

Dear PCI Evol. Biol., Dr. Meseguer,

Thank you very much indeed for this further input on our preprint. We have used your comments to further improve the ms.: this includes addressing points raised by the new reviewer by clearing up an error we had introduced in describing the methods (it was 1 minute, rather than what would have been a much bigger 1 degree of buffer around occurrences); testing the impact of using just the occurrences themselves; and by qualifying our use of the word “niche” in the context of realised versus fundamental niche. Detailed responses to these and the other more minor points are included below, and changes to the text are indicated as tracked changes in a version we will provide in addition to v.3 of the preprint.

It occurs to me to suggest that if you are generally satisfied with our next version of the ms., but still harbour differences in opinion on the issue of biogeographic model testing, you might want to consider addressing these in your recommendation text. I think this provides an excellent opportunity for a direct and open response, and it would give us an additional source to cite in order to be maximally open about such concerns in the final version.

On behalf of the authors,

Mike Pirie

Decision

by Andrea S. Meseguer, 2018-11-25 15:43

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Needs a revision

This paper has improved from the last version and the authors have taken into consideration and answered many of the concerns raised in the initial review. Reviewer 1 believes it is in good shape for recommendation after a few minor revisions. Reviewer 2 did not see the original, but only the revised version and agrees with Rev 1 that the paper is of general interest. However, Rev 2 has some substantive comments that need to be dealt with before the paper can be accepted for recommendation. The most critical comments centre on the niche modelling approach and how this affects your results. Rev 2 has a number of other critical but supportive and constructive comments that will make the paper more useful for the biogeographic community.

The authors' response to my critique of their use of the DEC+J models is satisfying. I agree that this ms is not the place to go into the detail of this argumentation, although I appreciate they acknowledge the controversy and provide the DEC results. Just as a note of caution, the

recent paper of Ree & Sanmartin (2018) shows that DEC and DEC+J models are not directly comparable using statistical methods such as AIC that assume probabilistic equivalency of events. Therefore, I recommend privileging arguments based on empirical (biological, geographic) considerations rather than AIC scores. AIC comparisons might otherwise work to compare DEC (and DEC+J) models among them.

Mike: Certainly we can act on this suggestion to emphasise the biological arguments already set out in the ms. However, in correspondence that we have had with Matzke he also took issue with this particular conclusion from R&SM, arguing strongly against abandoning statistical model comparison. The following changes in the results are a bit of a compromise:

“Assuming that AIC values of the differing models can be compared (but see Ree and Sanmartín, 2018), DEC/DEC+J models generally fit the data better than Bayarea-like or DIVA-like models and DEC+J models generally fit the data better than equivalent DEC ones (Appendix 8).”

“Adopting DEC+J as the generally better fitting and biologically more realistic model (see Discussion), we assessed the results given phylogenetic uncertainty represented by selected bootstrap trees.”

I regret however, the authors have not fully taken into account my comments about the adjacency matrix. I apologize if this is because I was not clear enough. The “Cape to Cairo” hypothesis (dispersal from Europe to the Cape, followed by migrations to the Drakensberg; Figure 1), could not be properly tested if the adjacency matrix does not allow ancestral connections between Europe and the Cape regions (0 values on this connection). By setting 0 values you are specifying that these two areas were not connected in the past (an ancestral distribution in Europe and the Cape is disallowed). Hence, although in theory dispersal is still allowed, in practice this constraint forces species to follow another route to disperse between these areas or forces jump dispersal. In my opinion this is a too strong assumption when the “Cape to Cairo” is the hypothesis to test, specially given the possibility that before the Miocene aridification of northern Africa, Erica was distributed in regions where it does not occur today. This limitation seems to apply only to DEC+J and not to DEC analyses where the adjacency matrix was not implemented. I suggest testing again the hypotheses without this constriction, which will make the results more solid.

Mike: I think we understood each other, but perhaps simply disagree here. Yes, under the besting-fitting DEC+J models dispersal from Europe (or indeed Tropical Africa) to the Cape can only be via jump dispersal, but I don't see a problem with that. Certainly it doesn't constrain the results to follow a particular route: the results showed jump dispersal from TA to the Cape, but they could have shown jump dispersal from Europe if that had fit the data better. Conversely, I do see a problem in allowing widespread distributions between non-adjacent areas, even if past distributions were wider. This may be unavoidable for the DEC models, but as we argue it doesn't make biological sense. What we will do is to present the ancestral area reconstructions for both the set of best-fitting models and the more poorly fitting unconstrained ones to show that those results are consistent irrespective of assumptions; these are now in the improved Appendix 13 (see below). We won't further discuss these in the context of hypothesis testing because they are just two of many suboptimal models.

I also have a few minor points: - The biogeographic reconstructions on Appendix 13 don't have any legend. You need to explain the symbols on the trees, the colours, the abbreviations or the analyses that have produced these figures. In addition, the size of the pie charts on the

trees is way too big and needs to be reduced. - The unconstrained biogeographic DEC and DEC+J reconstructions need to be presented the Appendix.

Mike: We have fixed the pie charts and expanded the caption for Appendix 13 – it was in the text, not embedded within the appendix itself – and now include the reconstructions based on the unconstrained models too:

“Appendix 13: Results: Ancestral area reconstructions inferred using BioGeoBEARS given the best tree under the best fitting model given A: DEC+J; B: DEC; and without range or dispersal constraint: C: DEC+J; D: DEC. For each model the single most probable state is shown first (boxes with areas at nodes) followed by the relative probability of each state represented with pie charts at nodes. Areas are represented by colours: Dark blue for Europe (E); green for Tropical Africa (T); yellow for Madagascar (M); light blue for Drakensberg (D); red for Cape (C); and further colours for widespread distributions as indicated in the legends.”

- Please, clarify if the “Cape to Cairo” model fits the data better than “Southerly stepping stone” model. Discussion lines 285-287 state: “Cape to Cairo” and “Drakensberg melting-pot” mostly fit the data better than “Southerly stepping stone”. Meanwhile, in the results: “Under DEC+J given the best tree, the Drakensberg melting pot, geographic distance, and southerly stepping stone models revealed the lowest AIC; under DEC the Drakensberg melting pot model alone scored best, but with higher AIC”. Moreover, in Table 1, the CtoC model does not even appear among the best models when considering the best tree.

Mike: I think we’re consistent – the results first report the best fitting models given the best tree (no CtoC), then go on to those given the set of trees (CtoC features but not SSS); in the discussion we refer to all the results. Clarified as follows:

“Of the stepping-stone-dispersal models, “Cape to Cairo” and/or “Drakensberg melting-pot” fit the data better than “Southerly stepping stone” **for all but the best tree,**”

I hope that the authors will find these comments helpful to improve their work.

Indeed we have – our thanks again!

Yours sincerely,

Andrea S. Meseguer

Reviews

Reviewed by Florian Boucher, 2018-10-05 11:00

[Download the review \(PDF file\)](#)

Text added here:

I have now assessed the revised version of the manuscript by Pirie and colleagues on the historical biogeography of the genus *Erica* in the Afrotemperate region. As stated in my original review, the writing of the ms is clear and I appreciate the robust hypothesis-testing setting of the study. I also think that the question(s) tackled here is important, especially in the era of statistical historical biogeography. It is pleasing to see that the authors have taken into consideration and answered most of the concerns I had raised in my initial review, and I think

that after these clarifications the manuscript would be publishable as is. I still have some comments that might help improve it further in my opinion.

In the Results section I still get the feeling that the two types of biogeographic hypotheses (distance/ climate vs. specific biogeographic scenarios) are presented together, which might be a bit difficult for the readers to follow. The authors might want to improve that a bit still. The distinction between both kinds of biogeographic explanations is however made much clearer in the Discussion, which is very good and which I think improves a lot the clarity of the paper.

Mike: we have them under separate subheadings before reporting the ancestral areas – not sure what more to do here.

While I am still doubtful about the performance of ‘+j’ models in Biogeobears (perhaps I need to see Matzke’s rebuttal first so that I understand his line of defense), the authors’ response to my critique of their use of these models is satisfying. They are taking some kind of a risk here, but they’ve investigated the question deeply and are aware of possible consequences. I appreciate the fact that they deal with this issue directly in the text and I also must say that the fact that most speciation events inferred are NOT founder event speciation makes me trust their results a lot: it is good choice to write it explicitly now in the revised version of the MS.

I would still recommend that the authors give the units of parameters j and d from the DEC+J model. I was asking for this in my first review but did not get an answer on this point. The parameter d is a probability of dispersal per unit time (Myrs probably here) and this is why I was asking about the typical branch length in the *Erica* phylogeny: since j is a probability of dispersal per node, its value would be better compared to $d \times \text{typical_Branch_length}$ I think.

Martha: We added the units for the d and e values [1/Ma] in the text and Appendix. J is the probability of jump dispersal per node. Text modified as follows:

“For example, the values for range expansion (parameter d) were similar and low (0.0030 and 0.0027 per Ma respectively; Appendix 9). Under DEC+J, cladogenetic dispersal (parameter j) was 0.0024 per node, i.e. lower than d (particularly given an average branch length across the *Erica* phylogeny of 1.78 Ma, variance of 11.67) and much lower than the maximum permitted value (3).”

Below are three more specific and minor comments, with line numbers referring to the tracked .docx file.

L. 78-79 : shall you briefly describe what both of these scenarios are for readers who are unfamiliar with them?

Bold text added:

(Bellstedt et al., 2012), might thus be best described by biogeographic scenarios emphasising vicariance processes, such as for example the “Rand Flora” representing plant lineages that show similar disjunct distributions around the continental margins of Africa (Sanmartín et al., 2010; Pokorný et al., 2015), or the “African arid corridor” hypothesis that seeks to explain disjunct distributions between the Horn of Africa and arid south-western Africa (Verdcourt, 1969; White, 1983)

L. 96-100: I still find that the description of the ‘niche similarity’ hypothesis for dispersal is too short and vague, even though one sentence describing it has been added compared to the previous version of the ms.

Expanded/modified this part just a little:

“Thus geographic distance and ecological suitability **might individually constrain the biogeographic history of plants, or the interplay between both factors** may be decisive (Donoghue, 2008; Carvajal-Endara et al., 2017), so much so that...”

L. 177: you should say here what is the region covered by PRECIS, most readers won’t know it.

Added:

“representing mostly southern African collections, held by the South African National Biodiversity Institute;”

I hope that the authors will find these last comments helpful and I wish them good luck with their manuscript, which definitely deserves attention from the community.

Yours sincerely,
Florian C. Boucher

Reviewed by anonymous reviewer, 2018-10-05 11:00

General comments

- (1) English sounds good. However, I am not a native English speaker and then I am unable to judge the quality of English language.
- (2) I am not a specialist of biogeographic models and then I am unable to give a strong opinion on biogeographic inferences and model selection.
- (3) As my specialty is niche comparison among species, I will overall focus my comments on this particular aspect of the MS.

Major comments

-L282: Authors depicted the biogeographic regions by using an arbitrarily set buffer of c. 1° lat/lon in radius around presence records.

I am afraid that a 1° radius buffer will introduce erroneous/unsuitable climate conditions for Erica species in analyses. It is worth to calculate niche dimensions using only real presence records ... My biggest concern is about the arbitrary selected 1°C buffer. It could have negative impact on inferences. This is particularly true for species occurring in tropical mountains where 1°C radius could mean an abrupt change in climate conditions. I invite the authors to run again models with true presence records only.

Nicolai: Thank you very much for this remark! There was a mistake in the manuscript: we actually used 1 minutes of arc (resulting in a buffer of ca. 11 km around presence records), not the erroneously stated 1° (~110 km buffer), which would indeed introduce very different climate conditions. This has been corrected in the manuscript: “...placing a buffer of one minutes of arc in radius (ca. 11 km) and 50 m elevation around the individual occurrences ..., conservatively aiming at a representative approximation of spatial extent and ecological conditions

of the species' distribution (Nakazato et al. 2010; Anacker & Straus 2014) in a respective biogeographic area".

Mike: I think this of itself basically addresses the point.

Nicolai: In choosing a buffer for distributional range approximation of species in a biogeographic area we followed other studies (citations added in the manuscript, see above). Because we used the climatic similarity of the 'area ranges' to constrain our biogeographic model, we are convinced that the 'buffered niche' is a more conservative approximation of the climatic conditions with which the ancestral Erica species had to cope with after dispersal from a distant area (e.g. Europe). Following your suggestion, we calculated the Schoener's D values using presence records only. Although values are generally lower in this case, there is a positive correlation ($R > 63$) and a linear relationship between both proxies.

-Are niche similarity/dissimilarity proxies (i.e. Schoener's D values) correlated to geographic distances? If there is correlation, it could impact inferences and model selection procedure. Collinearity is always a problem in modelling and the absence/presence of collinearity between both descriptors should be addressed in the MS. The presence of colinearity could make tricky results interpretation.

Nicolai: Yes, there is negative correlation between both proxies (Kendall's $R = -0.64$). That is why we designed the combined model. In my opinion this clearly indicates the importance of both geographic and environmental distance in shaping plant distributional patterns.

Text modified as follows:

Methods: "Finally, to consider both geographical and environmental distances in a joint model, **also accounting for a negative correlation between both geographic and environmental distances (Kendall's $R = -0.64$)**, we used two rate multiplier matrices"

Discussion: "**The generally better fit of the combined geographic and realized niche model affirms the concerted importance of both factors in shaping distributional patterns of plants (Donoghue 2008; Donoghue and Edwards, 2014).**"

- Authors could be a bit more careful when interpreting realized niche differences. Actually I would be happy to see at some point in the discussion a statement of differences between the realized and fundamental niche and implications of these concepts on the significance of their results. As authors use the term 'niche' without discriminating the fundamental and the realized niche, the MS is sometimes confusing.

Nicolai: Thanks for the comment; we agree the term 'niche' was imprecisely and often confusingly used. We have modified the text throughout for clarity using 'realized climatic niche' in cases when talking about the species and 'ecological conditions' when talking about the distributional ranges in a certain area, which are occupied by several species. However, regarding the scope of the study that does not address evolution of the fundamental niches (see comment below on the interpretation of niche similarity proxies), in my opinion a detailed discussion of realized versus fundamental niche appears misplaced.

Minor comments

L51-53: Authors say ‘The distribution pattern of the more than 800 *Erica* species across Europe and Africa provides an opportunity to disentangle the effects of geographical and ecological distance on biogeographic history’

I am not sure that this statement is pertinent. I would say that combination of genetics, distribution data and fossil information could help to disentangle....

Rephrased:

“The more than 800 *Erica* species across Europe and Africa provide an excellent example with which to test the impact of geographical and ecological distance on biogeographic history.”

L82-83: Authors say : ‘Nonetheless, similar distribution patterns across Europe and Africa are observed in different plant groups.’

References for that statement ?

Added: Gizaw et al 2016, Mairal et al 2017

L84-85: Authors say :Organisms adapted to different habitats respond differently to changing environmental conditions (Mairal, Sanmartín & Pellissier, 2017; Chala et al., 2017).

In my opinion, this statement is obvious and thus useless. Could be removed from the MS.

Obvious perhaps, but not useless to introduce this paragraph we’d argue.

L604: Authors say : ‘In this study, we modelled shifts between biomes and dispersals over larger distances in the evolution of *Erica*, in order to test six hypotheses for the origins of Afrotemperate plant groups (Fig. 1).’

Can we use the term biome here? I am not sure.

Mike: Biomes are a troublesome concept in general, but we do refer explicitly to them in the introduction, in the sense of White, who recognised the different regions under different biomes: “a single lineage dispersed across different biomes of the Afrotemperate (sensu White, 1981):”

L643: Authors say : The dispersals to Tropical Africa and to Madagascar both involved large shifts in niche (Schoener’s D of 0.298 and 0.274 respectively) .

Too speculative in my opinion. Authors use D Schoener index as a proxy for niche similarity. I would like authors to moderate the reliability of this index. In my opinion, strong differences in D schoener values among clades could just reflect very slight fundamental niche differences (or perhaps no differences at all) since all *Erica* species are adapted to temperate climates. I am pretty sure that niche similarity tests according Broenimann (2012) would indicate that all *Erica* lineages have climatic niche more similar than expected at random. Perhaps these realized niche differences could not reflect real differences in their fundamental niche. Again, the term ‘niche’ is used without accounting for potential differences between realized and fundamental niches.

Mike: this feels related to the point we've addressed previously, considering differences in niche within Erica as opposed to bigger differences between it and other clades. Yes, they're all temperate, but the conditions across regions differ nevertheless. However, the fundamental versus realised niche thing is kind of thorny in this context.

Nicolai: Agree, solely based on Schoener's D values we cannot conclude on niche shifts. This was superficial and speculative. We adjusted the respective statement in the discussion: "The dispersals to Tropical Africa and to Madagascar both might have involved shifts in realized niches (indicated by low Schoener's D values of 0.298 and 0.274 respectively)...". And in the conclusion: "...two potentially with shifts in the realized niche...". Testing for niche shifts in a phylogenetic framework (i.e. between clades, not sister species) demands further analyses (at least additionally to the niche similarity test according Broenimann 2012), which is far behind the scope of this study. See also above our answer to the comment regarding realized versus fundamental niche.