

1 **Evolutionarily younger and faster diversifying plants are more threatened by extinction**

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6

7 **Abstract**

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

## 20 **Introduction**

21 Much of the world's biodiversity is threatened to varying degrees by extinction [1]. In  
22 addition to present-day environmental pressures, some species may intrinsically face a higher  
23 risk of extinction because of at least two historical reasons. The first is that traits that were  
24 once advantageous became less adaptive as environments diverged from previous selection  
25 regimes [2], thereby making older species more likely to be threatened by extinction. A  
26 classic example is the loss of large-bodied Eurasian mammals, such as woolly rhinoceros  
27 (*Coelodonta antiquitatis*), at the end of the most recent glacial period. Woolly rhinoceros  
28 were presumably maladapted for changes to their steppe habitat arising from warmer  
29 temperatures [3]. However, older species that survived long-term environmental changes  
30 may also be less at risk of extinction because they tolerate a greater range of conditions and  
31 are ecologically more generalist [4,5]. A second historical explanation for variation in  
32 extinction risk is that younger species, which often arise from rapidly diversifying lineages  
33 [6], initially tend to have smaller geographic ranges. Small ranges are especially likely if  
34 speciation started from small reproductively isolated populations. These small populations  
35 can also occupy a narrower adaptive space. Together, small geographic and adaptive ranges  
36 can increase extinction risk in both younger species and rapidly diversifying clades with  
37 many young species [7-9].

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

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

53

## 54 **Methods**

### 55 *Data assembly*

56 We first selected genera for which we could confidently estimate the time of divergence from  
57 their sister clades (i.e. ‘stem age’) in the time-calibrated, species-level phylogenetic tree of  
58 Qian & Jin [12]. The selected genera came from densely sampled clades (i.e. families) to  
59 circumvent low sampling across the broader tree both at a species- and genus-level. For each  
60 family, we calculated the proportion of genera that were sampled in the phylogeny from the  
61 taxonomic database curated by the *taxonlookup* v1.1.1 R package and retained those with  
62  $\geq 60\%$  coverage. We also used stem ages because they only require one species to be  
63 sampled within each genus and reflect the entire evolutionary history of clades unlike crown  
64 ages that can have young age biases because they consider only extant species [13]. Taxa  
65 outside of an established “core clade” for each genus, as determined using *MonoPhy* in R,  
66 were removed prior to all calculations. After calculating ages from the large tree, we  
67 intersected the selected genera with 20,473 IUCN assessments [11] and calculated the  
68 proportion of species in each genus threatened with extinction. We further restricted our

69 analysis to genera with >1 species, of which  $\geq 20\%$  had sufficient data to be assessed for  
70 extinction risk. Overall,  $n=297$  genera had both reliable age and risk status data spanning  
71 2,679 IUCN species-level assessments.

72 We also estimated net diversification rates for each of our selected genera. We used a  
73 well-established method-of-moments estimator that assumed diversification rates were  
74 constant over time within genera given a known stem age and species richness [14].  
75 Following standard practice, we assumed three values of relative extinction  $\epsilon$  of 0, 0.5 and 0.9  
76 when estimating diversification [14]. Taxonomy was standardised to The Plant List  
77 nomenclature using the *Taxonstand* R package prior to processing all datasets.

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

85

#### 86 *Statistical analyses*

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

93 -0.79). We repeated this analysis in conifers and palms, and again did not simultaneously fit  
94 age and diversification rates given high correlations ( $r < -0.71$  when  $\varepsilon = 0.0$  or  $0.5$ ).

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

100

## 101 **Results**

102 We found that relatively more species were threatened with extinction in faster diversifying  
103 genera (for  $\varepsilon$  of 0.0, 0.5, 0.9:  $t_{295} = 2.25, 2.32, 2.40$  and  $p = 0.025, 0.021, 0.017$ ; respectively).

104 The mean proportion of a genus threatened with extinction doubled from 32% to 65%  
105 between the slowest and fastest diversifying genera (figure 1). These results did not arise  
106 simply because faster diversifying genera were younger, as genus age had no effect on risk  
107 status ( $t_{295} = -1.48, p = 0.141$ ). However, we found an age bias in our dataset. Sampled  
108 genera were older and more diverse on average than obtained by applying our sampling  
109 criteria to the initial tree (i.e. before intersecting with threat status; table S1), which may  
110 explain why we failed to detect an association between younger genera and extinction risk.

111 Diversification was also slower in our sample, but the sampling criteria did not lead to  
112 differences in risk status (table S1). Repeating our analyses with only the genera from the  
113 more complete species-level datasets was inconclusive, likely because of small sample sizes  
114 ( $n \leq 36$ ; table S2).

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

117 and  $z_{338} = -1.46$ ,  $p = 0.145$ , respectively; figure 2a). The mean effect  $\pm$  SE was more than  
118 twice as large in the conifers ( $-0.36 \pm 0.14$  vs  $-0.15 \pm 0.10$  on log-scale), leading to nearly a  
119 50% absolute reduction in the probability of being threatened over the range of observed ages  
120 (figure 2b).

121

## 122 **Discussion**

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

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

141 Another explanation is that palm species that were susceptible to environmental change have  
142 already gone extinct or traits that make species more prone to extinction are not  
143 taxonomically conserved [8]. Our results with conifers and palms were also not simply an  
144 artefact of biased sampling as ages and rates did not markedly differ from observations across  
145 entire clades, i.e. before filtering with IUCN data (table s3). Similar results to the larger  
146 phylogeny also suggest that our conclusions were robust to biases in IUCN assessments [24].

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

158

#### 159 **Ethics**

160 Does not apply.

161

#### 162 **Data accessibility**

163 Data will be deposited in the Dryad repository upon acceptance.

164

#### 165 **Authors' contributions**

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

169

#### 170 **Competing interests**

171 We have no competing interests.

172

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179

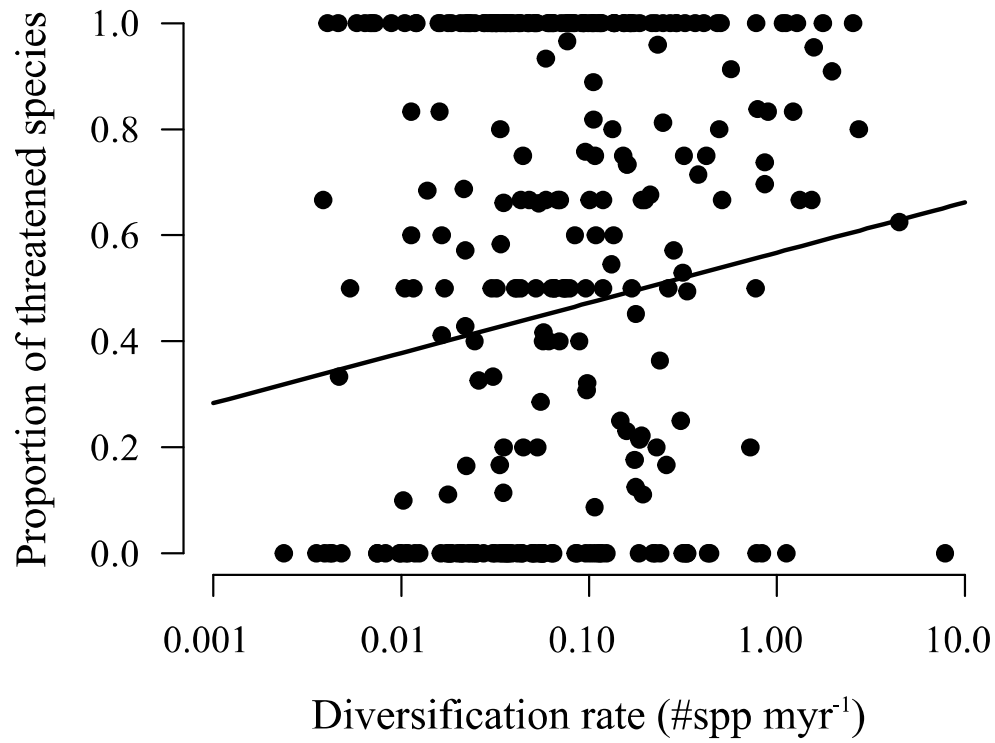
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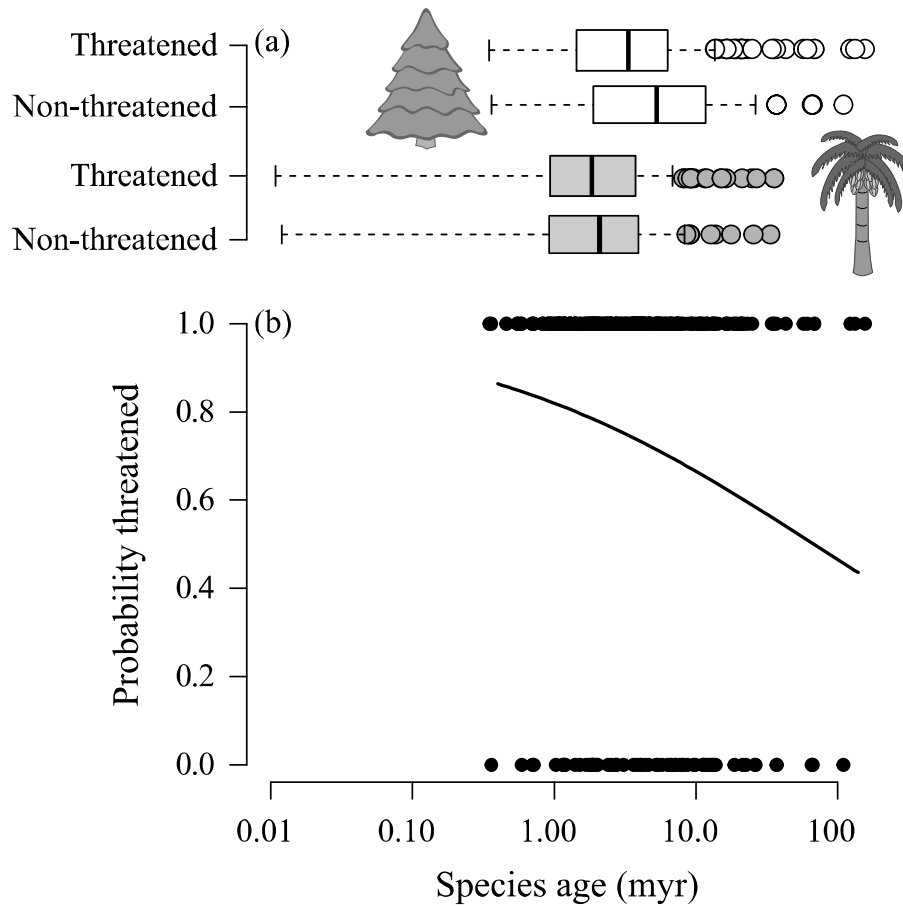
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236

237 **Figure 1.** More species are threatened with extinction in faster diversifying genera. Solid

238 line is mean association estimated by PGLS for  $\epsilon = 0.50$ .



239

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