Does Evolutionary History Correlate with Contemporary Extinction Risk by Influencing Range Size Dynamics?

Andrew J. Tanentzap,[1,*] Javier Igea,[1] Matthew G. Johnston,[1] and Matthew J. Larcombe[2]

1. Ecosystems and Global Change Group, Department of Plant Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EA, United Kingdom;   2. Department of Botany, University of Otago, Dunedin 9054, New Zealand

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 that range size dynamics may explain differing patterns of extinction risk across the ToL, with consequences for biodiversity conservation.

Keywords: conservation, environmental change, macroecology, macroevolution, phylogenetics.

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 associ-

ated 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 nonlemur primates showed the reverse pattern (Arregoitia et al. 2013). The only study in 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 nonrandomly 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 produce 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

* Corresponding author; email: ajt65@cam.ac.uk.

ORCIDs: Tanentzap, https://orcid.org/0000-0002-2883-1901; Igea, https://orcid.org/0000-0001-9493-2076; Johnston, https://orcid.org/0000-0003-1141-6135.

include fewer species with small ranges (Tanentzap et al. 2015), 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 (2018) Red List. Reliable taxon age estimates require sampling a large proportion of closely related taxa (e.g., ≥60% of congeneric species or confamilial genera for species and genus age estimates, respectively; fig. A1; figs. A1, A2, S1–S5 are available online). Only 483 species in 116 genera had ER data and met this sampling criterion 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 undersampled 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 require only 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 the subclade for each genus that contained ≥50% of all species were removed prior to calculations using MonoPhy in R (ver. 3.4; 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 (ver. 1.1.1; Pennell et al. 2016) and retained those with ≥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 (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, "nonthreatened"). 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 that 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 for all internal nodes reported in the 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 ≥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 (GBIF; http://www.gbif.org). Conifer data were supplemented by published records absent from GBIF (see the list of sources in the appendix, available online). All duplicate and spatially invalid records (e.g., nonnumerical, exceeding global extent, or 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 are provided in the appendix). 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; tables S1–S4, A1 are available online).

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 dif-

ference 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 regression 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 nonindependence 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 <2 from 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 were 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 faster-diversifying genera (for ε of 0.0, 0.5, and 0.9: $t_{492} = 4.46$, 4.45, and 4.30, respectively; $P < .001$ 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 that genus age was negatively associated with ER ($t_{637} = -3.38$, $P = .001$; fig. 1b). A caveat is that we found some bias in our data set. Sampled genera were older, slower diversifying, and less threatened, on average, than those 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 ($t_{128} = -1.92$, $P = .058$). Repeating our analyses at the genus level with the more complete conifer and palm data sets 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 species-level data sets revealed that older conifers but not palms were associated with greater ER (figs. 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 the 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 (supplemental PDF, "Text S1—Additional analysis of sister species").

Our results with conifers and palms were also not simply an artifact of biased sampling, as ages and rates did not markedly differ from observations across entire clades, that is, before filtering with IUCN data (table S4).

Discussion

Our study supports the idea that taxon age may explain the nonrandomness of ER across the ToL by influencing range size dynamics. We found younger and faster-diversifying 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
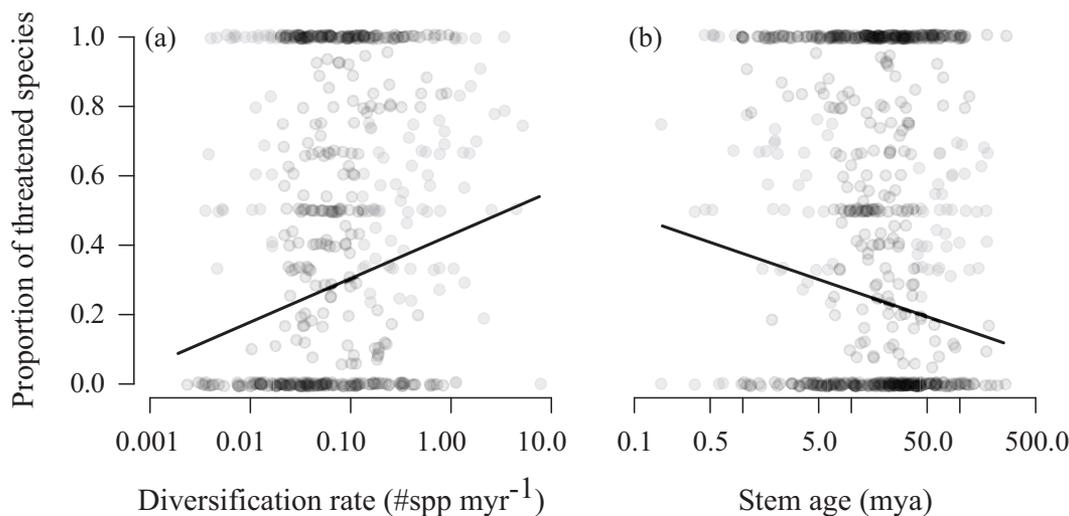

Figure 1: More species are threatened by extinction in faster-diversifying (*a*) and younger (*b*) genera. Diversification was estimated for $\varepsilon = 0.50$. Solid lines show mean associations estimated by phylogenetic least squares. Mean (SE) standardized slopes were 0.06 (0.01) and -0.05 (0.01) and $R^2 = 0.10$ and 0.08 in *a* and *b*, respectively.
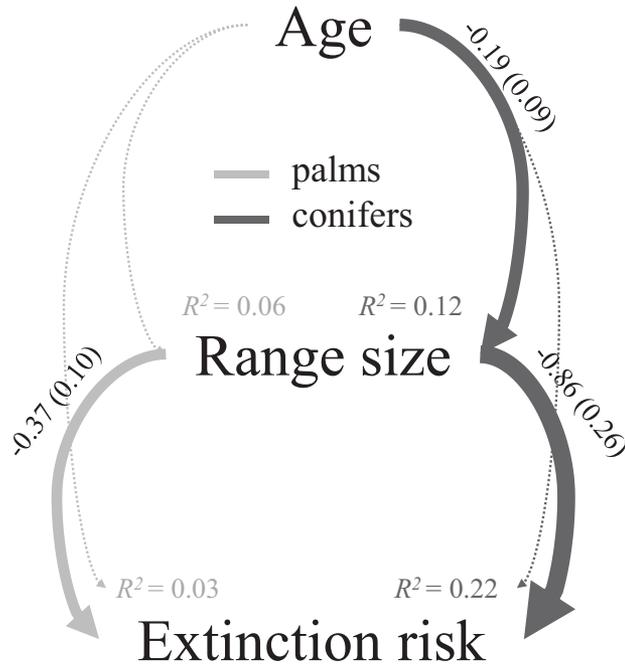
Figure 2: Phylogenetic path analysis of putative causal linkages among species age, range size, and extinction risk. The model was fitted separately for conifers ($n = 138$) and palms ($n = 455$). Path thickness is proportional to the mean (SE) standardized effect estimated from model averaging and pooling errors in the case of palms (see fig. S3). Dotted paths are not statistically significant. R^2 values are reported for modeled responses. As extinction risk was estimated with a logistic model, corresponding R^2 values were based on likelihood ratios between full and intercept-only models and are not directly comparable with those calculated for phylogenetic least squares based on explained variance (Ives 2019).

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, for example, parapatry or sympatry (Pigot et al. 2010), and if range expansion is not limited postspeciation (Schurr et al. 2007). Differences in speciation modes can also help explain the lack of consistent evidence for age-dependent 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 escaped extinction only 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 ER (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 become extinct or that traits that increase ER 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 overestimate ages in incompletely sampled groups. Our sampling coverage produced relatively accurate estimates of taxon age (i.e., <15% error for interquartile range), with error likely negligible for most genera ($n = 266/494$) with ≥80% sampling coverage (appendix). 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), although we took steps to minimize this concern (appendix). Finally, we used higher-level Red List classifications that ignore variation in ER within the threatened and nonthreatened categories. However, it has been argued that much of the variation in the lower-level categories can be attributed to classification
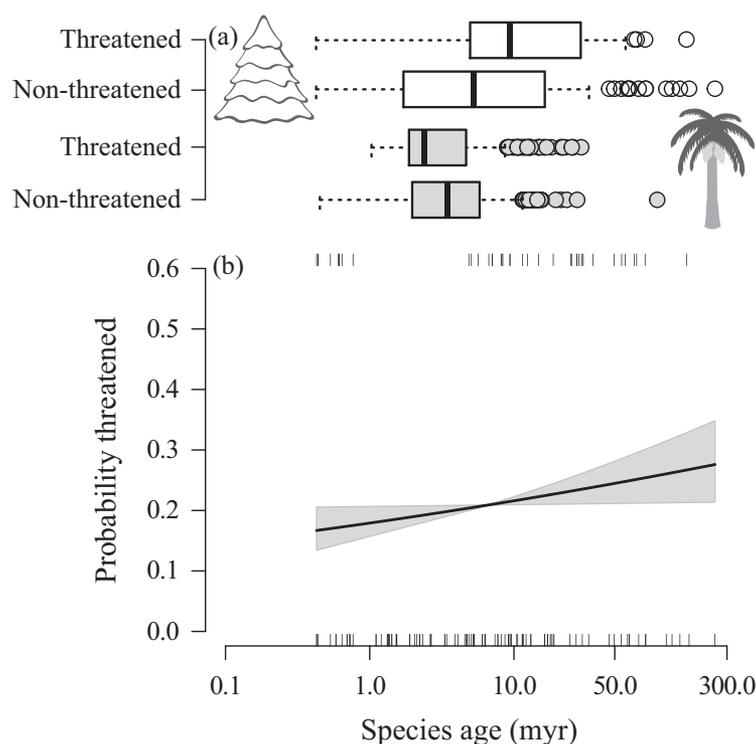
Figure 3: Older conifers but not palms have a greater probability of being threatened by extinction. *a*, Boxplot for stem ages of conifer (white; $n = 138$) and palm (gray; $n = 455$) species that were classified as either threatened or nonthreatened. Solid lines show medians, boxes show interquartile ranges, whiskers extend one and a half times the interquartile range, and points indicate 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. The solid line shows the mean effect of species age (with gray shading indicating the 95% confidence interval) estimated by model averaging of phylogenetic logistic regressions fitted within a path analysis framework. Rugs are observations of individual species either threatened or nonthreatened by extinction.

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 ER in plants and thereby emphasize its importance for biodiversity conservation.

Data and Code Availability

Data and R code to perform our analyses have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.k0p2ngf3z; Tanentzap et al. 2019).

Literature Cited

Anacker, B. L., and S. Y. Strauss. 2014. The geography and ecology of plant speciation: range overlap and niche divergence in sister species. Proceedings of the Royal Society B 281:20132980.

Arregoitia, L. D. V., S. P. Blomberg, and D. O. Fisher. 2013. Phylogenetic correlates of extinction risk in mammals: species in older lineages are not at greater risk. Proceedings of the Royal Society B 280:20131092.

Baker, W. J., and T. L. P. Couvreur. 2013. Global biogeography and diversification of palms sheds light on the evolution of tropical lineages. I. Historical biogeography. Journal of Biogeography 40:274–285.

Bennett, P. M., and I. P. F. Owens. 1997. Variation in extinction risk among birds: chance or evolutionary predisposition? Proceedings of the Royal Society B 264:401–408.

Castiglione, S., A. Mondanaro, M. Melchionna, C. Serio, M. Di Febbraro, F. Carotenuto, and P. Raia. 2017. Diversification rates and the evolution of species range size frequency distribution. Frontiers in Ecology and Evolution 5:147.

Ceolin, G. B., and E. L. H. Giehl. 2017. A little bit everyday: range size determinants in *Arachis* (Fabaceae), a dispersal-limited group. Journal of Biogeography 44:2798–2807.

Condamine, F. L., A. B. Leslie, and A. Antonelli. 2017. Ancient islands acted as refugia and pumps for conifer diversity. Cladistics 33:69–92.

Condamine, F. L., J. Rolland, and H. Morlon. 2013. Macroevolutionary perspectives to environmental change. Ecology Letters 16:72–85.

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

Farjon, A. 1996. Biodiversity of *Pinus* (Pinaceae) in Mexico: speciation and palaeo-endemism. Botanical Journal of the Linnean Society 121:365–384.

Faurby, S., W. L. Eiserhardt, W. J. Baker, and J.-C. Svenning. 2016. An all-evidence species-level supertree for the palms (Arecaceae). Molecular Phylogenetics and Evolution 100:57–69.

Garamszegi, L. Z., and A. P. Møller. 2010. Effects of sample size and intraspecific variation in phylogenetic comparative studies: a meta-analytic review. Biological Reviews 85:797–805.

Gaston, K. J. 1998. Species-range size distributions: products of speciation, extinction and transformation. Philosophical Transactions of the Royal Society B 353:219–230.

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

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

Higgins, S. I., R. B. O'Hara, O. Bykova, M. D. Cramer, I. Chuine, E.-M. Gerstner, T. Hickler, et al. 2012. A physiological analogy of the niche for projecting the potential distribution of plants. Journal of Biogeography 39:2132–2145.

Ho, T., L. Si, and C. Ané. 2014. A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. Systematic Biology 63: 397–408.

Igea, J., D. Bogarín, A. S. T. Papadopulos, and V. Savolainen. 2015. A comparative analysis of island floras challenges taxonomy-based biogeographical models of speciation. Evolution 69:482–491.

IUCN (International Union for Conservation of Nature). 2018. The IUCN Red List of Threatened Species. http://www.iucnredlist.org.

Ives, A. R. 2019. R^2s for correlated data: phylogenetic models, LMMs, and GLMMs. Systematic Biology 68:234–251.

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

Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters 12:334–350.

Kissling, W. D., W. L. Eiserhardt, W. J. Baker, F. Borchsenius, T. L. P. Couvreur, H. Balslev, and J.-C. Svenning. 2012. Cenozoic imprints on the phylogenetic structure of palm species assemblages worldwide. Proceedings of the National Academy of Sciences of the USA 109:7379–7384.

Leslie, A. B., J. Beaulieu, G. Holman, C. S. Campbell, W. Mei, L. R. Raubeson, and S. Mathews. 2018. An overview of extant conifer evolution from the perspective of the fossil record. American Journal of Botany 105:1531–1544.

Leslie, A. B., J. M. Beaulieu, H. S. Rai, P. R. Crane, M. J. Donoghue, and S. Mathews. 2012. Hemisphere-scale differences in conifer evolutionary dynamics. Proceedings of the National Academy of Sciences of the USA 109:16217–16221.

Liu, Y.-J., N. C. Arens, and C.-S. Li. 2007. Range change in *Metasequoia*: relationship to palaeoclimate. Botanical Journal of the Linnean Society 154:115–127.

Magallon, S., and M. J. Sanderson. 2001. Absolute diversification rates in angiosperm clades. Evolution 55:1762–1780.

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

Mounce, R., M. Rivers, S. Sharrock, P. Smith, and S. Brockington. 2018. Comparing and contrasting threat assessments of plant species at the global and sub-global level. Biodiversity and Conservation 27:907–930.

Orme, D. 2013. The caper package: comparative analysis of phylogenetics and evolution in R. https://cran.r-project.org/web/packages /caper/vignettes/caper.pdf.

Paul, J. R., C. Morton, C. M. Taylor, and S. J. Tonsor. 2009. Evolutionary time for dispersal limits the extent but not the occupancy of species' potential ranges in the tropical plant genus *Psychotria* (Rubiaceae). American Naturalist 173:188–199.

Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12:361–371.

Pennell, M. W., R. G. FitzJohn, and W. K. Cornwell. 2016. A simple approach for maximizing the overlap of phylogenetic and comparative data. Methods in Ecology and Evolution 7:751–758.

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

Pigot, A. L., and J. A. Tobias. 2013. Species interactions constrain geographic range expansion over evolutionary time. Ecology Letters 16:330–338.

Pittermann, J., S. A. Stuart, T. E. Dawson, and A. Moreau. 2012. Cenozoic climate change shaped the evolutionary ecophysiology of the Cupressaceae conifers. Proceedings of the National Academy of Sciences of the USA 109:9647–9652.

Purvis, A., J. L. Gittleman, G. Cowlishaw, and G. M. Mace. 2000. Predicting extinction risk in declining species. Proceedings of the Royal Society B 267:1947–1952.

Qian, H., and Y. Jin. 2016. An updated megaphylogeny of plants, a tool for generating plant phylogenies and an analysis of phylogenetic community structure. Journal of Plant Ecology 9:233–239.

Rabosky, D. L. 2010. Extinction rates should not be estimated from molecular phylogenies. Evolution 64:1816–1824.

Rabosky, D. L., and A. H. Hurlbert. 2015. Species richness at continental scales is dominated by ecological limits. American Naturalist 185:572–583.

Scholl, J. P., and J. J. Wiens. 2016. Diversification rates and species richness across the Tree of Life. Proceedings of the Royal Society B 283:20161334.

Schwery, O., and B. C. O'Meara. 2016. MonoPhy: a simple R package to find and visualize monophyly issues. PeerJ Computer Science 2:e56.

Schwartz, M. W., and D. Simberloff. 2001. Taxon size predicts rates of rarity in vascular plants. Ecology Letters 4:464–469.

Schurr, F. M., G. F. Midgley, A. G. Rebelo, G. Reeves, P. Poschlod, and S. I. Higgins. 2007. Colonization and persistence ability explain the extent to which plant species fill their potential range. Global Ecology and Biogeography 16:449–459.

Slatyer, R. A., M. Hirst, and J. P. Sexton. 2013. Niche breadth predicts geographical range size: a general ecological pattern. Ecology Letters 16:1104–1114.

Tanentzap, A. J., A. J. Brandt, R. D. Smissen, P. B. Heenan, T. Fukami, and W. G. Lee. 2015. When do plant radiations influence community assembly? the importance of historical contingency in the race for niche space. New Phytologist 207:468–479.

Tanentzap, A. J., J. Igea, M. G. Johnston, and M. J. Larcombe. 2019. Data from: Does evolutionary history correlate with contemporary extinction risk by influencing range size dynamics? American Naturalist, Dryad Digital Repository, https://doi.org/10.5061/dryad.k0p2ngf3z.

Valente, L. M., V. Savolainen, and P. Vargas. 2010. Unparalleled rates of species diversification in Europe. Proceedings of the Royal Society B 277:rspb20092163.

Vamosi, J. C., and J. R. U. Wilson. 2008. Nonrandom extinction leads to elevated loss of angiosperm evolutionary history. Ecology Letters 11:1047–1053.

van der Bijl, W. 2018. phylopath: easy phylogenetic path analysis in R. PeerJ 6:e4718.

Warton, D. I., and F. K. C. Hui. 2011. The arcsine is asinine: the analysis of proportions in ecology. Ecology 92:3–10.

Williams, S. E., Y. M. Williams, J. VanDerWal, J. L. Isaac, L. P. Shoo, and C. N. Johnson. 2009. Ecological specialization and population size in a biodiversity hotspot: how rare species avoid extinction. Proceedings of the National Academy of Sciences of the USA 106:19737–19741.

Willis, J. C. 1926. Age and area. Quarterly Review of Biology 1:553–571.

Wilson, E. O. 1959. Adaptive shift and dispersal in a tropical ant fauna. Evolution 13:122–144.

Yessoufou, K., B. H. Daru, R. Tafirei, H. O. Elansary, and I. Rampedi. 2017. Integrating biogeography, threat and evolutionary data to explore extinction crisis in the taxonomic group of cycads. Ecology and Evolution 7:2735–2746.

Zanne, A. E., D. C. Tank, W. K. Cornwell, J. M. Eastman, S. A. Smith, R. G. FitzJohn, D. J. McGlinn, et al. 2014. Three keys to the radiation of angiosperms into freezing environments. Nature 506:89–92.

Žliobaitė, I., M. Fortelius, and N. C. Stenseth. 2017. Reconciling taxon senescence with the Red Queen's hypothesis. Nature 552:92–95.

References Cited Only in the Online Enhancements

Ardia, D., K. Boudt, P. Carl, K. M. Mullen, and B. G. Peterson. 2011. Differential evolution with deoptim. R Journal 3:27–34.

Barbet-Massin, M., F. Jiguet, C. H. Albert, and W. Thuiller. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? Methods in Ecology and Evolution 3:327–338.

Farjon, A. A. 2010. Handbook of the world's conifers. Vol. 1. Brill, Leiden.

Hantemirova, E., A. Berkutenko, and V. Semerikov. 2012. Systematics and gene geography of *Juniperus communis* L. inferred from isoenzyme data. Russian Journal of Genetics 48:920–926.

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.

Kaufman, L., and P. J. Rousseeuw. 2009. Finding groups in data: an introduction to cluster analysis. Wiley, Hoboken, NJ.

Larionova, A. Y., A. K. Ekart, and A. N. Kravchenko. 2007. Genetic diversity and population structure of Siberian fir (*Abies sibirica* LEDEB.) in middle Siberia, Russia. Eurasian Journal of Forest Research 10:185–192.

Petrova, E., S. Goroshkevich, M. Belokon, Y. S. Belokon, and D. Politov. 2014. Distribution of the genetic diversity of the Siberian stone pine, *Pinus sibirica* Du Tour, along the latitudinal and longitudinal profiles. Russian Journal of Genetics 50:467–482.

Thornley, J. H. 1998. Modelling shoot:root relations: the only way forward? Annals of Botany 81:165–171.

Timoshok, E., E. Timoshok, and S. Skorokhodov. Ecology of Siberian stone pine (*Pinus sibirica* Du Tour) and Siberian larch (*Larix sibirica* LEDEB.) in the Altai Mountain glacial basins. Russian Journal of Ecology 45:194–200.

Zhao, X. Y., C. Wang, S. C. Li, W. Hou, S. Q. Zhang, G. J. Han, D. Pan, P. Wang, Y. F. Cheng, and G. F. Liu. 2014. Genetic variation and selection of introduced provenances of Siberian Pine (*Pinus sibirica*) in frigid regions of the Greater Xing'an Range, northeast China. Journal of Forestry Research 25:549–556.