

AE report:

The revised version of this interesting study connecting past diversification and present-day extinction risk offers contrasting patterns at two taxonomic levels, and tying the two patterns together is proving a bit difficult, at least for me.

The initial, taxonomic large-scale pattern – and what originally set the paper apart as potentially of note – is the following: across a large set of vascular plant genera, there is a consistent, if not strong, correlation between average diversification rate (or younger genus stem age) and the probability of being globally threatened (Figure 1a). This is consistent with patterns in Amphibians (Greenberg and Mooers) and plants (Schwartz and Simberloff and Davies et al.), and there are interesting mechanistic connections via ongoing and rapid peripatric speciation leading to small geographic ranges in young species.

However, after reviewing their data, the authors now report a (backwards from the previous version and) contrasting pattern for conifers – here species on longer terminal branches are more likely to be listed as globally threatened (Fig. 2). Conifers are an "old" taxon, associated with a warmer, wetter earth, and it is certainly possible that what drove their diversification and what drives their current global status might be different from vascular plants more generally.

The authors decide to compare the "potential" range size of pairs and threatened (TH) vs. non-threatened (nonTH) species, and lay out a particular scenario consistent with the results across plant genera (lines 188+): "For example, there may be greater disparity in the ranges of young species pairs under peripatric as opposed to allopatric speciation (Gaston 1998; Hodge and Bellwood 2015), resulting in a negative correlation between age and range disparity." This, to my mind, implies that younger species are both more likely to be at risk, and that, as time passes, and sister-species range sizes become more equal as the peripatric budding species increases its range, and the "younger" species of the pair becomes non-threatened. However, the first part of the scenario is not supported by the initial conifer data, so it is hard to gauge what to do with this model; confusingly, the difference in potential range between nonTH and TH sister species does seem to decrease with time (Fig. 3). So, if we combine the results from Fig. 2 and Fig. 3 together, we have younger nonTH-nonTH pairs and older nonTH-TH and TH-TH pairs (assuming there are some of this third class).

The authors interpret the Fig 3 pattern (expected from line 188 under peripatric speciation) as follows: because TH species will have small ranges by definition, the equalizing of ranges with age is consistent with the nonTH species in nonTH-TH pairs losing range via specialization or loss of habitat over paleontological time.

We apologise for the confusion. We believe the conifer results are entirely consistent with the model that we have tried to present. Specifically, younger conifer species do not have to be more at risk. Under a peripatric mode of speciation, a new budding species will have a smaller range than its sister species. As time passes, the ranges of the sister species can become more equal either because the peripatric budding species increases its range faster than the NT species (which we think lacks strong *a priori* support) or the larger-ranged species is disproportionately impacted by environmental change (consistent with the niche specialisation hypothesis and even the hat-like patterns of taxon history described by Žliobaitė et al. 2017 *Nature*). However, only the second scenario would be consistent with the observed negative correlation between age and extinction risk that we observe because only the second scenario predicts that species ranges decline over time and would be older species are greater risk of extinction.

As we hope is true in our case – that a picture is worth a thousand words – we have now added the following to page 4 the ESM:

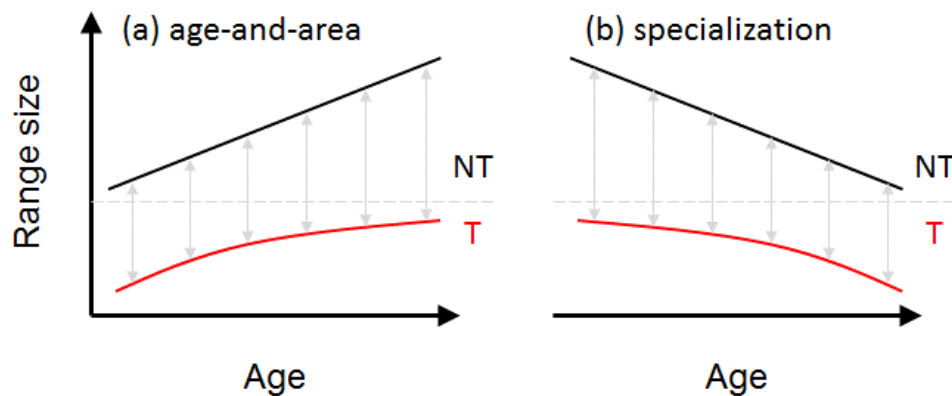


Figure A1. Hypotheses for how range size could vary with taxon age in non-threatened (NT, black) and threatened (T, red) taxa. Vertical grey arrows show how the disparity between NT and T sisters correlates either (a) positively (i.e. increases) or (b) negatively (i.e. decreases) with time. In this example, we use a binary threshold in range size to differentiate between NT and T taxa (above and below dotted horizontal line, respectively), while recognising that this classification is likely to be much more complex in reality.

In NT taxa, (a) the age-and-area hypothesis predicts that range size increases with more time for dispersal and range expansion, whereas (b) the evolutionary specialism hypothesis predicts traits that were once advantageous become less adaptive as environments change, resulting in smaller ranges in older taxa. We expect both trends to be weaker in T taxa (i.e. flatter slopes), because smaller ranged species should have fewer opportunities for range expansion and contraction and so should change proportionally less.”

We have also added the following on lines 186-190 to help clarify the underlying model: “For example, there may be greater disparity in the ranges of young species pairs under peripatric as opposed to allopatric speciation (Gaston 1998; Hodge and Bellwood 2015), resulting in a negative correlation between age and range asymmetry (fig. A1). This pattern may ultimately result in either a positive or negative association between age and extinction status, depending on whether species expand their ranges with time (i.e. age-and-area hypothesis) or contract their ranges as environments change (i.e. specialism hypothesis).”

Again, we regret that we didn’t include Fig. A1 in the previous submission. We hope that it clears away any remaining confusion.

I leave aside the issues surrounding "potential" vs. "realized" range size, as this is clearly articulated by the second reviewer below. My concern is with the interpretation of the range-size disparity vs. age plot.

We address this issue below where raised by the second reviewer.

My own initial (but perhaps faulty) interpretation of the pattern was that the non-TH vs. TH sister pairs were the appropriate controls for overall "niche breadth." Thinking out loud, it may be that nonTH-TH pairs arise (in any geographic context) in a context that is now deteriorating, the TH species is currently simply the more unlucky member, while the sister

species is also shrinking (and so might eventually become TH). In contrast, nonTH-nonTH pairs (the "controls") are pairs that arose in (large) stable niche space; these two ideas together would support Fig. 3. However, this links threatened status to niche contraction fairly indirectly by specifying a scenario where both members of the nonTH-TH contrast represent adaptation on a shrinking niche space. And, if shrinking niches were also older than stable ones, then we could get Fig. 2. Unfortunately there is no overall negative relationship between potential range size and lineage age (Table B1), implying that older conifer species generally are not losing out in this way.

As we have explained on lines 179-181, we think that this analysis is somewhat problematic given systematic differences in the ages of the two groups that can obviate any overall relationship.

(Perhaps a more focused test of this scenario would be to compare the average potential range size of the nonTH species in nonTH-TH pairs with the average of nonTH-nonTH pairs. I don't know, though.)

We do not entirely follow why a NT species would have a smaller range size when paired with a T sister. On the contrary, the fact that the NT species do not have smaller ranges when paired with T as compared with when they are paired with a NT supports our use of this analysis as a "control".

Added on lines 201-204:

"Reassuringly, potential range size of non-threatened conifers and threatened palms did not differ in our analysis when sister species had the same threat status, supporting their use as "control" contrasts (t-test: $t_{177} = 0.183$, $p = 0.855$ and $t_{124} = 0.597$, $p = 0.552$, respectively)."

Of course, this may not be the scenario the authors have in mind, but whatever model needs be made clearer, and then challenged with the data. Both I and the other reviewer are uncomfortable using TH species as controls here, at least without more justification.

Thank you for the opportunity to clarify the scenario that we wish to present.

Added on lines 190-196:

"For example, there may be greater disparity in the ranges of young species pairs under peripatric as opposed to allopatric speciation (Gaston 1998; Hodge and Bellwood 2015), resulting in a negative correlation between age and range asymmetry (fig. A1). This pattern may ultimately result in either a positive or negative association between age and extinction status, depending on whether species expand their ranges with time (i.e. age-and-area hypothesis) or contract their ranges as environments change (i.e. specialism hypothesis)."

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One additional thought: As I read through the paper once again, I keep getting caught up at line 115. Given that stem ages are being used to estimate age and diversification rates, why do you drop monotypic species – surely these are "low diversifiers" par excellence?

Added on lines 116-117:

"We excluded 154 monotypic genera because these would confound our analyses as they all had the same diversification rate irrespective of lineage age."

Report from Dan Greenberg:

The revised version of Tanentzap et al. "Range size dynamics can explain why evolutionarily age and diversification rate correlate with contemporary extinction risk in plants" addresses several issues raised in the previous review, but now raises several additional issues and outstanding questions with their updated analysis.

The revised introduction is a major improvement, as it sets up a clear rationale for the various ways in which speciation events, time since speciation, range size and extinction risk could be expected to interact under various hypotheses. My interpretation of the crux of their argument is that evolutionary 'age' can relate to extinction risk in two potential ways:

1. That recently diverged species are at a higher risk of extinction due to:

- a. Smaller geographic ranges due to recent speciation
- b. Less of their potential range being filled
- c. Potentially higher specialization/lower generalism compared to more ancestrally diverged species

2. That species which diverged earlier are at a higher risk of extinction due to:

- a. A declining environmental niche space, and
- b. Increasing specialization through time

The authors seem to find contrasting support for these hypotheses at different scopes: hypothesis 1 is supported as rapidly diversifying plant genera have a higher proportion of threatened species, but hypothesis 2 is supported within a species-level analysis of the conifers, with no clear relationships among palm species. Though some predictions of these hypotheses are indeed tested, I find the overall message of the manuscript to be confusing due to 1) contrasting patterns at different taxonomic levels without a clear explanation of why these would/should differ, and 2) a lack of realized range data to test the key predictions that range size either declines or increases with divergence time across species, and 3) the fact that it's unclear what the potential range size metric actually represents, presumably some measure of fundamental niche breadth, but without realized range data it's hard to grasp what is going on here.

We address each of these points below in response to the expanded comments.

With respect to 1):

The authors explain the contrasting age-risk patterns in conifers vs plants generally due to differences in speciation mode: conifers being highly vicariant rather than the more dispersal-driven palms going forth and colonizing new adaptive landscapes. However, a mode of speciation that relies on budding would expect the opposite relationship in my mind: lots of vicariance should result in higher risk in younger species that are range-restricted (as they are recently budded). Indeed, this is the mechanism Davies et al. 2011 invokes for the Cape Flora, and perhaps if anything we'd expect most plant lineages to follow this vicariance driven model (supporting the broader observation among plant genera). Is the difference in age-risk relationships due to a difference between peripatric vs. other forms of allopatric speciation? Are conifers unique or are they closer to the common rule amongst the other plant clades?

Added on lines 190-196:

“For example, there may be greater disparity in the ranges of young species pairs under peripatric as opposed to allopatric speciation (Gaston 1998; Hodge and Bellwood 2015), resulting in a negative correlation between age and range asymmetry (fig. A1). This pattern may ultimately result in either a positive or negative association between age and extinction

status, depending on whether species expand their ranges with time (i.e. age-and-area hypothesis) or contract their ranges as environments change (i.e. specialism hypothesis).”

Added on lines 260-274:

“The global status of conifers differs from palms and other plant clades, potentially explaining why older species had smaller potential ranges that made them more threatened by extinction. Conifer species are older on average than the rest of the Qian and Jin (2016) tree (Welch’s *t*-test: $t_{465.5} = 13.71$, $p < 0.001$), and many species are range-restricted (Farjon 1996; Jordan et al. 2016). Consistent with the evolutionary specialism hypothesis, most old conifers evolved during warmer wetter climates, where they occupied larger ranges than in the present day (Farjon 1996; Jordan et al. 2016). Old species may have only escaped extinction by inhabiting climatic refugia that have been historically stable (Leslie et al. 2012; Condamine et al. 2017). ... By contrast, most palm species have occupied relatively large areas of stable habitat since the Eocene (Kissling et al. 2012), potentially explaining the lack of age-range correlations. Speciation in palms may have also occurred largely by long-distance dispersal (Baker and Couvreur 2013), which can produce less range asymmetry (Gaston 1998). Consequently, palms may lack age-range associations that influence extinction risk.”

With respect to 2):

I think the authors need some measure of realized range size in here to make this all logical. Simply it's not clear how divergence time and range size relate in palms vs. conifers, but this is key to our understanding of the range-risk-age relationship. The potential range size metric doesn't seem to address the key predictions of the hypothesis, and it's hard to interpret as a "potential" metric (especially as a ratio between NT:T species, see below).

The Reviewer’s concern is that potential range size does not seem to address the predictions of the study hypotheses. We agree that this is the case for prediction 1a above, but this prediction is not actually presented in the MS. For predictions related to specialisation, potential range size is a better metric because it is not confounded by dispersal limitation and biotic factors that influence realised range size. Therefore, given that this point only addresses one potential prediction – which isn’t even explored in our study – we have made no further changes to the text.

Reviewing their previous version with the range filling metric I actually preferred this to the new "potential range size" metric, although I agree that the number of occupied cells is likely far underestimating the actual range size of these species. I'm not sure what the solution is here since I'm not familiar with plant biodiversity data - are there IUCN polygons for species or can they build a minimum convex polygon between GBIF points to estimate realized range size?

No IUCN polygons exist for plants nor are minimum convex polygons a robust approach. These concerns were raised by the other Reviewer in the previous round and, for these reasons, we removed these analyses from the MS. Reinstating these analyses would be tenuous given the previous discussion and anyway have ambiguous results. Correlations between age and range filling are non-significant in palms (consistent with the lack of age-extinction associations) and there is only a positive correlation for non-threatened conifers with no significant correlation when controlling for age (i.e. in the sister-contrast).

An additional reason to avoid using range filling is that it is, by definition, artefactually correlated with potential range size. If we let P = potential range size, and A = the actual

range size, and assume A and P are independent, then the covariance between P and A/P is given by $\text{cov}(P, A/P) = E[A] - E[P] E[A/P] = E[A] (1 - E[P] E[1/P])$ using independence. Jensen's inequality then gives $1/E[P] \leq E[1/P]$ as P is positive. Thus, $E[P] E[1/P] \geq E[P] 1/E[P] = 1$, and so $E[A] (1 - E[P] E[1/P]) \leq 0$. Under these assumptions, we would expect a negative covariance/correlation to arise without any real biological mechanism. Such an artefact would confound interpretation of any observed effects.

With respect to 3):

The authors then use an analysis of range potential to help explain this pattern. However, I'm not entirely sure why they had the NT:T species pairing as these are contemporary human distinctions, although they may reflect biological attributes as well. As well, it's not clear that there should be a difference in range potential changing over divergence time for threatened vs non-threatened groups.

We do not entirely understand this comment and would welcome further clarification. Our comparison of the NT and T distinctions is the basis of our study and reflects biological attributes, such as range size, by definition. This comment also seems unrelated to whether we are using potential or realized niche sizes, which we thought was the whole point of comment 3) according to the introductory comments above.

Similarly, is there a relationship between potential range size and threat status? Presumably a small potential range size indicates a high degree of specialization and subsequent extinction risk – it would be interesting to specifically test this.

Yes, there is a relationship between potential range size and threat status. We tested this idea in Table B1 and have now made it explicit in the text.

Added on lines 234-235:

“Larger potential ranges did, however, always reduce extinction risk (table B1).”

I think the manuscript could be made much clearer if an estimate of current range size were added, and potentially contrasted with the potential range size metric, to specifically test several predictions of the hypotheses that were presented.

We think that a current range size estimate might make the MS less clear because it involves new assumptions. Importantly, we do not understand why current range size is a better metric than potential range size in the context of our study hypotheses (i.e. 1a-c and 2a-b), and would welcome further guidance from the Reviewer.

It seems critical to know: whether recently diverged species have smaller range sizes on average, whether recently diverged species have filled more of their potential range size, and whether evolutionary range size patterns differ within palms and conifers.

We have tested all these ideas in relation to potential range size as explained on lines 172-175. The results are included on lines 229 and 234 and in Table B1.

Though the ideas and concepts presented in this manuscript are very compelling, I think there's further digging into the data that will be required to fully understand how range dynamics contribute to patterns of extinction risk in the plant tree of life.

We thank the Reviewer for their encouragement and hope that our clarification of the analyses will support the ideas and concepts that we present.