1 **Greater range filling can explain why evolutionarily older and slower diversifying**

2 **plants are less threatened by extinction**

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8 **Abstract**

9 Extinction threatens many species, yet few factors predict this risk across the plant Tree of

10 Life (ToL). Taxon age is one factor that may associate with extinction if occupancy of

11 geographic and adaptive zones varies with time. Age-dependent occupancy can also

12 influence diversification rates and thus extinction risk where new taxa have small range and

13 population sizes. Here we found that faster diversifying plant genera had more species

14 threatened by extinction across the ToL. Evolutionary age had no effect in 297 sampled

15 genera, potentially because they were older, on average, than expected. Repeating our

16 analyses in two large, well-sampled groups, we found that extinction risk decreased with

17 evolutionary age in conifer species but not palms. Range filling increased in older, non-

18 threatened conifers more strongly than in threatened taxa. Our results suggest contrasting

19 modes of speciation may explain differing patterns of extinction risk across the ToL with

20 consequences for biodiversity conservation.

21 **Keywords**: conservation, environmental change, macroecology, macroevolution,

22 phylogenetics

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Introduction

25   Much of the world's biodiversity is threatened by extinction because of small geographic

26   ranges and/or population sizes (Pimm et al. 2014).   In addition to having traits that promote

27   small ranges and population sizes independent of phylogeny, such as those associated with

28   life history and resource use, some species may be more threatened by extinction because of

29   their evolutionary history (Bennett and Owens 1997; Purvis et al. 2000; Johnson et al. 2002;

30   Arregoitia et al. 2013). Extinction is consequently non-randomly distributed across the Tree

31   of Life (ToL), evidence that chance events and human activities are not fully responsible for

32   explaining species losses (Bennett and Owens 1997; Purvis et al. 2000; Vamosi and Wilson

33   2008). Identifying macro-evolutionary predictors of extinction risk can therefore help to

34   assess future conservation status where range and population data are lacking and identify

35   reasons for its non-randomness across the ToL (Jetz and Freckleton 2015).

36   Taxon age is one measure of the amount of environmental and evolutionary change

37   that species have experienced and may be associated with extinction risk for at least two

38   reasons. The first relates to the idea that older taxa should be less at risk of extinction

39   because they have had more time to disperse across a greater range (Paul et al. 2009; Ceolin

40   and Giehl 2017), consistent with the age-and-area hypothesis (Willis 1926). Taxa that span a

41   greater area will also tend to occupy more environments (Slatyer et al. 2013). Occupancy of

42   more environmental space by older taxa (i.e. greater niche filling) can consequently limit

43   younger taxa from establishment opportunities through competition (Žliobaitė et al. 2017).

44   However, evidence of a correlation between age and range filling has been limited (Schurr et

45   al. 2007; Paul et al. 2009; but see Weber et al. 2014), and can alternatively be detected by

46   measuring rates of species diversification, which slow with clade age as niches are filled

47   (Tanentzap et al. 2015). As new taxa initially tend to have small range and population sizes,

48   especially if speciation started from small reproductively isolated populations that occupy

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49   narrow adaptive spaces (Valente et al. 2010; Castiglione et al. 2017), younger species in

50   rapidly diversifying clades should face a greater risk of extinction (Davies et al. 2011;

51   Greenberg & Mooers 2017).

52   A second historical explanation for variation in extinction risk relates to the

53   environment in which the geographic and adaptive ranges of species evolved. This idea can

54   result in two contrasting patterns that we group under the "evolutionary (mis)matching

55   hypothesis". Older species can be more threatened by extinction because traits that were

56   once advantageous became less adaptive as environments diverged from past selection

57   regimes, i.e. "mismatched" (Wilson 1959; Žliobaitė et al. 2017). A classic example is the

58   loss of large-bodied Eurasian mammals, such as woolly rhinoceros (*Coelodonta antiquitatis*),

59   at the end of the most recent glacial period. Woolly rhinoceros were presumably maladapted

60   for changes to their steppe habitat arising from warmer temperatures. Their potential range

61   size (i.e. total area of suitable steppe) consequently contracted, hastening extinction

62   (Lorenzen et al. 2011). Population densities could have remained unchanged in areas that

63   stayed climatically favourable, resulting in the same proportion of habitat occupancy and no

64   association between range filling and taxon age. In contrast to mismatching, older species

65   that survive long-term environmental changes may be less at risk of extinction because they

66   tolerate broader conditions and are ecologically more generalist (Gaston and Blackburn 1997;

67   Liow 2007). Species should be better "matched" to the environment in these cases and have

68   larger ranges with increasing taxon age because more sites will be favourable for dispersal

69   and colonisation. Again, range filling can be decoupled from range size (Gaston 1994;

70   Johnson 1998), such as if biotic interactions constrain eventual establishment. Thus, the

71   strength of the association between taxon age and both range size and filling can help identify

72   mechanisms that influence extinction risk.

73   Evidence that taxon age is associated with extinction varies among lineages, so testing

74   correlations in relation to range size and occupancy can help explain this variation and make

75   generalisations across different divisions in the ToL. Previous work in birds (Gaston and

76   Blackburn 1997) and marsupials (Johnson et al. 2002) found that older lineages were more

77   threatened by extinction, whilst the reverse was shown across non-lemur primates (Arregoitia

78   et al. 2013).   The only study on plants, to our knowledge, found a higher extinction risk in

79   younger, rapidly diversifying clades of the South African Cape (Davies et al. 2011). Broader

80   generalisations across plants have not been possible until now because of poor taxonomic

81   sampling that prevents reliable divergence times from being estimated.

82   Here, we tested whether younger and faster-evolving lineages were associated with

83   greater extinction risk across 297 genera. We did so by combining the largest time-calibrated

84   phylogenetic tree presently estimated for vascular plants with all available peer-reviewed

85   assessments of conservation status from the International Union for Conservation of Nature

86   (IUCN) *Red List* (2016). We complemented our findings with analyses for two large,

87   ancient, and widespread plant clades (conifers and palms). We collated data on range size

88   and range filling for these two groups to test the age-and-area and (mis)matching hypotheses,

89   and how they might explain differences in age-extinction correlations between taxonomic

90   groups with contrasting histories. Positive age-extinction correlations would implicate the

91   mismatching hypothesis, while negative correlations would implicate matching or the age-

92   and-area hypothesis, depending on the strength of underlying associations with range size and

93   filling. These analyses also allowed us to address concerns around estimating divergence

94   times and threat status from the larger but under-sampled phylogenetic tree.

95

96   **Methods**

97   *Data assembly*

4

98   We first selected genera for which we could confidently estimate the time of divergence from

99   their sister genera (i.e. 'stem age'). Genera were selected from the time-calibrated, species-

100   level phylogenetic tree of Qian and Jin (2016), which was an updated version of Zanne et al.

101   (2014). The selected genera came from densely sampled clades (i.e. families) to circumvent

102   low sampling across the broader tree both at a species- and genus-level. For each family, we

103   calculated the proportion of genera that were sampled in the phylogeny from the taxonomic

104   database curated by the *taxonlookup* v1.1.1 package in R v3.2 and retained those with ≥60%

105   coverage. We also used stem ages because they only require one species to be sampled

106   within each genus and reflect the entire evolutionary history of clades unlike crown ages that

107   can have young age biases because they consider only extant species (Scholl and Wiens

108   2016). Taxa outside of an established "core clade" for each genus, as determined using

109   *MonoPhy* in R, were removed prior to all calculations. After calculating ages from the large

110   tree, we intersected the selected genera with 20,473 IUCN assessments (IUCN 2016) and

111   calculated the proportion of species in each genus threatened with extinction. We further

112   restricted our analysis to genera with >1 species, of which ≥20% had sufficient data to be

113   assessed for extinction risk. Overall, $n = 297$ genera had both reliable age and risk status data

114   spanning 2,679 IUCN species-level assessments.

115   We also estimated net diversification rates for each of our selected genera. We used a

116   well-established method-of-moments estimator that assumed diversification rates were

117   constant over time within genera given a known stem age and species richness (Magallon and

118   Sanderson 2001). Following standard practice, we assumed three values of relative

119   extinction ε of 0, 0.5 and 0.9 when estimating diversification (Magallon and Sanderson

120   2001). Taxonomy was standardised to The Plant List nomenclature using the *Taxonstand* R

121   package prior to processing all datasets.

122   We also repeated our diversification analysis as above with two large clades that were

123   well sampled at a species-level in separate time-calibrated phylogenies. These clades

124   included 70% of all 651 accepted Pinales (extant conifers) (Leslie et al. 2012) and all 2,539

125   Arecaceae (palms) (Faurby et al. 2016). We intersected risk statuses of the two clades with

126   species stem ages, giving $n = 340$ and 346, respectively. For the palms, we used the

127   maximum clade credibility tree that we computed from the posterior distribution of trees that

128   was generated using topological constraints based on Govaerts taxonomy recommended in

129   Faurby et al. (2016).

130   Finally, we assembled range data for our two large clades. Georeferenced records

131   with no flagged issues were downloaded from the Global Biodiversity Information Facility

132   (www.gbif.org) using the R package *rgibf*. Conifer data were supplemented by published

133   records absent from GBIF (table A1 available online). All duplicate and spatially invalid

134   records (e.g. non-numerical, exceeding global extent, located in the ocean, urban areas, or

135   country centroids) were removed with the R package *sampbias*. Using the occurrences, we

136   estimated the actual range size as the total number of 0.25 decimal degree grid cells occupied

137   by each species (after Grossenbacher et al. 2015). To estimate potential range size, we

138   employed a mechanistic species distribution model (SDM) that predicts the physiological

139   tolerances of species for growth from distribution data (Higgins et al. 2012). Absence points

140   for the SDM were generated using standard approaches (full details given in Appendix A).

141   We then summed the total number of 0.25 decimal degree grid cells potentially occupied by

142   each species and calculated range filling as the ratio of the actual to potential range size.

143

144   *Statistical analyses*

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145   We separately tested whether genera with a greater proportion of threatened taxa were

146   correlated with younger ages and faster diversification rates using phylogenetic least squares

147   (PGLS). We fitted the PGLS using the *gls* function in R to account for different sample sizes

148   within each genus by weighting observations with the inverse square-root of the number of

149   IUCN assessments that they received (Garamszegi and Møller 2010). Following standard

150   practice, the PGLS was fitted with maximum-likelihood transformations of branch lengths

151   based on the strength of phylogenetic covariance estimated by Pagel's λ (Orme 2013). Both

152   ages and diversification rates were log-transformed. Models were not fitted with both

153   predictors simultaneously as they were highly correlated (Spearman's $r < -0.79$). We

154   repeated this analysis in conifers and palms, and again did not simultaneously fit age and

155   diversification rates given high correlations ($r < -0.71$ when $\varepsilon = 0.0$ or 0.5). Fit of the PGLS

156   was summarised by the correlation coefficient r between predicted and observed values.

157   For conifers and palms, we also tested whether extinction risk was associated with

158   younger species and how this was influenced by range dynamics. We first fitted logistic

159   regression models to threat status as a function of species age using penalised maximum-

160   likelihood and accounted for phylogenetic non-independence of species with the *phylolm* R

161   package. Predictors were scaled to a mean of 0 and standard deviation of 1 to compare

162   effects. We then tested how range size and filling were associated with species age. To

163   reduce potential biases in divergence time estimates that can confound associations with

164   range size (Hodge and Bellwood 2015), we focused our analysis on pairs of sister species

165   with contrasting risk status (i.e. non-threatened and threatened species of the same age). For

166   each sister pair, we calculated the difference in range filling and size. We expected

167   threatened species would, by definition, always have relatively small ranges, producing an

168   invariant or weak age-range association. By contrast, non-threatened species should reach

169   larger and/or more filled ranges with age if the age-and-area or matching hypotheses were

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170   supported, resulting in greater disparity between the two threat categories over time (i.e.

171   positive correlation). We tested if this correlation was different than expected by chance by

172   comparing it to the correlation calculated from randomly sampling the same number of sister

173   pairs 1,000 times, but choosing those where both members of the pair were non-threatened;

174   both members were threatened for palms as most pairs fell in this category. We also checked

175   signs of range-age correlations for each threat category individually using PGLS to verify

176   whether statistically significant correlations in our sister analysis arose from ranges

177   increasing or decreasing more slowly with age in one group as opposed to another.

178

Results

180   We found that relatively more species were threatened with extinction in faster diversifying

181   genera (for ε of 0.0, 0.5, 0.9: t_{295} = 2.13, 2.18, 2.24 and p = 0.034, 0.030, 0.026, respectively;

182   r = 0.15 for all). The mean proportion of a genus threatened with extinction doubled from

183   36% to 71% between the slowest and fastest diversifying genera (fig. 1). These results did

184   not arise because faster diversifying genera were younger, as genus age had no effect on risk

185   status (t_{295} = -1.66, p = 0.099, r = 0.13), but we did find an age bias in our dataset. Sampled

186   genera were older and more diverse on average than obtained by applying our sampling

187   criteria to the initial tree (i.e. before intersecting with threat status; table B1), which may

188   explain why we failed to detect an association between younger genera and extinction risk.

189   Diversification was also slower in our sample, but the sampling criteria did not lead to

190   differences in risk status (table B1). Repeating our analyses with only the genera from the

191   more complete species-level datasets was inconclusive, likely because of small sample sizes

192   ($n \leq 36$; table B2).

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193   Analyses with the more complete species-level datasets also revealed that younger

194   conifers but not palms were relatively more threatened by extinction (z_{344} = -2.67, p = 0.008

195   and z_{338} = -1.46, p = 0.145, respectively; fig. 2a). The mean effect ± SE was more than twice

196   as large in the conifers (-0.36 ± 0.14 vs -0.15 ± 0.10 on log-scale), leading to nearly a 50%

197   absolute reduction in the probability of being threatened over the range of observed ages (fig.

198   2b).

199   Greater range filling reduced extinction risk of older taxa, supporting the age-and-area

200   hypothesis. Range filling increased with taxon age in non-threatened conifers (i.e. positive

201   slope) more strongly than in threatened taxa, resulting in a greater difference than expected if

202   sisters had the same threat status (r = 0.15, p = 0.004; fig. 3a). By contrast, range size

203   differences did not vary over time (r = -0.16, p = 0.567; fig. 3b). Contrasting threat status did

204   not alter correlations between age and either range size or filling in palms, consistent with the

205   lack of an age-extinction association (r = 0.04, p = 0.379 and r = -0.13, p = 0.868,

206   respectively).

207

Discussion

209   Lineages that occupy less of their potential range face a greater risk of extinction (IUCN

210   2016), and our results suggest that this may depend on taxon age in at least two ways that are

211   consistent with the age-and-area hypothesis. First, young species tend to occupy narrower

212   geographic and adaptive spaces (Castiglione et al. 2017), particularly as most plant speciation

213   involves vicariance (Davies et al. 2011; Anacker and Strauss 2014; Igea et al. 2015). Time

214   may consequently be required for post-speciation range expansions despite much of the

215   available area remaining favourable for establishment (Pigot et al. 2010; Pigot and Tobias

216   2013; Anacker and Strauss 2014). Second, if species diversification is density-dependent,

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217   such as because of limited resources, then younger lineages that fill less of their range will

218   tend to produce relatively more young species (Rabosky and Hurlbert 2015). Faster rates of

219   species diversification will again elevate extinction risk in younger lineages if reproductive

220   isolation arises within small geographic and adaptive spaces. By contrast, time-dependent

221   range expansions may be unnecessary under other modes of speciation, e.g. parapatry or

222   sympatry (Pigot et al. 2010), and if range expansion is not limited post-speciation (Schurr et

223   al. 2007). These contrasting dynamics of different speciation modes can also help explain the

224   lack of consistent evidence for age-dependent extinction across the large taxonomic scale in

225   our study and across animals (Gaston and Blackburn 1997; Johnson et al. 2002; Davies et al.

226   2011; Arregoitia et al. 2013; Greenberg and Mooers 2017)

227   Palms and conifers have different biogeographic histories that can explain the

228   contrasting results between the groups. Conifer diversification is presumed to have depended

229   on range contraction and expansion (Leslie et al. 2012; Condamine et al. 2017), whereas

230   palms may have formed new species by dispersing into new habitats that were subject to

231   divergent adaptation rather than vicariance (Savolainen et al. 2006; Roncal et al. 2015).

232   Thus, older conifers may have had more time to fill their ranges and reduce their extinction

233   risk. The predominance of conifers in topographically complex regions, especially in the

234   Northern Hemisphere, further supports the importance of time-dependent range shifts in

235   fostering diversity (Leslie et al. 2012). Palms are also restricted to the more ecologically

236   stable tropics, where range dynamics may vary less over time (Couvreur et al. 2011), though

237   such stability may equally help explain the resilience to extinction of older conifers in the

238   Southern Hemisphere (Leslie et al. 2012; Jordan et al. 2016). Finally, we cannot exclude the

239   possibility that palm species that were susceptible to environmental change have already gone

240   extinct or traits that make species more prone to extinction are not taxonomically conserved,

241   resulting in no signature of taxon age on extinction (Arregoitia et al. 2013). Our results with

242 conifers and palms were also not simply an artefact of biased sampling as ages and rates did

243 not markedly differ from observations across entire clades, i.e. before filtering with IUCN

244 data (table B3). Similar results to the larger phylogeny further suggest that our conclusions

245 were robust to biases in IUCN assessments (Webb and Mindel 2015).

246 Our results suggest that macro-evolutionary dynamics have some value for

247 biodiversity conservation. Specifically, we found that these dynamics provided an indicator

248 of contemporary extinction risk that might be easier to derive for large numbers of taxa than

249 detailed species-level assessments. Macro-evolutionary dynamics might also offer insight

250 into the vulnerability of species to future change, as the smaller population and range sizes

251 that make some species prone to extinction are likely to be carried into the future (Condamine

252 et al. 2013). Although our results must be interpreted with caution, given biases inherent to

253 our datasets, they provide new evidence that lineages span a continuum from little species

254 turnover to producing fast diversifying and extinction-prone taxa (Greenberg and Mooers

255 2017). The consistent effect of age that we found at different taxonomic scales also suggests

256 similar patterns should emerge when the plant Tree of Life becomes more densely sampled.

257

258 **Data Accessibility**

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

260

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264

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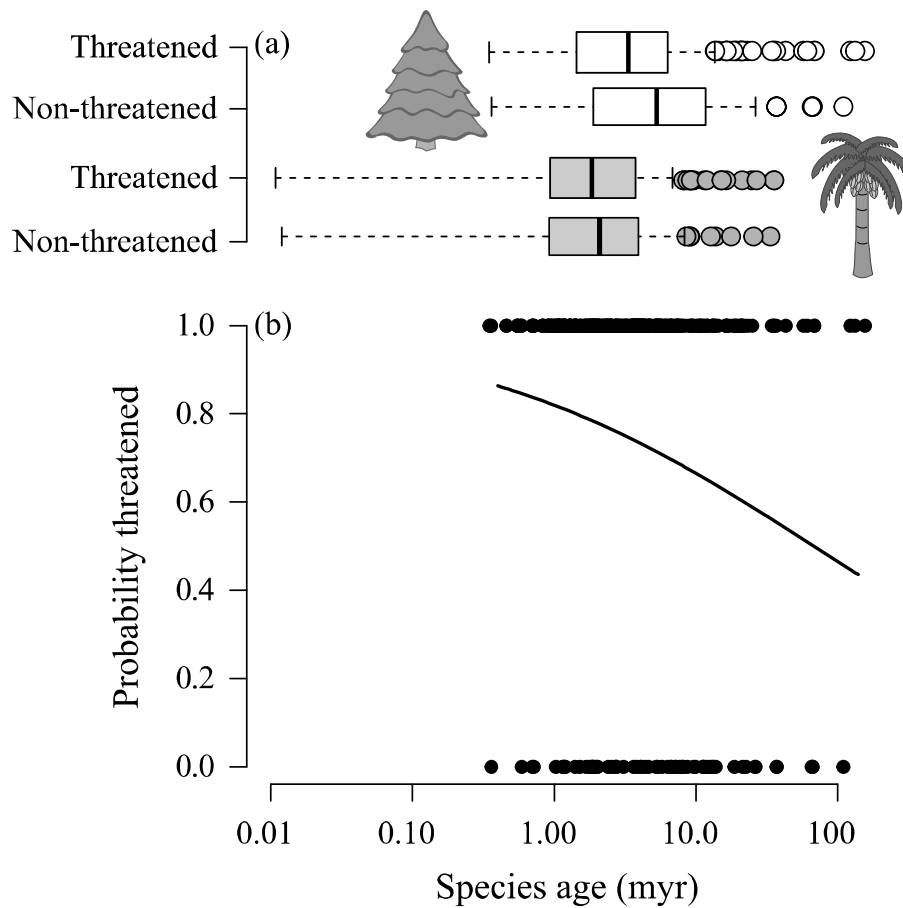
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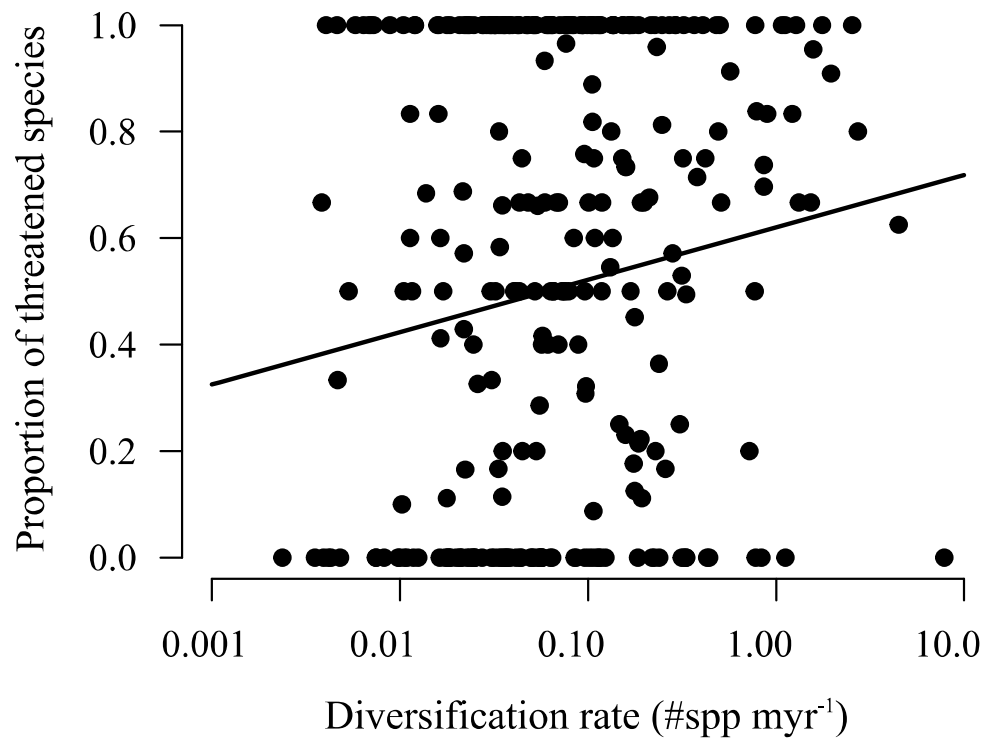
Figure 1. More species are threatened with extinction in faster diversifying genera. Solid line is mean association estimated by PGLS for $\varepsilon = 0.50$.

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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.

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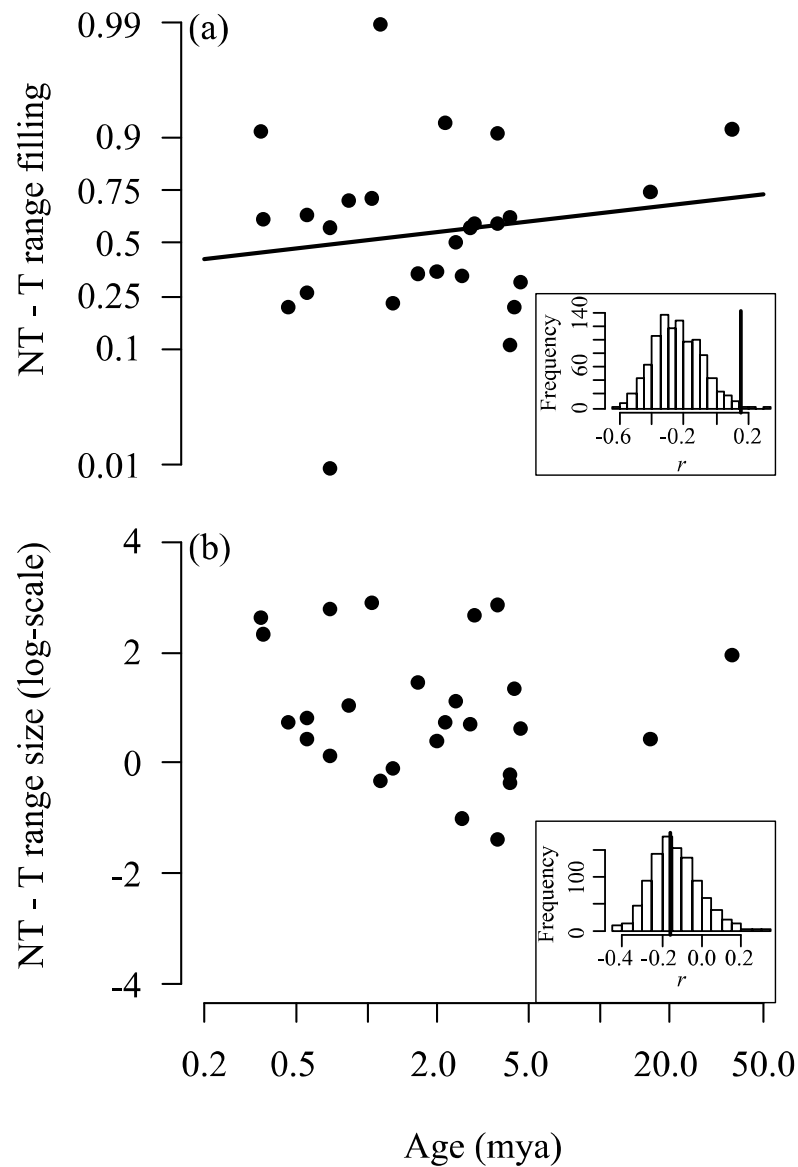
Figure 3. Differences in range characteristics between sister conifers of contrasting threat status changes with their age. For each sister pair of non-threatened (NT) and threatened (T) taxa we calculated the difference in the (**a**) proportion of their potential ranges that was filled and (**b**) the absolute size of log-transformed ranges. Solid line is the 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 threat status (i.e. corresponding to plotted data points).