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Article

Island biogeography and competition drive rapid venom complexity evolution across rattlesnakes

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Abstract

Understanding how human-mediated environmental change affects biodiversity is key for conserving evolvability. Because the most severe impacts are ongoing, such an understanding is proving exceptionally difficult to attain. Islands are natural, replicated experiments that serve as proxies for habitat fragmentation and, therefore, allow us to use historical changes in biodiversity under Island Biogeography Theory (IBT) to predict the consequences of immediate anthropogenic impacts on functional trait evolution. Rattlesnake venoms are molecular phenotypes that mediate interactions with prey, and diet and venom complexity are positively correlated. Consequently, rattlesnake venoms allow us to investigate how functional traits co-vary with changes in biodiversity according to IBT. We collected venom from 83 rattlesnakes across multiple species and 11 islands in the Gulf of California and estimated venom complexity using the Shannon Diversity Index. Using a mixed effects modeling approach, we found that the number of congenerics, island isolation, and island area best predicted venom complexity variability. All variables exhibited a negative relationship with venom complexity, contrary to predictions for island area under IBT. Larger islands with more congenerics exhibited reduced trait complexity, perhaps reflecting niche partitioning and venom specialization. Ultimately, we used a synthetic eco-evolutionary framework to predict functional trait evolution across fragmented landscapes.

Keywords: island biogeography, conservation, functional trait

Habitat loss is a major driver of the current biodiversity crisis (Ceballos *et al.*, 2015; De León *et al.*, 2023; Zhang *et al.*, 2024), contributing to extinctions and extirpations in many taxa worldwide (Haddad *et al.*, 2015; Laurance *et al.*, 2018; Young *et al.*, 2016). Habitat-based solutions to the biodiversity crisis have been described as crucial (Marske *et al.*, 2023), yet such solutions would require a thorough understanding of how changes and reductions in biodiversity within particular environments affect evolutionary potential (Forester *et al.*, 2022) and functional biodiversity (e.g., trait variation that affects ecosystem dynamics and structure in different environments). Such an understanding is proving exceptionally difficult to obtain considering the most severe biodiversity effects are occurring now (De León *et al.*, 2023; Marske *et al.*, 2023). Therefore, natural, past changes in species richness may provide us our best opportunity to understand how changes in biodiversity bias evolutionary trajectories, ultimately enabling us to make predictions regarding anthropogenic-induced effects occurring now and in the future.

Foundational ecological theories have historically been used to predict broad biological patterns (Caswell, 1978; Cohen

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et al., 1997; O'Connor *et al.*, 2019; MacArthur and Wilson, 2001; Margalef, 1963; Simpson, 1964), including species richness, and may offer essential perspectives for predicting evolutionary trajectories based on rapidly changing biodiversity dynamics. One such ecological theory is Island Biogeography Theory (IBT; MacArthur and Wilson, 1963, 2001) which has been used to explain patterns of migration and extinction, and may explain species persistence on islands across a variety of taxa (Burns, 2015; Gillespie and Baldwin, 2009; Helmus *et al.*, 2014; Holland and Cowie, 2009; Kadmon and Pulliam, 1993; Lenzner *et al.*, 2017; MacArthur and Wilson, 1963; Presgraves and Glor, 2010; Triantis *et al.*, 2012; Warren *et al.*, 2015; Weigelt *et al.*, 2016; Whittaker and Fernandez-Palacios, 2007; Whittaker *et al.*, 2017). IBT predicts that species richness positively correlates with island area and negatively correlates with island isolation (MacArthur and Wilson, 1963, 2001).

Islands provide natural, replicated experiments that can serve as a proxy for habitat fragmentation. Habitat fragmentation is conceptually analogous to island systems because relatively isolated habitat patches may be embedded within a larger landscape matrix made uninhabitable by anthropogenic activity (Bueno and Peres, 2019; Laurance, 2008; Powledge, 2003; Whittaker and Fernandez-Palacios, 2007). As a result, islands may allow us to use natural, historical changes in species richness under IBT to predict the evolutionary consequences of current habitat fragmentation on functional biodiversity, particularly for functional traits mediating species interactions. Indeed, functional traits are likely to be evolving under strong selection (Betzholtz *et al.*, 2013; Geber and Griffen, 2003; Nosil *et al.*, 2018; Vermeij, 1994; Spitz *et al.*, 2014) and, therefore, may respond rapidly to changes in species richness, as these changes should alter the nature, frequency, and/or strength of the interspecific interactions the traits are mediating (Jacquet *et al.*, 2017). On islands, where species richness varies predictably under IBT (MacArthur and Wilson, 1963, 2001), functional trait-based analyses provide a powerful framework for understanding how changes in ecological conditions and biodiversity influence organismal evolution and function (Adler *et al.*, 2013; Barnett *et al.*, 2019). By focusing on the relationships between habitat characteristics, species richness, and functional trait evolution, we can assess whether foundational ecological theories such as IBT explain the evolutionary consequences of biodiversity change.

Indeed, functional trait-based analyses in the context of IBT have been used to assess how species richness influences trait distributions across different island systems. For example, in the Azorean archipelago, functional diversity in spiders and beetles—measured through variation in traits such as body size, locomotion strategies, and feeding guilds—increases predictably with species richness, which positively and negatively scales with island area and isolation, respectively (Whittaker *et al.*, 2014). Plant functional diversity on islands, including traits such as leaf morphology, seed dispersal mechanisms, and growth forms, is shaped by dispersal limitation, environmental filtering, and species interactions, linking island characteristics and functional trait variation (Schrader *et al.*, 2021). Similarly, in reef fish communities, habitat area and isolation influence functional trait variation, with small and isolated reefs favoring large-bodied species due to resource limitations (Jacquet *et al.*, 2017). Collectively, these studies demonstrate that IBT can predict the patterns of functional trait diversity by associating species richness and ecological function, providing a foundation for testing how biodiversity change shapes functional traits.

Functional traits, however, may differ in the degree to which they are expected to co-vary with species richness under IBT. Traits such as body size or foraging strategy may be indirectly influenced by species richness through complex ecological interactions, including shifts in resource availability, competitive dynamics, and/or niche differentiation (Jacquet *et al.*, 2017; Schrader *et al.*, 2021; Whittaker *et al.*, 2014). In contrast, traits that directly mediate interspecific interactions may be more immediately shaped by changes in species richness. Animal venoms provide a uniquely direct system for testing how IBT-predicted variation in species richness influences functional trait evolution because venom functions solely following injection into another organism, resulting in direct species interactions.

Snake venoms are glandular secretions comprised of toxic proteins that collectively function to immobilize and digest prey (Barlow *et al.*, 2009; Casewell *et al.*, 2011; Daltry *et al.*, 1996; Mackessy, 2021; Munawar *et al.*, 2018). Toxin expression levels, which predict venom function, often vary due to adaptive differences against distinct prey species (Margres *et al.*, 2016, 2017), with genetic factors, rather than environmental (i.e., plastic), producing such variation (Gibbs and Mackessy, 2009; Margres *et al.*, 2015a). As complex mixtures of proteins, venoms can be quantified through chromatographic separation, allowing the application of diversity metrics such as Shannon's H index to investigate trait complexity (Berenbaum and Zangerl, 1998; Holding *et al.*, 2021; Richards *et al.*, 2015; Zancolli and Casewell, 2020). Snake venoms evolve largely as a function of diet, with more diverse diets favoring more complex venoms (Holding *et al.*, 2021). Consequently, we may expect that venomous snakes inhabiting larger, less isolated islands, which are predicted to have greater species richness under IBT (MacArthur and Wilson, 1963, 2001), have more complex diets and, therefore, more complex venoms compared with conspecifics on smaller islands (Figure 1). The putative connections between species richness, dietary breadth, and venom complexity underscore the utility of using venom to understand how functional traits may co-vary with changes in biodiversity.

Rattlesnake venoms have been extensively studied and characterized (Borja *et al.*, 2018; Durban *et al.*, 2017; Hirst *et al.*, 2024; Holding *et al.*, 2018, 2021; Mackessy *et al.*, 2003; Mackessy, 2010, 2021; Margres *et al.*, 2015b,a, 2019; Massey *et al.*, 2012; Meik *et al.*, 2018; Rautsaw *et al.*, 2019; Rokyta *et al.*, 2017; Schield *et al.*, 2022; Schonour *et al.*, 2020; Smith *et al.*, 2023; Wray *et al.*, 2015), and ≥10 rattlesnake species have been documented on islands, with the highest density of island populations found in the western Gulf of California (Case *et al.*, 2002; Grismer, 2002). Here, four species [Speckled Rattlesnakes (*Crotalus mitchellii*), Southwestern Speckled Rattlesnakes (*Crotalus pyrrhus sensu lato*), Red Diamond Rattlesnakes (*Crotalus ruber*), and Baja California Rattlesnakes (*Crotalus enyo*)] occur in different combinations across ≥20 islands (Glenn and Straight, 1985; Grismer, 2002; Meik *et al.*, 2018). Snake species richness on these islands has been shown to positively correlate with island area and negatively correlate with island distance from the mainland (Arnaud *et al.*, 2024; Grismer, 2002), consistent with expectations under IBT. Such patterns suggest that other taxonomic groups, including prey, may follow similar trends, making the Gulf of California islands an excellent system for

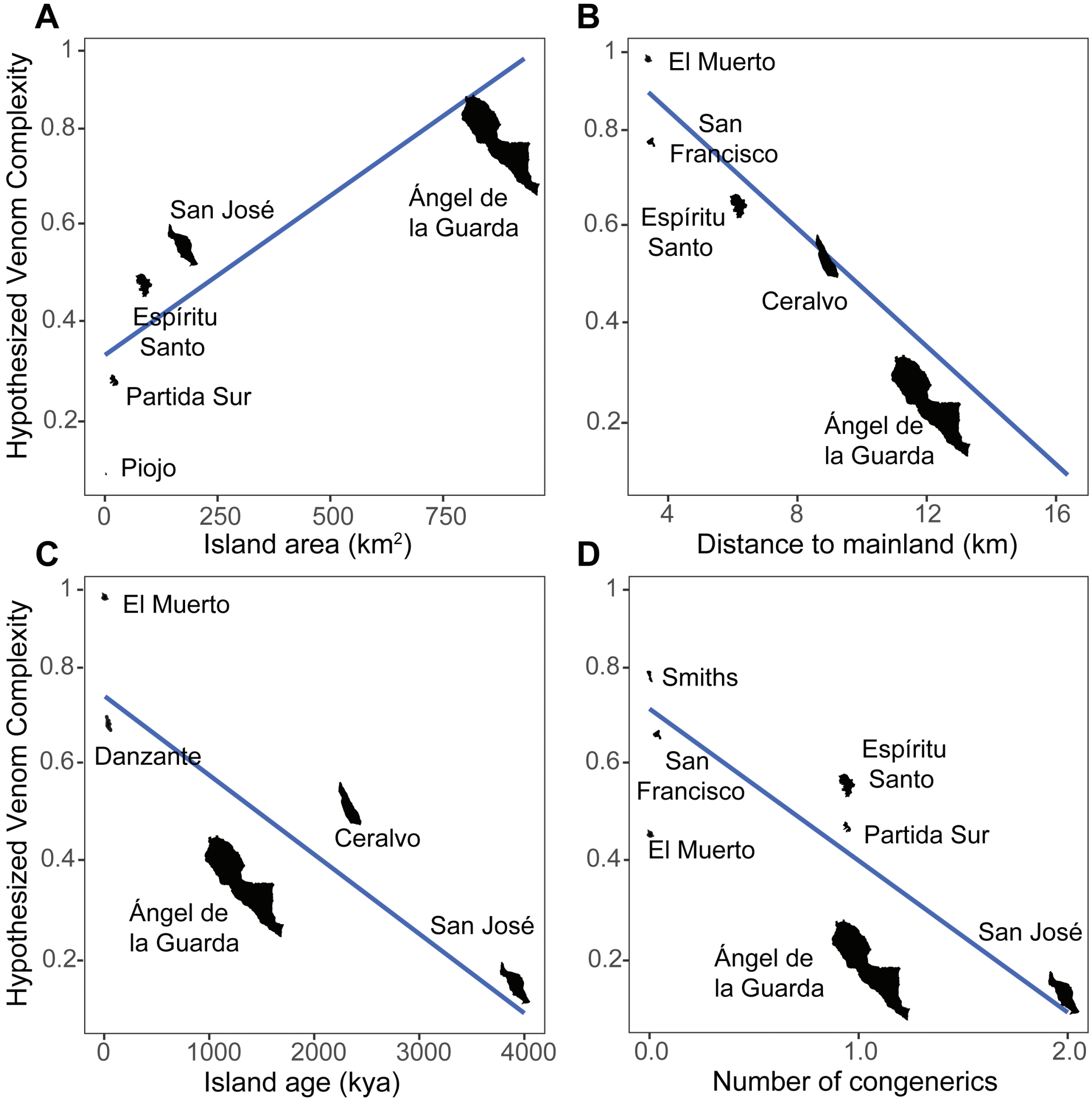

Figure 1. Hypotheses and predicted outcomes regarding the relationship between venom complexity and island (A) area, (B) distance to mainland (i.e., degree of isolation), (C) age, and (D) number of sympatric congenerics (i.e., other rattlesnake species found on the island). Note that our hypotheses represent competing predictions and may contradict one another. Specifically, putative competition from congenerics (D) introduces an alternative, non-IBT mechanism that could disrupt patterns expected under the other hypotheses. We expect that island area, isolation, age, and number of congenerics may each individually influence venom complexity, but the relative contributions and interactions of these factors remain unknown. Islands are drawn to scale, and only a subset of the islands is shown for clarity. *X*-axis values represent true values. *Y*-axis values represent simulated values consistent with each hypothesis.

testing whether IBT predicts functional trait evolution. Building on these trends, we made two key assumptions in this work: (1) prey diversity is positively correlated with species richness patterns under IBT (i.e., increases with island area and proximity to the mainland), and (2) higher prey diversity leads to broader dietary breadth in snakes. We recognize that either or both assumptions may be violated in certain or even many instances, yet such violations should result in the absence of a relationship between venom complexity and IBT predictors. Conversely, patterns consistent with IBT would support the use of IBT to predict functional trait evolution across fragmented landscapes. Ultimately, our framework allowed us to test whether IBT-driven patterns of species richness predict changes in venom complexity across islands; confirming the ultimate and proximate causes of such patterns requires additional work beyond the scope of this study (see Discussion).

We collected venom from 83 rattlesnakes across 11 islands (Figure 2) to investigate how venom complexity correlates with island area, distance from the mainland, age, and the number of sympatric, putative competitors. Island area has been shown to positively correlate with species richness across various taxa (Hannus and Von Numers, 2008; Kalmar and Currie, 2007; Kohn and Walsh, 1994; Triantis *et al.*, 2012), including in snakes across these islands (Arnaud *et al.*, 2024); therefore, we hypothesized that venom complexity positively correlates with island area (Figure 1A). Because increased island isolation can lead to reduced species richness

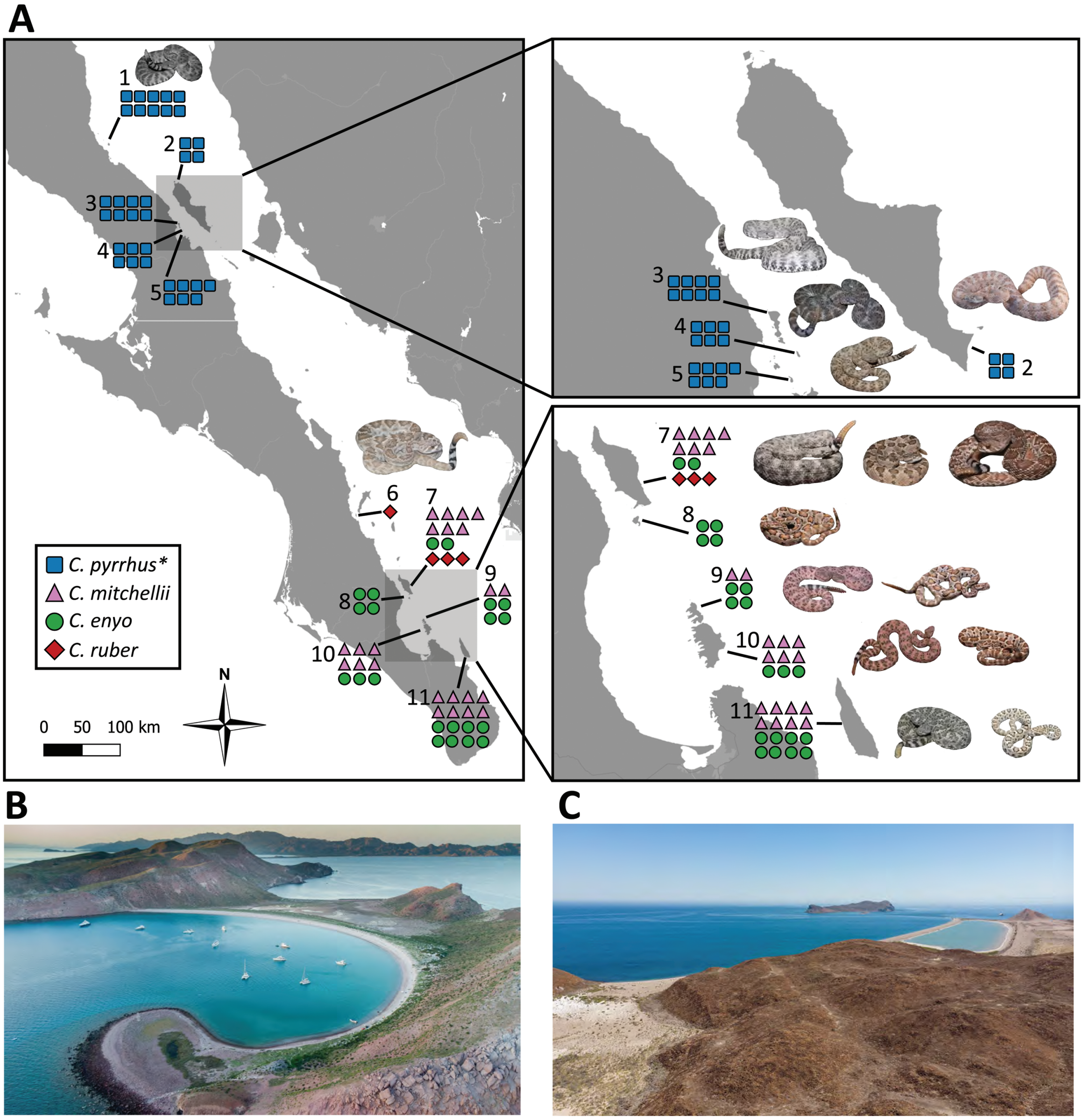

Figure 2. Sampling of 83 rattlesnakes collected across 11 islands. (A) Left map shows all islands along the Baja California Peninsula, and right maps show insets of two regions with high island density. Rattlesnakes were sampled on Isla El Muerto (1 on map; inhabited by *Cp*), Isla Ángel de la Guarda (2; **Ca*, *Cr*), Isla Smiths (3; *Cp*), Isla El Piojo (4; **Ct*), Isla Cabeza de Caballo (5; **Cpo*), Isla Danzante (6; *Cr*), Isla San Jose (7; *Cm*, *Ce*, *Cr*), Isla San Francisco (8; *Ce*), Isla Partida Sur (9; *Cm*, *Ce*), Isla Espiritu Santo (10; *Cm*, *Ce*), and Isla Cerralvo (11; *Cm*, *Ce*). Rattlesnake species sampled from each island reflect all known species present, except for *Cr* on Isla Ángel de la Guarda, which was not detected during surveys. Photos of rattlesnakes next to each island depict representative individuals of the species sampled from that specific island. Images of (B) Isla San Francisco (8) in the foreground and Isla San Jose (7) in the background, and (C) Isla Ángel de la Guarda (2). *Cp*: *Crotalus pyrrhus*, *Ce*: *C. enyo*, *Cm*: *C. mitchellii*, and *Cr*: *C. ruber*. Asterisks indicate insular endemics that were considered *C. pyrrhus* (*sensu lato*) in this study: *Ca*: *C. angelensis*, *Ct*: *C. thalassoporus*, and *Cpo*: *C. polisi*. Rattlesnake image credits: Ricardo Ramírez Chaparro and Víctor Vásquez-Cruz. Island image credits: Jacobo Reyes-Valasquez and Brandon Deitrich.

(Kadmon and Pulliam, 1993), we hypothesized that venom complexity would negatively correlate with island distance from the mainland (Figure 1B). Older islands harbor populations that may be long-isolated and subject to greater genetic drift, more frequent bottlenecks, higher levels of inbreeding, and/or prolonged selective pressures, all of which could erode genetic variation and reduce phenotypic diversity (Lohr *et al.*, 2014; Schlaepfer *et al.*, 2018); thus, we hypothesized that venom complexity negatively correlates with island age (Figure 1C). Alternatively, interspecific competition could oppose the effects of changes in prey diversity/abundance by favoring niche partitioning and more specialized phenotypes (Drury *et al.*, 2016). Competitive exclusion is strongest among closely related species (Violle *et al.*, 2011), meaning congenerics are likely to experience stronger competitive interactions. Notably, 5 of the 11 islands in our study harbor more than one rattlesnake species, providing opportunities for interspecific competition to influence venom evolution. Consequently, we hypothesized that venom complexity negatively correlates with the number of local congenerics (Figure 1D; see Materials and Methods). These simple predictions allowed us to use a synthetic eco-evolutionary framework to predict complex trait evolution while simultaneously assessing the extent to which habitat characteristics best explain variation in functional biodiversity across a fragmented landscape.

Sampling

We sampled venom from 83 individuals across 4 species: Speckled Rattlesnakes (*C. mitchellii*), Red Diamond Rattlesnakes (*C. ruber*), Baja California Rattlesnakes (*C. enyo*), and Southwestern Speckled Rattlesnakes (*C. pyrrhus sensu lato*) across 11 islands. Note that three insular *C. pyrrhus* populations that were recently described as endemic species (*C. angelensis* on Isla Angel de la Guarda, *C. thalassoporus* on Isla Piojo, and *C. polisi* on Isla Cabeza de Caballo; Meik *et al.*, 2015, 2018) were categorized as *C. pyrrhus* in this study to facilitate within species comparisons across islands. Snakes were captured via visual encounter surveys. All known rattlesnake species documented on each island were sampled, except for *C. ruber* on Isla Ángel de la Guarda, which was not encountered. Upon capture, sampling locality, snout-vent-length (SVL), total length, and sex were recorded. Venom was collected by allowing the snake to bite through a parafilm covered sample collection cup. Venom was transferred to a 2-mL microcentrifuge tube and immediately placed in a sealed container with silica drying crystals. Air was pumped out to accelerate drying, which occurred within 12–24 hr depending on venom yield. To prevent drying from exceeding 24 hours, venom was processed in quantities of 50 μL or less. Snakes were released at site of capture post-data collection. All snakes were collected under the following permits: Secretaría de Medio Ambiente y Recursos Naturales Oficio N SGPA/DGVS/06166/20; SGPA/DGVS/01178/20; SGPA/DGVS/04856/21; SGPA/DGVS/04999/22. The procedures outlined were approved by the University of South Florida Institutional Animal Care and Use Committee (IACUC) under protocol IS00011949 and Clemson University IACUC protocol 2017-067.

Characterizing venom differentiation across islands and life history

Venom samples were analyzed using Reversed-phase high-performance liquid chromatography (RP-HPLC) on a Dionex ultimate 3000 UHPLC DAD (Thermo Fisher Scientific, Waltham, MA) with a Jupiter® 5 μm C18 300 , LC Column 250 x 2 mm, and Ea column. Prior to analysis, dried venom was resuspended in HPLC grade water, and 50 μg of total venom protein were injected onto the column using a solvent system of A = 0.1% trifluoroacetic acid (TFA) in water and B = 0.075% TFA in acetonitrile. After 5 min at 5% B, a 1% per min linear gradient of A and B was run to 25% B, followed by a 0.25% per minute gradient from 25% to 65% B at a flow rate of 0.6 mL per min Margres *et al.* (2014). Column effluent was monitored at 220 nm. RP-HPLC peaks were quantified in the Chromeleon^{TM} software (Thermo Fisher Scientific, Waltham, MA). We estimated the relative abundance of each protein peak by measuring the area under the peak relative to the total area of all peaks identified (Dataset S1; Gibbs and Rossiter, 2008) as previously described Margres *et al.* (2014) and Margres (2017).

To determine whether venom expression was significantly different across island population and/or individual size within species, we used permutational multivariate analysis of variance (PERMANOVA). Raw peak quantification data were first transformed in R using the isometric Log-Ratio (ILR) transformation from the robCompositions package (Templ *et al.*, 2020). We then performed PERMANOVA via the “adonis2” function (Oksanen *et al.*, 2020) in R on the ILR transformed venom data as previously described (Margres *et al.*, 2014, 2019; Wray *et al.*, 2015).

Measuring venom complexity

We quantified venom complexity using the Shannon Diversity Index $H = -\sum_{i=1}^{s} p_i \ln(p_i)$; 97, 118.

Here, the proportional area of each nontransformed HPLC peak i represented p_i and the total number of peaks was represented by s (Holding *et al.*, 2021). Because we aimed to identify relative changes in venom complexity across islands regardless of species, we estimated a relative Shannon’s H for each individual by subtracting the min H of the species from the H value of the individual and then dividing this difference by the range of Shannon’s H for that species (see below).

$$H_{\text{relative}} = \frac{H_i - H_{\min}}{H_{\max} - H_{\min}} \tag{1}$$

Values of venom complexity across all species were therefore constrained from 0 to 1 (Dataset S1). For example, the highest venom complexity value for an individual *C. mitchellii* was 2.293 and the lowest was 1.610. The relative complexity value for an individual with an H value of 1.992 would then be 0.559 (1.992 – 1.610)/(2.293 – 1.610).

Using mixed effects multiple linear regression to identify factors of IBT that best explain venom complexity

Using a mixed effects multiple linear regression framework, we determined whether island area, island distance from the mainland, island age, and number of putative competitors best explained relative venom complexity across all four species simultaneously. Values for island age, area, and distance were obtained from Case *et al.* (2002) and confirmed using QGIS (version 3.36). Island area was measured in km^2, island distance was measured in km as the shortest distance between island and mainland, and island age was measured in million years ago (mya) based on the estimated geological epoch when formation occurred. The number of putative competitors on each island was obtained from Grismer (2002) and direct field observation (Dataset S2). We tested three different metrics for the number of putative competitors: (1) all snake species identified on the island, (2) all snake species identified on the island with predominantly vertebrate diets (i.e., excluding species with predominantly invertebrate diets), and (3) only congenerics (i.e., *Crotalus* sp.; see below). We also included the mechanism of island origin—categorizing islands as volcanic, block-faulted, or uplifted based on classifications from Case *et al.* (2002)—as a factor during model selection (see below).

We expected that conspecifics collected from the same island would likely exhibit similar venom complexities; such a pattern would potentially introduce the issue of pseudoreplication and violate the observation independence assumption of multiple linear regression (Berry, 1993; Poole and O’Farrell, 1971). Additionally, rattlesnake venoms often exhibit ontogenetic variation (Alape-Giròn *et al.*, 2008; Andrade and Abe, 1999; Barlow *et al.*, 2009; Borja *et al.*, 2018; Cipriani *et al.*, 2017; Durban *et al.*, 2017; Margres *et al.*, 2015a,b; Modahl *et al.*, 2016; Rokyta *et al.*, 2017; Schonour *et al.*, 2020; Wray *et al.*, 2015), thus introducing the possibility of ontogeny serving as a confounding factor in our analysis. To account for ontogeny and potential pseudoreplication, we employed a mixed effects modeling approach testing for spatial autocorrelation and included snake size as an additional explanatory variable. We began by determining the most suitable random effects structure for model selection following the approach of Zuur *et al.* (2009). We constructed six models with all fixed effects using a different combination of random effects and compared AICc values of each (Supplementary Material Table S1). We used the lme function from the nlme package in R (Stegmann *et al.*, 2018) to test models using (1) neither random effects nor spatial autocorrelation, (2) spatial autocorrelation but no species random effect, (3) spatial autocorrelation by individual species, (4) species random effect but no spatial autocorrelation, (5) island as a random effect nested within species, and (6) spatial autocorrelation by individual species with island origin as a random effect. Because the same fixed effects were used across each model for initial identification of the best random effects structure, we fit each model by maximizing the restricted maximum likelihood. We then used the dredge function from the MuMIn package in R (Bartoń 2023) to conduct model selection using spatial autocorrelation by individual species. We fit each model using the maximized log-likelihood due to differing fixed effects identified in each model. We included all fixed variables, including island distance, island age, island area, number of competing congenerics, and SVL.

We also tested for multicollinearity of explanatory variables in the model using the R program Performance Ludecke (2021) and generated a correlation matrix using the "cor" function in R. We removed the variables with the highest variance inflation factor (VIF) until VIF of all factors was ≤4. Two of the three metrics for the number of putative competitors, including all snakes found on the island (VIF= 351.88) and snakes with predominantly vertebrate diets (VIF= 324.45), exhibited high multicollinearity. Specifically, both metrics were highly collinear with the number of congenerics ($r = 0.79$ for all snakes; $r = 0.76$ for snakes with predominantly vertebrate diets; Supplementary Material Table S2), prompting their removal from the model. Number of putative competitors in model selection was therefore only represented by sympatric congenerics; congenerics likely reflect the strongest competitive interactions as competitive exclusion is typically stronger among more closely related species (Violle *et al.*, 2011).

To ensure that our results were unaffected by using a measurement of relative venom complexity, we replicated our mixed effects multiple linear regression framework using raw, unscaled Shannon's H values as the response variable rather than relative Shannon's H values. Unscaled Shannon's H values exhibited heterogeneous variances across species. To accommodate heterogeneous variances across species (Berry, 1993; Poole and O'Farrell, 1971), we incorporated variance modification using the varIdent function from the nlme package (Stegmann *et al.*, 2018) during our model selection process (Supplementary Material Figure S1).

To visualize the trends inferred using our top multiple regression model (Figure 3), we predicted relative Shannon's H values based on novel predictor values for island area, distance from the mainland, and number of congenerics. For each predictor, we generated 200 values for each species ranging from 0 to the maximum observed value. Using the expand.grid function in R, we created a matrix of simulated multivariate predictor data, ensuring that all predictors were de-correlated to accurately reflect the independent beta coefficients estimated in the top multiple regression model. This process resulted in a predictor matrix containing 3.2×10^7 unique combinations of predictor values. We then used the predict() function to calculate fitted values for Shannon's H based on each combination of predictor values in the matrix. For island area, distance from the mainland, and number of congenerics, we visualized the response–predictor relationships by averaging the predicted response values at each unique value of the focal predictor (i.e., for a given value of the focal predictor, multiple predicted response values exist due to variation in other predictors, which were averaged). These relationships were visualized in Figure 3A–C. Additionally, we used heatmaps to depict the relationships between Shannon's H and pairs of predictors simultaneously (Figure 3D–F). For each pair of focal predictors, we averaged the predicted response values across all unique combinations of values for the two predictors. This approach provided a clear visualization of the combined effects of island area, distance from the mainland, and number of congenerics on venom complexity.

Determining the contributions of IBT on venom variation through conditional redundancy analysis

In addition to investigating factors explaining variation in venom complexity, we also determined which of these same variables (island area, island age, island distance from the mainland, number of congenerics, and snake size) best predicted multivariate venom expression variation. By analyzing both metrics, we aimed to confirm that the factors driving complexity variation also influenced multivariate venom expression variation, thereby validating the biological significance of the observed complexity patterns. For instance, if venom complexity, representing one axis of venom variation, explained only a minimal portion of overall expression variation, then the factors identified as significantly driving venom complexity may not be biologically meaningful. We therefore estimated the contributions of island area, island distance from the mainland, island age, number of congenerics, and snake size on multivariate venom expression variation irrespective of venom complexity using conditional Redundancy Analyses (RDA; Capblancq and Forester, 2021; Liu, 1997; Van Den Wollenberg, 1977). These analyses differed from the mixed effects multiple linear regression analyses above through the venom response variable; here, the venom response variable was multivariate protein expression data representing abundance levels for multiple toxins, whereas above the venom response variable was the univariate relative Shannon's H. Similar to analyses of venom complexity, we aimed to identify factors associated with differences in venom expression across all species and islands within a single analysis rather than across individual species and multiple analyses. We, therefore, binned RP-HPLC peaks for each species according to retention time within 20-min intervals (Supplementary Material Figure S2, Table S3). Venom expression level per chromatography time interval was then used as the response variable for the conditional RDA. We also conditioned each explanatory variable in the model on all other explanatory variables to isolate the unique effect of a focal explanatory variable. We then conducted a marginal test using all explanatory variables and used forward model selection to identify the marginal (i.e., best) model and the factors that best explained venom expression variation across

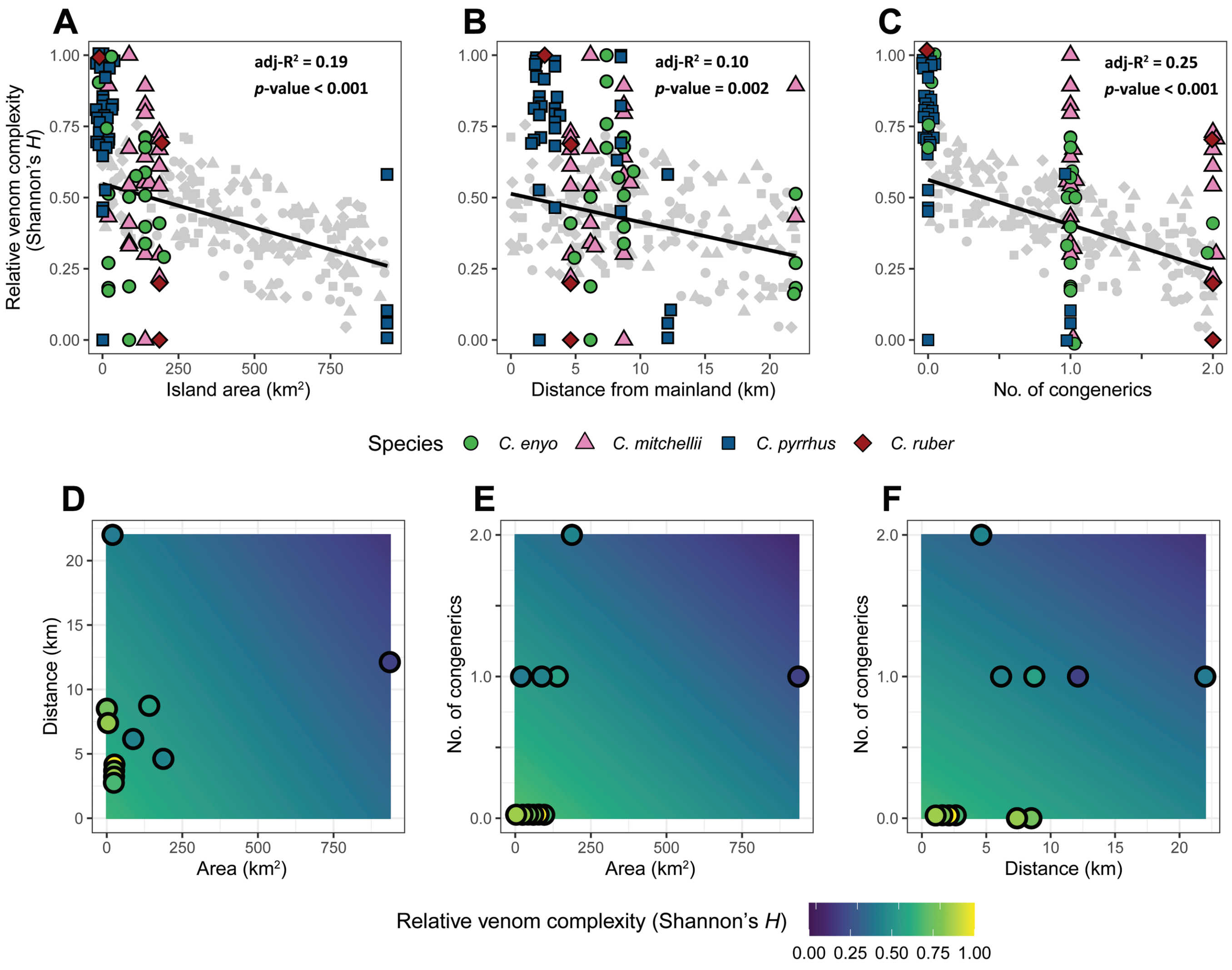

Figure 3. Relative venom complexity in rattlesnakes is best predicted by the number of sympatric congenerics, island distance from the mainland, and island area. (A–C) Relationships between relative Shannon's *H* and the three significant factors identified via our mixed effects multiple linear regression framework: (A) island area, (B) island distance from the mainland, and (C) number of sympatric congenerics. Colored points indicate empirical relative Shannon's *H* values from our dataset, and gray points indicate 200 predicted relative Shannon's *H* values using our top model. Note that there are multiple predicted values per value of the focal predictor due to variation at other predictor variables. Predicted relative Shannon *H* values do not take into account the error variance inferred by the model. Estimates of *p*-value and adj-R^2 shown are from simple linear regressions for visual purposes only; factors were identified as significant through our mixed effects multiple linear regression framework. (D–F) Heatmaps showing the relationship between relative venom complexity (tile color) and pairs of significant predictors (*x*- and *y*-axes): (D) island area and island distance from the mainland, (E) island area and number of congenerics , and (F) distance from the mainland and number of congenerics. Colored points represent islands with shading of each dot corresponding to the mean relative Shannon's *H* of that island across all species. See Methods for further details.

all 83 individuals. Conditional RDAs were conducted using the "rda" function from the Vegan package in R (Oksanen *et al.*, 2020), and included "ordiR2step" for forward model selection.

Results

Species exhibit significant venom differentiation across islands

To determine whether venom expression was significantly different across islands and/or snake size for each of our focal species independently, we performed a PERMANOVA on venom proteomic data. For each species, venom was significantly different across islands (*C. pyrrhus* [n = 35] across 5 islands: $p < .001$, $R^2 = 0.33$; *C. enyo* [n = 21] across 5 islands: $p < .001$, $R^2 = 0.55$; and *C. mitchellii* [n = 23] across 4 islands: $p < .001$, $R^2 = 0.37$). The effect of snake size on venom expression, however, was only significant for *C. pyrrhus* (*C. pyrrhus*: $p < .001$, $R^2 = 0.11$; *C. enyo*: $p = .315$, $R^2 = 0.03$; and *C. mitchellii*: $p = .091$, $R^2 = 0.05$). The interaction between island and snake size was also only significant for *C. pyrrhus* (*C. pyrrhus*: $p = .012$, $R^2 = 0.13$; *C. enyo*: $p = .197$, $R^2 = 0.10$; and *C. mitchellii*: $p = .190$, $R^2 = 0.12$), indicating that venom differentiation across islands for *C. pyrrhus* could not be disentangled from differentiation across snake size. Individual tests of venom differentiation for *C. ruber* could not be conducted due to low sample size (n = 4 across 2 islands).

Table 1. Mixed effects multiple regression model selection results for relative venom complexity. β coefficient values for island age, island area, island distance from the mainland, number of congenerics (Cong.), and snake size (SVL) with the degrees of freedom (df) and ΔAICc. NA indicates that factor was omitted from the model. All models ≤ 3 ΔAICc identified from model selection are shown. Models with ≤ 2 ΔAICc from the top model are bolded. See Supplementary Material Table S4 for all tested models.

Age	Area	Distance	Cong.	SVL	df	ΔAICc
NA	**−0.0003**	**−0.0103**	**−0.1485**	**NA**	**8**	**0**
NA	**−0.0003**	**NA**	**−0.1605**	**NA**	**7**	**0.96**
NA	**NA**	**−0.0113**	**−0.1815**	**NA**	**7**	**1.11**
NA	**NA**	**−0.0111**	**−0.1697**	**−0.0023**	**8**	**1.97**
NA	−0.0003	−0.0104	−0.1452	−0.0010	9	2.23
0.0173	−0.0003	−0.0104	−0.1604	NA	9	2.24
NA	NA	NA	−0.1995	NA	6	2.63

Table 2. Results of the conditional RDA across all species with venom expression per chromatography time interval (see Methods) as the multivariate response variable. The marginal (i.e., best) model was identified using forward model selection on all explanatory variables. Significant results are bolded.

Explanatory Variable	F	p-value	adj-R^2
Marginal Model			**0.26**
Congenerics	**15.57**	**.001**	**0.15**
Snake size	**12.43**	**.001**	**0.11**
Conditioned Individual Variables			
Snake size	**7.63**	**.001**	**0.06**
Island area	**7.43**	**.001**	**0.06**
Island distance	1.71	.168	0.01
Island age	0.15	.946	0.00
Congenerics	**13.44**	**.001**	**0.11**
Full model	**8.32**	**.001**	**0.31**

Venom complexity decreases, not increases, with island area, island distance, and number of congenerics

We used mixed effects multiple linear regression accounting for spatial autocorrelation by individual species (see Methods) to determine whether island age, island distance from the mainland, island area, and/or number of sympatric congenerics best predicted relative changes in venom complexity. Following model selection, the best model (defined as the model with the minimum AICc), included the number of congenerics ($\beta = -0.14851$), island distance from the mainland ($\beta = -0.01034$), and island area ($\beta = -0.00031$) as the most important factors explaining variation in relative venom complexity (Figure 3; Table 1). Here, β coefficients represent the change in relative Shannon's H per unit change of the predictor, and the sign indicates direction of change, meaning venom complexity negatively correlated with all three variables. Three additional models within ≤ 2 ΔAICc were also identified (Table 1) and included some combination of island area, island distance, and number of congenerics with the fourth model also including snake size (Table 1; Dataset S1). Age was not identified in any model ≤ 2 ΔAICc.

The role of island area in explaining venom complexity was robust to the exclusion of Isla Ángel de la Guarda, which is 5× larger than the next largest island ($936\ \text{km}^2$; Supplementary Material Figure S3, Tables S5 and S6). Additionally, we ensured that our results were unaffected by the use of a relative measure of venom complexity by repeating model selection using raw, unscaled estimates of venom complexity; congenerics ($\beta = -0.05514$), island distance from the mainland ($\beta = -0.00487$), and island area ($\beta = -0.00029$) were again identified as the most important factors in the top model (Supplementary Material Table S7).

Number of congenerics and snake size predict multivariate venom expression variation

Having determined that venom complexity (a univariate summary of multivariate data) was best predicted by the number of congenerics, island distance, and island area, we next determined which factors best predicted multivariate venom expression data irrespective of complexity. We used conditional redundancy analysis (RDA) with multivariate venom expression data as the response variable and found that the full model, including all variables, was significant ($p = .001$; $adj - R^2 = 0.31$; Table 2), indicating that our model captured at least one or more variables that significantly explained venom variation.

The marginal (i.e., best) model as determined via forward model selection ($adj - R^2 = 0.26$) revealed that the number of congenerics ($p = .001$; $adj - R^2 = 0.15$) and snake size ($p = .001$; $adj - R^2 = 0.11$) were the best predictors of multivariate venom expression variation (Table 2). After conditioning each explanatory variable in the model on all other explanatory variables to isolate the unique effects of each covariate, number of congenerics, snake size, and island area were individually found to be significant predictors of venom variation (Table 2; Supplementary Material Table S8).

Discussion

We present strong evidence that IBT, a foundational ecological theory used to predict species richness, can also be used to predict functional trait evolution across fragmented landscapes. Our results revealed that (1) venom expression was significantly different across islands within species, (2) number of sympatric congenerics, degree of island isolation, and island area significantly and negatively correlated with venom complexity, and (3) number of congenerics and snake size best predicted multivariate venom expression variation. Previous studies have demonstrated that IBT can predict functional trait variation across multiple taxa; however, most studies focused on traits that were likely to be indirectly influenced by species richness through habitat filtering, dispersal limitation, and/or environmental constraints (Jacquet *et al.*, 2017; Schrader *et al.*, 2021; Whittaker *et al.*, 2014). Our study tested whether IBT could predict the evolution of a functional trait that directly mediates species interactions (i.e., through injection) and has been shown to evolve to changes to such interactions at macroevolutionary scales (Holding *et al.*, 2021). Traits that directly mediate species interactions, such as venom, provide a clear link between biodiversity dynamics and functional evolution, allowing for more precise predictions of how changes in biodiversity may shape patterns of functional biodiversity.

We first established that venom expression was significantly different across islands for three of the four species using multivariate venom expression data (*C. ruber* was excluded due to low sample size). Venom expression differed across islands independent of snake size except for *C. pyrrhus*. Body size evolution in this species has been observed, with instances of both dwarfism and gigantism (Grismer, 2002; Meik *et al.*, 2010). Specifically, our sampling included dwarfed individuals from Isla el Muerto and giant individuals from Isla Ángel de la Guarda. Consequently, significant correlation between venom differentiation across islands and snake size in *C. pyrrhus sensu lato*, although interesting, was unsurprising.

Venom differentiation across islands has been identified in other snake populations (Chijiwa *et al.*, 2000; Franco-Servín *et al.*, 2021; Sunagar *et al.*, 2014), likely due to local adaptation to island prey (Margres *et al.*, 2017). However, predicting patterns of insular venom differentiation, which has yet to be systematically explored, should enhance our understanding of how functional traits may evolve in response to rapid ecological change. Our results revealed that patterns of venom differentiation in island populations can be predicted through IBT. Consistent with our predictions (Figure 1), venom complexity negatively correlated with island isolation and number of congenerics; however, contrary to expectations (Figure 1), island area also negatively correlated with venom complexity, and island age was not a significant predictor in our top models. Additionally, the mechanism of island origin—whether due to block–faulting, uplift, or volcanism—did not influence venom complexity across islands, indicating that functional trait evolution across islands is shaped by ecological and biogeographic processes rather than geological history and island formation.

Increased habitat area often provides greater habitat heterogeneity and/or resources to support a greater number of species (Thomsen *et al.*, 2022). For example, snake species richness positively correlates with island area among islands in the Gulf of California and elsewhere (Arnaud *et al.*, 2024). We, therefore, predicted that venom complexity would positively correlate with island area due to increased species richness and, therefore, dietary breadth on larger islands. However, we found that although island area was a significant predictor of venom complexity, increasing island area resulted in reduced venom complexity. We argue that this result was likely driven by area-induced increases in putative competition on more species rich, larger islands, and/or increased specialization on larger islands due to greater habitat heterogeneity. Specifically, the number of congenerics present on an island had the greatest effect on venom complexity variation, suggesting that increased species richness supported by larger island area intensified putative competition between closely related species on larger islands (Violle *et al.*, 2011), leading to niche partitioning and, ultimately, less complex, more specialized venoms. All four species are known to consume a combination of rodents, lizards, and occasionally birds and other mammals on the mainland, indicating the potential for dietary overlap on islands (Dugan and Hayes, 2012; Grismer, 2002; Klauber, 1997; Taylor, 2001). Although prey availability may vary across islands, putative dietary overlap suggests that sympatric rattlesnakes could experience strong interspecific competition for similar prey resources, reinforcing the potential for niche partitioning to drive venom differentiation on larger islands. Specific dietary data across multiple species and islands in sympatry and allopatry would be needed to confirm whether this pattern reflects competition-driven specialization.

Furthermore, the number of congenerics was the primary factor explaining multivariate venom expression variation in the RDA (i.e., irrespective of venom complexity) with area also having a significant effect. Confirming these patterns using multivariate venom expression data allowed us to ensure that biologically relevant variation was not lost by reducing a complex venom phenotype to a single complexity measure. Therefore, putative competition among local congenerics had the largest effect on venom evolution across multiple scales, highlighting the potentially important role of competition in driving phenotypic evolution (Drury *et al.*, 2016), particularly across islands (Losos and Ricklefs, 2009). Although our findings suggest that competition has strongly influenced venom evolution, determining whether specific toxin expression patterns converge in response to shared competitors would provide stronger evidence that competition has driven specific patterns of venom evolution (e.g., repeated character displacement). However, our sample sizes per species per island (Median 5; SD 2.7 individuals per species per island) were insufficient to robustly assess protein-level convergence (Margres *et al.*, 2015a), a limitation that future studies with larger sample sizes should address.

Although increased habitat area may promote species richness (Hannus and Von Numers, 2008; Kohn and Walsh, 1994; Lillywhite and Martins, 2023; Thomsen *et al.*, 2022), our results suggested habitat area may also promote increased competition, leading to niche partitioning and the distribution of functional diversity among multiple competitors, perhaps reducing the functional diversity of individual species. Similarly, increased island area may produce greater habitat heterogeneity, leading to microhabitat partitioning among species (Sfenthourakis *et al.*, 2021). Partitioning may lead to specialization and limit interspecies interactions (Holt, 2009), thereby reducing functional diversity of an individual species. Therefore, the negative correlation between island area and venom complexity may be attributed to the combined effects of increased competition and habitat heterogeneity, both of which may lead to specialization and ultimately reduce functional trait complexity within species.

Venom complexity was negatively predicted by island distance from the mainland, consistent with our expectations (Figure 1). Increased island isolation reduces local biodiversity due to dispersal limitations from the mainland and higher extinction rates (MacArthur and Wilson, 1963, 2001; Kadmon and Pulliam, 1993), potentially reducing snake diet diversity and leading to less complex venoms. Multiple factors, including fewer initial colonization events, reduced migration rates, and/or dietary specialization due to limited prey diversity, could all contribute to this pattern. Genetic drift may also play a role by eroding phenotypic variation where gene flow would otherwise maintain it (Schlaepfer *et al.*, 2018; Templeton *et al.*, 1990). Disentangling the relative contributions of these mechanisms would require population genetic data and explicit modeling of migration rates, colonization history, and local ecological interactions (Spurgin *et al.*, 2014) which is beyond the scope of the current study. Despite the effects of island isolation on venom complexity, island distance did not predict multivariate venom expression variation, indicating that degree of habitat isolation had significant effects on functional trait complexity but nonsignificant effects on functional trait variation.

Contrary to our expectations (Figure 1), island age was not identified as a significant predictor of venom complexity nor multivariate venom expression variation. Ultimate depletion of resources on islands can lead to gradual extinction, thereby reducing species richness (Whittaker *et al.*, 2017).

Additionally, genetic drift in small, isolated populations can reduce phenotypic and genetic variation over time as discussed above (Lohr *et al.*, 2014; Schlaepfer *et al.*, 2018). Due to the combined effects of stochasticity and putative reductions in diet diversity, we predicted age would negatively correlate with venom complexity; however, venom variation occurred across islands regardless of their age of emergence. Our results indicated that venom evolution may occur quite rapidly and that genetic drift may not play a significant role in reducing venom complexity, suggesting that even in isolated habitats, functional trait complexity can be maintained over long periods under putatively strong selection. Alternatively, island age may not directly reflect the age of snake populations inhabiting each island. Colonization timing and population persistence can vary independently of island geological emergence, and some islands may have experienced local extirpations and recolonizations over time (Burger *et al.*, 2019). However, island age still provides a lower bound on population age, as no population can predate the formation of its island. Without direct estimates of colonization timing or demographic history, island age serves as an approximation for how long populations may have been isolated. Ultimately, disentangling the effects of island age from population turnover would require understanding historical colonization and extinction dynamics. Future work should incorporate genomic data to reconstruct demographic history, identify genetic signatures of past bottlenecks and colonization events, and determine whether observed patterns reflect long-term isolation or more recent recolonization (Franks, 2010; Wang *et al.*, 2022).

Our study employed a robust statistical framework to establish significant relationships between venom complexity and island isolation, area, and putative competition. Although we used an island system to demonstrate these patterns, habitat fragmentation due to anthropogenic activity is conceptually analogous to scenarios described in IBT (i.e., human activity creates isolated patches of habitat in an otherwise uninhabitable landscape matrix; Laurance, 2008; Powledge, 2003; Whittaker and Fernandez-Palacios, 2007); therefore, we suggest that our results will be broadly informative for preserving functional biodiversity across fragmented landscapes. To further substantiate the broad evolutionary patterns identified in this study and address the assumptions outlined in the Introduction, future research should (1) confirm that diet diversity is predicted by IBT by precisely characterizing the diet composition of each species on each island, (2) verify that venom complexity evolves in response to local prey by determining whether, for example, more complex venoms exhibit greater toxicity to multiple local prey species, (3) incorporate genetic data to determine whether venom complexity is primarily shaped by selection or drift and to identify loci associated with changes in venom expression, and (4) confirm these patterns in other venomous taxa across similar island systems and habitat types to establish generality.

As habitat fragmentation continues to drive the current biodiversity crisis (Ceballos *et al.*, 2015; De León *et al.*, 2023), preserving the diversity of traits, particularly for traits involved in mediating species interactions, is essential for maintaining ecosystem functionality and resilience (Craven *et al.*, 2016; Gagic *et al.*, 2015; Gladstone-Gallagher *et al.*, 2019). Trait diversity enhances the ability of species to perform various ecological roles and adapt to changing environmental conditions (Forester *et al.*, 2022; Hoffmann and Sgrò, 2011; Milot *et al.*, 2020). Our findings suggest that to preserve functional biodiversity, conservation strategies should maintain interconnected habitats that minimize isolation while also balancing the advantages of increased habitat area with the potential for increased competition and microhabitat partitioning for particular (e.g., keystone) species. Such an approach would support evolutionary potential, promoting adaptability to rapid anthropogenic-induced environmental changes in the future.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

The data underlying this article are available in its online supplementary material. Metadata are provided in Supplementary Material Datasets S1 and S2. All analytical softwares are publicly available. The Dryad repository containing scripts used for statistical analyses and figure generation in this study is available at https://doi.org/10.5061/dryad.6q573n66g

Author contributions

S.R.H., J.L.S., and M.J.M. conceived and designed the study. All authors contributed to data collection and/or generation. S.R.H. and M.A.B. analyzed data. S.R.H. and M.J.M. led writing with input from all coauthors.

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