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**Running Title:** Island Biogeography and taxonomic effort

**Title:** Island Biogeography, the effects of taxonomic effort and the importance of island niche diversity to single island endemic species

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## ABSTRACT

Island biogeography theory is fundamentally reliant on measuring the number of species per island and hence has taxonomy at its foundation. Yet as a metric used in tests of the theory, island species richness ( $S$ ) has varied with time according to the level of taxonomic effort (a function of the rate of finding and describing species). Studies using a derivative of  $S$ , single-island-endemic species richness (SIE  $S$ ), may be even more prone to change in taxonomic effort. Decreases or increases in species numbers resulting from taxonomic revision or increased sampling are likely to have a large effect on values of SIE  $S$ , as they tend to be smaller than total  $S$  for the same island. Using simple biogeography models, we analysed estimates of SIE  $S$  in plants, land snails, beetles and fungi from comprehensive datasets for eight island groups, produced species accumulation curves and applied Bayesian regression over five time periods. Explanatory power differed across taxa, but area and island age were not always the best explanatory variables, and niche diversity appeared to be important. Changing levels of SIE  $S$  over time had different effects on models with different taxa and between island archipelagos. The results indicated that the taxonomic effort that determines SIE  $S$  is important. However, as this cannot often be quantified, we suggest Bayesian approaches should be more useful than frequentist methods in evaluating SIE  $S$  in island biogeography theory. Fundamentally, the paper highlights the importance of taxonomy to theoretical biogeography.

**Keywords:** species richness, evolution, modelling

## INTRODUCTION

Species richness ( $S$ ) is a fundamental metric used to validate many theoretical and empirical studies, particularly when the primary focus is to resolve why some areas have more species than others. The scientific foundation that allows the development, validation and testing of theories using  $S$  is taxonomy. Taxonomic and related research classifies species, defines their distributions and hence allows regional estimates of  $S$  to be derived. 2013 marks 50 years since the publication of MacArthur and Wilson's (MacArthur and Wilson 1963) groundbreaking paper that led to *The Theory of Island Biogeography* (MacArthur and Wilson 1967). From a few underlying principles, island biogeography theory (and other macroecological theories) aims to unify the relationships between island area, abundance and species richness ( $S$ ) by generating models of, for example, the species–area curve. Central to validation of these models are estimates of island  $S$ . More recently, as a step towards including indicators of island evolutionary dynamics, studies have begun to incorporate single-island endemic  $S$  (SIE  $S$ ) (Emerson and Kolm 2005, Whittaker et al. 2008) defined here as:

*“the total number of single island endemic species within any specified taxonomic group in a given area”*

Intuitively, SIEs have the potential to reveal within and between island evolutionary processes if these species are symptomatic of the individual islands' processes. From an analysis of SIE  $S$  from Hawaii and the Canaries, Emerson and Kolm (2005) provided evidence that endemic diversification was related to species richness. They suggested that, mostly through competitive mechanisms, high diversity stimulates high rates of speciation and that speciation rate and extinction rate are positively related. This created some controversy (Cadena et al. 2005, Emerson and Kolm 2007a, Emerson and Kolm 2007b,

Kiflawi et al. 2007, Pereira et al. 2007, Whittaker et al. 2007, Witt and Maliakal-Witt 2007, Gruner et al. 2008) but is also beginning to gain some empirical support (Forbes et al. 2009, Zobel et al. 2011) yet theoretically remains uncertain (see e.g. Chen and He 2009).

Incorporating factors such as the geological life cycle of islands have also been proposed as alternative models (Whittaker et al. 2007, Whittaker et al. 2008). This, however, has been questioned for high dispersive taxa and more recently SIE  $S$  of bryophytes and seed plants has been related more successfully to elevation than island age (Patiño et al. 2013, Steinbauer et al. 2013) suggesting that within-island processes may be important to evolution and hence SIE.

Regional species distributions are often summarised in checklists from which estimates of SIE  $S$  are usually drawn. However, there are several assumptions underlying these estimates that have yet to be fully explored. Of these, the most important is that available species counts for an island are a representative estimate of the ‘true’ SIE  $S$ . Estimates of SIE  $S$  may be particularly susceptible to differences in *taxonomic effort*, i.e. the effort that goes into finding, describing and revising endemic species. Furthermore, SIE  $S$  may be more susceptible than total island  $S$  because estimates of SIE  $S$  can be small, therefore small changes of one or two species can have disproportionately large effects. In addition, technological advances, particularly in molecular methods, and/or periods of intense taxonomic revision of island flora and fauna may cause SIE  $S$  to increase or decrease rapidly resulting in step changes through time. If single-island endemics are to be reliable indicators of evolutionary dynamics, any estimate of SIE  $S$  needs to be examined in detail, especially if the ultimate goal is to successfully combine evolutionary and biogeographic theories.

Taxonomic effort is composed of two parts: sampling effort and description effort. The first concerns the rate of sampling (collecting) between and within islands. This is a well-

known phenomenon and is directly analogous to sampling effort in distributional biodiversity studies (see e.g. Prendergast et al. 1993, Gotelli and Colwell 2001, Bush et al. 2004, Romo et al. 2006, Cardoso et al. 2009). Examination of taxonomic sampling effort involves the collation of data from geo-referenced specimens from any particular taxonomic group so that a spatial representation of collection effort can be assessed. The second component depends on the amount of effort, after collection, expended on describing new species i.e. taxonomic description effort. Many collections may be looked at once during collection and then left for decades (or longer), particularly in less charismatic taxa. Also, as technology advances, the resolution at which taxa are classified is being increasingly refined. The net effect of the two components of taxonomic effort could be to raise SIE  $S$  by identifying more species through increased collection effort, higher species description / revision rate and the consequent ‘taxonomic inflation’ caused by revising subspecies and raising them to the species level (Isaac et al. 2004). Or SIE  $S$  could be lowered by the revision and combination of previously separate endemic species or subspecies into one, more widely distributed species or by finding single-island endemics on more than one island.

Dealing with the spatial variation in sampling effort is analytically possible though there can be problems and data quality is an important issue and in particular sampling bias can lead to prediction errors (Hortal et al. 2007, Aranda and Lobo 2011). Schulman *et al.*, (2007) present an elegant example using electronic datasets of geo-referenced herbarium collections to quantify taxonomic sampling effort in Amazonia. However, for many areas and islands the type of data required to perform these analyses is simply not yet available.

Hypothetically, even for well-known island biotas, taxonomic effort may have a demonstrable effect on models involving SIE  $S$ . A useful first step in biogeographic analyses is to construct species accumulation curves; the accumulated number of species discovered and described over time. The resulting curves are a direct result of both aspects of taxonomic

effort which are likely to be dynamic over time. Nevertheless, a general assumption is that when species accumulation curves approach an asymptote that effort should be reaching saturation; thus estimates of  $S$  are stabilising (Gotelli and Colwell 2001).

It is likely that, for evolutionary processes to be meaningfully assessed in biogeographic models based on SIE  $S$ , locally important variables, such as within-island niche diversity, will need to be incorporated (see e.g. Steinbauer et al. 2012). This is because the rate of within-island speciation is not related only to island area for example, but is dependent on the selective pressure applied by factors such as environmental diversity and complexity. Hence, local data will need to be incorporated into models if the causative factors driving differences in diversity are to be successfully identified. Such assessments of the drivers of diversification are fundamentally important to the conservation of global biodiversity.

Using estimates of SIE  $S$  derived from comprehensive databases from eight groups of islands we attempt to answer the questions:

1. Are within-island processes (e.g. niche diversity and evenness) important for determining levels of SIE  $S$  and hence speciation?
  - (i) How common is an asymptotic relationship in SIE  $S$  data?
  - (ii) How does a temporally dynamic SIE  $S$  resulting from increasing taxonomic effort affect model results?
2. Finally we ask, should SIE  $S$  be used in biogeography?

## METHODS

Analyses were based on SIE *S* derived from checklists for eight well known island groups mainly for plants and land snails but also fungi and Coleoptera. Specifically the island checklist sources are: the Azores (9 islands), plants and land snails - Borges et al. (2010); the Canary Islands (7 islands), plants, land snails and fungi - Hernández et al. (2009); the Galapagos (14 islands), plants, land snails and Coleoptera - Bungartz et al. (2009); the Hawai'ian Islands (11 islands), plants Wagner et al. (2005) and land snails - Bishop Museum (2002); Marquesas Islands (9 islands), plants - Wagner and Lorence (2011); the Seychelles (8 islands), plants - Robertson (2005) and land snails - Gerlach (2006); St Helena (1 island) and Ascension (1 island) plants and invertebrates - Ashmole and Ashmole (2000), Cronk (1980, 2000) and Gray (2005); Tristan da Cunha (3 islands), plants and land snails - Holdgate (1965) and Wace and Holdgate (1958); Falkland Islands (2 main islands), plants (Broughton and McAdam 2005); Fernando de Norhona (1 island), Trinidad (1 island) and Martim Vaz (1 island) - Alves (1998, 2006); and finally the plants of the West Indies (13 islands) - Acevedo-Rodríguez (2007).

For Hawai'i, as in the analysis of Whittaker, R.J., Triantis, K.A., et al., (2008) we excluded all the small atolls, Kure, Midway, Pearl & Hermes, French Frigate Shoals and Kaula Island as they do not represent single islands but complexes of many small sand islets. The South Atlantic islands are included here as one group as the flora have some taxonomic affinities (particularly among the Pteridophytes and Poaceae and Cyperaceae) but note they are really a more diffuse and isolated grouping than the other archipelagos. In addition, note that the analysis across the South Atlantic island group was done for plants only. For land snail data we used both species with and without external shells. In addition to the above references, we also used online databases such as International Plant Name Index, Missouri Botanical Garden's Tropicos® database, the World Checklist of Selected Plant Families, the



Encyclopedia of Life, the Biodiversity Heritage Library, the Botanicus Digital Library, ZipcodeZoo, The Global Biodiversity Information Facility and the International Mycology Association's MycoBank database.

We used the checklists to identify the date of publication for each endemic species using the basionym. Nomenclatural synonymy was also researched in order to derive the date when each species was classified as endemic. This resulting dated reference allowed us to build up the number of single island endemic species described per year for each island. We included species, sub-species and varieties in our analyses but note that the results were qualitatively unchanged if sub-species and varieties were excluded.

## ANALYSES

All the analyses were conducted across the complete island dataset and for each of the archipelagos or island groupings separately.

### *Accumulation curves*

From the checklist data we quantified SIE  $S$  over time (1750 – 2012) and produced species accumulation curves for each island. Theoretically, several species accumulation curves are possible, including those that show asymptote, linear, exponential and step changes in species description (Fig. 1a). The asymptote assumes that the effort expended is finding fewer and fewer species over time and is hence approaching the true value of SIE  $S$ . It is widely regarded that this asymptotic relationship is the ideal from which to analyse species richness data. A linear relationship would arise if the number of species discovered remained constant. Under this scenario it is possible that the true SIE  $S$  value could be reached abruptly ending in a flattened line. However, a linear relationship may also indicate that a particular island is in the early stages of species discovery. An exponential curve indicates increasing discovery possibly as a result of increasing effort but may also indicate the early stages of species discovery. Step changes may also arise if there are sporadic bouts of species description in periods when, for example, a limited number of taxonomists are active and then either stop or slow down their activity.

We fitted robust locally weighted regression or LOWESS smoothers (Cleveland 1979) to show the relationship between the accumulated number of taxa described and time. Robust locally weighted regression is a method for smoothing a scatterplot,  $(x_i, y_i)$ ,  $i = 1, \dots, n$ , in which the fitted value at  $x_k$  is a polynomial fit to the data by weighted least squares, where the weight for  $(x_i, y_i)$  is large if  $x_i$  is close to  $x_k$  and small if it is not (Cleveland 1979).

### *Species-area curves*

We examined the effects of a temporally dynamic SIE  $S$  on Type IV species-area curves (Scheiner 2003) plotted separately for five differing time points (1849; 1899; 1949; 1999 and 2010); data were log transformed.. We chose an arbitrary 50-year period that we regard as sufficient for either revisions and/or new species to have been described resulting in a change to SIE  $S$ . Although power models appear to perform best in relation to species-area curves (Triantis et al. 2012), the authors also conclude that there is no definitive technique applicable to all situations. As such, we have largely retained simple linear models here as it is a widely understood and easily interpretable technique both within and outside the biogeography community but we also include comparison to power models in the supplementary material. We used the premise that taxonomic effort increases with time and will tend to increase SIE  $S$ . In addition, we assumed (for the species-area curves and the more complex models below) that this change to SIE  $S$  would affect models in a systematic way, i.e. we assume the model relationship to improve with time. Thus, taxonomic effort should have a minimal effect on model interpretation - an assumption that presumably underlies most analyses in the literature. However, we acknowledge this may not necessarily be the case and it is possible that the model interpretation could be affected by a varying SIE  $S$ . Our approach to this problem is to incorporate Bayesian methodology in our analyses. Although, Bayesian methods do not explicitly correct for a changing SIE  $S$ , they do allow models to be developed through time with the incorporation of prior knowledge in subsequent analyses (see below).

### *Biogeographic Modelling (1) Area and Island Age*

Here, we replicated a simple yet well known model from Whittaker *et al.*, (2008) that used a combination of area and island age ( $\text{Time} + \text{Time}^2$ ). An estimate of maximal geological age was derived from the literature and a bibliography of sources consulted is included in the supporting information. The model was fitted to the data using multiple regression of the form:

$$\text{SIE } S = a + b_1 * \log(\text{Area}) + b_2 * \text{Time} + b_3 * \text{Time}^2 + \varepsilon \quad (\text{equation 1})$$

We have one important distinction from the analyses of Whittaker et al.: we used a Bayesian approach to fit the multiple regressions and incorporate prior information (i.e. the results from preceding time periods) using OpenBUGS v3.2.1 (see Lunn et al. 2000). Data were analysed both across all islands and within each archipelago. The Bayesian approach was used to derive the intercept (a) and regression coefficients for the explanatory variable ( $b_{1-3}$ ) with 95% credible intervals based on prior information. In this case the prior information was based on the parameters and credible intervals from the regression models of previous estimates of SIE  $S$  from the preceding time period. In cases where quantification of taxonomic effort is impossible or impractical, we suggest that using a Bayesian approach is more useful and informative than frequentist approaches. This is because the effect of prior information on coefficients and credible intervals can be more intuitively assessed; in Bayesian terminology there is a 95% chance that the true parameter value will be within the given interval (McCarthy 2007). This type of prior information can be collated from previously published data or by incorporating previous checklist assessments of  $S$  into any analyses. For our analyses, if the prior information is uninformative then the regression parameters will remain similar and the credible intervals will tend towards constancy. We also consider that using Bayesian methods and presenting the data in this way, the results are much more useful for the meta-analyses (see McCarthy 2007 and references therein) that are routinely undertaken in biogeography and macroecology.

### *Biogeographic Modelling (2) Incorporating Island Isolation and Niche Diversity*

In the second approach, we extended the area/island age model by including an index of niche diversity calculated from the Shuttle Radar Topography Mission (SRTM) (CGIAR-CSI 2004, Farr et al. 2007). The SRTM is an international research effort to obtain and freely

disseminate digital elevation models on a near-global scale from 56° S to 60° N. The SRTM data represents approximately three-arcsecond, 90-m resolution digital elevation; note that data was available for most islands but not all. From the island SRTM data we calculated two altitudinal diversity metrics; Shannon-Wiener diversity index (Shannon 1948) and Buzas and Gibson's Evenness (Buzas and Gibson 1969). We made the assumption that these were suitable indicators of niche diversity as there is often a close coupling between island altitude and environment, particularly soils and climate (Steinbauer et al. 2012). Hence, if niche is defined in terms of resource availability (sensu Hutchinson 1957) we assume that niche diversity will correlate with the changing climatic conditions that are associated with altitude. It follows then that islands with more diverse elevation and topography would be expected to have greater niche diversity. Using the SRTM data we used elevation as an indicator of niche and assessed whether niche diversity (Shannon-Wiener) and/or niche evenness (Buzas and Gibson 1969) across islands were important explanatory variables.

A strong latitudinal gradient was evident in our complete dataset (from the southern Falklands to northern Azores) we therefore included latitude in the analysis (northern values positive and southern negative). In addition we included distance to nearest islands and distance to nearest continent, obtained from the UNEP island directory (<http://islands.unep.ch/isldir.htm>). When incorporating these variables we used a best subsets approach to the multiple regressions, thus our maximal model was:

$$\text{SIE } S = a + b_1 * \log(\text{Area}) + b_2 * \text{Time} + b_3 * \text{Time}^2 + b_4 * \text{Nrst}_{\text{isld}} + b_5 * \text{Nrst}_{\text{cont}} + b_6 * \text{Alt}_{\text{div}} + b_7 * \text{Alt}_{\text{even}} + b_7 * \text{Lat} + \varepsilon$$

(equation 2)

## RESULTS

### *Accumulation Curves*

The effect of increasing taxonomic effort over time for all archipelagos and taxonomic groups was clear in that all islands showed an increase in SIE  $S$  (Fig. 1; note, not all islands are shown). Very few of the islands appeared to approach an asymptote (Table S1 in Supplementary Material: doi:10.5061/dryad.cc47h). In only two of the island groups were asymptotes evident, however, a further five did appear to be approaching one. Interestingly, what we considered to be well worked islands did not show asymptotes, e.g. in Hawai'i, there appeared to be an almost linear relationship, the Canaries appeared to show step changes, and although most of the West Indies appear to at least be approaching asymptotes, Cuba was a notable exception (Fig. S1). Amongst all the islands we examined we found evidence for all the theoretical species accumulation curves illustrated in Figure 1a. The Marquesas were the only islands to show exponential-like curves (Fig. S2). Some islands also showed a very recent increase (post-1999), e.g. land snails in some of the Canary Islands (Fig. S3).

### *Species area curves*

The effect of a temporally dynamic SIE  $S$  influenced the species-area relationships in slightly different ways for each of the different archipelagos and taxa. In some archipelagos, but not all, the slopes and intercepts appeared to be converging at least in the latter time periods e.g. plant SIE  $S$  in Seychelles, Hawai'i, and Marquesas (Table S2). The variance explained by the species-area model did not show systematic increase over time across all islands or taxa (Fig. 2 and Table S2). For example,  $r^2$  values for the vascular plant SIE data for the Canary Islands decreased over time whereas that for the Hawai'ian flora tended to increase. This effect appeared to be consistent among Canarian plants and land snails, but the

fungi showed an increase to 1949, a decrease during the next period and a slight rise in the post-2000 period (Fig. 2).

### *Biogeographic modelling (1)*

Regression coefficients associated with the area and island age model appeared much more stable than species-area relationships but there was still a degree of change over the time periods examined (Table S3). Across all islands, it appeared that coefficients were reaching stability with decreasing width of credible intervals. The picture within island groups was again much more variable and mirrors the patterns shown in the species area curves above; perhaps as a consequence of the overall importance of area in this model. There appeared more general stability where the data were asymptotic. The results suggest that a Bayesian approach of incorporating prior information from previous time periods is an appropriate and useful approach, particularly for the incorporation of data into future studies and meta-analyses.

### *Biogeographic modelling (2)*

Using all the variables as single predictors suggested that there were important differences among taxa but also between island groups. Across all islands, for the SIE plant dataset, area was a strong explanatory variable with high adjusted  $r^2$  values that increase in each successive time period (Fig. 3 and Table S3). However for land snails, although area appeared to be a good single predictor there was no clear increase in  $r^2$  and altitudinal diversity was a close second in explanatory power. Also, island age in the land snail data only appeared to be important when included as a quadratic fit but with much less explanatory power than for plants. Both isolation from islands and continents and latitude had little explanatory power in comparison to the other variables.

The best subsets regression suggested that when model complexity was increased area, island age and isolation were not always the best combination of explanatory variables and that there were competing models with as much if not slightly more explanatory power (Fig. 3, Tables S2 and S4). This was the case for both the data across all the islands and within the island groups. For example, the best model as indicated by the AIC and adjusted  $r^2$  for all the snail data omitted area, whereas area was a component of most of the plant SIE models. The best model for the Canaries plant data also omitted area, although in every other island group area was a strong feature for plants. In contrast to the plant datasets, area was not always a clear predictor for the land snail data except for the Canary Islands. There was also an interesting contrast between the West Indies and the South Atlantic islands: in the West Indies, area, age, latitude, proximity to islands and niche diversity were important parameters. In contrast the best model for the South Atlantic omitted latitude altogether and nearest continent was more important than nearest island. For the land snail data, the estimates of SIE  $S$  for the Galapagos were not explained very well by any of the parameters, although the single parameter model of altitudinal evenness gave the best AIC and adjusted  $r^2$ . For the beetles of the Galapagos the models were similar to the plants with the addition of altitudinal diversity in the best overall model. The Canary Islands fungi showed a similar response to the Canary Islands land snails, as area, age, nearest island and altitude diversity were the most consistent explanatory variables. (Table S4).



## DISCUSSION

*Are within-island processes (e.g. niche diversity and evenness) important for determining levels of SIE  $S$  and hence speciation?*

The land snail and plant datasets – our two most comprehensive datasets – showed distinct responses that can best be explained ecologically and have consequences for estimations of evolutionary rates within these groups. Across all time periods, SIE  $S$  estimates for land snails showed a clear and consistent relationship with niche diversity. We suggest this may result from the land snail group including species with a variety of differing adaptations that allow survival in contrasting habitats. For example, included here are species that inhabit hot dry areas and avoid the driest seasons by aestivating inside their shell (dormancy). In addition there are also species that have a preference for cooler, wetter habitats because they are either unable to retreat into their shell (e.g. the genus *Plutonia* Stabile 1864) or have no external shell. The variability and sensitivity of this group to environmental conditions may explain its clear link to our measure of niche diversity. SIE  $S$  estimates for plant data showed a slightly different response, with niche evenness appearing to have more explanatory power than niche diversity. Island area and age were also important parameters for plants but age showed little explanatory power for land snails. Since plants are rooted and have potential for a plastic environmental response, they are expected to show less sensitivity to environmental variability. Borges & Hortal (2009) showed that analysing different arthropod ecological groups generates diverse patterns and conclusions indicating that ecological relationships are not always congruent. What is important to SIE  $S$  model interpretation is the inclusion of variables that are expected to be important within and between island ecological and evolutionary drivers even when these differ across taxa.

*How common is an asymptotic relationship in SIE  $S$  data?*

We expected that the effect of taxonomic effort would be evident, but that well-worked biotas would tend to reach asymptotes with increasing effort and time. However, even such well worked taxa as those on the Hawai'ian Islands appeared to show an almost linear relationship between SIE  $S$  and time; a relationship that has been observed previously in other systems (see e.g. Bebbier et al. 2007). The influence of time on species richness has mostly been considered on geological time scales (see Borges and Brown 1999 and references therein) but shorter term taxonomic influences also need consideration for model interpretation. Gotelli & Colwell (2001) suggest that raw species richness counts can only be validly compared when accumulation curves have reached a clear asymptote. However, this can only be the case when one knows that the effort expended is not a contributing factor to the shape of the curve. Clearly a well defined asymptote can be the result of a decrease in taxonomic effort. From experience we know this to be the case in St Helena which showed the clearest asymptote of any of the islands. Yet plant species are still being described and the number of endemics has been recently revised for St Helena (Lambdon et al. 2012, Lambdon 2013). In addition, we expect that the finer resolution offered by genetic techniques will reveal further distinct species that are as yet cryptically hidden. There is increasing molecular evidence from single-species studies to support the classification of intraspecific taxa without clear differentiation in the phenotype, i.e. cryptic species (Gibson and Dworkin 2004, Masel 2006, Bickford et al. 2007, Hayden et al. 2011, Schaefer et al. 2011), hence, SIE  $S$  is highly likely to change.

There are methods to deal with variations in taxonomic effort in addition to the example noted above (Schulman et al. 2007). Lobo and Borges (2010) used comparisons of the exponential and Clench functions (the two main species-accumulation functions) and asymptotic value to estimate the number of species still undescribed. Santos et al. (2010) dealt with unevenness of data quality by using completeness at high taxonomic levels,

congruence with well-established ecological relationships (such as species–area relationship) and publication effort. Nevertheless, many of these deal either with only one aspect of taxonomic effort or rely on a high proportion of the species to have been already described (e.g. see Bebbber et al. 2007). If our results are representative then the latter point is unlikely to be the case for SIE *S* datasets, and highlights the problem that much of the data needed for these methods is not widely available.

*How does a temporally dynamic SIE *S* resulting from increasing taxonomic effort affect model results?*

We also expected that increasing taxonomic effort would result in a decreasing influence on the models. However, regression coefficients did not always tend towards stability with increasing effort and time. Thus the effects on the SIE *S* area-time relationships did not appear to be systematic in relation to increasing taxonomic effort. Changes in slope have been attributed to changes in geographical scale (Williams 1943, Preston 1960, Rosenzweig 1995, Triantis et al. 2012). Our analyses show that taxonomic effort can also change these parameters when geographic scale is held constant. The application of Bayesian methods allowed us to assess how the parameters and credible intervals responded to the incorporation of prior information. In all cases credible intervals narrowed through time suggesting informative priors. This suggests that Bayesian approaches are likely to be very useful in the application of SIE datasets particularly where they are expected to be temporally dynamic.

Perhaps the most surprising result was that the explained variance in some archipelagos decreased with increasing time. The lack of consistent relationships among archipelagos implied that important processes are being omitted from current models of island biogeography. In particular, as many islands show incomplete saturation of taxonomic

effort (i.e. failure to reach SIE asymptote); it seems likely that quantification of currently unexplored levels of species diversity (both cryptic species and poorly known island flora and fauna) will tend to change these relationships further. The consequence would be that, for models of island biogeography, *in situ* speciation rate would take a much more prominent role in determining levels of diversity, via the physical proxies of island age, size and niche complexity. Recently, there have been attempts to take a more phylogenetic approach to biogeography models (e.g. Rosindell and Phillimore 2011). However, in most cases the extent of phylogenetic coverage is still too limited to allow entire island biotas to be fully evaluated and, where an extensive phylogenetic framework exists, problems of variable taxonomic or sampling effort are likely to undermine their value. There is a need to re-evaluate SIE  $S$  estimates for islands, using objective approaches systematically applied across multiple islands. Secondly, there is a need to reassess the causative factors driving the differences in diversity and to work these key local variables into revised models of island biogeography. This is especially the case if more meaningful ecological, evolutionary and geological processes are to be incorporated, as has been widely called for (Haila 1990, Cowie 1995, Borges and Brown 1999, Brown and Lomolino 2000, Heaney 2000, Lomolino 2000, Heaney 2007, Whittaker and Fernández-Palacios 2007).

#### *Should SIE $S$ be used in biogeography?*

Our results suggest that estimates of SIE  $S$  can be valuable biogeographic parameters when their quality is properly assessed and controlled for. This is true for both biogeography and other studies where SIE  $S$  has formed part or a major focus. It should be noted that using the basionym year, as we have done here, does not give an indication of the additional sampling effort through collections performed by taxonomists and ecologists on islands. We suggest that, when available, standardized island surveys (e.g. Borges et al. 2005, Ribeiro et al. 2005) should also be used to evaluate the relative knowledge of island floras and faunas.

However, we think the study of SIE  $S$  is likely to yield interesting results when variables of evolutionary consequence are included in models such as those that are indicators of niche diversity. We propose that island SIE  $S$  (and probably total  $S$ ) be regarded as an unknown and dynamic metric and that studies attempt to assess the level of taxonomic effort within the datasets they use and the influence this may have on the results. We also suggest that a systematic approach to evaluating SIE  $S$  on islands is also required, sampling across and within taxa to test model predictions and hypotheses. For example, we might ask: what is the importance of relictual isolation as the origin of endemism (paleo / neo-endemism) and selection versus drift as mechanisms of SIE speciation? Although this type of evidence has still to be collated for many islands, these are necessary data to allow within-island processes to be understood and biogeographic models interpreted appropriately (see also Rosindell and Phillimore 2011). That the effects of increasing taxonomic effort alone can influence species-area relationships, and hence biogeographic models, illustrates the drawbacks of accepting SIE  $S$  estimates *de facto*. However, by embracing a Bayesian approach the explanatory power of island biogeography theory can be compared and evaluated in a more objective manner. In particular, better collaboration between taxonomists and modellers presents exciting opportunities to test and develop the theory of island biogeography in new and dynamic ways, promising rapid development as we move into the next 50 years.

## **SUPPLEMENTARY MATERIAL**

Supplementary material can be found in the Dryad data repository (doi:10.5061/dryad.cc47h)

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## Figure Legends

Figure 1: Idealised (a) and actual species accumulation curves from 1750 until 2010 for selected islands (b, c and d). (a) Idealised species accumulation curves: decreasing towards asymptote, linear, exponential and step change rates of endemic species description (b) Species accumulation curves for single island endemic plant richness of the Hawai'ian archipelago; most Hawai'ian Islands exhibit near linear increase. (c) Species accumulation curve for single island endemic plant richness of the South Atlantic island group; most South Atlantic Islands exhibit a decreasing rate of discovery. (d) Species accumulation curve for single island endemic plant richness of the Canary archipelago; most Canary Islands exhibit step changes in the discovery rate, significantly slowing down in the 1850-1950 period. Note that the Marquesas Islands showed a near exponential increase (Fig. S1). Fitted lines (in b, c and d) represent a LOWESS smoother (Cleveland 1979) with degree of smoothing set to 0.1 and 10 steps.

Figure 2: Species-area relationships for selected island data using accumulated single island endemic richness over five different time periods. Both species richness and area were log transformed. (a) Species-area curve for single island endemic plant richness of the Hawaiian archipelago. (b) Species-area curve for single island endemic plant richness of the Marquesas archipelago. (c) Species-area curve for single island endemic plant richness of the Canary archipelago. (d) Species-area curve for single island endemic fungal richness of the Canary archipelago.

Figure 3: Results of univariate linear regression of single island endemic plant richness for different island groups and time periods, showing the variance explained by each explanatory variable. Note that both a simple fit to maximum age and a quadratic fit for island age were used here.

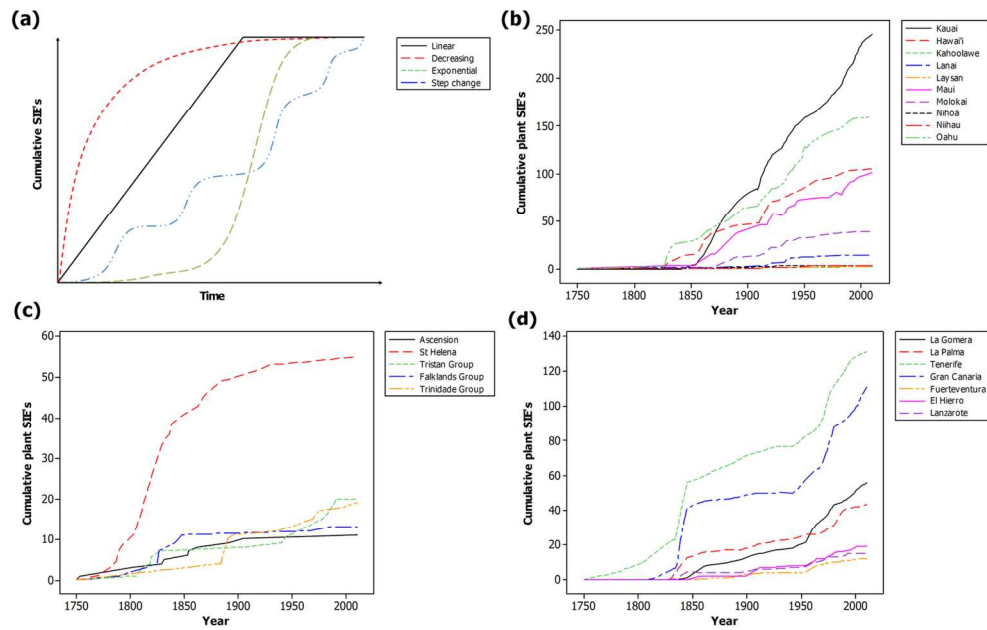


Figure 1

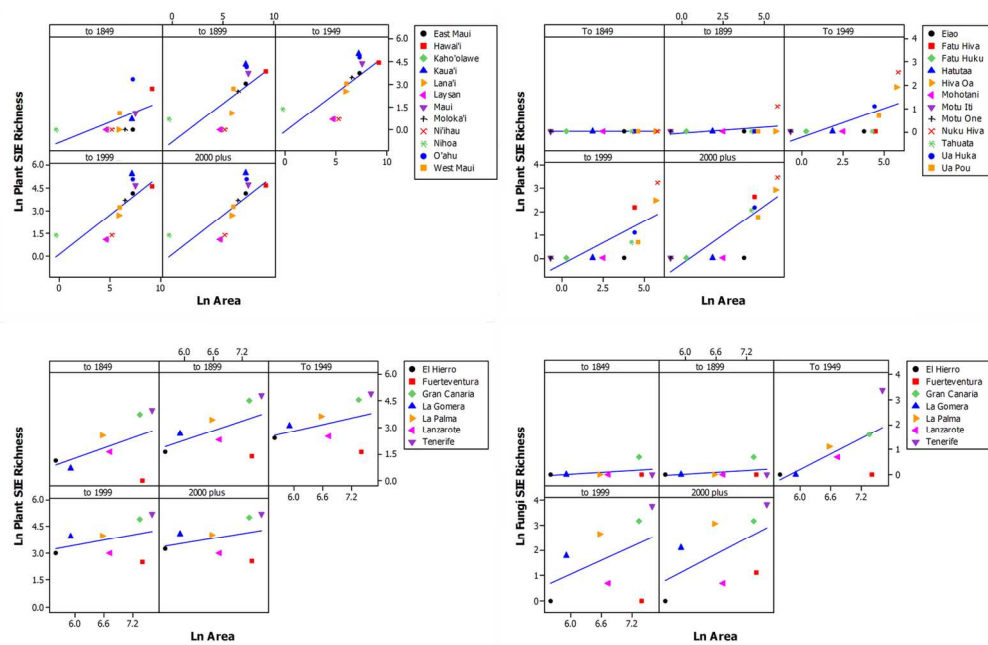


Figure 2



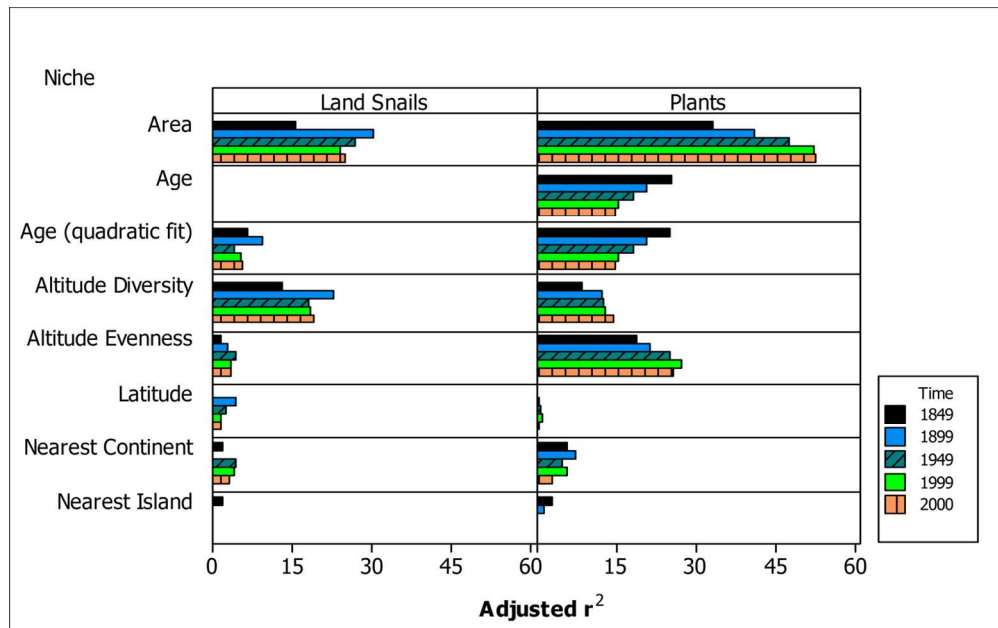


Figure 3

## **Supplemental Material**

### **Island Biogeography, the effects of taxonomic effort and the importance of island niche diversity to single island endemic species**

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## Method Note

*Island Geological Age:* We used the maximal geological age derived from the published sources found in the bibliography.

## Additional Results

Figure S1: Species accumulation curves for single island endemic plant richness of the West Indies. Fitted lines represent a LOWESS smoother (Cleveland, W.S. 1979) with degree of smoothing set to 0.1 and 10 steps.

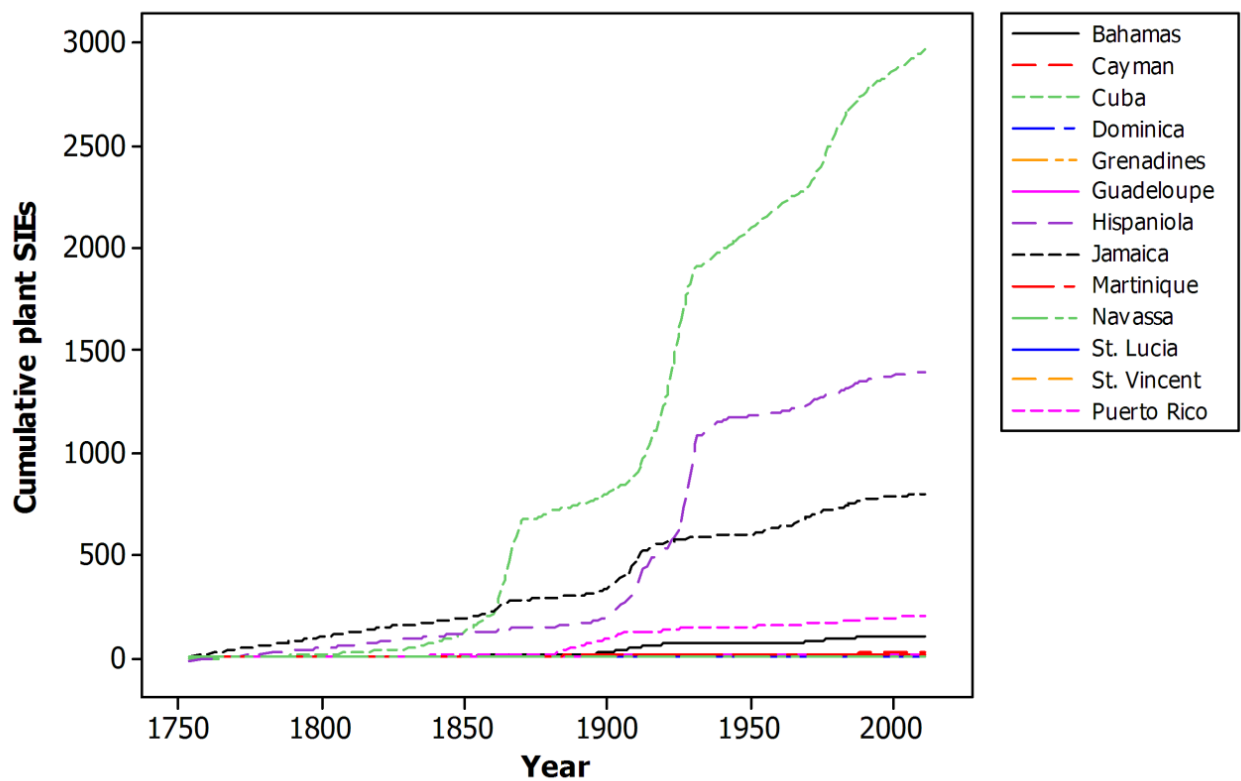


Figure S2: Species accumulation curves for single island endemic plant richness of the Marquesas archipelago note the near exponential increase. Fitted lines represent a LOWESS smoother (Cleveland, W.S. 1979) with degree of smoothing set to 0.1 and 10 steps.

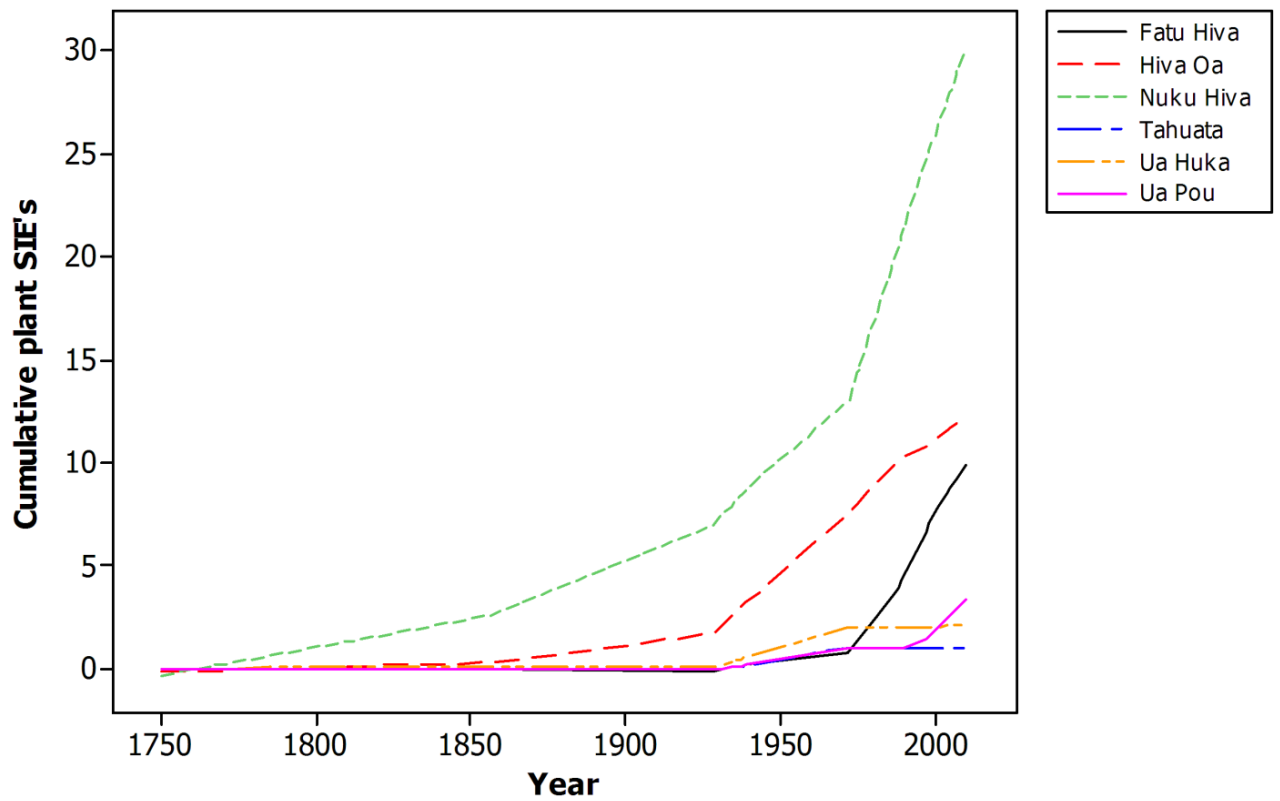


Figure S3: Species accumulation curves for single island endemic land snail richness of the Canary Islands. Fitted lines represent a LOWESS smoother (Cleveland, W.S. 1979) with degree of smoothing set to 0.1 and 10 steps.

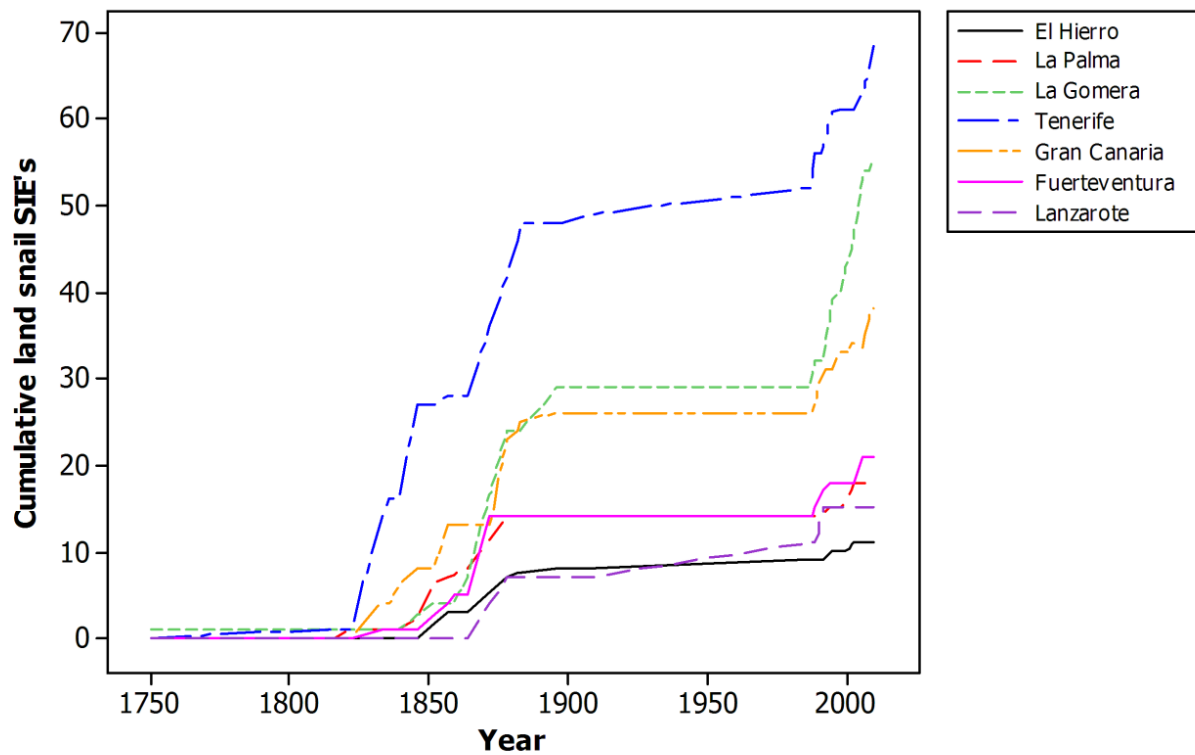


Table S1: Details of island groups: number of islands where at least 1 single island endemic was found in at least one taxonomic group (n), datasets included and whether the single island endemic accumulation curve reached an asymptote. Three categories were used for classifying asymptote, *Yes* for those islands definitely displaying an asymptote, *No* when an asymptote was not apparent and *Approaching* for those that were more ambiguous. \* St Helena & Tristan da Cunha only.

Ocean Region	Island System	Island Origins	<i>n</i>	Taxon	Asymptote
North Atlantic	Azores	Volcanic	9	Plants	No
				Land snails	No
	Canary Islands	Volcanic	7	Plants	No
				Land snails	No
				Fungi*	No
Pacific Ocean	Hawai'ian Islands	Volcanic	11	Plants	No
				Land snails	Yes
	Galapagos	Volcanic	14	Plants	Approaching
				Land snails	Approaching
				Coleoptera	No
	Marquesas	Volcanic	9	Plants	No
Indian Ocean	Seychelles	Continental	8	Plants	Approaching
		& Atolls		Land snails	Approaching
South Atlantic	All	Volcanic	6	Plants	Yes
		& Continental	2	Land snails*	Approaching
Caribbean	West Indies	Volcanic, Continental & Atolls	13	Plants	Yes or approaching (but Cuba still increasing)

Table S2: Results of univariate linear regression of single island endemic plant richness for different island groups and time periods, showing the variance explained by each explanatory variable note that a quadratic fit was used for Island Age here. \* indicates time periods for when no single island endemics were recorded therefore model not fitted.

Variable	Time Period	Adjusted r <sup>2</sup>								
		All Islands	Azores	Canaries	Galapagos	Hawaii	Marquesas	Seychelles	South Atlantic	West Indies
Area	1849	33.17	N/A	8.62	0.21	9.34	N/A	48.48	21.82	69.42
	1899	41.11	13.96	12.05	17.87	27.67	3.76	48.48	0	77.55
	1949	47.6	26.37	0	19.74	41.02	44.69	60.16	0	79.06
	1999	52.13	44.47	0	40.64	48.12	49.91	60.31	0	79.93
	2010	52.5	35.34	0	41.06	48.12	67.8	60.31	0	79.88
Latitude	1849	0	N/A	0	6.17	3.08	N/A	0	0	15.65
	1899	1.89	1.89	0	36.01	11.73	0	0	0	23.77
	1949	0.63	0	0	35.16	18.18	0	2.56	0	30.76
	1999	0.82	0	0	32.13	17.63	0	27.56	0	34.55
	2010	0.29	6.6	0	31.61	17.63	19.5	27.56	0	33.81
Nrst Continent	1849	5.73	N/A	0	0	0	N/A	0	8.06	0
	1899	7.16	7.22	0	0	4.2	0	0	0	0
	1949	4.75	16.82	0	4.09	7.74	0	0	0	0
	1999	5.69	0	0	10.43	12.57	0	0	5.18	0
	2010	2.67	0	0	10.39	12.57	0	0	7.28	0
Nrst Island	1849	2.94	N/A	24.03	0	0	N/A	0	0	56.21
	1899	1.36	27.37	13.57	0	1.89	0	0	0	51.69
	1949	0	9.64	29.12	0	13.61	0	0	0	44.64
	1999	0	0	27.08	0	18.79	0	0	0	46.94
	2010	0	14.9	34.08	0	18.79	0	0	0	46.62

Table S2 continued

Variable	Time Period	Adjusted r <sup>2</sup>								
		All Islands	Azores	Canaries	Galapagos	Hawaii	Marquesas	Seychelles	South Atlantic	West Indies
Island Age	1849	25.24	N/A	0	6.82	0	N/A	0	0	60.42
	1899	20.8	0	0	5.36	12.57	0	0	0	67.86
	1949	18.31	0	0	0	20.22	0	0	0	72.73
	1999	15.42	0	0	0	19.44	0	0	0	71.56
	2010	14.71	10.04	0	0	19.44	0	0	0	72.86
Island Age (quadratic)	1849	21.1	N/A	6.29	3.86	0	N/A	0	0	73.32
	1899	19.01	31.1	23.66	9.45	2.06	0	0	28.55	73.75
	1949	17.35	41.9	33.88	1.4	12.58	0	7.97	13.74	79.47
	1999	15.27	29.14	37.33	0	12.32	1.95	38.6	0	76.4
	2010	14.72	27.1	37.25	0	12.32	8.21	38.6	0	78.09
Alt Diversity	1849	8.41	N/A	31.78	0	5.97	N/A	0	14.64	27.81
	1899	12.07	0	36.8	11.4	35.76	0	0	0	0.73
	1949	12.4	0	52.87	9.61	49.45	19.27	0	0	0
	1999	12.72	14.64	52.47	33.43	51.17	23.78	12.51	0	0
	2010	14.51	0	56.84	33.71	51.17	1.23	12.51	0	0
Alt Evenness	1849	18.71	N/A	0	0	1.5	N/A	0	0	4.74
	1899	21.43	0	0	0	10.23	0	0	0	37.08
	1949	24.99	0	0	0	12.73	0	0	0	43.9
	1999	27.19	0	0	11.04	17.02	0	0	0	46.34
	2010	25.57	0	0	11.84	17.02	8.87	0	0	46.28



Table S3: Bayesian regression coefficients for the ATT<sup>2</sup> model of single island endemics species richness in eight island systems spanning five different time periods. Grey shaded rows signify that no single island endemics published and the model cannot be fitted. The fungal group here includes fungi, lichens and fungi imperfecta. CI's are Bayesian derived 95% credible intervals.

Island System	Time Period	intercept	SD	5% CI	95% CI	b [1] (area)	SD	5% CI	95% CI	b [2] (time)	SD	5% CI	95% CI	b [3] (time2)	SD	5% CI	95% CI
All Islands <i>n</i> = 80 (plants)	to 1849	0.729	0.112	0.546	0.913	0.211	0.042	0.142	0.280	0.025	0.011	0.006	0.043	0.000	0.000	0.000	8.16E-05
	to 1899	0.927	0.090	0.780	1.073	0.253	0.033	0.198	0.306	0.022	0.007	0.010	0.034	0.000	0.000	0.000	0.000
	to 1949	1.114	0.081	0.980	1.247	0.286	0.029	0.238	0.334	0.021	0.006	0.011	0.031	0.000	0.000	0.000	0.000
	To 1999	1.288	0.077	1.162	1.413	0.313	0.026	0.270	0.357	0.019	0.005	0.011	0.028	0.000	0.000	0.000	0.000
	2000 plus	1.438	0.072	1.319	1.555	0.334	0.024	0.293	0.373	0.018	0.004	0.011	0.025	0.000	0.000	0.000	0.000
Azores <i>n</i> = 9 (plants)	to 1849																
	to 1899	0.077	0.081	-0.046	0.202	0.072	0.076	-0.045	0.190	0.227	0.147	0.011	0.447	-0.025	0.017	-0.051	0.0012
	to 1949	0.123	0.052	0.036	0.206	0.104	0.048	0.024	0.181	0.273	0.079	0.141	0.399	-0.031	0.009	-0.046	-0.0151
	To 1999	0.161	0.051	0.077	0.245	0.127	0.046	0.052	0.202	0.278	0.061	0.178	0.378	-0.033	0.007	-0.045	-0.0214
	2000 plus	0.203	0.052	0.118	0.288	0.142	0.043	0.070	0.213	0.308	0.050	0.226	0.389	-0.030	0.006	-0.040	-0.0208
Canaries <i>n</i> = 7 (plants)	to 1849	1.956	0.398	1.448	2.466	1.891	0.706	0.979	2.803	0.231	0.226	-0.044	0.511	-0.020	0.011	-0.034	-0.0073
	to 1899	2.709	0.259	2.215	3.043	1.625	0.360	1.076	2.244	0.286	0.098	0.119	0.440	-0.021	0.005	-0.028	-0.013
	to 1949	3.059	0.174	2.743	3.310	1.401	0.249	1.016	1.830	0.279	0.058	0.183	0.375	-0.021	0.003	-0.025	-0.016
	To 1999	3.272	0.178	2.974	3.559	1.307	0.225	0.946	1.683	0.283	0.045	0.210	0.357	-0.020	0.002	-0.024	-0.016
	2000 plus	3.480	0.168	3.193	3.745	1.212	0.202	0.887	1.550	0.283	0.036	0.225	0.341	-0.020	0.002	-0.023	-0.017
Hawaii <i>n</i> = 11 (plants)	to 1849	0.746	0.378	0.138	1.358	0.300	0.214	-0.044	0.646	0.143	0.362	-0.442	0.729	-0.007	0.016	-0.033	0.019
	to 1899	1.356	0.338	0.774	1.886	0.414	0.157	0.150	0.666	0.165	0.218	-0.199	0.520	-0.011	0.010	-0.027	0.005
	to 1949	1.929	0.325	1.375	2.445	0.451	0.127	0.242	0.657	0.183	0.149	-0.064	0.427	-0.012	0.007	-0.023	-0.001
	To 1999	2.495	0.292	1.991	2.951	0.489	0.104	0.316	0.659	0.228	0.152	-0.024	0.475	-0.013	0.006	-0.023	-0.003
	2000 plus	2.839	0.230	2.449	3.202	0.515	0.085	0.374	0.655	0.248	0.100	0.083	0.412	-0.014	0.004	-0.022	-0.007
Marquesas <i>n</i> = 12 (plants)	to 1849																
	to 1899	0.091	0.081	-0.038	0.222	0.072	0.037	0.013	0.131	-0.410	0.184	-0.707	-0.113	0.051	0.028	0.005	0.097
	to 1949	0.138	0.079	0.008	0.267	0.095	0.036	0.036	0.154	-0.443	0.144	-0.679	-0.203	0.045	0.022	0.008	0.082
	To 1999	0.180	0.079	0.050	0.309	0.114	0.036	0.056	0.172	-0.442	0.142	-0.675	-0.207	0.021	0.042	-0.048	0.090
	2000 plus	0.215	0.079	0.085	0.344	0.129	0.036	0.070	0.187	-0.436	0.134	-0.656	-0.215	0.017	0.032	-0.036	0.071

Table S3 continued

Island System	Time Period	intercept	SD	5% CI	95% CI	b [1] (area)	SD	5% CI	95% CI	b [2] (time)	SD	5% CI	95% CI	b [3] (time2)	SD	5% CI	95% CI
Galapagos <i>n</i> = 14 (plants)	to 1849	0.206	0.114	0.022	0.391	0.071	0.049	-0.008	0.151	0.846	0.574	-0.091	1.777	-0.220	0.189	-0.527	0.08746
	to 1899	0.286	0.106	0.109	0.458	0.081	0.042	0.011	0.151	0.831	0.385	0.197	1.463	-0.209	0.130	-0.423	0.006
	to 1949	0.335	0.104	0.165	0.505	0.090	0.041	0.023	0.157	0.756	0.308	0.251	1.263	-0.227	0.105	-0.399	-0.055
	To 1999	0.385	0.103	0.216	0.554	0.103	0.040	0.037	0.168	0.653	0.264	0.222	1.089	-0.251	0.089	-0.397	-0.103
	2000 plus	0.432	0.101	0.266	0.598	0.115	0.039	0.052	0.179	0.612	0.229	0.236	0.990	-0.257	0.078	-0.385	-0.129
Seychelles <i>n</i> = 8 (plants)	to 1849	0.288	0.219	-0.049	0.629	0.246	0.158	0.000	0.490	2.482	1.984	-0.896	5.347	-0.040	0.032	-0.086	0.014
	to 1899	0.288	0.136	0.067	0.511	0.247	0.098	0.087	0.407	2.464	1.398	-0.064	4.415	-0.040	0.023	-0.064	4.415
	to 1949	0.332	0.111	0.147	0.513	0.293	0.081	0.158	0.423	2.737	1.172	0.726	4.342	-0.044	0.019	-0.070	-0.012
	To 1999	0.384	0.106	0.208	0.558	0.334	0.077	0.206	0.460	3.017	1.017	1.163	4.565	-0.049	0.016	-0.074	-0.019
	2000 plus	0.430	0.101	0.264	0.595	0.370	0.073	0.249	0.489	3.265	0.881	1.649	4.553	-0.053	0.014	-0.073	-0.027
South Atlantic <i>n</i> = 6 (plants)	to 1849	1.682	1.045	0.579	2.791	1.159	1.071	0.094	2.301	0.134	0.232	-0.107	0.399	-0.001	0.002	-0.004	0.001
	to 1899	2.442	0.242	2.055	2.773	0.452	0.237	0.124	0.839	0.146	0.050	0.071	0.223	-0.001	0.000	-0.002	-0.001
	to 1949	2.580	0.129	2.357	2.777	0.418	0.122	0.221	0.619	0.124	0.024	0.085	0.164	-0.001	0.000	-0.001	-0.001
	To 1999	2.666	0.113	2.475	2.845	0.402	0.100	0.240	0.567	0.111	0.016	0.085	0.139	-0.001	0.000	-0.001	-0.001
	2000 plus	2.726	0.099	2.560	2.885	0.392	0.085	0.254	0.531	0.106	0.012	0.087	0.125	-0.001	0.000	-0.001	-0.001
West Indies <i>n</i> = 13 (plants)	to 1849	1.738	0.274	1.297	2.181	0.292	0.162	0.031	0.555	0.056	0.025	0.016	0.096	0.000	0.000	0.000	0.000
	to 1899	2.155	0.221	1.775	2.500	0.359	0.112	0.171	0.539	0.045	0.014	0.021	0.068	0.000	0.000	0.000	0.000
	to 1949	2.545	0.234	2.152	2.917	0.364	0.092	0.216	0.519	0.039	0.010	0.023	0.056	0.000	0.000	0.000	0.000
	To 1999	2.986	0.240	2.582	3.371	0.371	0.079	0.240	0.500	0.034	0.008	0.021	0.048	0.000	0.000	0.000	0.000
	2000 plus	3.426	0.203	3.074	3.741	0.383	0.066	0.273	0.490	0.032	0.006	0.021	0.042	0.000	0.000	0.000	0.000
All Islands <i>n</i> = 51 (land snails)	to 1849	0.452	0.106	0.278	0.627	0.130	0.041	0.063	0.198	0.064	0.028	0.017	0.109	-0.001	0.000	-0.002	0.000
	to 1899	0.632	0.097	0.472	0.791	0.176	0.037	0.116	0.236	0.072	0.019	0.040	0.104	-0.001	0.000	-0.002	-0.001
	to 1949	0.763	0.092	0.612	0.914	0.202	0.034	0.146	0.258	0.069	0.015	0.045	0.094	-0.001	0.000	-0.002	-0.001
	To 1999	0.885	0.088	0.740	1.029	0.220	0.032	0.168	0.273	0.070	0.012	0.051	0.089	-0.001	0.000	-0.001	-0.001
	2000 plus	0.988	0.084	0.851	1.125	0.236	0.030	0.186	0.285	0.070	0.010	0.054	0.086	-0.001	0.000	-0.001	-0.001
Azores <i>n</i> = 9 (land snails)	to 1849	0.077	0.081	-0.046	0.202	0.072	0.077	-0.045	0.190	0.229	0.150	0.011	0.447	-0.025	0.018	-0.051	0.001
	to 1899	0.149	0.083	0.012	0.284	0.096	0.072	-0.023	0.213	0.347	0.112	0.163	0.529	-0.014	0.013	-0.035	0.008
	to 1949	0.229	0.083	0.092	0.364	0.118	0.066	0.009	0.227	0.373	0.085	0.234	0.513	-0.013	0.010	-0.029	0.004
	To 1999	0.296	0.083	0.160	0.432	0.136	0.063	0.032	0.240	0.396	0.071	0.279	0.513	0.011	0.008	-0.025	0.002
	2000 plus	0.357	0.082	0.222	0.491	0.153	0.061	0.053	0.253	0.359	0.061	0.259	0.460	0.005	0.007	-0.006	0.017

Table S 3 continued

Island System	Time Period	intercept	SD	5% CI	95% CI	b [1] (area)	SD	5% CI	95% CI	b [2] (time)	SD	5% CI	95% CI	b [3] (time2)	SD	5% CI	95% CI
Canaries <i>n</i> = 7 (land snails)	to 1849	1.037	0.500	0.399	1.678	1.069	0.887	-0.075	2.215	0.226	0.284	-0.120	0.577	-0.014	0.014	-0.030	0.003
	to 1899	2.089	0.521	1.134	2.814	0.709	0.600	-0.213	1.757	0.198	0.156	-0.055	0.459	-0.012	0.008	-0.024	0.000
	to 1949	2.739	0.255	2.285	3.106	0.539	0.358	-0.030	1.140	0.188	0.087	0.046	0.331	-0.011	0.004	-0.017	-0.004
	To 1999	3.052	0.156	2.772	3.280	0.406	0.229	0.046	0.795	0.205	0.052	0.118	0.289	-0.010	0.002	-0.014	-0.006
	2000 plus	3.172	0.124	2.961	3.367	0.358	0.183	0.061	0.663	0.209	0.037	0.149	0.270	-0.010	0.002	-0.013	-0.007
Galapagos <i>n</i> = 14 (land snails)	to 1849																
	to 1899	0.214	0.159	-0.043	0.471	0.102	0.069	-0.009	0.213	-0.429	0.800	-1.735	0.869	0.146	0.263	-0.281	0.575
	to 1949	0.186	0.133	-0.031	0.405	0.129	0.055	0.037	0.219	-0.754	0.516	-1.591	0.108	0.187	0.174	-0.102	0.469
	To 1999	0.168	0.114	-0.020	0.356	0.142	0.047	0.065	0.219	-0.850	0.363	-1.441	-0.251	0.215	0.123	0.011	0.416
	2000 plus	0.164	0.104	-0.007	0.335	0.154	0.042	0.084	0.223	-0.922	0.280	-1.380	-0.460	0.224	0.095	0.067	0.380
Hawaii <i>n</i> = 11 (land snails)	to 1849	0.935	0.377	0.336	1.538	0.243	0.154	-0.002	0.490	0.323	0.379	-0.281	0.935	-0.016	0.016	-0.042	0.010
	to 1899	1.343	0.337	0.766	1.873	0.395	0.134	0.167	0.608	0.208	0.223	-0.163	0.572	-0.015	0.010	-0.031	0.002
	to 1949	1.768	0.328	1.212	2.287	0.513	0.117	0.313	0.700	0.134	0.151	-0.115	0.382	-0.013	0.007	-0.024	-0.002
	To 1999	2.114	0.276	1.640	2.546	0.583	0.095	0.424	0.735	0.146	0.107	-0.032	0.321	-0.013	0.005	-0.021	-0.005
	2000 plus	2.294	0.224	1.917	2.651	0.614	0.077	0.486	0.740	0.159	0.078	0.030	0.287	-0.014	0.004	-0.019	-0.008
Seychelles <i>n</i> = 8 (land snails)	to 1849	0.173	0.184	-0.110	0.459	-0.059	0.132	-0.266	0.145	2.056	1.657	-0.756	4.463	-0.033	0.027	-0.072	0.012
	to 1899	0.370	0.121	0.157	0.551	0.086	0.087	-0.066	0.216	2.303	1.163	0.154	3.894	-0.037	0.019	-0.063	-0.002
	to 1949	0.484	0.114	0.293	0.667	0.124	0.075	-0.002	0.246	2.558	1.013	0.795	4.116	-0.041	0.016	-0.066	-0.013
	To 1999	0.594	0.115	0.404	0.781	0.135	0.069	0.022	0.248	2.784	0.891	1.167	4.166	-0.045	0.014	-0.067	-0.019
	2000 plus	0.705	0.111	0.520	0.884	0.145	0.062	0.042	0.247	2.989	0.794	1.548	4.220	-0.048	0.013	-0.068	-0.025
Galapagos <i>n</i> = 14 (Coleoptera)	to 1849	0.206	0.152	-0.039	0.452	0.080	0.066	-0.026	0.186	0.470	0.765	-0.779	1.708	-0.063	0.251	-0.471	0.347
	to 1899	0.092	0.087	-0.039	0.245	0.063	0.033	0.012	0.119	-0.113	0.363	-0.665	0.527	0.024	0.119	-0.186	0.206
	to 1949	0.085	0.071	-0.031	0.201	0.072	0.027	0.028	0.116	-0.262	0.242	-0.656	0.142	0.053	0.082	-0.083	0.186
	To 1999	0.105	0.071	-0.011	0.222	0.074	0.027	0.030	0.118	-0.299	0.224	-0.666	0.071	0.050	0.076	-0.074	0.174
	2000 plus	0.128	0.071	0.011	0.219	0.076	0.027	0.032	0.110	-0.350	0.211	-0.697	-0.079	0.041	0.071	-0.076	0.132
Canaries <i>n</i> = 7 (Fungi)	to 1849	0.099	0.235	-0.201	0.400	0.112	0.416	-0.426	0.650	0.032	0.133	-0.130	0.197	-0.002	0.006	-0.009	0.006
	to 1899	0.099	0.116	-0.090	0.289	0.113	0.207	-0.223	0.452	0.031	0.057	-0.063	0.125	-0.002	0.003	-0.006	0.003
	to 1949	0.141	0.116	-0.050	0.331	0.189	0.205	-0.147	0.525	0.032	0.050	-0.050	0.114	-0.002	0.002	-0.006	0.002
	To 1999	0.175	0.116	-0.015	0.367	0.219	0.202	-0.113	0.553	0.030	0.047	-0.046	0.107	-0.003	0.002	-0.006	0.001
	2000 plus	0.210	0.117	0.019	0.403	0.248	0.200	-0.081	0.578	0.031	0.044	-0.042	0.104	-0.003	0.002	-0.006	0.001

Table S4: The results of the best subsets regression for single island endemics datasets of plants, land snails, Coleoptera (Galapagos only) and fungi (Canaries only), which identifies the best combination of variables for each island group level. The candidate models are ranked by Akaike Information Criterion (AIC), which identifies the models which explain the most variance in the data with the fewest terms in the model. Candidate models with 0% adjusted  $r^2$  (Adj.  $r^2$ ) are not shown.

Taxa	Island Group	AIC	Adj. r <sup>2</sup>	Model															
Plants	All Islands	77.76	57.44	Area	+	Age	+	Nrst Isld											
	n = 80	78.08	56.63	Area	+	Nrst Isld													
		79.20	57.19	Area	+	Age	+	Latitude	+	Nrst Isld									
		80.35	57.11	Area	+	Age	+	Latitude	+	Nrst Cont	+	Nrst Isld							
		81.15	57.25	Area	+	Age	+	Latitude	+	Nrst Cont	+	Nrst Isld	+	Alt Even					
		83.00	56.72	Area	+	Age	+	Age <sup>2</sup>	+	Latitude	+	Nrst Cont	+	Nrst Isld	+	Alt Even			
		84.03	52.50	Area															
		85.00	56.08	Area	+	Age	+	Age <sup>2</sup>	+	Latitude	+	Nrst Cont	+	Nrst Isld	+	Alt Div	+	Alt Even	
Plants	Azores	15.00	99.85	Area	+	Age	+	Age <sup>2</sup>	+	Latitude	+	Alt Div	+	Alt Even					
	n = 9	17.00	99.70	Area	+	Age	+	Age <sup>2</sup>	+	Latitude	+	Nrst Isld	+	Alt Div	+	Alt Even			
		18.30	99.37	Area	+	Age	+	Latitude	+	Alt Div	+	Alt Even							
		44.30	97.43	Area	+	Age	+	Latitude	+	Alt Div									
		419.90	75.28	Area	+	Age	+	Latitude											
		952.20	52.67	Area	+	Age													
		1512.20	35.34	Area															
Plants	Canaries	10.47	89.09	Age	+	Age <sup>2</sup>	+	Alt Div											
	n = 7	10.70	84.46	Age	+	Alt Div													
		11.50	90.09	Area	+	Age	+	Age <sup>2</sup>	+	Alt Div									
		13.00	86.77	Area	+	Age	+	Age <sup>2</sup>	+	Nrst Isld	+	Alt Div							
		20.31	56.84	Alt Div															

Table S4 continued

Taxa	Island Group	AIC	Adj. r <sup>2</sup>	Model															
Plants	Galapagos	14.77	63.48	Area	+	Age	+	Age <sup>2</sup>											
	n = 14	15.74	65.14	Area	+	Age	+	Age <sup>2</sup>	+	Latitude									
		16.72	47.93	Area	+	Latitude													
		17.35	41.06	Area															
		17.37	62.74	Area	+	Age	+	Age <sup>2</sup>	+	Latitude	+	Nrst Cont							
		18.11	66.74	Area	+	Age	+	Age <sup>2</sup>	+	Nrst Cont	+	Nrst Isld	+	Alt Even					
		20.04	60.71	Area	+	Age	+	Age <sup>2</sup>	+	Nrst Cont	+	Nrst Isld	+	Alt Div	+	Alt Even			
		22.00	51.42	Area	+	Age	+	Age <sup>2</sup>	+	Latitude	+	Nrst Cont	+	Nrst Isld	+	Alt Div	+	Alt Even	
		Plants	Hawaii	15.87	71.60	Area	+	Age	+	Latitude	+	Nrst Isld							
n = 11	16.14		75.95	Area	+	Age	+	Latitude	+	Nrst Cont	+	Nrst Isld							
	16.65		64.09	Latitude	+	Nrst Isld	+	Alt Div											
	17.31		75.96	Area	+	Age	+	Latitude	+	Nrst Cont	+	Nrst Isld	+	Alt Div					
	17.42		58.53	Latitude	+	Alt Div													
	18.22		78.53	Area	+	Age	+	Latitude	+	Nrst Cont	+	Nrst Isld	+	Alt Div	+	Alt Even			
	19.13		51.17	Alt Div															
	20.00		70.96	Area	+	Age	+	Age <sup>2</sup>	+	Latitude	+	Nrst Cont	+	Nrst Isld	+	Alt Div	+	Alt Even	
	Plants		Marquesas	13.91	98.81	Area	+	Age	+	Age <sup>2</sup>	+	Alt Div	+	Alt Even					
n = 9		15.28	98.80	Area	+	Age	+	Age <sup>2</sup>	+	Nrst Isld	+	Alt Div	+	Alt Even					
		17.00	98.13	Area	+	Age	+	Age <sup>2</sup>	+	Latitude	+	Nrst Isld	+	Alt Div	+	Alt Even			
		18.61	95.97	Area	+	Age	+	Age <sup>2</sup>	+	Alt Div									
		40.04	88.01	Area	+	Nrst Isld	+	Alt Div											
		64.57	81.74	Area	+	Age													
		124.45	67.80	Area															

Table S4 continued

[illegible]

Taxa	Island Group	AIC	Adj. r <sup>2</sup>	Model																	
Land Snails	Azores <i>n</i> = 9	12.00	65.82	Age																	
		9.29	83.59	Age	+	Nrst Cont															
		10.02	87.93	Age <sup>2</sup>	+	Nrst Cont															
		11.16	91.34	Age	+	Age <sup>2</sup>	+	Nrst Cont		+	Nrst Isld										
		13.12	88.80	Age	+	Age <sup>2</sup>	+	Latitude	+	Nrst Cont		+	Nrst Isld								
		15.02	84.78	Age	+	Age <sup>2</sup>	+	Latitude	+	Nrst Cont		+	Nrst Isld		+	Alt Div					
		17.00	70.09	Area	+	Age	+	Age <sup>2</sup>	+	Latitude	+	Nrst Cont		+	Nrst Isld		+	Alt Div			
Land Snails	Canaries <i>n</i> = 7	10.74	89.46	Area	+	Age	+	Alt Div													
		11.54	91.16	Area	+	Age	+	Nrst Isld		+	Alt Div										
		12.68	80.76	Age	+	Alt Div															
		13.00	88.48	Area	+	Age	+	Age <sup>2</sup>	+	Nrst Isld		+	Alt Div								
		46.60	1.81	Area																	
Land Snails	Galapagos <i>n</i> = 14	8.84	26.26	Alt Even																	
		10.55	23.71	Area	+	Nrst Cont															
		12.42	17.79	Nrst Isld	+	Alt Div		+	Alt Even												
		14.37	8.55	Area	+	Age	+	Age <sup>2</sup>	+	Nrst Cont											
		16.05	2.99	Age	+	Age <sup>2</sup>	+	Nrst Cont		+	Nrst Isld		+	Alt Div							
		18.02	0.00	Area	+	Age	+	Age <sup>2</sup>	+	Nrst Cont		+	Nrst Isld		+	Alt Div					
		20.01	0.00	Area	+	Age	+	Age <sup>2</sup>	+	Latitude	+	Nrst Cont		+	Nrst Isld		+	Alt Div			
		22.00	0.00	Area	+	Age	+	Age <sup>2</sup>	+	Latitude	+	Nrst Cont		+	Nrst Isld		+	Alt Div		+	Alt Even
Land Snails	Hawaii <i>n</i> = 11	20.00	97.24	Area	+	Age	+	Age <sup>2</sup>	+	Latitude	+	Nrst Cont		+	Nrst Isld		+	Alt Div		+	Alt Even
		21.72	94.73	Area	+	Age	+	Age <sup>2</sup>	+	Latitude	+	Nrst Cont		+	Nrst Isld		+	Alt Div			
		27.99	90.34	Area	+	Age	+	Age <sup>2</sup>	+	Latitude	+	Nrst Cont		+	Alt Div						
		31.74	89.1	Area	+	Age	+	Age <sup>2</sup>	+	Latitude	+	Nrst Cont									
		38.62	86.83	Area	+	Age	+	Latitude	+	Nrst Cont											
		69.82	75.62	Nrst Isld	+	Alt Div		+	Alt Even												
		108.04	64.79	Alt Div	+	Alt Even															
		154.08	53.96	Alt Div																	

Table S4 continued

Taxa	Island Group	AIC	Adj. r <sup>2</sup>	Model															
Land Snails	Seychelles	13.70	99.98	Area	+	Age	+	Latitude	+	Alt Div	+	Alt Even							
	n = 8	15.00	99.98	Area	+	Age	+	Age <sup>2</sup>	+	Latitude	+	Alt Div	+	Alt Even					
		19.80	99.94	Area	+	Age	+	Latitude	+	Alt Even									
		2287.90	90.00	Area	+	Latitude	+	Alt Even											
		12027.20	57.83	Area	+	Alt Div													
		24367.20	28.78	Area															
Coleoptera	Galapagos	16.74	81.25	Area	+	Age	+	Age <sup>2</sup>	+	Alt Div									
	n = 14	17.53	82.42	Area	+	Age	+	Age <sup>2</sup>	+	Nrst Cont	+	Alt Div							
		18.66	82.71	Area	+	Age	+	Age <sup>2</sup>	+	Nrst Cont	+	Alt Div	+	Alt Even					
		19.25	72.20	Area	+	Age	+	Age <sup>2</sup>											
		20.11	81.70	Area	+	Age	+	Age <sup>2</sup>	+	Nrst Cont	+	Nrst Isld	+	Alt Div	+	Alt Even			
		21.60	65.31	Area	+	Age													
		22.00	77.75	Area	+	Age	+	Age <sup>2</sup>	+	Latitude	+	Nrst Cont	+	Nrst Isld	+	Alt Div	+	Alt Even	
		28.30	50.85	Area															
Fungi	Canaries	10.24	86.97	Area	+	Nrst Isld	+	Alt Div											
	n = 7	11.14	90.09	Area	+	Age	+	Nrst Isld	+	Alt Div									
		11.34	76.73	Area	+	Alt Div													
		13.00	82.56	Area	+	Age	+	Age <sup>2</sup>	+	Nrst Isld	+	Alt Div							
		22.70	34.77	Alt Div															



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