

Interactive comment on “Phylogeny of the Stipa and implications for grassland evolution in China: based on biogeographic evidence” by Qing Zhang et al.

Anonymous Referee #3

Received and published: 4 July 2018

General comments In this manuscript, the authors present an interesting analysis of grassland evolution and biogeography in relation to the Cenozoic history of China. Focusing on *Stipa* grass species, they 1) generate a time-calibrated phylogeny to estimate divergence times, 2) reconstruct ancestral geographic distributions, and 2) discuss ways in which landscape and climate events may have contributed to geographic expansions and speciation events. In general, this is an interesting question and the approaches appear sound; however, some questions remain about specific methodological decisions and the overall validity of the findings. Furthermore, more caution in inferring the biogeographic history of the *Stipa* group is encouraged so as not to overstate the study's findings. For example, what are the assumptions that go into the

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biogeographic model and what are the errors and/or uncertainties involved in the timing of divergence and geologic/climatic events? Finally, some changes to the figures and manuscript text are recommended for clarity's sake. Please find below suggested line and figure edits.

Introduction Line 32-35: There are a few confusing things in this statement. First of all, one cannot infer biogeographic processes based on molecular clocks/genetic information. A step - ancestral state reconstruction for geography, which the authors perform - provides this information, not the molecular clock or the genetic information itself. Next, what does isolation of organisms at a molecular level mean and how does one assess the importance of geologic events. This sentence would benefit from some editing and conceptual clarification.

Line 36: It is too strong to say that divergence times can be “basically confirmed” – they are inferred or estimated, based on some model of evolution and assumptions about molecular clocks.

Line 51: Suggest change of phrasing and clarification: “According to In relation to paleogeographical climate change...” What does paleogeographic refer to? There is nothing geographic in the statement being made here. Regional climate change in China?

Line 63-67: The rationale for this study is fairly clear, but I would suggest the authors moderate their language, especially with the use of “direct” evidence. Phylogenies and biogeographic models are built on a series of assumptions that enable us to infer the history of grassland expansion in relation to climate and landscape events; although these are often reasonable assumptions, this does not equate direct evidence. Direct evidence would comprise temporal and geographic series of grass fossils/biomarkers/etc., which is beyond the scope of this paper.

Lines 69-80: I am not familiar with the composition of grassland ecosystems in China – what do the authors mean, for example, by “constructive species in the typical grass-

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lands”? And when the authors describe *Stipa* species as dominant, what does this mean (abundance, diversity)? For readers unfamiliar with Chinese grasslands or *Stipa* more generally, what is a “typical” grassland (line 74) and what is the broader context for *Stipa* evolution/biogeography? What is the basis for the statement that “the evolutionary processes of Chinese grasslands are closely related to the evolution of *Stipa* species”? Can the authors describe more about regional grassland communities? Otherwise, *Stipa* species are just a case study of one group of grasses, rather than a proxy for all grasslands.

Lines 86-88: Please include references for BEAST and RASP.

Materials and Methods Line 139: Can you clarify how FigTree provided the divergence times for *Stipa* species. I was only aware that this program helped visualize trees.

Lines 147-148: Why did you assign a maximum number of distribution areas as 2? Please explain your rationale – is that the maximum number of areas any given extant species occurs in?

Results Line 161: What is meant by “the divergence time of *Stipa* species” in this sentence – I know what you mean when looking at the figure, but in the text it is unclear that this refers to the basal-most split in the studied clade. Since *Stipa* is a large, widely distributed group, what does this mean in the context of the whole group?

Line 162: I’m curious as to why the authors did not test for radiations/diversification rate shifts directly. If the primary evidence for an “explosive rapid radiation” is from visual inspection of the tree, I am somewhat unconvinced. It would be better to do a formal test for rate variation, such as using BAMM (Rabosky 2014 in PLOS One). If this kind of test is beyond the scope of the paper, I suggest reframing as an inference/hypothesis that could explicitly tested at a later date.

Line 168: I’m curious what the authors mean by isolated divergences – are they referring to a vicariance model? Can the authors clarify, and justify how they determined an

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event to be an isolated divergence event?

Line 171: It is unclear what the authors are referring to – stronger interaction than what? What kind of interaction? This brings up another point – for readers unfamiliar with the landscape of the 7 regions, the topographic setting may be unknown and thus hard to know what the strength of the elevational gradient from the “top and bottom” of the mountains means. Please provide a little more information about the regions (perhaps earlier in the Introduction?).

Line 182: Can the authors please explain how Figure 4 was generated? Does RASP provide frequency estimates of event types, and from there, authors generated what looks like a kernel density plot? In Figure 4, there is a “Standard” and “Extinction” line; however, these are not mentioned in the text. Can the authors please elaborate? Furthermore, the colors in the figure do not match the legend provided, so it is difficult to align what is in the text with the figure. Finally, the three geologic events illustrated in this figure seem to occur instantaneously, when in reality these events likely took >1myr. Instead of drawing a single line, I suggest providing the age range of geologic events (similar to how it is presented in the text as a range and not a single date).

Line 185-187: Can the author please clarify what is meant by “isolation events” – is this vicariance, founder event? Seems like the authors mean vicariance, but it would be helpful to be as clear as possible, and for the terminology in the manuscript to match that of the figures. Furthermore, I’m not sure that I see how the peak frequency (I’m assuming this is frequency, although the y-axis is not labeled) in dispersal and vicariance are “basically matched” in time - can the authors conduct a statistical test to verify this?

Discussion Line 195-198: This is an incomplete sentence, please rewrite.

Lines 212: Please include a reference for the changing climate conditions.

Lines 214: I don’t see this (short internodes) very clearly; again, this could be formally

tested. Until it is tested, I am unconvinced that this is a clear indication of an explosive, rapid radiation, especially given the large error bars on divergence age estimates. I recommend that the authors moderate their statement – perhaps point to a suggestion of a radiation, but that this remains untested.

Lines 221: There are a few qualitative statements here that I think can be removed: “Due to the crumpling effect of the uplift of the Qinghai-Tibet Plateau, the Tian Shan, Quilian, Altyn Tagh, and Kunlun Mountains all had large-scale elevation of fault-blocks, and many areas that were already elevated became medium-height mountains with around 4000m height.”

Line 225: What do the authors mean here? I suggest rephrasing to say that geographic isolation was likely. “Obvious” here in and elsewhere in this paragraph is kind-of a loaded term, and I suggest avoiding it.

Line 230/235: Is there evidence, other than the assumed absence of physical barrier, for ecological and/or sexual speciation? Ancestral state reconstruction of geographic areas helps inform geography of speciation, but not necessarily mode of speciation.

Line 237-239: This statement is too strong, better to be cautious and use language, such as we infer x or evidence supports y. . . I don’t think we can know this definitively, even with a formal test for rate shifts.

Line 240-244: This is an interesting idea. However, I am curious, if *Stipa* species have a high A+T content and A+T bonds are more prone to mutations, does this imply that the average evolutionary rate of herbaceous plants may be an underestimate of rates for the *Stipa* group? If so, how might that affect your findings? In general, a more developed discussion of the assumptions that went into the BEAST and RASP analyses would be good, as well as an explanation for the wide error bars on the reconstructed phylogeny.

Line 246-247: It is a little unclear what the division between discussion sections 4.1 and

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4.2 is, since geologic and climate history is brought up in 4.1 in relation the divergence dates and geographic expansions. This is up to the authors, but perhaps it would better serve the reader to include some of the background information about the landscape history of the Tibetan Plateau and regions of the study in the Introduction of the paper. Then, the authors could more freely discuss this history throughout the manuscript's discussion.

Line 248: I suggest removing the line “During the developmental process of the whole geological history” since it is a little unclear what this refers to (e.g., the scope of geological history is far greater in space and time than what is explored in this study).

Line 266-268: Can the authors elaborate on how Oligocene faunal turnover (to a rodent-lagomorph dominated fauna) supports their inferred Miocene *Stipa* expansion? It is still somewhat unclear, to me, how extensive Chinese grasslands were prior to divergence and expansion of the *Stipa* and/or whether *Stipa* are a major player in history of grassland expansion. Or, if they are an interesting group to study because of their dominance (?) today and history in relation to more recent (e.g., Miocene) geologic/climate events. I think this remains unclear throughout the manuscript – for example, in Lines 291-292, the authors surmise that the uplift of the Qinghai-Tibet Plateau and climate changes promoted the origin of grasslands, which appears to contradict an earlier origin inferred from faunal turnover and mentioned in Line 266. This confusion might be cleared up by clarifying early on the current state of knowledge (based on fossil evidence, other non-*Stipa* groups, etc.) and how *Stipa* specifically contributes to the grassland story in China – e.g., does it signal grassland expansion?

Line 284: Suggest replacing “outbreak” with expansion, shift in ecological dominance, etc. . .

Figures: In general, the text in the accompanying figures is small and difficult to read. Is it possible to enlarge the figures and figure text?

Figure 2: There are very wide error bars on divergence times; this should be mentioned

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in the results and should be discussed in detail in the results and/or discussion. What contributes to wide error on divergence age estimates and how does this influence your interpretations of evolutionary processes? *Stipa* should also be capitalized in the Latin names.

Figure 3: Can you make this figure larger? It is difficult to read as is, especially the ancestral states and landmark nodes on the phylogeny. Furthermore, the colors on the phylogeny seem to correspond with different regions. Can you color code the different regions on the map as well? Provinces appear to contain multiple biogeographic regions, so it is difficult to tell where the region boundaries are. Not necessary, but it might also help get the authors' message across if another panel is included with terrain, so that the readers can know where mountains ranges exist, etc. in relation to the biogeographic regions and inferred dispersal routes.

Figure 4: Please add y-axis and x-axis labels to this figure, and more detail as to how this figure was constructed. Are we looking at output from the RASP analysis? In addition, please change the colors of the curves to match those of the figure legend (for example, I cannot tell which curve is the extinction and which is the standard). In the figure caption, what does a time-geological time curve mean? Do the authors simply mean event curves over geologic time from 30 Ma to present? And, is it necessary to use the terminology "time abscissas and range ordinates"? I think this is confusing, when, I believe, the authors are just describing x and y coordinates.

Frequent typos: e.g., missing spaces between word and reference, missing punctuation; inconsistent pluralization of grasslands, area, etc.; "stipa" is lower case in the figures; comparative adjectives used without a comparison noun (e.g., lines 182-183 – "larger" should be "large" or the authors should state what the expansion is larger than); "MaBP" can just be "Ma"

Interactive comment on Biogeosciences Discuss., <https://doi.org/10.5194/bg-2018-140>, 2018.

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