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Re-evaluating the general dynamic theory of oceanic island biogeography

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Abstract. The general dynamic model of oceanic island biogeography integrates temporal changes in ecological circumstances with diversification processes, and has stimulated current research in island biogeography. In the original publication, a set of testable hypotheses was analysed using regression models: specifically, whether island data for four diversity indices are consistent with the 'B-ATT²' model, in which B is a diversity index, A is log(area) and T is time. The four indices were species richness, the number and percentage of single-island endemic species, and a diversification index. Whether the relationships between these indices and time are unimodal (i.e., 'hump-shaped') was a key focus, based on the characteristic ontogeny of a volcanic oceanic island. However, the significance testing unintentionally used zero, rather than the mean of the diversity index, as the null hypothesis, greatly inflating *F*-values and reducing *P*-values compared with the standard regression approach. Here we first re-analyze the data used to evaluate the general dynamic model in the seminal paper, using the standard null hypothesis, to provide an important qualification of its empirical results. This supports the significance of about half the original tests, the rest becoming non-significant but mostly suggestive of the hypothesized relationship. Then we expand the original analysis by testing additional, theoretically derived functional relationships between the diversity indices, island area and time, within the framework of the ATT² model and using a mixed-effects modelling approach. This shows that species richness peaks earlier in island life-cycles than endemism. Area has a greater effect on species richness and the number of single-island endemics than on the proportion of single-island endemics and the diversification index, and was always better fit as a log–log relationship than as a semi-log one. Finally, the richness–time relationship is positively skewed, the initial rise happening much more quickly than the later decline.

Keywords. Diversification, extinction, immigration, island evolution, island life-cycle, island theory, linear mixed-effects models, macroecology, oceanic archipelagos, space-for-time substitution

Introduction

MacArthur and Wilson's (1963, 1967) equilibrium theory of island biogeography was seminal in linking ecological processes with observable patterns and geographical features. It was also groundbreaking in providing a first comprehensive theory of island biogeography with testable predictions. However, the need to incorporate further proc-

esses (especially speciation) more fully into a more general theory of island biogeography has frequently been stressed (e.g. Brown and Lomolino 2000, Heaney 2000, 2007, Lomolino 2000, Whittaker 2000). Several recent contributions have aimed to advance new syntheses of a more general island biogeographical theory. Among the most important is Whittaker et al.'s (2007, 2008,

2010) general dynamic model of oceanic island biogeography (GDM), currently the most comprehensive theoretical model for the biodiversity of oceanic islands of volcanic origin.

The GDM integrates the processes of immigration, speciation and extinction in the temporal frame of the characteristic ontogeny of volcanic oceanic islands. After emergence from the sea, such islands are typically transformed by erosion processes, initially increasing topographical heterogeneity and later reducing it as the islands become flatter (Whittaker et al. 2007). In addition, for some volcanic hotspot island systems, the elevation is gradually reduced by subsidence of the underlying tectonic plate, once the hotspot responsible for its existence has passed by (Fernández-Palacios et al. 2011). The GDM is not an equilibrium theory and does not explicitly address interactions among the three fundamental processes of immigration, speciation and extinction. Instead, it postulates that the carrying capacity (for species diversity) of an island, which is related to its topographic heterogeneity, increases as the island grows in area and elevation and declines as the island erodes away, later in its life-cycle. Following this ontogeny of islands, the GDM predicts, among other things, unimodal ('hump-shaped', over the entire life-cycle of the islands) relationships between time (often measured as the age of the island) and biodiversity indices, specifically: species richness; number of single-island endemic species; the percentage of native species that are single-island endemic species; and a diversification index that represents the ratio of the number of single-island endemics to the number of genera containing single-island endemics (see Whittaker et al. 2008 for details).

To empirically test time-related explanations for island biodiversity, such as island ontogeny, time series of assemblage descriptors such as species richness and percentage of single-island endemics would be needed. Even if such data were available for some islands, they would need to span very long time-periods. Such data are not available. Space-for-time substitution is a commonly applied alternative strategy in such situations. To minimize confounding influences of spa-

tial or ecological context and regional biogeographic history, island archipelagos are often used for testing. This was the case for Whittaker et al. (2008), whose empirical evaluation of the GDM focused on the predicted unimodal relationship between time and the diversity-related indices, based on the typical ontogeny of volcanic islands. The relationship was expressed as:

$$\text{Biodiversity} \sim \text{Time} + \text{Time}^2 \quad (1)$$

[abbreviated here as **B~TT²**]

Since islands of different maximum size (over their life-cycles) will differ in their overall biodiversity, Whittaker et al. (2008) also tested a correction term for (logarithmic) island area, to account for semi-log version of the well-known species–area relationship:

$$\text{Biodiversity} \sim \log(\text{Area}) + \text{Time} + \text{Time}^2 \quad (2)$$

[abbreviated here as **B~lnATT²**]

(note: Whittaker et al. 2008 called this 'ATT²')

Whittaker et al. (2008) empirically tested these and several alternative models using linear regressions on the same variables. They found the predicted hump-shaped relationships, with the improved fit of the hump-shape over a linear relationship being significant in almost all cases. Further, the **B~lnATT²** model received the strongest empirical support (see their Table 4). However, in their hypothesis testing they unintentionally used a value of zero for the response variable as their null hypothesis. That is, they tested whether each model accounts for the values of the diversity indices significantly better than assuming all values of these indices to be zero. We consider this to be an inappropriate null hypothesis, which relegates to triviality the significance testing of the whole models versus the null—and involves some circularity, given that archipelagos with few species or no single-island endemics were implicitly excluded from the sampling. It is also likely to have distorted the comparison of models by causing the error variances to be unduly small, thus favouring the more complex models, including those with quadratic terms. We understand that zero was not

the intended null hypothesis; this is unfortunate, given how seminal the Whittaker et al. (2008) publication is proving to be. Here, we start by setting the record straight: we redo the modelling of Whittaker et al. (2008), using the same data and models, but applying the standard null hypothesis. That is, we evaluate the models and their constituent parts in terms of improved fit relative to the mean of the response variable, rather than zero.

We then expand upon the original analysis of Whittaker et al. (2008), and the reanalysis by Bunnefeld and Phillimore (2012), in two ways. First, we apply mixed-effects modelling to all the diversity indices used by Whittaker et al. (2008); Bunnefeld and Phillimore (2012) only analysed the number of single-island endemics. This allows a meaningful comparison of different aspects of the diversity patterns, and we particularly focus on endemism versus richness, which may be expected *a priori* to behave differently (Whittaker et al., 2001). Second, we test whether alternative theoretically based functional relationships between biodiversity indices and island area and time provide a better fit than those tested so far within the framework of the ATT² approach.

Methods

Ecological and biogeographical datasets typically contain much noise (Simberloff 1980). To separate an existing pattern from noise, large datasets are required. The limited number of suitable archipelago datasets and the small number of within-archipelago replicates (islands within defined age classes) strongly restrict the options for statistical tests of island biogeographical theories using standard linear regression, especially for oceanic islands. In order to overcome these issues, Whittaker et al. (2008) elected to test as many suitable oceanic archipelago datasets as possible. They used 14 datasets of different species groups on 5 archipelagos to test the GDM predictions outlined above. Each test had a small sample size, but some degree of generality was afforded by finding the same patterns repeatedly. An alternative is to pool data across archipelagos in one analysis, greatly increasing sample size. However,

biodiversity data within archipelagos are typically more similar to each other than between comparable islands from other archipelagos, for instance because of the influence of species pools; this violates the assumption of independence of observations. Here, we follow Bunnefeld and Phillimore (2012), who argued that mixed-effects models are a highly appropriate tool for hypothesis testing in island biogeography (see also Hortal 2012, Steinbauer et al. 2012). Mixed-effects models allow incorporation of all archipelagos under study into one analysis, thus increasing the statistical power. Regression coefficients representing the model of theoretical interest are fitted as fixed effects. Variation between archipelagos or species groups can be accounted for by adding random effects on the intercept and/or regression coefficients. This approach also allows additional testing because extra variables are included in the analysis (e.g., archipelago identity or taxonomic group).

Regarding functional relationships between the biodiversity metrics and island area and time, Fattorini (2009) argued that the species–area relationship is best expressed by a power function. Triantis et al. (2012) found the (logarithmic) power model to be the best supported out of 20 species–area models tested on 601 island datasets. This suggests that the response variable should be log-transformed, as well as area (at least for the two diversity indices that count species: species richness and the number of single-island endemics). This applies the log–log relationship, which is more commonly used than the semi-log version to linearize the species–area relationship:

$$\log(\text{Biodiversity}) \sim \log(\text{Area}) + \text{Time} + \text{Time}^2 \quad (3)$$

[abbreviated as *lnB~lnATT²*]

We further test whether log-transformed time values significantly improve model performance and normality of residuals because island building typically happens much more quickly than island erosion. This was mentioned by Whittaker et al. (2008: 980): “Note that the period of [island] growth is typically shorter than the period of decline, such that [...] the time axis should

best be considered as some form of log or power function." However, it was not incorporated into their statistical testing, and has not been subsequently, to our knowledge. We thus modified equation 3 to test whether a log-transformation of time fits the data better:

$$\log(\text{Biodiversity}) \sim \log(\text{Area}) + \log(\text{Time}) + \log(\text{Time})^2$$

[abbreviated as $\ln\mathbf{B} \sim \ln\mathbf{A} / \ln\mathbf{T}\mathbf{T}^2$] (4)

When re-evaluating the data used by Whittaker et al. (2008), we graphically inspected each relationship to identify spurious quadratic U-shaped relationships over the range of data sampled. U-shaped relationships are indicated by significant positive quadratic and negative linear terms for Time. A significant negative quadratic term in combination with a positive linear term for Time indicates a hump-shaped relationship with the response variable, as predicted by the GDM.

We then used generalized linear mixed-effects models to analyze all the islands and taxa together, with either the Gaussian error distribution and identity link (for the response variables species richness, number of single-island endemics and diversification index) or binomial error distribution and logit link (percentage of single-island endemics). Using the binomial error distribution for percentage values has the advantage of better reflecting the data by including information on the number of cases a percentage value is based on (a value of 10% is more reliable if it is based on 100 individuals than if it is based on 10). Response variables were $\log(x+c)$ transformed for models with a Gaussian error distribution, where $c = 0$ for species richness and $c = q1^2 / q3$ for the diversification index and number of single-island endemics (where $q1$ and $q3$ are the first and third quartile of those observations not equal to zero; Stahel 2002). We included random effects for archipelago and species group, which comprised plants, insects and snails. We excluded species groups that are subsets of other groups in the analysis (e.g., beetles and smaller order insects were analyzed both separately and jointly by Whittaker et al. 2008), in order to avoid pseudoreplication

within our single, overall analysis. Analyzing all the same groups as Whittaker et al. (2008) gave similar results, but overemphasized insects. For the Azores, we added insects to the analysis. Thus the final mixed-effects model is based on plants, insects and snails for Hawaii and the Canary Islands, insects and snails for the Azores, plants and insects for Galapagos and plants for the Marquesas. We did not include island as a random effect, despite several islands having datasets for more than one species group. This is because a random effect for island would interfere with the modeled effects of area and time (both also unique per island), which are the key foci of our analysis. We checked whether adding island as a random effect altered the findings qualitatively, which it did not (see Results). We evaluated the presence of hump-shaped relationships in the same way as for the linear regressions. We ranked models by their AIC (Akaike information criterion), where lower AIC values indicate better model performance. Statistical analyses were performed in R version 3.0.0 (R Development Core Team 2013) using LME4 version 0.999999-2 (Bates et al. 2013) for the mixed-effects models.

Results

According to our analyses based on the standard regression null hypothesis, roughly 50% of the models lost their significance, compared with Whittaker et al.'s results (Table S1 in the Appendix). Even so, in many cases the $\mathbf{B} \sim \ln\mathbf{ATT}^2$ model (equation 2) remained both significant and the model best fitting the data, out of the models tested by Whittaker et al. (2008). The general linear and non-linear mixed-effects models supported these results for the $\mathbf{B} \sim \ln\mathbf{ATT}^2$ model (Table S2). However, the $\ln\mathbf{B} \sim \ln\mathbf{A} / \ln\mathbf{T}\mathbf{T}^2$ model (equation 4; Table 1; Figure 1a) performed better than the $\mathbf{B} \sim \ln\mathbf{ATT}^2$ model when modelling species richness. For the number and proportion of single-island endemics (both diversification-related indices), the model without log-transformed time values performed best ($\ln\mathbf{B} \sim \ln\mathbf{ATT}^2$; Figure 1b,c). The diversification index was best fit by a model without any time variable ($\ln\mathbf{B} \sim \ln\mathbf{A}$; Figure 1d). The log-transformation of the diversity indices produced

Table 1. Comparison of model fits for the four diversity metrics, using generalized linear mixed-effects modelling (the type of GLME is noted for each analysis). 'SR' is species richness, 'nSIE' and 'pSIE' are the number and percentage of single-island endemic species respectively, and 'DI' is the diversification index (see text for explanation). Lower AIC values indicate better model performance, with the 'best' models indicated in bold font; those displayed in Figure 1 are marked with an asterisk. For model significance ('P') and the significance of the quadratic Time term ('P(hump)') the P-value is given. "Arch." and "Spec." indicate the variance accounted for by the random effects Archipelago and Species Group, respectively. "Res." indicates residual variance; note that this cannot readily be interpreted for the binomial model and is thus not reported for pSIE. Results for similar analyses for untransformed response variables (SR, nSIE, DI) or a "probit" (=normal) link function (pSIE) are in the appendix.

Model	SR (Gaussian)			Random variance			nSIE (Gaussian)			Random variance		
	AIC	P	P(hump)	Arch.	Spec.	Res.	AIC	P	P(hump)	Arch.	Spec.	Res.
<i>lnB~lnAlnTT²</i>	212*	<0.001	<0.001	0.27	2.65	0.27	282	<0.001	<0.001	1.06	1.24	0.54
<i>lnB~lnATT²</i>	223	<0.001	0.001	0.26	2.65	0.27	281*	<0.001	<0.001	1.12	1.24	0.48
<i>lnB~AlnTT²</i>	342	<0.001	<0.001	0.81	2.59	0.87	388	<0.001	<0.001	1.72	1.21	1.40
<i>lnB~ATT²</i>	356	<0.001	0.113	0.77	2.59	0.92	400	<0.001	0.001	1.78	1.21	1.43
<i>lnB~lnAlnT</i>	227	<0.001		0.25	2.65	0.33	298	<0.001		0.94	1.23	0.67
<i>lnB~lnAT</i>	221	<0.001		0.33	2.65	0.3	302	<0.001		1.39	1.23	0.67
<i>lnB~AlnT</i>	361	<0.001		0.65	2.57	1.13	410	<0.001		1.33	1.18	1.86
<i>lnB~AT</i>	347	<0.001		0.89	2.59	0.93	399	<0.001		2.23	1.20	1.57
<i>lnB~lnA</i>	221	<0.001		0.24	2.65	0.33	297	<0.001		1.17	1.23	0.69
<i>lnB~A</i>	362	<0.001		0.47	2.56	1.19	406	<0.001		1.16	1.18	1.86
<i>lnB~TT²</i>	352	<0.001	0.353	1.01	2.58	1.06	397	<0.001	0.009	2.57	1.20	1.66
<i>lnB~lnT</i>	356	0.001		0.83	2.56	1.28	407	0.042		2.09	1.18	2.12
<i>lnB~T</i>	341	<0.001		1.08	2.58	1.05	393	<0.001		2.90	1.20	1.75

Model	pSIE (Binomial)			Random variance			DI (Gaussian)			Random variance		
	AIC	P	P(hump)	Arch.	Spec.	Res.	AIC	P	P(hump)	Arch.	Spec.	Res.
<i>lnB~lnAlnTT²</i>	824	<0.001	<0.001	0.65	0.33		142*	<0.001	0.004	0.06	0.04	0.15
<i>lnB~lnATT²</i>	708*	<0.001	<0.001	0.76	0.33		150	<0.001	<0.001	0.07	0.04	0.15
<i>lnB~AlnTT²</i>	1027	<i>no convergence</i>		0.13	0.08		203	<0.001	<0.001	0.11	0.04	0.24
<i>lnB~ATT²</i>	850	<0.001	<0.001	0.94	0.35		215	<0.001	0.006	0.12	0.03	0.24
<i>lnB~lnAlnT</i>	916	<0.001		0.71	0.34		143	<0.001		0.06	0.03	0.16
<i>lnB~lnAT</i>	1029	<0.001		0.78	0.35		150	<0.001		0.09	0.03	0.17
<i>lnB~AlnT</i>	1165	<i>no convergence</i>		0.13	0.08		212	0.010		0.08	0.03	0.28
<i>lnB~AT</i>	1209	<0.001		0.98	0.36		209	<0.001		0.15	0.03	0.26
<i>lnB~lnA</i>	1031	<0.001		0.79	0.35		141	<0.001		0.08	0.03	0.16
<i>lnB~A</i>	1236	<i>no convergence</i>		0.13	0.08		206	0.002		0.07	0.03	0.28
<i>lnB~TT²</i>	981	<0.001	<0.001	1.05	0.35		201	<0.001	0.021	0.17	0.03	0.26
<i>lnB~lnT</i>	1209	<0.001		1.01	0.36		n.s.	0.308		0.13	0.03	0.30
<i>lnB~T</i>	1231	0.151		1.03	0.36		193	0.001		0.20	0.03	0.27

Table 2. Timing of the peak modelled value of the diversity indices, in millions of years. Abbreviations as in Table 1.

Model	SR	nSIE	pSIE	DI
$\ln B \sim \ln A \ln TT^2$	2.5	3.6	5.8	4.6
$\ln B \sim \ln ATT^2$	7.3	9.8	9.8	10.5

better-fitting models in all cases, with the transformation normalizing the residuals. Adding 'island' as an additional random effect did not change results qualitatively, except that, for the number of single-island endemics, the $\ln B \sim \ln A \ln TT^2$ model was slightly favoured over the

$\ln B \sim \ln ATT^2$ model.

The curve of the best model peaks much earlier for species richness than for the other three diversity indices (Table 2, Figure 1). In the $\ln B \sim \ln ATT^2$ model, the negative quadratic term for time (indicating the humped shape of the curve) is most significant for the proportion of single-island endemics ($P = 2.2 \times 10^{-72}$) followed by the number of single-island endemics ($P = 4.6 \times 10^{-9}$), the diversification index ($P < 1.4 \times 10^{-4}$) and species richness ($P < 8.5 \times 10^{-4}$).

Within the $\ln B \sim \ln A \ln TT^2$ models, the effect of $\log(\text{area})$ is more pronounced for the number

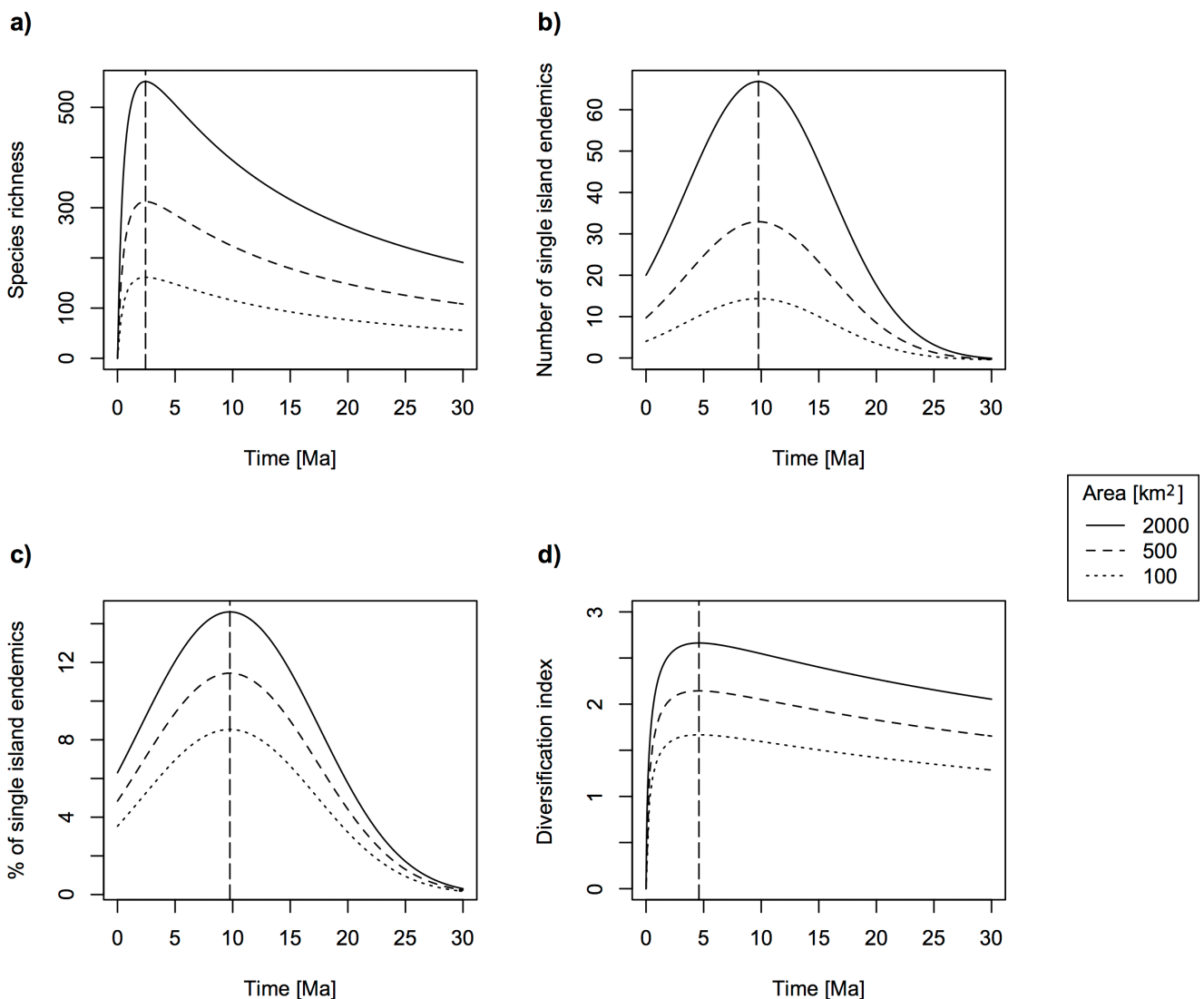


Figure 3. The modelled relationship between the diversity indices and both area and time (representing the developmental phase of a volcanic island). The 'best' model (see Table 1) is shown in each case for (a) SR, (b) nSIE and (c) pSIE. For the diversification index, a model independent of time performs as well as the one including time that is shown in (d). The lines shown on the graphs were derived from the fixed effects of the mixed-effects models of all archipelagos and taxonomic groups. A three-dimensional representation of these models, including the original data and differentiating between the archipelagos and the taxa, is presented in Figure S1 in the Appendix.

of single-island endemics (coefficient = 0.50 ± 0.03) and species richness (0.41 ± 0.02) than for the percentage of single-island endemics (0.26 ± 0.02) and the diversification index (0.16 ± 0.02). The same is true for the *lnB-lnATT²* models. In general, for the data tested, the effect of area on the diversity indices is more pronounced than that of time, according to the AIC values (Table 1).

Discussion

The *B-lnATT²* model examined by Whittaker et al. (2008), and others subsequently, is, in the original authors' words, "a simple model of diversity derived from the GDM" (Whittaker et al. 2008: 977). By applying log-transformations to different terms in the B-ATT² framework, we have focused entirely on testing GDM predictions, while departing from the original empirical model. By examining, in this way, the different forms of the fit between the various diversity variables and both area and time, we have tested different theoretical aspects of the GDM, yielding insights into its nature and applicability.

The simple model originally formulated by Whittaker et al. (2008) seems especially suited to modelling speciation processes on volcanic oceanic islands. The *lnB-lnATT²* model (i.e., as originally favoured by Whittaker et al. 2008, but with a log-transformed response variable) performs best for the diversification-related indices 'nSIE' and 'pSIE' (Table 1). When the response variables are not transformed, Whittaker et al.'s *B-lnATT²* model is much the best for the percentage of single-island endemics, but evidence for the hump shape is equivocal at best for the other diversity indices. For species richness, the increase with time appears to happen faster than its decline, as indicated by the better fit of log-transformed time (Figure 1a). The same may be true of the number of single-island endemics, for which the fit of the model with log-transformed time was indistinguishable from that with untransformed time. The peak in species richness is much earlier in the life-cycle of the volcanic oceanic island than the peaks in either the number or proportion of single-island endemics. Species gain on young volcanic islands may therefore typically be dominated by immigra-

tion from neighbouring, older islands or mainland sources (Fernández-Palacios et al. 2011), while the generation of endemic species via speciation needs more time (time for speciation effect; Stephens & Wiens 2003). On the other hand, net species loss may start earlier for species not endemic to the island than for single-island endemics. This could indicate either ongoing gain in endemic species via speciation (cladogenesis or anagenesis) while overall species richness is declining, or a lower extinction risk for species endemic to the island (e.g., by better adaptation to local conditions or smaller population sizes) than non-endemics, or both.

Within the ATT² modelling framework, the species–area relationship appears to be best modelled as a log–log relationship, which consistently resulted in more normal, unpatterned model residuals. This is consistent with other analyses of species–area relationships on islands, including those explicitly considering the GDM (e.g., Fattorini 2009; Triantis et al. 2012). Island area had greater explanatory power for species richness than did time, which is reassuring for the usefulness of fitting species–area relationships for islands or patches of differing ages. The fact that area also had greater explanatory power than time for all the diversification-related indices is consistent with the speciation–area relationship, as well as the standard species–area relationship. A direct effect of area on diversification has been suggested (Losos and Schluter 2000, Stuessy et al. 2006, Kisel and Barraclough 2010) and is consistent with our results. Interestingly, the 'diversification index' was most parsimoniously modelled by a time-independent species–area relationship (Tables 1 and S2). This index is calculated as the number of single-island endemic species divided by the number of genera to which these species belong. This index thus primarily reflects speciation within genera—cladogenetic speciation—which is considered especially dependent on area (Kisel and Barraclough 2010). Because island area is influenced by the ontogeny of the island, it may be that a combination of a strong modelled area effect with isolation influences masks a possible change in the diversifica-

tion index with time. More robust measures of cladogenetic speciation than the diversification index (e.g., see Kisel and Barraclough 2010) may yield greater insight.

Some of the predictions of the GDM have been supported for various taxa (Bunnefeld and Phillimore 2012, Cameron et al. 2013), but not for spore-producing plants, which have very high dispersal ability (Patiño et al. 2013; also S.C. Aranda, R. Gabriel, P.A.V. Borges, A.M.C. Santos, E. Brito de Azevedo, J. Patiño, J. Hortal and J.M. Lobo unpublished). Interestingly, none of these studies investigated patterns in the percentage of single-island endemics. This index has a large advantage compared with species richness and the number of single-island endemics. Species richness is strongly dependent on area, and the number of endemic species is correlated with species richness empirically, as well as directly related theoretically if one assumes a constant per-species diversification rate. The percentage of endemic species, however, is not dependent on area (or richness) in this way. A significant relationship between area and 'pSIE' can thus be directly associated with a change in diversification rate (per species) with area. If extinction rate is constant the percentage of single-island endemics may be a proxy for speciation rate per species and time (Emerson and Kolm 2005, Steinbauer et al. 2012, 2013).

Each island represents a specific developmental phase (time step) within the idealised ontogeny of volcanic islands. Archipelagos comprising solely old or young islands will thus reflect only a section of the postulated hump-shaped trajectory (Triantis et al. 2011). Where an island is placed on this time frame of an idealised ontogeny, however, has been a cause of debate (Anderson et al. 2009, Whittaker et al. 2007, 2008, 2010). Islands might sometimes have been sterilized by volcanic activity, setting species richness back to zero. Here, we followed the time estimates used by Whittaker et al. (2008), to favour a comparison of approaches. One of the reasons for uncertainty, when estimating the developmental phases of islands, is the fact that volcanic activity is often pulsed. In addition, originally separated volcanic island can merge to one composite island

as an effect of later eruptions (e.g., Tenerife) or sea-level changes (e.g., during the last glacial maximum Lanzarote and Fuerteventura were one large island, Mahan). Large volcanic events can sterilize entire islands a long time after their original emergence above the sea (e.g., Gran Canaria), or whole islands can be sterilized by being temporarily submerged by rising sea levels (as for many existing seamounts today). Furthermore, unstable young oceanic islands, in particular, can be strongly affected by large landslides. Besides these extreme events, climatic and ecological changes during an island's ontogeny influence topographic heterogeneity. The specific climatic history and geology of an island or archipelago also affects its ecological isolation from climates and ecosystems on a nearby continent (Fernández-Palacios et al. 2011). All these aspects add uncertainty to the space-for-time substitution approach.

In the light of these considerations, it is striking that the GDM appears to be so generally applicable. To some degree, a hump-shaped fit of diversity with time is inevitable for an oceanic island, given that it necessarily starts, and almost inevitably ends, with no species. The different nature of the fits and timing of the peaks for the different diversity indices suggest that time for diversification may be a key factor in generating biodiversity, at least on islands. However, the gradual conversion of colonist species to single-island endemics, via both anagenesis and their extinction in their source areas, may represent part of the explanation for later peaks of diversification-related indices than species richness. It is worth noting, for example, that some single-island endemics in the Hawaiian archipelago are thought to be much older than the island to which they are now endemic (Lerner et al. 2011). Oceanic islands, of course, are only one type of island; an expansion of the theory beyond the particularities of oceanic island ontogeny to temporal changes in island characteristics in general may be worthwhile, as may consideration of other taxonomic levels. As more evidence accumulates, it is likely that the simplicity and elegance of Whittaker et al.'s (2008) model will

provide a valuable framework for incorporating island dynamics into island biogeography theory.

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Supplementary materials

The following supplementary materials can be found online:

Figure S1. The modelled relationship between the diversity indices and both area and time.

Table S1. Adjusted R^2 values and significance of the alternative linear regression models.

Table S2. Comparison of model fits for the four diversity metrics, using generalized linear mixed-effects modelling on untransformed response variables.

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