Peer Community In
Ecology

Does information theory inform chemical arms race communication?

Rodrigo Medel based on reviews by Claudio Ramirez and 2 anonymous reviewers

A recommendation of:

Comment on "Information arms race explains plant-herbivore chemical communication in ecological communities"

Ethan Bass, André Kessler *(2022), EcoEvoRxiv, ver. 8 peer-reviewed and recommended by Peer Community in Ecology* ***https://doi.org/10.32942/osf.io/xsbtm***

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Recommendation

One of the long-standing questions in evolutionary ecology is on the mechanisms involved in arms race coevolution. One way to address this question is to understand the conditions under which one species evolves traits in response to the presence of a second species and so on. However, specialized pairwise interactions are by far less common in nature than interactions involving a higher number of interacting species (Bascompte, Jordano 2013). While interactions between large sets of species are the norm rather than the exception in mutualistic (pollination, seed dispersal), and antagonist (herbivory, parasitism) relationships, few is known on the way species identify, process, and respond to information provided by other interacting species under field conditions (Schaefer, Ruxton 2011).

Zu et al. (2020) addressed this general question by developing an interesting information theory-based approach that hypothesized conditional entropy in chemical communication plays a role as proxy of fitness in plant-herbivore communities. More specifically, plant fitness was assumed to be related to the efficiency to code signals by plant species, and herbivore fitness to the capacity to decode plant signals. In this way, from the plant perspective, the elaboration of plant signals that elude decoding by herbivores is expected to be favored, as herbivores are expected to attack plants with simple chemical signals. The empirical observation upon which the model was tested was the redundancy in volatile organic compounds (VOC) found across plant species in a plant-herbivore community. Interestingly, Zu et al.'s model predicted successfully that VOC redundancy in the plant community associates with increased conditional entropy, which conveys herbivore confusion and plant protection against herbivory. In this way, plant species that evolve VOCs already present in the community might be benefitted, ultimately leading to the patterns of VOC redundancy commonly observed in nature.

Bass & Kessler performed a series of interesting observations on Zu et al. (2020), that can be organized along three lines of reasoning. First, from an evolutionary perspective, Bass & Kessler note the important point that accepting that conditional information entropy, estimated from the contribution of every plant species to volatile redundancy implies that average plant fitness seems to depend on community-level properties (i.e., what the other species in the community are doing) rather than on population-level characteristics (I.e., what the individuals belonging a population are doing). While the level at which selection acts upon is a longstanding debate (e.g., Goodnight, 1990; Williams, 1992), the model seems to contradict one of the basic tenets of Darwinian evolution. The extent to which this important observation invalidates the contribution of Zu et al. (2020) is open to scrutiny. However, one can indulge the evolutionary criticism by arguing that every theoretical model performs a number of assumptions to preserve the simplicity of analyses. Furthermore, even accepting the criticism, the overall information-based framework is valuable as it provides a fresh perspective to the way coding and decoding chemical information in plant-herbivore interactions may result in arm race coevolution. The question to be assessed by members of the scientific community is how strong the evolutionary assumptions are to be acceptable. A second line of reasoning involves consideration of additional routes of chemical information transfer. If chemical volatiles are involved in another ecological function unrelated to arm race (as they are) such as toxicity, crypsis, aposematism, etc., the conditional information indices considered as proxy to plant and herbivore fitness may be only secondarily related to arms race. This is an interesting observation, which suggests that VOC production may have more than one ecological function, as it often happens in "pleiotropic" traits (Strauss, Irwin 2004). This is an exciting avenue for future research. Finally, a third category of comments involves the relationship between conditional information entropy and plant and herbivore fitness. Bass & Kessler developed a Bayesian treatment of the community-level information developed by Zu et al. (2020) that permitted to estimate fitness on a species rather than community level. Their results revealed that community conditional entropies fail to align with species-level indices, suggesting that conclusions of Strauss & Irwin (2004) are not commensurate with fitness at the species level, where the analysis seems to be pertinent. In general, I strongly recommend Bass & Kessler's contribution as it provides a series of observations and new perspectives to Zu et al. (2020). Rather than restricting their manuscript to blind criticisms, Bass & Kessler provides new interesting perspectives, which is always welcome as it improves the value and scope of the original work.

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Reviews

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Evaluation round #1

DOI or URL of the preprint: ***https://ecoevorxiv.org/xsbtm/***

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Author's Reply, None

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Decision by Rodrigo Medel, 08 Dec 2021

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

Download recommender's annotations

Reviewed by anonymous reviewer, 27 Oct 2021

Download the review

Reviewed by anonymous reviewer, 30 Nov 2021

Plant-herbivore chemical communication has been studied and modeled thanks to a information theory-based approach (Zu et al Science 2020). The model is based on the hypothesis that condional enthropies 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 developped 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 necessarly 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 neglegecting 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 ptrobably 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 evolutionnary process (phylogenetics for VOC and selection for insects).

In addition, before to discuss the hypothesis of Zu et al, Bass et al. estimated 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 redondant 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.

Reviewed by Claudio Ramirez, 30 Nov 2021

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 sclamble 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.