Received: 8 June 2021 | Revised: 12 July 2021 | Accepted: 29 July 2021

DOI: 10.1111/ele.13868

ECOLOGY LETTERS WILEY

LETTER

Evolutionary legacies in contemporary tetrapod imperilment

Dan A. Greenberg[1] | **R. Alexander Pyron**[2] | **Liam G. W. Johnson**[1] | **Nathan S. Upham**[3,4,5] | **Walter Jetz**[3,4] | **Arne Ø. Mooers**[1]

[1]Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada

[2]Department of Biological Sciences, George Washington University, Washington, District of Columbia, USA

[3]Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut, USA

[4]Center for Biodiversity and Global Change, Yale University, New Haven, Connecticut, USA

[5]School of Life Sciences, Arizona State University, Tempe, Arizona, USA

Correspondence
Dan A. Greenberg, Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada.
Email: dan.greenberg01@gmail.com

Funding information
Natural Sciences and Engineering Research Council of Canada; National Science Foundation, Grant/Award Number: DEB 1441719 and DEB 1441737

Editor: Tim Coulson

Abstract

The Tree of Life will be irrevocably reshaped as anthropogenic extinctions continue to unfold. Theory suggests that lineage evolutionary dynamics, such as age since origination, historical extinction filters and speciation rates, have influenced ancient extinction patterns – but whether these factors also contribute to modern extinction risk is largely unknown. We examine evolutionary legacies in contemporary extinction risk for over 4000 genera, representing ~30,000 species, from the major tetrapod groups: amphibians, birds, turtles and crocodiles, squamate reptiles and mammals. We find consistent support for the hypothesis that extinction risk is elevated in lineages with higher recent speciation rates. We subsequently test, and find modest support for, a primary mechanism driving this pattern: that rapidly diversifying clades predominantly comprise range-restricted, and extinction-prone, species. These evolutionary patterns in current imperilment may have important consequences for how we manage the erosion of biological diversity across the Tree of Life.

KEYWORDS
diversification, evolutionary age, extinction risk, extinction selectivity, phylogenetics, range dynamics, turnover, vertebrates

INTRODUCTION

Extinction is a crucial process in shaping the Tree of Life (Raup, 1994), and with humanity's recent rise to global ecological dominance we are now the principal driver of this evolutionary force (Barnosky et al., 2011). The 'rise and fall' of all lineages is one of evolution's few constants (Raup, 1986), but rates of extinction can differ considerably among clades due in part to legacies of heritable traits, niches and geographic distributions that subtly shape the tempo of this process (Jablonski, 1987, 2017; Liow, 2007; McKinney, 1997; Roy et al., 2009). Whether these evolutionary legacies also contribute to current anthropogenic extinctions remains an outstanding question.

There are several reasons to expect a broad concordance between patterns of ancient and modern species extinction. There are certain lineage characteristics that have consistently influenced ancient extinction rates – including geographic range size (Harnik, Simpson, et al., 2012; Jablonski, 1986; Orzechowski et al., 2015), niche specialisation (Heim & Peters, 2011; Smits, 2015) and global abundance (Kiessling & Aberhan, 2007) – and these same characteristics also consistently influence contemporary extinction risk (Böhm et al., 2016; Chichorro et al., 2019; Lee & Jetz, 2011). Extinction drivers now associated with humans are also not all evolutionarily novel: rapid biome shifts; the invasion of novel predators, competitors and parasites; and sweeping environmental changes have all been long-standing themes in Earth's biotic history (Harnik, Lotze, et al., 2012). Undoubtedly, the rate at which these extinction drivers are now exerted is magnitudes greater than in the past (Barnosky et al., 2011; Gaffney & Steffen, 2017), but regardless of pace those lineages that have repeatedly survived these historical extinction filters should be more resilient in the present (Balmford, 1996; Betts et al., 2019). Similar evolutionary patterns evident in deep-time extinction dynamics - including clade age, lineage turnover and recent speciation rates – may therefore also influence future species loss as the Anthropocene unfolds.

Extinction risk of both species and higher-order clades may be age-dependent (Pearson, 1995), changing over the course of a lineage's 'lifespan' (1. *Clade Age hypothesis*; Figure 1). There are several mechanisms that could elevate extinction risk in recently diverged lineages (*Prediction* 1.1): 'young' clades may have evolved into ephemeral or crowded adaptive zones (Stigall, 2014), possess narrow niches and geographic distributions (Davies et al., 2011; Heim & Peters, 2011), or have not yet passed through extinction filters that winnow out susceptible lineages compared to older clades (Balmford, 1996). Alternatively, ancient lineages may have higher extinction risks (*Prediction* 1.2): these 'older' clades may be adapted to declining relict niches (Foote et al., 2007; Tanentzap et al., 2020) and possibly exhibit slower rates of molecular and phenotypic evolution generally (Gingerich, 1983; Ho et al., 2011). Importantly, while van Valen (1973) presented evidence that extinction risk may be independent of age (but see: Hagen et al., 2018), his comparisons were within clades, and his proposed mechanism was competition between related taxa sharing an adaptive zone. Age-dependent extinction risk could still emerge among distantly related clades that occupy distinctive adaptive zones with respect to each other.

Extant clades also vary considerably in their history of past extinctions (Pyron & Burbrink, 2012; Quental & Marshall, 2013), and this might reflect differences in intrinsic resilience to extinction as associated with conserved traits in modern-day species. Phylogenies of extant species are shaped by both speciation and extinction, but there appears to be little information on past extinction that can be inferred from extant tree shape alone (Louca & Pennell, 2020, 2021). However, a pattern of a

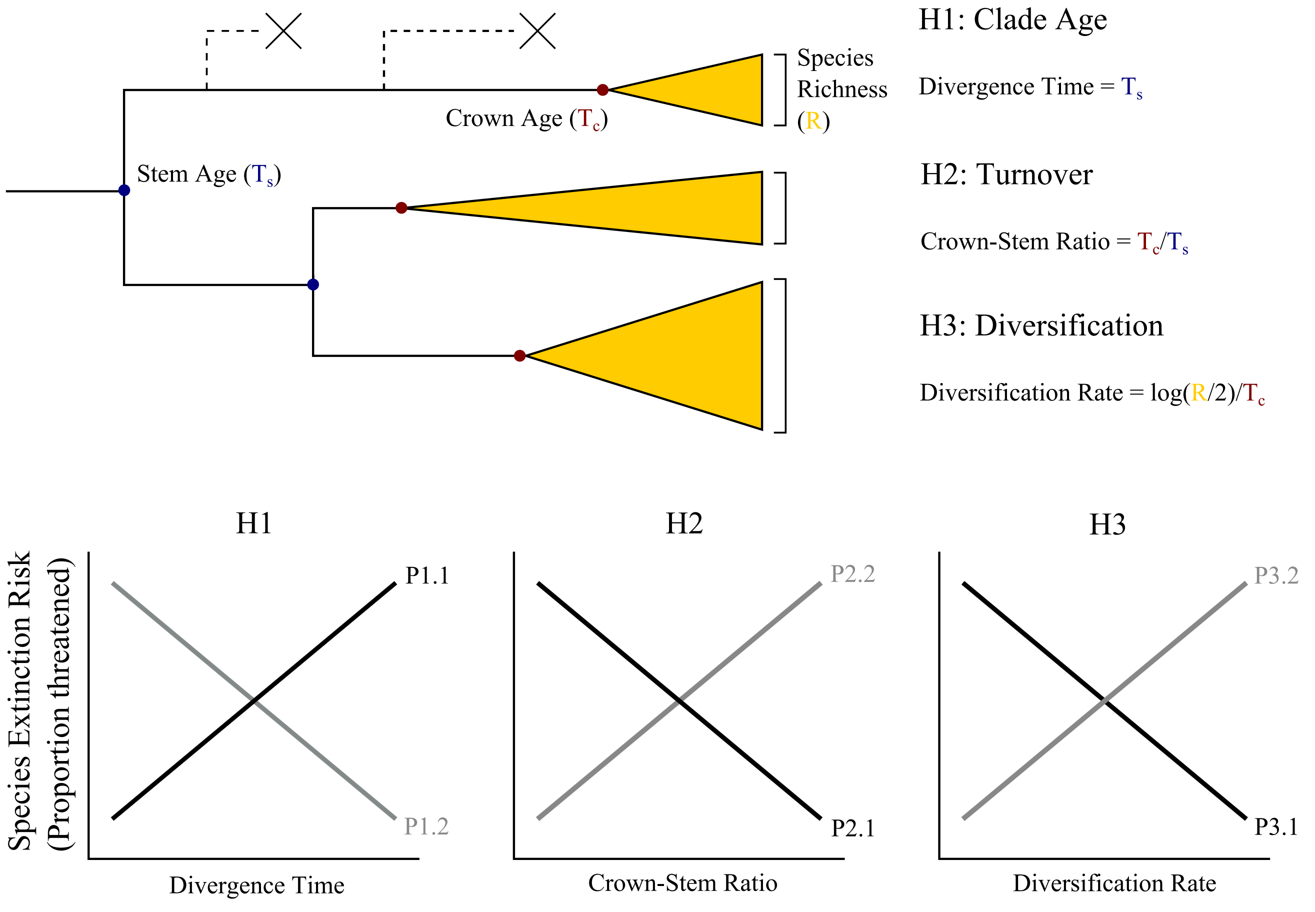

FIGURE 1 Predictions of how evolutionary dynamics may influence contemporary imperilment (proportion of threatened species) across extant clades. The Clade Age hypothesis (H1) posits that species' extinction risk may either increase (P1.1) or decrease (P1.2) from the time since their clade originated (stem age, T_s). Under the Turnover hypothesis (H2), extinction risk may be elevated in clades with a higher turnover of speciation and extinction events in their deep history (P2.1) – which may be reflected in a short clade crown age (T_c) relative to a long stem age (T_s), as ancient stem lineages (indicated as X) have been lost due to high extinction rates. Alternatively, a short clade crown-to-stem ratio may reflect a late adaptive radiation with a concurrent reduction in extinction risk (P2.2). The Diversification Rate hypothesis (H3) suggests that extinction risk may differ depending on the rate of lineage diversification ($\log(R/2)/T_c$): if faster diversification is due to low extinction, then one would predict lower extinction risk in these clades (P3.1). However, if speciation and extinction are positively correlated due to shared drivers, then we would predict higher extinction risk in faster diversifying lineages (P3.2)

long clade stem age (i.e. a lineage's time since divergence from its sister taxon) relative to crown age (i.e. the earliest divergence within a clade from which all extant taxa descend) is consistent with the loss of numerous stem lineages over time (Bennett et al., 2017; Budd & Mann, 2020). This ratio of crown to stem age may therefore be informative about lineage turnover: the rate of extinction relative to speciation. If true, then we may expect that groups with a low ratio of crown-to-stem age should have higher extinction risk in the present (2. *Turnover hypothesis*, *Prediction* 2.1; Figure 1). However, a low ratio of crown-to-stem age may also arise if an ancient lineage undergoes a late and sudden radiation (Nagalingum et al., 2011), potentially into new adaptive zones. In this scenario, we may expect extinction risk to instead be lower in these clades, as incipient species may be in the midst of expanding their distributions and niche space (*Prediction* 2.2; Figure 1).

Absolute differences in speciation and extinction rate across extant lineages might also shape contemporary extinction patterns (3. *Diversification hypothesis*; Figure 1). High net diversification rates may be due to exceptionally low rates of extinction relative to speciation within a lineage, predicting that clades with higher diversification may have lower modern extinction risk (*Prediction* 3.1). Alternatively, it has been suggested that speciation and extinction rates among lineages are broadly positively correlated (Stanley, 1979), as the same traits and environments (e.g. dispersal limitation, niche specialisation, peripheral habitats) that promote lineage divergence also tend to elevate the risk of lineage extinction (Jablonski, 1986, 2017; Stanley, 1990). Cladogenesis itself may also elevate extinction risk, as incipient lineages are likelier to exist in small initial populations with higher genetic loads (Lynch et al., 1995). Extinction must always lag speciation, and clades with high rates of recent speciation may therefore have a preponderance of 'walking dead' lineages with high intrinsic extinction risk (Nee et al., 1994). This 'macroevolutionary trade-off' between speciation and extinction across lineages would then predict that contemporary risk may be concentrated in clades with high rates of recent net diversification (*Prediction* 3.2). This prediction combines elements of both the age (of species, rather than clades) and lineage turnover hypotheses, where the toll of extinction for nascent species has just not yet been paid.

Support for the effects of evolutionary history on contemporary extinction patterns remains mixed across the various taxonomic scales and groups in which these hypotheses have been examined. Both younger clades in some plant groups (Davies et al., 2011; Tanentzap et al., 2020) and older clades in some vertebrates (Gaston & Blackburn, 1997; Johnson et al., 2002; Verde Arregoitia et al., 2013) have been associated with heightened modern extinction risk. Clade diversification rates also positively correlate with extinction risk in plants (genera: Davies et al., 2011; Tanentzap et al., 2020; families: Schmidt et al., 2021) and amphibians (Greenberg & Mooers, 2017). The leading mechanism explaining these associations between clade extinction risk and evolutionary dynamics is their joint associations with species' geographic range size.

Range size has been the most prominent predictor of lineage extinction in both the fossil record (Harnik, Simpson, et al., 2012; Orzechowski et al., 2015) and in modern history (Boyer, 2010; Loehle & Eschenbach, 2012). Geographic distributions can change with age, as incipient lineages first expand and then contract over time (Foote et al., 2007; Liow & Stenseth, 2007). This same pattern can also emerge stochastically with speciation and extinction (Pigot et al., 2012). Speciation rate and range size also tend to be related (Davies et al., 2011; Greenberg & Mooers, 2017; Jablonski & Roy, 2003), which could arise either directly from cladogenesis via the fission of ancestral ranges through vicariance or peripheral isolation (i.e. peripatry) of populations (Pigot et al., 2010), or indirectly through clade characteristics that simultaneously promote broad ranges and dampen speciation rates (e.g. high dispersal capability or ecological generalisation; Jablonski & Roy, 2003).

Curiously, many studies examining the relationship between threat and diversification rate at the species-level using evolutionary distinctiveness (ED), a measure that reflects the inverse of species-level diversification rate and divergence time (Jetz et al., 2012), generally find no association (among mammals: Verde Arregoitia et al., 2013; birds: Jetz et al., 2014; squamates: Tonini et al., 2016; amphibians: Jetz & Pyron, 2018; but, see Chondrichthyans, Stein et al., 2018, and non-avian Archosauromorphs, Colston et al 2020). This difference in reported evolutionary patterns between species-level and clade-level measures may be due to the underappreciated fact that, while a species' ED is highly correlated with its divergence time from its closest relatives, lineage divergence time can vary widely even under homogenous birth-death model rates (Weedop et al., 2019). This discrepancy between taxonomic levels may emerge then purely due to stochastic processes (Weedop et al., 2019), as the stochastic contribution to estimated diversification rates should decline with longer phylogenetic timescales (see Figures S1 and S2). Another key factor is that species-level divergences measured from a phylogenetic tree do not necessarily reflect the true 'origin' of a lineage (Ezard et al., 2012), particularly if the dominant form of speciation is through the asymmetrical budding of new lineages via peripatry (Hodge et al., 2012). In the latter process, species' divergence times (and species-level diversification rate) are expected to be highly decoupled from range size (e.g. widespread founder lineages will appear as recent originations from their daughter lineages), thereby obscuring the association between evolutionary dynamics and modern extinction risk at this phylogenetic scale. Both scenarios support testing these hypotheses in higher-order clades.

Here, we test for evolutionary legacies in contemporary extinction risk within the tetrapods, by comparing the distribution of modern species imperilment and geographic range size patterns to evolutionary dynamics among 4404 tetrapod genera, including amphibians (n = 458), birds (n = 1948), mammals (n = 1073), squamates (with *Sphenodon*, n = 821) and non-avian archosauromorphs (turtles and crocodiles, hereafter archosauromorphs, n = 104), collectively representing 29,763 species.

METHODS

Taxonomic and phylogenetic data

To understand how evolutionary dynamics may shape patterns of contemporary threat, we delineated genera for each major tetrapod group from available recent molecular phylogenies (Colston et al., 2020; Jetz & Pyron, 2018; Jetz et al., 2012; Tonini et al., 2016; Upham et al., 2019). We synonymised the tips of each tree with recent taxonomic datasets (AmphibiaWeb, 2020; Burgin et al., 2018; Colston et al., 2020; Handbook of the Birds of the World & BirdLife International, 2018; Uetz et al., 2020; Table S1) and elected to only include tips that had molecular data available to ensure that estimates of stem and crown ages were based on estimated, rather than imputed, branching times. We extracted crown and stem ages from a random sample of 100 phylogenies from the credible set of each tetrapod group. We only retained these estimates when a genus was monophyletic in a given phylogeny, and only examined genera with at least 10 monophyletic estimates across the set.

We delineated three evolutionary predictors that may shape contemporary threat across lineages, based on the hypotheses outlined (Figure 1). To test the Clade Age hypothesis (H1), we calculated the stem age for each genus – that is the time since divergence between a genus and its closest relative(s). Although this hypothesis should also apply for species, the overall high fraction of missing species precludes accurate estimates of species-level divergence times to test this. To test the Turnover hypothesis (H2), we calculated the ratio of genus crown age (the time since divergence of all extant species) to genus stem age (crown-to-stem ratio). When extinction is high relative to speciation then we may expect that clade to have a short crown age relative to its stem age, reflecting the frequent extinction of stem lineages since its origination. We confirmed through simulations of phylogenies from a birth-death process (detailed in the Supplementary Material) that, on average, a smaller crown-stem ratio can indicate high levels of turnover (Figure S4). We note that this metric does not measure absolute diversification rate, and so is distinct from diversification rate predictions.

To test the Diversification Rate hypothesis (H3), we calculated recent net diversification rates using the methods-of-moment (MoM) estimator based on clade crown age (Magallon & Sanderson, 2001). This estimates net diversification (the average rate of species accumulation from clade origin) based on clade richness (R, divided by the initial split) and crown age (T_c): ($\log(R/2)/T_c$). The MoM estimator is one of many approaches to quantify diversification rates, and it implicitly adopts some unrealistic assumptions – for example time-constant rates and unbounded diversity limits (Morlon, 2014; Rabosky & Benson, 2021). MoM estimates based on crown ages for relatively young clades (i.e. genera) will be more reflective of recent speciation (Nee et al., 1994), which is ideal when examining lagged pulses of impending extinction. Time-varying rates of speciation would be preferable, but identifying the temporal dynamics of speciation and extinction from molecular phylogenies of exclusively extant lineages appears to be intractable (Louca & Pennell, 2020). Similar identifiability issues exist for the MoM estimator (Rabosky & Benson, 2021), and we discuss our rationale for its use in this study in the Supplemental Material. As diversification rate estimates tend to be biased by clade age (Henao Diaz et al., 2019; Rabosky & Benson, 2021), we also ran separate models including crown age as an additional covariate to diversification rate in contributing to modern threat.

The MoM estimator relies on accurate estimates of clade crown ages in the phylogeny, which will depend on how many extant species are represented in the phylogeny (lower species representation will bias crown ages to be underestimated) in addition to the fossil dating and models of molecular evolution used to construct a dated phylogeny. We simulated how missing data may impact our estimates of crown age using a birth-death model among clades of varying extant richness (Figure S3) and set clade-size based cut-offs for species representation to reduce biases in genus crown age (Table S2). For genera that did not meet the representation cut-off, we censored their crown age estimates and therefore could not calculate net diversification rate or crown-stem ratios for these clades. We also excluded ditypic genera, as such clades do not have enough information to characterise their underlying diversification rates as the numerator is always zero. The MoM estimator requires an assumption on lineage turnover (eq. 7; Magallon & Sanderson, 2001) or relative extinction rate (ε); we present diversification rate with $\varepsilon = 0.5$, and results with $\varepsilon = 0$ or $\varepsilon = 0.9$ are included in Table S4.

Rather than extinction risk emerging as a byproduct of the characteristics that promote speciation rates within a clade, it may simply emerge from either the total number of speciation events, or the carrying capacity for species diversity, within a clade. The total extant species richness of a clade captures both of these mechanisms (Rabosky, 2009). As such, we also included $\log_e$ transformed extant richness (known as the Ω statistic; Rabosky, 2009) as a predictor in our models – both alone and in combination with diversification rates.

Threat and range data

To characterise extinction risk at the clade level, we determined the number of assessed species for each genus that were listed in 'threatened' or 'non-threatened' categories according to the International Union for the Conservation of Nature (IUCN, vers. 2020-2). We aggregated threat categories into a binary classification to have a more robust sample to detect differences in threat probabilities among genera. Threatened included any species listed as Vulnerable, Endangered, Critically Endangered, Extinct in the Wild, as well as confirmed historical extinctions (Extinct). Non-threatened included species listed as either Least Concern or Near Threatened. The total number of threatened species in our datasets included 1995 amphibians (41.5% of 4804 species), 1324 birds (14.6% of 9083), 206 turtles and crocodiles (79.5% of 259), 972 squamate reptiles (19.3% of 5030) and 1035 mammals (27.1% of 3818). We summarised species' extinction risk at the genus-level as the proportion of threatened species in the clade, that is ($N_{\text{threatened}}/N_{\text{assessed}}$), which is equivalent to the per-species probability of threat. We omitted species that were Data Deficient or Not Evaluated, assuming that the proportion of assessed species that are threatened is representative of the genus-wide threat distribution. We also used continuous probabilities of extinction based on these threat categories (e.g. Davis et al., 2018) and replicated our analyses to explore this methodological choice (see Table S3).

We used estimates of species range size (in km^2), based on the total area of species' extent of occurrence polygons, from the IUCN and additional compilations for amphibians (González-del-Pliego et al., 2019), birds (with distributions restricted to resident and breeding ranges; BirdLife International, 2018), turtles and crocodiles (Colston et al., 2020), squamate reptiles (Roll et al., 2017) and mammals (Upham et al., 2019). We note that these range sizes also included historical distributions where the species is now extirpated (primarily in birds and mammals). Details on characterising species range size for each group are available in the Supplementary Material.

Analysis

To test how different evolutionary metrics influence modern threat and range size, we conducted three primary sets of analyses. For our analyses we constructed Bayesian phylogenetic generalised linear models in Stan (Carpenter et al., 2017) using the *brms* package (Bürkner, 2017) in *R* version 4.0.2. Explicit model formulae and prior specifications are detailed in the Supplementary Material.

In our first set of analyses, we test whether genus extinction risk is influenced by lineage age, turnover or diversification rate, by modelling the proportion of threatened species in each clade using a negative binomial rate model. This approach models the number of threatened species in a clade with an offset for the ($\log_e$ transformed) number of assessed species in each clade – effectively modelling the probability of a given assessed species being threatened. The negative binomial distribution accounts for the higher variance (V) in the proportion of threatened species in species rich (i.e. higher μ) clades, which is captured by the overdispersion parameter (Φ) in the quadratic parameterisation as: $V = \mu + \mu^2/\Phi$. The proportion of threatened species was overdispersed in each group, except for the archosauromorphs (Figure S5).

We accounted for shared ancestry among genera with a phylogenetic correlation matrix in each model. To test our three hypotheses, we fit models where the proportion of threatened species was a function of the specific evolutionary predictor: stem age, crown-stem ratio or diversification rate. To formally incorporate the uncertainty of these evolutionary predictors among the 100 sampled phylogenies, we treat each metric as 'missing' data in our modelling approach – where the estimated geometric mean and standard deviation of each metric for each clade is treated as a prior distribution, from which an estimated 'true' stem age or diversification rate is sampled in each iteration of the Bayesian model. We applied $\log_e$ transformations to stem age and diversification rate, or a logit transformation for the crown-stem ratio. We assessed support for each hypothesis based on 95% credibility intervals of the posterior parameter estimates.

In our second set of analyses, we test whether evolutionary predictors were also linked to the range dynamics of clades. We modelled the geometric mean species' range size ($\log_{10}$ transformed) within each genus as a function of each evolutionary predictor with a Gaussian distribution, while accounting for phylogenetic heritability among genera. We applied the same model fit procedures for each predictor as for the threat models. Not all species within a genus had range size data available, and so to account for the uncertainty in mean range sizes we weighted the model contribution of each genus by the proportion of species with data.

Finally, given our results with both threat and range size, in our third set of analyses we aimed to assess the interdependency of range size and diversification rate in shaping genus extinction risk. We compared models of the proportion of threatened species as a function of mean range size and diversification rate, independently and with both terms included together. The combined model allows us to estimate the partial regression coefficients and assess whether the effects of diversification rate are mediated entirely or partially by the mean species' range size of genera. If the effects of diversification rate remain robust, based on the magnitude and credible interval of the partial regression coefficients, then this may suggest that mechanisms beyond range dynamics contribute to the relationship between modern threat and clade diversification rates among genera. We also note, however, that there may be additional variation in the range size distribution of clades that is simply not captured by the geometric mean.

RESULTS

Evolutionary patterns of contemporary imperilment

Among 4278 tetrapod genera, contemporary extinction risk appears to be shaped by historical evolutionary dynamics through several pathways (Table 1).

For most groups, clade age had no relationship with contemporary threat (Figure S6). In both birds and mammals, however, contemporary threat was higher for recently diverged genera and declined for older clades (birds: β_{AGE} = −0.273 [95% CI = −0.422, −0.129]; mammals, β_{AGE} = −0.163 [−0.305, −0.018]). However, the lack of broad consensus suggests that there is no general relationship between modern threat and clade age across the tetrapods.

Similarly, there was little support for the hypothesis that genera with low ancient turnover also exhibit lower contemporary extinction risk. This prediction had only weak support in birds (β_{CSR} = −0.132 [−0.266, 0.002]) and squamates (β_{CSR} = −0.174 [−0.356, 0.011]), and was insignificant in all other groups (Figure S7).

In contrast, the hypothesis that clade diversification rates may shape contemporary threat received near unanimous support across the tetrapods (Figure 2). We found a consistent positive relationship between contemporary extinction risk and diversification rate among genera in amphibians (β_{DR} = 0.397 [0.090, 0.720]), as reported by Greenberg and Mooers (2017), but also in birds (β_{DR} = 0.474 [0.287, 0.672]), squamate reptiles (β_{DR} = 0.491 [0.178, 0.816]) and mammals (β_{DR} = 0.288[0.033, 0.553]). Only the archosauromorphs showed a negative relationship between the proportion of threatened species and diversification rate (β_{DR} = −0. 072 [−0. 510, 0.388]), but we did not find strong evidence suggesting that this relationship significantly differed among the five groups (Table S5). Generic species richness was unrelated to modern threat for most clades (amphibians, β_S = 0.095 [−0.030, 0.221]; archosauromorphs, β_S = −0.024 [−0.283, 0.253]; squamates, β_S = 0.040 [−0.124, 0.210]; mammals, β_S = 0.021 [−0.136, 0.190]), but there was a significant positive association in birds (β_S = 0.159 [0.021, 0.300]). Nevertheless, the effect of genus diversification rate on modern threat remained unchanged for every major group when modelled jointly with both species richness (Table S6) and crown age (except mammals; Table S7). Collectively, the hypothesis that extinction risk and speciation rate are positively correlated through shared drivers is strongly supported by the distribution of modern threat status in tetrapods.

Evolutionary dynamics of range size

Across every tetrapod group, we found a negative relationship between the mean species' range size and net diversification rate of genera (Figure 3). This relationship was significant for amphibians (β_{DR} = −0.518 [−0.776, −0.254], birds (β_{DR} = −0.375 [−0.485, −0.264]), squamates (β_{DR} = −0.393[−0.599, −0.185]) and mammals (β_{DR} = −0.251 [−0.418, −0.078]), but was weaker and non-significant in the archosauromorphs (β_{DR} = −0.232 [−0.607, 0.148]). These effect sizes correspond to a considerable difference in the expected range size of a species from the slowest compared to fastest diversifying genera of each clade: 26-fold greater for amphibians, 55-fold for birds, 36-fold for squamates and 8-fold for mammals; there was no strong evidence that the scaling of mean species' range size with genus diversification rate significantly differed among the five tetrapod groups (Table S8).

Consistent with our extinction risk results, neither stem age nor turnover show strong relationships with patterns of contemporary range size across lineages. The only other significant pattern that emerged was in birds, where genera with older lineage ages had larger mean extant range sizes (β_{AGE} = 0.131 [0.039, 0.222]; Table S9).

Range size as a mediator of evolutionary patterns of threat

The effect of genus diversification rate on extinction risk in each tetrapod group was consistently weakened when also conditioning on mean species' range size (Figure 4) – with a greater shift for amphibians and squamate reptiles compared to birds and mammals. After accounting for mean range size, the confidence intervals for the partial effect of genus diversification rate crossed zero for amphibians (β_{DR} = 0.120 [−0.114, 0.359]), squamate reptiles (β_{DR} = 0.229 [−0.023, 0.506]) and mammals (β_{DR} = 0.230 [−0.017, 0.482]), but for birds the independent effect of diversification rate remained significant (β_{DR} = 0.317 [0.128, 0.519]). Overall, this suggests that the link between modern threat and diversification rate among tetrapod genera is partly mediated by evolutionary patterns in geographic range size.

DISCUSSION

The extinctions poised to occur in the coming centuries appear to be unfolding in an uneven manner across the tetrapod Tree of Life. Our results indicate that among four of the five major tetrapod groups, those genera that have diversified faster are poised to disproportionately lose this diversity in the near future. In part, this phenomenon can be explained by the evolutionary dynamics of species' range sizes, whereby species from genera with

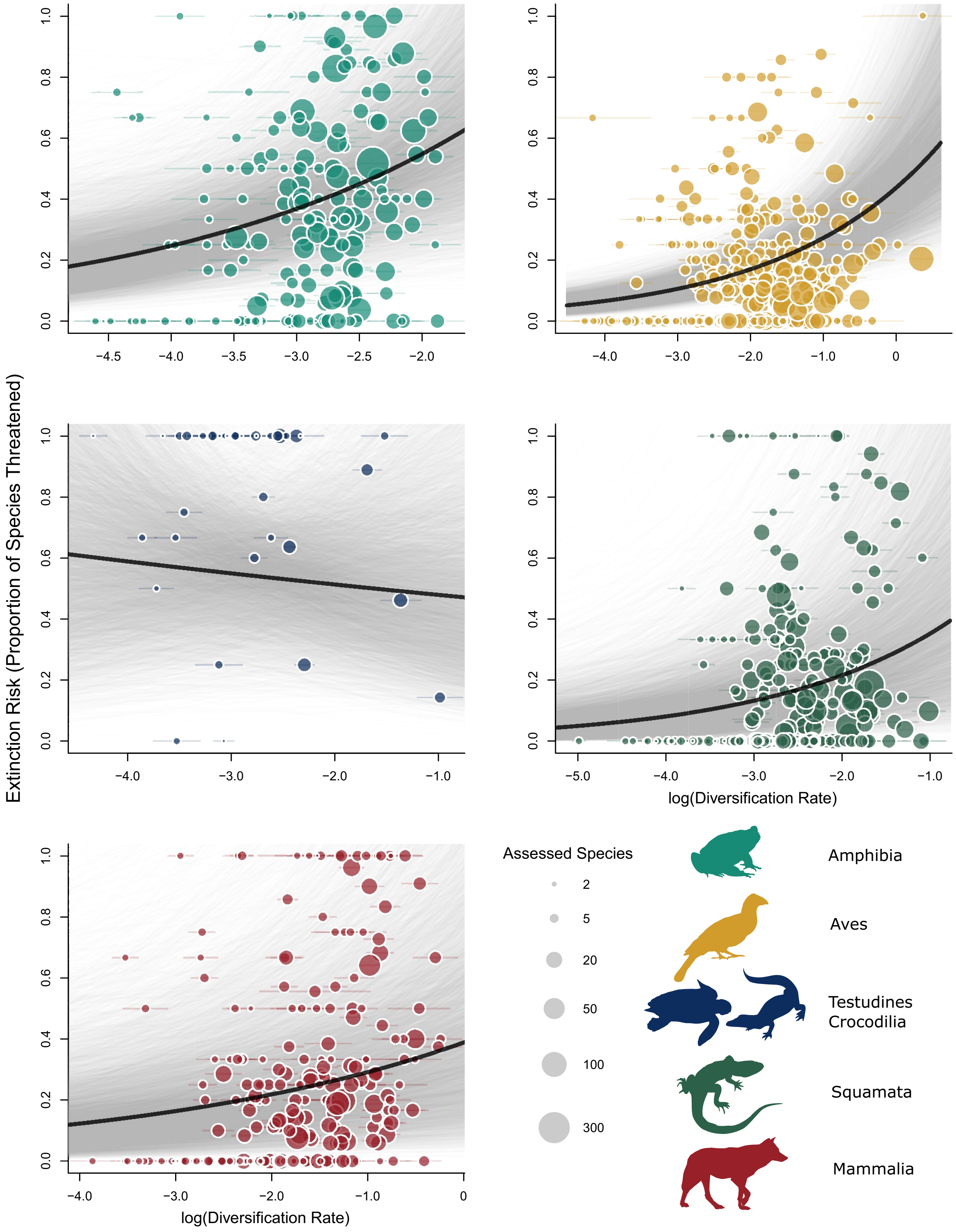

FIGURE 2 Genus-level contemporary extinction risk, measured as the proportion of species in 'threatened' IUCN categories, as a function of net diversification rate ($\log_e$ normalised, averaged across the phylogenetic distribution). Grey lines indicate model predicted relationships between the probability of a species being listed in a threatened category based on genus diversification rate from parameters drawn from the full posterior distribution of each model. The solid line indicates the relationship based on median parameter estimates. Points are scaled to the number of assessed species in a genus and horizontal point lines represent ±1 standard deviation in rate estimates

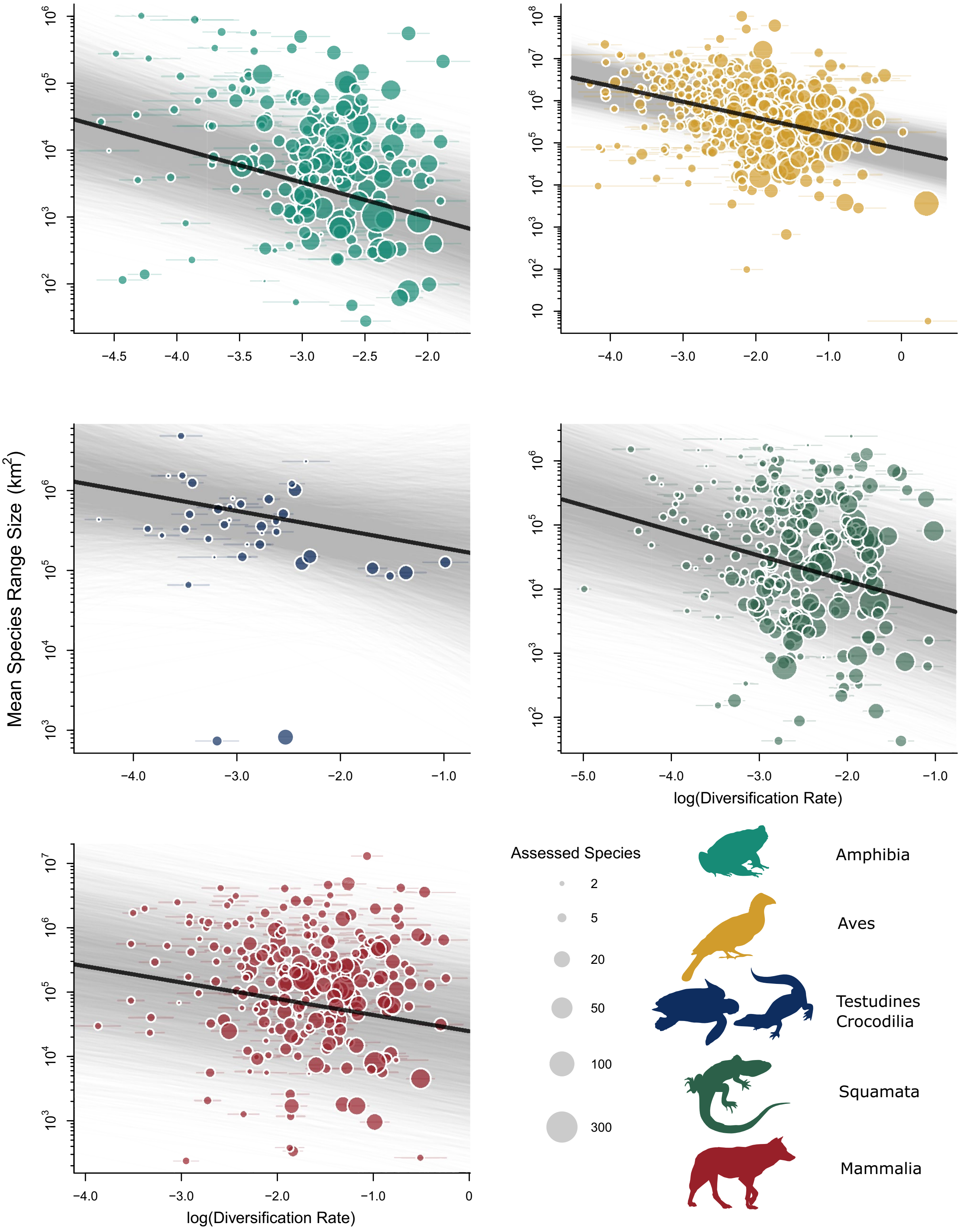

FIGURE 3 The mean range size of species within a genus (km^2, on a $\log_{10}$ scale) is broadly correlated with net diversification rate ($\log_e$ transformed, averaged across the phylogenetic distribution). Gray lines indicate model predicted relationships between mean species' range size and genus diversification rate from parameters drawn from the full posterior distribution of each model. The solid line indicates the relationship based on median parameter estimates. Points are scaled to the number of assessed species in a genus and horizontal point lines represent ±1 standard deviation in rate estimates

TABLE 1 Median coefficient estimates from the posterior distribution of models evaluating the lineage age (β_{AGE}), turnover (β_{CSR}), and diversification (β_{DR}) hypotheses on the proportion of currently threatened species for each of the five major Tetrapoda clades.

	Lineage age hypothesis		**Turnover hypothesis**		**Diversification hypothesis**	
	β_{AGE}	*n*	β_{CSR}	*n*	β_{DR}	*n*
Amphibians	−0.026 [−0.331, 0.274]	448	−0.079 [−0.225, 0.082)	206	**0.397 [0.090, 0.720]**	181
Aves	**−0.273 [−0.422, −0.129]**	1982	−0.130 [−0.263, 0.006]	644	**0.474 [0.287, 0.672]**	456
Archosauromorphs	0.163 [−0.253, 0. 569]	99	0.022 [−0.256, 0.317]	58	−0. 072 [−0.510,0.388]	38
Squamates	−0.163 [−0.424, 0.099]	742	−0.172 [−0.354, 0.013]	293	**0.491 [0.178, 0.816]**	245
Mammals	**−0.163 [−0.305, −0.018]**	1058	−0.020 [−0.162, 0.129]	359	**0.288 [0.033, 0.553]**	251

Note: Coefficient estimates correspond to the expected change in the probability of threat per assessed species on the $\log_e$ scale. Significant coefficient estimates, based on 95% credible intervals from the posterior (in brackets), are bolded.

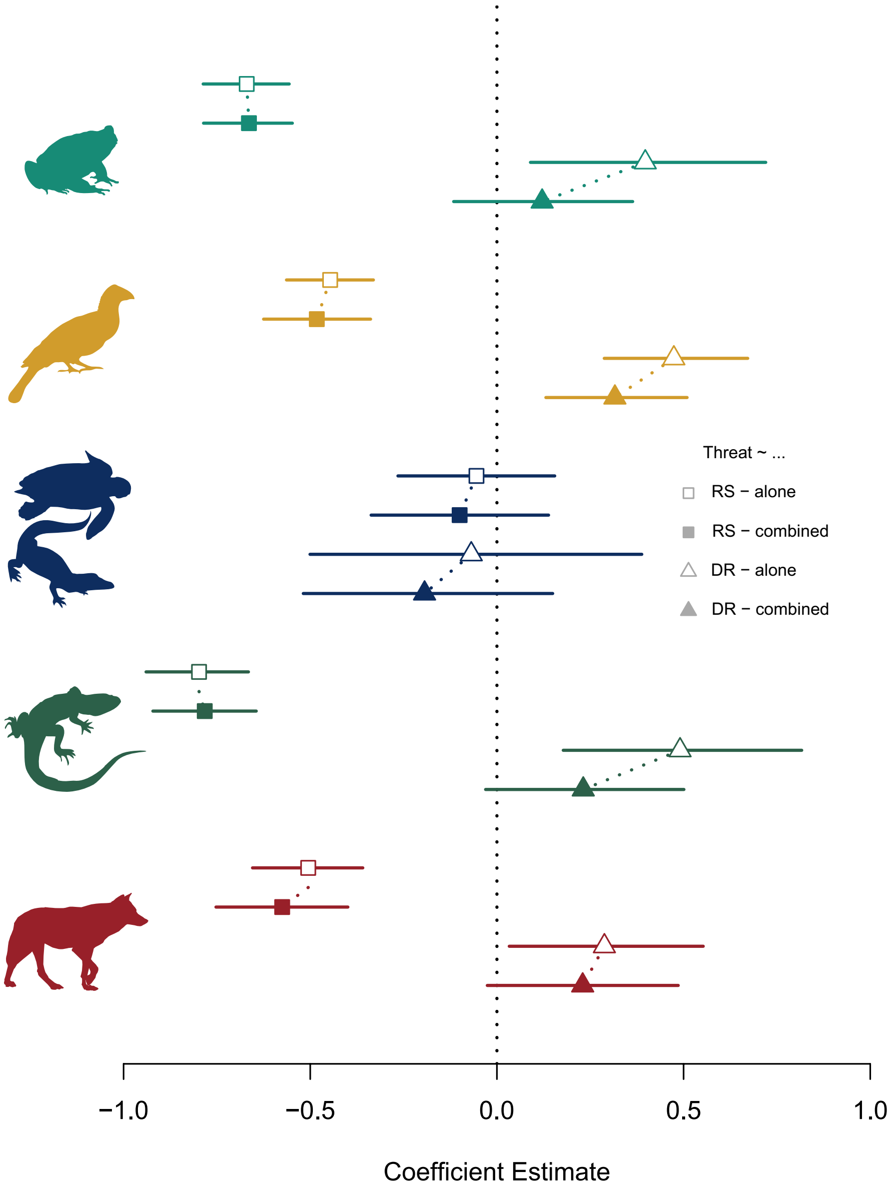

FIGURE 4 The independent and combined effects of mean range size (RS) and diversification rate (DR) on the proportion of threatened species within a genus. The empty and filled symbols indicate each predictor in a model either alone or when also accounting for the other variable (i.e. range size or diversification rate). The lines indicate 95% credible intervals for the estimated effect. The effect of diversification rate decreases when combined with mean range size for each group, with a greater shift for amphibians and squamate reptiles compared to birds and mammals, suggesting that the relationship between threat and diversification rate (Figure 2) is mediated at least in part by evolutionary patterns in geographic range size (Figure 3)

faster diversification rates tend to have more restricted geographic distributions on average. Range size itself is a category for assessing contemporary threat (under Criterion B, IUCN, 2020), which introduces a potential circularity. However, range-restricted species have also been shown to be disproportionately lost from environmental change at local scales (Newbold et al., 2018; Staude et al., 2020), and range size has consistently been the predominant predictor of ancient extinctions (Finnegan et al., 2015; Harnik, Simpson, et al., 2012; Harnik, Lotze, et al., 2012; Orzechowski et al., 2015), suggesting that small range size is a reliable risk factor for extinction. These patterns have important consequences for our understanding of both historical and contemporary biodiversity loss.

The consistent relationship between recent diversification rates and modern extinction risk across tetrapod genera supports the theory that speciation and extinction rates are in general positively correlated across lineages (Jablonski, 2017; Stanley, 1979, 1990), and is congruent with extinction patterns over deep evolutionary timescales (Knope et al., 2020; Marshall, 2017). This pattern suggests that, at least for some clades, there is a tendency towards both the rapid genesis and subsequent loss of incipient lineages – a high frequency of speciation and extinction events through time consistent with the ephemeral speciation model (Rosenblum et al., 2012). This same lineage turnover pattern could also emerge as an artefact of taxonomic inflation – for example if the elevation of certain populations to species status is driven by conservation concerns (Isaac et al., 2004) – but this seems unlikely to consistently be the case so broadly across tetrapods.

We show that many species in rapidly diversifying lineages generally have highly restricted geographic distributions, suggesting a clear mechanism whereby novel species would both be gained and lost quickly. Exceptions to this trend exist though, as there is considerable variation in modern extinction risk among clades across the diversification spectrum – some clades appear to be both rapidly expanding in diversity and apparently unimpeded by human impacts. These lineages might be in the midst of rapid expansions in species number, distribution and niche space (Schluter, 2000), and it is possible that lineages undergoing expansionary adaptive radiations (as opposed to non-adaptive radiations) are more robust to the unstable and highly modified ecosystems of the Anthropocene. How the temporal dynamics of diversification (i.e. accelerations and slowdowns) and concurrent changes to clade trait and niche space ultimately contribute to extinction risk is therefore an important outstanding question. There are many pathways to high diversification (Rundell & Price, 2009), and the relationship between modern extinction and diversification rate is also likely dependent on the specific eco-evolutionary drivers of each radiation.

A link between speciation and extinction rates is likely to arise as an emergent property of lineage characteristics (i.e. species selection; Jablonski, 2017), but rarely are these two processes considered in concert. Our results suggest that the relationship between extinction and speciation may in part arise from evolutionary range size dynamics in certain groups (e.g. amphibians and squamates) – but this phenomenon is itself likely a product of lineage traits (e.g. low vagility or niche specialisation) that may influence rates of gene flow, genetic fission and population loss in these lineages. Other proximate mechanisms likely drive this association as well, given that there was still a weakened positive effect of diversification rate on modern threat for bird, squamate reptiles and mammals even after accounting for mean species' range size in genera. In some cases, the mechanisms may be extrinsic: certain environments, like islands and tropical mountain ranges, are crucibles of diversification (Jetz et al., 2014; Quintero & Jetz, 2018), and also have a high concentration of historical extinctions and current imperilment (Blackburn et al., 2004; Faurby & Svenning, 2016; La Sorte & Jetz, 2010). The consistent evolutionary patterns we show here suggest a possible broad rule across the Tree of Life: that lineages fall along a macroevolutionary spectrum of low-to-high species turnover (Greenberg & Mooers, 2017; Jablonski, 2017). Whether the drivers of this macroevolutionary trade-off are universal, or represent epiphenomena from multiple pathways, also remains an outstanding question.

That the distribution of contemporary extinction risks across tetrapod clades aligns with extinction patterns from the fossil record suggests the possibility that human impacts are 'merely' accelerating the 'natural' extinction process. However, human activities can also reshape species' ancestral fitness landscapes, where once adaptive traits now become a liability for survival in the Anthropocene. Hunting and harvesting is one clear example, particularly for lineages with minimal extrinsic adult mortality in their evolutionary history before the emergence of human predators (Darimont et al., 2015). That turtles and crocodiles show a reversed evolutionary pattern compared to other groups is intriguing, as overexploitation is the predominant stressor for 60% of turtle and crocodile species (IUCN, 2020). Turtle and crocodile lineages with slow life histories may also have slower diversification rates, causing an elevated extinction risk in evolutionarily isolated lineages (e.g. as in chondrichthyans; Stein et al., 2018). This potential shift in the underlying evolutionary dynamics of extinction risk is almost certainly replicated among many at-risk tetrapod lineages that bear the brunt of our persecution.

If we aim to stanch this loss of biological diversity and history, how then should we prioritise lineages for conservation across the diversification spectrum? The concentration of threat within rapidly diversifying lineages is perhaps advantageous, as this may lessen the loss of overall tetrapod evolutionary history (Heard & Mooers, 2000). In contrast, evolutionarily distinct and threatened species may represent a departure from the norm, if these lineages generally exhibit exceptionally low rates of extinction (Bennett et al., 2017; Liow, 2007). Prioritising evolutionarily isolated lineages, as exemplified in the EDGE (Evolutionarily Distinct and Globally Endangered) of Existence program (https://www.edgeofexistence.org/), could therefore be a doubly shrewd strategy: both to protect evolutionary history and to rectify a potentially aberrant extinction burden on what may be historically resilient lineages. There are also many cases, however, of entire clades being threatened with imminent extinction, where a considerable loss of evolutionary history may occur without conservation intervention (Greenberg & Mooers, 2017). This dual strategy, to safeguard both ends of the diversification spectrum, may be an ideal compromise in a future where conservation triage is an unfortunate reality.

ACKNOWLEDGEMENTS

Thanks to the numerous curators and contributors of the various taxonomic, geographic and threat databases we relied upon for this study, whose efforts make these kinds of studies possible. Thanks also to A. Phillimore, two anonymous reviewers, and an associate editor for constructive feedback on this manuscript. This work was supported by NSF grant DEB 1441719 to RAP, NSF VertLife Terrestrial grant DEB 1441737 to WJ, the Biodiversity Knowledge Integration Center at Arizona State University (President's Special Initiative Funds) to NSU and a NSERC Discovery grant to AØM.

AUTHOR CONTRIBUTIONS

DAG, RAP and AØM conceived of the study. RAP, NSU and WJ contributed the data. LGWJ conducted the simulations. DAG collated and analysed the data. DAG led the manuscript writing, with editorial contribution from RAP, NSU, WJ and AØM.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13868.

DATA AVAILABILITY STATEMENT

Data and code for this study are available at https://doi.org/10.6084/m9.figshare.14727660.

ORCID

Dan A. Greenberg https://orcid.org/0000-0001-7489-1393
Nathan S. Upham https://orcid.org/0000-0001-5412-9342

REFERENCES

AmphibiaWeb (2020) Berkeley, CA: University of California. Available at: https://amphibiaweb.org [Accessed 20th January 2020].

Balmford, A. (1996) Extinction filters and current resilience: The significance of past selection pressures for conservation biology. *Trends in Ecology & Evolution*, 11, 193–196.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B. et al. (2011) Has the Earth's sixth mass extinction already arrived? *Nature*, 471, 51–57.

Bennett, D.J., Sutton, M.D. & Turvey, S.T. (2017) Evolutionarily distinct "living fossils" require both lower speciation and lower extinction rates. *Paleobiology*, 43, 34–48.

Betts, M.G., Wolf, C., Pfeifer, M., Banks-Leite, C., Arroyo-Rodríguez, V., Ribeiro, D.B. et al. (2019) Extinction filters mediate the global effects of habitat fragmentation on animals. *Science*, 366, 1236–1239.

Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L. & Gaston, K.J. (2004) Avian extinction and mammalian introductions on oceanic islands. *Science*, 305, 1955–1958.

Böhm, M., Williams, R., Bramhall, H.R., McMillan, K.M., Davidson, A.D., Garcia, A. et al. (2016) Correlates of extinction risk in squamate reptiles: the relative importance of biology, geography, threat and range size. *Global Ecology and Biogeography*, 25, 391–405.

Boyer, A.G. (2010) Consistent ecological selectivity through time in Pacific island avian extinctions. *Conservation Biology*, 24, 511–519.

Budd, G.E. & Mann, R.P. (2020) The dynamics of stem and crown groups. *Science Advances*, 6, eaaz1626.

Burgin, C.J., Colella, J.P., Kahn, P.L. & Upham, N.S. (2018) How many species of mammals are there? *Journal of Mammalogy*, 99, 1–14.

Bürkner, P.-C. (2017) brms: an R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, 80, 1–28.

Carpenter, B., Gelman, A., Hoffman, M.D., Lee, D., Goodrich, B., Betancourt, M. et al. (2017) Stan: a probabilistic programming language. *Journal of Statistical Software*, 76, 1–32.

Chichorro, F., Juslén, A. & Cardoso, P. (2019) A review of the relation between species traits and extinction risk. *Biological Conservation*, 237, 220–229.

Colston, T.J., Kulkarni, P., Jetz, W. & Pyron, R.A. (2020) Phylogenetic and spatial distribution of evolutionary diversification, isolation, and threat in turtles and crocodilians (non-avian archosauromorphs). *BMC Evolutionary Biology*, 20, 81.

Darimont, C.T., Fox, C.H., Bryan, H.M. & Reimchen, T.E. (2015) The unique ecology of human predators. *Science*, 349, 858–860.

Davies, T.J., Smith, G.F., Bellstedt, D.U., Boatwright, J.S., Bytebier, B., Cowling, R.M. et al. (2011) Extinction risk and diversification are linked in a plant biodiversity hotspot. *PLoS Biology*, 9, e1000620.

Davis, M., Faurby, S. & Svenning, J.C. (2018) Mammal diversity will take millions of years to recover from the current biodiversity crisis. *Proceedings of the National Academy of Sciences of the United States of America*, 115, 11262–11267.

Ezard, T.H.G., Pearson, P.N., Aze, T. & Purvis, A. (2012) The meaning of birth and death (in macroevolutionary birth-death models). *Biology Letters*, 8, 139–142.

Faurby, S. & Svenning, J.C. (2016) Resurrection of the island rule: human-driven extinctions have obscured a basic evolutionary pattern. *The American Naturalist*, 187, 812–820.

Finnegan, S., Anderson, S.C., Harnik, P.G., Simpson, C., Tittensor, D.P., Byrnes, J.E. et al. (2015) Paleontological baselines for evaluating extinction risk in the modern oceans. *Science*, 348, 567–570.

Foote, M., Crampton, J.S., Beu, A.G., Marshall, B.A., Cooper, R.A., Maxwell, P.A. et al. (2007) Rise and fall of species occupancy in Cenozoic fossil mollusks. *Science*, 318, 1131–1134.

Gaffney, O. & Steffen, W. (2017) The Anthropocene equation. *The Anthropocene Review*, 4(1), 53–61.

Gaston, K.J. & Blackburn, T.M. (1997) Evolutionary age and risk of extinction in the global avifauna. *Evolutionary Ecology*, 11, 557–565.

Gingerich, P. (1983) Rates of evolution: effects of time and temporal scaling. *Science*, 222, 159–162.

González-del-Pliego, P., Freckleton, R.P., Edwards, D.P., Koo, M.S., Scheffers, B.R., Pyron, R.A. et al. (2019) Phylogenetic and trait-based prediction of extinction risk for data-deficient amphibians. *Current Biology*, 29, 1557–1563.e3.

Greenberg, D.A. & Mooers, A.Ø. (2017) Linking speciation to extinction: diversification raises contemporary extinction risk in amphibians. *Evolution Letters*, 1, 40–48.

Hagen, O., Andermann, T., Quental, T.B., Antonelli, A. & Silvestro, D. (2018) Estimating age-dependent extinction: Contrasting evidence from fossils and phylogenies. *Systematic Biology*, 67, 458–474.

Handbook of the Birds of the World and BirdLife International. (2018). *Handbook of the Birds of the World and BirdLife International digital checklist of the birds of the world: version 3*. Available at: http://datazone.birdlife.org/userfiles/file/Species/Taxonomy/HBW-BirdLife_Checklist_v3_Nov18.zip [Accessed 22nd November, 2019].

Harnik, P.G., Lotze, H.K., Anderson, S.C., Finkel, Z.V., Finnegan, S., Lindberg, D.R. et al. (2012) Extinctions in ancient and modern seas. *Trends in Ecology & Evolution*, 27, 608–617.

Harnik, P.G., Simpson, C. & Payne, J.L. (2012) Long-term differences in extinction risk among the seven forms of rarity. *Proceedings of the Royal Society B-Biological Sciences*, 279, 4969–4976.

Heard, S.B. & Mooers, A.Ø. (2000) Phylogenetically patterned speciation rates and extinction risks change the loss of evolutionary history during extinctions. *Proceedings of the Royal Society B-Biological Sciences*, 267, 613–620.

Heim, N.A. & Peters, S.E. (2011) Regional environmental breadth predicts geographic range and longevity in fossil marine genera. *PLoS ONE*, 6, e18946.

Henao Diaz, L.F., Harmon, L.J., Sugawara, M.T.C., Miller, E.T. & Pennell, M.W. (2019) Macroevolutionary diversification rates show time dependency. *Proceedings of the National Academy of Sciences of the United States of America*, 116, 7403–7408.

Ho, S.Y.W., Lanfear, R., Bromham, L., Phillips, M.J., Soubrier, J., Rodrigo, A.G. et al. (2011) Time-dependent rates of molecular evolution. *Molecular Ecology*, 20, 3087–3101.

Hodge, J.R., Read, C.I., van Herwerden, L. & Bellwood, D.R. (2012) The role of peripheral endemism in species diversification: Evidence from the coral reef fish genus Anampses (Family: Labridae). *Molecular Phylogenetics and Evolution*, 62, 653–663.

Isaac, N.J.B., Mallet, J. & Mace, G.M. (2004) Taxonomic inflation: its influence on macroecology and conservation. *Trends in Ecology & Evolution*, 19, 464–469.

IUCN. (2020). The IUCN red list of threatened species. Version 2020-2. https://www.iucnredlist.org

Jablonski, D. (1986) Larval ecology and macroevolution in marine invertebrates. *Bulletin of Marine Science*, 39, 565–587.

Jablonski, D. (1987) Heritability at the species level: Analysis of geographic ranges of cretaceous mollusks. *Science*, 238, 360–363.

Jablonski, D. (2017) Approaches to macroevolution: 2. Sorting of variation, some overarching issues, and general conclusions. *Evolutionary Biology*, 44, 427–450.

Jablonski, D. & Roy, K. (2003) Geographical range and speciation in fossil and living molluscs. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270, 401–406.

Jetz, W. & Pyron, R.A. (2018) The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. *Nature Ecology & Evolution*, 2(5), 850–858.

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012) The global diversity of birds in space and time. *Nature*, 491, 444–448.

Jetz, W., Thomas, G.H., Joy, J.B., Redding, D.W., Hartmann, K. & Moeers, A.Ø. (2014) Global distribution and conservation of evolutionary distinctness in birds. *Current Biology*, 24, 919–930.

Johnson, C.N., Delean, S. & Balmford, A. (2002) Phylogeny and the selectivity of extinction in Australian marsupials. *Animal Conservation*, 5, 135–142.

Kiessling, W. & Aberhan, M. (2007) Geographical distribution and extinction risk: lessons from Triassic-Jurassic marine benthic organisms. *Journal of Biogeography*, 34, 1473–1489.

Knope, M.L., Bush, A.M., Frishkoff, L.O., Heim, N.A. & Payne, J.L. (2020) Ecologically diverse clades dominate the oceans via extinction resistance. *Science*, 367, 1035–1038.

La Sorte, F.A. & Jetz, W. (2010) Projected range contractions of montane biodiversity under global warming. *Proceedings of the Royal Society B*, 277, 3401–3410.

Lee, T.M. & Jetz, W. (2011) Unravelling the structure of species extinction risk for predictive conservation science. *Proceedings of the Royal Society B-Biological Sciences*, 278, 1329–1338.

Liow, L.H. (2007) Lineages with long durations are old and morphologically average: an analysis using multiple datasets. *Evolution*, 61, 885–901.

Liow, L.H. & Stenseth, N.C. (2007) The rise and fall of species: implications for macroevolutionary and macroecological studies. *Proceedings of the Royal Society B-Biological Sciences*, 274, 2745–2752.

Loehle, C. & Eschenbach, W. (2012) Historical bird and terrestrial mammal extinction rates and causes. *Diversity and Distributions*, 18, 84–91.

Louca, S. & Pennell, M.W. (2020) Extant timetrees are consistent with a myriad of diversification histories. *Nature*, 580, 502–505.

Louca, S. & Pennell, M.W. (2021) Why extinction estimates from extant phylogenies are so often zero. *Current Biology*, 31(14), 3168–3173.e4.

Lynch, M., Conery, J. & Burger, R. (1995) Mutation accumulation and the extinction of small populations. *The American Naturalist*, 146, 489–518.

Magallon, S. & Sanderson, M.J. (2001) Absolute diversification rates in Angiosperm clades. *Evolution*, 55, 1762–1780.

Marshall, C.R. (2017) Five palaeobiological laws needed to understand the evolution of the living biota. *Nature Ecology & Evolution*, 1, 1–6.

McKinney, M.L. (1997) Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annual Review of Ecology and Systematics*, 28, 495–516.

Morlon, H. (2014) Phylogenetic approaches for studying diversification. *Ecology Letters*, 17, 508–525.

Nagalingum, N.S., Marshall, C.R., Quental, T.B., Rai, H.S., Little, D.P. & Mathews, S. (2011) Recent synchronous radiation of a living fossil. *Science*, 334, 796–799.

Nee, S., Holmes, E.C., May, R.M. & Harvey, P.H. (1994) Extinction rates can be estimated from molecular phylogenies. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences*, 344, 77–82.

Newbold, T., Hudson, L.N., Contu, S., Hill, S.L.L., Beck, J., Liu, Y. et al. (2018) Widespread winners and narrow-ranged losers: Land use homogenizes biodiversity in local assemblages worldwide. *PLoS Biology*, 16, e2006841.

Orzechowski, E.A., Lockwood, R., Byrnes, J.E.K., Anderson, S.C., Finnegan, S., Finkel, Z.V. et al. (2015) Marine extinction risk shaped by trait-environment interactions over 500 million years. *Global Change Biology*, 21, 3595–3607.

Pearson, P.N. (1995) Investigating age-dependency of species extinction rates using dynamic survivorship analysis. *Historical Biology*, 10, 119–136.

Pigot, A.L., Owens, I.P.F. & Orme, C.D.L. (2012) Speciation and extinction drive the appearance of directional range size evolution in phylogenies and the fossil record. *PLoS Biology*, 10, e1001260.

Pigot, A.L., Phillimore, A.B., Owens, I.P.F. & Orme, C.D.L. (2010) The shape and temporal dynamics of phylogenetic trees arising from geographic speciation. *Systematic Biology*, 59, 660–673.

Pyron, R.A. & Burbrink, F.T. (2012) Extinction, ecological opportunity, and the origins of global snake diversity. *Evolution*, 66, 163–178.

Quental, T.B. & Marshall, C.R. (2013) How the Red Queen drives terrestrial mammals to extinction. *Science*, 341, 290–292.

Quintero, I. & Jetz, W. (2018) Global elevational diversity and diversification of birds. *Nature*, 555, 246–250.

Rabosky, D.L. (2009) Ecological limits and diversification rate: alternative paradigms to explain the variation in species richness among clades and regions. *Ecology Letters*, 12, 735–743.

Rabosky, D.L. & Benson, R.B.J. (2021) Ecological and biogeographic drivers of biodiversity cannot be resolved using clade age-richness data. *Nature Communications*, 12, 2945.

Raup, D.M. (1986) Biological extinction in earth history. *Science*, 231, 1528–1533.

Raup, D.M. (1994) The role of extinction in evolution. *Proceedings of the National Academy of Sciences of the Unites States of America*, 91, 6758–6763.

Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A.M., Bernard, R. et al. (2017) The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nature Ecology & Evolution*, 1, 1677–1682.

Rosenblum, E.B., Sarver, B.A.J., Brown, J.W., Des Roches, S., Hardwick, K.M., Hether, T.D. et al. (2012) Goldilocks meets Santa Rosalia: an ephemeral speciation model explains patterns of diversification across time scales. *Evolutionary Biology*, 39, 255–261.

Roy, K., Hunt, G. & Jablonski, D. (2009) Phylogenetic conservatism of extinctions in marine bivalves. *Science*, 325, 733–737.

Rundell, R.J. & Price, T.D. (2009) Adaptive radiation, nonadaptive radiation, ecological speciation and nonecological speciation. *Trends in Ecology & Evolution*, 24, 394–399.

Schluter, D. (2000) *The ecology of adaptive radiation*. Oxford, UK: Oxford University Press.

Schmidt, J.P., Davies, T.J., Farrell, M.J. (2021) Opposing macroevolutionary and trait-mediated patterns of threat and naturalisation in flowering plants. *Ecology Letters*, 24, 1237–1250.

Smits, P.D. (2015) Expected time-invariant effects of biological traits on mammal species duration. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 13015–13020.

Stanley, S.M. (1979) *Macroevolution, pattern and process*. San Francisco: W. H. Freeman.

Stanley, S.M. (1990) The general correlation between rate of speciation and rate of extinction: fortuitous causal linkages. In: Ross, R.M. & Allmon, W.D. (Eds.) *Causes of evolution: a paleontological perspective*. Chicago, IL: University of Chicago Press, pp. 103–172.

Staude, I.R., Navarro, L.M. & Pereira, H.M. (2020) Range size predicts the risk of local extinction from habitat loss. *Global Ecology and Biogeography*, 29, 16–25.

Stein, R.W., Mull, C.G., Kuhn, T.S., Aschliman, N.C., Davidson, L.N.K., Joy, J.B. et al. (2018) Global priorities for conserving the evolutionary history of sharks, rays and chimaeras. *Nature Ecology & Evolution*, 2, 288–298.

Stigall, A.L. (2014) When and how do species achieve niche stability over long time scales? *Ecography*, 37, 1123–1132.

Tanentzap, A.J., Igea, J., Johnston, M.G. & Larcombe, M.J. (2020) Does evolutionary history correlate with contemporary extinction risk by influencing range size dynamics? *The American Naturalist*, 195, 569–576.

Tonini, J.F.R., Beard, K.H., Ferreira, R.B., Jetz, W. & Pyron, R.A. (2016) Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. *Biological Conservation*, 204, 23–31.

Uetz, P., Freed, P. & Hošek, J. (2020) The reptile database. http://www.reptile-database.org

Upham, N.S., Esselstyn, J.A. & Jetz, W. (2019) Inferring the mammal tree: species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLoS Biology*, 17, e3000494.

van Valen, L. (1973) A new evolutionary law. *Evolutionary Theory*, 1, 1–30.

Verde Arregoitia, L.D., Blomberg, S.P. & Fisher, D.O. (2013) Phylogenetic correlates of extinction risk in mammals: species in older lineages are not at greater risk. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20131092.

Weedop, K.B., Mooers, A.Ø., Tucker, C.M. & Pearse, W.D. (2019) The effect of phylogenetic uncertainty and imputation on EDGE scores. *Animal Conservation*, 22, 527–536.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Greenberg, D.A., Pyron, R.A., Johnson, L.G.W., Upham, N.S., Jetz, W. & Mooers, A.Ø. (2021) Evolutionary legacies in contemporary tetrapod imperilment. *Ecology Letters*, 24, 2464–2476. https://doi.org/10.1111/ele.13868