0.05 | 0.21 | 0.08 | -0.23 | 1 | | |
| **δ13C** | 0.15 | -0.17 | -0.19 | 0.009 | **-0.44***** | -0.21 | 0.04 | 0.27 | 0.18 | 1 | |
| **FL** | -0.009 | -0.01 | **0.32*** | 0.28 | **0.41**** | 0.05 | -0.01 | -0.06 | -0.19 | -0.23 | 1 |

# Chapter 4

# Human species selection determines plant invasions in the Hawaiian islands

# Abstract

Biological invasions are considered one of the most important threats to biodiversity and ecosystem services. A primary goal of invasion science is to predict which alien species have a high potential to become invasive as a basis for intervening to prevent their introduction to new geographic areas. This is often done through correlative studies, which aim to identify traits overrepresented in invasive species. However, over the past few decades it has become evident that factors favouring non-native species may change during the course of an invasion, with different attributes being important for dispersal to a new region and subsequently for establishment and spread. In this study we compared characteristics of the introduced and invasive spermatophyte plants of European origin (specifically we studied species native in Switzerland) in one oceanic island archipelago, the Hawaiian islands in the Pacific ocean.

We checked for all spermatophyte plants native to Switzerland (2145 species) whether they were introduced (171 species) and became invasive (78 species) on any of the islands of the Hawaiian archipelago (excluding atolls). We then compared the traits of introduced species with those that were not introduced, and invasive with non-invasive species. For this, we compiled a database with species traits that characterized (i) the general biology of the plants (Raunkiaer life form, Grime life strategy, leaf duration, mode of dispersal and breeding system); (ii) habitat affinity, and (iii) ecological specialization (ecological indicators values for temperature, continentality, light, soil moisture, soil pH, soil nutrients, soil humus, soil aeration). We used model selection based on multiple logistic regressions to identify the most parsimonious set of variables for three presence-absence datasets: (1) species introduced to Hawaii among all native European (Swiss) species, (2) species invasive in Hawaii among those native European species that were introduced to Hawaii, and (3) species invasive in Hawaii among all native species.

Successful species in the introduction phase were mainly fertile meadow or weed species from the colline and montane zone (77% of terrestrial species), with evergreen species being over-represented compared to deciduous ones. Fertile meadow and weed species also had the highest invasiveness rates, followed by forest and mountain plants (>25%), and were relatively high even for plants from unfertilized dry meadows (14%). Indeed, if we exclude the category of fertile

meadow and weed species, only 2% of the European species from other natural habitats were introduced to Hawaii, but 27% of these became invasive. Besides habitat affinity, soil factors – especially adaptation to acidic soils – differentiated between invasive and non-invasive alien species of European origin.

Our data strongly indicate that some ecological groups of plants are less prominent than others in Hawaii's non-native flora, not because the species are less invasive but because fewer of them have been introduced. Because the proportion of a source flora that is introduced to a new area is much smaller than the proportion of introduced species becoming invasive, disregarding this distinction can produce misleading conclusions about the traits conferring invasiveness. Indeed, as human activities and technologies change, other types of plant may be transported internationally, and some these may prove invasive.

## Introduction

Biological invasions are considered one of the most important dimensions of anthropogenic environmental change threatening biodiversity and ecosystem services (Mack et al. 2000, Millennium Ecosystem Assessment 2005, Reaser et al. 2007, Caujapé-Castells et al. 2010, Pyšek et al. 2012). With the rise of international trade and transportation, the rate of the introduction of species to areas where they would not occur without human-assisted dispersal – i.e. alien species – is rapidly increasing (Hulme 2009, Hulme et al. 2009). In Europe, for instance, about 6-7 new plant species and a similar number of amphibian and reptile species are recorded each year (Hulme et al. 2009), while over 20 new insect species are detected annually in Switzerland alone (Wermelinger 2014). Most of these are unproblematic, but some of them spread rapidly and may negatively affect biodiversity or ecosystem services. These species are called invasive (Richardson et al. 2011, Brunel et al. 2013).

For over fifty years, invasion science has attempted to understand what distinguishes species that become invasive, as a basis for identifying and potentially problematic species and preventing their introduction (Mack et al. 2000, Kolar and Lodge 2001, Van Kleunen et al. 2010, Richardson 2011). However, predicting the invasive behaviour (invasiveness) of alien species has proved difficult (Daehler 2003, Kueffer et al. 2013). Several studies have shown that invasive species are usually readily dispersed, exhibit rapid population growth (e.g. small seeds, prolific seed production, fast growth rates and population cycles), and possess generalised traits that allow them to occupy a wide array of habitats (e.g. high phenotypic plasticity, or generalised seed dispersal and pollination mechanisms) (Baker 1974, Kolar and Lodge 2001, Van Kleunen et al. 2010, Richardson 2011). However, beyond these rather general conclusions, more precise information of what makes some species invasive remains elusive. In reaction, invasion biologist have tended to move away from identifying traits applicable across organism groups and invasion scenarios, and focused instead on understanding invasion processes in specific contexts (Daehler 2003, Kueffer and Daehler 2009, Kueffer et al. 2013). In particular, invasions have been depicted as a sequence of phases: introduction of species to new areas, establishment, spread across the landscape, and invasion into particular habitats (Richardson et al. 2000, Blackburn et al. 2011).

Based on such a conceptual model, it became possible to ask what characterises successful species in each of these phases (Dietz and Edwards 2006, Theoharides and Dukes 2007, Richardson and Pyšek 2012).

This new approach has underscored that invasions are strongly influenced by the ways humans select and transport species, since these processes determine which and how many species reach a new area (Kueffer 2013). Many species have been deliberately selected for particular land use or other economic activities, and these species often share ecological characteristics. Not surprisingly, therefore, economic development is one of the most important factors predicting the number of alien or invasive species in a place (Denslow et al. 2009, Kueffer et al. 2010, Pyšek et al. 2010, Essl et al. 2011). Also, species that are accidentally introduced to new areas – e.g. pests transported with plant material, or weeds in seed mixtures – are not a random subset of the source biota.

In this study we used comprehensive data on the spermatophyte plant species recorded as alien and as invasive species on the islands of the Hawaiian archipelago (Pacific ocean). We were interested in which species from Europe have been introduced to Hawaii, and which have become invasive. Because little or no ecological information is available for most of the 11’500 species in the European checklist, we confined our study to a subset of this flora, the native flora of Switzerland, for which excellent ecological databases were available. This flora can be divided into lowland species growing to an altitude of about 1500 m asl, most of which are widely distributed across Central Europe and the British Isles, and montane species, many of which occur across the Alpine arc and in other mountainous regions such as the Pyrenees. Only one species - a locally distributed allopolyploid *Draba ladina* - is endemic to Switzerland. Thus, the Swiss flora can be taken as representative of much of Western and Central Europe, and we refer to these species as being of European origin, to avoid implying that Switzerland was the direct source of Hawaiian populations.

Based on this dataset we addressed three questions:

- Which traits differentiate species that are recorded as alien species in the Hawaiian archipelago from the other species in the European ‘source’ flora?

- Which traits differentiate species that are recorded as invasive species in the Hawaiian archipelago from the non-invasive alien species (of European origin) found in the Hawaiian archipelago?
- How important is human selection in determining and predicting the composition of the invasive flora in the Hawaiian archipelago?

## Method

### *Species list*

We selected all spermatophyte plants native to Switzerland from the 2002 Swiss red data list (Moser and Genève 2002) and excluded all subspecies. From these 2341 species, we removed 196 due to incomplete trait data, leaving 2145 species that we used in our study (Fig. 1). For each of these, we checked whether it had been introduced (171 species) to any of the islands of the Hawaiian archipelago (excluding atolls), and whether it had become invasive (Curtis C. Daehler, University Hawaii at Manoa, unpublished data). Invasive species were defined as those that colonized natural areas, meaning areas without frequent deliberate anthropogenic disturbance (Kueffer and Daehler 2009). We included alien-dominated novel ecosystems without any current land use, but excluded ruderal sites, roadsides, agricultural land and urban areas.

### *Species traits*

Species traits were derived from Landolt et al. (2010) for all species (Appendix 1). We selected traits that characterized (i) the general biology of the plants (Raunkiaer life form, Grime life strategy, leaf duration [deciduous, evergreen, winter-green, summer-green], mode of dispersal [self, man, wind, animal, water], breeding system [apomictic, self-pollinating, monoecious, dioecious]); (ii) habitat affinity (habitat types, hemeroby, see Appendix 1), and (iii) ecological specialization (ecological indicator values for temperature [T], continentality [K], light [L], soil moisture [F], soil pH [reaction, R], soil nutrients [N], soil humus [H], & soil aeration [D]). Based on Cramer' s V calculated with the R package vcd (Friendly 2013), we checked the association between variables as a way of minimizing problems of multicollinearity (Appendix 2). Humus (H) and soil aeration (D) were the only two variables with a Cramer' s V higher than 0.6 (which we defined as a threshold). Based on ecological considerations we included D and excluded H.

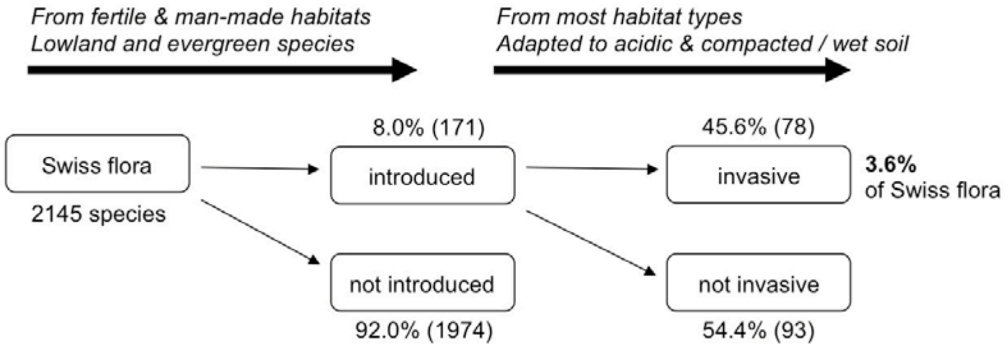


**Figure 1:** Conceptual model of two stages of the invasion process of the Hawaiian archipelago (Pacific ocean) by plant species native to Switzerland. The species from the total Swiss flora (2145 species) are either introduced to Hawaii or not. Among the introduced species some become invasive while others do not. The percentages indicate the proportion of species from the previous stage that are in either of two categories; with absolute species numbers in brackets. 3.5% of the Swiss species were recorded as invasive in Hawaii. Above the diagram, the main results about the traits that characterize species, which pass the respective stage, are summarized.

### *Data analyses*

We used model selection based on multiple logistic regressions (i.e. generalized linear models (glm) with a binomial error structure) to identify the most parsimonious set of variables for three presence-absence datasets: (1) species introduced to Hawaii among all native European (i.e. Swiss) species, (2) species invasive in Hawaii among those native European species that were introduced to Hawaii, and (3) species invasive in Hawaii among all native European species.

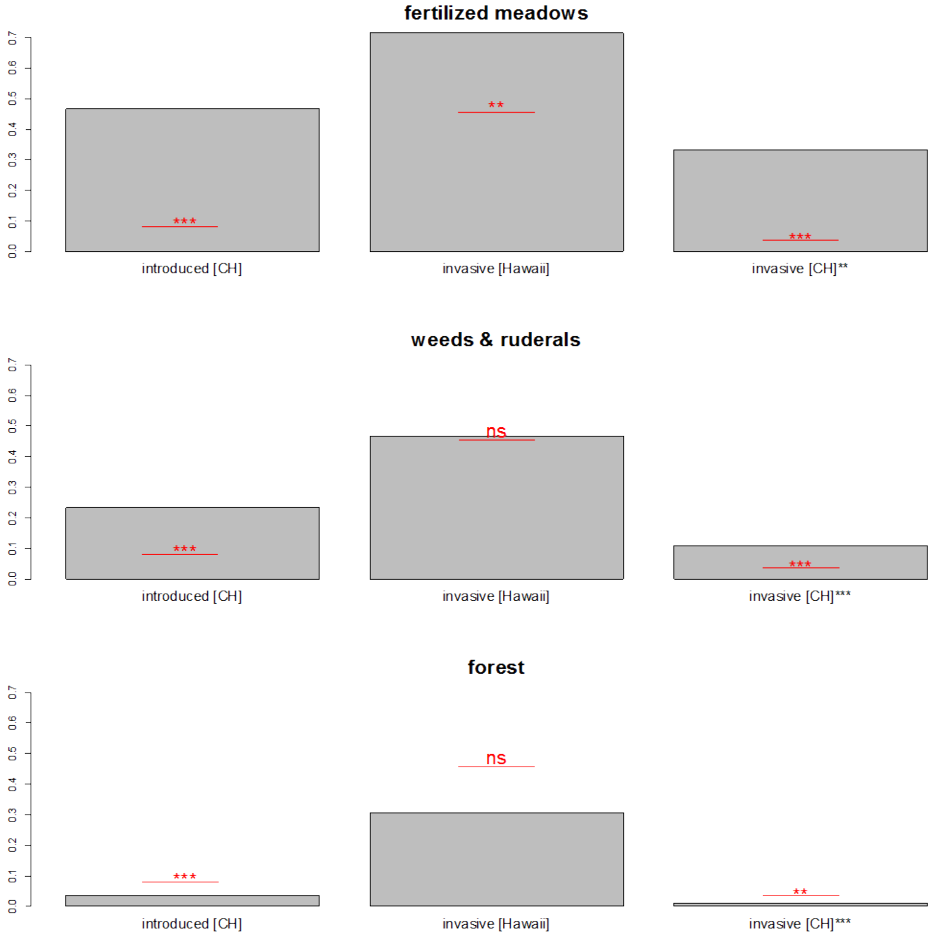
Model selection was done based on Akaike's Information Criterion (AIC), and chi-square tests were used to test whether models differed significantly from each other.

To illustrate the effect of the 'source' flora (i.e. complete Swiss flora, or those species introduced to Hawaii) on the identification of traits characterizing invasive species ('invasiveness'), we compared numbers of invasive species in five large families (Poaceae, Asteraceae, Fabaceae, Brassicaceae, Cyperaceae) with those predicted from null model simulations using two different source floras (Fig. 5). From each flora, we took random subsamples of 78 species (equal to the number of invasive species in Hawaii, Fig. 1) and repeated this process 10'000 times. From these samples, we calculated the geometric mean and the 97.5 and 2.5 percentile confidence intervals for the species number of the five selected families. All data analyses were performed in R (R Development Core Team 2012).

## Results

### *Which traits differentiated species that are recorded as alien species in the Hawaiian archipelago from the other species in the European 'source' flora?*

Leaf duration, habitat type, hemeroby, temperature (T), continentality (K), nutrients (N), and soil aeration (D) were retained as predictors in the final model (Table 1a, Fig. 1). Nearly half of the European fertilized meadow plants and one quarter of weed / ruderal species were recorded in Hawaii (Fig. 2). Together these two groups made up c. 70% of the introduced European plants in Hawaii. In contrast, the other terrestrial plant groups accounted for between 0.7% (mountain plants) and 4.7% (lowland pioneer species) of European species, and aquatic plants 8%. Species from the most human-influenced habitats were strongly over-represented in Hawaii relative to those from more natural habitats (Fig 3). In addition, evergreens were over-represented relative to deciduous and summer-green species, lowland relative to montane species, continental relative to oceanic species, and species of infertile and compacted soils relative to species of better soils (Table 1a).


fertilized meadows
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
***
**
***
introduced [CH]
invasive [Hawaii]
invasive [CH]**
weeds & ruderals
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
***
ns
***
introduced [CH]
invasive [Hawaii]
invasive [CH]***
forest
0.0
0.1
0.2
0.3
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0.5
0.6
0.7
***
ns
**
introduced [CH]
invasive [Hawaii]
invasive [CH]***

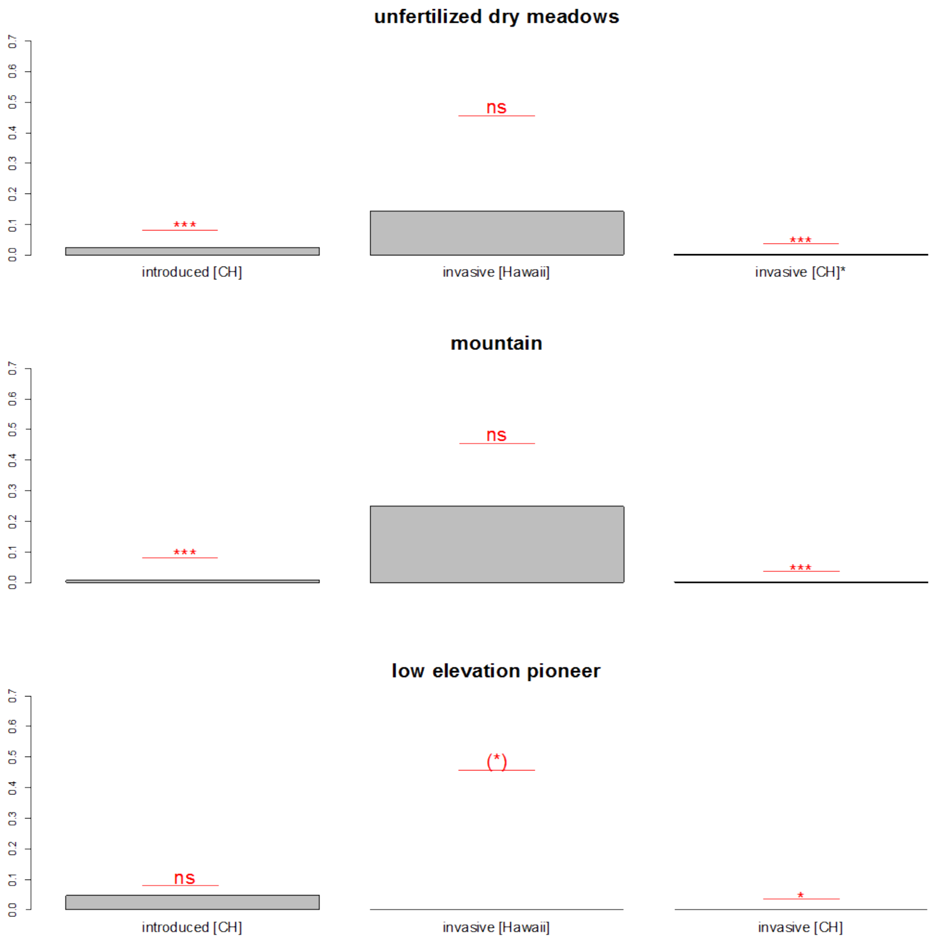


**Figure 2:** Introduction and invasion rates in Hawaii for the native Swiss flora separated by broad classes of habitat affinity (“ecological groups”, water and wetland plants are not shown). The three bars show from left to right (always for respective ecological group): proportion of the Swiss flora introduced to Hawaii, proportion of introduced species that are invasive, and proportion of Swiss flora that is invasive in Hawaii. Red bars show respective ratios across complete Swiss flora (i.e. all ecological groups). Indicated significance levels were derived from binomial tests that compared the ratio in the ecological group with the ratio across the complete flora. Significance levels indicated with the label of the third bar were derived from Fisher’s exact tests comparing the proportion of invasive species in the complete Swiss flora and in the introduced flora in Hawaii.

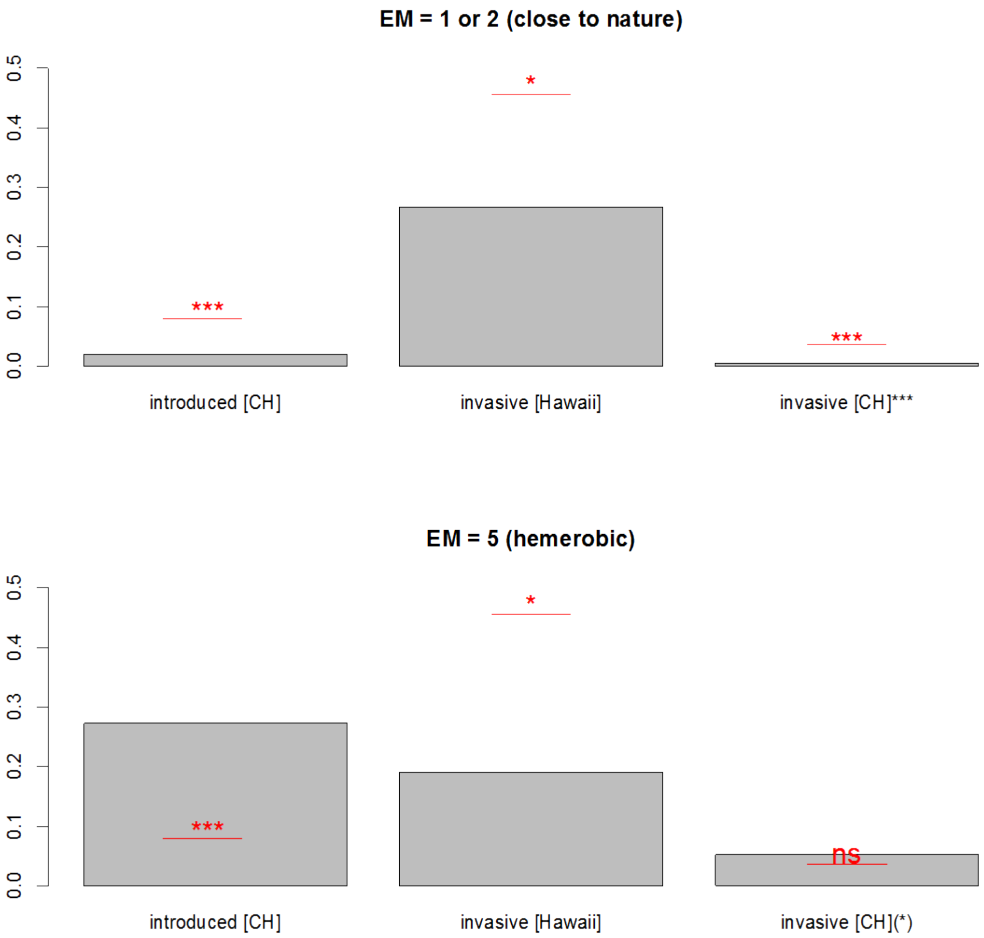
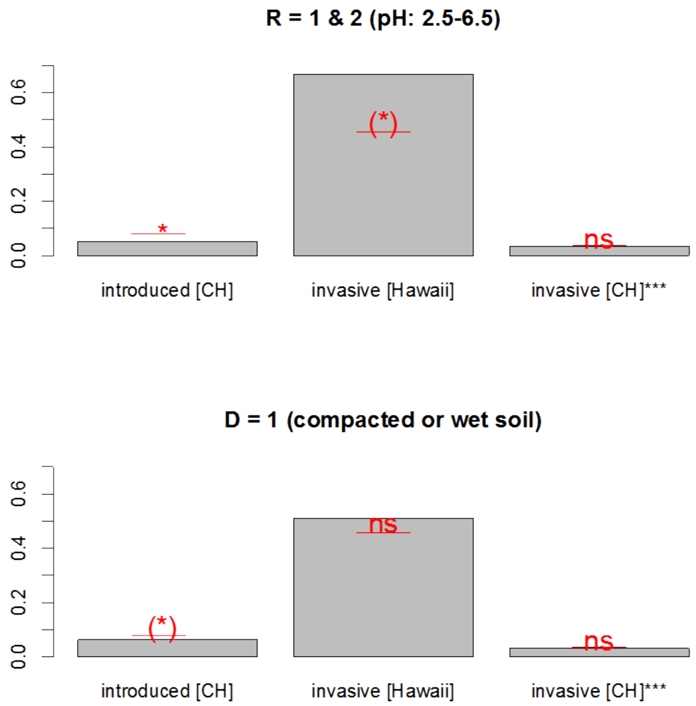


**Figure 3:** Introduction and invasion rates in Hawaii for the native Swiss flora separated by broad classes of affinity to man-made habitat (hemeroby, EM). Shown are the data for the least man-influenced (upper panel) and most man-influenced habitats (lower panel). For further information see legend of Figure 2 and main text.

### *Which traits differentiated invasive species in the Hawaiian archipelago from non-invasive alien species?*

The minimum adequate model for invasive species in the introduced flora in Hawaii retained habitat type, hemeroby, reaction (R), and soil aeration (D) (Table 1c). Fertile meadow, weed and ruderal species were the most successful ecological groups at this stage, but between one fifth and one third of introduced forest, mountain, and unfertilized dry meadow species also became invasive (Fig. 2). Species from the least disturbed habitats showed a higher invasiveness than those from the most anthropogenic ones, contrary to the pattern detected during introduction (Fig. 3), and species adapted to acidic and compacted / wet soils were more invasive than species from better soils (Fig. 4).



**<u>Figure 4:</u>** Introduction and invasion rates in Hawaii for the native Swiss species that are adapted to acidic (Ellenberg R indicator of 1 or 2, upper panel) and compacted or wet soils (Ellenberg D indicator of 1, lower panel). For further information see legend of Figure 2 and main text

**<u>Table 1:</u>** Logistic regression models for introduced versus non-introduced species in the Swiss flora (1a), invasive versus non-invasive species in the Swiss flora (1b), and invasive versus non-invasive species among species introduced to Hawaii (1c). Shown are for all retained factors the deviance and significance (based on a chi-square test); and for all factor levels the estimated coefficient, standard error, Z-value, and P-value (. P < 0.1; * P <0.05; ** P <0.01; *** P <0.001). The intercept factor level is shown in brackets. For explanation of factors see main text.

**Table 1a: introduced versus non-introduced species of the Swiss flora**

| Factor | Factor levels | Estimate | SE | Z | Deviance / P |
|---|---|---|---|---|---|
| Intercept | | -7.61 | 1.71 | -4.45 | *** |
| Leaf duration | (deciduous) | | | | 4.64 |
| | evergreen | 2.39 | 0.54 | 4.39 | *** |
| | summergreen | -1.48 | 1.05 | -1.42 | |
| | wintergreen | 0.26 | 0.20 | 1.30 | |
| Ecological group | (fertilized meadow) | | | | 260.32*** |
| | forest | -2.22 | 0.45 | -4.94 | *** |
| | mountain | -1.48 | 0.82 | -1.81 | . |
| | low elevation pioneer | -2.20 | 0.63 | -3.49 | *** |
| | unfertilized dry meadows | -2.36 | 0.54 | -4.34 | *** |
| | water | -0.55 | 0.59 | -0.93 | |
| | weeds and ruderals | -1.39 | 0.38 | -3.62 | *** |
| | wetland | -1.20 | 0.46 | -2.63 | ** |
| Influence of man | (close to nature) | | | | 65.04** |
| | moderately close to nature | 1.49 | 0.67 | 2.24 | * |
| | indifferent | 2.71 | 0.69 | 3.90 | *** |
| | moderately hemerobic | 3.18 | 0.73 | 4.34 | *** |
| | hemerobic | 3.15 | 0.77 | 4.11 | *** |
| Temperature (T) | (alpine) | | | | 13.40** |

| | | | | | |
|---|---|---|---|---|---|
| | colline | 2.42 | 1.31 | 1.85 | . |
| | montane | 2.18 | 1.30 | 1.68 | . |
| | subalpine | -0.10 | 1.32 | -0.08 | |
| Continentality (K) | (continental) | | | | 22.52*** |
| | intermediate | 2.70 | 1.04 | 2.59 | ** |
| | oceanic | 2.04 | 1.29 | 1.58 | |
| | subcontinental | 1.68 | 1.04 | 1.62 | |
| | suboceanic | 2.12 | 1.05 | 2.02 | * |
| Nutrients (N) | (fertile) | | | | 10.62* |
| | infertile | -1.20 | 0.35 | -3.49 | *** |
| | medium | -0.42 | 0.21 | -1.96 | * |
| | very fertile | 0.11 | 0.51 | 0.22 | |
| | very infertile | -0.64 | 0.69 | -0.93 | |
| Soil aeration (D) | (bad) | | | | 10.10** |
| | good | 1.05 | 0.40 | 2.61 | ** |
| | moderate | 0.73 | 0.26 | 2.81 | ** |
| Residual deviance | | | | | 806.36 |

**Table 1b: invasive versus non-invasive species of the Swiss flora**

| **Factor** | **Factor levels** | **Estimate** | **SE** | **Z** | **Deviance / P** |
|---|---|---|---|---|---|
| Intercept | | -19.25 | 2312.99 | -0.01 | |
| Ecological group | (fertilized meadow) | | | | 165.56*** |
| | forest | -2.40 | 0.61 | -3.95 | *** |
| | mountain | -3.15 | 2.16 | -1.46 | |
| | pioneer | -19.16 | 2471.09 | -0.01 | |
| | unfertilized | -3.37 | 1.07 | -3.13 | ** |
| | water | -0.21 | 0.85 | -0.25 | |
| | weeds | -1.14 | 0.42 | -2.70 | ** |
| | wetland | -1.58 | 0.57 | -2.78 | ** |
| Influence of man | (close to nature) | | | | 32.26*** |

| | | | | | |
|---|---|---|---|---|---|
| | moderately close to nature | 0.40 | 0.93 | 0.43 | |
| | indifferent | 2.82 | 0.99 | 2.84 | ** |
| | moderately hemerobic | 3.17 | 1.05 | 3.03 | ** |
| | hemerobic | 2.21 | 1.16 | 1.91 | . |
| Temperature (T) | Alpine | | | | 13.60** |
| | colline | -0.84 | 2.22 | -0.38 | |
| | montane | -0.58 | 2.21 | -0.26 | |
| | subalpine | -17.62 | 1313.91 | -0.01 | |
| Continentality (K) | (continental) | | | | 16.70** |
| | intermediate | 17.68 | 2312.99 | 0.01 | |
| | oceanic | 17.31 | 2312.99 | 0.01 | |
| | subcontinental | 16.67 | 2312.99 | 0.01 | |
| | suboceanic | 16.75 | 2312.99 | 0.01 | |
| Reaction (R) | (acid) | | | | 8.63. |
| | alkaline | -16.52 | 1839.28 | -0.01 | |
| | extremely acid | -16.79 | 4359.68 | 0.00 | |
| | neutral | -1.14 | 0.43 | -2.66 | ** |
| | weakly acid | -0.73 | 0.41 | -1.80 | . |
| Residual deviance | | | | | 433.39 |

**Table 1c: invasive versus non-invasive species of the introduced flora in Hawaii**

| **Factor** | **Factor levels** | **Estimate** | **SE** | **Z** | **Deviance / P** |
|---|---|---|---|---|---|
| Intercept | | 2.54 | 1.41 | 1.80 | . |
| Influence of man | (close to nature) | | | | 18.64*** |
| | moderately close to nature | -2.09 | 1.41 | -1.48 | |
| | indifferent | 0.48 | 1.36 | 0.35 | |
| | moderately | 0.25 | 1.37 | 0.18 | |

| | | | | | |
|---|---|---|---|---|---|
| | hemerobic | | | | |
| | hemerobic | -1.45 | 1.45 | -1.01 | |
| Reaction (R) | (acid) | | | | 13.16* |
| | alkaline | -17.34 | 1101.95 | -0.02 | |
| | extremely acid | -17.02 | 2399.54 | -0.01 | |
| | neutral | -2.27 | 0.71 | -3.22 | ** |
| | weakly acid | -2.04 | 0.70 | -2.93 | ** |
| Soil aeration (D) | (bad) | | | | 11.06** |
| | good | -2.47 | 0.83 | -2.98 | ** |
| | moderate | -0.66 | 0.44 | -1.51 | |
| Residual deviance | | | | | 192.89 |

### *How important is human selection in determining the composition of the invasive flora in the Hawaiian archipelago?*

A comparison between invasive and non-invasive species based upon the entire source flora (i.e. the traditional approach, Table 1b) yielded very different results from one restricted to species known to have been introduced into Hawaii (Table 1c). Not only did the traits associated with invasiveness differ significantly according to the source flora used in the analysis (Fig. 2-4), but also which plant families were most invasive (Fig. 5). For instance, although Poaceae and Fabaceae were substantially over-represented among invasive species when using the complete European (Swiss) flora, there was no such indication when only introduced species were considered. This indicates that the over-representation of Poaceae and Fabaceae in the alien flora of Hawaii was due to effects related to introduction rather than to higher invasiveness of plants in these families.

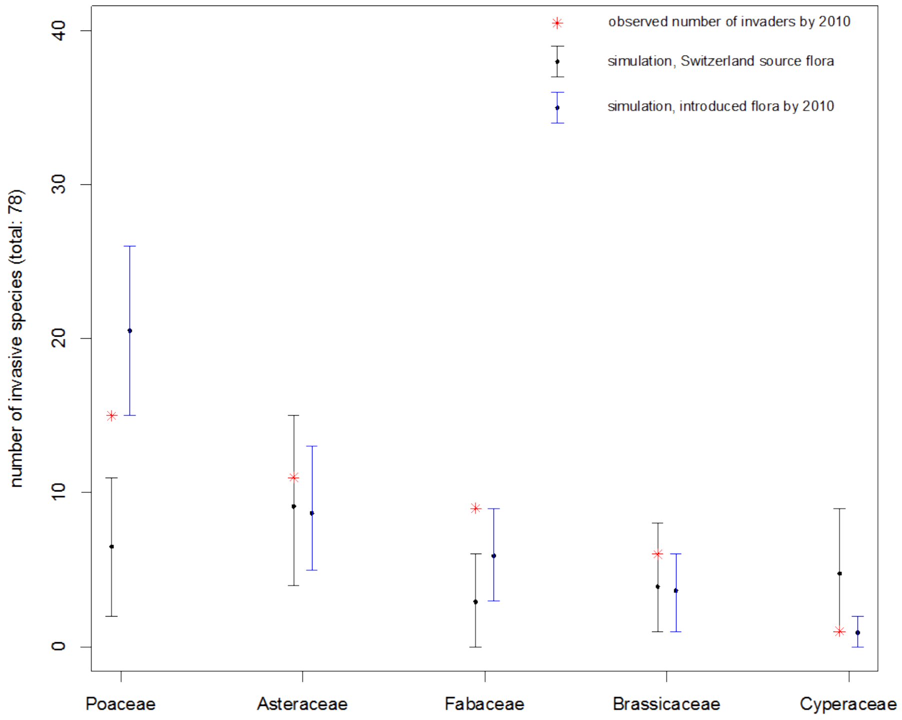


**Figure 5:** Number of invasive species in five large families (*Poaceae, Asteraceae, Fabaceae, Brassicacese, Cyperaceae*). Data is shown for observed values (red dots), and the simulated data generated through random sampling from two different source floras (black lines: native Swiss flora; blues lines: native Swiss flora introduced to Hawaii). The small black dots are mean values of simulations and the bars show the range for 95% of simulations.

## Discussion

Predicting which alien species have a high potential to become invasive – high invasiveness – is a primary goal of invasion science, which, if achieved, would enable managers to take steps to prevent them from being introduced into new areas (Mack et al. 2000, Hulme 2009). For this reason, the study of what makes non-native species invasive has been a major research focus for several decades (Kolar and Lodge 2001, Richardson 2011). While experimental studies – including large multispecies experiments (Schlaepfer et al. 2010) – have gained in importance, correlative studies that identify species characteristics which are over-represented among invasive species remain important in research (Kueffer et al. 2013) and as the basis of most weed risk assessment systems (e.g. Pheloung et al. 1999). However, over the past few decades it has been realised that the factors promoting the success of non-native species may change during the course of an invasion (Dietz and Edwards 2006, Theoharides and Dukes 2007, Richardson and Pyšek 2012). The aim of this study was to understand how invasiveness traits differ between the phases of introduction and invasion, using plants of European origin in the Hawaiian islands as the study system.

### *Do invasiveness traits differ between the introduction and invasive phases?*

After allowing for the relative frequency of traits in the European source flora and the correlation among traits, habitat affinity proved to be a better predictor of invasion success in both phases than biological characteristics. For instance, while over 50% of invasive species were therophytes, 95% of them were also fertile meadow or weed species, which proved to be the more important factor. Asteraceae was the second largest family of invasive species, but it is also the largest family in the European source flora and consequently is not more invasive than expected by chance (Fig. 5).

Successful species in the introduction phase were mainly fertile meadow or weed species from the colline and montane zones (77% of terrestrial species). An obvious explanation for this pattern is that these species are associated with human land use, and in particular with agriculture. Indeed, a majority of plants in the Hawaiian islands were introduced, deliberately or accidentally, in association with pastures and other forms of agriculture (Daehler 2005). Although the absence of subalpine and alpine species could be a result of climate matching – i.e. species establish successfully and later become invasive mostly in areas characterised by a similar climate as in the native range (Pheloung et al. 1999, Petitpierre et al. 2012) – it seems more probable that these species have rarely been introduced. Indeed, it has been argued that the composition of alien mountain floras around the world, which conspicuously lack species of mountain origin, reflects the dominant role of agricultural trade in assembling these floras (Alexander et al. 2011, McDougall et al. 2011).

Fertile meadow or weed species proved very invasive, but we also found high rates of invasiveness (> 25%) amongst forest and mountain plants, and even amongst plants from unfertilized dry meadows (14%). Indeed, while only 2% of European species from relatively natural habitats were introduced to Hawaii, 27% of these became invasive (Fig. 3). This demonstrates that the low representation of some groups of plant species on Hawaii reflects lower rates of introduction rather than lower invasiveness. Indeed, the invasive potential of ecological groups that have rarely been introduced to new areas might have been greatly underestimated by ecologists and managers (Kueffer 2010, Kueffer et al. 2013). Besides habitat affinity, soil factors – especially adaptation to acidic soils (Fig. 4) – differentiated between invasive and non-invasive alien species of European origin. This suggests that predictive models of potential alien distribution ranges, which are mainly based upon macroclimatic variables (e.g. Petitpierre et al. 2012), could be significantly improved by including local factors such as soil variables or microclimate (compare e.g. Kueffer and Daehler 2009, Titeux et al. 2009, Bertrand et al. 2012).

### *Disregarding the composition of introduced floras can lead to spurious results in correlative invasiveness studies*

It has long been recognised that data on the relative frequency of traits in the source flora are needed to identify those traits associated with invasiveness (e.g. Daehler 1998). However, our results indicate that such studies can be distorted by the effects of human introduction on the composition of alien floras. This is because the species introduced to a new area represent a much smaller proportion of the source flora than the proportion of introduced species becoming invasive (Fig. 1). Thus, although different traits, and therefore species, are favoured in the phases of introduction and invasion (Fig. 2-4), the alien flora is likely to exhibit predominantly those traits favoured in the former phase. Indeed, models that used the European flora as source flora instead of the European species introduced to Hawaii (Table 1b, Fig. 5) produced strongly differing results. This leads us to suggest that many of our ideas about what makes species invasive can only be reliably applied to past invasions. As human activities and technology change (e.g. due to changing land use), different ecological groups of species may be transported over long distances, whose behaviour we cannot predict from previous experience (Kueffer 2010, Kueffer et al. 2013).

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# Supporting Information

**Appendix 1:** Overview of the plant species attributes included in the study and their different factor levels.

| **Trait** | **Factor levels** |
|---|---|
| *Biological traits* | |
| Life form (Raunkiaer) | Hydrophyte; Epiphyte/Climber; Therophyte;<br>Geophyte; Chamaephyte; Hemicryptophyte; Phanerophyte; Others (Canivorous, Parasitic, Saprophytes) |
| Life strategy (Grime) | Competitors (C); Ruderals (R); Stress-tolerators (S); Intermediates |
| Leaf duration | evergreen; deciduous; wintergreen; summergreen |
| Dispersal mode | self; man; wind; animals; water |
| Reproduction mode | apomictic; self-pollinating; monoecious; dioecious |
| *Habitat affinity* | |
| Ecological group (EG) | forest; mountain; low elevation pioneer; water; wetland; unfertilized dry meadow; weeds & ruderals; fertilized meadows |
| Human influence (Hemeroby, EM) | Close to nature; moderately close to nature; indifferent; moderately hemerobic; hemerobic |
| *Ecological indicators* | |
| Temperature (T) | alpine; subalpine; montane; colline |
| Continentality (K) | oceanic; suboceanic; suboceanic to subcontinental; subcontinental; continental |
| Light (L) | deep shade; shade; semi-shade; well lit places; full light |
| Soil moisture (F) | dry; fresh; moist; wet; flooded |
| Soil pH (Reaction, R) | extremely acid; acid; weakly acid; neutral; alkaline |
| Soil nutrients (N) | very infertile; infertile; medium; fertile; very fertile |
| Soil humus (H) | little; moderate; high |
| Soil aeration (D) | bad; moderate; good |

**<u>Appendix 2:</u>** “Correlations” between plant traits included in the study. The table shows Cramer' s V (calculated with the R package vcd) that ranges from 0 (no association) to 1 (identity). For abbreviations and definitions see Appendix 1.

| | Life form | Leaf duration | Life strategy | Dispersal | Reproduction | EG | EM | T | K | L | F | R | N | H | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Life form** | 1 | | | | | | | | | | | | | | |
| **Leaf duration** | 0.38 | 1 | | | | | | | | | | | | | |
| **Life strategy** | 0.53 | 0.18 | 1 | | | | | | | | | | | | |
| **Dispersal** | 0.29 | 0.09 | 0.13 | 1 | | | | | | | | | | | |
| **Reproduction** | 0.24 | 0.10 | 0.17 | 0.14 | 1 | | | | | | | | | | |
| **EG** | 0.43 | 0.17 | 0.34 | 0.29 | 0.12 | 1 | | | | | | | | | |
| **EM** | 0.31 | 0.14 | 0.32 | 0.16 | 0.09 | 0.47 | 1 | | | | | | | | |
| **T** | 0.21 | 0.16 | 0.19 | 0.16 | 0.10 | 0.35 | 0.33 | 1 | | | | | | | |
| **K** | 0.11 | 0.06 | 0.06 | 0.07 | 0.05 | 0.24 | 0.09 | 0.16 | 1 | | | | | | |
| **L** | 0.21 | 0.16 | 0.17 | 0.14 | 0.05 | 0.38 | 0.23 | 0.34 | 0.10 | 1 | | | | | |
| **F** | 0.32 | 0.11 | 0.19 | 0.25 | 0.12 | 0.44 | 0.16 | 0.15 | 0.34 | 0.17 | 1 | | | | |
| **R** | 0.12 | 0.12 | 0.09 | 0.09 | 0.04 | 0.18 | 0.16 | 0.17 | 0.14 | 0.15 | 0.25 | 1 | | | |
| **N** | 0.19 | 0.16 | 0.17 | 0.13 | 0.09 | 0.26 | 0.23 | 0.17 | 0.12 | 0.19 | 0.35 | 0.26 | 1 | | |
| **H** | 0.30 | 0.10 | 0.20 | 0.12 | 0.05 | 0.39 | 0.21 | 0.21 | 0.15 | 0.24 | 0.40 | 0.24 | 0.22 | 1 | |
| **D** | 0.34 | 0.12 | 0.21 | 0.14 | 0.07 | 0.43 | 0.19 | 0.23 | 0.22 | 0.25 | 0.50 | 0.22 | 0.23 | **0.68** | 1 |

# General conclusions

The aim of this study was to identify general determinants of island plant diversity on oceanic islands at a global scale. For this purpose, I used comprehensive data of the species composition of oceanic islands around the world to test empirically very general patterns of biodiversity on islands. My work challenges several fundamental assumptions of island biogeography, and shows new research opportunities in a time of increasing data availability. It also highlights new aspects of the conservation value of island floras.

## Island biogeography: the importance of *in situ* speciation, chance, source areas, and functional diversity

My results show that island floras are not necessarily more disharmonic than continental floras (chapter 1), contrary to what has usually been supposed.  This in turn suggests that the role of dispersal limitation might be less important than previously thought (chapter 1), while *in situ* speciation might play an even greater role for species richness patterns on island than expected (chapter 2). Although not new to island biogeography, these observations question the great importance that has been given to dispersal limitation (Carlquist 1974) and the neglect of *in situ* speciation (McArthur and Wilson 1967).

This study also highlights the role that chance plays in shaping island floras around the world, with different plant families becoming dominant on different islands (chapter 2). It suggests that immigration history influences the outcomes of evolution on islands, with those families that arrive first profiting from empty niches and therefore proliferating through adaptive radiation. The consequence is the observed pattern of certain families being very species-rich and with high endemism on particular islands. Thus, immigration history, although recognized as an important factor in evolutionary biology, needs to be better integrated into island biogeography (Whittaker *et al.* 2008). In this respect, new molecular data will increasingly allow reconstructing immigration sequences for whole island floras (Emerson and Gillespie 2008).

The chapter on the assembly of an alien and invasive flora in the Hawaiian islands (chapter 4) points to another perspective for island biogeography research. The data indicate that accessibility of habitats of potential source species by the dispersal agent – in this case humans – can strongly affect the composition of alien floras. While up to 50% of plants characteristic of anthropogenic habitats in Switzerland (chosen to represent the Central European flora) were recorded in Hawaii, very few species from remoter habitats such as mountains made their way to the middle of the Pacific. Island biogeography has always been interested in knowing which are the source regions for island biotas (Carlquist 1965, 1974); my results suggest that of equal or even greater interest would be to know which are the habitats from which species originate (compare Fernández-Palacios *et al.* 2014).

Documenting and understanding patterns of species diversity is in itself an important topic but with the loss of species it becomes increasingly important to understand how species differ ecologically and consequently fill differing roles for ecosystem functioning and services (e.g. Hooper *et al.* 2012). I document in chapter 3 that adaptive radiations on island can produce high functional diversity. The questions of how and where functional diversity evolved on islands and how it is related to taxonomic diversity have been largely neglected. Finding answers would not only improve our understanding of island biodiversity but might suggest ways to conserve it more effectively. Furthermore, as with other aspects of island biogeography, this research would probably reveal more general ecological and evolutionary mechanisms that would be equally relevant to continental areas.

## The conservation value of oceanic islands

It is well recognized that island biotas are very significant for global biodiversity because of their high levels of endemism (Myers *et al.* 2000, Millennium Ecosystem Assessment 2005, Caujapé-Castells *et al.* 2010). This study highlights that these biota are of unique biodiversity value for three additional reasons. First, because of their small size, most island floras are harmonic or, in other words, phylogenetically diverse (chapter 1). On small islands most species are from different genera and families. Second, my results suggest that functional diversity on islands can be high (chapter 3), though this needs further study. Third, islands are unique model system for understanding mechanisms – including anthropogenic ones (chapter 4) – that shape biodiversity on islands as well as continents (especially chapter 1-2).

## Data-intensive ecology reaches island research

In conclusion, this study has shown the great potential of using global datasets to disentangle the factors determining patterns of biodiversity on islands. However, the analyses presented here are just the beginning of what could be done with additional types of data, including comprehensive species lists from all families, data on introduced and invasive floras from many more islands, and molecular data. This will require much greater coordination of researchers on islands around the world (Kueffer and Fernández-Palacios 2010, Kueffer 2012), which as this study indicates could be of huge benefit to ecology and conservation.

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