

Venomous Archipelagos: Integrating Adaptability and Island Biogeography Theory to Assess Persistence in the Anthropocene

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Introduction

Understanding how environmental change affects biodiversity is crucial for conserving evolvability, yet difficult to predict. Islands serve as natural experiments and proxies for habitat fragmentation, allowing us to apply Island Biogeography Theory (IBT) to investigate the effects of habitat fragmentation on functional trait evolution¹. Rattlesnake venom, a molecular phenotype linked to prey diversity, provides an effective model for testing the influence of IBT (island size, isolation, and age) on trait evolution². We analyzed venom complexity from rattlesnakes across multiple Gulf of California islands, examining its relationship with island size, isolation, age, and competition. Our findings integrate IBT with trait evolution to predict biodiversity loss impacts across fragmented landscapes.

Hypotheses

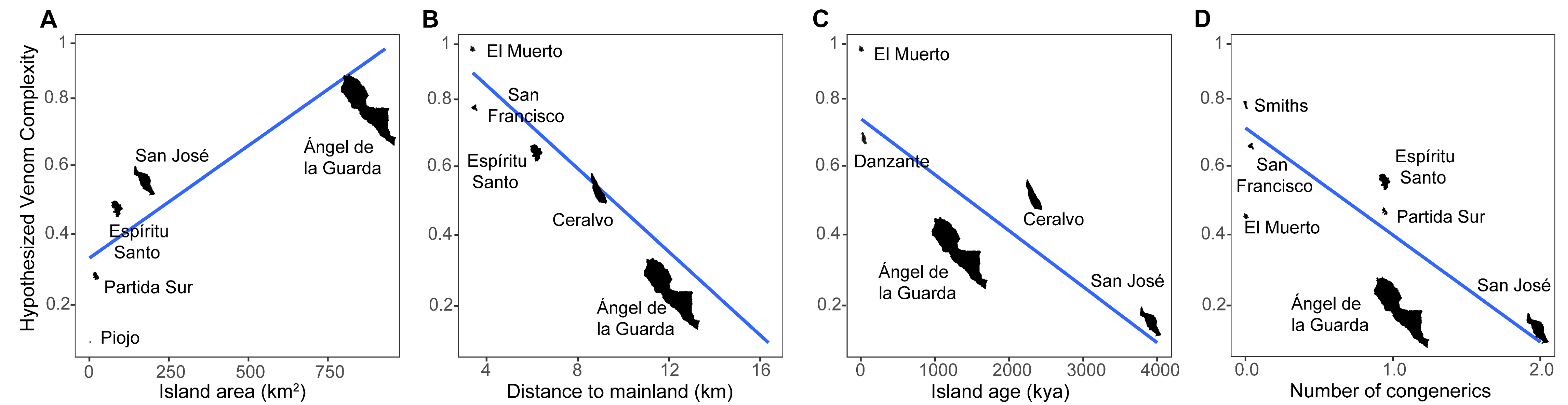


Figure 1: Hypotheses and predicted outcomes regarding the relationship between venom complexity and island (A) area, (B) distance to mainland (i.e., degree of isolation), (C) age, and (D) number of sympatric congeners (i.e., other rattlesnake species found on the island). Islands are drawn to scale. X-axis values represent true values. Y-axis values represent simulated values consistent with each hypothesis.

Materials & Methods

Data collection and processing: We sampled venom from 83 individuals across four rattlesnake species (*Crotalus mitchellii*, *C. ruber*, *C. enyo*, and *C. pyrrhus sensu lato*) on 11 islands. Venom was analyzed using reversed-phase high-performance liquid chromatography (RP-HPLC). Protein peak abundance was estimated as the area under each peak relative to the total area of all peaks. Venom complexity was quantified using the Shannon Diversity Index²(*H*).

Statistical analyses: Using a mixed effects multiple linear regression accounting for spatial autocorrelation by individual species, we determined whether island area, isolation, age, and number of competitors best explained relative venom complexity across all four species. To validate the biological significance of the observed complexity patterns, we determined which of the same factors best predicted multivariate venom expression variation using conditional redundancy analysis (RDA).

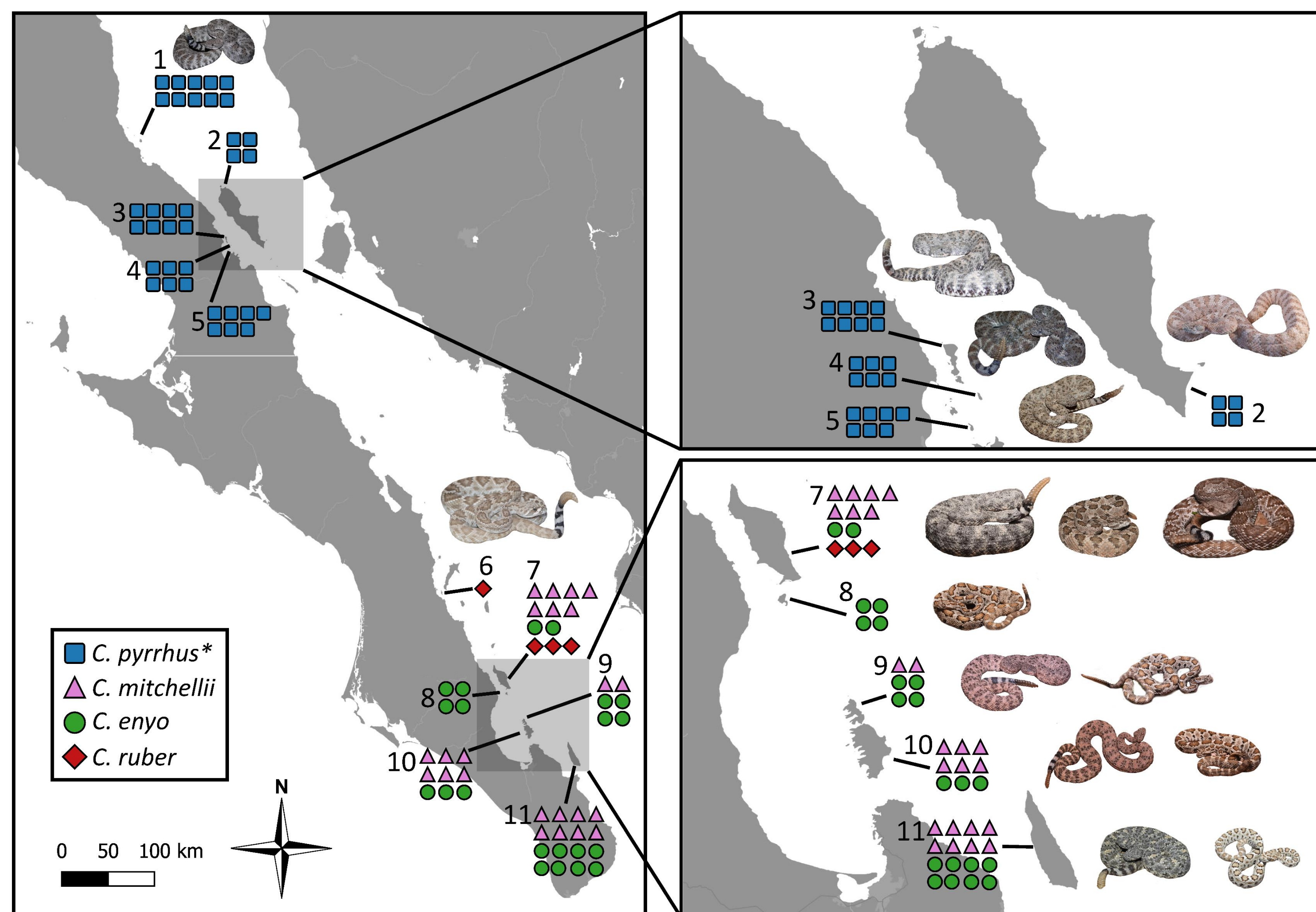


Figure 2: Sampling of 83 rattlesnakes collected across 11 islands. Left map shows all islands along the Baja California Peninsula, and right maps show insets of two regions with high island density.

Venom Complexity Predicted by Competition, Island Area, and Island Isolation

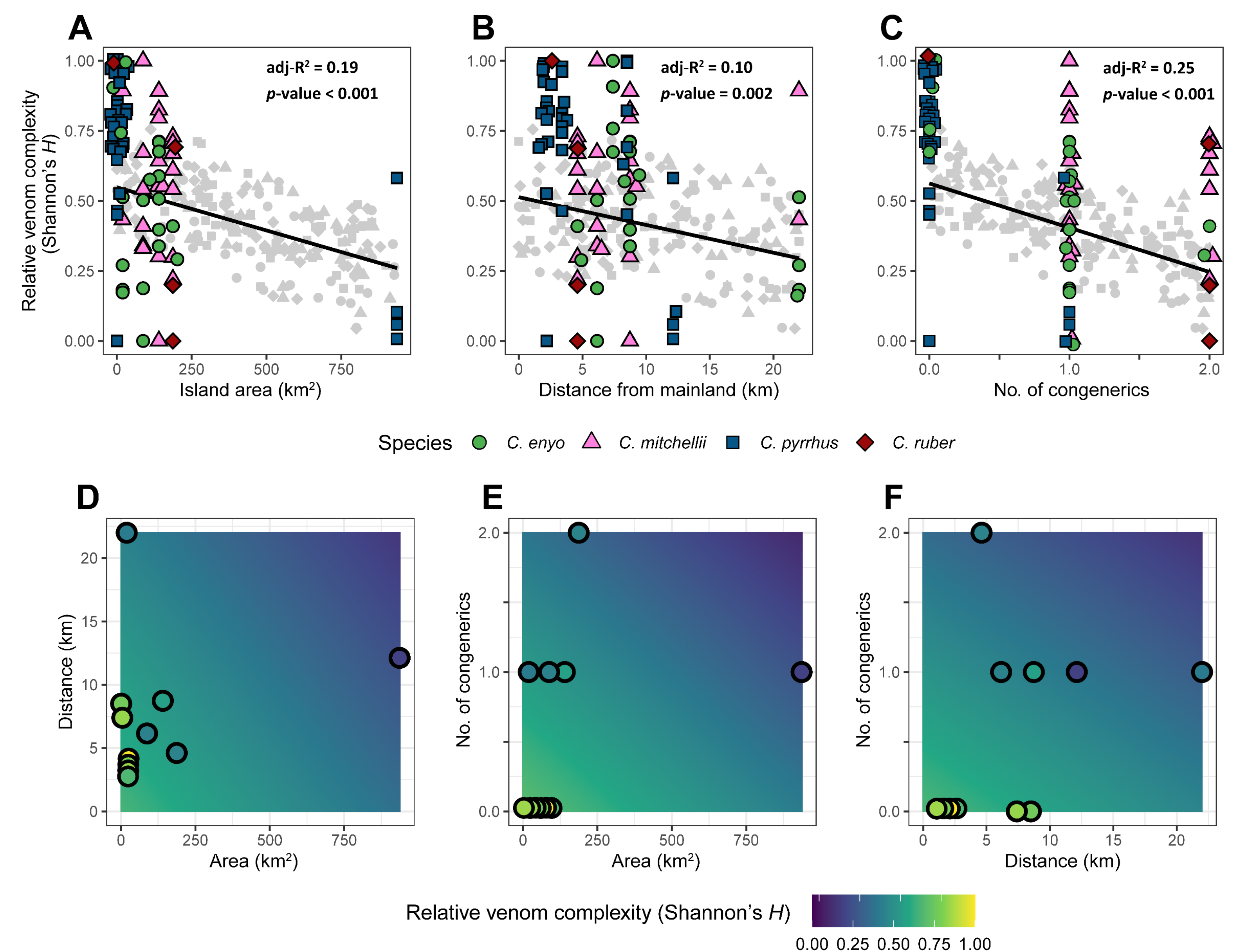


Figure 3: (A–C) Relationships between venom complexity and the significant factors identified via our MMLR. (D–F) Heatmaps showing the relationship between venom complexity (tile color) and pairs of significant predictors (x- and y-axes).

Age	Area	Distance	Cong.	SVL	$\Delta AICc$
NA	-0.0003	-0.0103	-0.1485	NA	0
NA	-0.0003	NA	-0.1605	NA	0.96
NA	NA	-0.0113	-0.1815	NA	1.11
NA	NA	-0.0111	-0.1697	-0.0023	1.97
NA	-0.0003	-0.0104	-0.1452	-0.0010	2.23
0.0173	-0.0003	-0.0104	-0.1604	NA	2.24
NA	NA	NA	-0.1995	NA	2.63

Table 1: MMLR model selection results for venom complexity. β coefficient values for island age, area, isolation, number of congeners (Cong.), and snake size (SVL) and $\Delta AICc$.

Explanatory Variable	F	p-value	adj-R ²
Marginal Model			0.26
Congenerics	15.57	0.001	0.15
Snake size	12.43	0.001	0.11
Conditioned Individual Variables			
Snake size	7.63	0.001	0.06
Island area	7.43	0.001	0.06
Island distance	1.71	0.168	0.01
Island age	0.15	0.946	0.00
Congenerics	13.44	0.001	0.11
Full model	8.32	0.001	0.31

Table 2: Results of the conditional RDA across all species with venom expression as the multivariate response variable.

Conclusions

- Venom complexity follows IBT predictions for isolation but contradicts expectations for island area, decreasing instead of increasing.
- Competition, more than island area, was the primary driver of venom evolution, suggesting that increased putative competition on larger islands leads to niche partitioning and specialization.
- Island age did not significantly predict venom complexity, highlighting the potential for rapid functional adaptation.
- Preserving functional trait diversity for conservation requires strategies that balance maintaining habitat connectivity while considering the effects of increased habitat area on competition and niche partitioning.

References & Funding

References:

1. MacArthur, R.H. and Wilson, E.O., 2001. *The theory of island biogeography* (Vol. 1). Princeton university press.
2. Holding, M.L., et al. 2021. Phylogenetically diverse diets favor more complex venoms in North American pitvipers. *Proceedings of the National Academy of Sciences*, 118(17), p.e2015579118.

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