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Research Article

Detecting functional diversity loss under directional, stabilizing, and disruptive models of nonrandom anthropogenic extinction of species

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Humans alter extinction pressures in ways that favor some species over others, causing nonrandom loss of functional diversity. While the three classic models of natural selection within species – directional, stabilizing, and disruptive – are widely used to explain trait evolution, it remains unclear whether they can also capture human-caused nonrandom functional diversity loss among species. Here we develop a framework to test for nonrandom extinction by tracking how trait means and variances change as species with different functional traits are sequentially lost. Applying this approach to the Caribbean lizard genus *Leiocephalus*, which has already lost eight of its 32 species and has 10 more threatened with future extinction, we found that past extinctions were directional with respect to ecomorphological traits, as large-bodied species were disproportionately eliminated, likely due to hunting and introduced predators. In contrast, predicted-future extinctions are best explained by stabilizing processes, with species exhibiting extreme appendage morphologies most at risk and species with intermediate appendage lengths least likely to go extinct in the future, possibly because this phenotype is better adapted to the deforested habitats that dominate Caribbean islands today. Such a shift from directional to stabilizing nonrandom extinction is expected when natural extinction pressures are replaced by anthropogenic pressures that directionally shift trait distributions to new adaptive optima. By linking trait-based extinction sequences to classic evolutionary models, our approach provides a generalizable framework for detecting and comparing nonrandom extinction across traits, clades, and ecosystems.

Keywords: adaptive landscape, Anthropocene, anthropogenic impact, body size, Caribbean, deforestation, functional diversity, hunting, introduced predators, island biogeography, land development, *Leiocephalus*, lizard, natural selection, nonrandom extinction, statistical methods

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Introduction

Non-random anthropogenic extinction is caused by extinction pressures that select against species with particular trait values compared to species without those values (McKinney 1997, Brook and Alroy 2017, Chichorro et al. 2019). Understanding nonrandom extinction is important because it is a common phenomenon under global change and results in loss of functional diversity (Gross and Cardinale 2005, Brook et al. 2008, Dirzo et al. 2014). For example, past extinctions and population declines have caused a reduction in the functional diversity of animal body-size and life-history traits (Cardillo 2003, Öckinger et al. 2010). Non-random anthropogenic extinction is often detected in contrast to random extinction by comparing trait values between extinct and extant species using null models, regressions, or other statistical methods (Purvis et al. 2000a, Cardillo et al. 2008, Sayol et al. 2020). Extinction, and its association with specific trait values in the context of natural selection, has been broadly addressed theoretically in quantitative genetics (Bürger and Lynch 1995, Chevin and Lande 2010, Chevin et al. 2010) and macroevolution (Foote 1997, Ciampaglio et al. 2001, Jablonski 2008, Simpson 2013, Chevin 2016). However, existing approaches for detecting nonrandom extinction of species caused by humans lack an underpinning in this evolutionary theory (Purvis et al. 2000b).

The three classic natural selection models describe what occurs to the mean and variance of a population's phenotype through time (Lush 1937, Arnold et al. 2001, Urry et al. 2017). Directional selection occurs when selection pressure changes to favor a new adaptive optimum, leading individuals with trait values far from this peak to have the lowest fitness (Lande 1976). This leads to reduced trait variance in the short term and the mean trait value of the population to shift (Kingsolver and Diamond 2011). In contrast, stabilizing selection occurs once a population is close to an optimal trait value, which reduces trait variance in the population but does not cause a mean shift (Covas et al. 2002). Finally, disruptive selection occurs when selection pressure changes to favor extreme phenotypes over an intermediate phenotype (Rueffler et al. 2006). Disruptive selection has a diversifying effect by increasing trait variance in the population without a mean shift. In the long term, it can cause sympatric ecological speciation if the population diverges into two subpopulations, each centered on separate trait value optima, sensu adaptive fitness landscapes (Bolnick and Lau 2008).

A broad empirical literature on trait selectivity across adaptive landscapes in both fossil and contemporary systems shows that species loss is often nonrandom with respect to traits (Monarrez et al. 2023, Payne et al. 2023, Martínez-Rubio et al. 2024). As such, trait selectivity provides a conceptual link between classic models of population natural selection and species-level patterns of trait-dependent extinction (Hansen 1997, Arnold et al. 2001, Ingram and Mahler 2013). Specifically, directional, stabilizing, and disruptive models can be extended to trait variation among species within a clade across macroevolutionary time (Jablonski 2008, Chevin 2016). Therefore, functional diversity loss due to anthropogenic extinction can be conceptualized as the selective removal of species from adaptive landscapes in ways analogous to directional, stabilizing, and disruptive models of natural selection.

Here, we articulate three general models of nonrandom anthropogenic extinction of species that are analogous to the three general models of natural selection (Fig. 1). To be clear, these proposed models are used as phenomenological analogies to describe patterns of trait change under nonrandom anthropogenic extinction, rather than as mechanistic equivalents of natural selection processes acting within populations, which operate at different spatiotemporal scales (Beissinger 2000, Congreve et al. 2018, Figueiredo et al. 2019). Directional nonrandom extinction occurs when extinction is greatest closer to one extreme phenotype. Data in support of the directional extinction model are common, such as the loss of large-bodied animals caused by invasive consumers, hunting, and other anthropogenic impacts (Pregill 1986, Cardillo 2003, Cardillo et al. 2005, Tingley et al. 2013, Kemp and Hadly 2015, Scheele et al. 2023). Stabilizing nonrandom extinction occurs when extinction pressure is highest for species with extreme phenotypes. Although data for stabilizing patterns of nonrandom extinction remain limited, insular vertebrate species with more extreme phenotypes can exhibit elevated extinction risk, consistent with stabilizing trait filtering (Rozzi et al. 2023). Further, predicted-future extinctions of vertebrates based on IUCN threat listings follow this model where both large- and small-bodied species are the most threatened (Ripple et al. 2017, Leclerc et al. 2018). Disruptive nonrandom extinction occurs when extinction is highest for species with intermediate trait values. Data in support of this model have been reported for extinctions of birds in Australia and New Zealand, where midsized species went extinct because of humans (Duncan and Blackburn 2004, Woinarski et al. 2017). European butterfly species also exhibit disruptive nonrandom extinction in dispersal ability; species of intermediate mobility declined the most since the 1980s (Thomas 2000).

We present a framework to test for the expected effects of directional, stabilizing, and disruptive non-random extinction on the loss of trait functional diversity measured from ecomorphological traits. Ecomorphology – the relationship between morphological traits and niches – is often studied in the context of natural selection across adaptive landscapes (Nosil and Crespi 2004, Mahler et al. 2013, Machado 2020). For example, ecomorphological traits like body size and limb length vary among lizard species due to natural variation in microhabitat usage and predation risk. Adaptive landscapes have been evoked to infer the selection mechanisms that maintain the ecomorphology of species within clades (Losos 1990, Melville and Swain 2000, Gifford et al. 2008, Goodman et al. 2008, Mahler et al. 2013, Lapiedra et al. 2018, Edwards et al. 2022). Under the framework, stabilizing selection maintains optimal adaptive ecomorphic trait values of species within a clade, directional selection causes species ecomorphology to track environmental changes, and disruptive selection

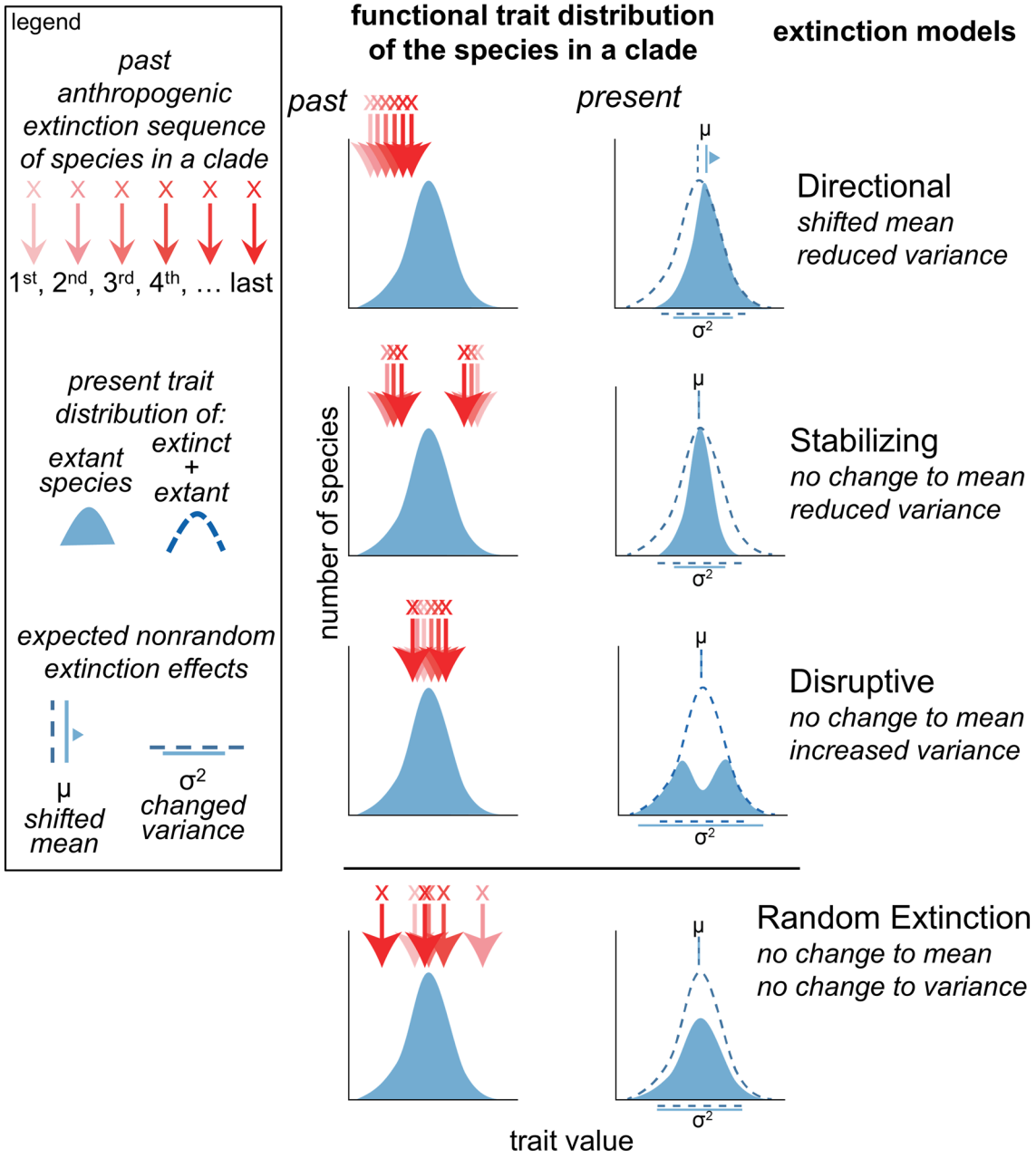

Figure 1. Three general models of non-random anthropogenic extinction. When the past distribution of functional trait values exhibited among the species of a clade (blue curves on the left) is associated nonrandomly with respect to anthropogenic extinction pressure, a sequence of extinctions (red arrows) will produce patterns analogous to directional, disruptive, and stabilizing selection in the present-day trait distribution (blue curves and dashed lines on the right). The expected statistical effects of extinction on shifting the mean and changing the variance of the trait distribution differs among the models depending on whether the species that went extinct were from one tail (directional), both tails (stabilizing), or the trait distribution center (disruptive). There is no expected effect on the mean and variance under a random extinction model.

drives clade ecomorphological diversification and speciation. Therefore, like for populations when the environment changes to a new regime (Sanjak et al. 2018), the species of a clade should exhibit directional change in their ecomorphology followed by stabilizing selection (Dumont et al. 2012, Rossoni et al. 2017). When such a shift is rapid, like the environmental changes caused by humans, the change in ecomorphology should be observable as directional followed by stabilizing patterns of non-random extinction.

We tested for past and predicted-future non-random loss of ecomorphological diversity in the curly-tailed lizards *Leiocephalus* of Caribbean islands. Curly-tailed lizards comprise 32 known species of which over half are extinct or threatened with extinction (Henderson and Powell 2009,

Köhler et al. 2016). *Leiocephalus* is primarily a ground-dwelling clade and documented extinction pressures on this genus include hunting, introduced mammal predators, and habitat loss (Steadman et al. 1984, Powell et al. 1999, Daltry 2007, Borroto-Páez and Woods 2012, IUCN 2020). Generally, land development and the introduction of predators causes ecomorphological shifts and the loss of lizard functional diversity (Berriozabal-Islas et al. 2017, Falvey et al. 2020, Lyndon-Gee and Jessop 2020, Balakrishna et al. 2021). Traits such as body size are commonly associated with lizard extinction risk (Böhm et al. 2016, Tingley et al. 2016, Senior et al. 2021, Caetano et al. 2022). Larger lizards with distinct functional traits have gone extinct from Caribbean lizard assemblages (Kemp and Hadly 2015, Kemp 2023). However, nonrandom extinction has not been assessed for most lizard clades including *Leiocephalus*, and no work has compared different models of non-random anthropogenic extinction for any taxa. Given known historical and ongoing anthropogenic pressures, we expected past extinctions to be predominantly directional due to size-selective pressures like hunting and predation, while future extinctions to reflect stabilizing patterns as environmental homogenization and habitat loss disproportionately filter species with more extreme trait values (Solar et al. 2015, Monarrez et al. 2023, Payne et al. 2023, Rozzi et al. 2023).

Material and methods

Nonrandom anthropogenic extinction

Directional, stabilizing, and disruptive nonrandom extinction vary in how trait means and variances of a population change as natural selection increases, which is analogous for species when extinction pressure non-randomly increases (Fig. 1). Thus, to conceptualize non-random anthropogenic extinction, suppose a clade of n species ($i = 1,...n$), with each species made up of many individuals that vary in a continuous trait, x. For simplicity, we disregard intraspecific trait variation to focus on trait means exhibited by each species, $\overline{x_i}$, that we assume follow a Gaussian distribution with a clade-specific mean, μ, standardized to zero, and clade-specific variance, σ^2, standardized to one. Assume an extinction scenario where a set of sequential extinctions has occurred over time that has removed k species in total from n. This extinction sequence: $j = 1,\ldots,k$ may shift the clade mean, μ_α, and change the clade variance, $\sigma^2{}_\alpha$, of the interspecific functional trait distribution to new present-day values, μ_ω and $\sigma^2{}_\omega$. The expectations of μ_ω and $\sigma^2{}_\omega$, $E[\mu_\omega]$ and $E\left[\sigma^2{}_\omega\right]$, after all k species have gone extinct, differ depending on the $\overline{x_j}$ values of the extinct species relative to the extant species (Fig. 1). Indeed, under a constantly applied extinction model, at each time point when one of the k species is lost, the mean shift, $\Delta\mu_{n-j}$, from the past distribution, will monotonically approach $\Delta\mu_{n-k} = \mu_\alpha - E\left[\mu_\omega\right]$ and similarly with $\Delta\sigma^2{}_{n-j}$.

By calculating the combination of mean shifts and variance changes for a given data set the extinction models can be distinguished from one another. The simplest model is random extinction. Sequential loss of k species is independent of $\overline{x_i}$ and leads to the same expected past and present means and variances ($\mu_\alpha = E\left[\mu_\omega\right]$, $\sigma^2{}_\alpha = E\left[\sigma^2{}_\omega\right]$), and $0 = \Delta\mu_{n-j} = \Delta\sigma^2{}_{n-j}$. There are two models for directional extinction because the mean shift caused by directional extinction depends on which tail is lost ($\mu_\alpha \lessgtr E\left[\mu_\omega\right]$). Sequential loss from the right tail (species with the largest trait values go extinct) results in all $\Delta\mu_{n-j} < 0$. Sequential loss from the left tail (species with the smallest trait values go extinct) results in all $\Delta\mu_{n-j} > 0$. Regardless of the mean shift, variance is reduced ($\sigma^2{}_\alpha > E\left[\sigma^2{}_\omega\right]$) and all $\Delta\sigma^2{}_{n-j} < 0$. The remaining two models, disruptive and stabilizing, do not shift expected means ($\mu_\alpha = E\left[\mu_\omega\right]$), but do change variances. Disruptive extinction increases variance ($\sigma^2{}_\alpha < E\left[\sigma^2{}_\omega\right]$) so that all $\Delta\sigma^2{}_{n-j} > 0$. Stabilizing extinction decreases variance ($\sigma^2{}_\alpha < E\left[\sigma^2{}_\omega\right]$) so that all $\Delta\sigma^2{}_{n-j} < 0$.

Detecting non-random extinction

To detect nonrandom extinction in observed data, we simulated sequential extinction. Sequential extinction simulations represent the ordered, stepwise loss of species from a clade, one at a time, with removal determined by extinction-model-specific rules based on species' positions within their trait distribution. For observed, empirical sequences, species were ordered by estimated extinction timing. When multiple species shared overlapping or identical extinction time estimates, ties were resolved by randomly sampling orderings among tied species across multiple replicates, and the resulting mean and variance changes were averaged across these replicates. Extinction sequences were simulated under the models, and we then statistically tested which models best fit the observed extinction sequence. For each model, we simulated n species of a clade of which k species go extinct sequentially under the model. The species of the simulated clade are assigned a functional trait value drawn from a normal distribution of mean zero and variance one. The n and k were the same as in the observed data, and the observed trait data were standardized to have a $\mu = 0$ and $\sigma^2 = 1$, and transformed if necessary to be normally distributed. We ran 10 000 simulations for each model. Finally, to assess model fits, the mean shifts, $\Delta\mu_{n-j}$, and variance changes, $\Delta\sigma^2{}_{n-j}$, of each simulation under each model were calculated and the simulated distribution for each model was statistically compared to the mean shifts and variance changes calculated for the observed clade.

The simulations of the models were as follows. For random extinction, k species were removed via random uniform sampling across n species independent of their functional

trait values. For directional nonrandom extinction, k species were lost in descending or ascending order based on their trait values for large-value or small-value directional extinction, respectively. For disruptive extinction, k species with the smallest absolute distance from the clade mean, $|\overline{x_i} - \mu|$, were sequentially removed. Finally, for stabilizing extinction, species with the largest absolute distance from the clade mean were sequentially removed.

To assess model fit, the observed data were compared to the simulated data with root-mean-square error (RMSE) goodness-of-fit statistics. First, for each model, the means of the $\Delta\mu^{sim_z}_{n-j}$ and $\Delta\sigma^{2sim_z}_{n-j}$ values across all $z = 1,\ldots 10\,000$ simulations, $\overline{\Delta\mu}^{sim}_{n-j}$ and $\overline{\Delta\sigma^2}^{sim}_{n-j}$, were calculated. The mean simulated trajectory was used to represent the central expected trajectory under each extinction model, while variation among simulations was retained in the subsequent distributions of simulated RMSE values. Then the RSME of the observed values, $\Delta\mu^{obs}_{n-j}$ compared to the means $\overline{\Delta\mu}^{sim}_{n-j}$ was calculated (Eq. 1) as:

$$\mathrm{RMSE}^{obs}_{\mu} = \sqrt{\frac{\sum_{j=1}^{k}\left(\overline{\Delta\mu}^{obs}_{j} - \overline{\Delta\mu}^{sim}_{j}\right)^2}{k}} \quad (1)$$

and similarly, for $\mathrm{RMSE}^{obs}_{\sigma^2}$ by replacing μ with σ^2. For an illustration, see Fig. 2 where colored lines are $\overline{\Delta\mu}^{sim}_{n-j}$ values for each model and the black lines are the $\Delta\mu^{obs}_{n-j}$ values. The RMSE values were then calculated for each simulated data set by replacing obs with sim_z in Eq. (1) to get $\mathrm{RMSE}^{sim_z}_{\mu}$ and $\mathrm{RMSE}^{sim_z}_{\sigma^2}$ for the 10 000 simulated values. Thus, for each nonrandom extinction model we produced a distribution of 10 000 simulated RMSE values for μ and σ^2 to compare to the observed RMSE of μ and σ^2. To better visualize these statistics for our observed data set, see the Supporting information plots for the observed and simulated RSME values for *Leiocephalus*.

We jointly consider the expected fit of both μ with σ^2 to differentiate among the models. To do this, we first calculated the mean of the errors across all 10 000 simulations, $\overline{\mathrm{RMSE}}^{sim}_{\mu}$, $\overline{\mathrm{RMSE}}^{sim}_{\sigma^2}$. Second, we calculated d_{obs}, which is the Euclidean distance between those means and the observed errors $\mathrm{RMSE}^{obs}_{\mu}$ and $\mathrm{RMSE}^{obs}_{\sigma^2}$. This metric, d_{obs}, is a goodness of fit statistic and is calculated for each of the five extinction models (i.e. random extinction and the four non-random extinction models). Smaller values of d_{obs} indicate a better model fit (black vertical lines in the Supporting information figures). Third, to assess the significance of d_{obs} for each model, we calculated the distance between the means and each of the 10 000 simulations, d_{sim_z} to produce a simulated distribution of goodness of fit values (colored distributions in the Supporting information figures). Fourth, if d_{obs} is significantly within the simulated distribution for a particular extinction model, then that model fits the observed data well. To assess significance, we used a non-parametric one-tailed Wilcoxon signed-rank test. This test was used as a non-parametric goodness-of-fit criterion to assess whether the observed distance was unusually large relative to the simulated distribution for a model, rather than to treat non-rejection as proof of model support. We used this non-parametric test to determine if the observed data fell within the distributions of the five simulated data sets because we found the distributions of d_{sim_z} for our system, *Leiocephalus* lizards, to be right skewed. The extinction model that best fit the observed data was the one with the highest Wilcoxon signed-rank test statistic that also failed to reject the left-tail null hypothesis, indicating that d_{obs} is significantly within the simulated distribution of that model.

Non-random extinction in *Leiocephalus* ecomorphology

Body size and several morphological traits were measured to estimated *Leiocephalus* ecomorphology. Body size was measured as the maximum observed snout–vent length (SVL), a common measure of lizard body size that is independent of tail length, from the literature, except the extant species *L. varius* for which we obtained a maximum value from museum specimens (Pregill 1981, Henderson and Powell 2009, Kemp and Hadly 2015, Köhler et al. 2016). Body size was the only morphological trait for which data could be obtained for all 32 species. For seven of the eight extinct species, maximum body size was the only trait available. For 21 extant and one extinct species, we accessed museum specimens to measure a suite of 15 morphological traits summarized with a principal component analysis (PCA). We measured fluid-preserved specimens for: SVL, fore–hindlimb distance, pelvis width, pelvis height, total tail length, head length, head width, head height, finger IV metatarsal length, upper arm length, forearm length, toe IV metatarsal length, toe IV width, thigh length, and shank length (see the table in Supporting information for specimens measured). Prior to conducting the PCA, we corrected for body size allometry by dividing trait values by SVL and log transformed SVL and the ratios. Note that we were neither able to perform phylogenetic PCA nor phylogenetic-size correction analyses (Revell 2009) because no phylogeny exists for all (or even a majority) of these species (Köhler et al. 2016). This ratio-based approach provides a simple and widely used correction for body size in comparative ecomorphological studies, particularly when sample sizes and trait availability are limited, although alternative methods such as regression-based allometric corrections may be appropriate when sufficient data are available (McCoy et al. 2006). We used the first two axes, PC1 and PC2, as synthetic morphological traits that we tested for non-random extinction. For body size, we evaluated all past extinctions starting with all described *Leiocephalus* species ($n = 32$, $k = 8$) and predicted-future extinctions starting with all extant species

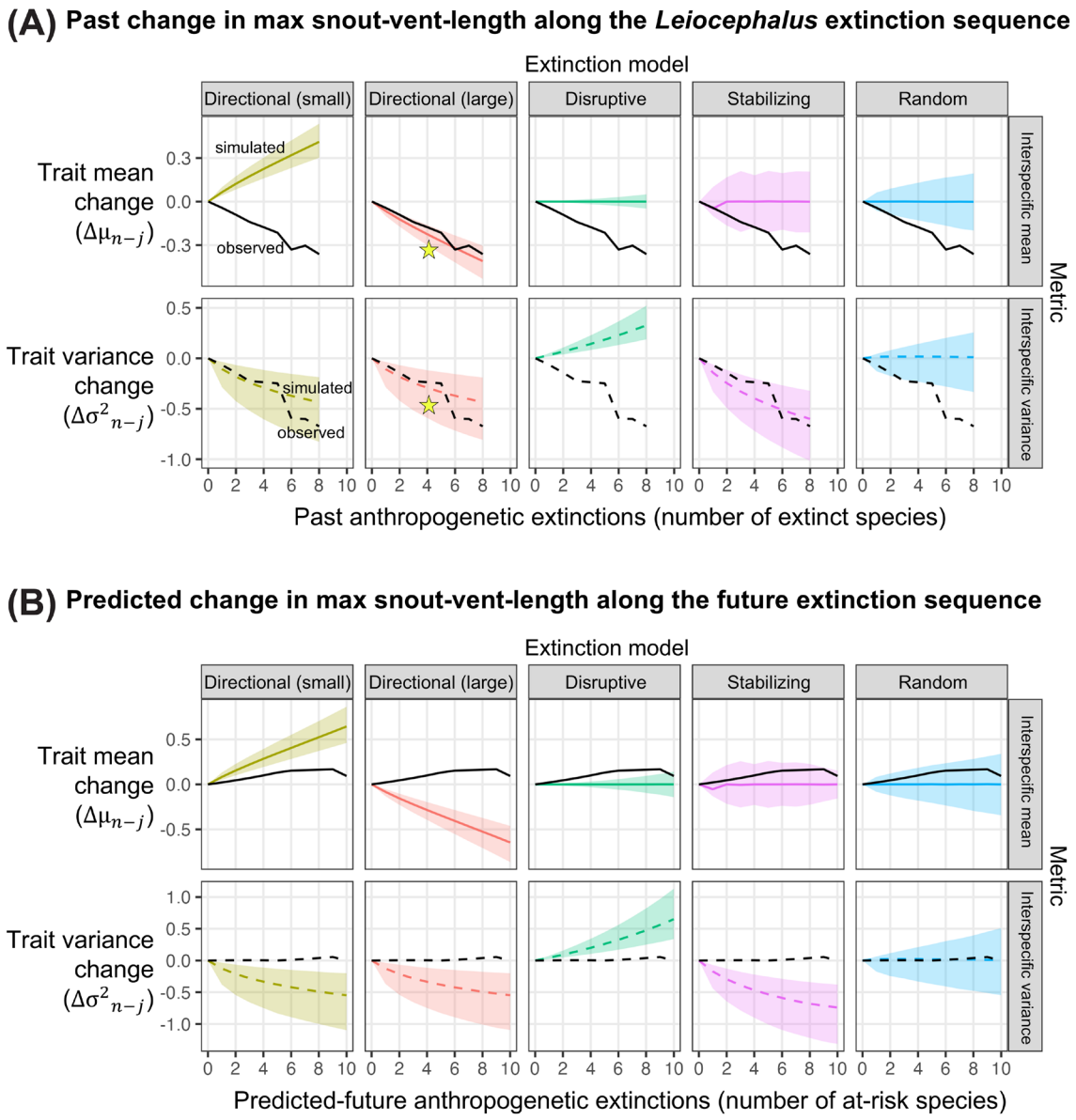

Figure 2. A) The largest *Leiocephalus* lizard species have all gone extinct and the extinction sequence exhibits strong directional nonrandom extinction. B) Predicted-future body-size loss was best explained by random extinction, but this simulation model was not significant. For each simulation model, changes in interspecific trait mean and variance metrics are plotted as species are lost for the observed data (black solid and dashed lines) and for a distribution of model simulations of the same species richness and number of extinctions for each extinction model. Median values of the simulations are the colored lines and the colored shading is the 95% confidence interval of all the simulations. Stars indicate best-fit and significant models.

until only IUCN Red List 'Least Concern' (LC) species remain ($n = 24$, $k = 10$). Similarly, for the two PCA axes we began with all extant species and ended with only LC species ($n = 22$, $k = 8$, based on available trait data).

We tested past maximum SVL, predicted-future maximum SVL, predicted-future PC1, and predicted-future PC2 for nonrandom extinction. We estimated the past and present extinction sequences of *Leiocephalus* lizards based on the IUCN Red List (IUCN 2020). Extinction scenarios that rely solely on IUCN Red List categories surely oversimplify extinction risk because these categories represent broad thresholds that can mask important variation among species (Pimiento et al. 2020). In the case of *Leiocephalus*, a refined statistical approach cannot be applied here, as few data on population variability and life history traits exist, limiting our ability with this clade to move beyond IUCN categories to generate quantitative extinction probabilities. Thirteen *Leiocephalus* species were IUCN categorized as 'Least Concern' (LC), one 'Near Threatened' (NT), two 'Vulnerable' (VU), one 'Endangered' (EN), five 'Critically Endangered' (CR), two 'Data Deficient' (DD), and eight 'Extinct' (EX). Published last occurrence years and ages

were used to order the eight *Leiocephalus* extinctions into a past extinction sequence (Etheridge 1965, 1966, Pregill 1981, 1984, IUCN 2020). For future-predicted extinction, we assigned the two DD species, *Leiocephalus sixtoii* to VU and *Leiocephalus varius* to LC, based personal observations of SBH (Cox et al. 2022). IUCN criterion E sets a probability of extinction within a particular number of years for CR ($p_{extinct} \geq 0.50$ within 10 years), EN ($p_{extinct} \geq 0.20$ within 20 years), and VU ($p_{extinct} \geq 0.10$ within 100 years) species (IUCN 2020). Corresponding probabilities are not published for NT species. Therefore, we followed Oliveira et al. (2020) for NT: $p_{extinct} \geq 0.01$ within 100 years.

To extrapolate the future year of likely extinction for each species, we solved for the year of extinction for $p_{extinct} = 0.95$ as extrapolated from criterion E probabilities, by assuming that the probability of extinction and remaining extant for a species over the same time interval sum to one. We treated the probability of remaining extant as an exponential decay function (Eq. 2):

$$P_{extant} = \left(1 - P_{extinct-E}\right)^{\frac{T}{Y_E}} \quad (2)$$

where $P_{extinct-E}$ is the probability of extinction, Y_E describes the time interval in years for each category from criterion E in years, and T describes the time in years it takes to fulfill P_{extant} at the set value. By algebraic manipulation of (Eq. 2), one can arrive at (Eq. 3):

$$T = Y_E \frac{\log\left(P_{extant}\right)}{\log\left(1 - P_{extinct-E}\right)} \quad (3)$$

We set $p_{extant} = 0.05$ and calculated the value of T for all extant *Leiocephalus* based on Red List categories. The resulting T values were treated as extinction date midpoints with a single year last seen ($T \pm 10$ years). These T values were then ordered to create the future-predicted extinction sequence.

The exact year of extinctions is unknown for past and future extinctions, causing ties in the extinction sequences. For species with overlapping date ranges, the species with the earliest year lower bound in the range was ordered first. If the earliest bounds were the same, then we ordered the species with the earliest upper bound first. For example, for a species with a range of 150–350 and one with a range of 150–200, we would order the second species before the first species. Finally, for species whose extinction year ranges were identical, we heuristically sampled ties in the extinction sequence and calculated the mean $\Delta\mu^{obs}_{n-j}$ and $\Delta\sigma^{2obs}_{n-j}$ across 10 000 tie-sampling replicates for empirical extinction (Supporting information). For each predicted-future extinction sequence replicate, species were sequentially removed according to their estimated extinction dates until only LC remained. We averaged the metrics across the tie-sampling replicates and calculated $RMSE^{obs}_{\mu}$, $RMSE^{obs}_{\sigma^2}$, and d_{obs} which we then tested against the simulations under the five extinction models – random, large directional, small directional, stabilizing, disruptive – to identify which models best fit the data. Links to all code and data to reproduce the method and all the analyses can be found at Dryad (https://doi.org/10.5061/dryad.j9kd51ctw) and GitHub (https://github.com/ieco-lab/extinctFD) and can be adapted for any observed data set.

Results

The past loss of body size diversity based on max SVL, observed for *Leiocephalus*, was significantly explained by the large directional model of nonrandom extinction and the best-fit model for the predicted-future pattern of body size was random (Fig. 2; Supporting information). Visually the random model best matched the predicted-future loss of body size diversity (Fig. 2; Supporting information). However, the predicted-future body size pattern differed significantly from all the models based on Wilcoxon signed-rank tests, indicating a more complex extinction scenario than random extinction and any of the general models (Table 1).

The first two axes of the morphological PCA explained 49.43 and 19.87% of the trait variance among species, respectively, and all other axes each explained < 10% of variance (Fig. 3). For PC1, body size-related traits loaded most heavily (e.g. SVL, head width). For PC2, limb-length traits loaded most heavily (e.g. upperarm length, shank length; see

Table 1. Extinction model fits for the loss of *Leiocephalus* lizard ecomorphology. Extinction models were fit for maximum observed snout–vent length (SVL) and the first two axes from a morphological diversity PCA conducted on 15 traits. Significant model fits are presented in bold and are followed by an asterisk based on a one sample Wilcoxon signed-rank test that compared the observed ecomorphological loss data to data simulated under each model.

Trait	Timeframe	Model	W statistic
Max SVL	Past	Directional (large)	**4.29E+07***
		Stabilizing	1.38E+05
		Random	2.10E+01
		Directional (small)	0.00E+00
		Disruptive	0.00E+00
	Future	Random	1.33E+07
		Stabilizing	6.81E+04
		Directional (small)	2.78E+02
		Disruptive	4.20E+01
		Directional (large)	0.00E+00
Morphological PC1 (body size)	Future	Random	**3.75E+07***
		Stabilizing	3.35E+05
		Directional (small)	4.40E+03
		Disruptive	2.10E+01
		Directional (large)	0.00E+00
Morphological PC2 (appendage length)	Future	Stabilizing	**3.35E+07***
		Random	7.39E+05
		Directional (large)	5.02E+03
		Directional (small)	0.00E+00
		Disruptive	0.00E+00

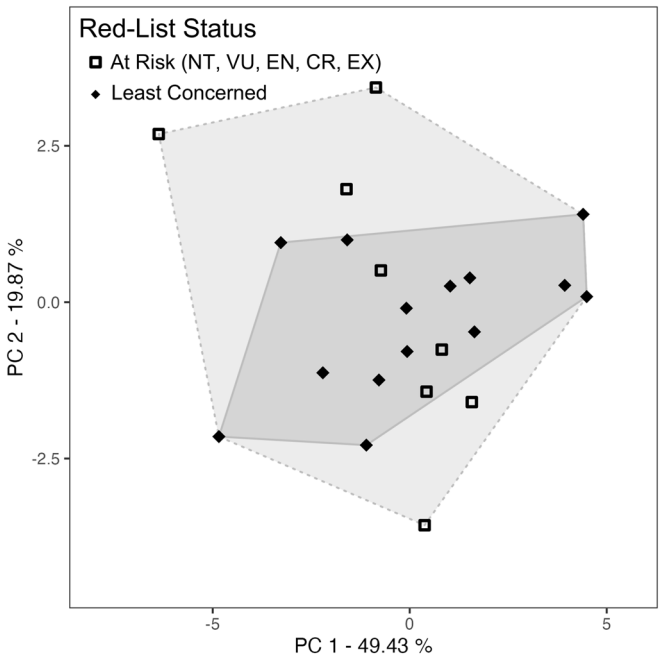

Figure 3. Predicted-future extinctions of *Leiocephalus* show a loss of ecomorphological diversity as measured with principal component analysis on 15 traits. The first two axes explained 59.30% of the variance and corresponded to morphological traits associated with body size (PC1) and appendage lengths (PC2). See Table S2 in Supporting information for trait loadings. The minimum convex polygons for extant species (dashed line and lighter grey fill) and predicted-future species after extinctions expected from IUCN Red List statuses (IUCN 2020) (solid line and darker grey fill) show considerable contraction, especially along PC2. Species are represented by black points that are shaped according to their grouped IUCN status.

loadings table in Supporting information). If all the threatened species went extinct, the morphological space that the genus comprises would shrink by 65%, primarily along PC2 (Fig. 3), where both long- and short-limbed species are more threatened than species with intermediate-sized limbs. Thus, stabilizing nonrandom extinction significantly explained the predicted-future pattern of PC2 loss (Fig. 4; Supporting information, Table 1). Like the result for predicted-future max SVL diversity loss (Fig. 2), the predicted-future loss of body size diversity explained by PC1 was best explained by random extinction (Fig. 4; see figures in Supporting information; Table 1).

Discussion

Human-caused extinctions in the Caribbean lizard genus *Leiocephalus* have been non-random with respect to ecomorphological traits. In the past, extinctions were strongly directional, with large-bodied species disproportionately lost (Fig. 2). Conversely, future extinctions – based on the IUCN Red List – are better explained by stabilizing processes (Fig. 4) that cull species with more extreme limb morphologies (Fig. 3). The approach that we developed to derive these conclusions provides a generalizable framework to understand non-random extinction based on classic models of natural selection (Fig. 1). A temporal change from directional to stabilizing non-random extinction based on the functional traits of species in a clade, like that observed in *Leiocephalus*, is expected when the adaptive landscape that gave rise to the species shifts. As such, this framework provides an avenue for forecasting future extinctions of species in clades based on functional traits when the past and future extinction sequences can be estimated.

The extinctions of the largest *Leiocephalus* were likely due to predation by introduced mammals and hunting by humans (Borroto-Páez and Woods 2012, Kemp and Hadly 2015). For instance, one of the largest species recorded, *L. cuneus*, was estimated at 200 mm SVL and was last seen in the 17th century on Guadeloupe. It was also known to inhabit three other islands (Anguilla, Antigua, and Barbuda; Henderson and Powell 2009, IUCN 2020). The last observations of *L. cuneus* correspond with the arrival of European settlers who introduced rats, cats, and dogs that all prey on large-bodied lizards (Steadman et al. 1984). Although direct evidence does not exist for the absolute cause of all *Leiocephalus* extinctions – one-third of the genus has gone extinct – examples like *L. cuneus* support that the largest species went extinct due to predation pressure and add to growing global trends of the anthropogenic loss of body size functional diversity that can impact ecosystem functioning (Séguin et al. 2014). Island food-webs and prey diversity were likely affected with the loss of large-bodied *Leiocephalus*, many of whom eat larger insect prey, lizards, snakes, and birds (Schoener et al. 1982, Henderson and Powell 2009). For example, *Leiocephalus* predation exerts selective pressure

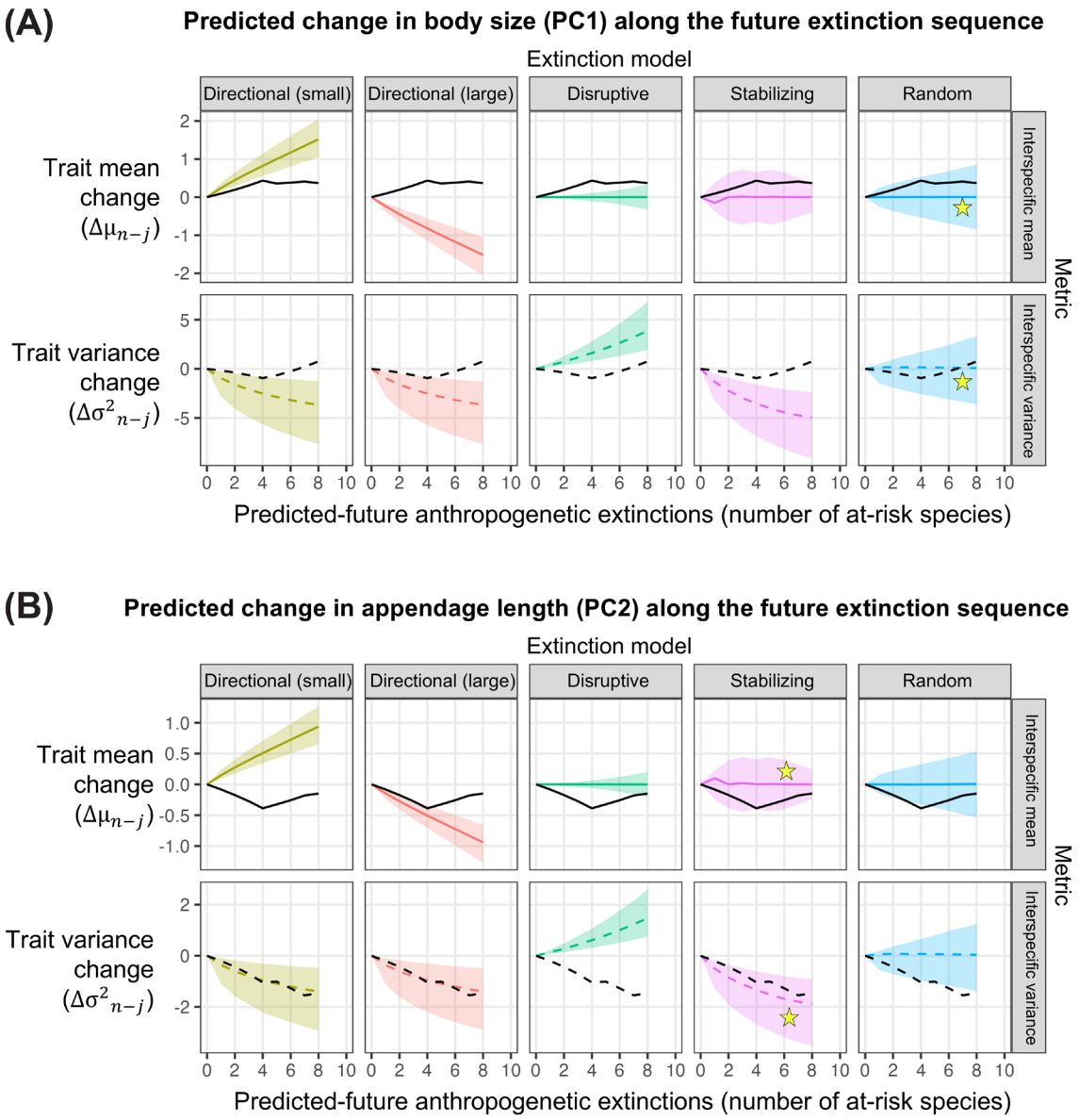

Figure 4. A) Predicted-future loss of body size ecomorphological diversity of *Leiocephalus* lizards is best fit by the random extinction model. B) In contrast, predicted-future loss of appendage length ecomorphological diversity matches the stabilizing non-random extinction model. Ecomorphological diversity was measured by the first two axes of a PCA conducted on 15 morphological traits (Fig. 3, Table S2). The first axis (PC1) corresponds with traits that measure body size. The second axis (PC2) is most strongly associated with appendage length traits (Table S2). Median values of the simulations are the colored lines and the colored shading is the 95% confidence interval of all the simulations. Stars indicate best-fit and significant models.

on fitness-related traits in *Anolis* and causes them to forage higher in vegetation (Schoener et al. 2002, Henderson and Powell 2009, Vanhooydonck et al. 2009).

More ecomorphological diversity will be lost from this lizard genus as more extinctions occur due to stabilizing non-random extinction. The predicted-future sequence of *Leiocephalus* extinctions best fit both random and stabilizing non-random extinction models. Random extinction best explained the predicted-future loss of functional diversity for both measures of body size traits (max SVL and PC1). In contrast, stabilizing non-random extinction explained the predicted-future loss of appendage length functional diversity based on PC2. Species with shorter or longer limb lengths are the most threatened with extinction. Stabilizing extinction of extreme limb lengths in *Leiocephalus* may reflect loss of species with more specialized locomotor performance on specific substrates and in specific unique habitats. For example, lizards with longer relative limb lengths perform better on firmer substrates like rocks; and lizards with shorter relative limb lengths perform better on sand (Irschick and Garland 2001, Goodman et al. 2008). Increased and decreased

limb length are also strongly associated with the adaptation of lizards to particular vegetation niches (Losos 1990, Melville and Swain 2000, Wiens et al. 2006, Losos 2009, Tulli et al. 2009, Edwards et al. 2022). It is unclear how such future loss of the extreme limb lengths could affect ecosystem functioning, because the ecosystems, like forests where such specializations arose, are now being lost at high rates (Hedges et al. 2018). These patterns suggest that *Leiocephalus* species with less specialized, more generalist morphologies may be more successful in navigating the novel habitats created by landscape transformation, reflecting a 'jack-of-all-trades is a master-of-none' strategy (MacArthur 1984, Davies et al. 2004, Böhm et al. 2013, van der Plas et al. 2016, Carmona et al. 2021).

Increased anthropogenic extinction pressures like habitat loss due to land development, charcoal production, and wood harvesting coincide with the observed past-to-future change from directional to stabilizing nonrandom extinction in *Leiocephalus* (Brooks et al. 2002, Leisher et al. 2013, IUCN 2020). Intensifying predation by invasive mammals like the mongoose, which can inhabit a wide range of habitats, has also exerted contemporary pressure (Borroto-Páez and Woods 2012, IUCN 2020). Such pressures are strong for Hispaniola, the most species-rich island for extant *Leiocephalus*, where deforestation and land development have become prolific over the last few decades (Sangermano et al. 2015, Hedges et al. 2018). Correspondence between habitat loss and extinction of species with extreme appendage lengths may result from loss of species that are more specialized to particular microhabitats (Blackburn and Gaston 2003). Additionally, invasive predators like the mongoose have now even penetrated remote mountains on islands like Hispaniola and prey readily on diurnal, ground-dwelling lizards like many species of *Leiocephalus* (Borroto-Páez and Woods 2012, Hedges and Conn 2012). Therefore, mongoose might indirectly benefit from the mismatch between more developed, less diverse habitats and *Leiocephalus* with more extreme phenotypes that are poorly suited to remaining habitats. Surviving *Leiocephalus* species then may be 'microhabitat generalists' (Arnold 1998, Tulli et al. 2012) that perform at an intermediate level across different microhabitats and consequently manage to avoid predation. The diverse habitats of these species need to be protected. We recommend that development plans include setting aside resources for dedicated protected areas and reserves to maintain such habitats that reduce stabilizing non-random extinction (Hedges et al. 2018). We urge that control plans be formed for invasive species like the mongoose, which have already demonstrated capacity to cause Caribbean lizard extinctions (Hedges and Conn 2012).

Future development of the methods and framework we propose to characterize non-random extinction in species' ecomorphological and functional trait data is needed. First, none of the five models significantly explained the predicted-future loss of max SVL diversity. Therefore, more complex extinction models should be developed and tested on data when none of the simple models we present fit. For example, the interaction among traits and extrinsic threats like habitat loss could be included in more complex models (Tingley et al. 2013, Zhong et al. 2022).

Second, future extinction sequences were based on IUCN Red List categories, which provide a standardized but coarse representation of extinction risk (Butchart et al. 2025). This approach assumes constant extinction risk through time, a fixed probability threshold for defining extinction timing, and subjectivity in the treatment of data-deficient species that could influence extinction ordering and limit the precision of inferred extinction regimes. If available, incorporating data on population dynamics, generation times, and range changes would improve estimates of extinction timing and refine model inference of non-random extinction processes (Edgar 2025). While we partially accounted for uncertainty in Red List extinction ordering by sampling across tied species, future work could incorporate probabilistic simulations and sensitivity analyses that explicitly model extinction risk and transitions among threat categories (Andermann et al. 2021).

Third, the current framework assumes normally distributed trait values to provide a common baseline; however, future applications could incorporate empirical trait distributions when sufficient data are available (McGill et al. 2006, Carmona et al. 2016). Fourth, the framework is applied at the clade level and does not distinguish among local, regional, or global extinctions. Future extensions could incorporate biogeography and range dynamics to account for scale-dependent patterns of non-random extinction (He and Hubbell 2011, Figueiredo et al. 2019). Fifth, phylogenetic non-independence may influence extinction conclusions if closely related species share similar trait values and extinction risks are related to unmeasured traits. Although a complete phylogeny for *Leiocephalus* was unavailable, such phylogenetic clustering could bias inference by amplifying or dampening apparent nonrandom trait patterns in anthropogenic extinctions (Bielby et al. 2010). Future work should incorporate phylogenetics where possible.

Finally, while there are distinct expected patterns for directional and disruptive non-random extinction even with few extinctions, it is difficult to distinguish random from stabilizing extinction if few extinctions have occurred. The expectations of the two models are nearly identical for short extinction sequences. As a result, statistical power to discriminate among these models is reduced when extinction sequences are short, and multiple models may be consistent with the observed data. This limitation is particularly relevant in *Leiocephalus* for predicted-future extinction scenarios, where relatively few species are projected to be lost and model identifiability is therefore constrained (Fig. 3). When data are available, sensitivity tests for nonrandom extinction could be assessed via simulation to determine the limitations in statistical power in clades with varying extinction levels, timescales, intervals, and confidence in estimated extinction sequences. Ultimately, addressing such questions will ensure confidence in extinction model fit that can be compared across taxa.

In conclusion, we identified evidence consistent with directional extinction in the past and stabilizing extinction in the future (Fig. 1). This pattern is expected when natural selection is replaced by anthropogenic extinction pressures that directionally shift trait distributions to new adaptive optima (Arnold et al. 2001). However, specimens are scant for the extinct *Leiocephalus*. Only body size could be measured for all extinct taxa, whereas multiple traits could be measured for extant species (Fig. 2). This limits direct comparisons of traits shifts and inference of extinction regimes across time periods (Fig. 4). Furthermore, the mechanisms underlying the observed patterns of directional and stabilizing extinction require further study, but observed non-random loss is consistent with expectations that past extinctions were predominantly large-size-selective from hunting by humans and predation by introduced vertebrates, whereas future extinctions reflect stabilizing processes as expected by land development and environmental homogenization that disproportionately selects against species with extreme ecomorphology (Solar et al. 2015, Monarrez et al. 2023, Payne et al. 2023, Rozzi et al. 2023). Regardless of data limitations and mechanisms, for this threatened insular clade, human actions look likely to further erode its unique ecomorphological diversity (Fig. 3).

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Data availability statement

Data are available from the Dryad Digital Repository: https://datadryad.org/dataset/doi:10.5061/dryad.j9kd51ctw (Huron et al. 2026).

Supporting information

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

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