

ARTICLE

A global analysis of land snail diversity on islands

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Abstract

Explaining spatiotemporal disparities in island species-richness (ISR) is a fundamental pursuit in (macro)ecology and biogeography. While most research has focused on vertebrates and vascular plants, invertebrates—representing ~70% of global species—remain understudied. Using data from 727 islands worldwide, we evaluate the impact of 14 key biogeographic variables, including island area, isolation, climate, energy, environmental heterogeneity, and human presence, on different insular land snail chorotypes: total indigenous richness, archipelagic endemics, including multiple- and single-island endemics, and native non-endemics. We find that these variables jointly explain 80%–84% of inter-island variation in endemic ISR, substantially enhancing explanatory power beyond what can be attributed to traditional species–area and species–energy relationships. In contrast, native non-endemic ISR, although partially explained by area or energy alone, is predominantly influenced by other unaccounted factors including source-pool effects. Driver significance varies among chorotypes, illustrating the capture of distinct biogeographic processes

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(speciation vs. colonization) per chorotype. Our findings show that factors influencing land snail ISR broadly align with those for vertebrates and plants while revealing significant variation in community assembly processes across chorotypes. Thus, our study provides a step towards a unified theory of diversity, encompassing chorotypes as fundamental ISR components, and invertebrates, which comprise most island animal diversity.

KEYWORDS

biodiversity patterns, endemism, environmental drivers, extinction, Gastropoda, historical contingencies, island biogeography, island macroecology, snail chorotypes

INTRODUCTION

Islands represent hotspots of global biodiversity within a small fraction of Earth's landmass (Whittaker et al., 2023). Globally they vary greatly in size, degree of isolation, climate, environmental characteristics, and species diversity (Weigelt et al., 2013). Explaining variation in species richness among islands has been a central research theme for decades. Yet investigation of the causes of this variation at the global scale—a prerequisite for obtaining a comprehensive overview of the macroecological and macroevolutionary processes involved independent of regional idiosyncrasies (e.g., locally variable evolutionary histories or environmental drivers of species richness)—has become possible only recently, and so far has only considered a few well-studied taxa, particularly birds, mammals, snakes, frogs, and vascular plants (Barreto et al., 2021; Kalmar & Currie, 2006; Kreft et al., 2008; Pyron & Burbrink, 2014; Rebouças et al., 2026). Invertebrates, which constitute approximately 70% of all known species (IUCN, 2022), have been overlooked in global-scale island species richness studies owing to the lack of comprehensive datasets (but see Guénard et al., 2017; Liu et al., 2023). In particular, and despite being the focus of numerous island biogeographic studies, we still lack an understanding of the drivers of variation in land snail richness across islands (see Proios et al., 2021; Whittaker et al., 2023).

The importance of land snails in understanding the mechanisms establishing biodiversity patterns was recognized long ago by Alfred Russel Wallace (1880, p. 77), who noted that “*If we take the whole globe, more species of land-shells are found on the islands than on the continents—a state of things to which no approach is made in any other group of animals...*”. This recognition dates back at least to the correspondence between Darwin and Wallace, with Darwin remarking that “*Land-Molluscs are a great perplexity to me*” (Holland, 2009). Insular land snails possess features that make them both tractable and fascinating for inferring processes determining broad scale island

diversity patterns, as they (1) are numerous—with >10,000 known species (Proios et al., 2021), (2) exhibit extraordinary levels of island endemism—for example, 99% in the Hawaiian and 92% in the Galápagos Islands (see Triantis et al., 2015), (3) are distributed across a variety of island types (e.g., land bridge vs. oceanic) and terrestrial ecosystems—from coastal sand dunes through to alpine moraines (Cameron, 2016), and (4) leave shell deposits of past presence that allow the reconstruction of the histories of different lineages and the quantification of natural and anthropogenic impacts on biodiversity. However, to date, most land snail island biogeography studies have been limited in geographical scope and have focused on patterns across single island groups (e.g., Astor et al., 2014; Cameron et al., 2007; Cook et al., 1972; Cowie, 1995, 1996; Peake, 1971; Waldén, 1984).

The few studies that have broadened their focus across multiple island groups have also revealed contrasting diversity patterns across different distributional groups (e.g., Cameron et al., 2013; Norder et al., 2019; Triantis et al., 2015, 2016), that is, chorotypes [i.e., single-island endemic vs. single-archipelagic endemic vs. native non-endemic vs. total indigenous (i.e., all native species) richness]. Examining chorotype-specific diversity patterns can provide evidence of how temporal effects—whether short-term ecological or long-term evolutionary legacies—may have left different imprints on currently observed species richness (Whittaker et al., 2017). For instance, in many taxa, total indigenous species richness can primarily be attributed to recent ecology (e.g., contemporary distance from mainland), whereas the distributions of single-island endemics and their overall richness often capture more historical legacies, such as those related to longer-term geodynamic processes (e.g., shifting neighboring island connectedness or past connection with continents due to sea-level changes; Fernández-Palacios et al., 2016; Norder et al., 2019; Weigelt et al., 2016). While insular land snails have played an important part in the development and evaluation of general island biogeographical models (see Cameron et al., 2013;

Norder et al., 2019; Triantis et al., 2015, 2016), we nonetheless still lack a comprehensive understanding of the mechanisms driving variation in their species richness at a global scale.

Previous global island richness studies of several vertebrate (see Barreto et al., 2021; Kalmar & Currie, 2006; Pyron & Burbrink, 2014; Valente et al., 2020) and vascular plant (Kreft et al., 2008; Weigelt et al., 2016) taxa have provided support for prevalent environment–richness hypotheses (e.g., MacArthur and Wilson’s equilibrium model, species–energy and species–habitat diversity theories; see Box 1)—typically explaining a large percentage (>65%) of the inter-island variation in species richness. These global analyses provide broad empirical support for theoretical expectations regarding the (1) positive relationships between species richness and island area, energy flow through ecosystems and environmental heterogeneity, and (2) negative relationship between species richness and island isolation (Box 1). Given their distinct ecological features compared to both vertebrates (e.g., smaller body size, shorter generation times, more complex life histories, larger population sizes) and vascular plants (e.g., fewer potential colonists, shorter generation time in most cases), snails (and more broadly, invertebrates) might be expected to respond differently to the dominant drivers of diversity of other taxa, whether in terms of directionality or in effect size and relative importance. Identifying similarities and discrepancies of how species richness of different taxa covary with classic biogeographic variables such as area, isolation, climate, energy, and environmental heterogeneity at broad scales can shed further light on the processes establishing global-scale biodiversity patterns.

Here, we aim to explore the main drivers of insular land snail richness using a newly collated global inventory including 11,139 species from 727 islands (Proios, 2020; Proios et al., 2021). We first produce global models for both total species (i.e., indigenous = IND; all native species, including endemics and non-endemics) and separately for each chorotype (i.e., single-archipelagic endemics = SAE, multiple-island endemics = MIE, single-island endemics = SIE, and native non-endemic richness = NAT), and examine the chorotype-specific responses of insular land snail richness to 14 environmental variables, capturing the full range of area, historical and current isolation, environmental heterogeneity, climate, energy, and human-presence effects. On theoretical grounds (Table 1), our main predictions may be grouped as follows. (1) Species richness and endemism of land snails will be positively associated with island area, environmental heterogeneity, favorable climate, and climate-based water-energy balance (Field et al., 2009; Hawkins et al., 2003; MacArthur & Wilson, 1963, 1967; O’Brien, 1998; Stein et al., 2014), with the effect of each

driver varying across chorotypes, reflecting the distinct biogeographical processes leading to chorotype-specific richness patterns. Specifically for area, we predict that its effect on richness should become stronger as we move from non-endemic to endemic land snail chorotypes (Triantis et al., 2015; Whittaker et al., 2017). (2) Isolation from mainland (current and past) should have negative effects on indigenous land snail species richness but positive effects on the number of endemic species (Fernández-Palacios et al., 2016; Norder et al., 2019), while past intra-archipelagic island connectedness is anticipated to facilitate the spread of MIE (positive effect on MIE richness) but reduce the richness of single-island endemics (negative effect). (3) Human impact (e.g., population density and road presence) is predicted to have negative effects on the species richness of all chorotypes except for native non-endemics, whose distribution is likely positively affected by cryptic human-assisted translocations (Capinha et al., 2015; see Appendix S1: Section S1.1 for further elaboration). (4) Simultaneously accounting for all 14 potential predictors of species richness and endemism will capture nuanced environmental differences among islands, thereby providing substantially greater explanatory power compared to two alternative explanations of ISR (see Whittaker et al., 2023; their Box 5.5): island area, which emphasizes resource availability, and the so-called species–energy hypothesis (Wright, 1983), which focuses on carrying capacity, alone (see Box 1). Finally, we discuss the results of our global models for land snails in the context of previous analyses of island birds, frogs, mammals, snakes, and plants and examine the extent to which snails adhere to island biogeographic trends established for other taxa.

METHODS

Species richness data

We used species richness data from a newly collated database that contains the occurrences of 11,139 indigenous (i.e., non-exotic) land snail species across 727 islands worldwide, spanning 11 biogeographic realms (Proios, 2020; Proios et al., 2021; see Appendix S1: Section S1.2.1 for further description). We first grouped the 727 islands into 86 archipelagos and then grouped these archipelagos into 40 meta-archipelagos (i.e., multi-archipelagic spatial groups sensu Whittaker et al., 2018) based on spatial proximity and overall biogeographic affinity. Considering the distribution of each species across archipelagos and islands, we categorized species in order of decreasing geographic extent as NAT ($n = 1123$), MIE restricted to a single archipelago

BOX 1 Predicted relationships between environmental drivers and species richness or endemism, based on theory.

Area and isolation: According to MacArthur and Wilson's (1963, 1967) seminal 'Equilibrium Theory of Island Biogeography' (ETIB) species richness of any island depends on the island area- and isolation-mediated rates of immigration, extinction, and speciation. The ETIB stresses that larger islands generally support greater species richness due to their ability to sustain larger populations and lower extinction rates. Later developments of the ETIB posit that larger islands may also be easier to reach—a phenomenon known as the target-area effect (Lomolino, 1990)—and offer greater opportunities for intra-island isolation, which can promote speciation and species richness. More isolated islands, on the other hand, are expected to have lower immigration rates, leading to lower species richness per unit area but higher endemism due to limited gene flow and greater opportunities for cladogenesis.

Theory/Model: Equilibrium theory of island biogeography (MacArthur & Wilson, 1963, 1967).

Expected effect direction: Area: ↑SR, ↑EN and isolation: ↓SR, ↑EN.

Climate: Several climatic factors shape biodiversity patterns and large-scale diversity gradients (Brodie & Mannion, 2023; Willig et al., 2003). Broad-scale regimes are typically described by temperature, precipitation, their seasonality, and composite metrics such as actual evapotranspiration (AET), which integrates thermal and water availability into a water–energy balance per unit area (O'Brien, 1998). Warm, wet tropical conditions maintained over long timescales are associated with higher richness and endemism, largely through reduced extinction and/or elevated speciation rates (Field et al., 2009; Grobler & Cowling, 2022; Ricklefs, 2006). Seasonality in temperature and precipitation can have mixed effects: extreme seasonal shifts may reduce productivity and limit consumer resources, whereas pronounced seasonality can also increase niche diversity and favor species with varied thermal and moisture adaptations.

Theory/Model: Climate-based diversity gradients (Hawkins et al., 2003; O'Brien, 1998; Willig et al., 2003).

Expected effect direction: ↑/↓SR, ↑/↓EN.

Energy: According to the species–energy hypothesis (Wright, 1983), inter-island variation in species richness reflects differences in carrying capacity driven by ecosystem energy flow. Although island area can approximate resource/habitat availability, Wright argued that carrying capacity is better captured by metrics of gross energy input: for plants, Island area × Total actual evapotranspiration (TAET), and for consumers, Island area × Total net primary productivity (TNPP). Hence, temperature on its own is just one physical variable governing the rates of biomass production (Brown, 2014; Clarke & Gaston, 2006; O'Brien, 1998). Following this framework, we use AET × Island area as a “productive energy” metric (sensu Evans et al., 2005) and examine the species–energy relationship independently of other climatic variables.

Theory/Model: Species–energy (Wright, 1983).

Expected effect direction: ↑SR, ↑EN.

Environmental heterogeneity: Intra-island heterogeneity in habitat, vegetation, soil and topography (collectively referred to as environmental heterogeneity; Stein et al., 2014)—which tends to be greater on larger islands—can potentially support a wider range of species through niche partitioning and lead to increased speciation rates through ecological specialization and increased reproductive isolation (Hortal et al., 2009). Thus, a positive relationship of EH with species richness and endemism is to be expected.

Theory/Model: Species–habitat diversity (Hamilton et al., 1963; Williams, 1964).

Expected effect direction: ↑SR, ↑EN.

Human impact: Islands are known to have suffered extensive anthropogenic extinctions, largely disproportionate for their area (Graham et al., 2017; Tershy et al., 2015; Whittaker et al., 2017). These extinctions have been linked with anthropogenic habitat modification, direct exploitation and the spread of invasive species, collectively causing the decline of both species richness and endemism (Graham et al., 2017; Whittaker et al., 2023).

Theory/Model: Global estimates of island species losses (Whittaker et al., 2023).

Expected effect direction: ↓SR, ↓EN.

Note: SR = species richness, EN = endemism. Arrows show the direction of effects: upwards (↑) = positive, downwards (↓) = negative.

TABLE 1 Predicted influence of each individual explanatory variable on land snail species richness across chorotypes, based on theory.

Effect group	Variable	IND	SAE	MIE	SIE	NAT	Theory/model (main references)
A	Island area	+	+	+	+	+	T1 ^b
EH	Elevation	+	+	+	+	+	T2 ^c
	TPI	+	+	+	+	+	T2
	No. of ecoregion types	+	+	+	+	+	T2
I	Current isolation	−	+	+	+	−	T1
	Past connectedness	+	+/−	+	−	+	T3 ^d
	Past connection	+	−	−	−	+	T3
C/E	T_{annual}	+	+	+	+	+	T4 ^e
	$T_{\text{seasonality}}$ ^a	+/−	+/−	+/−	+/−	+/−	T4
	P_{annual}	+	+	+	+	+	T4
	$P_{\text{seasonality}}$ ^a	+/−	+/−	+/−	+/−	+/−	T4
	AET	+	+	+	+	+	T4
HI	Human density	−	−	−	−	+	T5 ^f
	Road presence	−	−	−	−	+	T5

Note: Signs show the direction of effects.

Abbreviations: A, area; AET, actual evapotranspiration; C/E, climate/energy; EH, environmental heterogeneity; HI, human impact; I, isolation; IND, total indigenous; MIE, multiple-island endemics; NAT, native non-endemics; P , precipitation; SAE, single-archipelagic endemics; SIE, single-island endemics; T , temperature; TPI, topographic position index.

^aSee Box 1 for justification.

^bT1: Equilibrium theory of island biogeography (MacArthur & Wilson, 1963, 1967).

^cT2: Species–habitat diversity (Williams, 1964).

^dT3: Glacial sensitive model (Fernández-Palacios et al., 2016).

^eT4: Climate-based diversity gradients (Hawkins et al., 2003; O'Brien, 1998; Willig et al., 2003).

^fT5: Current estimates of human-driven species losses on islands globally (Whittaker et al., 2023).

($n = 1685$), or SIE ($n = 8331$). We then defined single-archipelagic endemic richness (SAE) as the combined richness of the two endemic chorotypes (SAE = MIE + SIE), and indigenous richness (IND) as the total richness across all mutually exclusive categories (IND = SAE + NAT). Across the 727 islands, mean richness values were 30 INDs per island (18 SAEs and 12 NATs), with MIEs, SIEs, and NATs representing an average of 30.7%, 13.6%, and 55.7% of total species per island, respectively (see Appendix S1: Section S2, Figure S1 for detailed view).

Geospatial and environmental data

We extracted geospatial data for all 727 islands from the Global Island Database (UNEP-WCMC, 2015) and, where needed, updated the data with the Global Shoreline Vector dataset (Sayre et al., 2019). Using Google Earth, we digitized small islets that had available occurrence data but were not contained in either source and added them to the dataset manually. The 727 islands span a broad range of geological settings, including oceanic islands ($n = 262$), continental-shelf islands ($n = 376$),

and islands associated with ancient continental-fragment regions ($n = 89$), following the broad terminology of Matthews and Triantis (2021). We note that this classification is used here as a simplified operational grouping to describe the geological setting of the sampled islands, rather than as a definitive island-by-island geological diagnosis.

We considered 14 environmental variables as potential determinants of observed richness patterns, with each falling into one of the following five categories. (1) Island area. (2) Environmental heterogeneity: elevation, topographic position index (TPI) and number of ecoregion types. (3) Isolation: current distance to mainland, past mainland connection (i.e., whether an island used to be connected to the nearest mainland), and past inter-island connectedness (i.e., a numerical predictor quantifying the number of present-day islands that used to be united in a single island). The sea level that we used for the latter two metrics was 65 m m.s.l., which represents the median—that is, most persistent—sea level across the last ~800 kyr and has been shown to have the stronger imprint on land snail endemic richness of oceanic islands relative to other depth values (Norder et al., 2019). (4) Climate:

mean annual temperature, temperature seasonality, annual precipitation, precipitation seasonality, and actual evapotranspiration (AET). AET is a measure of water-balance over the year, and can, within limits, be used as a proxy for energy flow or net primary productivity (see Field et al., 2009; Hawkins et al., 2003; O'Brien, 1998). (5) Human impact: human population density and road presence (see Appendix S1: Section S1.2.2 for details of variable extraction procedures, Section S1.2.3 for potential data limitations, and Section S2: Figure S2 and Section S3: Tables S1 and S2 for a description of each variable). These variables collectively capture the principal climatic, topographic, and historical dimensions of island environments, representing the putative major axes of environmental space relevant to patterns of species richness (see Appendix S1: Section S2, Figures S2–S4). The predicted relationships for each of the 14 variables are given in Table 1. Latitude was evaluated as an additional predictor of species richness by including both linear and quadratic terms (i.e., a second-degree polynomial). This allowed us to test for a single nonlinear latitudinal richness pattern consistent with the global latitudinal diversity gradient, including the possibility that richness peaks near, but not necessarily exactly at, the equator (Brodie & Mannion, 2023). Although island age has been shown to be an important determinant of island diversity patterns in various taxa (including snails) at the within-archipelago scale (Borregaard et al., 2017; Cameron et al., 2013; Whittaker et al., 2008), we did not include this variable in our analyses as the inclusion of land-bridge islands alongside oceanic islands makes ages non-comparable, and in any case, we do not have ages for all islands in our dataset. We extracted environmental data for each island from publicly available sources (Appendix S1: Section S3, Table S1) and processed them in ArcMap 10.7 (ESRI, 2019) and the R statistical programming environment (R Core Team, 2019).

Statistical analysis

We $\log_{10}$ transformed all continuous explanatory variables and subsequently standardized them to a mean of zero and unity (SD; i.e., $(x - \bar{x})/SD$), which allowed direct comparison of the magnitude of model coefficients (Schielzeth, 2010). We then checked for multicollinearity using non-parametric Kendall's tau coefficients of correlation, a preferred method when variables are non-normally distributed (Puth et al., 2015). Collinearity was below 0.7 in all pairwise relationships except for latitude and mean annual temperature (Kendall's tau $|r_{\tau}| = 0.73$; Appendix S1: Section S2, Figure S5). Latitude also showed considerable associations with temperature seasonality and AET ($|r_{\tau}| > 0.5$), overall indicating that it largely

reflects broad-scale climatic gradients already captured by the climate-specific drivers (Appendix S1: Section S2, Figures S3–S5). Thus, to maintain a mechanistic interpretation of environmental drivers ($|r_{\tau}| < 0.7$; see Dormann et al., 2013), latitude was not retained in the main models presented below. However, we explicitly tested its inclusion and verified that it did not effectively alter the magnitude or significance of other predictors (Appendix S1: Section S2, Figures S6 and S7).

We first tested whether the effect of each variable differs among land snail chorotypes. For this, we built a generalized linear mixed-effects model (GLMM), with the species richness of all chorotypes as a single response variable (i.e., a variable with $727 \text{ islands} \times 5 \text{ chorotypes} = 3635$ richness observations) and the 14 environmental variables along with chorotype identity fitted as fixed effects. To test whether the effects of the different predictors differ among chorotypes we allowed for interactions between chorotype identity (i.e., IND, SAE, MIE, SIE, and NAT) and each fixed effect. Archipelago/meta-archipelago identities were included as nested random-intercept effects to account for spatial pseudo-replication (*sensu* Bunnefeld & Phillimore, 2012). Overdispersion was accounted for through the inclusion of an observation-level random effect (OLRE). The GLMM was fitted with the 'glmer' function of the 'lme4' R package (Bates et al., 2015), using a log-link Poisson error structure. We calculated the difference in standardized beta coefficients (β) and associated *p*-values for each environmental variable across all chorotype pairwise comparisons using the function "emtrends" in the "emmeans" R package (Lenth et al., 2020). With five chorotypes, this resulted in 10 pairwise contrasts and, when evaluated across 14 environmental variables, a total of 140 pairwise comparisons, with *p*-values adjusted for multiple comparisons using a Tukey correction. It is important to note that two out of the five analyzed chorotypes overlap (e.g., SIEs and MIEs are included in SAEs; all species are included in INDs), meaning that there is some non-independence in chorotype richness in the full model. This nested structure is informative, as it allows us to identify how environmental drivers differentially influence broad-scale island richness and its constituent components.

Given that each chorotype responded differently to the 14 environmental variables (see Appendix S1: Section S1.3 and Section S3, Table S3), we then fitted five separate GLMMs, one for each chorotype (IND, SAE, MIE, SIE, and NAT), using the same model structure as above (i.e., 14 variables as fixed effects and archipelago/meta-archipelago identities as nested random effects).

In all GLMMs, we evaluated the spatial autocorrelation of model residuals by estimating Moran's I coefficient

using functions in the ‘ape’ R package (Paradis & Schliep, 2019). To further determine the extent of spatial autocorrelation and assess the sensitivity of the results to its effects, we also applied spatial mixed-effects models using the same model structure as above, whilst further incorporating a random spatial component based on the centroid longitude and latitude coordinates of each island (i.e., long-lat Matérn; see Appendix S1: Section S1.2.4). The results of this approach were highly congruent with the non-spatial GLMMs (Appendix S1: Section S2, Figure S8), revealing only small amounts of spatial autocorrelation (i.e., both Moran’s I and Matérn were below 0.10; Appendix S1: Section S2, Figure S9 and Section S3: Table S4), and therefore we do not consider them further.

To assess the relative importance of unaccounted factors specific to archipelagos and/or meta-archipelagos (i.e., random effects) and the selected environmental variables (fixed effects) on species richness patterns (see Bunnefeld & Phillimore, 2012), we computed conditional (fixed and random) and marginal (fixed-only) pseudo- R^2 values using the ‘r.squaredGLMM’ function from the ‘MuMIn’ R package (Barton, 2020), which incorporates adjustments for OLREs in GLMMs (i.e., `pj2014 = TRUE` argument; see Johnson, 2014). To get a measure of the directional response of species richness to each group of variables included in the fixed effects (i.e., area, environmental heterogeneity, isolation, climate, human impact), we summed the beta coefficients (β) of each individual environmental variable per effect group (e.g., environmental heterogeneity = $\beta_{\text{Elevation}} + \beta_{\text{TPI}} + \beta_{\text{No. of ecoregions}}$). We evaluated the significance of these composite contrasts using general linear hypothesis tests (GLHT), which estimate the combined effect and its uncertainty while accounting for covariance among coefficients (package `multcomp`; Hothorn et al., 2008). For isolation, we distinguished mainland, intra-archipelagic, and total isolation, to separately represent immigration limitation from the mainland ($\beta_{\text{Current isolation}} - \beta_{\text{Past connection}}$), dispersal within archipelagos ($\beta_{\text{Past connectedness alone}}$), and the overall biogeographic isolation ($\beta_{\text{Current isolation}} - \beta_{\text{Past connectedness}} - \beta_{\text{Past connection}}$) shaping species richness.

We evaluated the predictive power of chorotype-specific GLMMs (i.e., separately for the five chorotypes) by (1) calculating the goodness of fit as the ratio of predicted/observed richness (using the ‘predict’ R function) and (2) using a k -fold cross-validation approach. For the latter, we randomly put aside $k\%$ of the dataset as the test data and fitted the model to the remaining $100-k\%$ components (the training data). We subsequently used the resultant coefficients to predict the values of the species richness in the test data. The predictive power of the models was evaluated based on the Pearson’s correlation calculated

between the predicted and the observed richness values. This k -fold cross-validation process was then repeated 100 times and the mean correlation and its associated 95% CI value were taken. These analyses were undertaken separately for the five chorotypes IND, SAE, MIE, SIE, and NAT, and were implemented with $k = 10\%$, 25% , 50% , 75% , and 90% . Note that during the implementation of the analyses, k was adjusted during each run to avoid cutting an archipelago into training and test data but rather to assign the entire archipelago into either the training or the test data sets.

As a further step in the analysis, we compared the explanatory power of the five chorotype-specific GLMMs with the classical species–area and species–energy relationships. For this step, we modeled the species richness of each chorotype as a function solely of either island area or total available energy per island, respectively, using the same model structure as above (i.e., archipelago/meta-archipelago identities as nested random effects). We calculated the total available energy per island by multiplying island area with AET (sensu Wright, 1983). It is also worth noting that in the original test of the species–energy hypothesis, Wright (1983) used net primary productivity (NPP) in modeling richness for consumers (birds). However, because more direct estimates of NPP data were not available for all islands in this study, we used AET, which is often used as a proxy for NPP in similar correlative studies (Field et al., 2009; Luck et al., 2010). We compared the fit of the ‘full’ 14 variables model with the species–area and species–energy relationships using the Akaike’s information criterion (AIC) and the marginal pseudo- R^2 values.

RESULTS

Multi-chorotype analysis

Our GLMM including all chorotypes and allowing for an interaction between chorotype identity and each fixed effect showed that the predictor variable effect sizes and significance varied across chorotypes (Appendix S1: Section S3, Table S3). Notably, most pairwise chorotype comparisons (101/140) exhibited significant differences, substantiating insights drawn by the following separate (per-chorotype) analyses.

Chorotype-specific trends

We report these findings according to the four sets of predictions outlined at the end of the *Introduction*.

Prediction (1): Driver significance

Larger island area, greater environmental heterogeneity, and favorable climatic/energy conditions (i.e., warmer and wetter) had positive effects on richness for all

chorotypes (Figure 1), with island area ranking first among explanatory variables (i.e., having the largest absolute standardized β value) in all chorotypes except MIEs (see Appendix S1: Section S3, Table S4, and descriptions below). Specifically, the effect of area varied among

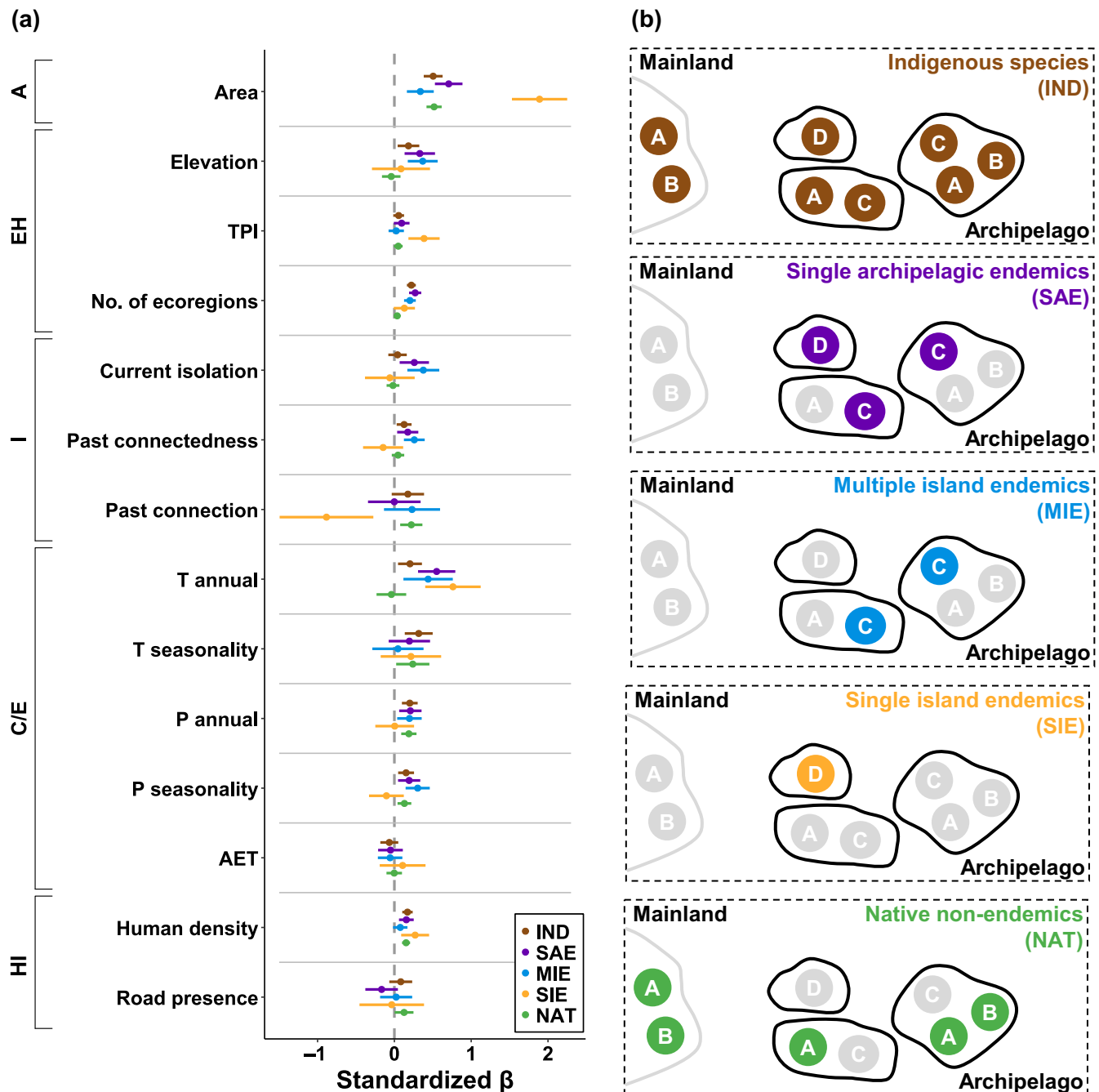


FIGURE 1 Environmental drivers of insular land snail species richness across chorotypes. (a) Standardized beta coefficients (β) of the fixed effects of generalized linear mixed-effects models (GLMMs) for each chorotype. Colors denote distinct models, one per chorotype. Dots indicate estimated β and error bars represent 95% CIs. See Appendix S1: Table S4 for values of standardized β and their SE. A, area; AET, actual evapotranspiration; C/E, climate/energy; EH, environmental heterogeneity; HI, human impact; IND, indigenous; MIE, multiple-island endemics; NAT, native non-endemics; SAE, single-archipelagic endemics; SIE, single-island endemics; TPI, topographic position index. (b) Conceptual figure illustrating chorotypes. Each letter denotes a species (A–D), circles mark its location, and the color highlights the definition of the chorotype.

the mutually exclusive chorotypes (MIE, SIE, NAT), being strongest for the most range-restricted group, SIE ($\beta = 1.89 \pm 0.18$ SE), markedly weaker for MIE ($\beta = 0.34 \pm 0.09$ SE), and intermediate for NAT ($\beta = 0.52 \pm 0.05$ SE). When considering composite groups, single-archipelagic endemics (SAE = SIE + MIE) were more strongly influenced by area ($\beta = 0.71 \pm 0.09$ SE), reflecting the dominant contribution of SIE, while indigenous richness (IND = NAT + SAE) showed intermediate effects consistent with contributions from both SAE and NAT ($\beta = 0.50 \pm 0.06$ SE). Area effects differed significantly among all chorotype pairs except IND–NAT and IND–MIE (Appendix S1: Section S3, Table S3). Partly consistent with our prediction that area effects should strengthen from non-endemic to endemic chorotypes, non-standardized area slopes (z), which capture the classic log–log species–area relationship, generally increased with endemism level (Appendix S1: Section S2, Figure S10 and Section S3, Table S5), rising from NATs and INDs ($z = 0.13$) to SAEs ($z = 0.18$) and peaking in SIEs ($z = 0.49$). However, MIEs deviated from this pattern, exhibiting the weakest slope ($z = 0.09$), despite being an endemic group. In particular, for MIEs, area ranked fourth ($\beta = 0.34 \pm 0.09$ SE), after annual temperature ($\beta = 0.44 \pm 0.16$ SE), current isolation ($\beta = 0.38 \pm 0.11$ SE), and elevation ($\beta = 0.37 \pm 0.10$ SE; Appendix S1: Section S3, Table S4).

The next most important predictors after island area were a measure of climate for INDs, SAEs, and NATs [$T_{\text{seasonality}}$ (positive effect, +ve) for INDs and NATs and T_{annual} (+ve) for SAEs], and isolation for SIEs [i.e., Past connection (negative effect, –ve); Appendix S1: Section S3, Table S4]. The effects of climate (i.e., T_{annual} , $T_{\text{seasonality}}$, P_{annual} and $P_{\text{seasonality}}$) on species richness varied among chorotypes (Figure 1 and Appendix S1: Section S3, Table S3). Of particular interest is that the effect of T_{annual} diminished greatly from SIEs (0.76 ± 0.18 SE) to MIEs (0.44 ± 0.16 SE) and again to NATs (-0.04 ± 0.10 SE), in the latter case becoming non-significant (Appendix S1: Section S3, Table S4). These varied effects were averaged out when either all endemic or all indigenous species were simultaneously considered in the SAE (0.55 ± 0.12 SE) and IND models (0.20 ± 0.08 SE), respectively. Notably, actual evapotranspiration (AET), often used as a proxy for energy flow, but reliably an indication of water balance, had no significant effect in any of these models (Figure 1 and Appendix S1: Section S3, Table S4).

Environmental heterogeneity variables were significant predictors of species richness for all chorotypes. Specifically, the number of ecoregion types present on an island and maximum elevation were the third strongest

predictors of INDs (0.22 ± 0.03 SE for the former), SAEs, and MIEs (0.33 ± 0.10 SE and 0.37 ± 0.10 SE for the latter), while topographic heterogeneity (TPI) had a significant positive effect only on SIEs, but no effect on INDs, SAEs, MIEs, and NATs (+ve for all; Appendix S1: Section S3, Table S4).

Combining the effects of different variables across five effect groups (i.e., area, environmental heterogeneity, isolation, climate and human impacts) showed that within the fixed effects, the relative contribution of each effect group as predictors of land snail diversity differed between chorotypes, consistent with our hypothesis that the influence exerted by each driver should vary substantially per chorotype (Figures 2a and 3a). This was particularly evident for isolation, where both total ($\beta_{\text{Current isolation}} - \beta_{\text{Past connectedness}} - \beta_{\text{Past connection}}$) and mainland ($\beta_{\text{Current isolation}} - \beta_{\text{Past connection}}$) isolation were negative for INDs and NATs, but positive for all endemic chorotypes (SAE, MIE, and SIE) (Figure 3a).

Prediction (2): Isolation effects

The effect sizes of standardized β for the three isolation metrics followed contrasting patterns across chorotypes. For IND and NAT, the effect sizes increased (became more positive) from current isolation to past inter-island connectedness to past mainland connection. In contrast, for SAE, MIE, and SIE the effect sizes decreased (became more negative) across the same metrics (Figure 1). Current isolation was significant (+) in the case of MIEs and, by extension, also influenced (+) SAEs. Past mainland connection was significant only in the SIE and NAT models, but the effect was positive for NATs (0.22 ± 0.07) and negative for SIEs (-0.88 ± 0.31) (Figure 1 and Appendix S1: Section S3, Table S4). Conversely, past inter-island connectedness had a significant positive effect on INDs, SAEs, and MIEs, but no effect on SIEs and NATs.

Prediction (3): Human effects

Regarding the variables associated with human impacts, the unexpected positive effect of human population density across IND, SAE, and SIE chorotypes (instead of only NATs) was significantly stronger for SIEs and NATs (Appendix S1: Section S3, Tables S3 and S4). Road presence had a significant positive effect only on NATs (0.13 ± 0.31), while its effect for SAEs, MIEs, and SIEs was small and nonsignificant (Appendix S1: Section S3, Table S4).

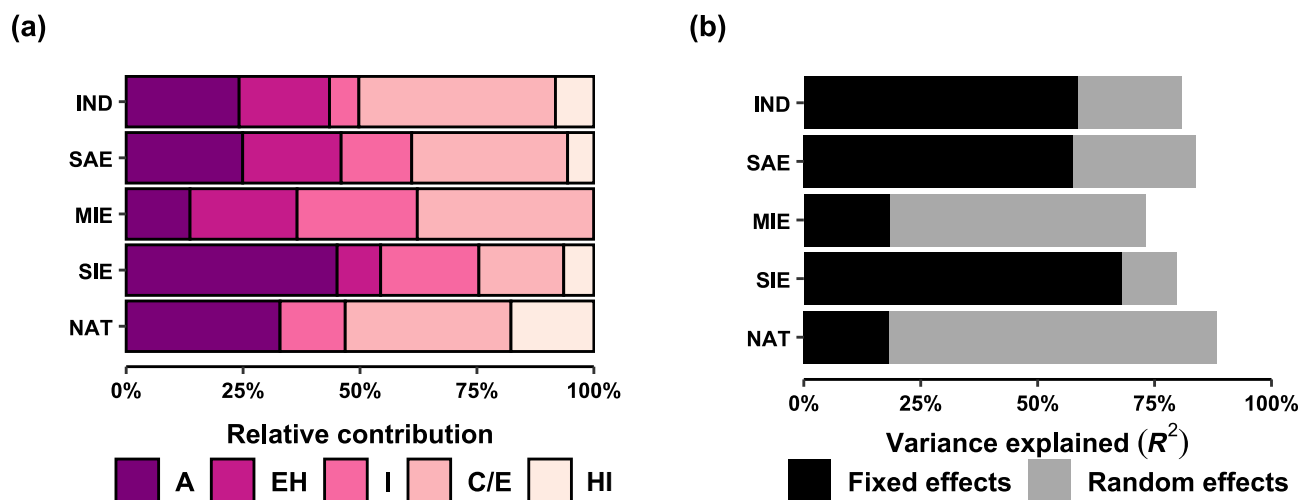


FIGURE 2 Relative importance of drivers and model performance across chorotypes. (a) Relative contribution of each effect group (fixed effects only) as predictors of land snail chorotype richness (see Appendix S1: Section S1.3 for further details). (b) Decomposition of the variance explained by the generalized linear mixed-effects models (GLMMs) ($R^2_{\text{conditional}}$) into its components assigned to the fixed (R^2_{marginal}) and random effects ($R^2_{\text{conditional}} - R^2_{\text{marginal}}$) with land snail chorotype richness as response variables. A, area; C/E, climate/energy; EH, environmental heterogeneity; HI, human impact; I, isolation; IND, indigenous; MIE, multiple-island endemics; NAT, native non-endemics; SAE, single-archipelagic endemics; SIE, single-island endemics. See Table 2 or Figure 1 for the variables considered within each effect group.

Prediction (4): Model performance and comparison with simpler models

In our ‘full’ 14 variables model, the predictors explained a very high proportion—between 80% and 88% depending on chorotype—of the variation in insular land snail species richness [Figure 2b; $R^2_{\text{conditional}}$ values (all factors, including the random effect) in Appendix S1: Section S3, Table S4]. There was an excellent correspondence between observed and predicted species richness in all cases (mean predicted/observed values were close to 1; Figure 4 for IND and Appendix S1: Section S2, Figure S11 for SAE, MIE, SIE, and NAT). Outputs of the k -fold cross validation showed that, for three of the k values tested (10%, 25%, 50%), the average correlation between the observed and the predicted richness was ≥ 0.67 in all chorotypes, and only started to decline drastically for k values $\geq 75\%$, with average correlations across chorotypes of 0.56 at $k = 75\%$ and 0.38 at $k = 90\%$ (overall mean across these two high- k scenarios = 0.47; Appendix S1: Section S3, Table S6).

The contribution of random and fixed effects varied substantially between chorotypes (Figure 2b). The 14 fixed effects captured much more variation than the random effects in the case of single-island endemic richness (SIE; $R^2_{\text{marginal}} = 0.68$, fixed factors only), followed by SAE and IND richness ($R^2_{\text{marginal}} = 0.58$ and 0.59, respectively), but they explained only small amounts of variation for MIE and NAT species richness ($R^2_{\text{marginal}} = 0.27$ and 0.18, respectively). For MIEs, most variance was explained by the random effects ($R^2_{\text{random}} = 0.54$), with

the archipelagic component capturing substantially more variation than in any other chorotype, while the meta-archipelagic component was negligible, as in IND, SAE, and SIE. For NAT, random effects also dominated the explained variance ($R^2_{\text{random}} = 0.70$), but in this case the variance attributed to the meta-archipelago was considerably higher than that of archipelago (Appendix S1: Section S3, Table S4). For INDs, SAEs, and SIEs, random effects accounted for little variance (R^2_{random} spanning from 0.12 to 0.26) and the meta-archipelago term was nonsignificant (likelihood ratio test: $\chi^2_1 < 1.54$, $p > 0.21$; Appendix S1: Section S3, Table S4).

Our ‘full’ 14 variables model consistently outperformed the single-variable species–area and species–energy models: they showed higher marginal pseudo- R^2 values, indicating greater explanatory power of the fixed effects, and lower AIC values, indicating that the improvement in fit outweighed the penalty for additional predictors (Table 2). Specifically, for the total indigenous (IND) and endemic chorotypes (SAE, MIE, and SIE), the full model performed substantially better than the energy-alone model, which in turn performed slightly better than the area-alone model. These differences were substantial, with $\Delta\text{AIC} > 30$ and $\Delta R^2_{\text{marginal}} > 0.12$ across chorotypes (Table 2). For native non-endemic richness (NAT), the ΔAIC indicated a notably higher explanatory power of the ‘full’ model ($\Delta\text{AIC} > 70$), but the differences in R^2_{marginal} were smaller. Here, the ‘full’ 14 variables model performed only slightly better than the energy model ($\Delta R^2_{\text{marginal}} = 0.03$), which itself marginally outperformed the area model ($\Delta R^2_{\text{marginal}} = 0.04$).

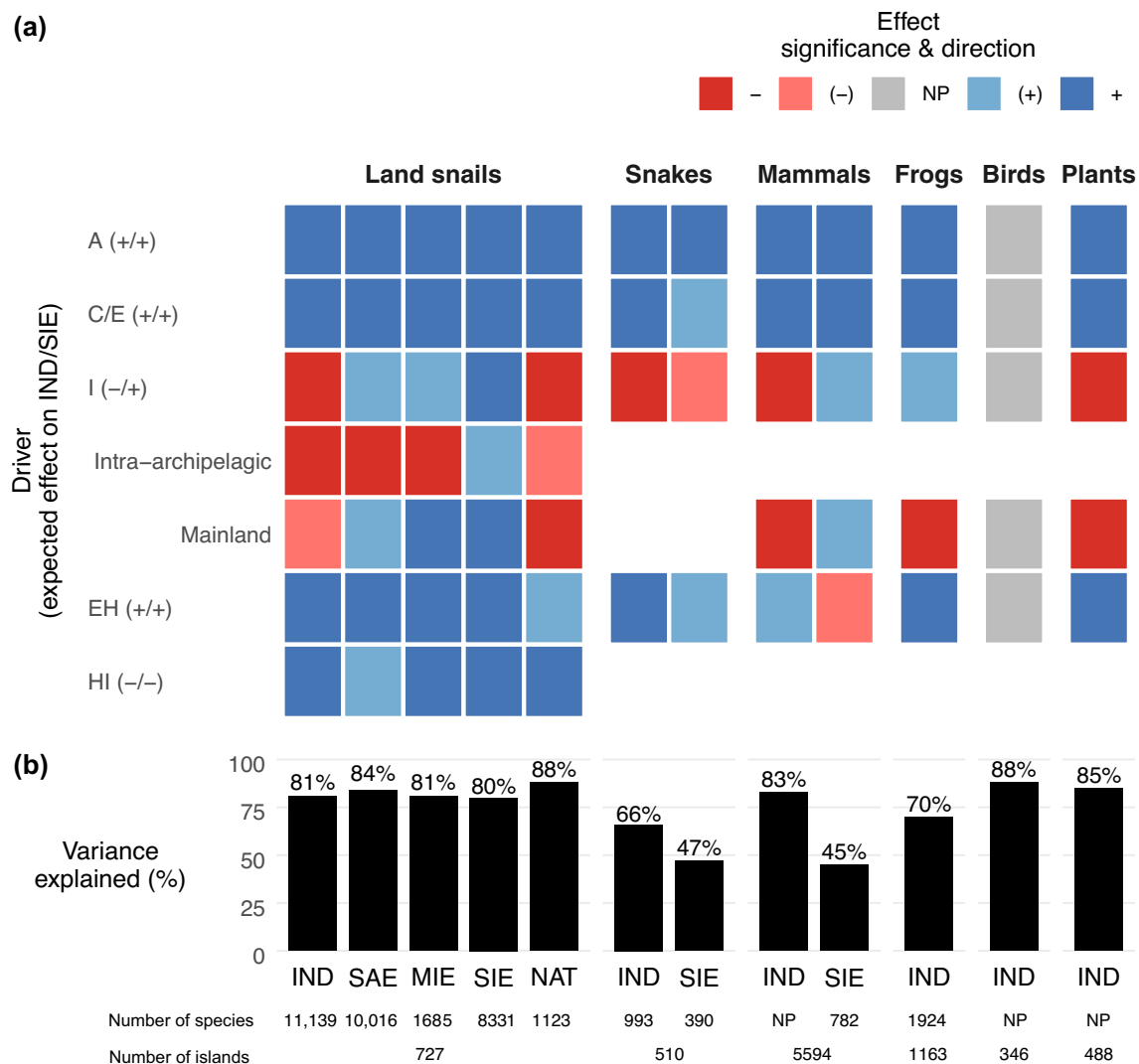


FIGURE 3 Effects of environmental drivers on insular species richness across six taxa and major chorotypes. (a) Documented effects are based on standardized β coefficients. Color indicates effect direction, and color saturation indicates statistical support. Saturated cells represent significant effects (based on contrast analyses), whereas paler cells indicate nonsignificant trends ($p \geq 0.05$; see [Methods](#) for their calculation). Empty (white) cells indicate drivers that were not tested for the corresponding taxon or chorotype. Data for taxa besides snails were derived from Kalmar and Currie (2006), Kreft et al. (2008), Pyron and Burbrink (2014), Barreto et al. (2021) and Rebouças et al. (2026); for frogs, effects shown here were derived from the species richness component of the structural equation models presented by Rebouças et al. (2026). We note that while overall isolation can be compared across taxa, separating intra-archipelagic and mainland components is not always possible due to differing isolation metrics. For snakes, isolation was measured using a composite index (“sum of the square root of distance to the nearest continent”; Pyron & Burbrink, 2014), which is not applicable here. For mammals and frogs, mainland connectivity during the Last Glacial Maximum (binary GMMC variable) aligns with our framework, whereas the alternative landmass-buffer metric does not distinguish intra-archipelagic from mainland isolation. For birds and vascular plants, isolation was quantified solely as distance to mainland, with directional effects reported only for vascular plants. (b) Variance explained (%) by the corresponding models for each taxon or chorotype. EH, environmental heterogeneity; HI, human impact; IND, indigenous; MIE, multiple-island endemics; NAT, native non-endemics; NP, not provided; SAE, single-archipelagic endemics; SIE, single-island endemics.

DISCUSSION

A global model of land snail species richness

Our analysis of indigenous land snails across 727 islands—covering a broad spectrum of island sizes, latitudes,

climates, degrees of isolation, and geo-environmental histories (Figure 4)—represents the first systematic, global-scale demonstration that the island diversity of an invertebrate group is regulated by the same environmental drivers (i.e., area, isolation, climate and environmental heterogeneity), and with similar overall effect sizes, as vascular plants and vertebrates

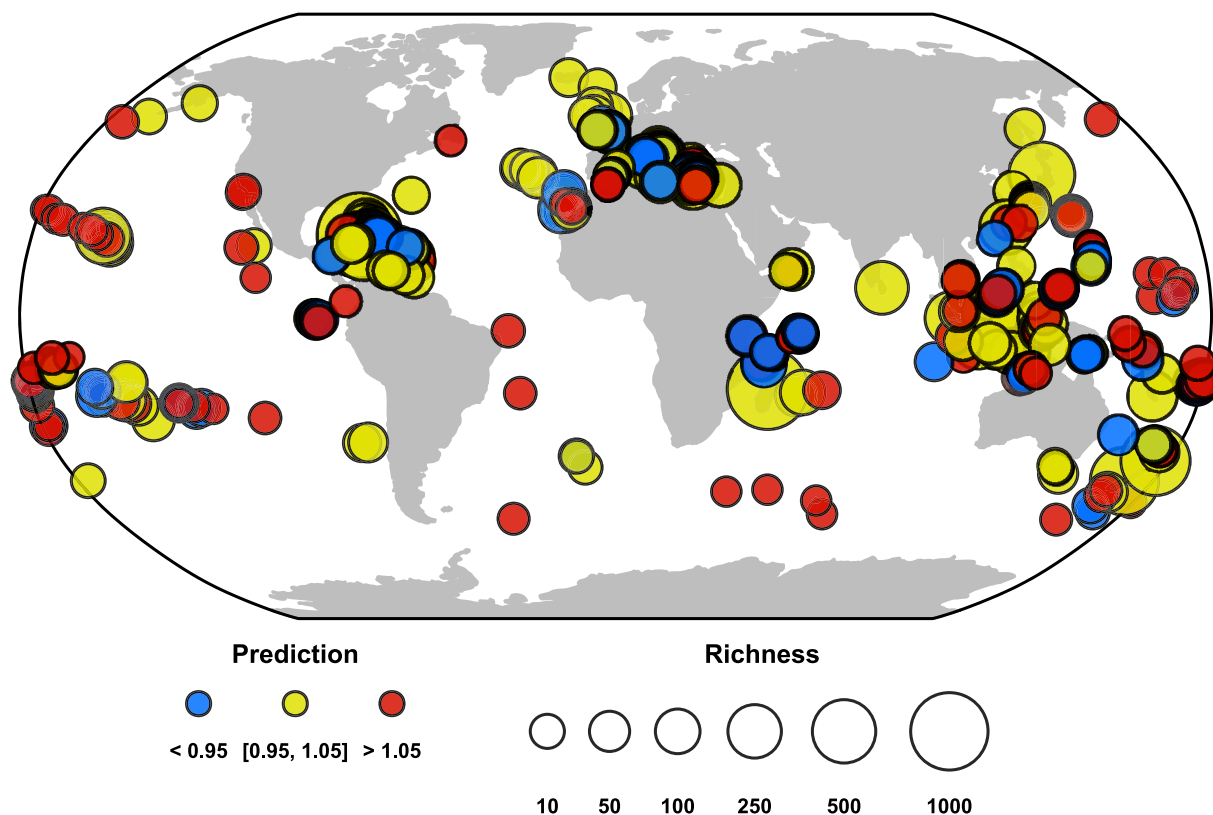


FIGURE 4 Goodness of fit of the model for indigenous land snail species richness (IND). Colors denote whether species richness is well-estimated (predicted/observed richness ratio between 0.95 and 1.05), underpredicted (predicted/observed richness ratio below 0.95), or overpredicted (predicted/observed richness ratio above 1.05). Mean predicted/observed richness ratio across all islands = 1.17, 95% CI = 1.13–1.21. Circle sizes are scaled relative to observed species richness.

(see Barreto et al., 2021; Kalmar & Currie, 2006; Kreft et al., 2008; Pyron & Burbrink, 2014; Rebouças et al., 2026). Besides these pivotal environmental drivers, the inclusion of archipelagic identity as a random effect in our analysis successfully captures other processes operating at regional spatial scales (e.g., the archipelagic-scale idiosyncratic effects of species pool sensu Bunnefeld & Phillimore, 2012), which substantially contribute to overall explanatory power (Figure 2 and Appendix S1: Section S3, Table S4). Notwithstanding possible inconsistencies among taxonomists working across the widely scattered islands and noise generated by the varying degrees of completeness of sampling of the faunas (see *Materials and Methods* and Proios et al., 2021), the predictive reliability of our models (Figure 4 and Appendix S1: Section S3, Table S6) suggests that the relationships established may extend to other archipelagos and island systems.

Land snail chorotype comparisons

Our analyses provide evidence that different chorotypes (i.e., single-island endemic, single-archipelagic endemic,

multiple-island endemic, native non-endemic, total indigenous) differ substantially in their responses to the same environmental factors. The response of each chorotype to each predictor differed for the majority of pairwise comparisons examined (101/140; Appendix S1: Section S3, Table S3), consistent with our hypothesis that partitioning diversity data in this way has the potential to shed light on the dominant underlying processes determining richness of different distributional groups. We note, for example, that Barreto et al. (2021) showed that indigenous mammal species richness on islands globally was mainly driven by physical conditions (island area and isolation), but environmental factors (e.g., temperature and precipitation patterns) were more important drivers of SIE richness. In a global analysis of island snakes, indigenous species richness was more strongly related to climate than to area, while for SIEs area was the major factor (see Appendix S1: Tables S1 and S2 in Pyron & Burbrink, 2014).

Our models show that narrow endemism—that is, single-island endemism, which accounts for 75% of the species in our dataset—is characteristic of large, tropical islands that at the median, most persistent –65 mean sea level across the last ~800 kyr, were not connected to the

TABLE 2 Comparison of explanatory power among full and single-variable models (species–area and species–energy) for five chorotypes of land snail richness.

Chorotype	Model	R^2_{Marginal}	$R^2_{\text{Conditional}}$	AIC	df	ΔAIC	$\Delta R^2_{\text{Marginal}}$
IND	Area	0.44	0.82	5288	5	120	0.15
	Energy	0.46	0.83	5291	5	123	0.13
	Full	0.59	0.81	5168	18	...	...
SAE	Area	0.30	0.83	4020	5	109	0.28
	Energy	0.34	0.82	4015	5	104	0.24
	Full	0.58	0.84	3911	18	...	...
MIE	Area	0.09	0.78	3385	5	95	0.18
	Energy	0.11	0.78	3381	5	91	0.16
	Full	0.27	0.81	3290	18	...	...
SIE	Area	0.51	0.77	2519	5	51	0.17
	Energy	0.56	0.77	2505	5	37	0.12
	Full	0.68	0.80	2468	18	...	...
NAT	Area	0.14	0.90	3907	5	72	0.04
	Energy	0.15	0.90	3912	5	77	0.03
	Full	0.18	0.88	3835	18	...	...

Note: ΔR^2 and ΔAIC values correspond to the differences of single-variable models from the ‘Full’ 14 variable models. Model names denote the full, area-alone, and energy-alone models per chorotype.

Abbreviations: AIC, Akaike information criterion; df, degrees of freedom; IND, total indigenous; MIE, multiple-island endemics; NAT, native non-endemics; SAE, single-archipelagic endemics; SIE, single-island endemics.

mainland (e.g., Cuba, Madagascar, Jamaica; note the effect of past connection in Figure 1 and see Appendix S1: Figure S1). The model for native non-endemic species (a non-overlapping and distinct chorotype representing just 10% of the species in our dataset) is distinct in that area is joined by temperature seasonality as a driver of increased richness of NATs, suggesting that islands with higher NAT richness are at higher latitude (see also Appendix S1: Section S2, Figure S7). While the SAE model is heavily driven by SIEs (as they constitute most of the SAEs—8331 against 1685 MIEs), the inclusion of MIEs in the SAE dataset decreases the amount of variation explained by area, while the relative importance of environmental heterogeneity and climate increases (Figures 2a). In addition, while the measure of isolation that features in the SAE model is current isolation, which appears to be driven by the pattern for MIEs (i.e., distance from mainland, +ve in both), for the SIE model it is past connection (–ve), suggesting that oceanic islands support more narrow endemics than continental shelf islands (Figure 1). Unsurprisingly, given that 90% of IND species are SAEs, the IND model is similar to the SAE model (Figures 1 and 2).

In line with our expectations, there is a grading of non-standardized area effects across the spatial scale of endemism [SIEs (0.49) > SAEs (0.18) > NATs (0.13) = INDs (0.13); Appendix S1: Section S3, Table S5 and Section S2, Figure S10], confirming the theoretically

expected lowering of the species–area slope as we move from speciation-dominated systems (those strongly shaped by evolutionary dynamics) to immigration/extinction systems and finally to dispersal-dominated systems (Rosenzweig, 1995; Triantis et al., 2012; Triantis et al., 2015; Whittaker et al., 2017). Notably, MIEs deviate from the otherwise monotonic gradient. Despite being endemic, MIEs showed the weakest area dependence ($z = 0.09$), weaker even than NAT and IND, and area had comparable explanatory power to that of past connectedness ($\beta = 0.34$ and 0.26, respectively). This suggests that MIE richness does not primarily scale with island size-mediated diversification but instead reflects processes related to dispersal among islands within archipelagic networks. Since SIEs form around 75% of the species in our data, we expected that the species–area slope of INDs would be similar to that of the SIEs. However, the majority (373/727) of islands are small ($<10 \text{ km}^2$), containing a mean of 4.5% SIEs (as many as 304 of the 373 small islands having zero endemics) and 61.6% NATs (the remaining 33.9% being MIEs), contributing to a steeper SIE species–area slope compared to IND (or NAT). This contrasts with the rest of the islands with an area $\geq 10 \text{ km}^2$ (354/727), which feature a mean of 23.2% SIEs and 49.5% NATs (the remaining 27.3% being MIEs).

Regarding climate, it is worth highlighting that AET failed to feature in any of the five main models, but significant relationships were observed involving mean

annual temperature, annual precipitation, and their seasonality (Appendix S1: Section S3, Table S4). Richness of archipelagic endemics (i.e., SAE) and MIEs increased with mean annual temperature, precipitation, and seasonality of precipitation, while the richness of SIEs is influenced only by mean annual temperature. Given the strong covariation between these climatic gradients and latitude, these results are consistent with a latitudinal diversity gradient, whereby species richness tends to increase towards lower latitudes (Brodie & Mannion, 2023). This interpretation is further supported by our supplementary models including latitude, which showed hump-shaped richness responses for SAE and SIE, with estimated peaks close to the equator, at approximately -4.6° and -4.9° , respectively (Appendix S1: Section S2, Figure S7). Thus, the climatic responses of endemic richness align with previous mechanistic explanations of the latitudinal diversity gradient, which interpret latitude as a composite descriptor of broad geographic gradients along which temperature, water availability, productivity, seasonality, historical climatic stability, and diversification processes covary (Field et al., 2009; Hawkins et al., 2003; O'Brien, 1998; Willig et al., 2003). In contrast, NAT richness is higher for islands of wetter and more thermally seasonal climates. Hence our findings reveal nuanced differences in the responses of each chorotype to climate variables, reflecting different underlying processes influencing biogeographical dynamics (see Clarke & Gaston, 2006; Evans et al., 2005) and in particular the importance of in situ speciation of land snails in tropical oceanic islands (Whittaker et al., 2023). Similarly, one measure of environmental heterogeneity used here, TPI, a measure of elevation variability within an island, had a significant positive effect only on the richness of SIEs, suggesting that speciation on islands is related to higher surface variation—and hence opportunities for both adaptive niche partitioning and/or non-adaptive radiation (Gittenberger, 1991; Whittaker et al., 2023)—but is of minor importance in the case of non-endemic richness. In contrast, MIE richness was more strongly associated with overall elevation, rather than TPI (Appendix S1: Section S3, Table S4). This pattern is consistent with the idea that the distribution and persistence of MIE lineages across archipelagos are shaped less by within-island ecological opportunity and more by island longevity through quaternary sea-level fluctuations: higher elevation islands were less frequently submerged or merged into larger paleoislands, providing longer-term refugia for regional persistence (Fernández-Palacios et al., 2016; Norder et al., 2019).

For isolation, depending on the metric used, the various components of richness responded differently, with current isolation (i.e., distance from nearest mainland shore) having a significant effect on MIEs and by

extension SAEs and, crucially, no effect on NATs. This indicates that increased contemporary distance from the mainland signifies the evolutionary uniqueness of more isolated archipelagos but captures limited biogeographical signal for non-endemic richness. The positive and significant effect of past inter-island connectedness for MIEs and SAEs shows that currently observed evolutionary uniqueness at the archipelagic level reflects long-term geodynamic processes (cf. Norder et al., 2019). That past inter-island connectedness had a significant positive effect on the richness of INDs and SAEs but not on SIEs and NATs (native non-endemics) and highlights the importance of MIEs, which are components of the former but not the latter, in observed richness patterns. This is as expected given that the joining together of separate islands into one land mass should encourage the sharing of former SIEs to become MIEs (and thus SAEs) when islands are separated once again (Norder et al., 2019). Richness of SIEs and NATs is better explained by whether an island was previously connected to the mainland. Specifically, NAT richness is elevated on formerly connected (land-bridge) islands, whereas SIE richness is reduced, consistent with the expectation that land-bridge islands support fewer narrow endemics for their size than oceanic islands that have never been connected to the mainland (Whittaker et al., 2023). Whether this discrepancy also translates to higher overall indigenous species richness on land-bridge islands—as expected by theory—is not supported by our analyses as, despite land-bridge islands tending to support more INDs, the effect of past connection on this chorotype is nonsignificant ($\beta_{\text{coef}} = 0.18 \pm 0.11$; Figure 3 and Appendix S1: Section S3, Table S4).

Partly confirming our expectation regarding human effects, land snail richness is positively affected by both road presence and human density, the former being significant only for NATs and the latter being significant for all land snail chorotypes except MIEs (Figure 1). The positive effect of human density on IND, SAE, and SIE richness is unexpected and we suggest four potential explanations. First, there may be a positive sampling bias, such that more densely populated areas are better studied and, hence, appear as more species-rich. Second, there may be an indirect correlation between human presence and various other environmental factors positively affecting snail species richness, such as productivity, energy availability, and habitat heterogeneity, as has been described for bird species richness in previous studies (Evans & Gaston, 2005; Luck et al., 2010). However, such a correlation was not apparent in the present study (all pairwise Kendall's τ $|r_\tau| < 0.7$; Appendix S1: Section S2, Figure S5). Third, species richness may covary with human density because species now considered as

indigenous were in fact introduced at some point in history by humans, and have since been naturalized, therefore substantially contributing to contemporary richness patterns (see e.g., Cameron, 2016; Sax & Gaines, 2008). This might be particularly an issue for islands where human presence extends deep in (pre-) historical times (Matthews et al., 2026). We lack the data needed to evaluate this possibility systematically, but it appears highly unlikely to apply to most endemic insular land snails. Finally, positive covariation of species richness with human density can be explained on the basis of the “replace then remove” framework. According to this, species richness might increase during a phase of intermediate human pressure—during which species assemblages are mostly affected by the replacement of indigenous losers by anthropophilous winner species—and then drastically decline when pressure becomes too high (Cazalis, 2022). This possibility appears likely, since almost half (48%) of the 727 islands considered host no permanent human populations, and as a result, average human pressure across all 727 islands—at least as depicted by population density—could be characterized as intermediate. We acknowledge that this is only a rough approximation of the intensity of human pressure and that further research is required to elucidate the causes of the positive human–snail species richness relationship described herein. It is important to note that because our richness data integrate both historical and contemporary records, the above patterns reflect long-term biogeographic legacies, with present-day richness (including species that are recently extinct or of uncertain status) still carrying the imprint of past colonization, persistence, and turnover dynamics. In this context, the influence of anthropogenic extinction dynamics—which are known to alter “natural” island biogeographic patterns (Chiba & Cowie, 2016; Matthews et al., 2020, 2026)—should be kept in mind when interpreting these results, although assessing their effects lies beyond the scope of the present study.

In addition to these core determinants, the random effects of archipelagic and meta-archipelagic identity improve the explanatory power of the models, substantially so for MIEs and NATs, less so for SIEs. This finding indicates that richness in groups shaped primarily by dispersal dynamics (e.g., MIEs and NATs) depends more strongly on their source pools, whereas the source-pool influence diminishes as endemism increases and diversification becomes the dominant process, in line with MacArthur and Wilson’s original formulation of the ETIB (MacArthur & Wilson, 1963, 1967). However, fixed effects explained a minority of the variance in MIEs and NATs (Figure 2; Appendix S1: Section S3, Table S4), suggesting a need to consider additional variables that

extend beyond those commonly considered in island biogeographic analyses.

Classical theories and integrative models for island species richness

Our study highlights the importance of incorporating multiple environmental drivers to better explain island species richness, demonstrating that integrative models may provide deeper insights into the underlying ecological mechanisms beyond that captured by classical species–area and species–energy relationships. Specifically, our models suggest that while island area and total energy account for a significant portion of the variation in richness, incorporating additional predictors substantially enhances explanatory power, particularly for total indigenous species (IND) and endemics (SAE, MIE, and SIE). Notwithstanding cross-study disparity in quantifications of “total available energy”, our findings echo recent studies in other taxa (e.g., Kalmar & Currie, 2006 for birds; Pyron & Burbrink, 2014 for snakes), which emphasize the dominant roles of area and energy in shaping global island richness patterns. Besides explanatory power, our results also highlight that the inclusion of additional predictors leads to a “corrected” effect of island area on species richness, as reflected in changes of the slope and intercept parameters of the species–area relationship (Δz ranging from -0.05 to -0.11 and $\Delta \log(c)$ from 0.1 to 0.31 ; Appendix S1: Section S2, Figures S12 and S13). This “correction” is particularly pronounced for indigenous and endemic species, suggesting that variation in within-island environmental heterogeneity and climatic conditions, modulate area effects to a degree not evident for native non-endemics (NAT).

Cross-taxon comparisons

Previous global analyses of vertebrates and plants have shown that island area, isolation, climate, and environmental heterogeneity are dominant drivers of island species richness. Our results are consistent with the hypothesis that these drivers are also of central importance for explaining variation in species richness of land snails, an invertebrate taxon. The explained variance in our models falls well within the range of explained variance reported in analyses of vertebrates and plants (R^2 varying from 45% to 88% depending on taxon and chorotype; Figure 3b). Interestingly, our model for land snail SIE richness explained a substantially higher percentage of the variance (80%) than the respective models for snakes (47%) and mammals (45%) (Figure 3b),

indicating that the global patterns of land snail endemism on islands are more predictable by comparatively simple models than those of larger vertebrates. This discrepancy may reflect that—notwithstanding differences in the model structure and the islands and variables included—speciation-related processes are likely of relatively greater importance in explaining land snail richness across islands globally. However, the extent to which this applies to other invertebrate groups remains to be determined.

The opposing trends of isolation between endemics (i.e., SAEs, MIEs, and SIEs) and non-endemics (i.e., NATs) that emerged in our models (Figure 3b)—which imply an increase in the importance of speciation and a decline in the importance of colonization as drivers of richness with isolation, respectively—are consistent with the current understanding of the effects of isolation on species richness, as expected by theory (Table 1) and reported for plants (Weigelt et al., 2016) and birds (Valente et al., 2020). Our findings of positive effects of larger areas, warmer and wetter climate, and greater environmental heterogeneity on land snail species richness and endemism also agree with trends found for vertebrates and plants (Figure 3b), giving support for disparate environment–richness hypotheses (e.g., species–area and species–energy relationships) being complementary rather than mutually exclusive. Taken together, these results reinforce the generality of biogeographic processes—colonization, extinction, and speciation—shaping eukaryote macro-organism island biodiversity, affirming that despite inherent cross-taxon ecological differences, the underlying mechanisms of community assembly remain remarkably consistent.

Future perspectives and conclusion

Reflecting on the factors affecting the broad-scale diversity of insular land snails—a taxon that stands out as one of the most imperiled among all plant and animal groups (Cowie et al., 2022; IUCN, 2022; Lydeard et al., 2004)—our results may also have implications for conservation. With the species–area relationship widely used in applied ecology (see Matthews et al., 2021), obtaining representative estimates of the effect of area and of the role of other modifying variables on land snail richness can facilitate their practical use in conservation biology. For instance, our dataset shows that single-island endemic species are disproportionately rare on very small islands ($<10 \text{ km}^2$, 4.5% SIEs), where indigenous assemblages are dominated by native non-endemics (61.6% NATs). This pattern is consistent with the idea that the persistence and diversification of SIEs requires a minimum habitat area, likely reflecting the need for both sufficient population

sizes and environmental heterogeneity (cf. Kisel & Barraclough, 2010). Understanding this area-dependence is important for designing protected areas of appropriate size, particularly in systems where small islands are numerous (Ladle & Whittaker, 2011). Additionally, further elaborating on the dependence of land snail richness on climate shown herein may be informative about future changes in species richness via climate change, and the fact that snails are highly threatened makes them especially valuable to study in this context.

Overall, our study comprises one of the first attempts to quantify patterns and processes of an invertebrate group across the world's islands and shows that after decades of research and accumulation of taxonomic land snail data (see Proios et al., 2021), the study of invertebrate diversity at global scales is now possible and can be used to complement and/or extend previous findings on better-studied vertebrate and plant taxa, towards a—taxonomically speaking—holistic assessment of the ecological ‘rules’ guiding the emergence of global-scale biodiversity patterns.

AUTHOR CONTRIBUTIONS

Konstantinos Proios, Albert B. Phillimore, Robert J. Whittaker, and Kostas A. Triantis designed the research. Konstantinos Proios and Kostas A. Triantis performed research. Konstantinos Proios, François Rigal, and Dimitris Poursanidis analyzed data with input from Albert B. Phillimore and Thomas J. Matthews. Konstantinos Proios, Thomas J. Matthews, and Robert J. Whittaker led the writing, and all authors substantially contributed to the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Proios, 2023) are available in the Harvard Dataverse repository at <https://doi.org/10.7910/DVN/XWZFZB>. Land-snail diversity data included in the

deposit were derived from Proios (2020), which is available in the Harvard Dataverse repository at <https://doi.org/10.7910/DVN/1KJQWJ>, and were curated for the purposes of this study. All environmental variables used in this work are referenced in Appendix S1: Table S1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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