

The intrinsic and extrinsic drivers of extinction risk in lemurs (*Lemuroidea*)

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ABSTRACT

Understanding why some species are more susceptible to extinction than others is critical for implementing effective conservation strategies. Phylogenetic comparative methods (PCMs) have been used to understand the drivers of extinction risk, and are most effective when applied to an entire lineage. Lemurs are a monophyletic group that evolved in Madagascar in relative isolation over millions of years, representing a unique and diverse lineage that provides an excellent case study for the drivers of extinction risk. We investigated the drivers of extinction risk in lemurs using intrinsic (species' traits) and extrinsic (environmental) variables related to ecology, life-history, and biogeography. We evaluated the tempo and mode of trait evolution and used PCMs to examine correlations between traits and extinction risk. We used models of trait evolution and historic and future climate data to predict how lemurs will fare under climate change. The predominant drivers of extinction risk in lemurs were diurnal activity and longevity, which were positively and negatively associated with extinction risk, respectively. Body size, as well as temperature mean and temperature variance across a species' range, were also predictors of risk. We found no evidence for evolution punctuated by short periods of rapid change in response to environmental shifts or other factors (punctuated equilibria), suggesting that traits will not evolve to track Madagascar's changing climate. These results may inform conservation strategies in Madagascar by differentiating the role of intrinsic vs. extrinsic traits in extinction risk. Moreover, findings may contribute to preventing declines in other endangered and endemic taxonomic groups.

1. Introduction

There is mounting evidence that the Earth is in the midst of a global biodiversity crisis. Estimates suggest that vertebrate species population sizes have halved in the past 40 years (McLellan et al., 2014), and that, at present, more than one million species face extinction (Montanarella et al., 2018). Determining why some species are more susceptible to extinction is critical for implementing effective conservation strategies to preserve biodiversity. Both evolutionary and ecological factors can influence the degree of threat that species face, and these factors can generally be categorized as intrinsic (species' traits and evolutionary history) or extrinsic (relating to the external environment) (Blackburn and Gaston, 2002; Fisher et al., 2003; Purvis et al., 2000a).

Common intrinsic factors include traits such as body size, longevity, and group size. Large body size is often cited as the prepotent intrinsic predictor of extinction risk (McKinney, 1997; Rapacciuolo et al., 2017). Studies have found that for species below 3 kg, extinction risk is generally driven by external threats, whereas in larger species it is

driven by a combination of external and intrinsic factors, and vulnerability to most threats increases sharply (Cardillo et al., 2005; Davies et al., 2008). Larger species tend to exhibit slower life histories than smaller species, meaning they reach sexual maturity later, have longer gestation periods and interbirth intervals, as well as smaller litter sizes. These factors reduce resilience, making it more difficult for them to offset high mortality with high fecundity, thus rendering them more vulnerable to extinction (McKinney, 1997). Intrinsic factors also comprise aspects of the ecology of large species that may increase their extinction risk, such as trophic level, activity cycle, habitat breadth, and home range size. For example, Atwood et al. (2020) found a correlation between body size and herbivory. Both these factors independently influence threat status in mammals, yet because of their shared evolutionary history they are not completely independent. When this is controlled for, some of this effect disappears, meaning that herbivory may be a spurious driver in such groups. Furthermore, diurnal species display a host of attributes that may predispose them to extinction, such as large body size, high predation rates, and vulnerability to hunting

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(Purvis et al., 2000a).

Extrinsic factors, such as biogeographic and climatic variables as well as anthropogenic disturbance, also drive species towards extinction. Human activities have likely contributed to species extinctions since the late Pleistocene, as evidenced by a mean body mass decline in taxa (Barnosky et al., 2004). Currently, the primary human-caused drivers that threaten biodiversity are habitat loss and fragmentation, hunting, invasive species, disease, pollution, and climate change (Baillie et al., 2004; Koch and Barnosky, 2006). While habitat loss is regarded as the primary threat, some analyses indicate that climate change is already affecting many species (Parmesan and Yohe, 2003) and may soon be the predominant driver of extinction (Thuiller, 2007; Urban, 2015). Thus, understanding species' climate niches and tolerances is necessary for predicting their responses to changing temperatures.

Extinction risk analysis is used to assess the probability of species' extinction, calculated as a function of their intrinsic biological characteristics and extrinsic factors. Over the last several decades, phylogenetic comparative methods (PCMs) have emerged as a powerful framework to model how threat status is affected by such factors (Garamszegi, 2014), with the goal of identifying the causes of species declines and predicting how changes in stressors will affect threat status (Fisher and Owens, 2004; Purvis, 2008). PCMs can be used to elucidate the evolution of biological traits, the intrinsic and extrinsic factors that contribute to speciation and extinction, and to account for the phylogenetic non-independence of taxa (Cornwell and Nakagawa, 2017). These methods can also be used to examine the “tempo” (speed) and “mode” (manner) of evolution in traits (Simpson, 1984), informing us how traits are evolving. A popular model of trait evolution is Brownian Motion (BM), which can be described as a ‘random walk’ through time (Revell et al., 2008). This model is often used due its application to a wide range of evolutionary scenarios, as well as being relatively straightforward to statistically fit to data (discussed in Harmon, 2019). In this model, trait values change randomly over time and descendent species drift away from each other following a speciation event (Felsenstein, 1985). A modification of this model is the Ornstein–Uhlenbeck (OU) model, which posits that trait values are being “pulled” towards an optimum (Butler and King, 2004). We can also evaluate evolution using metrics such as Pagel's λ , a measure of phylogenetic signal (Pagel, 1999), which measures the extent to which closely related species resemble each other, as approximated by BM. Additionally, Pagel's κ can signal whether evolution is occurring in a more punctuated manner, i.e. trait change is concentrated at speciation events, rather than constant over time. This may signify a case of adaptive radiation, in which diversification of lineages is associated with diversification of traits (Gavrillets and Losos, 2009).

PCMs are most effective when dealing with a complete monophyletic clade within which a single process is operating, such as when species evolved in relatively remote and circumscribed ranges. An example of this is the lemurs of Madagascar. Madagascar is the world's fourth-largest island, and an ideal natural laboratory for exploring evolutionary processes (Vences et al., 2009). It is home to an exceptional number of endemic species, making it one of the greatest biodiversity hotspots (Myers et al., 2000). Several entirely endemic clades have been evolving across the landscape in relative isolation for millions of years, including lemurs, carnivores, tenrecs, reptiles, and amphibians, which are 92–100 % endemic (Antonelli et al., 2022; Goodman and Benstead, 2005). Thus, conservation in Madagascar is important not only for safeguarding living species, but also for preserving deep lineages and important pieces of evolutionary history (Davies et al., 2013).

As Madagascar's endemic primates, lemurs have been a predominant target of evolutionary theory and research. Lemurs belong to the Strepsirrhini suborder of primates, comprising over 100 known extant species, approximately 94 % of which are vulnerable to extinction (Davies et al., 2013). Indeed, lemurs have been cited as the most endangered vertebrates (Davies et al., 2013). Lemurs are widely distributed throughout the forested habitats of Madagascar, including eastern

rainforests, western tropical dry forests, and southern arid spiny forest. This steep geographic and climatic gradient of the landscape may have had a considerable impact on the evolution of lemur traits (Dewar and Richard, 2007; Wright, 1999). Consequently, lemurs are taxonomically and phenotypically diverse. Body size in extant species ranges from 30 g (*Microcebus berthae*, the smallest living primate) to nearly 10 kg (*Indri indri*), while recently extinct lemurs have been recorded as weighing up to 160 kg (*Archaeoindris fontoynontii*) (Godfrey and Jungers, 2003). Lemurs also exhibit wide interspecific variation in dietary preferences, habitat breadth, and activity patterns which likely coevolved with body mass (Herrera, 2017a). Concerning activity patterns, some species are classified as strictly nocturnal/diurnal, whereas others are cathemeral, meaning their activity occurs at irregular times (Santini et al., 2015). Climate change over deep time may play a role in how lemurs have evolved and diversified (Godfrey et al., 2020; Herrera, 2020). This is relevant because temperature continues to rise across Madagascar, causing hotter dry seasons, wetter rainy seasons, and increases in number and severity of cyclones and droughts (Nematchoua et al., 2018).

Although many of the intricacies of lemur origins and evolution remain unknown, there is evidence that this clade has been evolving in relative isolation for approximately 50–60 million years (Herrera and Dávalos, 2016; Yoder and Yang, 2004). To date, there have been no analyses of the drivers of extinction risk across a nearly complete lemur phylogeny that considers both biological and environmental factors. In fact, lemurs have been excluded from research to ensure results would not be driven by this extremely threatened and unique group (Verde Arregoitia et al., 2013). Discerning the factors that predispose lemur species to greater extinction risk will help fill these research gaps, allow for more effective planning of conservation action in Madagascar, and aid our understanding and prevention of declines in other endemic or at-risk taxonomic groups. Thus, the fundamental goal of this project was to investigate the various drivers of extinction risk in these endemic primates. First, using extensive phenotypic data on species traits related to their intrinsic biology, as well as environmental data related to the external environments they live in, we investigated the tempo and mode of trait evolution across the entire lemur phylogeny. We then investigated the drivers of extinction risk by regressing extinction risk against intrinsic and extrinsic factors. Additionally, we used climate forecasts and rates of trait evolution to predict how lemurs will respond to anticipated climate change. Based on existing studies of extinction risk and evolution, we made the following hypotheses:

- 1) With respect to trait evolution, we expected to find evidence of high phylogenetic signal in life-history traits, consistent with past research in lemurs and other primates (Kamilar et al., 2012; Kamilar and Cooper, 2013).
- 2) We hypothesized that both intrinsic and extrinsic factors will predict extinction risk. The former would be consistent with past research in other mammals (Purvis et al., 2000b), whereas the latter is based on more recent studies that concluded narrow climate niches and human pressure were positively correlated with extinction risk (Chichorro et al., 2020; Di Marco et al., 2018).
- 3) Based on recent projections of rapid climate change, we predicted that climate niches, along with all other intrinsic and extrinsic factors, are evolving at a slower rate than the climate in Madagascar is changing.

The results of this study should advance the understanding of the factors contributing to lemurs' vulnerability to extinction and serve as a case study for other endangered or endemic island species.

2. Methods

We evaluated the drivers of extinction risk in lemurs using a dataset of intrinsic and extrinsic factors. We examined collinearity among

variables to select which traits to incorporate in analyses, and then fitted statistical models to test the tempos and modes of trait evolution. To determine how these traits relate to extinction risk, we conducted a phylogenetic regression analysis to examine correlations between traits and extinction risk, defined as IUCN Red List Status. Finally, we estimated rates of lemur trait evolution and projected forward to predict how lemurs will fare under climate change. All analyses were conducted using R version 4.0.2 (R Core Team, 2020); R package names are given in 'single quotes' while function names are in *italics*.

2.1. Trait data and phylogeny

This study included traits compiled from the literature (Table 1), based on two datasets to encompass the range of traits across species. The primary dataset was compiled from original literature sources (Table B1). We filled in some missing data from this dataset using a secondary dataset, Razafindratsima et al. (2018), which was a compilation of traits representing the ecological and geographical diversity of all extant mammal and bird species of Madagascar. As an index of extinction risk, we used data from the IUCN Red List of Threatened Species (IUCN, 2021), which includes 107 lemur species. The Red List is comprised of categories (ranging from least concern to extinct) that classify risk of extinction based on five criteria: population reduction, geographic range, small population size and decline, very small or restricted population, and probability of extinction (IUCN, 2012). Following Atwood et al. (2020), we incorporated all lemurs' IUCN Red List extinction statuses as data (IUCN, 2012). To incorporate phylogenetic information into the models, we used a time-calibrated maximum clade credibility phylogeny of 114 lemur species (Herrera and Dávalos, 2016).

2.2. Geographic range and environmental data

To extract environmental variables from within lemur geographic distributions, we used polygon shapefiles of extant lemur distribution maps (IUCN, 2021) and obtained climate data from WorldClim (Hijmans et al., 2005). Using *extract* in 'raster' (Hijmans, 2022), we extracted climate data (collected from 1970–2000) for all species. We calculated the mean and variance of annual temperature (BIO1), as well as the means for temperature range (BIO7), annual precipitation (BIO12) and precipitation seasonality (BIO15). We included precipitation variables to capture climates that may not vastly differ in temperature alone. We also retrieved WorldClim future climate projections. We extracted the projected mean temperature for the years 2061–2080 under the best case (rcp 2.6) and worst case (rcp 8.5) climate change scenarios and calculated the mean for each species (Taylor et al., 2012; van Vuuren et al., 2011). We used data from the 'IPSL-CM5A-LR' model, with a spatial resolution of 10 min of a degree of longitude and latitude (approximately 320 km²). Lemur distributions ranged from around 20 km² to 101,442 km². Lastly, to measure anthropogenic pressures within species' ranges, we obtained the 2009 Human Footprint index (HFP) data which measures cumulative human pressures, such as population density, and the spatial extent of railways, roads, and electrical infrastructure (Venter et al., 2016).

Missing values are common in trait data, and excluding species on the basis of missing data not only reduces sample size and thus statistical power, but risks introducing bias into analysis (Little and Rubin, 2002). To account for gaps in the datasets, we imputed missing values for all continuous trait data based on ancestral character reconstruction using *phyEstimate* in 'picante' (Garland and Ives, 2000; Kembel et al., 2010). In total, 29.6 % of the data was missing and imputed. Refer to the Appendix for the percentage of imputed data for each trait (Table A1) and the pre- and post-imputation data tables (Tables C1 and C2, respectively). Since imputing using phylogeny would introduce obvious biases in our analyses of the tempo and mode of trait evolution across phylogeny (Section 2.3 below), we did not use such imputed estimates in

Table 1

A description of all traits included in the dataset that were deemed as possibly important to extinction risk. * = Predictor variables used for regression analyses.

Trait	Description	Range	Units
Intrinsic traits			
Brain size	Estimates of the cranial capacity	1.7–135.6	cm ³
* Body mass	Body mass averaged across sexes. Midpoints used if averages were unavailable	30.6–161,200	g
* IBI	Interbirth interval. The length of time between successive births of the same female(s) after a successful or unspecified litter	210–1460	days
* AFR	Average age of first reproduction	321.4–1964.4	days
Gestation length	Length of time of fetal growth from conception to birth	52–321.2	days
Weaning days	Age at which infants are weaned	37.8–1095	days
* Longevity	Maximum adult longevity	103–472.6	months
* Litter size	Average number of offspring per female per litter	1–4.4	#
* Home range	Mean size of the area in which daily activities are generally restricted for a social group	0.0019–13.3	km ²
* Group size	Average number of individuals in a social group	1–17	#
* Trophic level	Based on diet: (0) herbivore; (1) omnivore		N/A
* Habitat breadth	Number of habitat layers used by each species. Layers include above-ground dwelling, aquatic, fossorial and ground dwelling. Coded as single habitat layer (0) or multiple layers (1)		N/A
* Activity cycle	Activity cycle of each species. Activity cycles include: (1) nocturnal only; (2) nocturnal/crepuscular, cathemeral, crepuscular or diurnal/crepuscular and (3) diurnal only		N/A
Extrinsic traits			
* Mean temperature	Mean annual temperature (BIO1) across each species' geographic range	17.4–26.8	°C
* Temperature variance	Variance in mean annual temperature across each species' geographic range	0.003–106.3	°C
Maximum temperature	Max Temperature of Warmest Month (BIO5)	25.7–35.5	°C
Minimum temperature	Min Temperature of Coldest Month (BIO6)	8.3–19.8	°C
Temperature range	Mean annual temperature range (BIO7) across each species' geographic range	11.4–24.4	°C
* Annual Precipitations	Mean annual precipitation (BIO12) across each species' geographic range	507.2–2770.6	mm
* Precipitation seasonality	Precipitation Coefficient of Variation (BIO15). A measure of the variation in monthly precipitation totals over the course of the year across each species' geographic range	41.6–124.2	mm
* HFP	Human Footprint Index of cumulative pressures on the environment in 2009 across each species' geographic range	3.3–10.1	N/A

those analyses, but only in our regression analyses (Section 2.4 below). All trait-evolution analyses were conducted using the original data without imputation.

2.3. Trait evolution

The ultimate goal of this study was to understand the factors that

render lemur species to be more susceptible to extinction, part of which includes understanding the evolution of these factors. A fundamental goal in PCM involves determining the model, or mode, of evolution under which traits are evolving (Hernández et al., 2013). To test the most likely mode of trait evolution, we fit several models. We estimated σ^2 – a measure of the variance in a macroevolutionary time scale under the BM model. σ^2 measures the tempo of evolution by evaluating the rate at which trait values of related species will diverge from each other. We also estimated α , a parameter of the OU model that measures the strength of return towards a theoretical optimum (Hansen, 1997). Larger values of α signify a faster approach towards the optimum and constraint around the optimal trait value. When α is 0, the OU model is equivalent to the BM model. Lastly, we fit a white-noise (null) model that assumes no phylogenetic relationship.

Evaluating the extent to which closely related species resemble each other, or their ‘phylogenetic signal’, is another fundamental part of PCMs (Münkemüller et al., 2012). We estimated Pagel's λ , a metric for measuring patterns of phylogenetic signal (Pagel, 1999), on continuous traits across the entire lemur phylogeny. λ is measured on a scale of 0–1, where traits with a value closer to 1 exhibit strong phylogenetic signal consistent with a BM model of evolution, and values closer to 0 are consistent with a white-noise model. For binary traits, we measured phylogenetic signal using D statistic (Fritz and Purvis, 2010). D and λ are conceptually linked, although D is anchored with 0 reflecting the expectation under BM (unlike λ , where the expectation is 1), and so we follow Díaz et al. (2013) in reporting $1-D$ for ease of comparison with λ . We also estimated Pagel's κ , a metric of mode that reflects a punctuational versus gradual mode of evolution. Like λ , a κ value of 1 refers to gradual evolution under a BM model, while a value of 0 signals that character change may be more concentrated at speciation events, consistent with adaptive radiation, for example.

We used Akaike Information Criterion (AIC) scores to assess models' fit (Burnham and Anderson, 2004; Richards, 2005) and determined the best model as the one with the lowest AIC score. We conducted likelihood ratio tests to determine if λ and κ values differed significantly from 0. Prior to analyses, we log-transformed all values to reduce skew. All models of continuous traits were fit using *fitContinuous* in ‘geiger’ (Pennell et al., 2014) and binary traits were measured using *phylo.d* in ‘caper’ (Orme et al., 2018).

2.4. Phylogenetic regression

We constructed a Phylogenetic Generalized Least Squares (PGLS) model to determine what factors best predict extinction risk in lemurs. We calculated variation inflation factors (VIF) to assess collinearity among continuous predictor variables (Kock, 2015), and thus removed all variables with a VIF greater than three: temperature range, maximum temperature, minimum temperature, weaning days, brain size, and gestation length. We used Red List statuses as a measure of extinction risk. Following Purvis et al. (2000a), we converted these ratings into an ordinal index. We chose not to include species that fell under Least Concern or Near Threatened, as these groups only included 3 species in total (2.5 % of our data) and were insufficient for analyses. We also excluded Extinct species, due to insufficient trait data, and Data Deficient species, reducing the sample size to 97 species. Our final index used for the regression analysis was: Vulnerable (VU) = 1, Endangered (EN) = 2, Critically Endangered (CR) = 3.

We modeled Red List status as a continuous measure of threat status following Purvis et al. (2000a). While there is the potential for this to introduce type I errors, Matthews et al. (2011) found that these error rates did not increase when ordinal data were used for PGLS. Using the *pgls* function in ‘caper’ (Orme et al., 2018), we tested the relationship between Red List status and predictor variables. PGLS corrects for phylogenetic nonindependence during model-fitting using the maximum likelihood estimate of Pagel's λ (Pagel, 1999). We first constructed a maximal PGLS model, with 12 continuous predictor variables

and three discrete variables (variables with asterisks in Table 1). Before analysis, all continuous variables were log-transformed. To make model coefficients for continuous variables with different units comparable, we z-transformed the data to a distribution with a standard deviation of 0.5 (Gelman, 2008). We assessed diagnostic plots of the residuals for goodness of fit.

It is important to note that range size is used as a criterion (criterion B) for assessing IUCN Red List status. We acknowledge that this introduces some biases and limits our discussion of range size. It also presents an issue when incorporating temperature variance into our regression models, as larger temperature variance may be due to a larger range size (because a larger range potentially exposes the species to a greater variation in temperature). We cannot exclude species classified under criterion B from our analyses as that would remove a large proportion (45 of 97) of species. We also recognize that incorporating range size directly into our model would create circularity issues. To mitigate these challenges, we divide temperature variance by the number of grid cells within each species' range. This approach aims to reduce the correlation between temperature variance and range size, particularly addressing the problem of larger temperature variances in species with expansive ranges.

To determine which predictor variables best explained extinction risk, we fit all possible simpler model combinations of the maximal model using ‘MuMin’ (Bartoni, 2022). Model performance is measured using small-sample corrected Akaike Information Criterion (AICc) weights. We compared the full model-averaged coefficients to determine the relative importance of all predictor variables, averaged across coefficient and parameter uncertainty. In addition to our continuous PGLS model, we modeled extinction risk as a binary response to account for any potential errors or inaccurate interpretations associated with modeling extinction risk as a continuous variable, as well as to identify any differences between any two Red List Categories. The methods and results for these analyses can be found in Appendix D.

2.5. Projections

We compared the estimated macroevolutionary diversification rates of lemurs against the rate of projected climate change. We used the estimated σ^2 values (estimated as described in Section 2.3; found to be the best-supported model of trait evolution as outlined in Section 3.1) to determine the rate at which trait values of related species will diverge from each other. It should be noted that these estimates assume traits are evolving at a constant rate, consistent with BM. Although it has been argued that BM is not the best model for trait evolution (Elliot and Mooers, 2014), we found support for the BM model across all traits (although, as discussed below, some support for OU and one trait almost as well-explained by a κ transformation as a λ). Thus, we suggest that these estimates are reasonable. Models of continuous traits were fit using *fitContinuous* in ‘geiger’ (Pennell et al., 2014). To understand how rates of trait evolution compared to rates of climate change, we converted trait rates into units of ‘felsens’, which makes traits directly comparable. A felsen is the variance among log-transformed trait values per million years (Ackerly, 2009), such that greater values indicate faster evolution and so greater variation among species' traits. Using historic climate data and future projections, we calculated the rate of climate change per century. We divided estimated felsens by 10,000 to convert from units of millions of years to centuries. Finally, we compared rates of trait evolution to rates of climate change for each species' distribution to deduce if climate is changing faster than traits are evolving.

3. Results

The full dataset used for analyses included 114 lemur species: 101 extant and 13 extinct, representing at least 93 % of all known species. Across the lemur phylogeny, 26 % of species fall into VU, 41 % fall into

EN, and 33 % fall into CR. Fig. 1 shows a breakdown of extant species by family and Red List status.

3.1. Trait evolution

We found that λ models best explained trait evolution for nine of the 12 traits (Table 2). The values from these models support that traits are evolving closer to a BM model of evolution (Fig. 2), since λ is a measure of phylogenetic signal, and a value of 1 is consistent with pure BM evolution. While the Pagel transformations (λ , δ , and κ) are technically metrics that summarise phylogenetic transformations, for simplicity of presentation and to highlight that they relate to evolutionary models, we refer to them as ‘models’ here, since we are modeling the fit to our data. Of our 12 traits, all but one (temperature variance; $\lambda = 0.18$, $p < 0.01$) showed moderately strong phylogenetic signal (all $\lambda > 0.6$, $p < 0.05$), indicating that traits are evolving closer to BM. The D estimate (Table A2) for trophic level ($1-D = 1.44$) signalled significant and extreme phylogenetic clumping, while habitat breadth ($1-D = 0.35$) indicated significant, yet weak phylogenetic signal. Body mass ($\lambda = 1$, $p < 0.0001$) had the strongest signal, suggesting that it is evolving under “perfect” BM. According to AIC values, the OU model was the best model for temperature range, mean precipitation, mean temperature, and precipitation seasonality (mean temperature and precipitation seasonality showed equal support for λ). However, none of these traits exhibited a strong alpha value ($\alpha < 0.43$ for all). While the BM model was best only for body mass, λ , α , and κ values indicated that many traits are evolving close to BM. Other exceptions include HFP (the only trait for which the null model was among the best), AFR and home range (both of which show high α values consistent with OU), and temperature variance (which displayed low phylogenetic signal.) Notably, group size showed most support for λ and κ transformations, with estimates of λ close to 1 (supporting BM evolution) and κ of 0 (supporting punctuated evolution). Values of σ^2 indicate that home range is evolving much more rapidly than any other trait. Fig. 2 displays comparisons of λ , σ^2 , α , and κ across all traits (exact values displayed in Table A3).

Table 2

Results of model comparison testing tempo and mode of trait evolution. AIC values for each trait, under five different models (λ , BM, OU, κ , and a null model). ‘BM’ is measured from σ^2 values, and ‘OU’ from α . AIC values within two units of each other are considered equivalent. For most traits, the best supported model (indicated in bold) was λ .

	λ	BM	OU	κ	null
Body mass	144.50	142.50	144.50	144.50	465.94
Age at first reproduction	28.90	56.66	42.13	31.96	40.11
Interbirth interval	29.40	50.86	41.81	31.42	53.06
Longevity	42.25	75.47	57.98	50.04	66.80
Litter size	25.59	43.94	31.60	28.98	51.91
Home range	204.35	315.24	218.24	210.09	212.87
Group size	69.87	113.90	105.05	69.17	143.65
Temp. mean	-137.61	-85.69	-135.69	-129.62	-134.22
Temp. variance	363.77	431.08	368.31	385.23	370.38
Annual precipitation	63.20	84.53	54.19	68.03	62.76
Precipitation seasonality	31.57	88.81	33.62	42.08	35.52
Human footprint	-18.80	65.67	-19.54	21.02	-20.80

3.2. Phylogenetic regressions

From the PGLS ($n = 97$, only extant species included), Pagel's λ was estimated at $\lambda = 0$, which indicates no phylogenetic signal in the residuals of the model (Uyeda et al., 2018). The model-averaged coefficient estimates in the full-model showed that diurnal activity cycle, longevity, temperature mean, body mass, and temperature variance were the strongest predictors (meaning they had the greatest standard effect sizes) of extinction risk (Table 3; Fig. 3). Being diurnal was the most important variable in the model, exhibiting a positive correlation with extinction risk. Longevity was the second most important predictor, with a negative correlation. Temperature mean, body mass, and temperature variance were all positively correlated with extinction risk and displayed relatively strong importance in the model, according to the standard effect sizes from the full model-averaged coefficients.

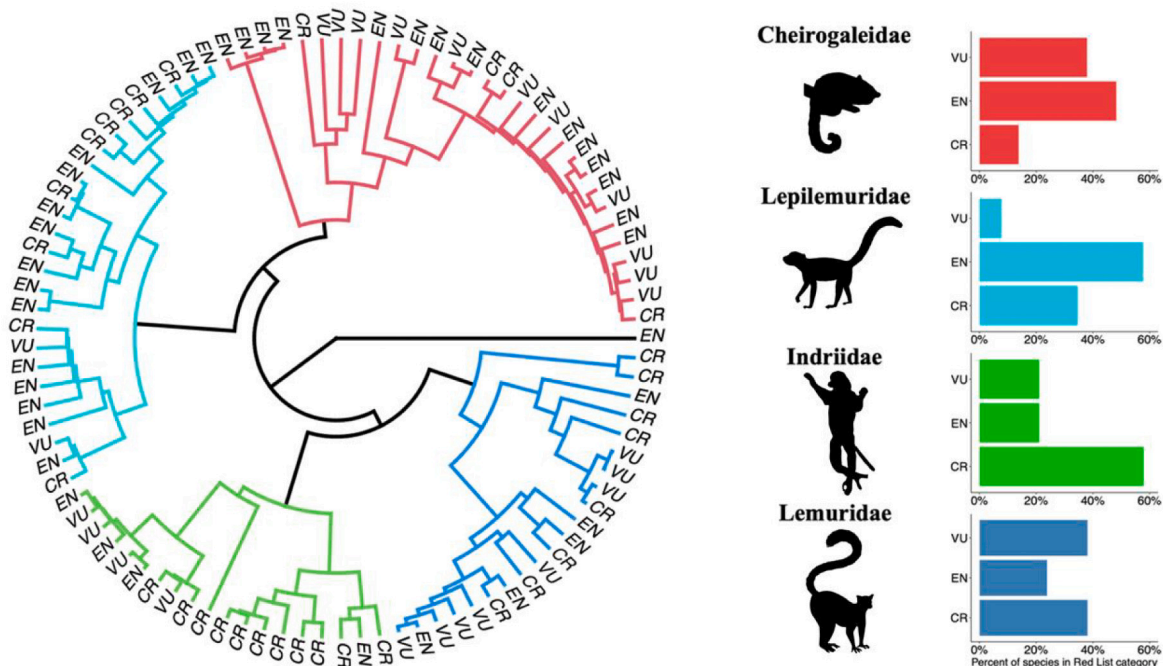


Fig. 1. Visualizations of Red List status distribution among families. (Left) Extant lemur phylogeny of the 97 species with Red List statuses. The four largest families are shown with Red List status at the tips. Colors of families on phylogeny correspond to colors in the family graphs. (Right) Bar chart displaying the percentage of species in each family that fall into each Red List category. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

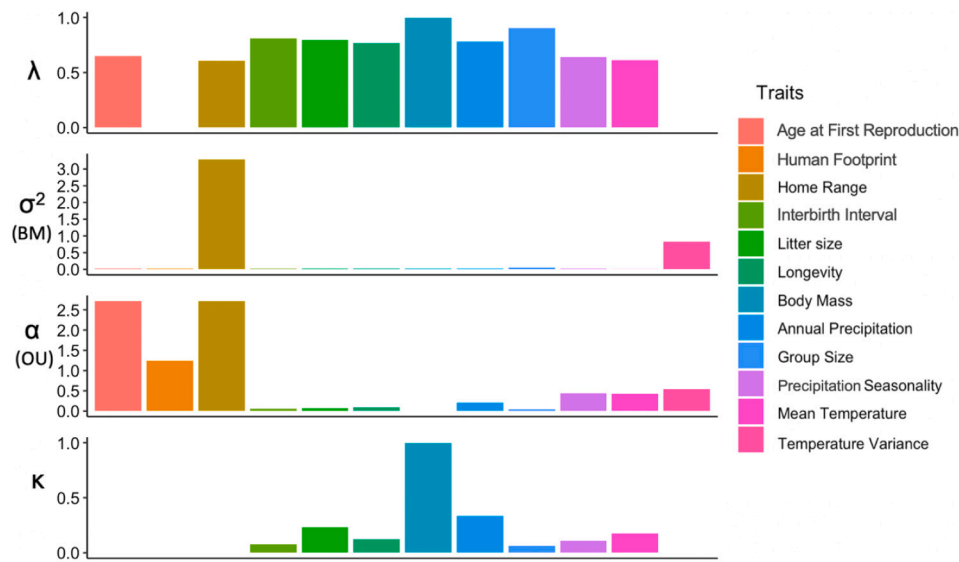


Fig. 2. Comparison of λ , σ^2 , α and κ values for each trait across the lemur suborder. Traits are plotted along the x-axis. The λ plot shows that all traits, with the exception of human footprint (HFP) and temperature variance, display intermediate phylogenetic signal ($\lambda > 0.6$). The σ^2 plot shows that home range, followed by temperature variance, is evolving at the fastest rates under the BM model. The α plot indicates multiple traits are experiencing a “pull” towards an optimum, however of these, HFP is the only variable where the α model had the lowest AIC value, indicating this model is the best fit. The κ plot indicates that body mass is evolving consistent with the BM model.

Table 3

Phylogenetically-controlled regression model, showing the major predictors of threat status. The estimate column refers to standard effect size, and $\Pr(>|z|)$ refers to p -value associated with the value in the z value column. The intercept acts as a reference (meaning the different factor levels are contrasts against it), and in this case refers to a nocturnal only activity cycle. Since (as described in the text) our explanatory variables are scaled so as to make their coefficients estimates of relative importance, we highlight in bold those variables that are noticeably larger (>0.3) and so are more important in the model.

	Estimate	Std. Error	Z value	$\Pr(> z)$
Intercept – activity cycle (nocturnal)	3.961	0.117	33.426	0
Activity cycle (crepuscular/cathemeral)	0.117	0.222	0.526	0.599
Activity cycle (diurnal)	0.642	0.345	1.863	0.062
Longevity	−0.422	0.172	2.454	0.014
Body mass	0.361	0.275	1.314	0.189
Temperature mean	0.381	0.169	2.262	0.024
Temperature variance	0.336	0.173	0.942	0.052
Interbirth interval	0.048	0.122	0.390	0.696
Habitat breadth	0.026	0.089	0.291	0.771
Precipitation seasonality	−0.004	0.044	0.093	0.926
Age at first reproduction	−0.004	0.102	0.035	0.972
Human footprint	0.002	0.032	0.070	0.944
Home range	−0.002	0.038	0.050	0.960
Trophic level	−0.013	0.089	0.148	0.883
Annual precipitation	0.001	0.031	0.022	0.982
Litter size	−0.013	0.086	0.149	0.882
Group size	−0.0003	0.063	0.004	0.997

Violin plots showing comparative distributions of species in each Red List category (VU = Vulnerable, EN = Endangered, CR = Critically Endangered) for log-transformed (A) longevity, (B) body mass (C) temperature mean, and (D) temperature variance. Boxplots represent the median and interquartile range for each group. Red circles are labelled with the mean value for each trait in each category. Significant values from a pairwise Games-Howell test are displayed, which were calculated using *ggbetweenstats* in ‘*ggstatsplot*’ (Patil, 2021). Here, we see that there is a positive relationship between extinction risk and body mass, temperature mean, and temperature variance, as well as a negative

relationship between extinction risk and longevity. (E) Stacked bar graph showing the percentage of species in each activity level for each Red List category. From this we can visualize how extinction risk is positively and negatively associated with diurnal and cathemeral species, respectively.

3.3. Projections

To make predictions about how lemurs will fare in the future given climate change, we estimated rates at which traits were evolving, as well as the rate at which climate is changing under the best- and worst-case climate change scenarios. All rates of change were converted to felsen units to allow for direct comparison. For all 12 traits in each of the 114 species, the rate of trait evolution was slower than the rate of temperature change expected for the geographic range of the species (Table A4). This held true for both temperature change scenarios. The mean rate of temperature change across all species' range was 0.093 felsen units per 100 years under the best-case scenario, and 0.192 units under the worst-case scenario. For comparison, the fastest evolving trait, home range, is changing at a rate of 0.00033 units per 100 years. Thus, temperature is projected to change faster by two to three orders of magnitude than the fastest evolving trait (Fig. 4).

4. Discussion

Using an extensive dataset of intrinsic and extrinsic factors, we applied PCMs to a focused clade to investigate the drivers of extinction risk in lemurs. We found that home range and temperature variance are evolving fastest, and most traits appear to be evolving under the BM model of evolution. We found that the strongest predictors of extinction risk were diurnal activity cycle and longevity, along with temperature mean, body mass, and temperature variance. Analysis of climate projections and rates of trait evolution revealed that, even under a best-case climate change scenario, through the macro-evolutionary past lemur traits have been evolving slower than the climate is currently changing.

4.1. Trait evolution

We investigated the tempo and mode of evolution across traits. We

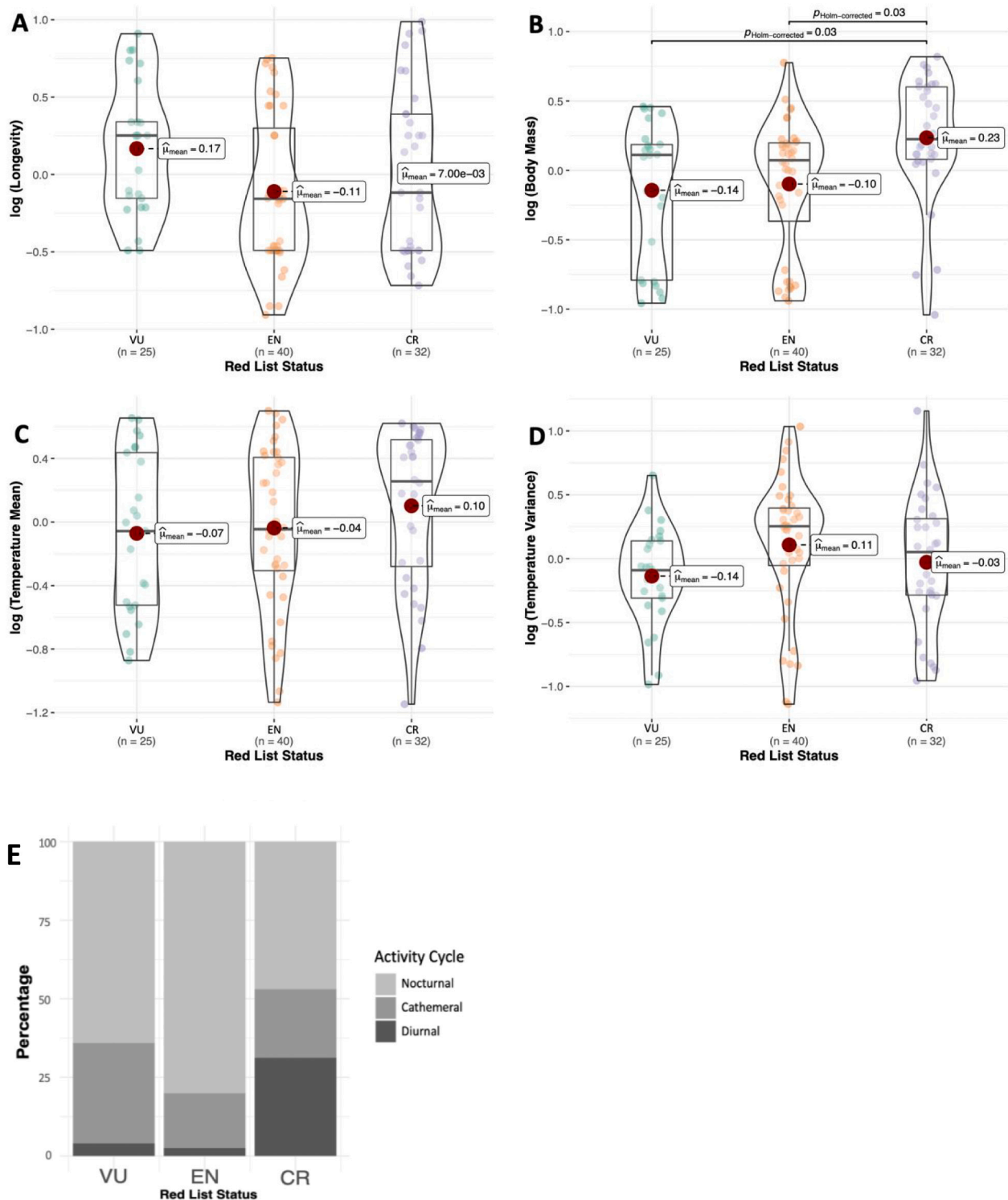


Fig. 3. Visualisation of the most important predictor variables across all regression models.

found that across all traits, life-history traits generally exhibited the strongest phylogenetic signal. However, signal was still moderately high ($>0.6 \lambda$, Table A2) across most traits, indicating that phylogeny influences similarities in lemur life history, morphology, ecology, as well as in some environmental niches. Some of this phylogenetic structure may have been lost over time (Freckleton et al., 2002), and there are likely other covariates related to trait evolution. Notably, body mass appeared to be evolving under pure BM. Similarly, Kamilar et al. (2012) found high phylogenetic signal in lemur body mass, and Kamilar and

Cooper (2013) found relatively high phylogenetic signal in primate body mass compared to most other traits. Other studies found differing results. Kamilar and Muldoon (2010) detected weak phylogenetic signal across lemur environmental niche traits, but this may be due to multiple convergent optima in environmental niches across lineages, rather than a single rate across the whole clade (Herrera, 2020). Similarly, while Kamilar et al. (2012) found a BM model for body mass across the whole clade, Herrera (2017b) found evidence of OU evolution in lemur body mass. In this study, we used a more complete trait dataset compared to

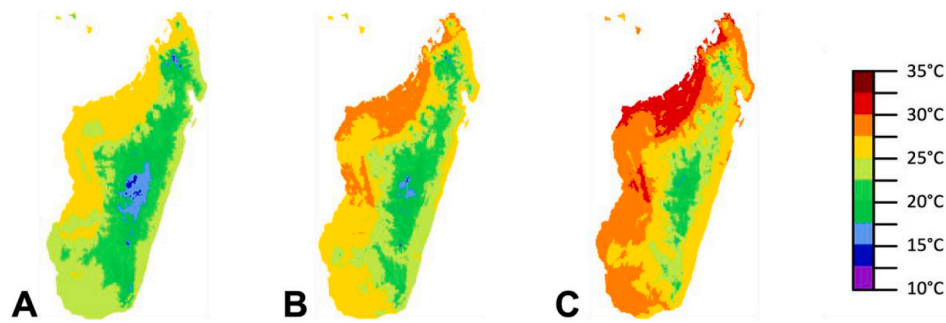


Fig. 4. Visualizations of mean annual temperature in Madagascar under historic and projected future conditions. (A) Mean annual temperature from 1970 to 2000. (B) Projected mean annual temperature in 2070 under the 'best case' scenario. (C) Projected mean annual temperature in 2070 under the 'worst case' scenario.

Kamilar and Muldoon (2010), which analysed only 43 species and used range maps that are now considered outdated. Similarly, differences in methodology may explain these discrepancies. For example, in this study we assumed a single rate of trait evolution across lineages, while a multi-peak OU model showed that body mass evolved under different rates for species with different diets and activity patterns (Herrera, 2017b). Additionally, Cooper et al. (2016) caution that the OU model is often incorrectly favoured over simpler models in smaller datasets. In summary, our results may differ from previous studies because of our more complete dataset, as well as assuming a single rate of trait evolution across the whole clade. We feel that these results reflect the varying degrees to which species' niches evolved according to simple models of variation through time and warrants the use of phylogenetic regression in further analyses.

4.2. Extinction risk regression analysis

Regression analysis revealed that both intrinsic and extrinsic factors predicted extinction risk, as hypothesized. Activity cycle was identified as an important predictor of extinction risk, indicating that diurnal species have a significantly higher extinction risk than nocturnal or cathemeral species. This was expected, as some of the most endangered lemur groups are diurnal (e.g., *Indri* and *Varecia*), and diurnal species in general are more likely to become functionally extinct compared to nocturnal, crepuscular, and cathemeral species (Cox et al., 2022). This is due to factors such as increased vulnerability to hunting and typically larger body size (Cox et al., 2022; Purvis et al., 2000a). Notably, Cox et al. concluded that the eradication of diurnal primates, in particular, will result in major functional losses in global trait space. Many of the nocturnal species (e.g., Cheirogaleidae) are abundant, and the greatest threat they face is loss of habitat. Species that are cathemeral (e.g., *Eulemur collaris*) have the greatest plasticity in their behaviour which confers several advantages, including flexible foraging over a 24-hour period (Donati et al., 2007). In support of this, a significant negative correlation between cathemeral species and extinction risk was detected when comparing Vulnerable and Critically Endangered species.

Somewhat surprisingly, we found that longevity is negatively associated with extinction risk. Most literature (González-Suárez et al., 2013; Purvis et al., 2000a) suggests that extinction risk increases with longevity. However, it could be that controlling for other confounding variables reveals that the pattern is not the same for lemurs. It is also possible that the more generalist species, which tend to be comparatively longer-lived, are faring better than the more specialized species, which include short-lived species. For example, *Eulemur fulvus* (listed as VU) is a generalist species that inhabits both dry forests in the northwest and eastern montane rainforests and has been recorded to live up to 37 years. Along with *E. fulvus*, several other *Eulemur* species that are not highly endangered are also generalist species, as well as wide-ranging. Importantly, *E. fulvus* is not listed under IUCN criterion B, thus range size was not considered in determining its Red List status. In contrast,

more range-restricted species, including mouse and sportive lemurs (*Microcebus* and *Lepilemur*), tend to be rather short-lived and more endangered. Notably, these species are nocturnal, a trait we've already factored into our analysis, thereby eliminating the influence of activity patterns. By accounting for the variance explained by the most highly endangered diurnal species, we allow for some of the effects of other variables, such as longevity, to be observed. Furthermore, our findings align with a study by Morris et al. (2008), which investigated longevity across 15 plant and 21 animal taxa, finding that long-lived species exhibit greater resilience to changes in climate variability compared to their short-lived counterparts. They concluded that the stability in survival rates and consistent reproductive patterns of long-lived species shields them from the adverse effects of environmental fluctuations, making them less susceptible to variations in survival and reproduction rates.

We also found partial support for our expectation that climate niches and high HFP would be predictive of threat status. Although human pressure is cited as an increasing threat to biodiversity (Ceballos et al., 2015; Di Marco et al., 2018), HFP was not a significant predictor in any model. This is possibly because HFP measures factors such as high population density, light density, and roads – characteristics that are rare in Madagascar given the predominance of rural populations with low densities and low road and electrical infrastructure [e.g., over 80 % of the population is rural, and fewer than 38 % of people have access to electricity ("INSTAT", 2022).] It also excludes the greatest human pressures, including deforestation (Morelli et al., 2020) and hunting (Borgerson et al., 2022). Additionally, the effects of anthropogenic disturbance may not be immediately reflected in wildlife populations, meaning that current extinction risk is mostly a product of the past as opposed to recent human pressure (Turvey et al., 2017). However, Sanderson et al. (2002) and Woolmer et al. (2008) highlight the limited value of applying global maps of human footprint to regional studies, due to poor accuracy and resolution of maps developed at the global scale. Thus, we acknowledge that we likely under-estimate their importance in driving lemur declines.

Supporting our hypothesis that extrinsic factors will predict extinction risk, we found that temperature mean and temperature variance were positively correlated with extinction risk. The positive relationship between temperature mean and extinction risk could indicate that species from the western regions of Madagascar are most endangered, since these regions are the hottest. Temperature mean and variance predicting extinction risk bodes poorly with respect to climate change, given that climate change is associated with increases in both temperature and temperature variability (Bathiany et al., 2018). Further, if species track their current climate niche in the future, 60 % of examined species will experience range reductions (Brown and Yoder, 2015). These results highlight the importance of closely monitoring species that live in areas where temperatures are, or are expected to be, rising. As noted in the methods, temperature variance across a species range is potentially correlated with range size. While we did our best to control for this, we

acknowledge that we may still observe some of this effect in the model results. Additionally, [Faurby and Araújo \(2018\)](#) discuss the importance of including historical range data in analyses of species distributions and climate change. While this is beyond the scope of the current study, future research should delve deeper into the role of the anthropogenic influences and recent range contractions in order to better inform our understanding of the correlation between species ranges and traits.

Body mass was another important predictor of risk. We found a positive association between body mass and extinction risk, consistent with past studies in primates which concluded that primates with larger bodies, as well as smaller litter sizes and longer gestations, experience higher extinction risk ([Matthews et al., 2011](#); [Purvis et al., 2000a](#)). As discussed in the introduction, the slower life history traits that tend to be correlated with body size may reduce their resilience, making it challenging to compensate for high mortality rates with high reproduction rates. Additionally, larger lemur species are often the target of hunters, since they are easier to spot and more sought after due to the larger amount of meat they provide for the same amount of effort ([Isaac and Cowlishaw, 2004](#); [Ripple et al., 2016](#)). This finding, coupled with the positive correlation between extinction risk and diurnal activity patterns, emphasizes the urgency of tailored conservation efforts for these larger, diurnal species. Specifically, these efforts should focus on countering threats such as hunting. Implementing targeted protection measures, such as intensified anti-poaching initiatives and the preservation of their habitats, becomes imperative to safeguard these at-risk lemurs effectively.

The results from binary GLMM analyses (Appendix D) partially aligned with the results from the PGLS analysis. Consistent with the PGLS results, the GLMM analyses indicate a positive correlation between temperature variance and temperature mean with extinction risk. This reinforces the finding that temperature-related variables significantly contribute to extinction risk, similar to previous findings that changing temperature is associated with risk of extinction ([Hill and Winder, 2019](#); [Ozgul et al., 2023](#); [Urban, 2015](#)).

The binary GLMM analyses also revealed that annual precipitation and precipitation seasonality are negatively correlated with extinction risk – a trend that was not observed in the PGLS analysis. However, various studies across different species ([Hill and Winder, 2019](#); [Hordley et al., 2023](#); [Román-Palacios and Wiens, 2020](#)) have reached similar conclusions regarding changes in precipitation associated with increased extinction risk. This finding holds particular significance given the environmental context of Madagascar, which has witnessed a decrease in annual precipitation, an increase in interannual precipitation variability, and an increase in the duration of droughts ([Arias et al., 2021](#)).

The disparities in identified variables between the PGLS and binary GLMMs may be due to some variables exhibiting a more pronounced effect when extinction risk is treated as a binary outcome. A binary model may capture situations where the association between predictors and extinction risk is non-linear or characterized by abrupt changes under specific conditions. Variables identified as important predictors of risk by only the PGLS, such as activity cycle and longevity, may become apparent only when considering the entire spectrum of species as opposed to comparing only two Red List groups at a time.

Sample size limited the extent of our model. First, we did not include interactions between intrinsic and extrinsic drivers in the regression model, as the statistical power would have been greatly reduced. It is also important to note that the value of the IUCN Red List status as the dependent variable is limited by its accuracy in capturing true extinction risk, which has limitations ([Collen et al., 2016](#)). Future studies should investigate using different response variables to gauge extinction risk, possibly using EDGE scores ([Isaac et al., 2007](#)), which incorporate estimates of the expected loss of evolutionary history with endangered status.

4.3. Projections

We found that, under both the best-and worst-case climate change scenarios, climate is changing faster than the evolutionary rate of all examined traits, consistent with our hypothesis. This implies that, based on past rates of evolution under a BM model and projected climate information, lemurs are not evolving fast enough to adapt to the changing climate. Although this sounds alarming, these results are based on lemurs' realized rather than fundamental niches ([Hutchinson, 1957](#)). Thus, current distributions may be restricted by other factors such as rivers ([Goodman and Ganzhorn, 2004](#)). Additionally, mapping macro-evolutionary rates of evolution onto micro-timescale changes may not be the most appropriate measure of risk. There are many reasons to suppose that estimates of trait evolutionary rate on phylogenies are under-estimates ([Li et al., 2018](#); [Pearse et al., 2018](#)), in particular because estimates of macro-evolutionary rates are often much slower than evolutionary rate estimates in the present day. We do note, however, that our felsen approach maps onto Brownian Motion evolution, which the majority of our traits (but not all) were found to be consistent with. Thus, while we are in no way claiming to have proven that lemurs cannot evolve to track climate change, given ongoing threats and population declines these results underscore the importance of immediate preservation of habitat lemurs can survive within right now. We should not assume, or perhaps even hope, that they will evolve to be able to better survive within more marginal habitat. At this time, we cannot tell if the assumption holds for group size, which our analyses suggest is either evolving in a punctuated fashion or under BM, but importantly group size is not a major predictor of extinction risk here and so this assumption is unimportant. [Revell \(2013\)](#) argues that estimates from BM models are prone to be biased to be more similar to each other than the underlying generating values. [Revell et al. \(2008\)](#) also points out that support for a BM model would also be consistent with past, strong selection to track environmental conditions changing according to a Brownian walk. We suggest that is unlikely in this case, since were lemurs able to track changing conditions so well, we wouldn't expect them to be so highly threatened with extinction as a result of recent anthropogenic (environmental) stressors. We emphasise that finding support for OU evolution in three of our extrinsic (environmental) traits does not suggest that changes in climate regime are more likely to be tracked on the basis that OU models describe how selection operates across the phylogeny ([Cooper et al., 2016](#)). If anything, support for OU models indicates that lemur evolution is likely to be constrained and thus unable to respond to future change.

It is also important to consider that traits' evolution could produce either additive or synergistic adaptive effects, meaning that one trait by itself may not be able to evolve fast enough to outpace climate change, but a combination of traits evolving might. Conversely, drivers can also be multiplicative. [Chen et al. \(2015\)](#) found synergistic effects of human egg-harvest and climate change were driving Chinese Crested Terns close to extinction, demonstrating how human pressure and climate can interact to manifest in a 'perfect storm'.

Finally, it is important to mention that, while much of this paper has focused on trait evolution and adaptation, species may also respond to changing climates and environments through behavioral changes or range shifts. For example, [Eppley et al. \(2022\)](#) found that rising temperatures and deforestation pressures are causing many species of monkeys and lemurs, which typically find shelter and food high up in the tree canopy, to spend more time searching for food on the forest floor. Nevertheless, it is possible that there will be scenarios where behavioral adaptations won't suffice as climate patterns continue to change and deforestation further reduces species ranges.

5. Conclusion

We applied phylogenetic comparative methods to a unique monophyletic clade to determine the intrinsic and extrinsic factors that

contribute to species extinction risk. This study has several important implications. First, we found that a diurnal activity cycle, followed by a shorter lifespan, and large body size, are all predictors of high extinction risk. Temperature mean and temperature variance – both of which are expected to increase with climate change – are also important predictors of risk. Additionally, we found that, based on past evolution, lemurs' traits are evolving too slowly to track climate change. Importantly, both intrinsic and extrinsic variables were predictors of risk. In fact, predictors were not clustered around any particular type of trait, but were a mix of evolutionary, ecological, and environmental factors. This finding highlights the need for more focused research that examines specific threats to specific species. In the face of a possible 6th mass extinction event, determining species extinction risk is critical. Antonelli et al. (2022) highlight the importance of understanding Madagascar's biodiversity and evolutionary history to protect the many unique, yet highly threatened species inhabiting this island. Moreover, the current study not only contributes to our understanding and prevention of the threats facing lemurs, but it serves as a case study for island species more generally. This is particularly important given that islands are more susceptible to the extreme effects of climate change. Thus, findings are relevant for discerning the drivers of extinction of species in Madagascar and beyond, setting the stage for future conservation efforts.

CRedit authorship contribution statement

Clara J. Brandon: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **William D. Pearse:** Conceptualization, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – review & editing. **James P. Herrera:** Conceptualization, Data curation, Investigation, Methodology, Supervision, Validation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. WDP and the Pearse Lab are funded by UKRI BB/Y008766/1, NE/X00547X/1, and NE/X013022/1.

Data availability

Data will be permanently archived at the Dryad data depository if the paper is accepted for publication.

Appendix. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2023.110408>.

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