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Discordance between morphological and taxonomic diversity: land snails of oceanic archipelagos

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ABSTRACT

Aim Morphological and taxonomic diversity are intuitive measures of biological diversity. Previous studies have shown discordance between these measures at large spatial and temporal scales, but the implications of this pattern for the underlying processes are not understood. Using oceanic archipelagos as spatial units, we examine potential links between the morphological and taxonomic diversity of their land snail faunas in a biogeographical framework.

Location Eleven major oceanic archipelagos.

Methods For each archipelago, we assembled lists of indigenous land snail species, classified by family and genus, with shell height and width for each species (1723 species in total). We used biogeographic and climatic variables as potential predictors of diversity patterns. We employed regression analyses to evaluate (1) whether morphological diversity scales with taxonomic diversity at the species, genus or family level, and (2) whether morphological and taxonomic diversity correlate similarly with biogeographic/climatic factors. We also assessed which taxonomic level contributes most to morphological variation within archipelagos.

Results Morphological diversity across archipelagos was strongly related to genus but not species richness. Within archipelagos, morphological variation reflected differences among genera and families but not species. Species richness was best explained by archipelago area, but morphological diversity was not significantly related to any of the physical features of archipelagos.

Main conclusions Across archipelagos, species richness and morphological diversity of land snail faunas are decoupled. The relationship between species richness and the available ecological space (captured mainly by area) indicates the prevalence of niche-based processes while, for morphological diversity, the strong conservatism of morphology at the genus level suggests the presence of diversification-based limits. Assuming genera effectively reflect diversification, our findings indicate that morphological space on oceanic archipelagos depends primarily on the number of evolutionary units that have colonized and/or diversified through time.

Keywords

ecological space, evolutionary units, Gastropoda, limits, morphological space, niche conservatism, oceanic islands, shell morphology, species diversity

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INTRODUCTION

In the search for global patterns of biodiversity, adopting a range of approaches provides the greatest insight. Macroecological and macroevolutionary patterns, in both neontological and palaeontological studies, are revealed mainly by the two most intuitive measures of biological diversity: (1) taxonomic diversity, most readily assessed as species richness, and (2) morphological diversity (e.g. Foote, 1993; Jablonski, 2007; Derryberry *et al.*, 2011; Ricklefs, 2012; Rabosky, 2013; Ruta *et al.*, 2013). Variation in both species richness and morphological diversity across major organismal groups constitute global yet poorly understood patterns in the large-scale organization of biodiversity.

Morphological diversity of a group of organisms is assessed by the multidimensional space that encompasses its morphological variation, that is, morphospace (McClain *et al.*, 2004). Although there are many species concepts (de Queiroz, 2007), most species descriptions are based on morphology; consequently a relationship between taxonomic richness and morphological diversity might therefore be expected. However, palaeontological (e.g. Foote, 1993; Jablonski, 2007) and neontological (e.g. Derryberry *et al.*, 2011) studies have shown that, in comparisons across large spatial and temporal scales, discordance between these two measures of diversity may arise, particularly during episodes of intense diversification when wide morphological variation appears well in advance of peak taxonomic diversity (e.g. Roy *et al.*, 2004; Erwin, 2007). These observations have led to the hypothesis that at coarse spatial and/or temporal scales morphological diversity of clades can approach functional limits – that are not necessarily strict – while taxonomic richness, especially at the species level, continues to accumulate, increasing the density of morphospace occupation over time (Foote, 1997; Roy *et al.*, 2004; Erwin, 2007). For most living organisms, however, there have been few tests of how large-scale spatial patterns of taxonomic richness are related to patterns of morphological diversity (Ricklefs, 2012).

Limits to morphological diversity, and diversity in general, can be extrinsic or intrinsic. Intrinsic constraining factors are properties of organisms that influence the dynamics of lineage splitting or extinction, including developmental, physiological, genetic or architectural constraints. Such properties can lead directly to niche conservatism reflected, for instance, in high niche retention across higher taxonomic levels (Prinzing *et al.*, 2001; Hadly *et al.*, 2009). Extrinsic factors are environmental features, for example, availability of niches and biotic interactions that are not biological or ecological properties of a lineage (Wagner, 1995; Valentine *et al.*, 1999; Jablonski, 2007; Vamosi & Vamosi, 2011; Rabosky, 2013). Intrinsic and extrinsic constraints are linked, respectively, to diversification and niche-based hypotheses for explaining geographical patterns in biodiversity (Erwin, 2007; Ricklefs, 2012). Therefore, if species richness were primarily constrained by extrinsic niche-based limits, one would expect that it would be related to the total ecological space available (Ricklefs, 2004, 2012); but if morphological diversity were primarily constrained by intrinsic factors, ecological space should have little influence and metrics quantifying diversification should prevail in explaining the diversity.

A key challenge to unification and generalization of our understanding of mechanisms that drive and constrain morphological disparity and taxonomic diversity is recognition of both the appropriate spatial and temporal scale at which to study these processes and the appropriate units of analysis. Oceanic archipelagos offer an opportunity to address this challenge (Whittaker *et al.*, 2014; Triantis *et al.*, 2015). Most oceanic islands are of volcanic origin, have never been connected to continental land masses and support some of the most isolated biological systems in the world (e.g. Cowie & Holland, 2006; Parent *et al.*, 2008; Whittaker *et al.*, 2008; Cameron *et al.*, 2013). Most taxa in these archipelagos exhibit high levels of endemism arising from the typically small number of founder species that become the source of local diversification, thereby leading to independently diversified regional biotas. Thus, oceanic archipelagos can be considered as biotic provinces, that is, self-contained areas within which diversity primarily reflects a balance between speciation and extinction, with colonization from outside playing a minor role (Whittaker *et al.*, 2008; Cameron *et al.*, 2013; Triantis *et al.*, 2015). Oceanic archipelagos provide tractable opportunities to detect and quantify large-scale relationships between taxonomic and morphological diversity.

Terrestrial snails provide an excellent system for quantifying patterns of taxonomic and morphological diversity, as they are numerous – about 24,000 described and up to 40,000 undescribed species world-wide (Lydeard *et al.*, 2004; Rosenberg, 2014) – and exhibit a wide spectrum of shell shapes that results in high morphological diversity. Shell size ranges over three orders of magnitude (Cain, 1977) and mass over more than five (Cameron, 2013).

In this study, we collated taxonomic and morphological data for the indigenous terrestrial snail faunas of 11 oceanic archipelagos to examine the potential links between taxonomic diversity (from species to higher levels), morphological diversity and biogeographic/climatic factors. The faunas of each of the archipelagos diversified essentially independently, as they are scattered widely across the globe.

We addressed the following questions:

1. Does morphological diversity among archipelagos correlate with taxonomic diversity and, if so, at which taxonomic level(s)?

2. Do morphological and taxonomic diversity scale with biogeographic and climatic variables such as total archipelago area and, if so, do they scale in similar fashion?

METHODS

Data collection

We collated complete species lists of the indigenous (endemic and native non-endemic) land snail faunas of 11

oceanic archipelagos (Azores, Canaries, Comoros, Galápagos, Hawaii, Juan Fernandez, Madeira, Mascarene, Revillagigedo, Samoa (American Samoa and independent Samoa), Tristan da Cunha), with each species classified at super-family, family and genus levels (see the full list of species at the Harvard Dataverse, http://dx.doi.org/10.7910/DVN/LOJT2Y; and Appendix S1 with Table S1.1 for data sources and Fig. S1.1 for archipelago locations in Supporting Information). The malacofaunas of these archipelagos are relatively well-studied, and reliable faunal lists for each of them are available. Oceanic island snail faunas have suffered widespread extinction because of human activities both recently (e.g. Solem, 1990; Cowie, 2001; Régnier *et al.*, 2015a, b) and during prehistory (e.g. Preece, 1998). Described species known to have gone extinct were included, but we cannot know about species that left no record as fossils or empty shells, nor about cryptic species that might have been discovered had modern molecular techniques been available (e.g. Richling & Bouchet, 2013). Introduced species and slugs lacking or with a reduced external shell were excluded. Our final dataset comprised 1723 indigenous species, including 1620 endemic and 103 native non-endemic species (species that arrived naturally, unaided by humans) from 52 islands of the 11 archipelagos (Table 1). The dataset may be made available on request to the corresponding author.

For every species, values of shell height and width were obtained from the original descriptions if possible, from subsequent publications, or from direct measurement. If multiple measurements or a range were provided, average values were used. Similarly, for species with valid subspecies, average values were estimated. The preferred measurements were taken parallel and perpendicular to the columellar axis (Cain, 1977; Fig. 1; see Table 1). Some authors may have not measured shell height and width using this exact protocol, but this variation is small relative to differences among species (Cowie, 1995).

Table 1 The number of indigenous species, genera and families of land snails, and the range of shell height and width, for each archipelago in the study.

	Species richness	Genus richness	Family richness	Height range (mm)	Width range (mm)
All	1723	192	49	0.5–78.5	0.5–52
Azores	89	23	17	0.7–19.5	0.9–15
Canaries	227	30	20	0.77–26.03	0.8–32.2
Comoros	102	30	14	1–37	1–20
Galápagos	97	12	11	1.25–24.2	1–15.5
Hawaii	752	44	10	0.5–78.5	0.8–24.3
Juan Fernandez	42	8	5	0.6–18.5	1.05–11.5
Madeira	161	30	10	1.17–33	0.8–52
Mascarene	162	46	17	0.75–42.5	0.7–41
Revillagigedo	17	11	11	0.75–15.5	0.5–10
Samoa	67	24	14	0.96–26.9	0.8–20.4
Tristan da Cunha	11	2	2	5–10	1.9–4.4

For each archipelago, we assembled data for 11 abiotic variables: six biogeographical variables, that is, geological age (as the maximum age of the currently existing oldest island), isolation (as the distance to the closest possible source; see Triantis *et al.*, 2015), total area (sum of the areas of all islands of an archipelago), number of islands, maximum elevation (highest point in the archipelago) and latitude (see Triantis *et al.*, 2015); and five climatic variables, that is, annual mean temperature, annual precipitation, annual range in temperature, the coefficient of variation in precipitation (unitless) (see Weigelt *et al.*, 2013 and Cabral *et al.*, 2014 for details) and the environmental volume of each archipelago as a measure of its environmental heterogeneity. Environmental volume was estimated as the three-dimensional convex hull occupied by the islands of each archipelago in the ordination space of a principal component analysis that included 17,883 islands world-wide and 10 bioclimatic and physical variables (see Weigelt *et al.*, 2013 and Cabral *et al.*, 2014 for details). All statistical analyses were implemented in R version 3.1.0 (R Core Team, 2014; see Appendix S2) and performed using numbers of indigenous species (94% of these being archipelago endemics).

Assessing taxonomic and morphological diversity

Taxonomic diversity for each archipelago was assessed by the number of species, genera and families. Morphological diversity was assessed using two measures (McClain *et al.*, 2004): (1) the size of the surface of the smallest polygon enclosing all species of an archipelago in the two-dimensional morphospace (MS) defined by shell height and width, calculated using the convex hull algorithm (Cornwell *et al.*, 2006); and (2) the mean morphological distance (MMD) among species in each archipelago calculated by averaging the Euclidean distances between all species pairs in the two-dimensional morphospace defined by shell height and width. Shell height and width were log-transformed to minimize distortion caused by outliers.

MS refers to the amount of morphospace occupied by a given sample, while MMD measures the dispersion of the different morphological forms within the sample (Foote, 1997). In contrast to morphological diversity measures based on mean pairwise distance (e.g. MMD) that are considered minimally sensitive to species richness (Pavoine *et al.*, 2013), measures based on ranges, surfaces or volumes (e.g. MS) are usually strongly positively correlated with species richness. Indeed, morphological space should be larger with more species simply because of the sampling effect (Foote, 1992). Similarly, differences in genus and family richness among samples may also be affected by differences in species richness (Foote, 1992; Alroy, 2010). Therefore, we applied a correction via a rarefaction analysis to estimate MS, MMD, genus richness and family richness at the same species richness (Foote, 1992; Kowaleski & Novack-Gottshall, 2010). For each archipelago species richness was down-sampled by randomly selecting 11 species 1000 times, 11 being the spe-

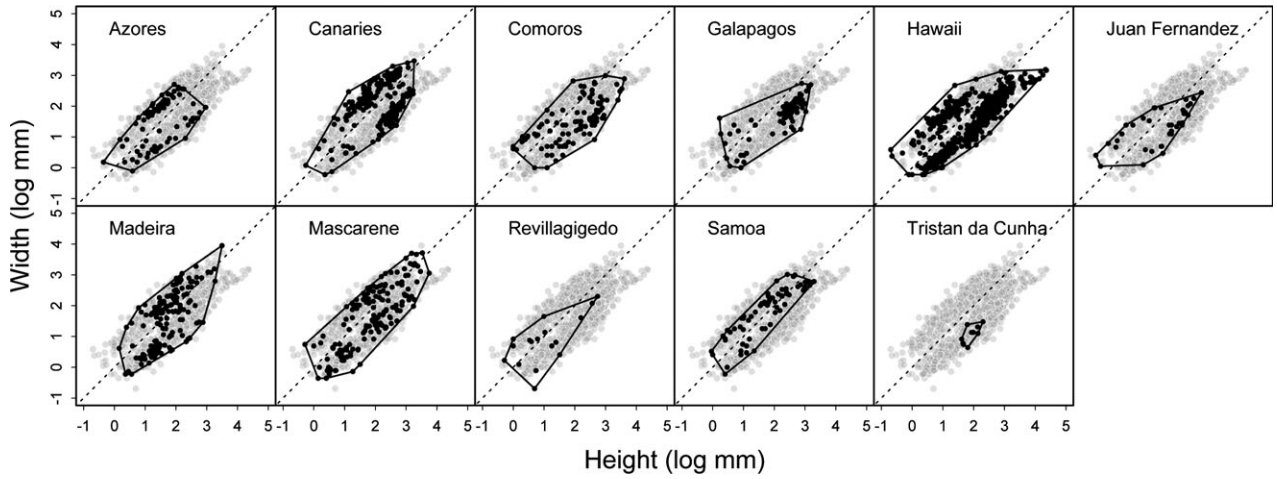

Figure 1 Projections of the morphological surfaces of each archipelago in the two-dimensional morphospace defined by log-transformed shell height and width. The solid black lines delimit the smallest polygon that encloses all indigenous species of a given archipelago defined by the convex hull algorithm (Cornwell *et al.*, 2006). Black dots indicate species. The surface area of the polygons corresponds to the measure of morphological diversity (MS) used in the study. The grey background dots represent the entire dataset (N = 1723). The black dotted line is the isocline (height = width).

cies richness of Tristan da Cunha, the least rich archipelago in our dataset. For each random sample, MS, MMD, genus richness and family richness were calculated, such that the rarefied values for these four variables corresponded to the averages of the 1000 random samples. To test the robustness of this approach, we repeated the rarefaction analysis by down-sampling species richness with different sample sizes. See Appendix S2 for details of the rarefaction analysis.

Assessing the relationships among morphological diversity, taxonomic diversity and biogeographical factors

All these analyses were conducted for both observed and rarefied (i.e. controlled for any species richness effect) MS, MMD, genus and family richness. We investigated the relationships between morphological diversity (MS and MMD) and the taxonomic variables (taxonomic model including species, genus and family richness) and the abiotic variables (biogeographic/climatic model including the 11 variables) using ordinary least squares (OLS) multiple regression analyses. We also assessed the relationships between the taxonomic and abiotic variables. For rarefied data, species richness was excluded from the analyses of the taxonomic model. Taxonomic, biogeographic and climatic variables were log-transformed if necessary to approximate normal distributions of residuals (see Appendix S2). Pairwise Pearson's correlations were explored to assess multicollinearity between the abiotic variables (see Appendix S2 and Table S2.2 for details). We retained for the ensuing analyses area, age, isolation, latitude, number of islands, annual mean temperature and annual range in temperature (pairwise correlations between these variables were < 0.56, see Appendix S2). The strong correlation between environmental volume and area (r_p = 0.769) is another indication that area is an approximate surrogate for available ecological space (Triantis *et al.*, 2012). Among taxonomic variables, correlation between log-transformed species richness and genus richness was high (r = 0.845), but because relationships between taxonomy and morphological diversity are the focus of our investigation, we retained all variables in our analysis, while acknowledging that collinearity may increase uncertainty in model selection (see below). We employed an information theoretic approach to capture the best set of variables explaining our dependent variables by fitting all possible models and calculating Akaike's information criterion (AICc) corrected for small sample size for each model; the best model being the one with the smallest AICc (Burnham & Anderson, 2002). However, all models with a ΔAICc value < 2 (the difference between each model's AICc and the lowest AICc) were considered as receiving equal statistical support (Burnham & Anderson, 2002).

Quantifying the contribution of species, genus and family level to morphological variation

For each archipelago, we quantified the contribution of each taxonomic rank (species, genus, and family) to the morphological variation in order to quantify the level of conservatism in shell form. At low levels of conservatism, most of the variation should be at the species level, while at high levels most of it should be at higher taxonomic levels. However, the considerable heterogeneity of variance in our morphological measurements among genera and families, as well as the imbalanced nature of the data (e.g. 3% of genera have > 50 species while 80% have < 10), precluded using nested ANOVA-like analyses commonly performed to partition variation across taxonomic levels (Prinzing *et al.*, 2001; Ricklefs, 2012).

We therefore used an alternative approach to estimate the extent to which species, genus and family richness explained

morphological variation within each archipelago. Independently for genera and families, we computed the index τ_{ST}, originally developed to assess β-diversity (Hardy & Senterre, 2007; Baraloto *et al.*, 2012), which expresses the ratio between the mean dispersion within and among groups. τ_{ST} was calculated as:

$$\tau_{ST} = 1 - \frac{\Delta_w}{\Delta_a}$$

with Δ_w being the mean MMD within genera/families and Δ_a the mean morphological pairwise distance separating species for all pairs of genera/families. In our case, $\tau_{ST} < 0$ indicates that species within genera/families are morphologically less similar than species from different genera/families, suggesting that morphological variation occurs primarily at the species level, while $\tau_{ST} > 0$ indicates that species within genera/families are morphologically more similar than species from different genera/families suggesting that morphological variation mostly occurs at the genus/family level.

For each archipelago, we compared the observed τ_{ST} values with those calculated based on 1000 randomizations of species among taxa. Because at least two species are needed to measure morphological distance, all genera/families that did not meet this criterion were excluded from this analysis: 13–63% of the genera (representing 1–41% of the species) and 0–63% of the families (representing 0–41% of the species) among archipelagos. The Tristan da Cunha archipelago has only two genera belonging to two families with one of them represented by only one species and it was therefore excluded from the analysis. Finally, we also assessed the relationship between both the biogeographic/climatic and taxonomic variables and τ_{ST} using OLS multiple regressions and model selection as described above.

Assessing taxonomic bias related to shell morphology

In land snails, the main diagnostic characters at the generic, or higher, levels have traditionally not been simple shell height and/or width measurements but more complex conchological characters and, more recently, internal anatomical characters, notably the morphology of the reproductive organs (e.g. Schileyko, 2013). Nevertheless, we applied a 'random forest' method (Breiman, 2001) to assess the correct assignment of species to their actual genera and/or families based on shell height and width (see Appendix S2). We performed the analysis considering the whole dataset and for each archipelago independently. If the majority of species at the global and especially at the archipelago level were indeed correctly assigned to genera and/or families by just shell height and width, this would imply a strong taxonomic bias in our results regarding morphological diversity.

RESULTS

The morphological space on each archipelago is presented in Fig. 1. The taxonomic models showed that MS was best explained by species and genus richness, but a second best model (ΔAICc = 1.26) included only genus richness (Table 2, Fig. 2a). In contrast, MMD was best explained by genus richness, but a second best model (ΔAICc = 0.69) included both species richness and genus richness, the former having no significant effect (Table 2, Fig. 2b). Rarefied MS and MMD were explained exclusively by genus richness (Table 2, Fig. 2c, d), demonstrating that the relationships between observed MS/MMD and genus richness were not due simply to differences in species richness among archipelagos. The results obtained with rarefied data were only minimally sensitive to the sample size used to rarefy species richness (see Appendix S3, Table S3.3).

For the biogeographic/climatic models, analyses emphasized a combined effect of total area (positive) and, to a lesser extent, number of islands per archipelago (negative) in explaining both observed MS and the three taxonomic variables. We therefore re-ran our analysis using mean island area (total area divided by number of islands), which combines the positive effect of area and the negative effect of the number of islands (Triantis *et al.*, 2015). Results were

Table 2 Best taxonomic model(s) for observed and rarefied morphological diversity (MS and MMD).

	Intercept	Species richness	Genus richness	Family richness	Adjusted R^2	ΔAICc	*w*AICc
Observed variables							
MS	4.8 (0.19)***	0.97 (0.38)*	1.08 (0.38)*	–	0.90	0	0.48
	4.8 (0.25)***	–	1.9 (0.26)***	–	0.84	1.26	0.25
MMD	1.24 (0.06)***	–	0.24 (0.06)**	–	0.58	0	0.48
	1.24 (0.05)***	−0.21 (0.10)	0.42 (0.10)**	–	0.69	0.69	0.34
Rarefied variables							
MS	0.18 (0.36)	NI	0.29 (0.05)***	–	0.74	0	0.90
MMD	0.39 (0.13)*	NI	0.13 (0.02)***	–	0.79	0	0.93

Best models with a ΔAICc less than 2 are the ones presented (see details in Materials and Methods). For each model, standardized regression coefficients (intercept and slope) are given along with their respective standard errors (in parentheses) and significance levels (***$P \leq 0.001$; **$P \leq 0.01$; *$P \leq 0.05$; in all other cases $P > 0.05$). The adjusted R^2 value, the ΔAICc and the AICc weight (*w*AICc) are given for each model. For the models with rarefied data, rarefied MS and MMD were tested against rarefied genus and family richness. NI: non-included (see Materials and Methods). MS, morphospace; MMD, mean morphological distance.

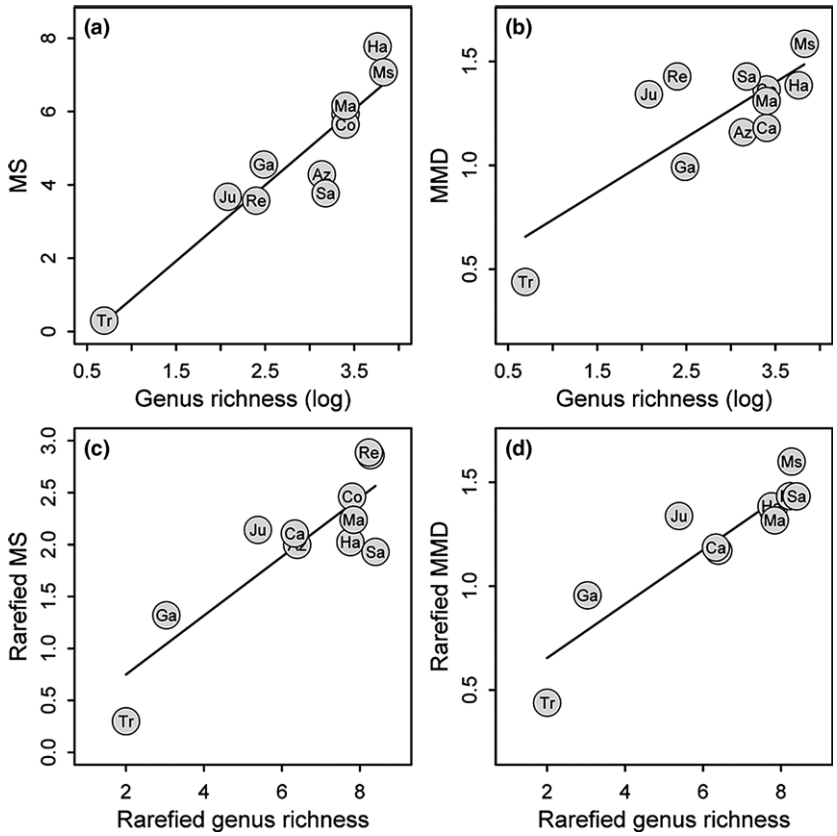

Figure 2 Relationships between genus richness and morphological diversity measurements, morphospace (MS) (a, b) and mean morphological distance (MMD) (c, d) for both observed (a, c) and rarefied (b, d) data. Standardized regression coefficients (intercept and slope), significance levels and adjusted R^2 are given in Table 1. The four relationships were highly significant. Az = Azores, Ca = Canaries, Co = Comoros, Ga = Galápagos, Ha = Hawaii, Ju = Juan Fernandez, Ma = Madeira, Ms = Mascarene, Re = Revillagigedo, Sa = Samoa, Tr = Tristan de Cunha.

Table 3 Best biogeographic/climatic model(s) for both taxonomic and morphological diversity. Analyses were performed for both observed and rarefied diversity measures.

	Intercept	Mean area	Age	Isolation	Latitude	AMT	ART	Adjusted R^2	ΔAICc	*w*AICc
Observed variables										
Species richness	4.46 (0.13)***	1.17 (0.15)***	–	–	–	–	0.33 (0.15)	0.86	0	0.34
	4.46 (0.16)***	1.07 (0.17)***	–	–	–	–	–	0.80	0.03	0.34
Genus richness	2.89 (0.17)***	0.75 (0.18)**	–	–	–	–	–	0.64	0	0.54
Family richness	2.33 (0.13)***				0.34 (0.14)*	0.37 (0.14)*		0.57	0.00	0.28
	2.33 (0.16)***	0.44 (0.17)*						0.37	0.19	0.25
	2.33 (0.16)***					0.41 (0.17)*		0.32	0.97	0.17
	2.33 (0.17)***				0.39 (0.18)			0.27	1.85	0.11
	2.33 (0.14)***	0.46 (0.15)*		−0.26 (0.15)				0.49	1.98	0.10
MS	4.80 (0.38)***	1.68 (0.40)**	–	–	–	–	–	0.63	0	0.44
	4.80 (0.33)***	1.92 (0.36)***	–	–	–	–	0.73 (0.36)	0.73	0.69	0.31
MMD	1.24 (0.08)***	–	–	–	–	0.18 (0.08)	–	0.28	0	0.38
	1.24 (0.09)***	–	–	–	–	–	–	–	0.77	0.26
Rarefied variables										
Genus richness	6.49 (0.57)***	–	–	–	–	1.27 (0.6)		0.26	0	0.38
	6.49 (0.66)***	–	–	–	–			–	0.53	0.29
Family richness	5.11 (0.48)***	–	–	–	–	1.05 (0.5)		0.25	0	0.40
	5.11 (0.55)***	–	–	–	–	–		–	0.44	0.32
MS	2.04 (0.22)***	–	–	–	–			–	0	0.32
	2.04 (0.17)***	–	–	–	–	0.61 (0.21)*	0.47 (0.21)	0.41	0.85	0.21
	2.04 (0.20)***	–	–	–	–	0.35 (0.21)		0.15	0.98	0.20
MMD	1.24 (0.08)***	–	–	–	–	0.18 (0.09)		0.26	0	0.36
	1.24 (0.09)***	–	–	–	–			–	0.50	0.28

Best models with a ΔAICc less than 2 are the ones presented (see details in Materials and Methods). AMT, annual mean temperature; ART, annual range for temperature. For each model, standardized regression coefficients (intercept and slope) are given along with their respective standard errors (in parentheses) and significance levels (***$P \leq 0.001$; **$P \leq 0.01$; *$P \leq 0.05$; in all other cases $P > 0.05$). The adjusted R^2 value, the ΔAICc and the AICc weight (*w*AICc) are given for each model. MS, morphospace; MMD, mean morphological distance.

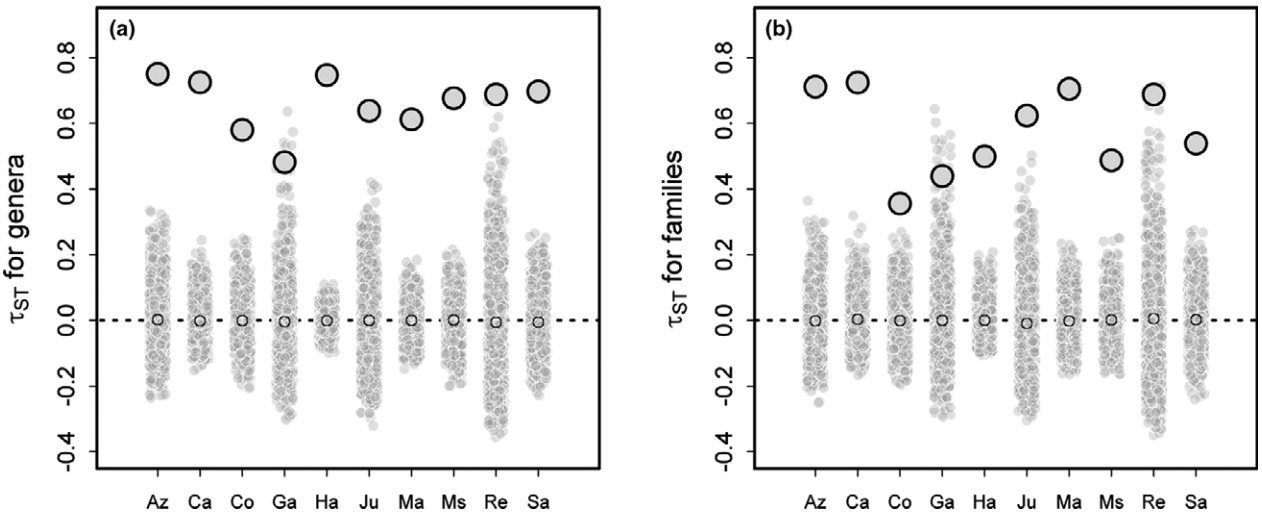

Figure 3 τ_{ST} values among archipelagos computed at genus (a) and family (b) levels for indigenous land snail species. Only genera/families having a minimum of two species were considered since at least two species are required to compute the mean dissimilarity between species (see formula of τ_{ST} in the main text). The Tristan da Cunha archipelago has only two genera belonging to two families with one of them represented by only one species and was therefore excluded from the analysis. Large grey circles represent the observed τ_{ST} values while small grey circles indicate the values of the 1000 randomizations and the open circles indicate the means of the 1000 random values. The black horizontal dotted lines represent the null hypotheses of $\tau_{ST} = 0$. Archipelagos coded as in Fig. 2.

unchanged and for simplicity we only present the analysis using mean area. Observed MS and species and genus richness were best explained by mean area (Table 3), while family richness was best explained by several combinations of variables including mean area, latitude and annual mean temperature (Table 3). In contrast, none of the abiotic variables significantly explained MMD (Table 3). Once rarefied, MMD, genus richness and family richness showed no significant relationship with any biogeographic/climatic variable (Table 3) while, for MS, a marginal effect of annual mean temperature was found in the second best model (Table 3). Again, the results obtained with rarefied data were not sensitive to the choice of sample size used to down-sample species richness (see Appendix S3, Table S3.4).

In all cases and on all archipelagos, τ_{ST} was > 0, that is, 0.659 ± 0.083 and 0.584 ± 0.128 at genus and family levels respectively (Fig. 3a, b). All τ_{ST} values were significantly higher than expected from our null model. Neither taxonomic nor biogeographic/climatic models revealed any significant relationship with τ_{ST}, except that at the family level it was marginally significantly explained by latitude and annual mean temperature (see Appendix S3, Tables S3.5, S3.6).

According to the random forest analysis, for the whole dataset, no species were correctly assigned for 74% of the genera and 64% of the families (see Appendix S3, Table S3.7). When archipelagos were considered separately, species were correctly assigned to more than 50% of the genera and families in five and eight archipelagos respectively. For the remaining archipelagos, few species were correctly assigned to the majority of the genera and families (see Appendix S3, Table S3.7).

DISCUSSION

Based on morphological data from 1723 species of land snails on 11 major oceanic archipelagos across the globe, we found that diversity at higher taxonomic levels, especially the genus level, is the most important variable determining morphological diversity. Rarefaction analyses controlling for species richness confirmed this finding with only the rarefied number of genera being significantly correlated with rarefied MS and MMD (Table 2). Assuming that genera effectively reflect diversification, the overall relationship between morphological diversity and generic richness indicates that archipelago morphological space depends primarily on the number of independent evolutionary units (genera and higher taxa) colonizing and/or diversifying within an archipelago. For example, the indigenous Hawaiian fauna, with more than 750 species (Cowie *et al.*, 1995), is thought to have arisen from just 22–24 ancestral colonizations (Zimmerman, 1948), with 44 genera recognized (Cowie *et al.*, 1995), 23 of which are endemic to the archipelago.

Genera and higher taxonomic ranks have been considered to be subjective constructs with boundaries inconsistent among taxonomists and thus lacking informative evolutionary significance (Lee, 2003; Coyne & Orr, 2004; Bertrand *et al.*, 2006). However, genera may indeed effectively reflect natural evolutionary processes (Simpson, 1953) and in this regard have been critical instruments in palaeobiology, macroecology and macroevolution (e.g. Alroy, 2010; Maruvka *et al.*, 2013). Recently, the validity of the genus as a morphologically recognized level in the taxonomic hierarchy that can effectively reflect diversification dynamics has been

reinforced (Maruvka *et al.*, 2013; Humphreys & Barraclough, 2014). Moreover, it has been shown for mammals and molluscs (including terrestrial gastropods) that morphologically defined genera are, for the most part, congruent with molecular phylogenies (Jablonski & Finarelli, 2009; but see their discussion of non-marine bivalves and also Smith & O'Meara, 2009). Jablonski & Finarelli (2009) also demonstrated that morphologically defined genera showed a strong correlation of body size and latitudinal range with genera defined on the basis of phylogeny. This implies that, although morphologically defined genera may not perfectly reflect phylogenies, their use in large-scale analyses of diversity is unlikely to be misleading. Maruvka *et al.* (2013) also discussed the advantages of morphologically defined genera and families in the study of macroevolutionary dynamics. However, few analytical frameworks have been developed to explicitly assess whether or not genera (and other higher taxonomic groupings) represent real biological entities, and these methods rely on resolved phylogenetic trees with dense sampling of species (Humphreys & Barraclough, 2014). Such trees were not available for our taxa.

The current family and super-family level taxonomy of land snails is closely supported by the most comprehensive molecular phylogenetic analysis available (Wade *et al.*, 2006). The same stands for one of the major groups of land snails, Helicoidea, at the subfamily level (Steinke *et al.*, 2004), despite many incongruences between morphological and molecular classifications at the species level (Hirano *et al.*, 2014; Köhler & Criscione, 2015). Accordingly, the observed correlation between morphological diversity (shell height and width) and generic richness, not documented before, was somewhat expected. However, most taxa are assigned to species based on more subtle features (e.g. shell aperture shape, microsculpture and apertural lamellae, reproductive system structure and dimensions, radular characters) that are not easily captured by shell size measurements (e.g. Yanes *et al.*, 2011; Martins *et al.*, 2013). Concordantly, the results of the random forest analysis indicate that assignment of species to the correct genus (according to current classification) solely based on shell height and width was low, suggesting a weak to moderate dependence between the morphological measurements used and taxonomy (see Appendix S3, Table S3.7). Furthermore, the possible inconsistencies among taxonomists working across these widely scattered archipelagos, along with the varying degrees of completeness of knowledge of the faunas (e.g. Cowie, 1995, 1996), add to the underlying stochasticity and thus provide further support that our findings appear to be ecologically meaningful and that generic richness is the main driver of morphological diversity. Rarefaction analyses (Appendices S2, S3, Table S3.4) also showed that MS and MMD did not exhibit significant relationships with any of the abiotic variables (the single statistically significant relationship, between MS and archipelago mean island area (Table 3), was probably due to its dependence on species richness). These results point to an absence of extrinsic ecological constraints controlling morphological diversity at an archipelago scale, at least regarding the biogeographic/climatic variables analysed.

The prevalence of genus and family diversity correlating with morphological variation within archipelagos (τ_{ST} analyses, Fig. 3) suggests conservatism in the morphological form of land snail species reflecting intrinsic constraints. Shell size and shape of terrestrial gastropods may have been selected over evolutionary time mainly by the mechanics of shell balance for locomotion (Cain & Cowie, 1978; Okajima & Chiba, 2011), channelling gastropod evolution towards a restricted set of architectural attractors. For example, shells with height and width approximately equal are not well balanced, and presumably this is why snails with such shells are rare (Cain, 1977; Okajima & Chiba, 2011), Furthermore, terrestrial, marine and freshwater species tend to occupy optimal regions of the morphospace, allowing the animals to achieve both stable postures and sufficient space for the soft body within the shell (Noshita *et al.*, 2012). Therefore, intrinsic limitations to morphological transitions, as well as to morphospace occupation, impose constraints on morphological diversification; species in particular genera/families are generally unable to diversify into morphospace beyond the bounds of their lineage (e.g. Wagner, 2010; but see Cowie, 1995). Hughes *et al.* (2013) analysed 98 metazoan clades radiating throughout the Phanerozoic and verified that clades reach their maximum morphological diversity relatively early in their evolutionary history. Although this pattern is consistent with both the intrinsic and extrinsic limits hypotheses, it implies constraints on the range of forms within a clade and that the limits are most commonly reached early in its life. Thus, for morphological diversity to increase in a region, new clades must be added.

Conversely to morphological diversity, the significant relationship between species richness and archipelago mean island area suggests the predominance of available ecological space in determining the packing of colonizing and diversifying species (Ricklefs, 2004; Triantis *et al.*, 2015). Area, to a large degree, captures multiple variables that together determine the available ecological space, encompassing both abiotic and biotic environmental conditions (Triantis *et al.*, 2012, 2015). Therefore, our results point towards the classic hypotheses that partitioning of the overall resource space constrains coexistence and that species richness consequently reflects the variety of available resources. Thus, for land snail faunas of oceanic archipelagos, taxonomic richness at the species level is mainly constrained by extrinsic, niche-based limits.

Intrinsic constraints can lead morphological diversity to reach an asymptote before species richness. Species richness can, however, continue to accumulate by speciation and/or colonization in response to continued expansion into new niche space or by a finer partitioning of available niche space, ultimately increasing the density of morphospace occupation (Foote, 1993, 1997; Roy *et al.*, 2004; Jablonski, 2007; see Appendix S3, Fig. S3.2). The Mascarene and Hawaiian archipelagos illustrate this pattern, with similar genus richness (46 and 44 genera, respectively) and accord-

ingly both having almost the same MS size (MS of the Mascarene islands is only 10% smaller than that of the Hawaiian islands). However, the Mascarenes host only 162 indigenous species while the Hawaiian Islands have > 750 (> 4 times more), which matches the difference in total area (4481 and 16,570 km^2 respectively). Similarly, the Canaries and Comoros have the same number of genera (30) and similar MS size (MS of Comoros is 5% smaller than that of Canaries), but the Canaries have more than twice as many species (226 and 102 respectively), being ~3.5 times larger (7496 and 2097 km^2 respectively).

Interpreting the decoupling between morphological diversity and species richness of these faunas, a pattern commonly reported in palaeontological studies (e.g. Foote, 1993; Ruta *et al.*, 2013) nonetheless remains challenging. Besides the niche-based and diversification-based limit hypotheses considered herein, it is possible that the shell measurements used in our study might not adequately characterize species niches. Concerning resource preferences, additional shell dimensions such as aperture shape and size (Chiba & Davison, 2007) might show a different pattern. Furthermore, partitioning of resources among species and individuals could also be reflected in niche axes unrelated to shell morphology, such as gut physiology (Charrier & Brune, 2003). However, lacking more complete measures of ecological niche, such issues cannot be further explored.

Our results provide support for the idea of species richness being determined by extrinsic, niche-based limits and morphological diversity by intrinsic, diversification-based limits. Furthermore, the high proportions of variation in species richness and morphological diversity explained by area and the number of genera, respectively, indicate that the faunas of these archipelagos have converged independently on the same relationships, supporting the idea that the patterns documented herein are rooted in fundamental limits to the processes establishing diversity (Ricklefs, 2004; Triantis *et al.*, 2015). In conclusion, holistic approaches to the study of diversity, especially at coarse temporal and spatial scales, are required for neontological as well as palaeontological studies, as considering taxonomic and morphological diversity independently may result in missing important patterns (Hughes *et al.*, 2013; Rabosky, 2013; Ruta *et al.*, 2013). In this context, oceanic archipelagos provide excellent opportunities for synthetic analyses in biogeography, macroecology and macroevolution.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

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

Appendix S1 List of data sources, biogeographic and climatic variables and geographical location of the archipelagos.
Appendix S2 Supplementary methods.
Appendix S3 Supplementary results.

DATA ACCESSIBILITY

The full species list with the archipelagic distribution of each species is available at Harvard Dataverse, http://dx.doi.org/10.7910/DVN/LOJT2Y.

BIOSKETCHES

Kostas Triantis has a long-term fascination with the biogeography of islands and also works on conservation and functional biogeography. He is currently working on diversity patterns of oceanic archipelagos.

François Rigal is an assistant professor at Université de Pau et des Pays de l'Adour. His research interests include island biogeography, macroecology and functional ecology.

All the authors are interested in understanding the processes that shape terrestrial snail biodiversity through a range of approaches, including molecular biology, palaeontology, phylogeography, taxonomy, population and community ecology and biogeography.

Author contributions: K.A.T., F.R. and R.H.C. designed the research; K.A.T., F.R., C.E.P., R.A.D.C., B.L., A.P., N.W.Y., M.R.A., M.I., A.M.F.M., D.N.F.T., O.L.G., Y.Y., K.A.H., R.C.P. and R.H.C. performed the research; F.R., B.L., A.P. and K.A.T. analysed the data; and K.A.T., F.R. and R.H.C. led the writing, with significant input from the rest of the authors.

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