Evolutionarily younger and faster diversifying plants are more threatened by extinction

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Abstract

Many species are threatened by extinction, yet few factors have been identified to explain this risk across the plant Tree of Life (ToL). Lineages that are evolutionarily younger or occurring within rapidly diversifying clades may have elevated extinction risk because they occupy smaller geographic ranges and adaptive zones as compared with older lineages that have tolerated longer periods of environmental change. Here we find that faster diversifying plant genera had more species at risk of extinction. Evolutionary age had no effect in the 297 genera that we sampled, potentially because of sampling older genera, on average, from across the ToL. Repeating our analyses in two well-sampled and large groups, we found that extinction risk decreased with evolutionary age in conifer species but not palms. Small sample sizes limited our power to detect effects of lineage diversification in these groups. Our results suggest that contrasting modes of speciation may explain differing patterns of extinction risk across the broader ToL and have consequences for biodiversity conservation.

Introduction

Much of the world's biodiversity is threatened to varying degrees by extinction [1]. In addition to present-day environmental pressures, some species may intrinsically face a higher risk of extinction because of at least two historical reasons. The first is that traits that were once advantageous became less adaptive as environments diverged from previous selection regimes [2], thereby making older species more likely to be threatened by extinction. A classic example is the loss of large-bodied Eurasian mammals, such as woolly rhinoceros (*Coelodonta antiquitatis*), at the end of the most recent glacial period. Woolly rhinoceros were presumably maladapted for changes to their steppe habitat arising from warmer temperatures [3]. However, older species that survived long-term environmental changes may also be less at risk of extinction because they tolerate a greater range of conditions and are ecologically more generalist [4,5]. A second historical explanation for variation in extinction risk is that younger species, which often arise from rapidly diversifying lineages [6], initially tend to have smaller geographic ranges. Small ranges are especially likely if speciation started from small reproductively isolated populations. These small populations can also occupy a narrower adaptive space. Together, small geographic and adaptive ranges can increase extinction risk in both younger species and rapidly diversifying clades with many young species [7-9].

Previous work in birds [4] and marsupials [10] found that older lineages were more threatened by extinction, whilst the reverse was shown across non-lemur primates [8], but there is no reason for these patterns to hold at a large taxonomic scale across other divisions in the Tree of Life. The only study on plants, to our knowledge, found a higher extinction risk in younger, rapidly diversifying clades of the South African Cape [7]. Broader generalisations across plants have not been possible until now because of poor taxonomic sampling coverage that prevents reliable divergence times from being estimated.

Here, we combined the largest time-calibrated phylogenetic tree presently estimated for vascular plants with peer-reviewed assessments of conservation status from the International Union for Conservation of Nature (IUCN) *Red List* [11] to test whether younger and faster-evolving clades were associated with greater extinction risk across 297 genera. We complemented our findings with analyses for two large, ancient, and widespread plant clades (conifers and palms). These analyses allowed us to address concerns around estimating divergence times and threat status from the larger but under-sampled phylogenetic tree.

Methods

Data assembly

We first selected genera for which we could confidently estimate the time of divergence from their sister clades (i.e. 'stem age') in the time-calibrated, species-level phylogenetic tree of Qian & Jin [12]. The selected genera came from densely sampled clades (i.e. families) to circumvent low sampling across the broader tree both at a species- and genus-level. For each family, we calculated the proportion of genera that were sampled in the phylogeny from the taxonomic database curated by the *taxonlookup* v1.1.1 *R* package and retained those with ≥60% coverage. We also used stem ages 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 [13]. Taxa outside of an established "core clade" for each genus, as determined using *MonoPhy* in R, were removed prior to all calculations. After calculating ages from the large tree, we intersected the selected genera with 20,473 IUCN assessments [11] and calculated the proportion of species in each genus threatened with extinction. We further restricted our

analysis to genera with >1 species, of which ≥20% had sufficient data to be assessed for extinction risk. Overall, *n*=297 genera had both reliable age and risk status data spanning 2,679 IUCN species-level assessments.

We also estimated net diversification rates for each of our selected genera. 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 [14]. Following standard practice, we assumed three values of relative extinction ε of 0, 0.5 and 0.9 when estimating diversification [14]. Taxonomy was standardised to The Plant List nomenclature using the *Taxonstand* R package prior to processing all datasets.

We also repeated our genus-level diversification analysis as above with two large clades that were well sampled at a species-level in separate time-calibrated phylogenies. These clades included 70% of all 651 accepted Pinales (extant conifers) [15] and all 2,539 Arecaceae (palms) [16]. Using these data, we also intersected risk statuses with species stem ages, giving *n*=340 and 346, respectively. For the palms, we used the maximum clade credibility tree that we computed from the posterior distribution of trees that was generated using topological constraints based on Govaerts taxonomy recommended in ref. [16].

Statistical analyses

We separately tested whether genera with a greater proportion of threatened taxa had younger ages and faster diversification rates using phylogenetic least squares regression (PGLS) in the R *caper* package. Following standard practice, we fitted the PGLS with maximum-likelihood transformations of branch lengths based on the strength of phylogenetic covariance estimated by Pagel's λ [17]. Both ages and diversification rates were log-transformed. Models were not fitted with both predictors simultaneously as they were highly correlated (Spearman's r <

-0.79). We repeated this analysis in conifers and palms, and again did not simultaneously fit age and diversification rates given high correlations ($r < -0.71$ when $\varepsilon = 0.0$ or 0.5).

For conifers and palms, we also tested whether threatened status was associated with younger species ages using logistic regression. Models were fitted with penalised maximum-likelihood that accounted for the phylogenetic non-independence of species using the *phylolm* R package. Predictors were scaled to a mean of 0 and standard deviation of 1 to compare effects.

Results

We found that relatively more species were threatened with extinction in faster diversifying genera (for ε of 0.0, 0.5, 0.9: $t_{295} = 2.25, 2.32, 2.40$ and $p = 0.025, 0.021, 0.017$; respectively). The mean proportion of a genus threatened with extinction doubled from 32% to 65% between the slowest and fastest diversifying genera (figure 1). These results did not arise simply because faster diversifying genera were younger, as genus age had no effect on risk status ($t_{295} = -1.48$, $p = 0.141$). However, we found an age bias in our dataset. Sampled genera were older and more diverse on average than obtained by applying our sampling criteria to the initial tree (i.e. before intersecting with threat status; table S1), which may explain why we failed to detect an association between younger genera and extinction risk. Diversification was also slower in our sample, but the sampling criteria did not lead to differences in risk status (table S1). Repeating our analyses with only the genera from the more complete species-level datasets was inconclusive, likely because of small sample sizes ($n \leq 36$; table S2).

Analyses with the more complete species-level datasets also revealed that younger conifers but not palms were relatively more threatened by extinction ($z_{344} = -2.67$, $p = 0.008$

and z_{338} = -1.46, p = 0.145, respectively; figure 2a). The mean effect ± SE was more than twice as large in the conifers (-0.36 ± 0.14 vs -0.15 ± 0.10 on log-scale), leading to nearly a 50% absolute reduction in the probability of being threatened over the range of observed ages (figure 2b).

Discussion

Our finding that faster diversifying lineages faced greater extinction risk, which the IUCN associates with smaller range and/or population sizes [11], may arise because most plant speciation is allopatric or peripatric [18,19]. Therefore, where these modes occur more often, species will ultimately have smaller geographic ranges and greater extinction risk [7]. Age effects on extinction risk should also prevail for allopatric speciation, which requires post-speciation range expansions that necessarily take time to accumulate [20]. Under peripatry, time-dependent range expansions are unnecessary for ancestral taxa to continue generating many new species with small range sizes [20]. These dynamics can also help explain varying age effects on extinction risk in other studies that span disparate taxonomic groups [4,7-10] and between conifers and palms. Conifer diversification is presumed to have been more dependent on range contraction and expansion [15,21] than in palms, where dispersal into isolated populations, consistent with peripatry, might better explain speciation [22].

Palms and conifers have contrasting biogeographic histories that can explain our differing results between the groups. Conifers mostly occupy temperate habitats as opposed to the predominately tropical distribution of palms. The greater ecological stability of the tropics may therefore result in little influence of evolutionary age on palm extinction [23]. For example, older palm species would have not been exposed to the repeated glacial cycles that fragmented temperate conifer populations [5] and could have elevated extinction risk.

Another explanation is that palm species that were susceptible to environmental change have already gone extinct or traits that make species more prone to extinction are not taxonomically conserved [8]. 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 s3). Similar results to the larger phylogeny also suggest that our conclusions were robust to biases in IUCN assessments [24].

Our results suggest that macro-evolutionary dynamics have some value for biodiversity conservation. Specifically, we found that these dynamics provided an indicator of contemporary extinction risk that might be easier to derive for large numbers of taxa than detailed species-level assessments. Macro-evolutionary dynamics might also offer insight into the vulnerability of species to future change, as the smaller population and range sizes that make some species prone to extinction are likely to be carried into the future [25]. Although our results must be interpreted with caution, given several biases inherent to the size of our datasets, they provide new evidence that lineages span a continuum from little species turnover to producing fast diversifying and extinction-prone taxa [9]. The consistent results we found at different taxonomic scales also suggests that similar patterns should be uncovered in the future when the plant Tree of Life is more densely sampled.

Ethics

Does not apply.

Data accessibility

Data will be deposited in the Dryad repository upon acceptance.

Authors' contributions

AJT conceived the study. All authors designed the study. AJT carried out the data analysis and drafted the manuscript with input from JI and MGJ. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Competing interests

We have no competing interests.

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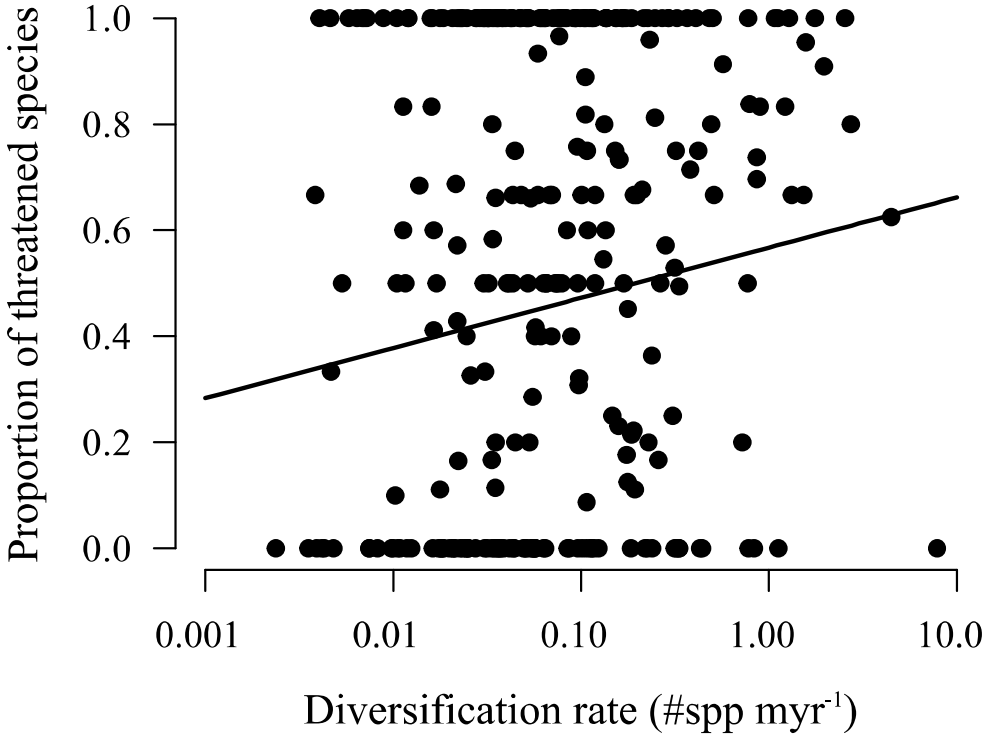

Figure 1. More species are threatened with extinction in faster diversifying genera. Solid line is mean association estimated by PGLS for $\varepsilon = 0.50$.

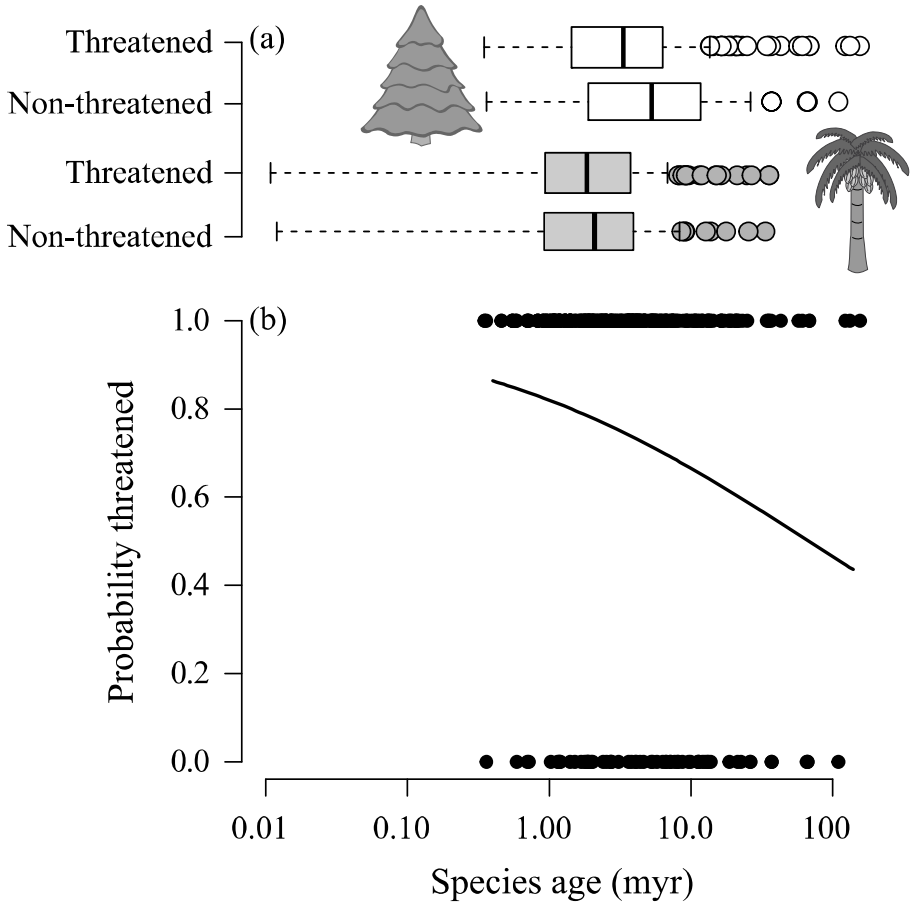

Figure 2. Younger conifers but not palms have a greater probability of being threatened by extinction. (**a**) Boxplot for stem ages of conifer (white, *n*=346) and palm (grey, *n*=340) species that were classified as either threatened or non-threatened. Solid line is median, box is inter-quartile range, whiskers extend 1.5-times the interquartile range, and points are outliers. (**b**) Change in probability of a conifer being classified as threatened with species age. Solid line is mean association estimated by phylogenetic logistic regression.