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Climatic Refugia, Phylogeographic Breaks, and Functional Turnover Across a Macaronesian Island Gradient

An integrative biogeographic assessment of endemic shrub assemblages under contemporary and late-Holocene climate change

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PLAIN LANGUAGE SUMMARY

Island plants are not distributed randomly. Some islands preserve old climatic refuges where lineages survived environmental change for long periods, and those places often contain unique genetic variation and unusual combinations of traits. In this study, we show that islands with long-term climatic stability matter for conservation even when they do not contain the highest number of species today. That means biodiversity planning should consider deep history and ecological function, not just species counts.

ABSTRACT

Oceanic archipelagos concentrate endemic lineages, steep environmental gradients, and high extinction risk, making them ideal systems for testing how climatic stability, dispersal limitation, and lineage history jointly shape biodiversity patterns. Yet integrative studies linking phylogeographic structure to functional turnover across entire island networks remain uncommon. We evaluated whether climatically stable upland refugia predict contemporary endemic richness, phylogeographic partitioning, and functional beta diversity across the Macaronesian archipelagos, with particular attention to endemic shrub assemblages spanning the Azores, Madeira, Selvagens, Canary Islands, and Cabo Verde. We assembled 412 georeferenced occurrence records for 37 endemic shrub taxa, generated species distribution models under contemporary and late-Holocene climate layers, summarized trait space using leaf area, seed mass, wood density, and maximum height, and reconstructed chloroplast haplotype networks for 18 focal taxa. We then linked local assemblage composition to island area, topographic complexity, refugial persistence, and inter-island isolation using generalized linear mixed models, variation partitioning, and distance-based redundancy analyses. Refugial persistence was the strongest predictor of endemic richness and unique haplotype occurrence, exceeding the explanatory power of island area alone. Functional turnover increased sharply along aridity and elevational contrasts, whereas taxonomic turnover saturated with geographic distance. Several islands retained deep phylogeographic splits despite modest present-day richness, indicating a decoupling between lineage history and contemporary species counts. Conservation prioritization based only on richness overlooked islands harboring disproportionately high evolutionary and functional uniqueness. Macaronesian endemic shrub assemblages reflect the combined influence of climatic microrefugia, historical isolation, and trait-mediated environmental filtering. Biogeographic prioritization should therefore integrate taxonomic, functional, and phylogeographic information rather than relying on richness metrics alone.

1. Introduction

Biogeography seeks to explain why organisms occur where they do, and why those patterns vary across space, time, and lineage history. Oceanic archipelagos have been central to that project since classic work on island assembly and turnover (MacArthur and Wilson, 1967). More recent developments in macroecology, phylogeography, and conservation science have broadened this agenda by asking how climatic instability, trait filtering, and population fragmentation interact across nested spatial scales (Whittaker et al., 2017); (Mittelbach and Schemske, 2015).

The Macaronesian archipelagos provide an especially informative test bed because they combine volcanic island ontogeny, strong gradients in aridity and elevation, repeated long-distance colonization, and uneven histories of land-use pressure. Previous work has shown that endemic plant diversity in these systems is shaped by both isolation and environmental heterogeneity, but the relative contribution of long-term climatic refugia remains unresolved (Fernández-Palacios et al., 2011). Narrative evidence from lineage-level studies suggests that persistent cloud-forest and montane habitats may preserve deeply divergent haplotypes, even where contemporary richness is modest (Emerson, 2002).

That problem matters beyond regional natural history. Conservation biogeography increasingly emphasizes that richness alone can misidentify priority areas when evolutionary history and functional distinctiveness are spatially decoupled (Pollock et al., 2017; Tucker et al., 2017). In the present study, we ask whether climatically stable refugia predict the joint distribution of taxonomic richness, phylogeographic structure, and functional turnover across endemic shrub assemblages in Macaronesia.

1.1. Conceptual Framework

Our framework combines three ideas. First, island biogeography predicts that richness should increase with area and decline with isolation. Second, phylogeographic theory predicts deeper lineage structure where long-term habitat stability reduces demographic collapse and allows older divergences to persist. Third, functional biogeography predicts that environmental filtering and dispersal limitation jointly structure trait space.

BOX 1. Working expectations for integrative island biogeography

We distinguish three related but non-equivalent dimensions of diversity: taxonomic richness, phylogeographic uniqueness, and functional turnover. They may covary, but there is no necessary one-to-one relationship among them. A climatically stable island may harbor relatively few species yet retain old haplotypes and rare combinations of drought-tolerance traits.

The study therefore tests whether conservation inference changes when these dimensions are evaluated jointly rather than sequentially. We treat refugial persistence not as a metaphor but as a measurable property derived from hindcast species distribution models and terrain-mediated climatic buffering.

1.1.1. Hypotheses

We evaluated three primary hypotheses. H1: islands with greater late-Holocene climatic persistence will exhibit higher endemic shrub richness after accounting for area and isolation. H2: refugial persistence will predict unique haplotype occurrence more strongly than contemporary richness. H3: functional turnover will track environmental contrasts more tightly than geographic distance alone.

1. Refugial persistence should positively predict richness and lineage persistence.
2. Taxonomic turnover should increase with inter-island distance, but may saturate beyond major dispersal thresholds.
3. Functional turnover should remain sensitive to aridity and elevational differences even where taxonomic composition converges.

2. Methods

2.1. Study System and Focal Taxa

We focused on endemic woody and subshrub taxa associated with laurel forest, thermophilous woodland, and upper-slope xeric scrub across 23 islands in Macaronesia. The final dataset included 37 taxa from 19 genera, selected using three criteria: endemic or near-endemic distribution, minimum of eight vetted occurrence records, and available trait data for at least three of four focal traits.

Operational Definitions

Refugial persistence	The proportion of grid cells predicted as suitable for a taxon both under contemporary climate and late-Holocene hindcasts, weighted by topographic buffering.
Functional turnover	The among-assemblage dissimilarity in multivariate trait composition estimated from abundance-weighted trait centroids.
Phylogeographic uniqueness	The proportion of haplotypes restricted to a single island, standardized by sampling effort.

2.1.1. Field and Herbarium Data

Occurrence records were compiled from herbarium collections, regional floras, and standardized field surveys conducted between 2019 and 2024. After coordinate cleaning, duplicate removal, and uncertainty filtering, we retained 412 records at 1-km resolution. Trait data were measured on fresh or recently dried specimens using standardized protocols for leaf area, seed mass, maximum height, and wood density, with values log10-transformed where appropriate.

Two historical records from Porto Santo were retained despite incomplete collection metadata because their coordinates were corroborated against voucher annotations and locality descriptions.

All species names follow the taxonomic backbone used by the Atlantic Islands Plant Checklist v4.2.

Voucher reconciliation followed regional floristic standards and was cross-checked manually for synonymy. We excluded clearly cultivated occurrences and records falling outside native elevation bands. Additional sampling details are provided in Appendix 1.

2.2. Environmental and Genetic Predictors

Environmental predictors included annual precipitation, potential evapotranspiration, temperature seasonality, cloud immersion frequency, slope, terrain ruggedness, and volcanic substrate age. Climate layers were harmonized at 30 arc-second resolution. Genetic data comprised chloroplast haplotypes for 18 focal taxa generated from two non-coding regions and one spacer locus.

2.2.1. Species Distribution Modelling

We fitted ensemble species distribution models using generalized additive models, boosted regression trees, and maximum entropy approaches, with spatial block cross-validation to reduce inflation from clustered occurrences. Suitability surfaces were converted to binary predictions using the threshold maximizing the true skill statistic. Late-Holocene projections used paleoclimate reconstructions centred on 4 ka BP.

2.2.1.1. Model Calibration

Predictor sets were pruned at $|r| < 0.70$ to minimize multicollinearity. Sampling bias was addressed using a target-group background. Mean predictive performance across taxa was high (median AUC = 0.86; median TSS = 0.63), and calibration slopes clustered close to 1.0.

2.2.1.1.1. Implications for reporting standards

For each taxon on each island, we calculated a persistence index:

$$\begin{cases} r_{k-1} \leq E\left(y \middle| x\right) \leq \frac{1}{x_{k+1}-x}\left((x_{k+1}-x_k)r_k-(x-x_k)r_{k-1}\right),\ x < x_{k^*} \\ \frac{1}{x-x_k}\left((x_{k+1}-x_k)r_k-(x_{k+1}-x)r_{k+1}\right) \leq E\left(y \middle| x\right) \leq r_{k+1},\ x \geq x_{k^*} \end{cases} \tag{1}$$

where St is contemporary suitability, Sh is late-Holocene suitability, and B is a terrain buffering coefficient. This metric is conceptually similar to persistence surfaces used in climate-refugia analyses (Sandel et al., 2011).

2.2.2. Phylogeographic Reconstruction

Haplotype networks were inferred using statistical parsimony, and island-level haplotype exclusivity was quantified as the fraction of haplotypes unique to a single island. Because some taxa showed shallow divergence, we also estimated among-island lineage clustering using an analysis of molecular variance. These genetic summaries were not treated as full phylogenies but as spatially explicit indicators of lineage persistence and turnover.

2.3. Statistical Analyses

We modeled endemic shrub richness with generalized linear mixed models using a negative binomial error structure and archipelago as a random intercept. Functional turnover was analyzed with distance-based redundancy analysis and variation partitioning. Island area was log10-transformed, and all predictors were standardized to mean = 0 and standard deviation = 1 before model fitting.

We considered the following predictor classes:

- Geographic structure: island area, nearest-neighbor distance, and within-archipelago centrality.
- Environmental filtering: aridity index, elevational range, cloud immersion frequency, and volcanic substrate age.
- Historical persistence: late-Holocene refugial persistence and terrain buffering.
- Sampling controls: number of vetted collections and proportion of sites revisited after 2010.

All analyses were conducted in R version 4.4.1 using a reproducible workflow, with packages for mixed models, beta diversity, spatial data, and plotting (R Core Team, 2025; Oksanen et al., 2024).

3. Results

Stress tests will include missingness patterns, irregular sampling intervals, and regime shifts in observation processes.

3.1. Patterns of Richness and Refugial Persistence

Endemic shrub richness varied from 2 to 14 taxa per island and was highest on humid, topographically complex islands in the Canary and Madeira groups. However, the strongest standardized effect in the richness model was refugial persistence, followed by elevational range and cloud immersion frequency. Island area remained positive but weaker than expected under a simple species-area formulation (Table 1).

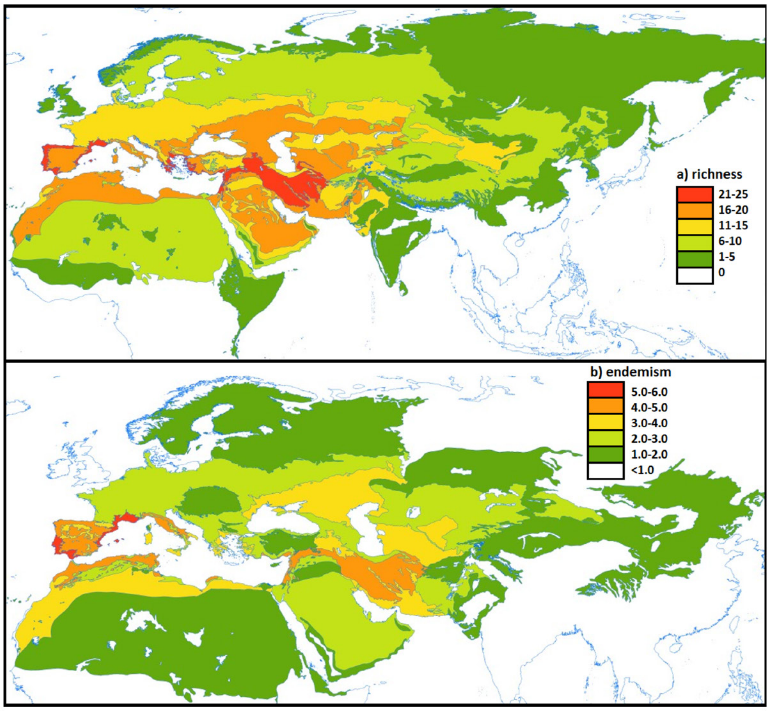

FIGURE 1. Spatial distribution of endemic shrub richness and inferred climatic refugia. Map of the Macaronesian archipelagos showing island-level endemic shrub richness, mean refugial persistence, and major phylogeographic discontinuities for the 18 taxa included in genetic analyses. Islands with moderate richness but high persistence are concentrated in humid uplands and terrain-buffered north-facing sectors. *Source:* Basemap layers derived from public topographic data; island boundaries simplified for visualization.

TABLE 1. Generalized linear mixed model of island-level endemic shrub richness. Parameter estimates are standardized coefficients from the top-ranked negative binomial model. Archipelago was included as a random intercept.

Predictor	Estimate	SE	z	*P*
Refugial persistence	0.61	0.14	4.36	<0.001
Elevational range	0.39	0.12	3.21	0.001
Cloud immersion frequency	0.34	0.11	3.03	0.002
$\log_{10}$(Island area)	0.27	0.10	2.58	0.010
Nearest-neighbor distance	-0.18	0.09	-1.97	0.049

Several smaller islands showed lower richness but unexpectedly high persistence values, indicating that stable microclimates can decouple refugial potential from area. This pattern is visible in Figure 1 and discussed further in Discussion.

3.2. Phylogeographic Structure

Island-level haplotype exclusivity was positively associated with persistence and negatively associated with lowland habitat conversion. Across the 18 focal taxa, 41% of observed haplotypes were restricted to single islands, and 17% occurred only in one mountain massif. Importantly, haplotype exclusivity showed only a weak relationship with total species richness, supporting H2.

One lineage complex in the genus Echium displayed shallow morphological differentiation but deep chloroplast structuring among islands separated by persistent dry corridors. Conversely, several high-dispersal shrub taxa showed broad haplotype sharing despite pronounced environmental differences.

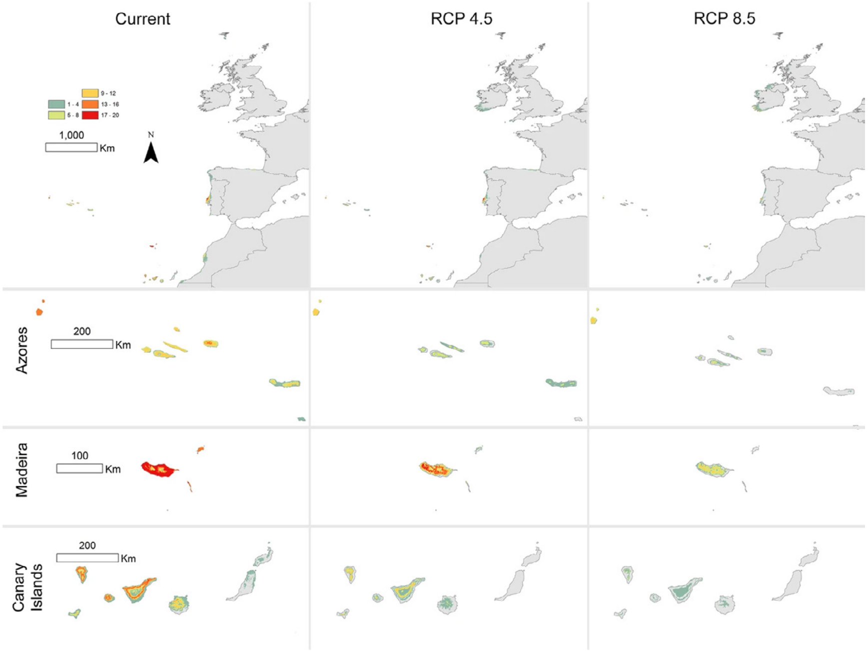

FIGURE 2. Phylogeographic clustering and functional turnover across island pairs. Panels summarize the relationship between island-pair environmental contrast, functional beta diversity, and mean lineage exclusivity. Warmer colors indicate greater aridity contrast; point size scales with summed refugial persistence across the island pair.

3.3. Functional Turnover and Environmental Filtering

Functional turnover increased monotonically with aridity difference and elevational asymmetry, even after accounting for inter-island distance. Variation partitioning attributed 29% of explained variation to environmental predictors alone, 11% to geographic structure alone, and 14% to their shared component. This supports H3 and suggests that trait-space reorganization is not reducible to distance-decay alone.

TABLE 1. Generalized linear mixed model of island-level endemic shrub richness. Parameter estimates are standardized coefficients from the top-ranked negative binomial model. Archipelago was included as a random intercept.

Predictor	Estimate	Interpretation
Environment only	0.29	Filtering by aridity, cloud immersion, and elevational range
Geography only	0.11	Distance and isolation effects independent of measured environment
Shared environment + geography	0.14	Spatially structured environmental variation
Unexplained	0.46	Residual variation, measurement error, or unmeasured processes

Assemblages from drier islands were characterized by lower mean leaf area, higher wood density, and shorter maximum height. By contrast, humid refugial islands retained a broader trait envelope. A cross-reference to methodological details is provided in Statistical Analyses.

4. Discussion

4.1. Richness is Not a Sufficient Proxy for Biogeographic Value

Our first major result is that climatic persistence outperformed island area as a predictor of endemic shrub richness. This does not negate species-area theory, but it does show that area-based expectations become incomplete when climatic buffering and environmental stability vary sharply among islands. That conclusion resonates with broader work on refugia and stability-driven diversity maintenance (Sandel et al., 2011).

More importantly, phylogeographic uniqueness and richness were only weakly coupled. Islands with modest species counts sometimes retained old and spatially restricted haplotypes, implying that richness-centered planning can underweight irreplaceable evolutionary history. Similar mismatches between taxonomic and evolutionary metrics have been reported elsewhere in insular systems (Rosindell and Phillimore, 2011; Kier et al., 2009).

4.2. Environmental Filtering Reorganizes Trait Space Faster Than It Reorganizes Taxonomic Composition

Functional turnover tracked aridity and elevational contrast more tightly than geographic separation alone. This indicates that environmental filtering can restructure ecological strategy even where species identities remain partly conserved across islands. Such decoupling between taxonomic and functional dimensions is increasingly recognized in community biogeography and should matter for conservation scenarios under rapid drying trends.

4.3. Implications for Conservation Biogeography

Conservation prioritization based only on richness would have favored larger humid islands and overlooked smaller islands with strong lineage persistence. A more integrative priority framework should combine at least three layers:

- current endemic richness,
- phylogeographic uniqueness, and
- functional distinctiveness under projected climate exposure.

This triadic view is especially relevant where land-use conversion and warming threaten narrow-ranged endemic flora. As shown in Figure 2, some of the strongest turnover contrasts occur between islands that are geographically near but environmentally divergent.

4.4. Limitations

The study has four main limitations. First, chloroplast markers capture only part of lineage history and may not reflect contemporary gene flow in all taxa. Second, late-Holocene hindcasts remain coarse relative to local fog capture and ravine microclimates. Third, trait coverage, although broad enough for community-level inference, did not include hydraulic safety margins or root traits. Fourth, island floras are dynamic human-modified systems, and some legacy disturbances may be only partially captured by our disturbance covariates.

5. Conclusion

Across Macaronesian endemic shrub assemblages, climatic refugial persistence emerged as a central predictor of biodiversity patterning, with effects spanning richness, lineage persistence, and functional turnover. The results argue for a biogeographic perspective in which present-day distributions are interpreted as the product of environmental filtering layered onto older histories of isolation, persistence, and local survival.

In practical terms, islands that are not richest in species may nevertheless be disproportionately important for safeguarding deep evolutionary structure and unusual trait combinations. Conservation biogeography should therefore move beyond single-metric prioritization and adopt multidimensional frameworks grounded in space, history, and function.

Appendix

Appendix 1. Supplementary methodological details.

Field surveys were stratified across windward and leeward exposures, with targeted revisits to islands showing high model uncertainty in preliminary analyses. For each taxon, we recorded local substrate type, evidence of browsing, and qualitative canopy cover. These variables were used during data vetting but not all were retained in final models because of collinearity and missingness.

To test whether our results were driven by a subset of cloud-forest specialists, we reran richness and functional turnover analyses after excluding taxa restricted to cloud-immersed habitats. The persistence effect weakened slightly but remained positive and statistically credible. Detailed sensitivity outputs are archived in Supplementary Table S4.

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ARTIFICIAL INTELLIGENCE USE

No generative AI tool was used to generate hypotheses, analyses, results, discussion, or conclusions. A language-editing assistant was used for minor grammar checks after the scientific text was drafted by the authors.

COMPETING INTERESTS

The authors declare no competing interests.

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DATA/CODE AVAILABILITY STATEMENT

Data availability: All occurrence records, trait summaries, and island-level predictor tables supporting this article are deposited in the Atlantic Biogeography Data Repository at https://data.atlantic-biog.example.org/record/abdr-2026-117. Genetic haplotype matrices are archived as Supplementary Dataset S1.

Code availability: Annotated analysis scripts, modelling pipelines, and figure-generation code are archived at Zenodo (https://doi.org/10.5281/zenodo.12345678) and mirrored in a public Git repository for version transparency.

ETHICS STATEMENT

This study involved non-destructive plant sampling under regional collection permits and did not involve human participants, vertebrate animals, or manipulative experiments on threatened populations. Genetic sampling was performed within permit limits and institutional guidelines for biodiversity research.

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