

Snails on oceanic islands: testing the general dynamic model of oceanic island biogeography using linear mixed effect models

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ABSTRACT

Aim We collate and analyse data for land snail diversity and endemism, as a means of testing the explanatory power of the general dynamic model of oceanic island biogeography (GDM): a theoretical model linking trends in species immigration, speciation and extinction to a generalized island ontogeny.

Location Eight oceanic archipelagos: Azores, Canaries, Hawaii, Galápagos, Madeira, Samoa, Society, Tristan da Cunha.

Methods Using data obtained from literature sources we examined the power of the GDM through its derivative ATT² model (i.e. diversity metric = $b_1 + b_2\text{Area} + b_3\text{Time} + b_4\text{Time}^2$), in comparison with all the possible simpler models, e.g. including only area or time. The diversity metrics considered were the number of (1) native species, (2) archipelagic endemic species, and (3) single-island endemic species. Models were evaluated using both log-transformed and untransformed diversity data by means of linear mixed effect models. For Hawaii and the Canaries, responses of different major taxonomic groups were also analysed separately.

Results The ATT² model was always included within the group of best models and, in many cases, was the single-best model and was particularly successful in fitting the log-transformed diversity metrics. In four archipelagos, a hump-shaped relationship with time (island age) is apparent, while the other four archipelagos show a general increase of species richness with island age. In Hawaii and the Canaries outcomes vary between different taxonomic groups.

Main conclusions The GDM is an intentionally simplified representation of environmental and diversity dynamics on oceanic islands, which predicts a simple positive relationship between diversity and island area combined with a humped response to time. We find broad support for the applicability of this model, especially when a full range of island developmental stages is present. However, our results also show that the varied mechanisms of island origins and the differing responses of major taxa should be taken into consideration when interpreting diversity metrics in terms of the GDM. This heterogeneity is reflected in the fact that no single model outperforms all the other models for all datasets analysed.

Keywords

General dynamic model, island biogeography theory, island evolution, land snails, mixed effect models, model selection, oceanic islands, speciation, species diversity dynamics.

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INTRODUCTION

Islands are prime reservoirs of land snail diversity

Alan Solem (1984, p. 9)

The biotas of oceanic islands have provided ideal material for studying ecological and evolutionary processes and their analysis has profoundly influenced the development of subjects ranging from species formation to biogeography (Whittaker & Fernández-Palacios, 2007). Whittaker *et al.* (2008) recently developed a model, the general dynamic model of oceanic island biogeography (hereafter GDM), to account for the development of species richness on oceanic islands. Building on the dynamic equilibrium theory of MacArthur & Wilson (1967), the GDM explicitly places the outcome of the processes of immigration, speciation and extinction in a temporal context dictated by the geological development of the islands.

The GDM is based on three premises: (1) that emergent properties of island biotas are a function of predictable trends in rates of immigration, speciation and extinction; (2) that evolutionary dynamics predominate in large, remote islands/archipelagos; and (3) that oceanic islands are relatively short-lived landmasses showing a characteristic humped trend in carrying capacity over their life span. The model predicts that several key diversity metrics (e.g. the number of native species, the number of archipelagic endemic species etc.) should show a general hump-shaped trend over time, driven largely by changing carrying capacity over the life cycle of the island itself. As we are unable to follow the behaviour of a single island over millions of years, Whittaker *et al.* (2008) suggest that certain predictions could be tested by examining contemporary data from across the different aged islands of an oceanic archipelago. This, in turn, generates an expectation of a positive relationship between these diversity metrics and island area combined with a parabolic relationship with time, i.e. $\text{diversity} = b_1 + b_2\text{Area} + b_3\text{Time} + b_4\text{Time}^2$ (where 'Time' is time elapsed since island emergence and 'Area' is island area), provided that the archipelago(s) concerned display a full range of island developmental stages. As this is not always the case, the relationship with time may vary according to the extent of the geological ages involved, from positive, to hump-shaped, or negative. Thus, fits employing this ATT² model framework can take different forms, such as simple linear area–time dependence (i.e. without the quadratic term of time), or a negative dependence on time (i.e. with a positive relationship with area and a negative relationship with time) (see Fig. 1; Whittaker *et al.*, 2008, 2010; Borges & Hortal, 2009; Cardoso *et al.*, 2010; Triantis *et al.*, 2010). Relationships may also be influenced by the specific ecological requirements and dispersal powers of the taxa studied (e.g. cave-adapted Azorean arthropods compared to other arthropods; see Borges & Hortal, 2009).

Land snails are among the better known and studied groups of invertebrates within oceanic archipelagos (Solem, 1984, 1990; Cameron *et al.*, 1996; Cowie, 1996; Chiba, 1999;

Martins, 2005; Alonso *et al.*, 2006; Parent & Crespi, 2006, 2009). Many land snail species are endemics with tiny geographical ranges, a feature that is even more apparent in snails inhabiting oceanic islands (Solem, 1984). In this paper we examine the patterns of snail species diversity and endemism of oceanic islands, within the context of the GDM, and we test the predictions and the generality of the mathematical models arising from the GDM, using first, the overall faunas, and second, certain taxonomic subsets. We do so using linear mixed models, an analytical approach pioneered in this context by Bunnefeld & Phillimore (2012).

MATERIALS AND METHODS

The archipelagos

Data from 56 islands from eight oceanic archipelagos were selected based on the availability of reliable faunal lists, and an estimated age of origin (maximum age) of each of the islands (see Appendix S1 in Supporting Information). Oceanic islands are generally considered to be those that have formed over oceanic crust and that have never been connected to continental landmasses (Whittaker & Fernández-Palacios, 2007): they are typically relatively short-lived landmasses and relatively few last longer than a few million years before subsiding and/or eroding back into the sea. Despite the relative simplicity of the geological history of some oceanic island groups, e.g. Hawaii, the dynamics of most archipelagos are more complex than assumed within the GDM (e.g. Courtillot *et al.*, 2003; Neall & Trewick, 2008). Even for hotspot archipelagos with a more or less linear arrangement of islands, at least three distinct types have been identified, based largely on the origin of the plumes (Fig. 4 in Courtillot *et al.*, 2003). Nevertheless, for the majority of the islands considered here, the age of origin (maximum age) is more or less agreed upon (below), and thus we use maximum age for all the analyses here (Table 1).

Island age data were derived as follows: (1) **Hawaiian Islands:** Clague (1996). (2) **Galápagos Islands:** Geist (1996 and unpublished data). (3) **Azores:** although Johnson *et al.* (1998) suggest an age of just 0.8 Ma for São Miguel, we use 4.01 Ma and the other ages adopted by Borges *et al.* (2009) for the rest of the archipelago in formal analyses. (4) **Madeira group:** Geldmacher *et al.* (2005). (5) **Canary Islands:** Carracedo *et al.* (2002). In the case of Gran Canaria, an age of *c.* 3.5 Ma has been used in some previous analyses (see Whittaker *et al.*, 2008 and discussion therein) based on the hypothesis of near-complete sterilization in the catastrophic Roque Nublo ash flow (Marrero & Francisco-Ortega, 2001). However, Anderson *et al.* (2009) demonstrate that this hypothesis is implausible, hence we use the maximum sub-aerial age of Gran Canaria, i.e. *c.* 14.5 Ma (Carracedo *et al.*, 2002; for discussion see Fernández-Palacios *et al.*, 2011). (6) **Samoan Islands:** Workman *et al.* (2004), and Neall & Trewick (2008). (7) **Society Islands:** Clouard & Bonneville (2005). (8) **Tristan da Cunha:** Ryan (2009).

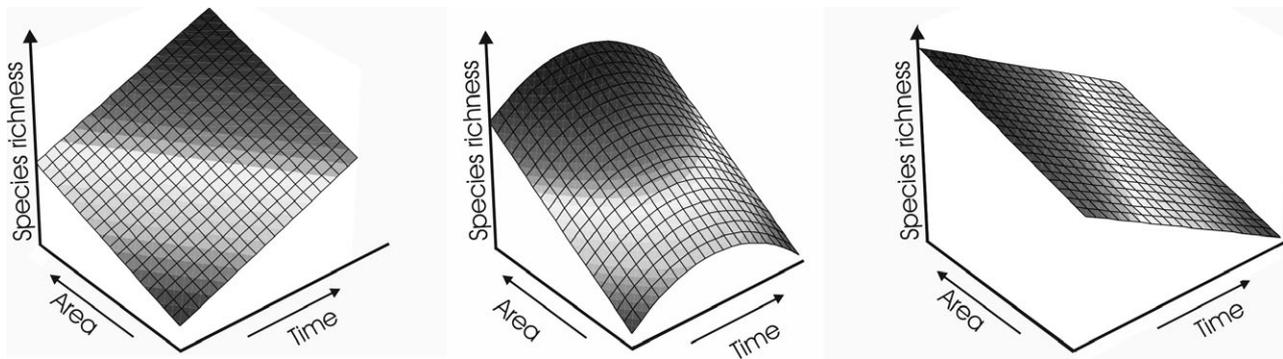


Figure 1 The three different forms of the species–area–time relationship for oceanic island groups predicted within the context of the general dynamic model of oceanic island biogeography (Whittaker *et al.*, 2008, 2010; Triantis *et al.*, 2010). The first and the third are described by simple log (Area)–Time relationship (AT; with a positive and negative relationship with time for the first and the third model, respectively), and a log(Area)–Time–Time² model (ATT²) for the second (adapted from Triantis *et al.*, 2010).

Sources and treatment of snail data

Our sources of data on snail faunas were as follows:

(1) **Hawaiian Islands:** Cowie *et al.* (1995) and Cowie (1995), updated by reference to Pokryszko (1997) for *Lyropupa*. (2) **Galápagos Islands:** Dall & Ochsner (1928), Smith (1966), Coppo (1985), Parent & Crespi (2006) and references therein. (3) **Azores:** Cunha *et al.* (2010), updated with unpublished data of A.M.F. Martins, R.A.D. Cameron and B. M. Pokryszko. (4) **Madeira group:** Seddon (2008) with some corrections and minor modifications (following Goodfriend *et al.*, 1996; Cameron *et al.*, 2007). (5) **Canary Islands:** Núñez & Núñez (2010), updated by Vega-Luz & Vega-Luz (2008), Holyoak & Holyoak (2009), Neiber *et al.* (2011), and unpublished data of M.R. Alonso and M. Ibáñez. (6) **Samoa Islands:** Cowie (1998) with additional records from Cowie (2001) and Cowie *et al.* (2002). (7) **Society Islands:** Peake (1981) provided overall species numbers, but did not discriminate introduced species. Thus, we use total number of species for this group of islands in our analyses. We have updated this list adding the recently described species from Gargominy (2008). Species lists are available only for the native family Partulidae (Coote & Loève, 2003). (8) **Tristan**

da Cunha: Holdgate (1965) and Preece & Gittenberger (2003).

Many oceanic island snail faunas have suffered extensive extinctions due to human activity (Solem, 1990; Cowie, 1995, 2001; Coote & Loève, 2003). We have included described species extinguished by such activity, but we cannot know about species that became extinct before they had been described, or about segregations that might have resulted had modern techniques been available at the time. Nevertheless, detailed studies of island mollusc faunas started earlier than for most invertebrate groups, and early inventories, including species now extinct, are remarkably complete (Seddon, 2008). Furthermore, in each case we have excluded from the analysis species thought to have been introduced. Fossil evidence for early occurrence of non-endemic snails is available in some cases; in others the judgement of the local workers has been used. All slugs have been excluded because nearly all are introduced (e.g. for Hawaii, see Cowie *et al.*, 1995).

We have generally followed the taxonomic status as given in the source publication, considering only full species. For each dataset, we compiled and recorded three diversity metrics (D), i.e. number of native species/species richness (SR),

Table 1 Properties of the oceanic island systems included in the analyses on land snail diversity and endemism. For a full list of data sources, see text.

Island group	No. of islands/units*	Area (km ²)	Total area (km ²)	Elevation (m)	Geological age (Ma)
Azores	9 (9)	17–750	2324	2351	0.25–8.12
Canary	7 (6)	278–2058	7601	3711	0.70–20
Galápagos	10 (3)	4.99–4588	7847	1707	0.30–6.3
Hawaii	10 (4)	0.2–10,433	16397	4205	0.60–23.4 (All) 0.60–4.7 (Large)
Madeira	3	15–740	795	1860	4.60–14
Samoa	7 (4)	0.3–1717.6	3049	1858	0.40–3.2
Society	6 (6)	38–1000	1486	2231	1.19–3.6
Tristan da Cunha	4 (4)	4–96	179	2060	0.20–18

*Number of islands and island units as used for the two analyses of the data followed (see text). For the archipelago of Hawaii ‘(All)’ refers to the maximum geological age for all the 10 islands considered herein, and ‘(Large)’ for the maximum age of the largest islands only (see Appendix S3).

number of archipelagic endemic species (nEnd), and the number of single-island endemic species (nSIE). The nSIE is a simple metric indicative of evolutionary dynamics that reflects the outcome of *in situ* speciation, extinction and migration within the islands of an archipelago. Additionally, for Hawaii and the Canaries, we subdivided faunas into major taxonomic groups.

We recognize that our data are incomplete (e.g. Neiber *et al.*, 2011). However, insofar as the data are incomplete, or subject to excessive taxonomic splitting or lumping, we assume that there is unlikely to be significant bias across the islands within a particular archipelago as the same taxonomists usually work on material from all the islands within an archipelago. Small numbers of additional or deleted species make little difference to the trends shown here. A possible exception is shown by Cowie's (1995) path analysis of variation in species richness of Hawaiian land snails, in which the densely populated island of Oahu appears oversampled in comparison to the much larger but sparsely populated island of Hawaii.

Island groupings

The configurations of islands vary through time, not just because of the ontogeny of the islands, but also due to the influence of other factors, e.g. tectonics and eustatic change. In particular, sea-level minima during the Pleistocene produced connections between some adjacent islands, turning them into single islands, while volcanism can both join and sometimes subdivide island territories (general review in Whittaker & Fernández-Palacios, 2007). For some analyses (detailed below), we have treated such groups as single islands so as to test the possible effects of varying configuration of the archipelagos through time (see Appendix S1, Table S2 & Appendix S2).

Statistical analyses

In studies such as this, the small number of islands per archipelago can lead to low power in detecting trends, instability in parameter estimation and model over-fitting (e.g. Burnham & Anderson, 2002). Bunnefeld & Phillimore (2012) recently suggested the use of linear mixed effect models (LMMs) to overcome such limitations. LMMs are designed to detect general patterns where data come from grouped sources (Bolker *et al.*, 2009; Zuur *et al.*, 2009). We follow their lead in applying LMMs to allow the simultaneous consideration of data from eight archipelagos comprising 56 islands.

LMM predictors are classified into (1) fixed effects: those for which we aim to estimate regression parameters, i.e. slope and intercept; and (2) random effects: those that identify groups conceptually drawn from a larger population (e.g. archipelagos or taxa) within the data and for which we examine variation in a parameter (i.e. slope and intercept) across levels (Bunnefeld & Phillimore, 2012; Hortal, 2012). When considering a factor as fixed we are interested in estimating

and comparing regression parameters for the different levels of the factor (e.g. different archipelagos). Considering a factor as a fixed effect leads to the estimation of different regression parameters for continuous variables, such as area, time or elevation for each level of the factor. When studying the fixed effect of a factor, the implicit assumption is made that the levels of the factor considered in the analysis are exhaustive (e.g. contain all the possible oceanic archipelagos), or alternatively that one is not interested in generalizing the results to other levels of the factor not included in the study (e.g. other oceanic archipelagos not included in the study). When a factor is studied as a random effect, instead of fitting regression parameters for each level of a factor, one is interested in estimating the variation in the regression parameters induced by the different levels of the factor (e.g. the variation around the general slope considering all the islands belonging to the same virtual global archipelago). The random effects can be seen as grouping factors drawn as a random sample from a larger (conceptual) population, such as the eight archipelagos considered here (adapted from glossary in Bunnefeld & Phillimore, 2012). In this context, one is not primarily interested in estimating and comparing the relationships under study for the different levels of the factor. The random effect is seen as a source of pseudoreplication [non-independence of data points (here islands) belonging to the same level of the factor (here archipelagos)] that needs to be taken into account.

Bunnefeld & Phillimore (2012) demonstrated the advantages of LMMs when applied to the data that were originally used for testing the ATT² model (i.e. $D = b_1 + b_2\text{Area} + b_3\text{Time} + b_4\text{Time}^2$). Here we follow the same methodological steps: our response variables were the three diversity metrics (SR, nEnd and nSIE). The fixed effects were island area (Area, in km²; log-transformed as generally supported by previous work, e.g. Whittaker *et al.*, 2008; Triantis *et al.*, 2012a), time elapsed since island formation (Time, i.e. date of emergence of each island, in million years ago, Ma), a quadratic term for the time elapsed (Time²), and we also considered elevation (Elevation, in metres, m) as a proxy of environmental heterogeneity. The grouping factor considered as a random effect was the archipelago that each island belongs to, as the values of the intercept and the slopes of the relationships between the diversity metrics, area, time and elevation may vary across archipelagos. To select the best models for describing the diversity metrics we followed a two-step procedure: first, the most parsimonious random effects structures (with all fixed effects included) were selected using model selection based on the small-sample corrected Akaike's information criterion (AIC_c) (Burnham & Anderson, 2002). The model with the lowest AIC_c value is considered to fit the data best. However, all models with a ΔAIC_c value < 2 (the difference between each model's AIC_c and the lowest AIC_c) must be considered as having relatively similar levels of support and thus belong to the group of 'best models' (i.e. equally parsimonious; Burnham & Anderson, 2002). Accordingly, when several random structures provided indistinguishable AIC_c values (ΔAIC_c value < 2), they were

considered as part of the 'best random structure group', and subsequent fixed effect structures were compared. To find the most parsimonious random effect structures we compared models with and without a varying intercept among archipelagos and all possible combinations of varying slopes across archipelagos for the different variables considered (i.e. $\log(\text{Area})$, Time, Time^2 and Elevation). We used the 'lmer' function in the 'lme4' library (version 0.999375-39) in R 2.14.1 (R Development Core Team, 2011) using restricted maximum likelihood (REML).

After determining the best random effect structures, the most parsimonious combinations of fixed effects were found using model selection based on AIC_c (models fitted using maximum likelihood). We used the 'dredge' function in the 'MuMIn' library in R (version 0.13.17) to run a complete set of models with all possible combinations of the fixed effects and determined the subset of 'best models' as the ones with ΔAIC_c value < 2 (as above). We additionally used Akaike weights derived from the AIC_c ($w\text{AIC}_c$) to evaluate the relative likelihood of each model, given the dataset and the set of models considered, and to estimate the relative importance of each variable by summing these $w\text{AIC}_c$ across the models in which they were included. Akaike weights are directly interpreted in terms of each model's probability of being the best at explaining the data (Burnham & Anderson, 2002).

To facilitate comparison with the previous LMM applications of the ATT^2 (Bunnefeld & Phillimore, 2012), we have applied the above methodological steps for the log-transformed values of the diversity metrics considered ($\log n + 1$ was used for datasets that contain at least one zero value for

the diversity metric considered) and also for the untransformed values. As we employ log-area in the analysis, this particular implementation of the ATT^2 assumes a power law species–area relationship, the most general and widely applied species–area relationship model (Rosenzweig, 1995; Triantis *et al.*, 2012a).

We have undertaken additional analyses for separate snail families for the two most species-rich archipelagos, i.e. Hawaii (10 islands) and the Canaries (7 islands), following the above steps, but with the random effect being 'Family' instead of 'Archipelago', in order to compare the diversity patterns within the same archipelago but for different taxonomic groupings. For the Hawaiian Islands the taxonomic groupings considered were: Succineidae, Pupilloidea, Helicariionidae, Helicinidae, Endodontoidea, Amastridae and Achatinellidae. For the Canary Islands they were: Vitrinidae, Helicoidea, Ferussaciidae and Enidae.

RESULTS

Linear mixed effect models: archipelagos

Random effects

For the log-transformed values of the diversity metrics, the random effect structures selected based on the lowest AIC_c scores were as follows. For SR two random effect structures were selected, a random intercept and a random slope for $\log(\text{Area})$, and a random slope for $\log(\text{Area})$, separately. For nSIE only a random slope for $\log(\text{Area})$ was selected. For

Table 2 Parameter estimates for the fixed effects of the most parsimonious linear mixed effect models for the land snails of the 56 islands considered (eight archipelagos). The models with a ΔAIC_c of less than two are presented (see Materials and Methods). The random structure (intercept or slopes varying across archipelagos), the number of parameters in the model (p), AIC_c and the AIC_c difference (ΔAIC_c) and Akaike weights ($w\text{AIC}_c$) are given for each model. NI indicates that the variable was not included in the model. The results remain identical for island groupings (see Appendix S3). The ATT^2 model is highlighted in bold. All diversity metrics were log-transformed. The importance of each variable is estimated by summing, for each combination of diversity metric and random structure, the Akaike weights of the models in which it was included. Time refers to the maximum surface age of each system (see Table 1).

Metric	Random structure	Intercept	Time	Time^2	$\log(\text{Area})$	Elevation	p	AIC_c	ΔAIC_c	$w\text{AIC}_c$
1. SR	$\log(\text{Area})$	0.414	0.039	−0.003	0.471	<0.000	7	22.131	0.000	0.369
		0.359	0.051	−0.003	0.424	NI	6	22.185	0.054	0.359
		0.538	NI	−0.001	0.481	<0.000	6	22.736	0.605	0.272
Variable importance			0.727	1	1	0.641				
2. SR	Intercept & $\log(\text{Area})$	0.491	0.054	−0.003	0.357	NI	8	22.383	0.000	0.449
		0.537	0.042	−0.003	0.403	<0.000	9	22.719	0.336	0.380
		0.672	NI	−0.001	0.417	<0.000	8	24.328	1.945	0.170
Variable importance			0.829	1	1	0.550				
1. nEnd	$\log(\text{Area})$	0.322	0.060	−0.003	0.393	NI	6	26.049	0.000	1
		Variable importance			1	1	1	0		
2. nEnd	Intercept	0.279	0.055	−0.003	0.431	NI	6	26.649	0.000	0.71
		0.323	0.047	−0.003	0.462	<0.000	7	28.439	1.789	0.29
		Variable importance			1	1	1	0.290		
1. nSIE	$\log(\text{Area})$	−0.150	0.109	−0.005	0.359	NI	6	43.034	0.000	1
		Variable importance			1	1	1	0		

SR, number of native species; nEnd, number of archipelagic endemic species; nSIE, number of single-island endemic species; Area, island area in km^2 .

nEnd, two random effect structures were selected: a random intercept and a random slope for $\log(\text{Area})$, separately (Table 2). The random effects variation distribution for the linear mixed effect models selected is given in Table S3 in Appendix S3. The results are similar for the island groupings (results not shown).

Fixed effects

According to the AIC_c -based model selection procedure, the ATT^2 model was always amongst the most parsimonious for all the diversity metrics considered (Table 2; see also Fig. 2).

Interestingly, for the log-transformed values of the diversity metrics, no simpler model than the ATT^2 (such as species–area or species–area–time) was included in the group of the best models. This is the only major difference between the results for transformed and untransformed diversity values because in some cases simpler models were selected for the untransformed diversity metrics (results not shown). The results are similar when all islands are considered individually and when the island groupings are considered (Table S4 in Appendix S3). Considering the coefficients for the ATT^2 model for the three different diversity metrics, using the same random structure, i.e. random slope for $\log(\text{Area})$, we

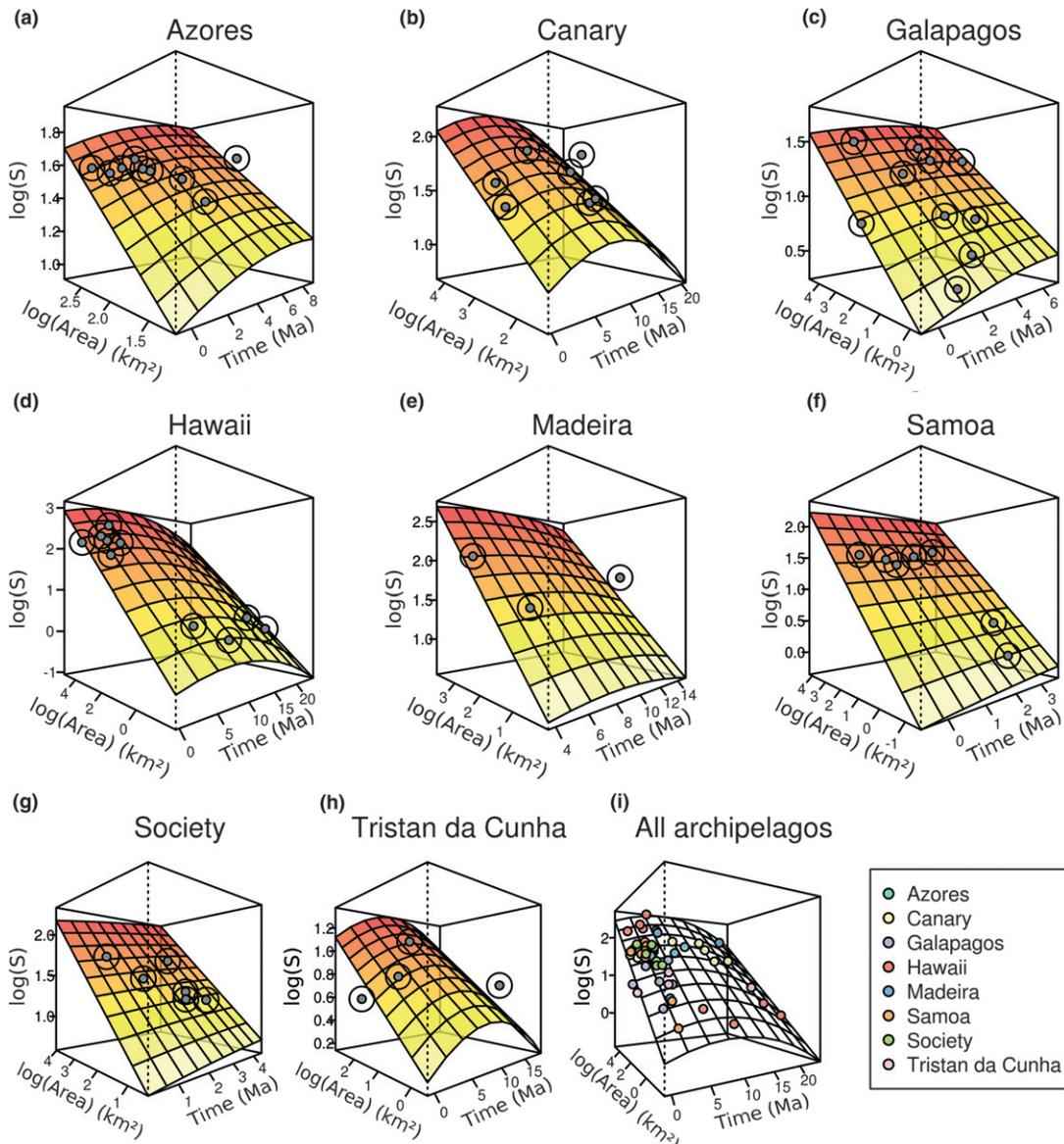


Figure 2 Species–area–time relationships (ATT^2) for the native land snail species of the eight oceanic archipelagos considered in this study. The surface is the prediction from the linear mixed effect model including a random slope for $\log(\text{Area})$ varying across archipelagos (Table 2), with number of species and area log-transformed. Points represent the observed data. Time is date of emergence of each island in million years ago (Ma). For panels (a)–(h) the colour shading indicates the species richness predicted by the model [from white (low) to red (high)]. Note that for panel (i) the slope corresponds to the grand mean fitted by the linear mixed effect model.

Table 3 Parameter estimates for the fixed effects of the most parsimonious linear mixed effect models based on AIC_c values for Hawaii (10 islands and seven families) and the Canary snail families (seven islands and four families; see text). The random structure (intercept or slopes varying across families), the number of parameters in the model (p), and the AIC_c difference (ΔAIC_c) and Akaike weights ($wAIC_c$) are given for each model. NI indicates that the variable was not included in the model. The results based on the untransformed diversity values remain identical. Diversity metrics were log-transformed. A variable importance is estimated by summing, for each combination of diversity metric and random structure, the Akaike weights of the models in which it was included.

Archipelago	Random structure	Intercept	Time	Time ²	Elevation	Log(Area)	p	AIC_c	ΔAIC_c	$wAIC_c$
Hawaii	Log(Area)	-0.600	0.134	-0.005	NI	0.426	11	66.595	0.000	1
Variable importance			1	1	0	1				
Canaries	Intercept	0.476	0.083	-0.004	NI	NI	5	35.912	0.000	0.435
		0.710	NI	NI	NI	NI	3	36.060	0.149	0.403
		0.586	NI	NI	<0.000	NI	4	37.900	0.161	0.160
Variable importance			0.435	0.435	0.160	0				

Time, geological age of the island in million years since emergence; Area, island area in km².

observe: (1) a progressive decrease of the log(Area) effect in turn considering natives, archipelagic endemics and SIE, and (2) an increase of the effect of Time², and especially of Time, from natives to SIE.

Among the selected models, log(Area) and Time² were always included and consequently have maximum relative variable importance values. Time and elevation were always the less important variables, with elevation having lower importance across all models (Table 2).

Linear mixed effect models: taxonomic subdivisions

Random effects

For the log-transformed values of the species richness for the main taxonomic groups for Hawaii and the Canaries the random effect structures selected were: Hawaii, random slope for log(Area); the Canaries, random intercept (Table 3).

Fixed effects

According to the AIC_c -based model selection procedure, for Hawaii the most parsimonious model was the ATT² (Table 3, see Fig. 3). By contrast, TT² was the most parsimonious model for the Canarian taxonomic groupings (Table 3, Fig. 4), signifying area as a non-essential descriptor of snail richness on this archipelago. For untransformed values, simpler models than ATT² were sometimes within the group of best fit, although the ATT² was always amongst the most parsimonious models (results not shown).

DISCUSSION

The general dynamic model of oceanic island biogeography seeks to provide a robust framework within which to consider species diversity of oceanic island biotas but at the same time it is an intentionally simplified representation of both the geological development and of species diversity dynamics (Whittaker *et al.*, 2008, 2010). Details of pattern are expected to vary both among archipelagos and among

groups of organisms due to factors other than time and area (and aspects of environment and history closely correlated with them) that may influence the diversity and composition of the biotas. The theory does not yet allow us to generate precise predictive models in the absence of relevant, quantitative data on properties of the taxa considered (cf. Rosindell & Phillimore, 2011). Thus, differences in the responses of biotas to time and area among both archipelagos and taxa not only interrogate the model, but also offer clues to understanding variation in the relative magnitude of the influence of the factors involved. Here, we examine the patterns shown in relation to the GDM and then consider the outstanding issues that arise from our analyses.

Snails, oceanic archipelagos and the GDM

Within the framework of the GDM, the shape of the relationship between key diversity metrics and time can vary according to the degree to which the archipelago encompasses the full range of island stages (Fig. 1; see: Whittaker *et al.*, 2008; Borges & Hortal, 2009; Fattorini, 2009; Triantis *et al.*, 2010). The two models (Fig. 1a, c) considering only a linear relationship with time (either positive or negative) can be viewed as special cases of the general model (Fig. 1b). For the data considered here, the ATT² model has in most cases greater generality than the traditional richness–area models, or time-only models. Plotting the ATT² for the native species richness (with a random slope for log(Area) only; Table 2) for all the archipelagos (Fig. 2) illustrates the positive relationship with area, and the full range of relationships with time, from hump-shaped to almost linear (as Fig. 1). While the ATT² formulation thus provides a good general description of the data, it should be emphasized that we cannot rule out alternative models (cf. Bunnefeld & Phillimore, 2012).

All the archipelagos considered are composed of true oceanic islands, yet their mechanisms of formation vary, contributing to inter-archipelago differences in diversity processes and patterns. For all the diversity metrics, and for all the archipelagos and island groupings, the most parsimonious random effect structures included invariant coefficients

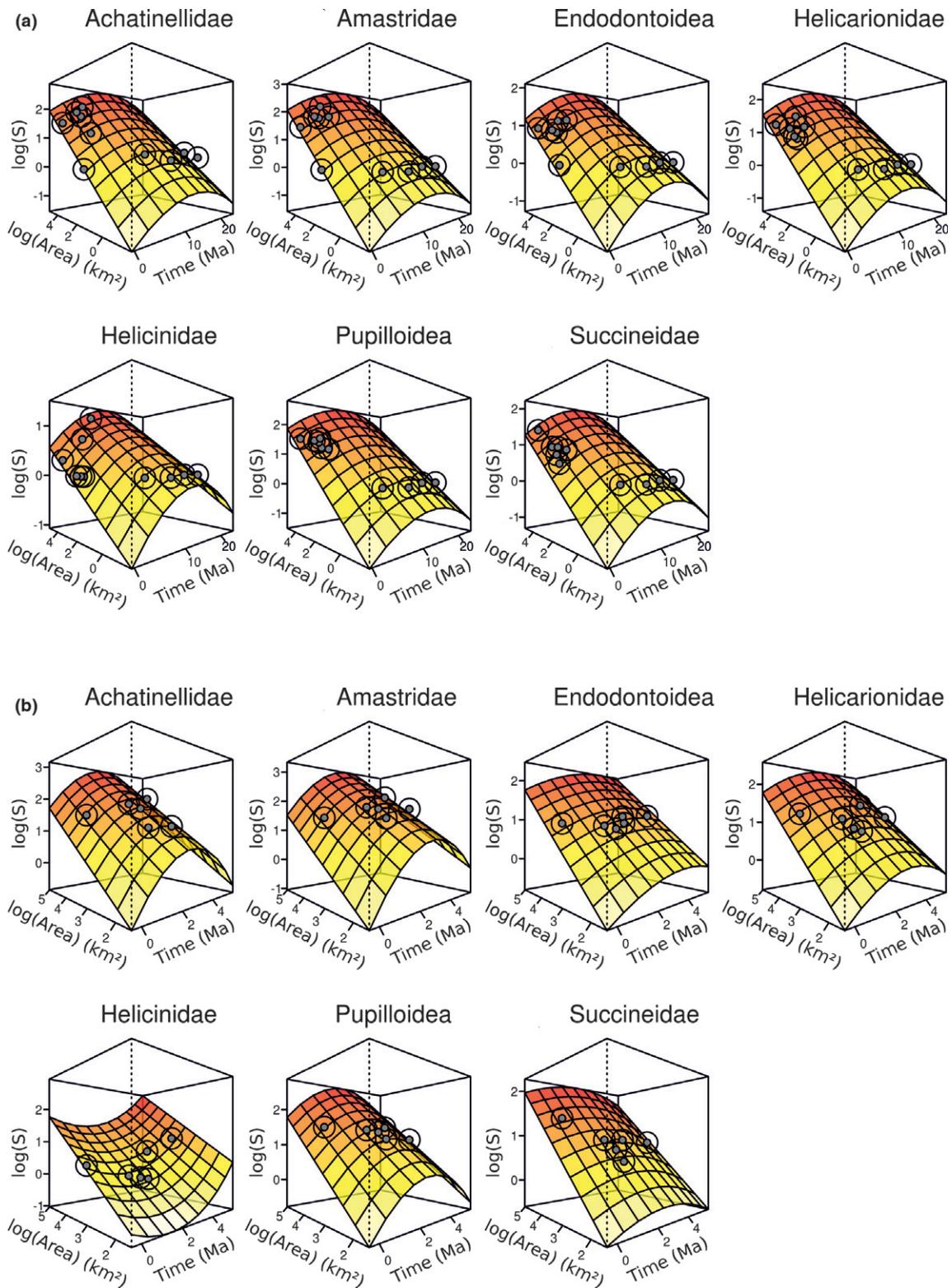


Figure 3 Species–area–time relationships (ATT^2) for the richness of the native species of the seven land snail families of the Hawaiian Islands: (a) for all the 10 islands considered, and (b) only for the six large islands. For the former the surface is the prediction from the linear mixed effect model including a random slope for $\log(\text{Area})$ varying across families (Table 3). For the latter, the surfaces are the prediction from a model including a random slope for Elevation, Time and Time^2 varying across families and including $\log(\text{Area})$, Elevation, Time and Time^2 as fixed effects: elevation values were averaged and multiplied by the respective coefficients for each family to produce the surfaces. Points represent the observed data. The numbers of species and area values are log-transformed. Time is in million years ago (Ma). The colour shading indicates the species richness predicted by the model [from white (low) to red (high)].

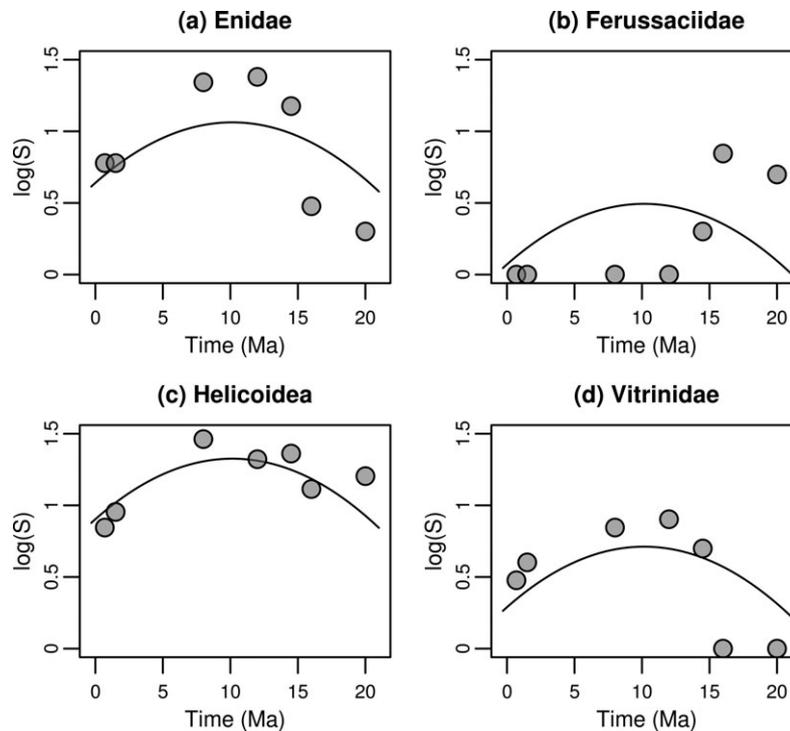


Figure 4 Species–time relationships (TT^2) for the richness of the native species of the four land snail families of the Canary Islands. The solid line represents the most parsimonious model based on the data for all families (see Table 3). Time is date of emergence of each island in million years ago, Ma (see Materials and Methods for details on island groupings). The number of species (S) is log-transformed.

for both Time and Time² across archipelagos (Table 2). This indicates the consistency of the effect of geological age on the processes generating and maintaining diversity of snails, regardless of the particularities of the geological setting in each archipelago considered here. Especially for the archipelagic endemic species and the SIE, this result signifies the importance of island areas to evolutionary dynamics (e.g. Rosenzweig, 1995; Triantis *et al.*, 2008a), and at the same time suggests that the inter-archipelagic differences in absolute geological ages are less important. On the other hand the sequential increase of the time effect as we move from natives to SIE (Table 2) signifies the critical role of time for the formation of new species.

For Hawaii, Canaries, Madeira and Tristan da Cunha, diversity rose and fell with increasing time, as predicted by the GDM (Table 2, Fig. 2). For the other archipelagos, i.e. Azores, Galápagos, Samoa and Society, we found only an increase with time (Fig. 2; see also Borges & Hortal, 2009; Triantis *et al.*, 2010; Bunnefeld & Phillimore, 2012). The main dichotomy between the two main groups of archipelagos identified above is the presence or absence of a full range of island stages, from ‘young’ to ‘old’ islands, which is not simply a matter of the time elapsed since island origination. For example Terceira in the Azores (c. 3.5 Ma, 400 km²) is a volcanically active island, whereas Bora Bora, an island of similar age in the Society Islands (c. 3.4 Ma, 30 km²), is a highly eroded, inactive shield volcano.

Taking two islands of the same size, Madeira and São Miguel (Azores), Cameron *et al.* (2007) has previously accounted for differences in snail richness as a product of effective island age and the range of available habitats. While the notional geological age of both islands is c. 4.5 Ma, São Miguel reached its current shape just 0.05 Ma, by the formation of a land bridge between an older eastern island, only part of which originated 4 Ma and a younger western island that originated 0.55 Ma. It has even been suggested that the whole island is less than 1 Myr old (Johnson *et al.*, 1998). Given all of which, the expectation would be that São Miguel is still accumulating diversity. This is indeed confirmed by detailed anatomical and molecular studies within generic clades (Martins, 2005; Van Riel *et al.*, 2005; Jordaens *et al.*, 2009). The relationship of age and ontogeny within the Azores in fact demands further comment. Assuming São Miguel to be in part around 4 Myr old, the only other old island is Santa Maria, which is estimated to have a maximum age of 8.12 Ma (Borges *et al.*, 2009). However, extensive volcanic activity occurred on Santa Maria around 4 Ma. Thus, the entire Azorean archipelago is essentially still in relative youthful stages of the island life cycle, while more than 60% of the land area of the archipelago is < 1 Myr old. Nevertheless, a synthetic consideration of these and other explanations (e.g. climatic effects) are required for a full explanation of these patterns (e.g. Triantis *et al.*, 2012b).

The effects of taxonomic subdivision

Plotting the ATT^2 for the native species richness for the seven taxonomic groups in Hawaii illustrates a consistent pattern of positive relationships with area and hump-shaped relationships with time (Fig. 3a). The pattern owes much to the diversity differences between the large main islands of the archipelago and the small north-west islands. When the small islands are removed, the relationship with time varies from highly humped for Amastridae and Achatinellidae, almost linear for Succinidae, to a shallow u-shape for Helicinidae (Fig. 3b). The overall humped pattern with island age is thus demonstrated to be due largely to the two richest families, the Achatinellidae and Amastridae (Table S1 in Appendix S1). The former, tree snails confined to the Pacific Basin, and the latter, all endemic to Hawaii, appear to have very limited powers of dispersal. Succineids tend to occupy open and at least seasonally wet habitats: they are most diverse on the youngest (and largest) island where these habitats are widely available. The ecology of the Helicinidae, which fits poorly with the ATT^2 model (Fig. 3b) is little known (see Cowie, 1996).

For the Canaries, the general success of the TT^2 model (see Results) again demonstrates some interesting variability according to family, with the Ferussaciidae standing out as an exception for having their greatest richness on the oldest islands (Fuerteventura and Lanzarote; Fig. 4). The Ferussaciidae are usually found in subterranean environments in warm and dry areas, more typical of the two oldest islands, in part reflecting their topography and in part their more easterly location. In contrast, forest-dwelling forms such as vitrinids are now entirely missing from Fuerteventura and Lanzarote and are more diverse in the intermediate-aged forested islands such as Tenerife. Similar patterns are observed in the Madeiran archipelago, with the composition of the Porto Santo and Desertas faunas resembling those of the dry eastern islands of the Canaries. Moreover, while Porto Santo is much smaller in size than the most humid island of the group, i.e. Madeira, the dominant superfamily, Helicoidea, is actually richer on Porto Santo (see Cook, 2008).

Interestingly, the taxonomic decomposition of the snail faunas of Hawaii and the Canaries revealed that the coefficients associated with time vary across the different taxonomic groupings (see Table 3 and note that for the Canaries there is not a single best random structure, although one of them includes time). This is in contrast to the structure selected for the snail faunas across the different archipelagos. These findings indicate that whatever the emergent whole system pattern, within the same archipelago the relationship of the diversity of the different taxonomic groupings with time varies in accordance with their different ecological requirements.

Future directions and hypotheses

In general, we have shown that the ATT^2 formalization of the GDM can successfully describe patterns in snail diversity among islands within these archipelagos. Inevitably, given

the complexity of the geological and ecological processes involved and the diverse histories of colonization and speciation and extinction, there are a number of exceptions. The challenge is thus to identify the factors involved in oceanic island diversity dynamics without resorting to a mass of ad hoc speculations and post hoc rationalizations. Such factors will include aspects of the islands themselves, and, as shown already for the Azores (Borges & Hortal, 2009; Triantis *et al.*, 2010), differences in life histories and dispersal abilities among subsets of organisms. We see the following as themes worth further consideration in this context.

1. The GDM is cast at the level of the emergent whole-system dynamics, and disaggregation into taxonomically or ecologically distinct groups may be expected to show varying responses to long-term island-environmental dynamics (e.g. Borges & Hortal, 2009). Ideally, hypotheses for such distinctive responses should be formulated in advance of analysis based on ecological characteristics of the groups concerned.
2. Analyses should seek to place alternative hypotheses into a multiple working hypothesis framework. For instance, Kim *et al.* (2008) identified three discrete waves of colonization by monophyletic endemic plant lineages of Macaronesian islands from the western Mediterranean, offering support to the 'colonization window hypothesis' (Carine, 2005), according to which, the opportunity for island colonization may have been largely constrained to one or more distinct periods of time (e.g. glacial era sea-level low stands; Fernández-Palacios *et al.*, 2011). This alternative theoretical case to the GDM makes specific predictions regarding the temporal development of island phylogenies distinct from the GDM, which should be testable if genetic analyses of multiple separate clades are undertaken (Whittaker *et al.*, 2010).
3. Other variables (apart from area) can be used for a more effective approximation of the available ecological space, e.g. habitat diversity. For example, in a recent study of taxa from a variety of island groups (including the Canaries, Azores and Cape Verde islands), Triantis *et al.* (2008b, 2010) concluded that the precise quantification of factors such as climate, habitat diversity and evolutionary history (that may partially covary with area) is necessary to develop a more predictive model of how species numbers vary across insular systems (see also Losos & Parent, 2010).
4. According to the GDM, lineage radiation (leading to multiple SIEs on individual islands) should be most prevalent after the initial colonization phase, in the period leading up to island maturity, coinciding with maximal species carrying capacity and the development of maximal topographic complexity (see also Fig. 4.5 in Whittaker *et al.*, 2010). There is support to be found for this general scenario (e.g. see Givnish *et al.*, 2009), although the specific characteristics of each island and archipelago play a significant role in the timing and the magnitude of radiation events. Whittaker *et al.* (2008, p. 983) argued that the GDM predicts that 'Adaptive radiation (AR) will be the dominant process on islands where the maximum elevational range occurs, as it generates the greatest richness of habitats (major ecosystem types),

including novel ones that few colonists have experienced, whereas non-adaptive radiation (NAR) will become relatively more important on slightly older islands, past their peak elevation, owing to increased topographical complexity promoting intra-island allopatry'. Testing these predictions provides a significant challenge (but see Givnish *et al.*, 2009; Rabosky & Glor, 2010).

5. There is some evidence of variation in the effectiveness and dynamism of habitat barriers within islands in different archipelagic settings. For instance, in the Galápagos, the first stages of adaptive differentiation within bulimulid species can be detected in the early history of islands, related to the availability of as yet unoccupied niches (Parent & Crespi, 2009). Evidence from other archipelagos, however, suggests that non-adaptive radiation in snails can also peak at an early stage. For example, Martins (2005) suggested that recurrent volcanism played a significant part in the build-up of single-island diversity in the relatively young Azorean snail faunas. There may be several episodes of partial differentiation followed by some introgression in early stages. Later, the rate of differentiation/speciation slows down (Martins, 2011). Cook (2008) similarly suggested that a coincidence of the rates of volcanic and erosive events with the speed of genetic differentiation in snail populations (the 'geodetic rate') accounts for diversity in the Madeiran snail fauna (see also Carson *et al.*, 1990, on drosophilids in Hawaii). There is some evidence in these studies of initially high rates of diversification, facilitated by temporary barriers caused by intermittent volcanic episodes, and by the exceptionally poor powers of active dispersal in snails (Kisel & Barraclough, 2010). Once again, the challenge will be to develop models that retain generality in the face of such system-specific differences.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Datasets used for the land snails of eight oceanic archipelagos (Tables S1 & S2).

Appendix S2 Island groupings considered for the land snails of eight oceanic archipelagos.

Appendix S3 Supplementary analyses and results (Tables S3 & S4).

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BIOSKETCH

Robert A. D. Cameron has a long-term fascination with the ecology, biogeography and evolutionary biology of land snails.

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