

Dear editor,  
dear referees

First of all, we, the authors, would like to thank you for your helpful comments and the time and work invested in our manuscript.

Below, we copied both referees' comments and added our answers in blue colour. Please don't hesitate to contact us in case of any additional questions.

Kind regards,  
Peter Biber

on behalf of all authors

### **Interactive comment on “Relationships between substrate, surface characteristics, and vegetation in an initial ecosystem”**

by

P. Biber et al.  
Anonymous Referee #1  
Received and published: 22 March 2013

General comments. The most prominent studies of primary succession take advantage of dunes, volcanoes, and glacial forelands. Only a handful of these have managed to simultaneously study geomorphic, biological, and ecosystem processes from the initiation of a barren landscape, and I would argue that none have done so in a coordinated and integrated way. Moreover, these natural disturbances often leave extremely complex landscapes that are difficult to understand thoroughly. Many other studies have focused on anthropogenic primary successional sites such as mine spoils or mine reclamation. While generally encompassing much smaller spatial scales, many important insights have derived from these study systems. Such systems have some advantages too in that they are often in more convenient locations, sometimes more uniform, and sometimes more replicable. There too, however, few if any studies have simultaneously studied geomorphic, hydrological, biological, and ecosystem processes in an integrated way.

The present study of the initial ecosystem at Chicken Creek is impressive in that it does integrate detailed study of these diverse processes from the time of initiation of a controlled, relatively homogenous ecosystem. Because the abiotic system is constructed, its initial structure is extremely well understood. It is also unusual among such reconstructions in that biological colonization is allowed to occur unassisted. Another key feature is that it comprises a complete sub watershed (catchment) and includes an impermeable lower layer, features that will allow thorough understanding of hydrogeologic processes. This manuscript is the latest in what is already an impressive body of work focused on this site, even though the site and research programme is still in its infancy. In the authors' words, this system allows “Tracing the development of .. young ecosystems and observing how new relationships and feedbacks emerge with increasing complexity.

I concur. In addition, it may provide numerous insights with more theoretical perspective or that unite previously separated disciplinary views of ecology and geology. The group's recent American Naturalist paper is a good example of this. The current manuscript helps to achieve the integrated view of geological and ecological processes. There are no ground-shaking findings, but the work provides a very thorough understanding of the transition from

a system dominated completely by hydrological and geological features and processes to a system that is much more influenced by vegetation, and in doing so elucidates a number of interesting relationships.

For example, the non-linear effects of total cover, spatial location, relief energy, and time on different vegetation categories are particularly well documented. Hence, the paper will certainly be of interest to ecologists interested in primary succession and land reclamation.

**Authors:** Thanks for these encouraging comments.

Specific Comments. Below, I make a few comments that I hope can improve the manuscript. For the most part I really enjoyed reading the manuscript, but there are a number of issues that should be addressed. These are almost all issues of omitted information that make the presented results difficult to interpret and thus less valuable.

**Authors:** We are confident that we can cover all issues raised.

1. There are some methods I did not evaluate critically because they are either new to me (terrestrial laser scan) or that I did not have the time to evaluate because I would need to review the technique (GAM). Other than this, I found the field and statistical techniques to be appropriate generally well described.

**Authors:** Thanks. We apply terrestrial laser scanning (TLS) and GAM's as standard methods and thus believe that we described them adequately.

2. In an ordinary printed journal article, I would recommend that the authors could save space by omitting much of the presentation of statistical models, as these are standard and could be incorporated by references. However, if space is available, I think it is worth including.

**Authors:** We share that opinion, but we believe that the results of the paper are by far easier to understand if readers can switch between the result graphs, tables and model presentations.

3. The authors are carefully to honestly state that they conducted preliminary analyses to choose the best variables. That honesty is to be encouraged, but I to be clear when such preliminary analyses are done that the true p values are inflated relative to the ones presented. I think a statement to that effect should be included

**Authors:** Our preliminary analyses were just explorative and performed on a descriptive visual basis, without formal statistical inference. We will be clearer about that in the revised version.

4. What is soil skeletal content? 4739: 1. Is it a description of physical structure, or is actual content of biological skeletal material? I searched for this on the web, and after 20-30 minutes could not find a clear definition. Use of the term primarily occurs in work from Germany, Switzerland, Czech republic, but I could not find a definition. Most ecologists reading this paper will not know the term, so please define it.

**Authors:** There seems to be a misunderstanding. The skeletal fraction of a soil is the gravel content with grain diameters > 2 mm. If expressed in percent, this means mass percent of the soil. We will add this definition in the revised version.

I was especially interested to understand why the presence of Fabaceae would be related to skeletal content.

Authors: The higher the skeletal content, the more unfavourable conditions (in terms of water and nutrient supply) for plant growth can be expected. On soils with higher skeletal percentages, plants belonging to the Fabaceae family should possess a pronounced competitive advantage: A symbiotic relationship with root nodule bacteria (Rhizobiaceae) allows for the utilisation of atmospheric nitrogen and thus raises the supply of this typically limited nutrient.

5. 4733-4744: what are the explanatory variables for H1? Similarly, explanatory variables are not provided for H2. Thus the description of the analyses here is unclear.

Authors: In the revised version, we will present the explanatory variables earlier, namely at the end of the methods section where we also introduce the response variables.

6. Figs. 2-4. It is standard to show the data points along with the fitted line, that is not done here. In the absence of that is very difficult to gauge how well supported the results are.

Authors: In the context of GAMM's this is not the standard, because it is not possible. The lines in the mentioned figures show the nonlinear influence of a given explanatory variable as a part of an overarching fitted model. Figure 2 might serve as an example: As indicated in the diagram's y-axis, the line represents the nonlinear effect of  $f_1(\text{DISTA})$  exactly as shown in equation 8. The point of these smoother diagrams in the GAMM context is to show how significant nonlinear effects are shaped.

I recognize that CIs are provided in the figures, but these obscure data structure.

Authors: The purpose of the CIs is to show how precise a nonlinear effect could be estimated, and they are perfectly good for that. Their meaning is comparable to the standard errors we give for the linear parameter estimates e.g. in Table 2 which corresponds to the above-mentioned Figure 2.

I recognize also that with a mixed effects model the raw data do not always provide an actual visualization of the actual relationships, but perhaps this can be improved by graphing data corrected for the random effects.

Authors: The data could be corrected for the random effects but even then plotting them with the fitted lines would be not meaningful. It is crucially important to understand that the lines do not show predictions from a complete model but only effects that are parts of an overarching model. Presenting such lines is fully analogous to presenting parameter estimates for a linear model.

I also found the figures took more time to understand than they should have.

Authors: In that case we strongly suggest not to leave out the presentation of the statistical models (see comment #2), because for readers who are not so familiar with GAMM's it would be even more time consuming to understand what actually has been done.

In any case, when revising the manuscript, we will try to clarify the points raised here as far as possible.

Y labels do not indicate the actual dependent variable.

Authors: They can't. See our arguments above.

Also valuable would be to back-transform the axes so that we can see the actual proportion cover.

Authors: Even if it would be done accordingly, not the actual (estimated) proportion cover (and other response variables) would ultimately be visible, because, as explained above, the lines do only represent a part of a model, not the whole.

From our point of view, the information gain by such a back-transformation would be marginal since the transformations are monotonous and would therefore not alter the general shapes of the curves (e.g. maxima and minima wouldn't vanish). On the other hand, we would lose the analogy with the linear model parameters from the overarching models where the fitted lines belong to, and we would also lose the direct match with the presented model equations.

If it were actually biological skeletal content then it would suggest an important role of P limitation for primary successional colonists. In this event, see the recent paper by Lambers et al. 2012 *Annals of Botany*.

Authors: This is a misunderstanding of the term "skeletal content". See our explanation above. We will provide an unambiguous definition of the term in the revised version.

7. A major omission from this manuscript is the complete lack of summary data of the variables. This makes interpretation of the results very difficult and the entire work becomes very abstract. In my opinion these must be included for this manuscript to be publishable. For vegetation should include species list with % covers (maybe at end point) and categories (ann, grass, etc).

Authors: For the revision, we will make a concept of descriptive summary statistics to present. We are not sure if a complete species list would exceed the available space, and feel that maybe a restriction to the response and explanatory variables directly used in this study would be best.

8. 4746 effect of organic C weakens with time, but I thought there was initially no organic C. Is organic C highest near upper site edge?

Authors: Initially, organic C (mostly from fossile sources) was not completely absent. However, the concentrations were low. They are not highest near the upper site edge.

9. 4746: So is rill formation driven by organic carbon or by relief energy?

Authors: This question concerns the results section. We feel we should concentrate in that section on describing the results and leave interpretations to the discussion. However, concerning rill formation and relief energy, this is probably a chicken-egg-who-first-question, which cannot be ultimately answered by statistical analyses. Actually, a feedback process is most probably in effect here: Higher relief energy means a more channelled surface water runoff which intensifies rills, which in turn increases relief energy and so on. This kind of feedback is already mentioned in the discussion but we will emphasize this point more in the revised version. In the discussion we also argue that the percentage of organic carbon seems to be a proxy for the general substrate properties (4751:14-27).

10. Figs. 2-3 – why only show effects of distance, why not show effects of other key explanatory variables?

Authors: There seems to be fundamental misunderstanding concerning the methods. Self-evidently we show the effects of all significant explanatory variables. Please note, that GAMM's are mixed models (MM) which are generalized (G) in order to be not restricted to normally distributed response variables. The "A" stands for "additive" which means that the effect of different explanatory variables can be modelled either in the classic linear way or as nonlinear smoothers in the same model.

For all our fitted models we show the nonlinear smoothers as diagrams (there is no other way to do that) and the linear effects in a standard table format. Take for example the model with RILLR as the response variable: Equation 8 is the mathematical representation of the whole model, Table 2 shows the linear effects and refers to Figure 2 for the nonlinear effect in the model (clearly it refers also to Equation 8). Figure 2 shows the nonlinear effect and refers to Equation 8. We do exactly the same for each model.

11. 4751 5-10: I am having trouble forming a mental image – perhaps including a photograph or two would help visualize how local conditions cause rills perpendicular to the main slope and the nature of the gullies channeling runoff?

Authors: During catchment construction such a structure, a plain or maybe slightly opposite-tilted strip perpendicular to the main slope direction was created unintentionally by the caterpillars levelling the surface. We mention that in the discussion (4751:4-8). However, we don't think that a photograph of these structures which are nothing more than non-relevant (given the purpose of the paper) exceptions would reveal anything interesting.

12. related to point 7 the authors should provide a species list that includes plant family and classifications for purposes of this manuscript.

Authors: We feel that – considering the required space – we should refer to published studies in this respect (see our answer to point 7). However, if editors and reviewers advice, we will provide such a list.

It seems quite strange to me to include *Rubus* in the same category as tree-form woody plants.

Authors: As *Rubus* species in general have woody stems they were allocated to the group of woody plants (in contrast to “grasslike “ and “herbaceous” according to Rothmaler (2000)).

Rothmaler, W.: Exkursionsflora von Deutschland Gefäßpflanzen: Atlasband, vol. 3, 10th edn., edited by: Jäger, E. J. and Werner, K., Spektrum Akademischer Verlag, Heidelberg, Berlin, 753 pp., 2000.

The authors single out Fabaceae but do not make clear whether these are the only N-fixing plants or organisms in the system.

Authors: Fabaceae are the only N-fixing vascular plants found on the catchment. Other N-fixing organisms are cyanobacteria, which participate in biological soil crusts, which - to some extent - were also present at the study site. However, in this regard, Fabaceae is the most important group by far.

I realize the authors provide this information in other publications, but it is important enough for interpreting the results in this paper that the information needs to be provided here.

Authors: See above.

4749: p(woody plants) decreases as total plant cover increases

Authors: We are not sure what you really mean. But the discussion at 4754:3-16 clarifies our ideas about the reasons behind this observation.

13. No information is provided about the surrounding plant communities, sources of carbon input and propagules, local climate, local atmospheric N deposition, etc. I recognize that many of these attributes are described in other publications, but they should nevertheless be

briefly described here before referring to those publications. This is especially true if any of these descriptions are in books that are hard for most readers to access.

Authors: For the revised version we will compile all relevant available information.

14. Abstract: the abstract does not need to include the names of the specific statistical techniques or even that your hypotheses were confirmed. The abstract would much improved by including some specific results that support the statement “transition from a geo-hydro towards a bio-geo-hydro system, where pure geomorphology or substrate feedbacks are changing into vegetation-substrate feedback processes”.

Authors: We will rework the abstract following your advice.

Technical corrections. Here are some minor suggestions to improve language use. There Discussion section had quite a few English phrasing issues that I did not take time to recommend corrections for. unproductivity not an english word, change to low productivity or something similar.

Authors: Thanks.

4735 10: influences back – change to just influences or feeds back to influence or in turn influences.

Authors: Will be changed.

4735 20: are the starting conditions at point zero known exactly?

Authors: The initial characteristics like geomorphology, substrate distribution and properties, inner structures, and boundary conditions of the chicken creek area are very well known and documented. However, the point we want to make here is that in natural watersheds these informations about starting conditions are usually very weak.

Is it really called Chicken Creek, or is it something like Huehnchen Bach? Should German language place names be translated?

Authors: Actually, it is called “Hühnerwasser” in German (we like your suggestion “Huehnchen Bach”☺), but in international publications it has been consistently called “Chicken Creek” so far. Thus, we see no alternative to sticking to the latter name.

4737 5: across the catchment area

Authors: Will be changed.

4740: 5 change despite to Although or While and move roughly to 4740: 9: typo: laser

Authors: Will be changed.

4741: 17 - replace further on with thereafter or subsequently 4742: 23 replace with The way that ..transformed

Authors: Will be changed.

4743 20 the question of whether the initial ... or H1: Do the initial ...

Authors: Will be changed.

4744 5: what does “most useful” actually mean? It shouldn’t just mean “gave the best fit or lowest p-value” but instead should mean “best satisfied model assumptions”.

Authors: Will be rephrased.

4744: Nitrogen fixing or Dinitrogen fixing, not nitrogen collecting.

Authors: Will be changed.

4745: overarching important .... - incorrect phrasing.

Authors: Will be rephrased.

## **Interactive comment on “Relationships between substrate, surface characteristics, and vegetation in an initial ecosystem”**

by

P. Biber et al.

Anonymous Referee #2

Received and published: 28 March 2013

General comments This is an interesting and thorough study of plant-environment interactions in the early stages of primary succession. As the authors mention, high resolution, spatiotemporal studies of initial ecosystem development are rare. Studies based on direct observations are vital to complement chronosequence studies, and, as a consequence, the findings of this paper have great value. Interactions between vegetation and geomorphological processes are frequently alluded to in research articles, but rarely have they been studied in such detail. The research methodology is sound and the combination of techniques used (particularly the laser scanning) is innovative. The results are not revolutionary (e.g. it is well established that vegetation growth stabilises slopes) but the careful integration of a wide range of factors make this important research.

**Authors:** Thanks, this is very encouraging.

I think the hypotheses, whilst generally sound, could have been framed more precisely (see Specific Comments, below). Clarifying the goals of the research, perhaps by including predicted responses, might have been useful.

**Authors:** We are surprised that the goal of our research remains unclear after 4736:4-12, but we will do our best to improve the presentation. Two out of the three main research hypotheses are scrutinized with more than one model. Breaking the hypotheses down to the variable-level when describing the overall goals of the research would be very confusing for the reader. We will work out a useful compromise.

The formulation of models is commendable, but I felt that this data could have been deployed more effectively. Specifically, I felt the selection of response variables should have been accompanied by an a priori ecological justification (this could have been done in the Introduction, for example). The response variables studied seem to have been selected by EDA, rather than a careful consideration of ecologically meaningful criteria.

**Authors:** This impression is wrong. The response variables were a priori defined and calculated. In the revised version we will clarify that.

The proliferation of response variables, and the complexity of the resulting models (e.g. equation 17), sometimes obscures the underlying ecological processes and makes the Methods and Results sections hard work to read. The inclusion of some basic summary statistics (e.g. showing the relationships between key variables) would have helped. The situation is redeemed somewhat by a clear, well-argued Discussion.

**Authors:** We don't feel at all that our models are overly complex (each is as scarce as possible) and obscuring ecological processes. If this were the case, our discussion could not be clear. Even the model based on equation 17 gives very clear and meaningful results for all variables involved ( $p < 0.001$ ). What would be the point of leaving some of them out as long as this is the case? This would bear the danger of misinterpretations. All models exactly show what you are asking for: relationships between key variables.

We agree that the methods and results section are not easy to read, and we will try our best to improve the presentation during revision, however, we are talking about state-of-the-art



methods, and we can't exonerate the reader from understanding what actually has been done.

#### Specific comments

P4735, line 4: I do not believe degraded ecosystems are inherently unstable, as a disturbed ecosystem can be simple but stable. However, land surfaces in these areas are likely to be unstable.

Authors: The cited literature (see below) indicate instability and low productivity of these disturbed sites unless measures of restoration or rehabilitation are taken.

Bradshaw, A. D.: The reconstruction of ecosystems, *J. App. Ecol.*, 20, 1–17, 1983.

Hüttl, R. F. and Weber, E.: Forest ecosystem development in post-mining landscapes. A case study of the Lusatian lignite district, *Naturwissenschaften*, 88, 322–329, 2001.

Schaaf, W.: What can element budgets of false-time series tell us about ecosystem development on post-lignite mining sites?, *Ecol. Eng.*, 17, 241–252, 2001

Walker, L. R. and Willig, M. R.: An introduction to terrestrial disturbances, in: *Ecosystems of Disturbed Ground, Ecosystems of the World 16*, edited by: Walker, L. R., Elsevier, Amsterdam, 1999.

Zikeli, S., Jahn, R., and Kastler, M.: Initial soil development in lignite ash landfills and settling ponds in Saxony-Anhalt, Germany, *J. Plant Nutr. Soil Sci.*, 165, 530–536, 2002.

P4736, line 2: The authors include pedogenesis, but they only measured soil properties once, so cannot really talk about the development of the soils.

Authors: This is true and we will remove pedogenesis in the revised version.

P4736, lines 6-7: I think a precise definition of what the authors mean by “surface structure and properties of the terrain” would have been useful (e.g. mentioning the importance of rills). The authors seem to use ‘surface structure’ to mean small-scale features and ‘geomorphology’ to mean large scale topographic variation. I would argue that the term ‘geomorphology’ encompasses all surface features, regardless of scale.

Authors: We will strive for more precision in the revised version.

P4736, line 9-10: A deterministic response to the environment seems reasonable, but I wonder if spatial differentiation/segregation is necessarily expected on young terrain? Pioneer species are, by necessity, very tolerant of stressful conditions, and spatially random distributions (a null model) might be more realistic on relatively homogeneous terrain such as this.

Authors: We don't use that as an a priori true statement but as an open hypothesis which could be rejected or accepted. According to our results it seems to be partly true. In addition this hypothesis directly relates to one of the main research hypotheses of the overarching project. Thus we strongly feel that we should keep it as it is.

P4744, line 1 onwards: I think the significance of rills could have been briefly discussed in the Introduction, to justify why so much emphasis is placed on this landscape component.

Authors: Will be done in the revision.

Furthermore, some basic graphs showing the empirical relationships between variables (e.g. rill density vs DISTA) would have been helpful.

Authors: We don't quite understand. Figure 2 is a relationship between rill density and DISTA as resulting from an empirical model which (the model) also takes into account significant influences of other explanatory variables. Thus, this is the best empirical relationship you can get from the data, because it is not confounded with influences from other variables.

P4747, line 5: Does the increase in surface elevation with increasing DISTA equate to deposition? It might be worth making this explicit.

Authors: This is what our results indicate. We will discuss that in the revised version.

P4749, line 10: The Authors should say why the peak coverage of Fabaceae in 2008 and 2009 was remarkable (this isn't self evident).

Authors: We don't explain that in this place, because in the results section, we restrict ourselves just to present the results and leave the interpretation to the discussion. There (4753:1-13) we offer an explanation for this observation.

P4752, line 18: Can soil processes really be regarded as exogenous to ecosystem development?

Authors: We agree. The idea was to contrast the processes directly happening in the plant community from others. We will change the wording accordingly.

I have to say that it is a shame soil properties were not monitored along with vegetation change because, as the Authors point out, the soil is the interface between the atmosphere/biosphere and substrate.

Authors: We also agree.

P4753, line 9: It isn't clear to me what the term 'preferential cover range' means in this context.

Authors: We mean the range of cover which is typical for a given plant species' performance in the time series so far. The term will be explained in the revised version.

P4753, line 15: Disproportionately high, or disproportionately low?

Authors: Disproportionally high. Will be clarified in the revised version.

P4753, line 27: What do the Authors mean by 'severely habitable'? Stressful, perhaps?

Authors: Thanks, will be re-worded.

P4755, lines 1-7: How were the heights of individual plant species measured? The Authors only mention measuring the height of vegetation, not individual taxa.

Authors: Individual species' heights were not measured systematically. However, some measurements on individual plant parameters were done in the catchment itself and especially an adjacent experimental site (recapitulating the catchment's development) since its onset in 2008. As we do not aim to cause an information overload to the reader, we consider our explanation in L 6-7 "still existing prior-year shoots" as adequate.

P4755, line 21: Why is the connection between skeletal content and the incidence of Fabaceae plausible?

Authors: A higher soil skeletal content (mineralic components with grain size > 2 mm) means more unfavourable conditions in terms of water and nutrient supply. Fabaceae, due to their ability to collect N, can be to have a competitive advantage under such conditions (see our response to referee #1).

Fig. 1: Changes in surface elevation are frequently referred to in the manuscript. I think Fig. 1 would have benefitted from a cross section showing the slope from A to Q.

Authors: Will be included in the revised version.

Technical points

P4736, line 1: Replace 'since nearly seven years' with 'over a period of seven years'?

Authors: Will be changed.

P4740, line 3: Replace 'Despite' with 'Although'?

Authors: Will be changed.

P4740, line 6: Replace 'vegetation period' with 'growing season'?

Authors: Will be changed.

P4740, line 9: Replace 'leaser' with 'laser'.

Authors: Will be changed.

P4741, line 14: What is meant by the term 'or seed'? Consider omitting this?

Authors: Thanks, this is not needed. Will be omitted.

P4741, line 17: Replace 'cells further on' with 'cells for further analysis'?

Authors: Will be changed.

P4742, line 23: Replace 'how' with 'in which'?

Authors: Will be changed.

P4743, line 20: Replace 'the question if' with 'i.e. that'?

Authors: Will be changed.

P4746, line 5: Replace 'probability to encounter rills' with 'probability of encountering rills'? Similar comments apply whether the term 'probability to' is used (e.g. P4747, line 21: 'probability of finding'.

Authors: Will be changed.

P4747, line 2: Replace 'where 2005 more medium sand has been found' with 'where more medium sand was found in 2005'?

Authors: Will be changed.

P4752, line 10: Replace 'prove' with 'match'? The term 'prove' seems a bit strong.

Authors: True. Will be changed.

P4754, line 5: Replace 'latest' with 'in the later stages of succession' or 'in the future'?

Authors: We mean "at the latest". Will be changed.

P4754, line 7: Replace 'prevail about' with 'prevail over'?

Authors: True. Will be changed.