Dear Dr. Medel,

We are herewith submitting the revised version of our manuscript " Comment on "Information arms race explains plant-herbivore chemical communication in ecological communities" for your consideration. Thank you and the referees for all the helpful recommendations. We have found these reviews very helpful in pinpointing areas where the clarity of our manuscript could be improved. We have addressed all concerns and suggestions in this revised version and detailed our changes or responses in the text below. When going back over our simulations we found a coding error that somewhat affects the results of one of our analyses, though not our conclusions. The affected figures are Fig. 2A & B in the original manuscript (now 1B & C due to the reorganization of our manuscript). In our corrected analysis, the correlation between specific conditional entropies and community conditional entropies is higher, but there are still many instances where they do not align. Again, thank you for the suggestions and the opportunity to resubmit our manuscript.

P.S. I'm not quite sure if I am supposed to submit track changes in addition to the completed draft (which is posted on *ecoevorxiv*). I am included them here in case they are helpful.

Sincerely,

Ethan Bass

Recommender

The three peer reviewers found that this manuscript will make an important contribution to the plant-herbivore arms-race literature as it provides a solid observation to the Zu et al. manuscript. However, they also performed a number of commentaries that may contribute to improve the clarity and organization of the main messages conveyed. I am attaching their main observations in the spirit of helping authors to present their message in the clearest way possible.

Best regards

Thank you for your support and suggestions. To address the comment on general clarity, we have adopted the suggestion by reviewers 1 and 3 to organize our critique into sections with clear headings and have sought to further clarify several areas that were confusing to the reviewers. We have re-organized the paper into four sections: "Misleading usage of evolutionary nomenclature"; "Alternative functions of chemical information"; "Are conditional entropies related to fitness?"; and "Alternative explanations of VOC redundancy and herbivore specialization".

Reviewer 1

The Bass and Kessler manuscript makes an informed critique of the work of Zu et al. However, in my opinion, the manuscript in some parts its a bit confusing, which makes it *difficult to read and to distinguish the main potentially flawed aspects of Zu et al. model. My recommendation is to organize the criticism into groups of aspects, namely assumptions and implications. On the one hand, each of the key assumptions should be listed in terms of how each of them would not be supported by current evidence. Criticisms should be prioritized in terms of which ones affect the validity of the model the most.*

Thank you for this suggestion. We have restructured the paper to make the priority of our criticisms more clear. For example, we now start with the discussion of how "fitness" is defined in the model, which from our point of view, is the major problem with the proposed model. Moreover, we now include subheadings that represent the different areas of critique as well as adjusting the text within each of those sections for more clarity.

As Bass and Kessler (line 69-70) state, a critical assumption by Zu et al. model is that plants share a common interest in confusing all herbivores in the community. However, in my opinion, this is not an assumption but a possible implication of the model (Taken from Zu et al: "Our work is based on hypotheses and suggests that an information arms race between plants and herbivores can lead plants to produce VOCs that are commonly shared by other species, increasing the difficulty for herbivores to identify suitable plants and potentially putting pressure on herbivores to specialize in a few plants").

While Zu et al do indeed state that the common interest of plants is an implication rather than an assumption of the model, we believe that the actual form of the model suggests otherwise. This is because of the way the model defines plant and herbivore fitnesses as a function of community conditional entropies, which are calculated by averaging across the columns of the AV matrix and are thus a property of the community as a whole. In fact, this is one of the most important problems with the model as we see it. The referee is correct however that this is not clearly stated as an assumption in the paper. We have tried to clarify this point in the text by drawing out our explanation of the way fitness is defined in the model (L 53-62) and why it is inconsistent with the way "evolutionary arms-races" are usually understood.

In my opinion, the main contribution of Bass and Kessler is related to the use of matrices calculating conditional entropies and fitness relationships based on simulated matrices using the average values, assuming selection at different levels other than the individual one (community level). Despite of this, Zu et al. included paired rewards for the plant and the insect (as sender and receiver) in terms of individual fitness, from which the average emerges as community parameter that alter individual fitness, which in the loop produce antagonistic dynamics (the arm-race). At some point, the overall pattern emerges from paired individual interactions. I would encourage to address with more detail this issue.

This is a very important point. Actually, the Zu et al model does not include individual fitnesses (or pairwise interactions) at any point – only the community conditional entropies, which determine whether or not mutations in the PV and AP matrices become fixed. This failure to account for individual fitnesses is one of the main points we aim to highlight in our comment. We do agree that this point is treated very confusingly in the original Zu et al manuscript, which is why we felt it necessary to write a comment addressing these issues. We have tried to further emphasize and clarify this point in our revision, where we have rewritten the relevant section and given it a new heading: "**Misleading usage of evolutionary nomenclature**" (L 53)**.**

If you consult the appendix to the Zu et al paper, where they describe the mathematical details of their model, plant and herbivore traits are modeled using two matrices: the PV matrix containing information about the distribution of VOCs in plants and the AP matrix containing information about the host range of each herbivore. One or more cells in each matrix are then mutated on each turn and the community conditional entropies (H(AIV) and H(VIA) are calculated to decide whether or not each new mutation is fixed. **At no point in this process do they model individual finesses based on specific interactions between plants and herbivores.** Whenever they talk about plant or herbivore fitness in the paper they are referring to these community level metrics.

In our comment, we derive an equivalent metric that can be calculated at the species level (drawing on the relevant literature in information theory). We propose that this species level conditional information can be used to test the model's assumption that conditional entropies are somehow related to fitness. As we point out in the text of our comment, "community fitness" is not a standard concept in ecology or evolutionary biology and is poorly defined in the Zu et al paper and thus cannot be directly measured to test whether the proposed indices are appropriate as metrics of fitness.

I think Bass and Kessler's critique should also focus on the problems of using assumptions that lack supporting empirical evidence. In other sections of the manuscript, Bass and Kessler (lines 78-87) questioned the lack of addressing behavioral effects of VOCs on herbivorous insects in Zu et al. model. However, Zu et al. only consider the outcome in terms of fitness without specifying the behavioral effect of the VOC.

The entire theoretical justification for choosing 1-H(VIA) and H(AIV) as "fitness" metrics is that they are assumed to affect insect behavior -- specifically they are supposed to reflect herbivore confusion, which is hypothesized to affect fitness. For example, when Zu et al introduce these fitness relationships, they write: "A high decoding efficiency can increase the attack rates and decrease the fitness of plants. By contrast, low efficiency can increase the searching time and decrease the fitness of herbivores."

Apart from this assumed link with behavior, there is no basis to assume that H(VIA) has anything to do with herbivore fitness or that it will determine evolutionary trajectories. The "fitness" effects are thus completely predicated on assumed behavioral effects, though we agree that these effects are not proven with any direct evidence. Again, this lack of evidence for their modeling framework is one of our major criticisms of the manuscript. We have added a short paragraph to make our criticism about the lack of empirical evidence for their chosen fitness metrics more explicit (L 161-166).

In my opinion, the model does not predefine the homogenization or diversification of the chemistry of the plant group, but this emerges as a product of the degree of effective information transfer between sender and receiver evaluated in terms of individual fitness.

As we have detailed above, there is no consideration of individual fitnesses in the Zu et al model – only community-level averages. We believe that homogenization is in fact predetermined due to the way that plant and herbivore "fitness" are defined in the model (see discussion beginning L 53). This is because a more homogeneous VOC distribution will always increase H(A|V). We have sought to clarify our reasoning around the homogenization of VOCs by making our reasoning more explicit (L 91-93).

However, as mentioned by Bass and Kessler, their own alternative model "demonstrates that the fitness of individual species does not always align with the fitness of the community", which means that this alternative model does not falsify Zu et al. model because, at least under some specific conditions, both conditions could align.

This is correct. However, these two figures are intended to convey the inconsistency of the proposed community "fitness" metrics with individual level concepts of fitness required to describe evolution by natural selection. While they may sometimes align, this is irrelevant to our broader point that the community "fitness" concept promoted by Zu et al is misleading and inconsistent with any common definition of fitness in biology. We have tried to clarify this point in the manuscript by rewriting the first sentence of this paragraph to better explain our intent: "The specific conditional information (Equation 3) can also be used to assess whether the community fitness concept proposed by Zu et al can be reconciled with the equivalent species-level fitness metric" (L 236).

The comment on the "information processing hypothesis" is not appropriate here or in Zu et al. This hypothesis addresses the idea of a trade-off between the ability to process information (formerly erected by Elizabeth Bernays as Neuronal Limitation Hypothesis) and the diet breadth of the insect. I don't see where Zu et al. use this information processing hypothesis.

In Zu et al, they state that "the conceptual framework for our study is based on… [the hypothesis that] plants aim to decrease the decoding efficiency of herbivores by changing PV associations, whereas herbivores aim to increase this efficiency" and that "a high decoding efficiency can increase the attack rates and decrease the fitness of plants" whereas "low efficiency can increase the searching time and decrease the fitness of herbivores". The only way that herbivores can increase this decoding efficiency is by “changing AP interactions” – i.e. narrowing their host range. Thus, the reader has to conclude that the basic framework of the Zu et al study is based on the hypothesis of a tradeoff between diet breadth and the ability to process information, and they explicitly advance this tradeoff as an explanation for herbivore specialization. We see this as being very closely related to the information processing (or neuronal limitation) hypothesis as proposed by Bernays and would thus like to keep this line of argumentation in the text.

There are some arguments that confuse the reader. For example, in line 6-70 Bass and Kessler say: "Most importantly, it also assume that the plants somehow share a common interest in confusing all herbivores in the community, ignoring the fact that plants compete with one another". If the model does not include variation within individual plants but only VOCs, this represents a scenario where all plants in a population interact identically, which does not mean that competition was not considered. It could be assumed that they interact as scramble competition. So, this does not affect Zu et al. model.

Thank you for raising this important point. We have tried to expand and clarify our argument (L 66-73). Our point here is not related to individual variation in VOCs, but rather to the fact that all plant species in the proposed model are arbitrarily assumed to evolve with the goal of optimizing community-level information indices, under the assumption that this increases herbivore confusion, thus reducing herbivory. Herbivores similarly are assumed to evolve to decrease the confusion of the entire herbivore community across species lines.

The assumption that plant and herbivore communities should evolve traits that collectively benefit their guild assumes an unrealistic level of common interest between species, contradicting much of what we know about species interactions and evolution by natural selection. For example, these assumptions imply that plants can derive a fitness benefit from confusing herbivores that eat only their competitors, contradicting basic logic (see L 71-73). Thus, our critique is not that Zu et al fail to explicitly model competition between plants, but rather that the way evolution is assumed to promote collective benefits in the model is inconsistent with basic ecological and evolutionary theory. In addition, there cannot be scramble competition in a model that does not include population sizes or density.

A critique of Zu et al. could include the observation that the insect-plant matrix used to validate the model was based on insects collected from plant leaves (tropical forest), meaning that the insects already selected the plant when the sampling took place. Therefore, the matrix is not related to the ability of insects to perceive signals (VOCs) from the host before settling on the leaves, something that is relevant for flying insects. Insects use VOCs during the host selection process prior to host use (feeding or oviposition) and information processing occurred at that step, and in a lesser extent afterward. In other words, the use of the insect-plant matrix refers to post-communication events between plant and insects.

Thank you for this suggestion. You are certainly correct that there could be other factors downstream of host-finding that affect herbivore distribution. However, we find that this is a fairly minor issue in comparison with the fundamental problems with model discussed in our comment.

After all, Bass and Kessler's comment to Zu et al. model is a valuable contribution and will surely help to improve the that model.

Thank you very much for pointing out areas where our commentary was unclear. We have tried to clarify these points in the main text as well as restructuring our arguments to improve the overall flow and clarity of our letter.

Reviewer 2

Plant-herbivore chemical communication has been studied and modeled thanks to an information theory-based approach (Zu et al Science 2020). The model is based on the hypothesis that conditional entropies can be considered as proxies of plant and animal fitnesses. In particular, plant fitness is related to the efficiency of coding a signal by the plant and animal's fitness is related to their capacity to decode a signal. The fitness is modeled at the community level (encompassing several species).
In this article, Bass et al. demonstrate that hypotheses of Zu et al are not realistic. In particular, Zu et al. considered plants and animals as communities and their model and the metrics used as fitness proxies does not depend on the species. These hypotheses does not consider that species compete with each other in a community. Arguments of Bass et al. are supported by strong biological references. In addition, they developed a model based on species conditional information and compare it with Zu et al. model (based on community condition information). Comparisons of fitness estimated from both of these models demonstrate that fitness of a given species does not necessarily correlate with fitness of its community.

Thank you, this is a very cogent summary of the Zu paper and of our response.

Authors of this paper also consider Zu et al. did not take into account the knowledge regarding the benefit of diversification of volatile components by neglecting the toxic or repellent nature of VOC for herbivores. I agree that this toxicity is not considered in the original paper, however I am not sure to understand the link between this assumption and its consequence on the diversification / homogenization of volatiles.

Thank you for pointing out this gap. We have tried to clarify our reasoning by adding the following: "The decision to disregard toxicity leads naturally to the homogenization of plant chemistry in the resulting model, since plants can increase herbivore confusion (and thus their own fitness) primarily by increasing VOC redundancy" (L 90-92). The key point here is that redundancy reduces the information content associated with a particular volatile (thus increasing the conditional entropy, $H(A|V_j)$). The conditional entropies for each volatile are then averaged to obtain the average conditional entropy $H(A|V)$, which is equated with plant fitness in the model. Thus, the model's assumptions lead inevitably to chemical homogenization because plants can maximize their primarily fitness by increasing VOC redundancy.

Authors did not show any relation between the number of insect on a plant and the specific information associated to this plant and conclude that volatile information is probably not a major determinant of plant resistance. Once again I am not sure to understand their reasoning (probably out of my skills for this part).

We certainly did not mean to imply that volatile information cannot affect plant resistance. Our purpose here was instead to emphasize that the particular information theoretic indices proposed by Zu et al as "fitness" metrics are not supported by any direct evidence. We clarify this point by adding a paragraph leading into this section (L 161-166) to better frame the discussion as well as revising the sentences leading into this section to better explain our line of thinking (L 168-173). We also added a concluding sentence summing up our argument in this section: "Thus, we find no support for the assumption that specific conditional entropies are related to plant fitness" (L 188).

Interestingly, authors cite references already supporting the fact that VOC redundancy and insect specialization an arise from evolutionary process (phylogenies for VOC and selection for insects).

In addition, before to discuss the hypothesis of Zu et al, Bass et al. estimated the connectedness of the matrices presented in the original paper thanks to field data and constructed a null model based on these parameters. This model correspond to any situation where volatiles components are redundant among plant and animals are specialized. The fitted values of this null model is similar to those obtained in the original paper, demonstrating that the information arms race is not the only explanation leading to a good fit between predicted and observed values.

Thank you. This is a very clear summary of the major point we intended to make in this section.

All the code and documentation needed to perform their analysis is available on line but I did not managed to test the script due to a technical problem on my computer.

Thank you for your attention to this. We found some small errors in the code and updated the repository on Zenodo. It should run now! Our conclusions remain unchanged.

Reviewer 3

I really enjoyed reading this response letter by Bass and Kessler; it is rigorous, well-written, relevant, and to the point. This letter is a response to the work presented recently by Zu et al. 2020. Latter authors propose that a “stable information structure explains the evolution towards redundancy of volatile organic compounds in plants”. The results of Zu et al. suggest
that the large diversity of VOCs in nature is explained by the ability of the herbivores to “quickly tell all plant species apart by making use of the few most informative VOCs, and plants can, in turn, respond to this potential by adding more VOCs to their profile. Under the same process, herbivores themselves can also be identified using a set of informative VOCs”. Nevertheless, there are several concerns about the assumptions and analyses that Zu et al. present in their work, as the authors of this letter have pointed out. This letter summarizes in relevant and polished manner biases in the results found by Zu et al. 2020.

Thank you very much for this cogent summary (and we are glad to hear that you enjoyed our letter).

I would suggest that authors explain what a “stable information structure” is in a few words.

Rather than endeavoring to explain what “stable information structure” means we have instead rewritten this sentence to remove this language, since we believe it is not clearly very defined in the original Zu et al paper.

Likewise, I would suggest that in the line 33, authors start pointing out their responses in a list manner or with subheadings, although this is just a writing style.

Thank you for this suggestion. We have restructured our major points as suggested and added subheadings.

Line 37. Please add a short explanation of what evolutionary principles authors are referring.

We have re-written the preceding sentence (L 33-35) to clarify our major issue here, which is that plants and herbivores are assumed to evolve toward collective goals (due to the way fitness is defined in the model). We have also sought to clarify and expand our discussion of these issues in the following section (under the heading **Misleading usage of evolutionary nomenclature**, beginning on line 53 in the revised MS). We now explicitly mention differential fitness (between species) as the evolutionary principle we believe is violated (L 57).

Line 38. As I have pointed out, it could be more informative for the readers if authors split the document by concerns/subtitles (e. g., “the null model”, “evolutionary theory of plant-insect interactions”).

This is a very helpful suggestion. We have split the document into four sections as you propose.

Line 65. Please clarify what hierarchical selection is.

We have rewritten this section and taken out the reference to hierarchical selection.

Line 67. I would reduce this sentence: Moreover, a model based on this assumption cannot explain the evolution by natural selection, since all plant species are assumed to have identical fitness in the model.

We have rewritten this sentence to clarify our meaning (L 58-62). We think it is important to emphasize that all species within a guild have identical fitness under the information arms race model because this conflicts fundamentally with basic assumptions of evolutionary theory.

Line 90. Or by convergent evolution, non-related species in the same environment can evolve the same VOCs. Indeed, the very well-supported studies on the diversification of secondary metabolites indicate that they originate from a small group of precursor compounds, which eventually become modified into diverse end-products. For example, all 40 000+ isoprenoid compounds originate from pyruvate and d-glyceraldehyde 3-phosphate entering the methylerythritol phosphate pathway in the chloroplast or from acetyl-CoA entering the mevalonate pathway reviewed in Moore et al. 2013. Another important thing that could be important to remark is what is happening at the genetic/genomic level. Gene duplications can lead to neofunctionalization of VOCs, hence increasing the chemical diversity.

Good point. We’ve added two sentences (L 408-410) reflecting that convergent evolution is also a possibility here, however we don’t want to get too deep into the weeds on the mechanics of chemical diversification, since our focus is intended to be fairly narrow in this letter.