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Research article

Rainfall increases conformity and strength of species–area relationships

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The positive relationship between species richness and area is regarded as one of the few laws in ecology. Therefore, deviations from predictable species–area scaling, evident as high residual variance in species–area curves, are often interpreted as anomalous behaviour. Small-island systems often do not conform to species–area relationships, yet the high stochasticity in their species–area curves is frequently treated as unexplainable noise or attributed to idiosyncratic extinction rates. Here, we introduce a statistical framework that incorporates the degree of stochasticity in species–area relationships as an explicit, interpretable model parameter. Using a global island plant dataset for atolls (378 islands across 19 atolls) – prototypical examples for small-island dynamics – we show that the degree of residual variance in species–area curves can be captured, modelled, and linked to environmental conditions. Our heteroscedastic modelling approach demonstrates that apparent stochasticity in species–area relationships is not random but predictable through environmental drivers. Specifically, we found that increased rainfall reduces the residual variance around the species–area curve, indicating that resource availability is a critical factor enabling conformity to species–area scaling. Cyclone disturbance frequency did not drive stochasticity, challenging the prevailing view that disturbance regimes drive the stochasticity in species–area scaling on small islands. By treating residual variance as an explicit model parameter in species–area relationships rather than unexplainable noise, our approach provides new insights into the conditions enabling biological communities to conform to species–area scaling. Shifting the focus in species–area studies on the residual variance as an interpretable model parameter that captures the degree of conformity to species–area scaling offers novel perspectives into the environmental factors prerequisite for species–area scaling. This contributes to unifying the apparent anomalous, stochastic nature of small-island systems with the general law of linear species–area scaling.

Keywords: atoll, Bayesian distributional regression, island biology, small-island effect, species assembly, species–area scaling

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Introduction

Species–area relationships constitute a fundamental and almost universally observable pattern in ecology and are thus often considered among the few general 'laws' governing ecological communities (Schoener 1976, Tjørve and Tjørve 2017). The most common representation of the relationship between species richness and area is Arrhenius' power law, which relates species richness (S) to area (A) through a log-log-linear equation of the form $\log(S) = c + z \times \log(A)$. In this formulation, the parameters c and z are estimated empirically and correspond to the intercept and slope of the relationship, respectively (Arrhenius 1921, Matthews et al. 2021a).

Islands have proven particularly instructive for studying the law of species–area scaling, with numerous studies documenting species–area relationships and quantifying the slope and intercept parameters across diverse geographies, spatial scales, and taxonomic groups (Triantis et al. 2012, Matthews et al. 2019a, Gooriah et al. 2021). At the same time, it also became well established that many small islands (and other small island-like systems) do not strictly conform to the predicted scaling between area and species richness (Lomolino and Weiser 2001, Triantis et al. 2006). This deviation from the canonical species–area relationship is typified by the 'small-island effect', a foremost descriptive framework for high stochasticity in species–area scaling due to species richness on many small islands being only weakly correlated with area (Morrison 2014). Conventionally, this effect is demonstrated by identifying a breakpoint in the species–area curve, below which the slope parameter z is lower (incl. $z = 0$) than above the threshold, as species richness becomes unexplained by area (Dengler 2010, Schrader et al. 2020).

One of the first documentations of highly stochastic species–area relationships on small islands was provided by William A. Niering (1956, 1963) in his studies of vascular plant diversity on 33 islands within Kapingamarangi atoll, Micronesia. Niering (1956) observed that the smallest islands did not conform to a linear species–area scaling. He posited that limited edaphic conditions and insufficient groundwater availability on these islands restrict the assembly of plant communities in a manner that is only weakly conforming to area-governing factors ('resource prerequisite hypothesis'; Niering 1963). Subsequent reanalyses of the Kapingamarangi data reinforced the notion that water availability is a critical resource prerequisite, governing the conformity of these island communities to predictable species–area scaling (Wiens 1962, Whitehead and Jones 1969).

Approximately a decade after Niering's work, MacArthur and Wilson (1967) incorporated Niering's data from Kapingamarangi atoll into their seminal 'Theory of island biogeography'. However, rather than attributing the nonconforming species–area relationship to resource prerequisites in the form of water scarcity as per Niering's original interpretation, MacArthur and Wilson (1967) concluded that island instability from recurrent catastrophic disturbances creates extinction rates that are not area-dependent, driving the high stochasticity in the atoll's species–area relationship

('disturbance hypothesis'). This extinction-centred interpretation has been questioned repeatedly (Stoddart and Fosberg 1981, Lee 1984, McGuinness 1984, Woodroffe and Stoddart 1992) but nonetheless prevails as a common explanation for the observed high stochasticity in species–area relationships of small oceanic islands, and particularly for atolls (Whittaker 1995, Kreft et al. 2008, Neufeld et al. 2017, Whittaker et al. 2023, Larrue 2024).

Critically, no study has directly tested the resource prerequisite hypothesis against the disturbance hypothesis to identify the underlying mechanism driving the high stochasticity of small islands in species–area relationships (see, however, Woodroffe and Stoddart (1992) for a qualitative discussion). This is a key knowledge gap, as mechanistically integrating these small-island dynamics into the theoretical frameworks of island biogeography is key to understanding the boundary conditions and limits underlying the law of species–area scaling at the smallest island sizes, which inherently cannot be inferred from, or tested through, the study of larger islands (Lomolino 2000).

To directly address this knowledge gap regarding the primary driver of stochasticity in small-island species–area relationships, our work introduces an analytical framework – distributional (or heteroscedastic) regression modelling (Klein 2024) – to species–area research. This approach draws attention to the overlooked role of the residual variance (or, colloquially, 'stochastic noise') in species–area relationships, as a measure of the conformity of biological communities to the law of species–area scaling. We reframe Arrhenius' power law as a sampling process with an explicit error term ε (i.e. $\log(S) = c + z \times \log(A) + \varepsilon$). By focusing on the magnitude of ε as a measure of the degree of conformity of island communities to species–area scaling (i.e. the amount of stochasticity around a species–area curve), we can model the extent to which observed species richness conforms to, or deviates from, the expected scaling. This enables us to identify environmental drivers that predictably increase or decrease the stochasticity – or, conversely, increase or decrease conformity – in species–area relationships.

To demonstrate the utility and power of this statistical approach, we address the long-standing opposition between Niering's (1963) and MacArthur and Wilson's (1967) interpretations of the highly stochastic species–area scaling proposed for atoll islands. The small reef islands of coral atolls are strongly subjected to both water-resource limitation and episodic instability from tropical cyclone disturbances (Steibl and Russell 2024, Steibl et al. 2024). With atolls widely distributed across the tropical oceans, and thus across major rainfall gradients and cyclone belts, and with each atoll comprising sometimes hundreds of individual reef islands (i.e. each atoll constituting an archipelago of small islands), atolls are a capable and powerful model system for contrasting the effects of resource limitation and disturbance regimes on the stochasticity in species–area scaling. Additionally, we assessed the effects of rainfall versus cyclone disturbance on the strength (slope) of the species–area relationship and contrasted those effects at the scale of individual atoll islands (i.e.

α-diversity) versus whole atolls (i.e. γ-diversity) (Cabral et al. 2014).

Material and methods

Data acquisition

We compiled a global dataset of vascular plant species richness from individual islands within atolls. Island-level atoll vascular plant species inventories were primarily sourced from Steibl and Russell (2024), which contain species lists for 16 atolls across the Indo-Pacific and Caribbean. Three additional datasets of island-level species richness from Ontong Java (Bayliss-Smith 1973), Rongelap (Releford et al. 2009), and Manuae atolls (Steibl et al. 2025a) were added, creating a final dataset of vascular plant species richness from 378 individual islands across 19 atolls (i.e. 'archipelagos'). Island area measurements were obtained either from published literature or using Google Earth ver. 10.66.0.0 (https://earth.google.com/web, last accessed 10 November 2024). Total atoll ('archipelago') land area was calculated as the sum of the land areas of their constituent islands. Atoll isolation was quantified as the minimum distance from the atoll to either the nearest larger volcanic island landmass or continent (Weigelt and Kreft 2013).

Vascular plant species names from the different literature sources were harmonised following the taxonomy of Kew Royal Botanical Gardens 'Plants of the World' (POWO 2024). We excluded introduced plants from the dataset based on available distribution classifications (Fosberg and Sachet 1980, POWO 2024), as these were mostly cultivated, agricultural, or ornamental taxa that typically adhere to anthropogenic rather than ecological drivers and therefore risk obscuring the natural patterns of native species assembly (Burns 2015, Blackburn et al. 2016). Introduced plants constituted between zero and 87% (median 13%) of species per island, but even though prevalent and often covering large fractions of total atoll island area, few behave invasively on atoll islands, and none has ever been documented to cause native plant extinctions, which would interfere with species richness data and analyses (Russell and Kueffer 2019, Burnett et al. 2024).

Annual precipitation data for each atoll were obtained from published meteorological data. The basin-wide long-term (1981–2010) gridded annual rainfall pattern was obtained from the Global Precipitation Climatology Project (GPCP) monthly analysis product (NOAA; https://psl.noaa.gov/data/gridded/data.gpcp.html, last accessed 3 December 2024).

Cyclone frequency data for each atoll were obtained from the Historical Hurricane Tracks database of the National Oceanic and Atmospheric Administration (NOAA; https://coast.noaa.gov/hurricanes/, last accessed 10 November 2024). The number of cyclones (categories 1–5) passing each atoll within a 50-km radius, measured from the outer polygon of the atoll and over the entire available time range of the database (1942–2021), was used as a conservative yet robust measure of the long-term disturbance regime affecting each atoll (Steibl and Russell 2024). Sampled atolls exhibited pronounced variation in annual rainfall (445–3304 mm year⁻¹) and in cyclone disturbance frequency (0–13 cyclones over an 80-year period), contingent upon their location along tropical oceanic rainfall gradients and tropical cyclone belts (Fig. 1).

Statistical analysis I. Rationale behind the approach and simulations

Species–area relationships are conventionally expressed using Arrhenius' power law or its derivations. Historically, research has been focused on empirically estimating slope and intercept parameters (Connor and McCoy 1979, Matthews et al. 2021b), and in the case of small islands, identifying area breakpoints (Losos and Schluter 2000, Schrader et al. 2020, Gao and Wang 2022). However, when Arrhenius' power law is interpreted not as a deterministic law but as emerging from a sampling process, another relevant parameter, the error term ε, should also be explicitly considered. This leads to an augmented formulation of the species–area relationship as $\log(S) = c + z \times \log(A) + \varepsilon$ (Fig. 2).

While ε is commonly treated as unexplainable 'noise' in the species–area relationship and cannot be further analysed in classic homoscedastic linear models, distributional regression models (or heteroscedastic regression models) allow us to investigate whether explanatory variables predict variation
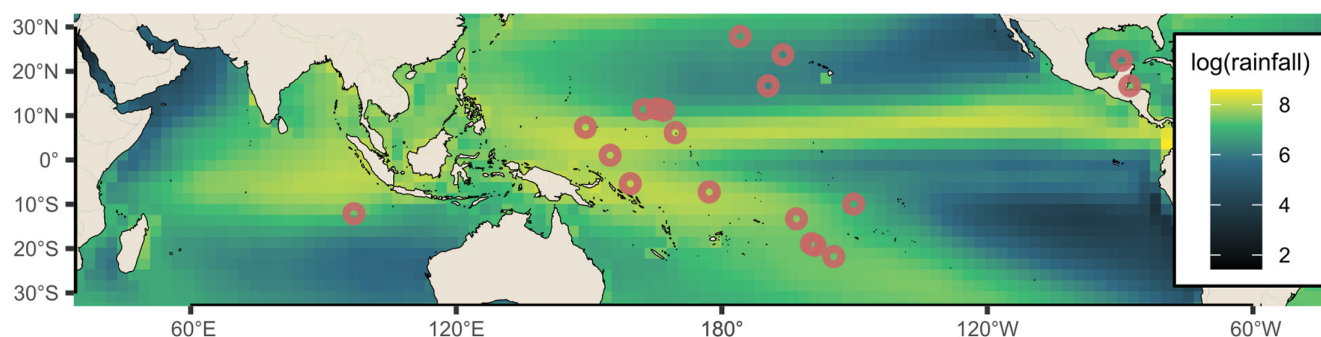

Figure 1. Long-term rainfall patterns and the location of atolls used in this study. Red circles indicate the location of the n = 19 atolls used in this study to test for effects of rainfall and cyclone frequency on species–area relationships. Colour-coded background indicates log-scaled annual rainfall amount [mm year⁻¹] across the tropical oceans.
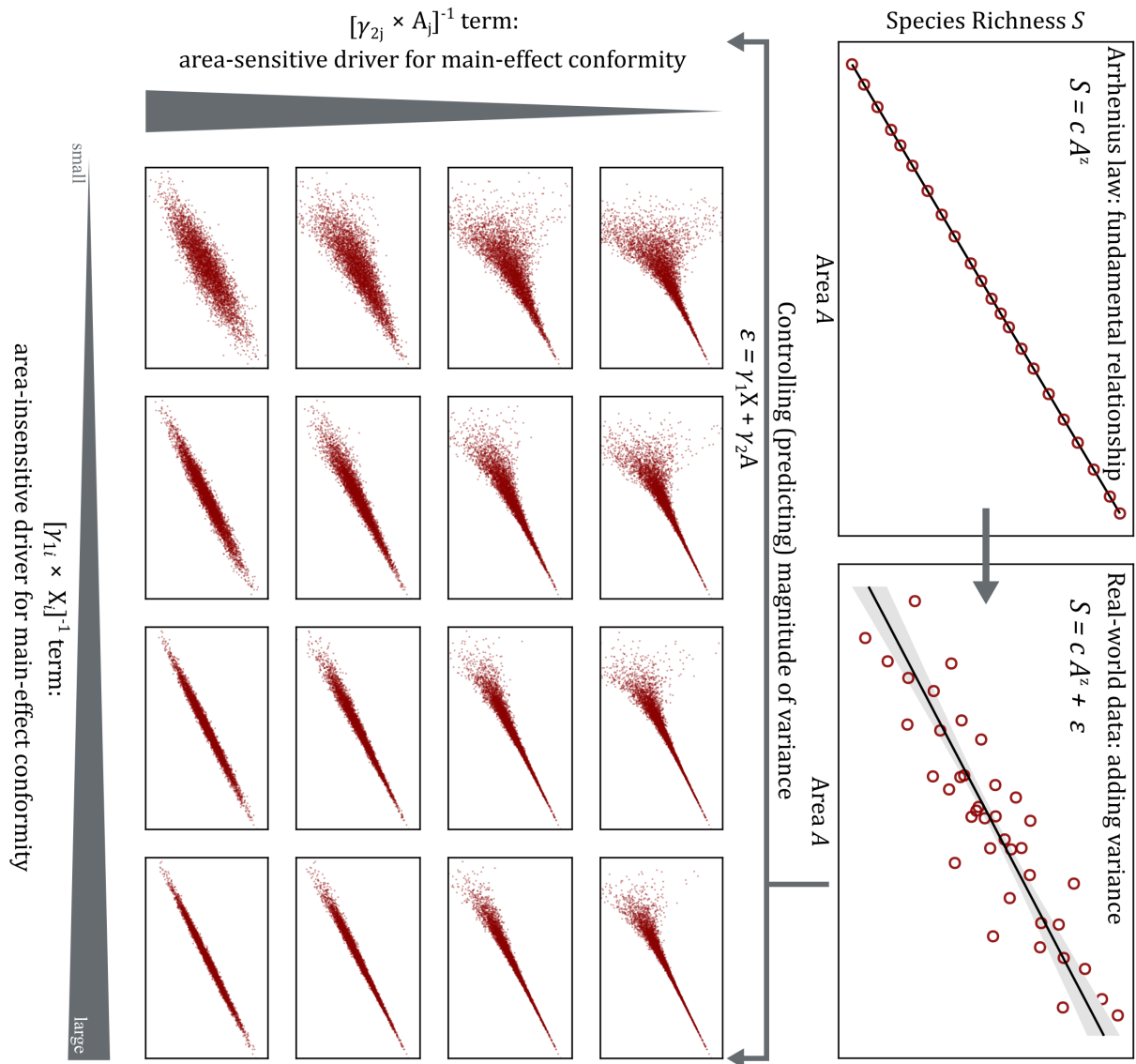
Figure 2. Simulating the data-generating process behind conformity in species–area relationships. Each panel represents a hypothetical island archipelago where the x-axis indicates the area of its islands, and the y-axis indicates species richness. Red points indicate the observed species richness for a hypothetical island within the archipelago. Across the 4 × 4 panels, we increased the area-insensitive term for main effect conformity to the species–area fit from left to right, and the area-sensitive term from top to bottom. The resulting species–area relationship for each panel (archipelago) shows the behaviour of species–area scaling under different effect sizes for the conformity parameters. Hypothetical effect sizes are exaggerated to visualise the behaviour of species–area scaling under different configurations.

in ε (Klein 2024). To the best of our knowledge, modelling heteroscedasticity, i.e. the conformity of data to a linear relationship (or the spread of observed datapoints around the predicted linear fit), has not yet been utilised to identify predictors of stochasticity in species–area relationships (but see HSARX models in Sólymos and Lele (2012), which quantified the magnitude of variation).

To demonstrate the utility of this approach for identifying drivers of conformity to species–area scaling, we first provide a series of simulations to showcase the rationale and procedure. We express species richness S of island i in archipelago j

as a function of area A_i with intercept c and slope z according to Arrhenius' power law, and an error term ε_{ij},

$$\log(S_{ij}) = c + z \times \log(A_i) + \varepsilon_{ij}$$

Rather than considering ε_{ij} as an unexplainable parameter as in conventional (homoscedastic) statistical frameworks for species–area studies, we considered ε_{ij} to be a distributional parameter, the magnitude of which can be expressed by a set of linear predictors:

$$\varepsilon_{ij} \sim N\left(0, \sigma_{ij}\right)$$

$$\log\left(\sigma_{ij}\right) = \sigma_0 + \gamma_{1j} \times X_j + \gamma_{2i} \times A_i$$

In this formulation, σ_0 is the intercept on the log scale, while the coefficients γ_1 and γ_2 quantify the effects of a hypothetical predictor X and island area A on the residual variance of the main effect of area on species richness, respectively. In other words, in our example the $[\gamma_1 \times X]$-term influences the magnitude of deviation (or the conformity) of observed island species richness around the predicted species–area curve. The $[\gamma_2 \times A]$-term modulates the magnitude of deviation contingent upon island area, allowing smaller islands to deviate more strongly from the predicted species–area mean effect than larger islands when values of γ_2 are negative. This also offers a continuous, single-process alternative to area breakpoints. While our example uses two predictor variables for the residual error, any number of predictors could theoretically be added, as in any conventional linearised modelling framework. Figure 2 shows a set of simulated species–area relationships with 16 distinct parameter configurations for γ_1 and γ_2. These simulations illustrate how varying the distributional parameter ε through changing γ_1 and γ_2 can yield species–area patterns with different magnitudes of conformity to the predicted species–area curve, while also capturing greater deviations of smaller islands from a species–area curve. Importantly, this is achieved under a single continuous model, i.e. under a single data-generating process, with just one slope parameter across the entire island size range. Analogous heteroscedastic modelling approaches can also be formulated for other species–area functions (e.g. power or logistic model) by modelling the residual error term as an explicit distributional parameter. Future studies can validate the performance and robustness of other functions, but this methodological testing was outside the scope of the present study. Simulations were done in the Julia programming language and the 'Turing' ecosystem for Bayesian modelling (Bezanson et al. 2012, Fjelde et al. 2025).

Statistical analysis II. Empirical data analysis

Statistical analysis of the empirical atoll island data was carried out in R ver. 4.4.3 (www.r-project.org). We used a Bayesian hierarchical regression framework to analyse the effects of rainfall and cyclone frequency on the conformity and slope of the species–area relationships, as well as to determine drivers for atoll-level (γ-diversity) species richness, using the 'brms' package (Bürkner 2017). We log-transformed and z-standardised all predictor variables (area, rainfall, cyclone frequency) prior to regression analysis.

In the first model ('conformity model'), we evaluated how rainfall and cyclone frequency influence the conformity of the species–area relationship (i.e. Arrhenius' power law) across the islands within atolls. Let S_{ij} be the observed log species richness for island i in atoll j. The expected log species richness $\hat{S}_{ij}$ is then modelled using Arrhenius' power law

augmented by an error term: a function of a random intercept c_j of each atoll j and the effect z of the area A of each island i in atoll j, with error term ε_{ij}:

$$\hat{S}_{ij} = c_j + z \times A_{ij} + \varepsilon_{ij}$$

$$\tau \sim \text{Normal}_+\left(0, 0.5\right)$$

$$c_j \sim \text{Normal}\left(\bar{c}, \tau\right)$$

$$\varepsilon_{ij} \sim N\left(0, \sigma_{ij}\right)$$

where $\bar{c}$ and τ are the corresponding hyperparameters of the random intercept parameter c_j. The hyperparameter prior for the global intercept was set at mean zero because the response variable was internally centred at zero. To test robustness, a separate model with a flat (uninformative) global intercept hyperparameter prior and a non-centred response variable was tested, reproducing the same results as in the initial model.

The effects of rainfall, cyclone frequency, and island area on the degree of conformity to the species–area relationship were then expressed as:

$$\log\left(\sigma_{ij}\right) = \beta_0 + \beta_1 \times A_{ij} + \beta_2 \times \text{rainfall}_j + \beta_3 \times \text{cyclone}_j$$

$$\beta_k \sim \text{Normal}\left(0, 0.25\right) \text{ for } k = 1, 2, 3$$

$$\beta_0 \sim \text{Cauchy}\left(0, 1\right)$$

where the β parameters are the intercept and main effect slopes of area (β_1), rainfall (β_2), and cyclone (β_3) frequency on the log-standard error of the species–area relationship. We used a Cauchy prior for the intercept because its heavy-tailed, weakly informative nature accommodates potential extreme values while providing adequate regularization in the absence of strong prior knowledge. We reproduced the same results using the 'brms'-default flat (uninformative) priors.

In the second model ('slope model'), we evaluated the interaction between rainfall and cyclone frequency with the species–area relationships across the islands within atolls. That is, we quantified the degree to which rainfall and cyclone frequency increase or decrease the slope of the species–area scaling. This analysis was separated from the conformity model, as the objective of the conformity model was to determine whether rainfall and/or cyclone frequency uniquely explain residual variance in the species–area relationship, rather than the residual variance given the interactive effect between area, rainfall, and cyclone frequency. Let S_{ij} be the observed log species richness for island i in atoll j, where $\hat{S}_{ij}$ is the expected log species richness for island i in atoll j, and σ the standard deviation of islands with homogenous variation:

$$S_{ij} \sim N\left(\hat{S}_{ij}, \sigma\right)$$

The expected mean log species richness $\hat{S}_{ij}$ is then expressed as:

$$\hat{S}_{ij} = c_j + z \times A_{ij} + \beta_1 \times \text{rainfall}_j + \beta_2 \times \text{cyclone}_j$$
$$+ \beta_3 \times \left(A_{ij} \times \text{rainfall}_j\right) + \beta_4 \times \left(A_{ij} \times \text{cyclone}_j\right)$$

where c_j is the random intercept of each atoll j, z the main effect of area according to Arrhenius, and the β parameters the main effect slopes of rainfall (β_1) and cyclone (β_2), and their interaction terms with area (β_3 and β_4, respectively). We used uninformative (flat) 'brms'-default priors for the slope parameters.

In the third model ('archipelago model'), we combined island-level species richness (α-diversity) per atoll to obtain an atoll-level measure of vascular plant species richness (γ-diversity). Let Y_j be the observed log species richness (γ-diversity) of atoll j and σ be the standard deviation:

$$Y_j \sim N\left(\hat{Y}_j, \sigma\right)$$

where $\hat{Y}_j$ is the expected log species richness on atoll j. We then tested the effect of total atoll land area, isolation, annual rainfall, and cyclone frequency on γ-diversity as:

$$\hat{Y}_j = c + \beta_1 \times \text{total\_area}_j + \beta_2 \times \text{isolation}_j$$
$$+ \beta_3 \times \text{rainfall}_j + \beta_4 \times \text{cyclone}_j$$

where c is the intercept, and the β parameters the main effect slopes for total atoll land area (β_1), isolation (β_2), rainfall (β_3), and cyclone frequency (β_4) on atoll j. We used uninformative (flat) 'brms'-default priors.

For each model, we ran four MCMC chains with 5000 iterations and a warmup of 2500 iterations, and all HMC diagnostics (R-hat, ESS, BFMI) indicated reliable MCMC sampling. We performed standard model validation steps, including prior predictive checks, computed Gelman and Geweke diagnostic metrics, checked for model convergence, performed leave-one-out (LOO) cross-validation, and conducted posterior retrodictive checks. All model (slope) parameters were un-z-standardized and are reported on the log-log scale.

Results

The number of native vascular plant species per island (α-diversity) ranged from just a single species to a maximum of 80 species. The area of individual islands ranged from 0.01 ha to a maximum of 623.0 ha. At the atoll ('archipelago') level, native vascular plant species richness (γ-diversity) ranged from 12 to a maximum of 86 species.

As expected, island area had a clear positive effect on island species richness, with both the conformity model and slope model generating the same slope parameter estimate ($z = 0.27$ [95% credible interval of the posterior: 0.24–0.29], posterior probability PP ($\beta > 0$) = 100%; Fig. 3A). The conformity of islands to the estimated species–area curve was strongly driven by island area and rainfall (conformity model; Fig. 3B–C). Atolls with higher annual rainfall showed a better linear fit of their species–area relationship across their constituent islands, i.e. lower residual variance of the species–area relationship within the atoll and thus higher conformity to Arrhenius' power law ($\beta_2 = -0.20$ [$-0.45 - 0.05$], PP ($\beta < 0$) = 94%). At the same time, we found little support for the hypothesis that cyclone frequency increases stochasticity in the species–area relationship ($\beta_3 = -0.06$ [$-0.21 - 0.10$], PP ($\beta > 0$) = 24%; Fig. 3D). Furthermore, we found that larger island size itself also decreased residual variance from the predicted species–area relationship ($\beta_1 = -0.11$ [-0.15 to -0.08], PP ($\beta < 0$) = 100%), thus capturing a continuously greater deviation of smaller islands from linear species–area fits within this single-model approach.

We identified a positive interactive effect of island area and rainfall on species richness (slope model; $\beta_{\text{area x rainfall}} = 0.06$ [$-0.02 - 0.14$], PP ($\beta > 0$) = 97%), showing that the slope of the species–area relationship is steeper on atolls with higher rainfall, i.e. islands under a higher rainfall regime accumulating species faster with increasing area than under lower rainfall regimes. At the same time, we found little support for the expected negative interactive effect of island area and cyclone frequency on diversity ($\beta_{\text{area x cyclone}} = 0.03$ [$-0.02 - 0.08$], PP ($\beta < 0$) = 10%), indicating that the slope of the species–area relationship is not depressed on atolls under higher cyclone disturbance frequency.

When combining island-level vascular plant species richness measures (α-diversity) into an atoll-level ('archipelago-level') measure for species richness (γ-diversity), we found that total atoll land area had no positive effect on γ-diversity (archipelago model; $\beta_{\text{atoll-area}} = 0.01$, [$-0.10 - 0.13$], PP ($\beta > 0$) = 59%; Fig. 4A). In other words, atolls with larger total land area are not more diverse at the atoll (i.e. archipelago) level. The distance of the atoll to the nearest volcanic island or continental landmass did not negatively influence γ-diversity ($\beta_{\text{atoll-isolation}} = -0.04$ [$-0.25 - 0.18$], PP ($\beta < 0$) = 63%). At the same time, rainfall had a clear positive effect on γ-diversity ($\beta_{\text{atoll-rainfall}} = 1.03$ [$0.49 - 1.56$], PP ($\beta > 0$) = 100%; Fig. 4B), while cyclone frequency exerted a less clear positive effect on γ-diversity ($\beta_{\text{atoll-cyclone}} = 0.19$ [$-0.23 - 0.60$], PP ($\beta > 0$) = 82%; Fig. 4C).

Discussion

Species–area relationships are central to understanding, predicting, and evaluating biodiversity patterns and thus are a foundational framework for ecology and biogeography (Storch et al. 2012, Matthews et al. 2021a). Given that species–area scaling is a near-universally occurring pattern,
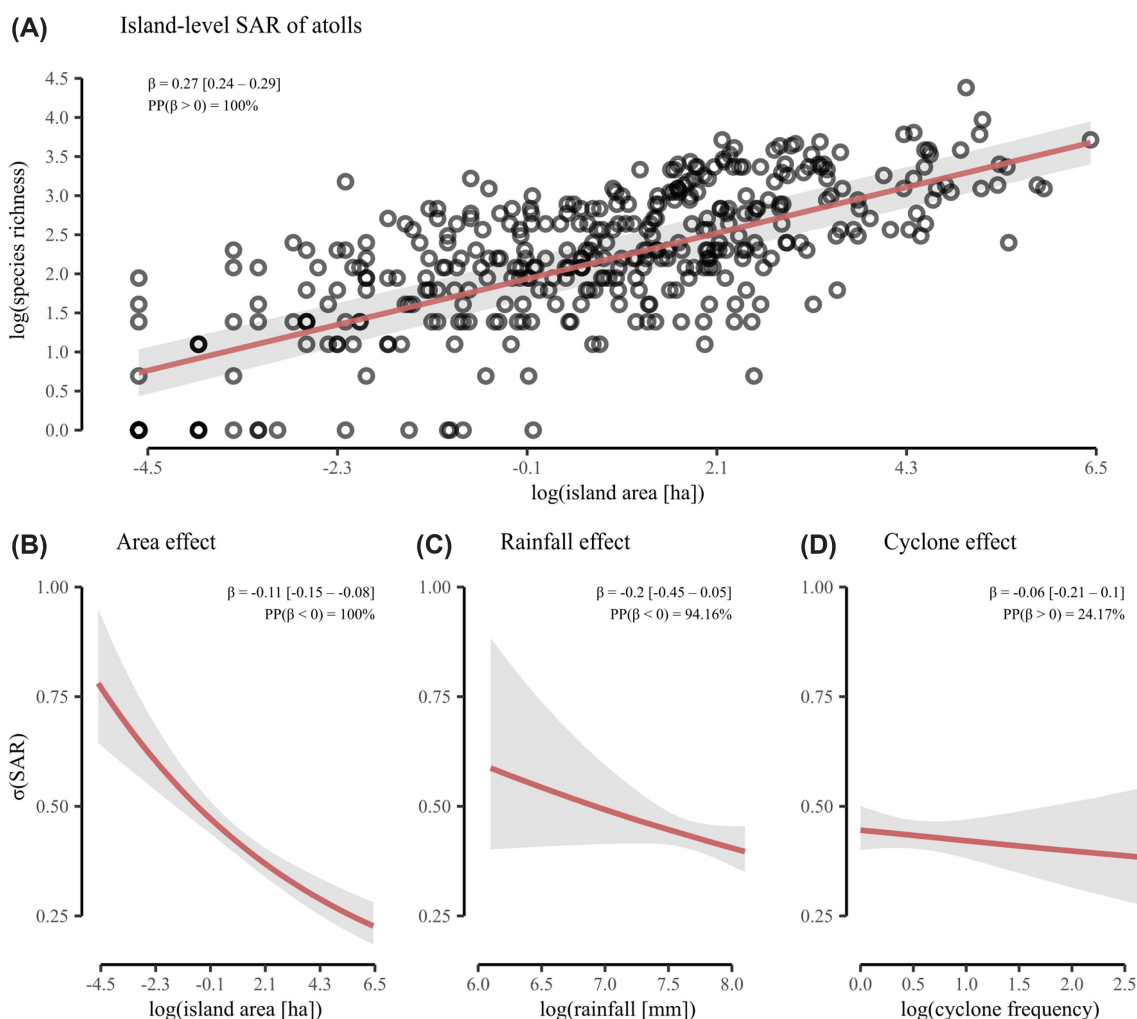
(A)   Island-level SAR of atolls

Figure 3. Species–area relationship (SAR) of the islands within atolls (α-diversity), and drivers for their residual variance. (A) The islands within each atoll follow a clear positive log–log-linear species–area relationship, whereby the atolls ('archipelagos') are treated as random intercept terms. (B) Area, (C) rainfall amount, and (D) cyclone frequency influence to varying degrees the residual variance of the species–area relationship (σ(SAR)) of the islands within atolls. Red lines indicate the mean posterior conditional effect, and grey ribbons the 95% credible intervals of the posterior slope estimate.

deviations from this general relationship are often perceived as anomalous behaviour to a fundamental law (Sfenthourakis and Triantis 2009). Small islands, in particular those of atolls, are prototypical and commonly used examples for deviations from predictable species–area relationships (Lomolino 2000, Tjørve and Tjørve 2017, Matthews et al. 2019b). However, rather than being entirely stochastic and unpredictable small–island communities, our heteroscedastic modelling approach reveals that rainfall predictably enhances the degree to which island species richness conforms to the law of linearised species–area scaling. Furthermore, rainfall increases the rate at which species are being accumulated with increasing area. Moreover, the differential effects of area and rainfall on island-level (α-diversity) versus atoll-level (γ-diversity) richness underscore the importance of scale in interpreting biodiversity patterns on these island ecosystems (Bunnefeld and Phillimore 2012, Cabral et al. 2014).

The study of small islands has been critical for developing, advancing, and refining island biogeography theory and our understanding of the law of species–area scaling (Lomolino and Weiser 2001, Triantis et al. 2006, Triantis and Sfenthourakis 2012). The distinct species–area relationships of atoll islands were among the prototypical examples for developing the original theoretical frameworks (Niering 1956). MacArthur and Wilson (1967) posited that these small islands experience episodic instabilities that create idiosyncratic extinction rates, which disrupt a predictable accumulation of species richness governed by area, creating high stochasticity around the species–area curve. However, the original hypothesis for the observed species–area curve on atolls, proposed by Niering (1956, 1963), followed an immigration model, arguing for water availability as a prerequisite for predictably accumulating species based on area. Our findings provide the first empirical test contrasting both
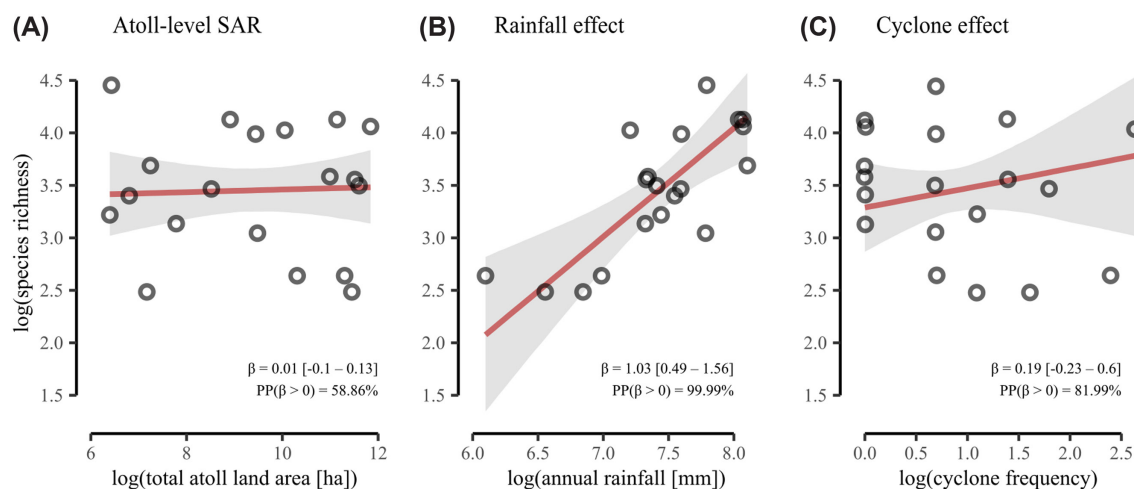
Figure 4. Drivers of atoll-level species richness (γ-diversity). Figure panels show the effects of (A) total atoll land area, (B) annual rainfall amount, and (C) cyclone frequency on the atoll-level species richness (n = 19 atolls). Points indicate observed values, red lines indicate the linear relationship, and grey ribbons the 95% credible intervals of the posterior slope estimate.

hypotheses, and strongly support Niering's resource prerequisite hypothesis while finding little support for MacArthur and Wilson's disturbance hypothesis. Atolls with higher rainfall showed greater conformity in their constituent islands to the species–area curve (Fig. 3C), meaning the islands' observed species richness more closely matched the values expected for a given island area.

Water availability is a well-established, known limiting resource for species richness, biomass, and productivity on atolls (Fosberg 1948, Amerson 1969, Frith 1979, Shekeine et al. 2015). Given the absence of permanent, open freshwater reservoirs and only shallow groundwater lenses on atoll islands, the year-round availability of water is closely tied to rainfall amounts, which recharge and maintain the islands' freshwater reservoirs (Oberle et al. 2017, Werner et al. 2017). Therefore, the observed positive effect of rainfall on the conformity of islands to the species–area curve likely reflects the increasing alleviation of energetic constraints that enables more predictable species establishment, accumulation, and persistence governed by the overarching limits of available land area (Fraser and Currie 1996, Sfenthourakis and Triantis 2009, Schrader et al. 2019).

At the same time, we found no correlation between disturbance frequency in the form of cyclones and the degree of stochasticity around species–area curves (Fig. 3D). This challenges the extinction-centred explanation for stochasticity in the species–area relationships of small islands (MacArthur and Wilson 1967). Previous theoretical work has pointed out that if disturbances were the driver for the apparent stochasticity, relatively larger islands should consistently recover more species than smaller ones due to lower extinction rates (Chisholm et al. 2016), yet our results indicate that even relatively larger islands within atolls conform less to species–area curves under lower rainfall conditions. Overall, our data suggest that energetic constraints from water availability are more critical than disturbance regime in enabling species richness to scale predictably with area. Rainfall enhances the

conformity of island communities to the species–area curve, suggesting that sustained resources are a prerequisite for the manifestation of this fundamental law of species–area scaling, whereas disturbance frequency is not creating persistent stochasticity in species–area curves (Niering 1963, Wright 1983). However, our modelling approach only incorporated cyclone frequency as a disturbance variable. Other types of disturbances such as droughts or salinisation of groundwater may exert measurable effects on the species–area scaling, sensu MacArthur and Wilson's disturbance hypothesis (Fosberg 1948, Amerson 1969).

Beyond conformity, we show that rainfall also modulated the strength of the species–area relationship (see slope model). In ecological theory, the rate at which species accumulate with increasing area can be constrained by available energy or resources (Wright 1983). In atoll ecosystems, freshwater is a fundamental constraint for terrestrial productivity and biomass (Fosberg 1948, Frith 1979, Shekeine et al. 2015). Therefore, atolls that receive higher rainfall can accumulate more species per unit area, allowing species richness to scale more strongly with area (Kalmar and Currie 2006), while the disturbance regime exerts no negative effect on the species–area scaling. Instead, recent work suggested that disturbances from cyclones may even promote species richness by increasing compositional turnover and introducing historical contingency in the assembly of atoll island communities (Steibl and Russell 2024).

Previous efforts to reconcile predictable species–area relationships with the apparent stochasticity in small-island systems have focused on species-centric approaches, addressing the role of traits, life histories, or sampling scales below which the monotonic relationship between area and richness breaks and apparent stochasticity arises (Drakare et al. 2006, Sfenthourakis and Triantis 2009, Schrader et al. 2020). Our approach shifts the focus to the environmental factors that linearly facilitate species–area conformity through a continuous process and with a single scaling parameter (z) across

the entire island size range. We show that resource limitation exerts predictable effects on the stochasticity around the species–area scaling. Whether these findings are directly transferable to other non-atoll systems, or whether species–area conformity in other contexts is governed by alternative resource prerequisites (e.g. temperature, photoperiod) or by disturbance regimes, becomes an important future research endeavour to delimit and determine generalisable constraints of species–area relationships (Wright 1983).

Our results also underscore the importance of distinguishing between island-level (α-diversity) and atoll-level (γ-diversity) determinants of species richness (Cabral et al. 2014, Triantis et al. 2015). While island area strongly influences α-diversity, the total land area of an atoll ('archipelago') and its degree of geographic isolation exert relatively minor effects on γ-diversity. Instead, rainfall is the most important driver of atoll-level species richness, supporting earlier assessments that emphasized water availability in shaping atoll terrestrial diversity (Fosberg 1948, Amerson 1969, Lee 1984, Kreft et al. 2008). This distinction highlights the potential pitfalls of conflating atoll data at its archipelago-level (γ-diversity) with individual volcanic-island (α-diversity) data in macroecological analyses across multiple island types. Such comparisons may obscure processes operating at different spatial scales where the nested structure of individual islands within atolls is not correctly considered, as previously demonstrated by Cabral et al. (2014) and Triantis et al. (2015) for other island archipelago systems.

In addition to the critical new perspectives on a disturbance versus resource prerequisite model for explaining the elevated stochasticity of small-island species richness in species–area relationships, our modelling approach has broad relevance for future biogeographical and ecological studies. Conventional frameworks for studying species–area relationships in small islands rely on breakpoint analyses, suggesting that species–area relationships manifest only above a given threshold of island size, implying that nature operates with two or three separate scaling factors z dependent upon area (Dengler 2009, Chisholm et al. 2016). By explicitly modelling the magnitude of the error term (ε) in Arrhenius' power law, our approach provides a more parsimonious framework for species–area studies that obviates the need for bi- or triphasic models (Tjørve and Tjørve 2011, 2017). We demonstrate that smaller islands are not inherently non-conforming to species–area relationships, nor require a separate process and slope parameter, nor that any non-conformity depends on a particular (and arbitrary) threshold value of island area, i.e. breakpoint. Instead, the degree of conformity increases continuously as limiting resources – specifically here rainfall on atoll islands – are progressively alleviated. This perspective, which emphasizes the analysis of the drivers of residual variance over area breakpoint thresholds, offers a more parsimonious explanation of species–area scaling (Tjørve and Tjørve 2011). Similar propositions to favour single-process, continuous frameworks have also recently emerged in island speciation models for large islands (Valente et al. 2020).

Our study highlights the utility of the residual variance parameter for more deeply understanding species–area relationships. When explicitly considered as a parameter of interest rather than dismissed as a nuisance parameter or unexplainable 'stochastic noise', the statistical analysis for the drivers of the magnitude of residual variance enables insights into the prerequisites for one of the fundamental laws in ecology (Schoener 1976). Modelling conformity (or heteroscedasticity) is well established in other research fields (Rosopa et al. 2013, Voncken et al. 2021, Klein 2024) yet remains unexplored in species–area research. By utilising this method, we identified environmental factors that modulate the conformity of biological communities to species–area relationships, thus gaining a novel perspective into the prerequisites for predictable ecological assembly.

Author contributions

Sebastian Steibl: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Software (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Simon Steiger**: Formal analysis (equal); Investigation (equal); Methodology (equal); Software (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Luís Valente**: Writing – original draft (equal); Writing – review and editing (equal). **James C. Russell**: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

Transparent peer review

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Data availability statement

All raw data and statistical code, as well as tutorials for the application of heteroscedastic modelling in species–area research, are available from the Zenodo repository: https://doi.org/10.5281/zenodo.15129175 (Steibl et al. 2025b) and the GitHub repository: https://github.com/simonsteiger/SAR-conformity.

Supporting information

The Supporting information associated with this article is available with the online version.

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