Temporal niche influences higher extinction risk among diurnal tetrapods from tropical regions

Jacinta Guirguis[1], Catherine Sheard[2] and Daniel Pincheira-Donoso[1,3]

[1]MacroBiodiversity Lab, School of Biological Sciences, Queen's University Belfast, 19 Chlorine Gardens, Belfast, BT9 5DL, United Kingdom

[2]School of Biological Sciences, University of Aberdeen, Tillydrone Avenue, Aberdeen, AB24 2TZ, United Kingdom

[3]Corresponding author: Daniel Pincheira-Donoso, email: D.Pincheira-Donoso@qub.ac.uk

Abstract

The extinction rates of Anthropocene biodiversity vary dramatically through geographic and phylogenetic space, with certain regions and lineages concentrating high defaunation rates, while others remain nearly unchanged. This heterogeneity results from (spatial and phylogenetic) variation in the interactions between species fitness-relevant traits and environmental threats that trigger the pathway to extinction. Existing evidence reveals that factors including life histories, ecophysiology, and resource-use generalism influence variation in species declines under rapidly changing environments. An emerging hypothesis predicts that species spread across different 'locations' of the 24h diel spectrum are exposed to different anthropogenic pressures on demographic stability (e.g. daytime contact with humans), which can trigger differential extinction risk among diurnal, nocturnal and cathemeral (day-night actives) species. However, this prediction remains largely neglected. Only a single large-scale test of this hypothesis, on mammals, exists, which documented higher declines in diurnal species, driven by primates. Here, we address this hypothesis across the world's tetrapods, spanning >23,000 species across both endotherms and ectotherms for the first time. Our results reveal that extinction risk is higher across diurnal species from tropical regions with greater human footprint. Collectively, extinction risk is the synergistic outcome of the interplay between extrinsic human-induced pressures and species traits.

Keywords: temporal niche, diurnal, nocturnal, cathemeral, tetrapods, Anthropocene, global change

Introduction

Human-induced erosion of animal biodiversity is structured into 'defaunation hotspots' –disproportionate concentrations of threatened species– heterogeneously distributed across regions of the planet. Traditionally, the identification and driving factors shaping these hotspots have focused on their distribution across geographic [1–3] and phylogenetic (i.e., differential aggregation of threatened species across clades) space [4–6]. However, whether defaunation hotspots are predictably distributed across 'temporal space' –which we define as the spread of phylogenetic diversity in the same geographic region over the 24h diel cycle– has rarely been considered. Therefore, the hypothesis that the likelihood for populations to undergo demographic collapses that lead to extinction is influenced by their temporal niche (i.e., nocturnal, diurnal, cathemeral) remains fundamentally untested.

Overlooking this temporal dimension can potentially eclipse the role of critical processes underlying the effects of human perturbations on species declines. Firstly, the greater concentration of human activities during the daytime has led to the prediction that diurnal species may experience higher extinction risk [7,8]. Secondly, the flexibility that cathemeral species –essentially, 'temporal generalists'– require to remain active throughout day and night may facilitate avoidance of threats in certain parts of the 24h cycle [8–14]. Incorporating temporal niche may, consequently, shed light on the role that the position of species along the generalist (cathemeral)-specialist (diurnal/nocturnal) continuum plays in their resilience under human perturbations and thus, in their risk of undergoing declines. In fact, a parallel can be made between species with small geographic range sizes (i.e., intrinsically susceptible to extinction) and day- or night-specialists, relative to species with large geographic ranges and cathemeral temporal generalists. From this parallel, we derive the prediction that cathemeral species have lower risk of extinction than species that are inflexibly restricted to either a diurnal or a nocturnal temporal niche.

Surprisingly, only one large-scale study, on mammals worldwide, has addressed the hypothesis that extinction risk varies across the 24h cycle [7]. Cox et al (2023) observed that population declines are associated with diurnal activity. This effect, however, vanished when primates were removed from the analysis, suggesting that results were influenced by phylogenetic biases [7]. In addition, the role of cathemerality in contributing to demographic resilience was not considered, and thus, the role of temporal generalism remains entirely unknown. Finally, no tests of any of these hypotheses exist for ectothermic animals (e.g., reptiles and amphibians). Therefore, the major components of this 'temporal extinctions' hypothesis remains untested.

Here, using a novel global scale dataset spanning >23,000 species from across the entire tetrapod tree of life (mammals, birds, reptiles and amphibians), we address these hypotheses with both IUCN Red List conservation categories and population trends as alternative proxies for extinction risk [3] under a phylogenetic Bayesian approach, accounting for the widely known role that body size (as an 'catch all' life history proxy) and geographic range size (GRS) perform on demographic stability [15–19]. We implement models aimed at detecting signals for the influence of temporal niche on extinction risk expressing in either of three ways. Firstly, as a direct consequence of characteristics relating to temporal niche; secondly, via synergistic interactions with human footprint (HF) as proxy for human activities; and thirdly, with traits (body mass, GRS) [7,20].

Results

Distribution of threatened and decreasing species across the 24h diel spectrum

Threatened species and species undergoing decreasing populations are generally not uniformly distributed among temporal niches. For both IUCN Red List categories and population trends, our data revealed that the diurnal niche space accommodates the greatest proportion of species at risk of extinction among amphibians and mammals, with a disproportionally higher frequency for population trends (Figure 1; Table S1). Specifically, 52% of diurnal amphibians and 34.4% of diurnal mammals are threatened based on IUCN Red List categories, while 66.5% of diurnal amphibians and 67.5% of diurnal mammals were decreasing in population sizes (Figure 1; Table S1). When defining extinction risk as population declines, diurnal niche space across tetrapods consistently accommodated the highest proportions of species at risk (Figure 1; Table S1). Yet, while these differences were pronounced in amphibians and mammals, they appear marginal in lizards and birds (Figure 1; Table S1). When defining extinction risk using threat categories, diurnal niche space accommodated the highest proportions of species at risk among amphibians and mammals (see above), but not in lizards and birds (Figure 1; Table S1). Among lizards, 22.6% of nocturnal species, 20.0% of diurnal species and 18.1% of cathemeral species

were threatened with extinction (Figure 1; Table S1). Among birds, 24.1% of cathemeral species, 11.0% of diurnal and 9.1% of nocturnal species were threatened with extinction.

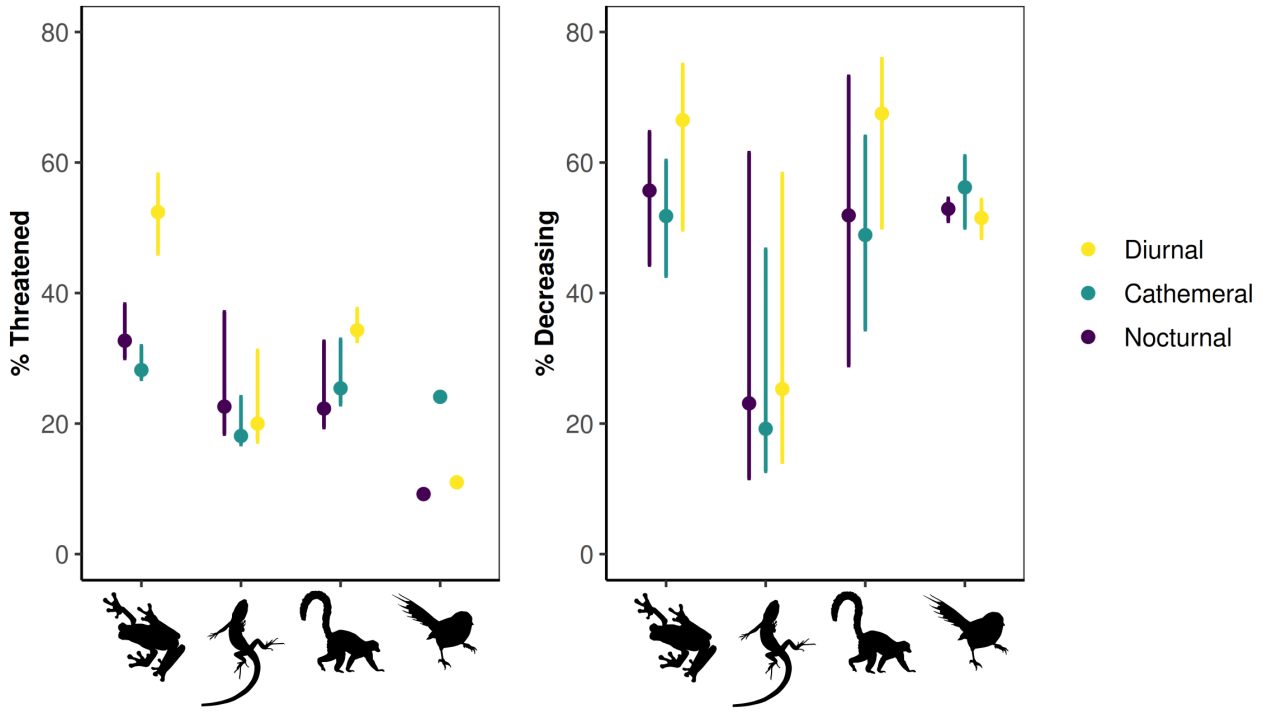

Figure 1. The percentage of species in each temporal niche that are considered at risk of extinction, which we defined as the as the of being threatened (based on IUCN categories) and probability of experiencing population declines (based on IUCN population trends). Using population trends, we assigned species listed as 'Decreasing' as 'declining', whilst those listed as 'Increasing' and 'Stable' were assigned 'not declining'. Similarly, using categories, we considered species listed as 'Vulnerable', 'Endangered', 'Critically Engendered', 'Extinction in the Wild' and 'Extinct' as 'threatened', whilst species listed as 'Least Concern' and 'Near Threatened' were assigned 'not threatened'. We incorporated species assigned 'Unknown' population trends or 'Data Deficient' category using the formula in Böhm et al. (2013). The lower error bar represents a 'best case scenario', where all species assigned 'Unknown' or 'Data Deficient' are assumed to be not threatened/not declining, whereas the upper error bar represents a 'worst case scenario', where those species were instead assumed to be threatened/declining. Silhouettes representing taxonomic groups were obtained from phylopic.org.

Effect of temporal niche alone on extinction risk

Our analyses failed to identify a signal that diurnal tetrapods are inherently at greater risk of extinction. Significant differences emerged only when extinction risk was modelled based on threat categories in temperate regions. Diurnality increased extinction risk among ectotherms, but decreased risk among mammals (Figure 2; Tables 1, S2 & S3). This effect among ectotherms was relative to nocturnal species in amphibians, and cathemeral species in lizards (Figure 2; Tables 1, S2 & S3). In contrast, among mammals, both diurnality and cathemerality were significantly associated with reduced extinction risk relative to nocturnality (Figure 2; Tables 1, S2 & S3).

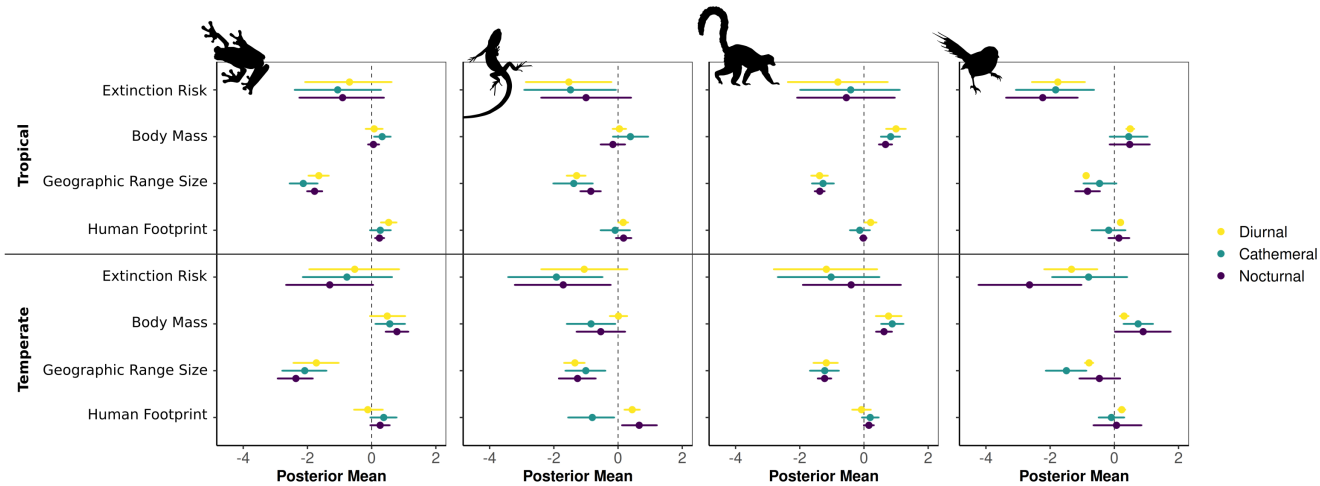

Figure 2. Coefficient estimates from fixed effects of Bayesian phylogenetic models, where extinction risk (binary, based on either IUCN Category) was modelled under a liability-threshold specification, with the R package 'MCMCglmm'. We ran separate models for amphibians, lizards, mammals and birds. We allowed the predictors of body mass, geographic range size and human footprint to vary by temporal niche (diurnal, cathemeral or nocturnal) within each biome (tropical or temperate). Prior to analysis, body mass and geographic range size were log-transformed then *z*-transformed, while human footprint was *z*-transformed. The extinction risk coefficient represents the absolute effect of the biome-temporal niche interaction shown on the latent scale, which when back-transformed would reflect the mean outcome of each group when all predictors are at their mean values (0). The dots represent the posterior mean, while whiskers show the 95% credible interval. Predictors are considered significant when the 95% credible interval does not include zero (represented by the dashed grey line). Silhouettes representing taxonomic groups were obtained from phylopic.org.

Table 1. Significant outputs from the test of posterior differences among posterior distributions of models that allowed for temporal niche variation. For each parameter component displayed ('Body Mass', 'Geographic Range Size' and 'Human Footprint'), we performed pairwise tests between temporal niches ('Diurnal > Nocturnal', 'Diurnal > Cathemeral', as well as 'Nocturnal > Cathemeral', as well as their reverses). We calculated the mean difference of two marginal posterior distributions accounting for the fact that model parameters are estimated jointly. Firstly, we determined the proportion (or probability, as odds) that the hypothesis is supported. For each iteration, we assigned '1' if the test was supported (e.g., for 'Diurnal > Nocturnal', if the value for diurnal was greater than the value for nocturnal), '0' if the test was not supported, and '0.5' if the parameter estimates were exactly equal. We then calculated the mean of these assigned values, which when converted to odds, represents the probability that the the hypothesis is supported. Secondly, we determined the average magnitude of differences by subtracting the values of one posterior from the other, and taking the mean, the 2.5% and 97.5% quantiles for the resulting distribution. We considered the difference between two posteriors to be significantly different from zero when the 95% credible interval did not include zero, which is indicated below in bold-face text. Note that for parameters that were negative in predicting extinction risk (e.g., geographic range size), a significant positive difference (e.g., in the test Diurnal > Cathemeral), indicates that the effect for diurnals is closer to zero (i.e., the effect is diminished by diurnality) whereas for parameters that were positive (e.g., body mass and most often time human footprint), a significant positive difference would indicate that the effect for diurnals is further from zero (i.e., the effect is intensified by diurnality). Table shows test, mean difference, 95% credible interval, as well as the probability and odds that the test is supported. Table shows only significant tests of significant predictors of extinction risk. Full outputs are displayed Table S3.

Model & Parameter Component	Test	Mean Difference	95% CI	Pr	Odds
1 Category					
1.1 Amphibians					
Tropical:Geographic Range Size	Diurnal > Cathemeral	0.484	0.018, 0.979	0.979	47.3
Tropical:Human Footprint	Diurnal > Nocturnal	0.285	0.023, 0.553	0.983	58.1
1.2 Lizards					
Tropical:Geographic Range Size	Nocturnal > Diurnal	0.444	0.117, 0.792	0.996	254.1
Temperate:Body Mass	Diurnal > Cathemeral	0.853	0.099, 1.663	0.987	78.9
Temperate:Body Mass	Cathemeral > Diurnal	-0.853	-1.663, -0.099	0.013	0.0
Temperate:Human Footprint	Diurnal > Cathemeral	1.243	0.567, 2.094	>0.999	99999.0
Temperate:Human Footprint	Nocturnal > Cathemeral	1.462	0.625, 2.456	>0.999	11110.1
1.3 Mammals					
Tropical:Body Mass	Diurnal > Nocturnal	0.328	0.019, 0.641	0.981	51.9
Tropical:Human Footprint	Diurnal > Nocturnal	0.228	0.028, 0.431	0.987	75.0
Temperate:Extinction Risk	Nocturnal > Diurnal	0.772	0.143, 1.44	0.992	131.3
Temperate:Extinction Risk	Nocturnal > Cathemeral	0.625	0.112, 1.166	0.993	137.9
1.4 Birds					
Temperate:Geographic Range Size	Diurnal > Cathemeral	0.706	0.089, 1.362	0.988	83.2
Temperate:Geographic Range Size	Nocturnal > Cathemeral	1.028	0.152, 1.933	0.989	93.3
2 Population Trends					
2.1 Amphibians					
Tropical:Body Mass	Nocturnal > Diurnal	0.315	0.019, 0.614	0.981	51.7
Temperate:Geographic Range Size	Cathemeral > Diurnal	0.94	0.357, 1.613	0.999	1665.7
Temperate:Geographic Range Size	Cathemeral > Nocturnal	0.894	0.147, 1.724	0.991	107.2
2.2 Lizards					
Temperate:Human Footprint	Diurnal > Cathemeral	0.597	0.062, 1.178	0.985	67.8
Temperate:Human Footprint	Nocturnal > Cathemeral	0.815	0.034, 1.671	0.979	47.4
2.3 Mammals					
Tropical:Geographic Range Size	Diurnal > Nocturnal	0.326	0.111, 0.539	0.998	624.0
2.4 Birds					
Tropical:Human Footprint	Diurnal > Nocturnal	0.427	0.17, 0.691	0.999	1135.4
Tropical:Human Footprint	Cathemeral > Nocturnal	0.904	0.356, 1.481	0.999	1665.7

The synergies of human footprint, biome and temporal niche on extinction risk

Our analyses support the core prediction that diurnality interacts with human footprint (HF) to increase extinction risk. Our models revealed parameter estimates that consistently support the prediction among tropical tetrapods, when using IUCN threat categories (Figure 2; Table S2). However, models of population trends did not consistently reveal significant diurnality-HF interactions (for details see Table S2).

When modelling extinction risk based on threat categories, we found that increases in HF significantly increase extinction risk among tropical, diurnal tetrapods (Figure 2; Table S2). HF was never observed to significantly increase extinction risk in cathemeral species, and was found to increase risk of tropical, nocturnal species only among amphibians (Figure 2; Table S2). However, our findings revealed the effect of HF on increasing risk was significantly greater in diurnal than nocturnal amphibians (Figure 2; Tables 1, S2 & S3). Among temperate tetrapods, the effect of HF was inconsistent across tetrapods and temporal niches. Specifically, among amphibians, HF was not associated with extinction risk (Figure 2; Table S2). Among lizards, HF increased risk for both diurnal and nocturnal species, but decreased risk significantly for cathemeral species (Figure 2; Table S2). Among mammals, HF increases risk in nocturnal species only, whereas in birds, HF increases risk in diurnal species only (Figure 2; Table S2).

Interacting effects of temporal niche with traits

We observed no consistent role for temporal niche interacting with the effects of traits (body mass, GRS) among tetrapods combined. In contrast, diurnality and cathemerality were observed to intensify or diminish the effects of body mass and GRS on extinction risk, depending on extinction risk proxy, taxa and biome (Table 1; Table S3).

Discussion

Our study provides the first tetrapod-wide, global-scale test of the 'temporal extinction' hypothesis that extinction risk is influenced by the temporal niche of species. As predicted by theory, our analyses reveal that the concentration of human activities in the daytime differentially increases extinction risk in diurnal vertebrates in the tropics. Therefore, however, no general effect of daytime across all contexts (e.g. for all tetrapods, across the globe generally) was observed. In addition, our analyses reveal that temperate, diurnal ectotherm tetrapods are under higher risk of extinction, even after the effects of HF, body size and GRS are accounted for. Further findings show inconsistent support for the hypothesis that temporal generalism (cathemerality) buffers against the impact of HF [8,21]. Finally, we found no evidence of a consistent role for the interacting effects of temporal niche and traits (body size, GRS) in increasing extinction risk.

Demographic mechanisms underpinning the diurnality-human footprint interaction

The mechanism underlying extinctions can be framed as the process when the onset of environmental pressures (i.e., the extrinsic trigger) exert stress on a population's functional (fitness-relevant) traits beyond their capability to maintain viable levels of demographic stability. When this process persists, populations can enter trajectories of progressive decline until they reach a demographic 'tipping point', beyond which a demographic collapse is expected to be inevitable, thus consolidating risk of extinction, or extinction [3,22,23]. Therefore, hypotheses aimed to identify signals of the role that an environmental trigger plays in shaping variation in extinction risk require a connection with some demographic feature or process within the population (i.e., intrinsic triggers). For instance, hypotheses on the role of body size and GRS in driving extinction risk are intrinsically linked with demography, as body size scales with reproductive output, while species with progressively smaller geographic ranges are progressively more vulnerable to demographic and genetic erosion caused by environmental factors [2,16–19,24–28].

While our analyses support the hypothesis that human activities during the day increase risk in diurnal, tropical species, we note that a demographic mechanism which links human activities to population erosion among diurnal species is required for the hypothesis to be considered as more mechanistically supported. Such a link could be that, in the same geographic space, the concentration of human activities in the daytime results in diurnal species experiencing a greater degree of habitat fragmentation than species active at other times. While in general, species may increase or decrease movement distances and home range sizes in response human activities, species in highly disturbed or urbanised areas tend to exhibit reductions in home range sizes, potentially interfering with their ability to forage, disperse and reproduce [29–31]. Our findings are consistent with a hypothesis that this effect may be influenced by or aggravated in diurnal species, potentially due to the physical presence or movements of humans during the daytime.

Conclusions

The Anthropocene is defined by the emergence of human-induced environmental erosion driven by the aggregated effects of industrial activity, which has triggered alterations to biodiversity across the globe. These effects have been consistently shown to alter the distribution and composition of biodiversity through an expanding phenomena of populations and species erosion worldwide. While these extinctions are predicted to cluster in certain geographic and phylogenetic regions [1–6], we hypothesised that they may also cluster predictably over different regions of the 24h diel spectrum. Based on this hypothesis we addressed the prediction that in diurnal niche space, due to the aggregation of pressures involving human activities will increase extinction risk [7,8,32]. While we found no evidence that extinction risk globally is concentrated in diurnal niche space, our analyses revealed that tropical, diurnal tetrapods in areas where human footprint is high have increased risk of extinction. In light of our findings, we call for action aimed towards understanding how the demographic impacts of urbanisation and human disturbances may vary across the day-night cycle. We emphasise that extinction risk is the (often synergistic) outcome of the interplay between extrinsic, anthropogenic pressures and intrinsic, evolutionary predispositions, and that

signals of extinction risk hypotheses may not emerge until these dependencies are accounted for.

Methods

Data collection

We assembled a novel database spanning ecological (temporal niche, geographic range size, biome, human footprint), phenotypic (body mass), and extinction risk (IUCN Red List conservation status) data for 23,042 species from across all four classes of tetrapod vertebrates – amphibians, 'reptiles' (restricted to lizards), mammals and birds. These data were obtained from the scientific literature (field guides, journal articles, books), existing class-specific databases (see details below), as well as field and museum records collected by the authors. Firstly, for temporal niche data (defined as the range of time at which a species is active over the 24h diel spectrum), we employed the high-level category system [33], where each species was classed as either diurnal (active during the day hours), nocturnal (active during the night hours), or cathemeral (active throughout the 24h of the day). We excluded crepuscular species due to low sample sizes. Temporal niche data were collated from existing databases for mammals [7,34] and lizards [35,36]. For lizards, these sources of data included both cathemeral and crepuscular species within the same category. Therefore, these species were re-classified into the separate categories of cathemeral and crepuscular, but only cathemeral species were retained for analyses. Global-scale databases for birds and amphibians are not currently available, and thus, bird data were obtained primarily from the Handbook of the Birds of the World [37], whereas amphibian data were collated as part of the Global Amphibian Biodiversity Project (GABiP [27,38]). Secondly, geographic range size (i.e., geographic surface over which a species is known to occur in km^2, GRS hereafter) and latitudinal midpoint data were extracted from species distribution polygons from the IUCN archive (www.iucnredlist.org) for amphibians and mammals, from GARD [39] (www.gardinitiative.org) for lizards, and from Birdlife International (www.datazone.birdlife.org) for birds. We assigned 'tropical' biome to species with latitudinal midpoints below the tropic of Cancer (23.43601°) and above the tropic of Capricorn (-23.43601°), whereas 'temperate' biome was assigned to species with latitudinal midpoints above the tropic of Cancer or below the tropic of Capricorn. Thirdly, we used human footprint (i.e., the overall pressure of human activities on the environment, HF hereafter) as a proxy for human activities, provided by Mu et al (2022)[40]. In this dataset, the calculation of HF incorporates eight variables (built environment, population density, nighttime lights, cropland, pasture, roads, railways, and navigable waterways). Using the R package 'raster', we averaged the entire dataset (spanning 2000 – 2018) into a single raster, then extracted the mean value for each species range.

Given that variation in extinction risk across animals (particularly among vertebrates) has consistently been associated with variation in body size [16,18,19,27,41], we collated a database of body mass of tetrapods. For amphibians, we calculated species body mass from snout-vent length (SVL) for frogs and salamanders [15,17,38,42–44], and from total body length for caecilians [45]. We then converted maximum SVL and maximum total body length into body mass using the approach presented by Pough (1980) [46] based on order-specific allometric formulas [18,19]. Body mass data for lizards was gathered from Meiri et al. (2020) [47]. For mammals, we used body mass from Cox, Baker, et al. (2023) [48], defined as mean adult body mass. For birds, we obtained body masses from the AVONET database [49], where it was defined as average species body mass. We excluded all imputed data. Data distributions were visualised using violin plots (Figure 3).

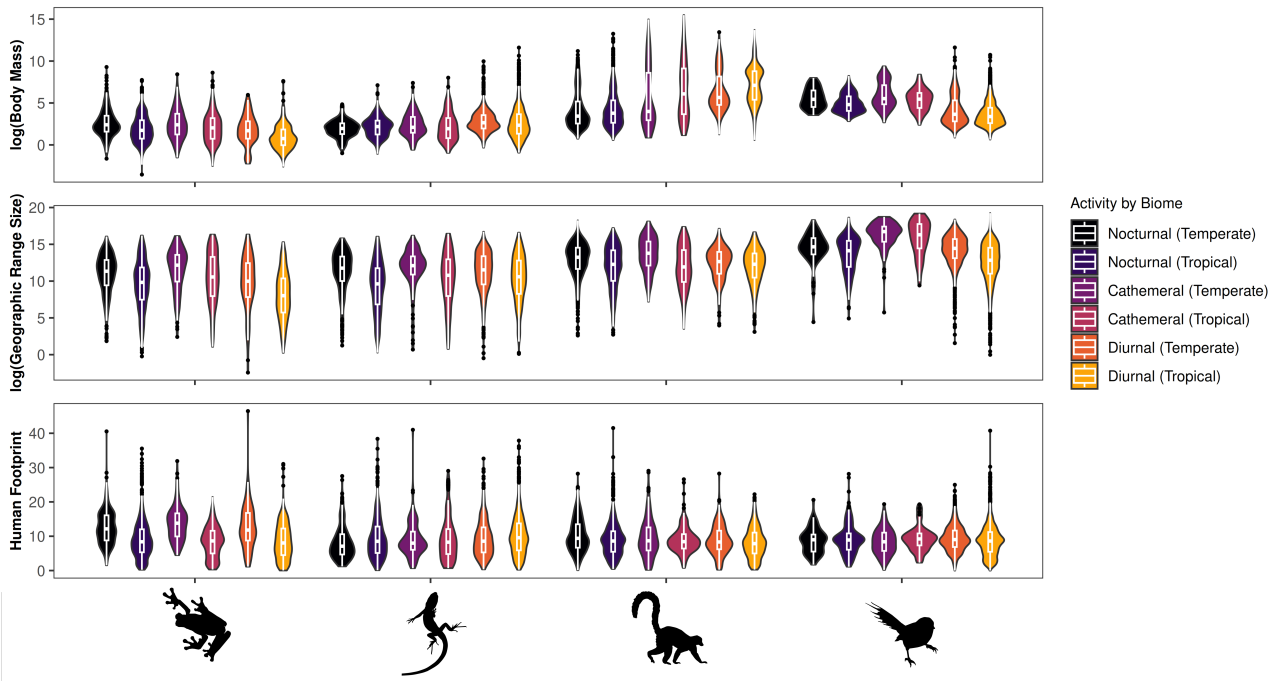

Figure 3. Violin plots showing the distributions of body mass, geographic range size, and human footprint by activity (diurnal, cathemeral or nocturnal) and biome (tropical or temperate) across tetrapods (amphibians, lizards, mammals and birds). The width of each violin represents the probability density of values at each level, estimated using kernel density estimation. Overlaid box plots display the median (horizontal line), first and third quartiles (box boundaries), while whiskers extend to the most extreme data points within 1.5 times the interquartile range from the box edges and outliers are represented by dots. Body mass and geographic range size were log transformed prior to visualisation. Silhouettes representing taxonomic groups were obtained from phylopic.org.

We employed two alternative proxies for extinction risk from the IUCN Red List for all tetrapod species for which these assessments exist [3]. Firstly, we used the classic conservation categories (the current estimated position of a species over an extinction risk spectrum). This proxy consists of two categories of non-threatened species ('Least Concern' or LC, and 'Near Threatened' or NT), and three categories of threatened species ('Vulnerable' or VU, 'Endangered' or EN, and 'Critically Endangered' or CR). Secondly, population trends (the trajectory of population sizes of a species through time), which assign species to either of the three categories of 'Decreasing', 'Stable' and 'Increasing' in population size (see [3]). We downloaded IUCN Red List data using IUCN API 2024-1, accessed with the R package 'rredlist' [50].

Finally, the taxonomic nomenclature used in our database follows a range of primary repositories of tetrapod taxonomy. For amphibians, we follow Frost (2023) [51]. For lizards, Uetz et al. (2022) [52]. For birds, we follow version 8.1 (January 2024) of the HBW Birdlife taxonomic checklist, maintained by Birdlife International. Finally, for mammals, we follow version 1.12.1 of the Mammal Diversity Database species checklist [53]. Mismatches in names between our data sources and these taxonomies were dealt with individually (see Supplementary Methods). All data are available in Table S4.

Phylogenetic trees

For phylogenetic analyses, we used consensus trees. For amphibians, we used Jetz and Pyron (2018) [6] phylogenetic supertree that contains ~82% of known extant species diversity. For lizards, mammals and birds, we summarised entire posterior distributions of time-calibrated trees available from Tonini et al. (2016) [54], the Phylacine 1.2 database [55], and the Birdtree database [56], respectively, using median node heights with the TreeAnnotator app of Beast 2.5 [57]. For birds, we used the Hackett backbone. These phylogenies represent ~85% of squamate, ~90% of mammal and ~89% of bird diversity.

Model specification

We performed our analyses using a Bayesian Markov chain Monte Carlo (MCMC) phylogenetic generalised mixed modelling approach, implemented in the package 'MCMCglmm' version 2.21.0 [58] in R version 4.4.2 [59]. We used MCMC to sample the posterior distributions of mixed models which included the phylogeny, in

form of an inverse-relatedness matrix produced by the function 'inverseA()', as a random effect. We modelled extinction risk as a binary response variable under a liability-threshold framework. In other words, we assume extinction risk is expressed by a latent, normally distributed continuous process which contains a threshold value at which species are separated into the binary outcome. We chose this approach because directly modelling the threshold or 'tipping point' [3,22,23] more accurately represents the mechanism of demographic decline to extinction. Our fixed effects included temporal niche, biome, body size, GRS, and HF.

Regarding response variables, we incorporated extinction risk into our models as the response variable using two proxies based on the IUCN Red List. Thus, each test ran twice. For our first proxy, we used the probability of being threatened, based on the IUCN threat category. We assigned '1' to species if their threat status was 'Vulnerable', 'Endangered' and 'Critically Engendered' and '0' to species if their threat status was 'Least Concern' and 'Near Threatened' while excluding 'Data Deficient' species. For our second proxy, we used the probability of experiencing population declines, based on the IUCN population trend. We assigned '1' to species if their population trend was listed as 'Decreasing' and '0' if their population trend was 'Increasing' or 'Stable' while removing species with a population trend of 'Unknown'.

For each proxy of extinction risk, we modelled the scenario in which predictors of extinction risk are influenced by the interaction with biome and temporal niche. Using this model structure, we tested whether temporal niche performs a direct role (i.e., as a fixed effect which simultaneously represents the absolute effect of a given temporal niche as well as the baseline variation in extinction risk of that temporal niche) or an interacting role (i.e., by modifying the effects of body size, GRS and HF) in predicting extinction risk. Thus, the fixed effects were specified to include the interaction between biome and temporal niche; the interaction between biome, temporal niche and body size; the interaction between biome, temporal niche and GRS; as well as the interaction between biome, temporal niche and HF. We excluded the global intercept. Therefore, the coefficients for the interaction of biome and temporal niche simultaneously represent absolute effects (i.e., as predictors) and baseline variation (i.e., as intercepts). This specification essentially models the effects of body mass, GRS and HF, separately for each temporal niche of each biome, in a single model that accounts for the entire phylogeny. As body size and GRS are highly positively skewed (with skewness of ~25 observed in each tetrapod group), these variables were transformed using natural logarithms prior to *z*-transformation.

While priors are less influential in analyses on large datasets, they may aid convergence and improve sampling efficiency by reducing the complexity of the parameter space. Therefore, for fixed effects, we selected weakly informative priors using a normal distribution. As continuous predictors were *z*-transformed, their priors were centred on zero. Priors for temporal niche and biome were centred on the proportion of species in each temporal niche and biome that were threatened or decreasing in population trend based on our data, transformed onto the liability scale. We used standard deviations of 2 (for continuous predictors) and 3 (for absolute effect terms), which allocates approximately 95% of the probabilities to coefficient values of +/- 4 and +/- 6, respectively. For the random effects phylogeny variance parameter, we specified an inverse-Wishart distribution with a scale parameter of 1 with 0.02 degrees of freedom. We employed the redundant working parameter 'alpha.V', using alpha.V = 1,000 (for models of lizards using categories) and alpha.V = 1 (for all other models), but kept alpha.mu = 0. The parameter 'alpha.V' uses parameter expanded algorithms to aid MCMC in searching complex parameter space while having minimal impact on inference. For models on lizards using population trends, we increased the parameter on the degrees of freedom to 100, due to the increase in phylogenetic clustering of declining species in this group. Given that our outcome was binary, we fixed the residual variance parameter to 1. We selected these distributions because macroecological data is typically highly variable and often exhibits weak correlations between predictors. These priors provide regularisation while avoiding the imposition of strong beliefs on coefficients.

We subsetted our data for vertebrates into amphibians, lizards, mammals and birds, and analysed each group separately. The package 'MCMCglmm' employs a single chain to sample the posterior of each model, which we ran for 500,000 iterations with a thinning interval of 10, discarding the first 50% of iterations as burn-in. Iterations were increased to 2 million for models on lizards, while maintaining the same thinning interval and percentage of burn-in. Convergence was determined by visually examining trace plots and ensuring effect sample size was greater than 1,000. Full model outputs are displayed in Table S2.

Hypothesis test

We tested for significant differences among the effects of temporal niche and biome by calculating pairwise differences between posteriors. For each model component (the absolute effect of temporal

niche, body mass, GRS and HF), we performed pairwise hypothesis tests between temporal niches ('Diurnal > Nocturnal', 'Diurnal > Cathemeral', 'Nocturnal > Cathemeral'). We performed these tests accounting for the fact that model parameters are estimated jointly. Firstly, we determined the proportion (or probability, as odds) that the hypothesis is supported. For each iteration, we assigned '1' if the test was supported (e.g., for 'Diurnal > Nocturnal', if the value for diurnal was greater than the value for nocturnal), '0' if the test was not supported, and '0.5' if the parameter estimates were exactly equal. We then calculated the mean of these assigned values, which when converted to odds, represents the probability that the hypothesis is supported. Secondly, we determined the average magnitude of differences by subtracting the values of one posterior from the other, and taking the mean, the 2.5% and 97.5% quantiles for the resulting distribution. We considered the difference between two posteriors to be significantly difference from zero when the 95% credible interval did not include zero. We applied this significance test to determine temporal niche variation among the continuous predictors that significantly predict extinction risk, and also to examine differences in the absolute effects of temporal niches on extinction risk. Full hypothesis test outputs are displayed in Table S3.

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