

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 ϵ 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 λ [17]. Both ages and diversification rates λ 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 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).

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 ± 0.14 vs -0.15 ± 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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175

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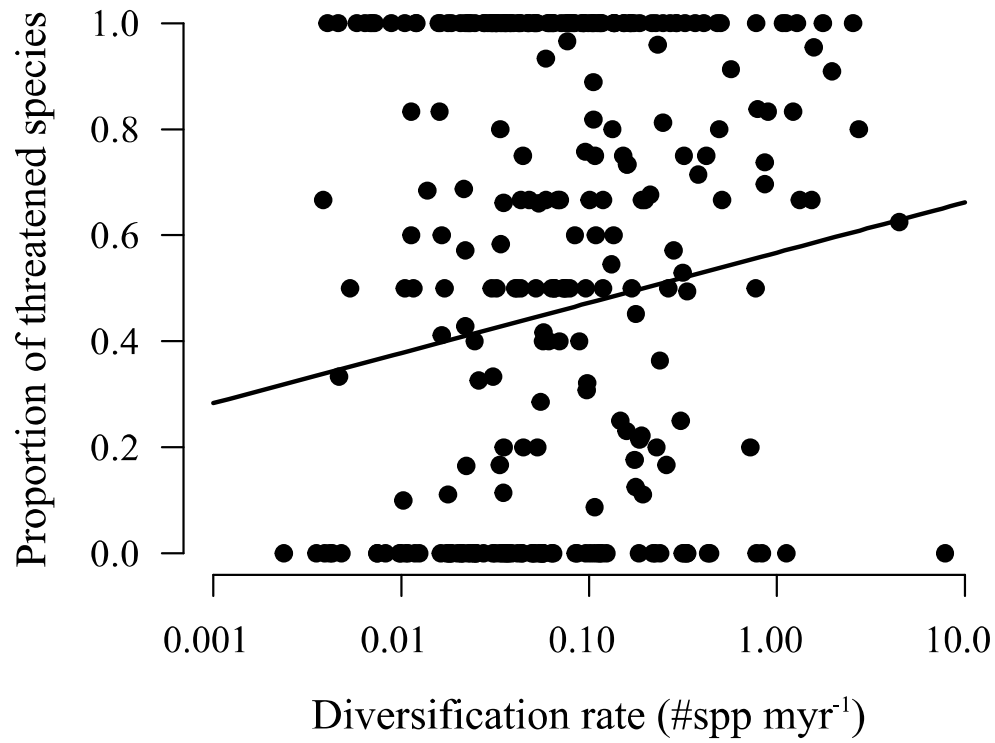
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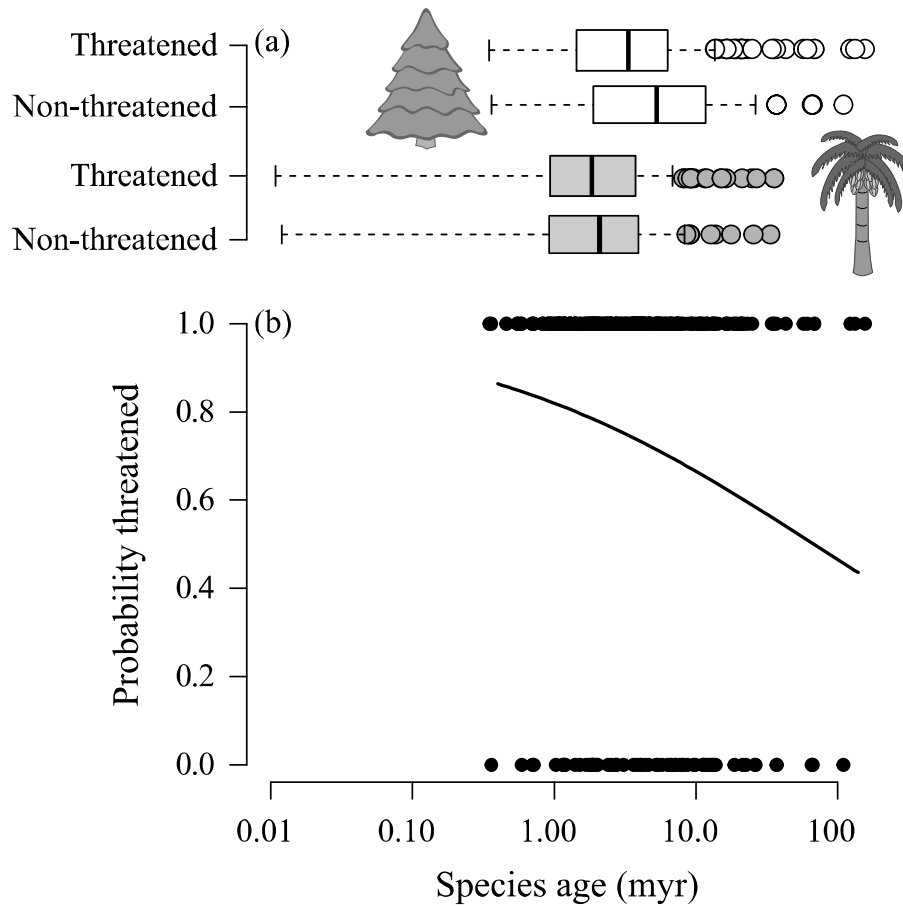
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236

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.