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Does evolutionary history correlate with contemporary extinction risk by

influencing range size dynamics?

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ABSTRACT

Extinction threatens many species, yet is predicted by few factors across the plant Tree of Life (ToL). Taxon age is one factor that may associate with extinction if occupancy of geographic and adaptive zones varies with time, but evidence for such an association has been equivocal. Age-dependent occupancy can also influence diversification rates and thus extinction risk where new taxa have small range and population sizes. To test how age, diversification, and range size were correlated with extinction, we analyzed 639 well-sampled genera representing 8,937 species from across the plant ToL. We found a greater proportion of species were threatened by contemporary extinction in younger and faster-diversifying genera. When we directly tested how range size mediated this pattern in two large, well-sampled groups, our results varied. In conifers, potential range size was smaller in older species and was correlated with higher extinction risk. Age on its own had no direct effect on extinction when accounting for its influence on range size. In palm species, age was neither directly nor indirectly correlated with extinction risk. Our results suggest range size dynamics may explain differing patterns of extinction risk across the ToL with consequences for biodiversity conservation.

Introduction

Some species are at greater risk of contemporary extinction than others (Bennett and Owens 1997; Purvis et al. 2000; Vamosi and Wilson 2008). By definition, species are threatened by extinction when their geographic range or population size is small and fragmented or undergoing relatively large declines (IUCN 2018). In addition to traits that promote small ranges and populations, such as those associated with life history and resource use, evolutionary history may influence extinction risk (ER) (Bennett and Owens 1997; Purvis et al. 2000). Previous work in birds (Gaston and Blackburn 1997) and marsupials (Johnson et al. 2002) found that species in older lineages were more threatened by extinction, while non-lemur primates showed the reverse pattern (Arregoitia et al. 2013). The only study on land plants, to our knowledge, found a higher ER for younger, rapidly diversifying clades in South Africa (Davies et al. 2011).

The amount of time elapsed since a taxon originated (hereafter "taxon age") can explain why extinction is non-randomly distributed across the Tree of Life (ToL) because it influences, among other factors, range size dynamics. For example, the age-and-area hypothesis proposes that older taxa have had more time to disperse across a greater range (Willis 1926; Paul et al. 2009; Ceolin and Giehl 2017). This idea leads to our prediction **P1**: older taxa may have larger ranges that make them less threatened by extinction. While the association between age and range size may weaken over millions of years as taxa become less dispersal-limited, younger taxa may encounter less available space and resources as niches fill through time irrespective of dispersal ability (Tanentzap et al. 2015). A negative age-extinction correlation can conversely arise if older taxa become maladapted as environments diverge from past selection regimes (Wilson 1959; Žliobaitė et al. 2017), limiting the range of habitats they can occupy (Slatyer et al. 2013). This idea leads to our prediction **P2**: older species may have smaller ranges that make them more threatened by extinction and thereby persist over long time periods in refugia or by having large local populations (Williams et al. 2009). Importantly, **P1** and **P2** are not mutually exclusive and may both operate in the same lineage, resulting in no age-extinction correlation, or occur in different groups and result in mixed results across different levels in the ToL.

The association between age and extinction is likely to scale from species to clades. For the same reason that older species may face less extinction (i.e. **P1**), older clades can include fewer species with small ranges (Tanentzap et al. 2014), especially if they arose by centrifugal or peripatric speciation. Following these modes of speciation, if differences in the range sizes of ancestral and daughter species diminish as more time elapses for range expansion (Anacker and Strauss 2014), then the proportion of species in a clade that are threatened by extinction should decrease with taxon age as predicted by **P1**. Relatedly, rapidly diversifying clades should have proportionally more taxa at risk of extinction (Davies et al. 2011; Greenberg and Mooers 2017). New taxa tend to have small range and population sizes, especially if speciation starts from small reproductively isolated populations that occupy narrow adaptive spaces (Valente et al. 2010; Castiglione et al. 2017). Thus, our prediction **P3** is that clades with more species arising (e.g. faster diversification) should face a greater ER (Schwartz and Simberloff 2001).

Here we tested how taxon age and diversification rate were associated with ER in plants and whether this was mediated by range size. Our approach incorporated two taxonomic scales. First, we analyzed genus-level age-extinction correlations to maximize sampling breadth across the plant ToL. We combined the largest time-calibrated phylogenetic tree presently estimated for vascular plants (Zanne et al. 2014) with all available peer-reviewed assessments of contemporary ER from the IUCN *Red List* (2018). Reliable taxon age estimates require sampling a large proportion of closely-related taxa (e.g. $\geq 60\%$ of congeneric species or confamilial genera for species and genus age estimates, respectively; Appendix A1, fig. A1). Only 483 species in 116 genera had ER data and met this sampling criteria at the species-level versus 639 genera representing 8,937 species at the genus-level, so we focused on the latter. Focusing on contemporary ER also allowed us to explore the association with present-day geographic distribution data to test explicitly how range size might influence age-extinction correlations predicted by **P1** and **P2**. We performed these analyses at the species-level for two large, ancient, and widespread plant clades (conifers and palms). These analyses allowed us to address concerns around estimating divergence times from the larger but under-sampled phylogenetic tree and ER from incompletely sampled genera.

Methods

Genus-level data

We first selected genera for which we could confidently estimate the time of divergence from their sister genera, i.e. 'stem age'. We used stem ages to estimate taxon age because they only require one species to be sampled within each genus and reflect the entire evolutionary history of clades, unlike crown ages that can have young age biases because they consider only extant species (Scholl and Wiens 2016). Species ages were also generally captured by genus ages (fig. A2), allowing us to use genera to characterize taxa (i.e. groups of organisms) with different ages and levels of ER to test **P1** and **P2**. Genera were selected from the time-calibrated, species-level phylogenetic tree of land plants from Qian and Jin (2016), which updates Zanne et al. (2014). Taxa outside of the subclade for each genus that contained \geq 50% of all species were removed prior to calculations using *MonoPhy* in R v3.4 (Schwery and O'Meara 2016). Selected genera

came from densely sampled clades (i.e. families) to circumvent low sampling across the broader tree. For each family, we calculated the proportion of sampled genera in the phylogeny from *taxonlookup* v1.1.1 (Pennell et al. 2016) and retained those with \geq 60% coverage. We explored the trade-off between sampling coverage and error with a simulation study, which showed no substantial errors in the age estimates with our applied threshold (Appendix A, fig. A1).

After age estimation, we collated 25,452 Red List assessments of ER. We classified ER in extant species using higher-level Red List categories, and only considered species to be threatened by extinction from small range sizes (i.e. meeting at least Criterion B or D2 of IUCN 2018). Species were consequently classified as either "lower risk" (includes lower-level categories of "least concern" and "near threatened") or "threatened" (includes lower-level categories of "vulnerable", "endangered", and "critically endangered"). This approach can be more robust to uncertainty in lower-level species categories (Mounce et al. 2018), and more readily interpretable at the clade-level by resolving to proportions of species in one as opposed to five different categories. We then calculated the proportion of species in each genus classified as "threatened" by extinction as opposed to facing "lower risk" (hereafter non-threatened). We restricted our analysis to genera where ≥20% of species were assessed for ER. Overall, 639 genera had both reliable age and ER data spanning 4,962 IUCN species-level assessments.

We also estimated net diversification rates for 494 genera to test **P3**. We excluded 145 monotypic genera because these would confound our analyses as they all had the same diversification rate irrespective of taxon age. We used a well-established method-of-moments estimator that assumed diversification rates were constant over time within genera given a known stem age and species richness (Magallon and Sanderson 2001). Following standard

practice, we assumed relative extinction ε of 0.0, 0.5 and 0.9 (Magallon and Sanderson 2001). All taxonomy was standardized to The Plant List nomenclature.

Clade-level data

We repeated our data assembly for two large clades that were well-sampled at the species-level in separate time-calibrated phylogenies. These clades included 81% of all 651 accepted Pinales (extant conifers) (Leslie et al. 2018) and all 2,539 Arecaceae (palms) (Faurby et al. 2016). The conifer topology was estimated using maximum-likelihood, with bootstrapped support of all internal nodes reported in supplementary information of Leslie et al. (2018). No topological or divergence time uncertainty information were available in Leslie et al. (2018). We therefore constrained our analysis to only those tips derived from nodes with a bootstrap support of \geq 90%. By contrast, the palm tree was estimated using Bayesian inference, and so we repeated our analyses across a posterior distribution of 1,000 phylogenetic trees available in Faurby et al. (2016). We used palm phylogenies based on Govaerts taxonomy, as recommended in Faurby et al. (2016). We then combined ERs of the two clades from the IUCN (2018) with species stem ages.

We also assembled range data for our two large clades. Georeferenced records with no flagged issues were downloaded from the Global Biodiversity Information Facility (www.gbif.org). Conifer data were supplemented by published records absent from GBIF (see list of sources in Appendix A). All duplicate and spatially invalid records (e.g. non-numerical, exceeding global extent, located in ocean, urban areas, or country centroids) were removed with the R package *sampbias* (https://github.com/azizka/sampbias). As species occur in many more

areas than recorded in GBIF, we estimated potential range size with a mechanistic species distribution model (SDM) that predicted the physiological tolerances of species for growth from distribution data (Higgins et al. 2012). Absence points for the SDM were generated using standard approaches and we took steps to minimize falsely inflating species ranges (details in Appendix A). We then summed the number of equal-area (Mollweide projected) 0.25 decimal degree grid cells occupied by each species. We found no evidence that sampling varied systematically with species age in a way that would bias our subsequent analyses (table S1).

Statistical analyses

We separately tested whether genera with a greater proportion of threatened taxa were correlated with younger ages and faster diversification rates (i.e. **P1-P3**) using phylogenetic least squares (PGLS) regression. Although the least squares model assumed normally distributed errors, and the response variable was a proportion with binomial errors, it is still appropriate for testing the null hypothesis of no statistically significant effect of an independent variable (Warton and Hui 2011). Repeating our analysis with an angular transformation of the proportions made no difference to our results (table A1). We also fitted the PGLS regression using the *gls* function in R because this approach, unlike other functions that incorporate phylogenetic information (e.g. *phyloglm*), could account for different sample sizes across genera by weighting observations with the inverse square-root of the proportion of species assessed by the IUCN (Garamszegi and Møller 2010). Following standard practice, the PGLS was fitted with maximum-likelihood transformations of branch lengths based on the strength of phylogenetic covariance estimated by Pagel's λ (Orme 2013). Ages and diversification rates were log-transformed to reduce right

skew and approach normality. Models were not fitted with both predictors simultaneously as parameter estimates were highly correlated (r = 0.74-0.88 depending on ε). We repeated the analysis in conifers and palms, and again did not simultaneously fit age and diversification rates given correlations in parameter estimates (r = 0.52-0.93 and 0.53-0.79, respectively; values for palms are medians across the posterior at each ε).

For conifers and palms, we also tested whether ER was associated with younger species and how this was influenced by range size to test **P1** and **P2**. We used phylogenetic path analysis from the *phylopath* R package to fit three models that described a hypothesized network of causal linkages for each group (van der Bijl 2018). First, we tested a model where age influenced ER indirectly by changing range size. We thus fitted a logistic regression model to ER as a function of species age using penalized maximum-likelihood and accounted for phylogenetic non-independence of species with the *phylolm* R package (Ho et al. 2014). We used PGLS to test whether older ages correlated with larger potential range sizes. Second, we tested a model where both species age and range size directly influenced ER using phylogenetic logistic regression. Finally, we tested a model where only range size influenced extinction without any direct or indirect effect of age. We then averaged across the three models to estimate standardized path coefficients. Weighting was performed with the C-statistic information criterion corrected for small sample sizes (CICc) for all models with a CICc of <2from the best-supported model (van der Bijl 2018). For palms, model averaging was performed for each of the 1,000 phylogenetic trees in the posterior distribution obtained from Faurby et al. (2016) and the corresponding estimates pooled. Explained variance was calculated for all models as recommended by Ives (2019).

Results

We found that relatively more species were threatened by contemporary extinction in fasterdiversifying genera (for ε of 0.0, 0.5, 0.9: $t_{492} = 4.46$, 4.45, 4.30, respectively; p < 0.001 for all). The mean proportion of species in a genus threatened by extinction more than quintupled from 10% to 54% between the slowest and fastest diversifying genera (fig. 1a). We also found genus age was negatively associated with ER ($t_{637} = -3.38$, p = 0.001; fig. 1b). A caveat is that we found some bias in our dataset. Sampled genera were older, slower diversifying, and less threatened, on average, than obtained by applying our sampling criteria to the initial tree (i.e. before intersecting with ER; table S2), but the proportions of both genera sampled in each family and species in each genus threatened by extinction were uncorrelated ($t_{128} = -1.92$, p = 0.058). Repeating our analyses at the genus-level with the more complete conifer and palm datasets revealed no age-extinction associations, unlike the positive plant-wide correlation (table S3), potentially because of small sample sizes (fig. S1). Many conifer genera were instead highly threatened despite being old and slowly diversifying (fig. S2). In palms, faster diversifying genera were more threatened by extinction, consistent with the plant-wide findings (table S3).

In contrast to our finding across the plant ToL, analyses with the more complete specieslevel datasets revealed that older conifers but not palms were associated with greater ER (fig. 2, 3a). The path analysis suggested that this correlation arose because older conifers were associated with smaller range sizes rather than age having a direct effect on ER (fig. 2). Consequently, the mean probability of being threatened by extinction increased by 61% in the oldest relative to youngest conifer species (fig. 3). These findings were supported by a separate analysis of selected sister species pairs with contrasting ER, which controlled for systematic differences in the ages of these two groups (Appendix C). Our results with conifers and palms

were also not simply an artefact of biased sampling as ages and rates did not markedly differ from observations across entire clades, i.e. before filtering with IUCN data (table S4).

Discussion

Our study supports the idea that taxon age may explain the non-randomness of extinction risk (ER) across the ToL by influencing range size dynamics. We found younger and fasterdiversifying genera had greater ER across the wider plant ToL, supporting P1 and P3 respectively. In contrast, older conifers had smaller ranges and were indirectly associated with greater ER because of a negative range-ER correlation, supporting P2. In palm species, age was not correlated with ER or range size. Although our findings across plant genera contrasted with those in conifer and palm species, they were consistent with the age-and-area hypothesis in at least two ways. First, young species tend to occupy narrower geographic and adaptive spaces (Castiglione et al. 2017), likely because most plant speciation involves vicariance (Davies et al. 2011; Anacker and Strauss 2014; Igea et al. 2015). Time may consequently be required for postspeciation range expansions and reductions in genus-wide ER despite much of the available area remaining favorable for establishment (Pigot et al. 2010; Pigot and Tobias 2013; Anacker and Strauss 2014). Second, if species diversification is density-dependent, such as because of limited resources (Rabosky and Hurlbert 2015), then younger lineages that diversify faster and produce more young species within initially small geographic and adaptive spaces will have elevated ER. This result provides new evidence that lineages span a continuum from little species turnover to fast diversifying and extinction-prone (Greenberg and Mooers 2017). Time-dependent range expansions may be unnecessary under other modes of speciation, e.g. parapatry or sympatry

(Pigot et al. 2010), and if range expansion is not limited post-speciation (Schurr et al. 2007). Differences in speciation modes can also help explain the lack of consistent evidence for agedependent extinction across the large taxonomic scale in our study and across animals (Gaston and Blackburn 1997; Johnson et al. 2002; Davies et al. 2011; Arregoitia et al. 2013; Greenberg and Mooers 2017).

The historical biogeography of conifers differs from palms and other plant clades, potentially explaining why older species had smaller ranges that could make them more threatened by extinction. Conifers originally evolved at high latitudes during warmer wetter climates (Farjon 1996; Liu et al. 2007). As these habitats became more temperate, the traits of older taxa may have diverged from their environment and restricted range sizes (Leslie et al. 2012; Pittermann et al. 2012), contributing to a negative age-range correlation (i.e. P2). Old species may have only escaped extinction by inhabiting climatic refugia (Leslie et al. 2012; Condamine et al. 2017). Cycadales, which are closely related to conifers, have undergone similar range contractions because of global cooling, resulting in presently high extinction risk (Yessoufou et al. 2017). By contrast, palms occupy more tropical habitats that have been larger and more climatically stable since the Eocene (Kissling et al. 2012). Tropical clades may therefore depend less on time to expand their ranges, explaining the lack of support for P1. Speciation in palms may have also largely involved long-distance dispersal (Baker and Couvreur 2013), which can produce less range asymmetry (Gaston 1998). Consequently, palms may lack age-range associations that influence ER. We also cannot exclude the possibility that palm species that were susceptible to environmental change have already gone extinct or traits that increase extinction risk are not taxonomically conserved, resulting in no signature of taxon age on extinction (Arregoitia et al. 2013).

At least four sources of bias may have affected our analyses. First, accurate estimates for our definition of taxon age depend on phylogenetic trees with few unsampled extant/extinct taxa and lineage-splitting accompanying speciation. While virtually all large-scale macroevolutionary studies will be prone to the "known unknowns" of both extinction and speciation without lineage-splitting, our sensitivity analyses indicated that we did not strongly over-estimate ages in incompletely sampled groups. Our sampling coverage produced relatively accurate estimates of taxon age (i.e. <15% error for inter-quartile range), with error likely negligible for most genera (n = 266/494) with $\geq 80\%$ sampling coverage (Appendix A). Second, contemporary ER estimates can be heavily influenced by factors that have mostly emerged over the past century, such as local habitat loss and climate change. However, despite these drivers differing from those in the paleontological record, the same traits, such as geographic range size, may predispose lineages to both ancient and modern extinctions (McKinney 1997). Therefore, extant species with high contemporary ER can also have faced high ER throughout their history (Greenberg and Mooers 2017). This assumption could be further strengthened by comparing contemporary and phylogenetic (i.e. macroevolutionary) estimates of extinction, but the methods for generating the latter remain controversial (Rabosky 2010). Third, the SDM could have falsely inflated ranges of young species that have not yet dispersed into available niche space (Pearson and Dawson 2003; Kearney and Porter 2009), though we took steps to minimize this concern (Appendix A). Finally, we used higher-level Red List classifications that ignore variation in ER within the threatened and non-threatened categories. However, it has been argued that much of the variation in the lower-level categories can be attributed to classification error rather than meaningful biological differences (Mounce et al. 2018).

The association between extinction and both taxon age and diversification rate may ultimately help inform biodiversity conservation. Specifically, these associations might make it easier to derive or refine contemporary ER estimates. Taxon age and diversification rate might also offer insight into the vulnerability of species to future change, as the range size that makes a species prone to extinction is likely to be carried into the future (Condamine et al. 2013). Although the genus-level results differed from conifer and palm species, they included a larger portion of the plant ToL and so may represent a general pattern. More generally, our results implicate range size in explaining different patterns of extinction risk in plants and thereby emphasize its importance for biodiversity conservation.

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Data Accessibility

Data and R code to perform our analyses are deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.k0p2ngf3z.

Appendix A – Additional methodological details

Sensitivity of genus age estimates to family-level sampling coverage

There is no specific threshold for taxon sampling that must be satisfied in phylogenetic analyses. Rather, the goal of any study should be to balance sample size against error in divergence time and diversification rate estimates. We therefore performed a simulation study to test the sensitivity of different family-level sampling coverage on estimates of genus age. Our approach was to select 17 non-monotypic families for which 100% of genera were sampled in the Qian and Jin (2016) tree, and so we were confident that we could recover accurate genus stem ages. There was a median of 6 genera (range: 4 to 17) and 91 (16 to 836) species per family for the subset groups. We then separately subset each family to between 10 to 90% of the original genera, at random, and re-calculated genus stem ages. We repeated this sampling 50 times for each 10% interval in sampling coverage, and calculated the relative difference between the subset ages and those estimated when sampling coverage was 100%. We found that ages were recovered with negligible error (i.e. inter-quartile range was <15%) when \geq 60% of genera in our focal families were sampled (fig. A1).

Estimating potential ranges

Our approach uses the Thornley Transport Resistance (TTR) model of plant growth to estimate the niche traits that match the observed distribution of species (Higgins et al. 2012). The TTR model is an ordinary differential equation model that considers how plant growth is influenced by carbon uptake, nitrogen uptake, and the allocation of carbon and nitrogen between roots and shoots (Thornley 1998). It explicitly separates the physiological processes of resource uptake from biomass growth. The implementation by Higgins *et al.* (2012) relates the uptake and growth processes to environmental forcing variables to predict the potential biomass of an individual plant at each site. Specifically, the model considers how carbon uptake might be limited by temperature, soil moisture, solar radiation, and shoot nitrogen; nitrogen uptake might be limited by temperature, soil moisture, and soil nitrogen; and growth and respiration loss might be influenced by temperature. The model runs on a monthly time step, which allows it to explicitly consider how seasonal fluctuations in the forcing variables interactively influence plant resource uptake and growth. Higgins *et al.* (2012) provide a full description of the model and its assumptions.

We used the cleaned presence dataset described in the main text to identify locations where species occurred. Several methods exist for simulating absence points (often called pseudoabsence points), but the choice is regarded as a relatively small source of error (Barbet *et al.* 2012). Our method balanced the number of presence and absence points and stratified the selection of absence points by environment types. To define environment types, we used a partitioning algorithm *clara* (Kaufman and Rousseeuw 2009) to classify the TTR input variables into 25 environmental zones. We further restricted the selection of absence points to the zoological realm(s) taken from the WWF map in the R package *rworldmap* where the species occurred and to distances >0.25 km from the presence points. This approach helped to ensure that a representative range of environmental zones were included in the absence samples and that they were selected within a dispersal zone that was reachable on an ecological time scale (i.e. the zoological realms). We also restricted projection of potential ranges to the subset of the 25 environmental zones present in each species' occurrence dataset (see above). As biotic interactions and dispersal limitation prevent species occupying the full extent of their potential

range, this restriction prevents predictions beyond the data domain used for estimating the model parameters.

We used the differential evolution optimization algorithm of Ardia *et al.* (2011) to estimate the set of model parameters that maximized the likelihood of each species' distribution across all sites. Following Higgins *et al.* (2012), we assumed that the probability of a species p_i occurring at site *i* was described by the complementary log–log of the modelled plant biomass at site *i*. The likelihood of observing the presence-absence data at site *i* could then described by a Bernoulli distribution. Model fits were evaluated by examining the confusion matrix that compares the number of true positives, true negative, false positives and false negatives, with particular weight given to the false negative rate, i.e. instances where the model predicts the species to be absent but it is actually present. All the species that were retained in the final model had suitable fits (data available at <u>https://doi.org/10.5061/dryad.k0p2ngf3z</u>; Tanentzap et al. 2019).

List of sources for georeferenced conifer records

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Table A1. Angular transformation does not change correlations between extinction risk (ER)

 and either diversification rate or genus age.

	Untransform	ned	Arcsine transformed		
Predictor of ER	Mean slope (SE)	<i>p</i> -value	Mean slope (SE)	<i>p</i> -value	
Diversification rate ($\varepsilon = 0.0$)	0.06 (0.01)	< 0.001	0.06 (0.02)	0.001	
Diversification rate ($\varepsilon = 0.5$)	0.06 (0.01)	< 0.001	0.06 (0.02)	0.002	
Diversification rate ($\varepsilon = 0.9$)	0.05 (0.01)	< 0.001	0.04 (0.02)	0.009	
Genus age	-0.05 (0.01)	0.001	-0.07 (0.02)	0.002	

Note: We refitted the four PGLS regressions predicting the proportion of taxa in a genera threatened by extinction after an arcsine transformation of the response variable to ensure our analysis was robust to using untransformed values. Reassuringly, there was little difference in the mean slopes, standard errors (SE), and statistical significance of model predictors.

[Figure A1 goes here]

[Figure A2 goes here]

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Figure Legends

Figure 1. More species are threatened by extinction in (**a**) faster-diversifying and (**b**) younger genera. Diversification was estimated for $\varepsilon = 0.50$. Solid lines are mean associations estimated by PGLS. Mean standardized slopes (± standard error) were 0.06 (0.01) and -0.05 (0.01) and $R^2 = 0.10$ and 0.08 in (**a**) and (**b**), respectively.

Figure 2. Phylogenetic path analysis of putative causal linkages between species age, range size, and extinction risk. The model was fitted separately for conifers (n = 138) and palms (n = 455). Path thickness proportional to mean standardized effect (\pm standard error) estimated from model averaging and pooling errors in the case of palms (see fig. S3). Dashed paths were not statistically significant. R^2 s reported for modelled responses. As extinction risk was estimated with a logistic model, corresponding R^2 s were based on likelihood ratios between full and intercept-only models and were not directly comparable with those calculated for PGLS based on explained variance (Ives 2019).

Figure 3. Older conifers but not palms have a greater probability of being threatened by extinction. (a) Boxplot for stem ages of conifer (white, n = 138) and palm (grey, n = 455) species that were classified as either threatened or non-threatened. Solid line is median, box is inter-quartile range, whiskers extend 1.5-times the interquartile range, and points are outliers. For palms, we plotted the mean age for each species estimated across 1,000 phylogenetic trees. (b) Change in probability of a conifer being classified as threatened with species age. Solid line is mean effect \pm 95% confidence interval of species age estimated by model-averaging of

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phylogenetic logistic regressions fitted within a path analysis framework. Rugs are observations of individual species either threatened or non-threatened by extinction.

Figure A1. Error in estimates of genus age becomes negligible when at least 60% of genera in a family are sampled. Solid horizontal lines are medians, with boxes denoting inter-quartile range, and lines denoting 90% confidence intervals from 50 simulations at each level of taxon sampling. Each simulation subset each of 17 families and compared the corresponding genus ages to estimates when groups were complete (i.e. 100% coverage).

Figure A2. Species ages are closely associated with genus ages in 4,139 species that come from relatively well-sampled (i.e. >60% coverage) genera or families (if monotypic genera). Sampling points were selected before intersecting ages with IUCN extinction risk data. Pearson's correlation coefficient r = 0.69.



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Figure A2





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ONLINE SUPPLEMENTARY MATERIAL

Does evolutionary history correlate with contemporary extinction risk by influencing range size dynamics?

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Text S1 – Additional analysis of sister species

To further analyse how potential range size was associated with species age and test P1 and P2, we undertook an additional comparison that focused on pairs of sister species with contrasting extinction risk. Focusing on sister pairs was desirable because it can minimize factors that confound direct age-range associations, such as unobserved extinctions (Hodge and Bellwood 2015). We expected both the potential increase in range size with more time for dispersal and expansion predicted by P1 and the potential decline in the adaptiveness and thus range size with time predicted by P2 would be weaker in species threatened by extinction (i.e. flatter slopes in fig. S4). Our reasoning was that smaller ranged species should have fewer opportunities for range expansion and contraction and so should change proportionally less.

We first identified all sister species pairs in the conifer and palm phylogenies used in the main text for which extinction risk was known for each species. Consequently, we retained only those conifer tips derived from nodes with \geq 90% bootstrap support and separately analysed each of the 1,000 posterior palm phylogenies. For each pair, we then calculated the difference in potential range size between sister species pairs with variable extinction risk (i.e. one was non-threatened and the other threatened) and correlated this value with their age. In conifers, we tested if this correlation between age and range asymmetry was different from randomly sampling the same number of sister pairs, but choosing those where both members of the pair were non-threatened, because most identical species pairs fell into this category (i.e. 23/25). We repeated the random sampling 1,000 times as there were many more pairs with identical than contrasting extinction risk: 23 vs 8, respectively. In palms, there were more pairs with contrasting than identical extinction risk (median ratio across posterior distribution of trees: 2.0, 95% CI: 1.3-3.1), so we could not subsample the latter group as in conifers. We instead tested if the absolute correlation between age and range asymmetry in pairs of contrasting extinction risk was larger than the absolute correlation when both sister pairs were non-threatened across all samples in the posterior tree. Reassuringly, the range size of non-threatened conifers in our contrasting pairs did not differ from the values of sister species that had the same extinction risk, supporting their use as "control" contrasts (test: $t_{52} = -0.95$, p = 0.347). We found the same result when comparing the range size of palm species that were threatened by extinction in sister pairs with contrasting extinction risks to the range size of palms in pairs where both species were threatened by extinction (median: t = 1.32, df = 78, p = 0.190; 95% CI: t = -0.33 to 2.77, df = 60 to 89, p = 0.007 to 0.890).

A smaller potential range size increased the extinction risk of older conifers, supporting **P2**. We specifically found that non-threatened conifers had narrower ranges as their age increased relative to sister species that were threatened (fig. S5). As the age of conifers increased, this difference between sister-species pairs of contrasting extinction risk was larger than expected if sisters had the same extinction risk (r = -0.63, p = 0.031; n = 8, fig. S5). We found comparable results when we subset to the sister pairs that also came from genera with >90% sampling (r = -0.57, p = 0.007, n = 7). Contrasting extinction risk did not alter correlations between age and potential range size in palms, consistent with the lack of an age-extinction association (median: r = -0.01, 95% CI = -0.35 to 0.36, p = 0.603).

Reference

Hodge, J., and D. R. Bellwood. 2015. On the relationship between species age and geographical range in reef fishes: are widespread species older than they seem?Global Ecology and Biogeography 24:495–505.

Table S1. No evidence of an age bias in geospatial records. We predicted the number of occurrences in GBIF from each species' extinction risk and age using PGLS in conifers (n = 138) and palms (n = 455). Rows are mean estimates (standard error, SE) for the effects of being threatened relative to non-threatened by extinction (i.e. change in intercept), species age, and change in the species age slope for species threatened by extinction (i.e. age × extinction risk interaction). Bolded values denote statistically significant effects.

	Conifers			Palms		
Effect	Mean	t	р	Mean	t	р
	estimate (SE)			estimate (SE)		
Threatened	-1.21 (0.25)	-4.93	<0.001	<0.01 (0.14)	0.02	0.985
Species age	0.03 (0.30)	0.10	0.921	0.01 (0.10)	0.13	0.897
Age \times threatened	-0.17 (0.23)	-0.73	0.465	0.03 (0.14)	0.23	0.819

Table S2. Sampling biases in genus-level datasets. We compared the dataset that was intersected with IUCN risk assessments and filtered for high sampling coverage (n = 494) with a dataset of genus-level characteristics derived from applying our sampling criteria to the full genus-level phylogeny derived from Qian and Jin (2016), i.e. before intersecting with extinction risk (n = 2,466). We also compared our filtered data with the percent of species threatened in each genus when we did not filter for high sampling coverage and only IUCN criteria (n = 1,403). For each dataset, we report the mean ± standard error, and compared means either with two sampled *t*-tests or Wilcoxon rank sum tests, denoted by *, where data were not normally-distributed. df = degrees of freedom for *t*-tests. Bolded parameters indicate statistically significant differences.

Parameter	Filtered data	Unfiltered data	t / W^*	df	p
Log genus age	2.76 ± 0.06	2.57 ± 0.02	3.19	2,958	0.001
Log species per genus	2.03 ± 0.05	2.37 ± 0.03	532,4	480*	< 0.001
Log diversification rate ($\varepsilon = 0.5$)	-2.56 ± 0.06	-2.23 ± 0.03	-4.84	2,958	< 0.001
Percent threatened species	$36 \pm 2\%$	$41 \pm 1\%$	371,	360*	0.015

Table S3. Faster diversifying genera were more threatened by extinction in palms with no correlations in conifers. We separately correlated net diversification rates and genus age with the proportion of species that were threatened by extinction in 40 conifer and 59 palm genera using PGLS (for genus age analysis, n = 68 and 78, respectively). Net diversification rates were calculated with relative extinction ε of 0.0, 0.5, or 0.9. For palms, we repeated analyses for 1,000 phylogenetic trees, and so report medians from across this posterior distribution.

	= 3	0.0	= 3	0.5	= 3	0.9	А	ge
Group	t	р	t	р	t	р	t	р
Conifers	-1.30	0.203	-1.50	0.142	-1.71	0.095	-0.66	0.510
Palms	2.49	0.013	2.58	0.011	2.70	0.008	-0.43	0.495

Table S4. Sampling biases in species-level datasets. We compared the dataset that was intersected with IUCN risk assessments with a dataset of species- and genus-level characteristics derived from the complete clade phylogenies, i.e. prior to intersecting with extinction risk. For each dataset, we report the mean \pm standard error, and compare means either with two sampled *t*-tests or Wilcoxon rank sum tests, denoted by *, where data were not normally-distributed. df = degrees of freedom for *t*-tests. Bolded values indicate statistically significant differences; for palms, determined from the median of *p*-values across the posterior distribution of phylogenetic trees.

Parameter	Filtered data	Unfiltered data	t / W*	df	р
Conifers					
Log species age	1.46 ± 0.06	1.47 ± 0.06	-0.07	869	0.946
Log genus age	2.75 ± 0.16	2.88 ± 0.17	-0.55	81	0.581
Log species per genus	1.98 ± 0.17	2.15 ± 0.19	-0.63	81	0.528
Log diversification rate ($\varepsilon = 0.5$)	-2.57 ± 0.14	-2.62 ± 0.14	0.26	81	0.793
Palms					
Log species age	0.79 ± 0.06	0.59 ± 0.03	-2.89	2,992	0.005
Log genus age	2.07 ± 0.11	2.13 ± 0.08	0.42	186	0.664
Log species per genus	1.73 ± 0.12	2.06 ± 0.10	3,20	52*	0.115
Log diversification rate ($\varepsilon = 0.5$)	-2.05 ± 0.12	$\textbf{-1.93}\pm0.08$	-0.86	186	0.393

Figure S1. Power analysis of association between extinction risk and diversification rate. We used the dataset of 494 genera with high-quality divergence time estimates and IUCN data. We sampled between 25 and 400 genera at a time, repeating each sampling intensity 100 times at random. For each replicate, we fitted the same PGLS model described in the main text and extracted the *p*-value associated with the effect of diversification rate on extinction risk to generate a distribution of values at each sampling intensity. Points are mean *p*-values \pm 95% confidence intervals. Dashed line denotes *p* = 0.05.



Figure S2. Associations between the proportion of species threatened by extinction and both (a) diversification rate and (b) genus stem age. Diversification was estimated for $\varepsilon = 0.50$. Points are scaled to the proportion of species assessed in each genus, which is used to weight the PGLS. Green and brown points denote conifers and palms, respectively. Solid lines are mean associations estimated by PGLS.



Figure S3. Probability densitiy functions of effects estimated in the phylogenetic path analysis for palms. We estimated a mean (μ) and standard deviation (σ) for standardised coefficients linking (a) species range to extinction risk, (b) species age to range size, and (c) species age to extinction risk. Estimates were generated for each of 1,000 phylogenetic trees. Red curves are generated from pooling means and variances across the 1,000 phylogenies, with corresponding parameter estimates inset.





Figure S4. Predictions for how range size could vary with taxon age in non-threatened (NT, black) and threatened (T, red) taxa. Vertical grey arrows show how the disparity between NT and T sisters correlates either (**a**) positively (i.e. increases) or (**b**) negatively (i.e. decreases) with time. In this example, we use a binary threshold in range size to differentiate between NT and T taxa (above and below dotted horizontal line, respectively), while recognising that this classification is likely to be much more complex in reality.



Figure S5. Differences in range size between sister conifers of contrasting extinction risk decrease with their age. For each sister pair of non-threatened (NT) and threatened (T) taxa we calculated the difference in log-transformed potential range sizes, i.e. log-ratio or NT divided by T as we express on the y-axis (n = 8). Solid line is slope for the corresponding correlation coefficient *r*. Inset shows frequency distribution of *r* calculated for 1,000 random simulations of sister pairs of the same threat category, with vertical line denoting observed correlation for contrasting extinction risk, i.e. corresponding to plotted data points.