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Reply on RC1

David Kienle et al.

Author comment on "Geodiversity and biodiversity on a volcanic island: the role of scattered phonolites for plant diversity and performance" by David Kienle et al., Biogeosciences Discuss., <https://doi.org/10.5194/bg-2021-107-AC1>, 2021

The authoring team would like to thank the reviewer for the constructive and thoughtful review of the manuscript "Geodiversity and biodiversity on a volcanic island: The role of scattered phonolites for plant diversity and reproductive fitness". Based on the reviewer's comments, we edited and complemented the manuscript. The discussion and the conclusion received the most changes. Below we addressed all comments in detail.

Anonymous Referee #1, 15 Jun 2021

General comments

The authors present an experimental study conducted on the island of La Palma, where they studied the effect of different substrates in the form of phonolitic and basaltic rocks on plant performance and species abundance. I think the study is relevant, the experiment well set-up and the conclusions interesting. I do have suggestions to potentially improve the paper, particularly regarding the framing and discussion of the results presented in the paper.

The first point of attention is that the overall conclusion of the paper, formulated as 'Phonolites host distinct vegetation compared to equivalent areas of neighbouring basaltic rocks', is not supported by the data, in particular the Detrended Correspondence Analyses presented in Figure A3, which shows 'no clear difference between phonolite and basaltic rock vegetations'. I think the conclusions of the paper should be reformulated to better reflect the results of the study.

Reply: Thank you very much for this comment concerning the conclusion. We agree that it is not the distinct vegetation that makes phonolites unique, but higher species numbers (including endemics) and plant performance. The term 'distinct vegetation' was removed from the conclusion (now L. 394). The focus is now only on higher species numbers and plant performance on phonolites compared to volcanic outcrops of basaltic origin.

A second point of attention is the lack of detail provided in the differences in the

petrographic and geochemical differences of the phonolites and basaltic substrates. I think that in particular, the availability of nutrients in these two substrates should be reported, as this information is key to the interpretation of the results discussed in 3) (L.243-253). It would be preferable to conduct and report measurements of the nutrient contents in the plots, but if not possible, I would at least expect a more detailed description of the chemical differences in nutrient availability reported in literature. Given the results of this study and it's potential to reach a more biologically minded audience, I also think it is worth elaborating how phonolites differ from the basaltic substrates in their chemical composition (in L.74 for example), which is mentioned, but not elaborated on. Also, the presence of heavy metals is discussed in L.281-287 to explain the differences that are reported in the paper, which calls for these to be measured as well.

Reply: Thank you very much for this remark on differences in chemical characteristics between phonolites and basalt. We followed your advice and included literature on nutrient availability and chemical composition of both rock types in the discussion (now L. 271ff.). We anticipate that we now have a more detailed description of the chemical differences in nutrient availability, allowing a profound basis for the discussion of our results. Measurement of nutrient availability in the field was not possible under the given sampling constraints, and therefore studies like Schoen et al. (2016) and Manning (2009) serve as sources on phonolites' chemical composition. Furthermore, we included literature on nutrient release from basalt and phonolite rock powder (Hinsinger et al. 2001, Tavares et al. 2018, Nogueira et al. 2021).

Statements concerning the presence of heavy metals were removed from the manuscript (L. 56 and 371) as we cannot provide measured petro-chemical evidence that support what can be found in literature.

I think the introduction can be streamlined. Currently, the introduction works towards the knowledge gap that is introduced in L.109. However, in between the introduction and the knowledge gap there is a considerable amount of text that introduces the study site of La Palma, which in my opinion, breaks the flow of the introduction. I would suggest to bring the paragraph where the knowledge gap is formulated forward, then following with a statement along the lines of: 'To this end, we investigated the occurrences and traits of plant species in a comparative study matching basaltic and phonolitic rock formations on the island of La Palma.' Followed by an introduction of the study site and its relevance to this study. Also, I think the paragraph in L.113-122 lead to the knowledge gap and should be integrated in the previous paragraph, and should be directly followed by the knowledge gap.

Reply: Thank you very much for these suggestions on improving the introduction. Accordingly, we moved the paragraph concerning the knowledge gap (now L. 123 ff.) forward and put paragraph lines 113-22 (original line numeration) directly above this part of the text. Additionally, paragraph lines 113-22 (original line numeration) were integrated into the previous paragraph to streamline the introduction.

I object to how the second hypothesis is currently formulated. The hypothesis is currently introduced with species *reproductive* fitness, which is then stated to be proxied with plant height and canopy diameter. I fully understand the choice to measure these two metrics due to the time constraints of a field work abroad, I don't think these can be used as a proxy for *reproductive* fitness. Instead, I suggest presenting these as proxies for plant performance, or maybe as proxies for plant fitness (not reproductive fitness), stating that these metrics are good proxies for the different components that make up plant fitness

(e.g. survival and reproduction, see Laughlin 2020). I would also introduce the use of plant height and canopy diameter as proxies for plant performance/fitness in the methods section.

Laughlin, D. C., J. R. Gremer, P. B. Adler, R. M. Mitchell, and M. M. Moore. 2020. The net effect of functional traits on fitness. *Trends in Ecology & Evolution*.

Reply: We appreciate this advice very much, especially the hint to the paper from Laughlin et al. (2020). We agree that the term plant performance fits better to our study. The authoring team had several discussions on the terms reproductive fitness, fitness, etc. before submission, and again after receiving this comment. We will follow your suggestion to use the term 'plant performance' but give additional information that we wanted to address what can be called 'plant fitness'.

In addition, we replaced the word "fitness" with "performance" in the title of the manuscript.

Indeed, trade-offs between growth, survival and reproduction make it more sophisticated to use traits as proxies to quantify the effects of fitness. Thus we rephrased the second hypothesis as following (now L. 163): "Plant performance: Plant species populations on phonolites show a larger abundance of individuals that are taller and have greater canopy diameter than neighbouring basalts due to their advantages in resource availability and porosity. We used plant performance as a surrogate for plant fitness."

Furthermore, we added the details to why we measured plant performance using the proxies plant height and canopy diameter with reference to Laughlin et al. (2020) (methods, now L. 202-204).

I fail to see the relevance of the specific introduction and discussion of the SIE *Cheirolophus junonianus* to the story of this paper. Appendix A1 shows that more species occur on only basalts or phonolites, but this is only discussed in the context of this one species. I would expect this to lead to differences in the species composition of the different substrates, yet the data presented in appendix A3 shows no compositional differences between substrates. This is highly relevant to the paper, and I would like to see this discussed more, and maybe also analysed in more detail. In the paper, the authors also mention that the basaltic rocks house more generalists, but no analysis is presented that shows the what species are considered specialists or generalists.

Reply: Thank you for this substantial and detailed comment. We rephrased paragraphs about *Cheirolophus junonianus* to make it more understandable why this species was chosen to be part of the storyline (L. 128, 337ff). The species is emphasised in the paper, as it is known to almost exclusively grow on phonolites. We kept this species as it initially stimulated the development of our hypotheses, and it adds an ecosystem perspective to our paper. However, at the same time, we also clarify that one species does not lead to significantly distinct vegetation on phonolites and basalt and instead seems to be the exception than the rule. Furthermore, we added a paper by Eriksson (2000) to show why remnant populations of plants, such as *Cheirolophus junonianus* on phonolites, can be of importance for community stability and even influence nutrient cycling.

We furthermore conducted some more analyses on the compositional data on phonolites and basalt. Interestingly, a posthoc permutation test (10,000 repetitions) between the DCA ordination axes and the environmental variables (substrate, inclination, aspect, relief) showed no significant differences between phonolite and basalt (p-values: DCA2~DCA1: 0.623; DCA3~DCA1: 0.503; DCA4~DCA1: 0.768; DCA3~DCA2: 0.289; DCA4~DCA2:

0.959; DCA3~DCA4: 0.439). The variation shown in the DCA does not depend on the substrate (but there is a relationship between northerness and the fourth dimension DCA4).

We agree that the data presented it not supporting any assumptions concerning generalists vs. specialists. We, therefore, deleted this part from the manuscript to stick to the assumptions we can draw from our data.

I would suggest restructuring the discussion The wording in L.226 suggests that these four drivers are expected to have an effect, so I was disappointed to then read the conclusions on the first two paragraphs (1. and 2.), telling me that these aspects didn't play a role. While not irrelevant, I would start with the points 3 and 4, which are more relevant to the discussion, and then bundle points 1 and 2 into a paragraph highlighting some other drivers that were not expected to play a role in this system.

Reply: Yes, we agree that changing the order of points 1-4 increases the quality of the discussion. The discussion now starts with the more relevant aspects, which in its new order are 1) chemistry and 2) age. In point 3 we discuss rock surface structure and colour in one paragraph as suggested.

I think the point discussed in 4) is very relevant and interesting, and I see an opportunity to place this research into a broader context that the authors didn't explore in full. I think the result on species abundances can be caused by either a lower than expected species richness on the basalts, or a higher than expected species abundance on phonolites, or both. The age difference between these two substrates might suggest that there are unfilled niches in on the basalt substrates (which is mentioned, but I think can be elaborated on), but also that there might be an extinction deficit in the phonolite habitats due to habitat decrease and habitat fragmentation. I think this opens up the possibility to discuss how geological history affects evolutionary processes. In line with that, I think the discussion can come back to the relevance of this work to understand how geological diversity affect biodiversity, as introduced in the opening paragraphs of the introduction.

Reply: Thank you very much for this inspirational comment that adds tremendous value to the discussion of the paper. Due to the importance of this point, we now mentioned age differences between substrates potentially affecting vegetation earlier on in the discussion (L. 265f). We added aspects on discussing the possibility that it might not be only phonolites exhibiting higher species numbers, but that it might also be that basalt hosts lower species numbers due to age.

The aspect of phonolites hosting vegetation with potential extinction debt has been included in L. 364ff.

To close the circle in the discussion and come back to the initial questions of how geodiversity is affecting biodiversity lead to a slightly changed order of paragraphs in the manuscript.

Detailed comments

Comment: The line numbering follows the document first submitted to Biogeosciences.

I also have some specific and technical comments:

L.40: chemical composition

Reply: Thank you. We changed 'geological elements (i.e., composition)' to 'chemical components'.

L.55: Omit 'also'

Reply: We rephrased the sentence to avoid 'also'.

L.56-59: I think this sentence needs to be rewritten to better connect to the previous sentence and align with the rest of the paragraph. Perhaps change the other of the sentence? 'This underlines the relevance of understanding the importance of geodiversity for insular biodiversity, which is particularly vulnerable to extinction due to restricted ranges and small population sizes of insular endemic species (Paulay, 1994).'

Reply: Thank you for this excellent idea to improve the connection between the two sentences. We followed your advice and kept 'highly restricted ranges'.

L.65: 'Distinctive to phonolites is fine-to-medium grain size'- Is there any relevance of this characteristic to this study?

Reply: Thank you for this comment. We decided to delete this sentence.

L.97: What does hyper-endemic means in this context? I suspect the authors mean this is a single-island endemic, and I would refer to it as such. (Note that hyper-endemic is a term used in epidemiology, referring to persistent, high levels of disease occurrence).

Reply: Thank you for asking this question. We wanted to underline with "hyper-endemic" that the species occurs only on two rock samples on La Palma. Nevertheless, in the same paragraph, we explain that the species "occurs within a range of only 3500 m²" so we decided to delete "hyper" to avoid any misunderstanding since the term is commonly used in epidemiology.

L.153: Move '(northernness and easternness)' to the first mention of aspect.

Reply: Thank you. We have implemented the changes as suggested.

L.163-164: 'Height, diameter, and species abundances were measured for species to

ensure that vegetational differences evolved through long-term processes and did not reflect the short-term variability of environmental conditions' – On its own, this statement is not correct. In short-lived annuals, these metrics will most certainly reflect short-term variability in environmental conditions. I suspect the plant species living on these rocks to be long-lived perennial species, and therefore one can assume that the height, diameter and abundance of individuals reflects long-term processes and is not solely influenced by short term environmental variability.

Reply: We agree with this point. Annuals may have a distinct trait response (height, diameter) and, on La Palma, depended strongly on occasionally occurring precipitation events. However, even if some annual species were found, our plant community is dominated by perennial plants, as you correctly assumed. We, therefore, changed these lines to: "Height, diameter, and species abundances were measured for all vascular plant species. As plant communities were dominated by perennial species, we can expect that vegetational differences evolved through long-term processes and did not reflect the short-term variability of environmental conditions."

L.221: 'This makes the greater number on phonolite even more remarkable.' I find this statement a little out of place, given that the results align with your hypothesis, and with the statement that follows.

Reply: You are right, this sentence sets up a contradiction that does not exist in this way. We deleted the sentence.

L.223-224: I think this result can be caused by either a lower than expected species richness on the basalts, or a higher than expected species abundance on phonolites, or both.

Reply: Thank you for raising this valuable point. We added that in addition to the unique properties of phonolites enhancing species numbers and plant performance, it might also be that basalt hosts less than expected species. Including this explanation adds another dimension to the discussion.

L.226: I would suggest changing 'colour' to 'temperature'

Reply: We see your point that it is not the colour itself but rather rock surface temperature that we discuss as a driver of vegetation differences between basalt and phonolites. However, as we only know for sure that colour differs and we have no measurements for temperature, we prefer to keep the term "colour".

We also checked out if satellite imagery measuring land surface temperature could be an option to obtain temperature data for our target phonolitic and basaltic outcrops. Such data could be calculated from Sentinel-8 imagery. However, the resolution of 90 m (reaching a resolution of 30 with interpolations) is too coarse for our analysis.

However, we added the following explaining term in parenthesis: "...colour (potentially translating into differing rock surface temperature)..."

L.269: I would omit the clause 'though the numbers of endemic species were significantly higher.' I would focus on relative abundance of endemics, which is the relevant metric for the discussion.

Reply: Yes, we fully agree with this suggestion and deleted this reference to the number of endemic species. The paragraph is now focused solely on the percentage of endemic species.

L.270: 'and the functioning of phonolites as islands of speciation within a sea of basalt does not seem to apply.' Which makes sense given the geological history of the island?

Reply: We agree. The sentence was deleted as we restructured the discussion.

L.271-273: 'However, as most individuals of the typical variety of *Cheirolophus junonianus* occur on one isolated outcrop and individuals of var. *isoplexiphyllus* on another one (personal observation), a very local allopatric speciation by adaptive radiation or an ongoing genetic drift could be the underlying cause.' Given the geological history of the island, I would expect the occurrence of these species on one single outcrop to be caused by habitat fragmentation and subsequent extinction in other habitats, rather than speciation on these two outcrops. This is discussed in the subsequent sentence, but the order suggests the authors think speciation is the most likely cause, with which I disagree.

Reply: We apologise for the confusion. We agree with you that the occurrences of two *Cheirolophus junonianus* varieties on two separate outcrops result from habitat fragmentation rather than small-scale speciation. We rephrased several sentences in the whole paragraph to clarify this point and emphasise that we reject the explanation of small-scaled speciation. The explanation of a burial event of formerly larger and connected phonolite habitats seems more likely. However, we have preserved the order of the two explanations, but we are sure to make the point clearer here with the new sentences:

"As most individuals of the typical variety of *Cheirolophus junonianus* occur on one isolated outcrop and individuals of var. *isoplexiphyllus* on another one (personal observation), **it could be supposed that** a very local allopatric speciation by adaptive radiation or an ongoing genetic drift could be the underlying cause (Vitales et al., 2014a; 2014b). **However, considering the geologic history of the islands South (Garantje et al., 1998) it is a more** possible explanation for that this singularity presumes *Cheirolophus junonianus* belongs to a relict population of plants that were once widely distributed on phonolitic rock before these were covered mainly in a basaltic matrix. **Consequently, lessons learned from other outcrops (Kruckerberg, 1991) cannot be adapted to the phonolitic rocks on La Palma, and the functioning of phonolites as islands of speciation within a matrix of basalt does not seem to apply."**

L.293-295: 'Contrasting, plants growing only on phonolites did not experience larger environmental gradients. In accordance, we observed plants on basaltic rocks to be more generalist than plants on phonolitic rocks.' Neither of these aspects are shown in the results, I suggest to either omit these statements or show the data to support them.

Reply: This is an observation from the field. Unfortunately, we have no tested data on this. Therefore, we followed the suggestion here and removed the last sentence.

L.305: 'plant growth responses' be consistent in your terminology, this was called reproductive fitness in the rest of the paper.

Reply: Thank you. We now use the term "plant growth response" consistently throughout the paper.

L.306: 'of these rocks for the vegetation on these islands which are globally dispersed', I was a bit confused by this sentence. The grammar suggests the islands are globally dispersed, can you mention why is that relevant?

Reply: Thank you for making us aware of this confusion. To simplify the sentence and to give it more clarity, we changed it to: "Higher species numbers and abundances as well as higher **plant fitness** underlines the importance of these rocks for the vegetation on **oceanic** islands."

L.307: 'Despite the small area covered by phonolites they play a significant role in enhancing plant biodiversity' add 'on the island of La Palma.'

Reply: Done, thank you for this comment.

L.307-308: 'Our results contribute to a better understanding of the distribution and plant diversity drivers on islands through exceptional rock outcrops like phonolites' I suggest toning down this statement. The results suggest that these outcrops play a role in the formation of plant diversity on volcanic islands such as La Palma, but the lack of additional data on, in particular, the chemical composition of the different substrates means that your results do not directly contribute to a better understanding of the drivers that lead to this effect.

Reply: Thank you. We deleted the sentence referring to the underlying drivers and rephrased the sentence following your suggestion. It now reads: "Our results suggest that exceptional rock outcrops like phonolites contribute to a better understanding of the formation of plant diversity on volcanic islands such as La Palma."