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. 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”).

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.

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. 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. 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.

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.

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.

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.

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.

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.

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. 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).

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.

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.

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.

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

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

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”).

Line 65. Please clarify what hierarchical selection is.

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.

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.