Peer Community In Ecology

Complex interactions between ecosystem productivity and herbivore diets lead to non-predicted effects on nutrient cycling

Sébastien Barot *based on peer reviews by* ***Manuel Blouin*** *and* ***Tord Ranheim Sveen***

Sébastien Ibanez, Arnaud Foulquier, Charles Brun, Marie-Pascale Colace, Gabin Piton, Lionel Bernard, Christiane Gallet, Jean-Christophe Clément (2022) The contrasted impacts of grasshoppers on soil microbial activities in function of primary production and herbivore diet. bioRxiv, ver. 2, peer-reviewed and recommended by Peer Community in Ecology. https://doi.org/10.1101/2022.07.04.497718

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The authors present a study typical of the field of belowground-aboveground interactions [1]. This framework has been extremely fruitful since the beginning of 2000s [2]. It has also contributed to bridge the gap between soil ecology and the rest of ecology [3]. The study also pertains to the rich field on the impacts of herbivores on soil functioning [4].

The study more precisely tested during two years the effect on nutrient cycling of the interaction between the type of grassland (along a gradient of biomass productivity) and the diet of the community of insect herbivores (5 treatments manipulating the grasshopper community on 1 m2 plots, with a gradient from no grasshopper to grasshoppers either specialized on forbs or grasses). What seems extremely interesting is that the study is based on a rigorous hypothesis-testing approach. They compare the predictions of two frameworks: (1) The "productivity model" predicts that in productive ecosystems herbivores consume a high percentage of the net primary production thus accelerating nutrient cycling. (2) The "diet model" distinguishes herbivores consuming exploitative plants from those eating conservative plants. The former (later) type of herbivores favours conservative (exploitative) plants therefore decelerating (accelerating) nutrient cycling. Interestingly, the two frameworks have similar predictions (and symmetrically opposite predictions) in two cases out of four combinations between ecosystem productivities and types of diet (see Table 1). An other merit of the study is to combine in a rather comprehensive way all the necessary measurements to test these frameworks in

combination: grasshopper diet, soil properties, characteristics of the soil microbial community, plant traits, vegetation survey and plant biomass.

The results were in contradiction with the "diet model": microbial properties and nitrogen cycling did not depend on grasshopper diet. The productivity of the grasslands did impact nutrient cycling but not in the direction predicted by the "productivity model": productive grasslands hosted exploitative plants that depleted N resources in the soil and microbes producing few extracellular enzymes, which led to a lower potential N mineralization and a deceleration of nutrient cycling. Because, the authors stuck to their original hypotheses (that were not confirmed), they were able to discuss in a very relevant way their results and to propose some interpretations, at least partially based on the time scales involved by the productivity and diet models.

Beyond all the merits of this article, I think that two issues remain largely open in relation with the dynamics of the studied systems, and would deserve future research efforts. First, on the "short" term (up to several decades), can we predict how the communities of plants, soil microbes, and herbivores interact to drive the dynamics of the ecosystems? Second, at the evolutionary time scale, can we understand and predict the interactions between the evolution of plant, microbe and herbivore strategies and the consequences for the functioning of the grasslands? The two issues are difficult because of the multiple feedbacks involved. One way to go further would be to complement the empirical approach with models along existing research avenues [5, 6].

References:

[1] Ibanez S, Foulquier A, Brun C, Colace M-P, Piton G, Bernard L, Gallet C, Clément J-C (2022) The contrasted impacts of grasshoppers on soil microbial activities in function of primary production and herbivore diet. bioRxiv, 2022.07.04.497718, ver. 2 peer-reviewed and recommended by Peer Community in Ecology. https://doi.org/10.1101/2022.07.04.497718

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[6] Schweitzer, J. A., Juric, I., van de Voorde, T. F. J., Clay, K., van der Putten, W. H., Bailey, J. K., and Fox, C. 2014. Are there evolutionary consequences of plant-soil feedbacks along soil gradients? Func. Ecol., 28, 55-64. https://doi.org/10.1111/1365-2435.12201

Reviews

Evaluation round #1

DOI or URL of the preprint: https://doi.org/10.1101/2022.07.04.497718

Version of the preprint: 1

Authors' reply, 10 December 2022

Download author's reply

Decision by Sébastien Barot, posted 17 October 2022, validated 17 October 2022

Revision needed

I concur with the two reviewers to think that the manuscript is interesting and based on a sound experiment. I particularly like the way two contrasted hypotheses are tested and the fact that the impacts of the treatments are documented through many relevant variables. Working on the impact of herbivore insect on soil functioning is relatively original. Nevertheless, the two reviewers have made numerous valuable comments that should help improving the manuscript. Overall, my general comment is that the theory behind the hypothesis to be tested is relatively complicated, that the data and the combinations of treatments are also relatively difficult to understand. Therefore, any effort to make the text crystal clear and to fully clarify each step of the rationale would be welcomed.

Sébastien Barot

Reviewed by Manuel Blouin, 20 September 2022

Reveiwer comments

The study of Ibanez et al. deals with the effect of herbivores on soil functioning in relation to primary production and herbivore diet. It is a complex experiment, given the number of compartments (plants, herbivores, decomposers) and the processes (primary production, diet differences, decomposition of organic matter) that are considered. The experimental design is fine, statistical analyses also, the conceptual background is well exposed and the paper is well written. It misses some coherence between the collected data and the tested conceptual framework.

Title

I suggest changing "ecosystem productivity". First, from available information, the authors did not measure productivity, nor production, but aboveground biomass. Second, it is restricted to plant, not ecosystem which include several trophic levels. If the authors can justify that the protocol allows to estimate a Δ of biomass per year, then they could talk about aboveground production.

Abstract

L38: This sentence give the feeling that the "productivity model" prediction is validated, which is misleading. The authors could precise "but were influenced by primary production, in a way that differed from the "productivity model", or something equivalent.

Introduction

The Introduction is quite long and could be shortened. The authors could stress less on productivity and herbivore diet theories when the same results are expected from both the interpretation, while insist on cases where predictions diverge. They could end the Introduction by diverging predictions from the two conceptual frameworks.

From my knowledge, productivity is high in "juvenile" stages, with many exploitative species, and relatively low in "mature" stages, with exploitative species (cf Odum, 1959). The authors could better explain how they will decorrelate productivity and species composition in terms of adaptive strategy.

L80: “recalcitrant litter”. The intrinsic recalcitrance of organic matter has been shown to be a concept that poorly explains the degradation of organic matter. From a quick reading, I did not found references to this recalcitrance in the paper of Reich (2014). The authors could be more precise to justify the association between plant types (conservative vs exploitative) and decomposition rates.

The authors could precise, from the Introduction, that they will consider forbs and grasses as exploitative and conservative groups of species. That will help to make a link between the tested conceptual frameworks and the experimental design.

Line 179: I was surprised that the authors chose managed and fertilized grasslands among their sites. This could bring an additional complexity through the interaction between fertilizer and soil processes. The impact of this choice on the results could be discussed.

Lines 210: the experiment has been repeated in 2016 and 2017. In the Materials and Methods, it is not precised (for example in the Statistical analysis section) how the authors managed the data from the two years. Are there differences? Are the data pooled? Did the authors chose one year and if so, why and based on which criteria? Results and Discussion could be completed accordingly, to make it more clear the nature of presented data.

Line 183-185: The authors say “We hypothesized that the effect of herbivory on these soil microbial characteristics depends on the interaction between herbivore diet and ecosystem productivity.”. It is not what I understood from the Introduction, which was more a confrontation of two conceptual frameworks to determine which one fit the best with observations. Since the authors identified situations where the two frameworks provide opposite expectations, they should focus on these different predictions and decide to support one hypothesis rather than the other, based on literature.

Materials and Methods

Lines 195-197: “All grasslands were composed of a mixture of forbs and grasses, although the dominant functional group depended on the grassland type (Sup. Fig. 2A).”. Sup Fig 2A is about leaf C/N ratio. Supp Fig 1 is about the percentage of eaten leaves. There is no clear information about the relative importance of forbs and grasses in each site. This requires an additional Supp. Figure.

Lines 200-201: The authors could explain better what is the rationale to consider three grasshopper species AND their mixture.

Lines 205-206: The authors should justify why they adjusted the density of grasshopper to the aboveground biomass.

Lines 206-207: A reference for the maximal density in this area would be welcome.

Line 276: The authors could better explain the experimental design. There are four types of grasslands, each with three replicates, and five points per replicates (five pseudoreplicates). Does the three replicates come from the same “region”? I mean is there a spatial correlation of the three replicates, which could have an impact on the results and conclusion? Is so, it should be precised. A map as supplementary information could be helpful. Strictly speaking, the five pseudoreplicates should have been averaged since the statistical individual is the site. A comment on this would be appreciated.

Lines 354-356: Precise RV=0.29 is lower than what, since you are talking about the RV=0.22 just before.

Results

Lines 358-360: Supp. Fig. 3 indicates the variation of the % of forbs in response to grasshopper species, not what you say here.

Discussion

Line 405: Given that you refer several times to this new microbial resource acquisition strategies, it could be interesting to present them briefly. This would also help to understand Y-strategists (line 409).

Lines 407-410: As an alternative explanation to root exudates, could it be that the plant-microbes competition

is stronger at high SOM levels? If the plant is more efficient than microbes to uptake mineralized nutrients, microbes could be constrained to mineralize more while they can not uptake more because of the plant.

Lines 447-449: the role of depolymerization is not clear to me.

Line 462: Please, keep PNM, instead of NMP, as in the whole text.

Line 477: Is it Supp. Fig. 3 insteadof Supp.Fig. 2?

Lines 477-482: All along the paper, I have not been convinced by reference/discussions about plant succession. The duration of the experiment is clearly not sufficient to get into these considerations. I suggest removing these elements to get a more focused paper.

Lines 490-494: This intellectual construction works, but it is not very convincing.... Some references to support the link between the TDN and leaf C/N ratio could help.

Line 506: "In the present study, high quality plants characterized by low leaf C/N ratio". This should be stated earlier, otherwise the reader does not understand before the discussion why the Introduction is so developed regarding high versus low quality of plants, and why different herbivore species are considered.

Lines 519-523: This paragraph could be shortened.

Conclusion

Lines 540-542: "We did not find any interaction between ecosystem productivity and herbivore diet on soil microbial characteristics, contrary to our expectation.". Regarding the last comment on the Introduction, I feel that the hypothesis was more than one model was better than the other since it can predict observations in some conditions whereas the other one can not. I did not understand why you expected to find an effect of the interaction.

Figures

Please, indicate the contribution of each axis in explaining the variance, for the three panels, and the number of observations for Figures 1 and 2, as well as the number of observation in Figure 3.

There were several problems with the Supp. Figures, pointed in previous comments.

Reviewed by Tord Ranheim Sveen, 16 October 2022

This is a very interesting study that is generally well written, researched, and presented. On the strong side is the anchoring of the study in the contrasting frameworks of herbivore impact on microbial functional characteristics and plant communities, which is a line related to and followed throughout the paper. The methods are solid and, coming from a soil ecology background, well motivated and sound. Your discussion relates well to your results and your research question and I learnt new interesting things. In particular, the indication of threshold values in SOM and N driving herbivory responses is very interesting and should be investigated further. I have some concerns and questions on details but overall, I am happy to recommend this study for publication. Well done.

Issues

The presentation of the contrasting frameworks (diet vs productivity) could be made easier to follow through a cross-table to explain when the models align and when they contrast. Something like a power analysi table used to explain Type I and Type II errors (example: https://www.scribbr.com/statistics/type-i-and-type-ii-errors/)

Since time scales is an issue when comparing your results with the productivity model, it would be good to provide an explanation for why you chose to do a 2-year study and not longer.

Could there be any effects of mineral fertilizers introduced into the soil that affects the microbial functions

you measured? For example, easily accessible mineral N would presumably affect the resource acquisition strategy of the microbial communities by itself.

l151: I would avoid using the term ”infertile” as this is implies there is no or very little productivity. I suggest changing this throughout to ”less productive” or similar.

l388-389: SOM does not equal C sequestration (which is a rate measured over time). Why would you talk about C sequestration at all in this context?

L418-420: The adoption of the A vs Y strategies is really interesting and can be fruitful in this context, but it would be good to introduce it more clearly with e.g. a definition of what you consider an A strategist community vs a Y strategist in terms of the functions you measured. What motivates you to say that ”the A strategy comes along with plant communities having higher C/N leaf ratios”? Basically, at what EEN is a community A strategists? at l441-442 you then go on to directly say that ”A strategists invested even more in extracellular enzymes in response to herbivory”. Again, this use of the term is quite careless, since you have not defined any thresholds for your strategies.

Figure 1 and figure 2A: you should better explain the differences in color of the arrows in the legend.

The paper could benefit from one last round of language editing, as some of the words and sentences are a bit clunky at times. I made some notes on this with line references below, but please note that this is not exhaustive.

l33: with contrasted productivities
l87: unclear wording ”different axis of variation”. What is the variation implied here?
L106: provide instead of provided
L312: change ”on a large part” to ”to a large extent”
l386: revise sentence, too many ”differences” and ”different”
L389-392: This is trivial and does not need an explanation. Usually, 95% of total N (or TDN) consists of DON.
l393: fertilized with what? Presumaly with mineral N? This should be stated.
L402-405: Good explanation and reference, you could also mention the carbon use efficiency concept which talks around this.