Title: Comment on “Information arms race explains plant-herbivore chemical communication in ecological communities”

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Abstract:

Zu et al (*Science*, 19 Jun 2020, p. 1377) propose that an ‘information arms-race’ between plants and herbivores explains plant-herbivore communication at the community level. However, our analysis shows that key assumptions of the proposed model either a) conflict with standard evolutionary theory or b) are not supported by the available evidence. We also show that the presented statistical patterns can be explained more parsimoniously (e.g. through a null model) without invoking an unlikely process of community selection.

Main Text:

Zu *et al* (*1*) propose that a (dis)information arms race between plants and herbivores leads to the emergence of a “stable information structure” in ecological communities and that this process explains the evolution of plant volatile organic compound (VOC) redundancy and insect dietary specialization. In support of this hypothesis, the authors present a mathematical model of plant-herbivore coevolution, where “fitness” is tied to conditional entropies derived from information theory. Conditional entropies measure the uncertainty associated with a random variable (e.g. herbivore identity), given knowledge of a second random variable (e.g. VOC composition). Specifically, the authors propose that plant fitness can be related to $H(A|V)$ – the average conditional entropy of herbivores with respect to the VOC profiles of their host plants. $H(A|V)$ can thus be understood as a reflection of the average difficulty of host-finding by herbivores. Herbivore fitness meanwhile is equated with $1 - H(V|A)$. As evidence for their hypothesis, the authors compare the conditional entropies derived from a simulation with empirical values estimated from their field data, finding that the two sets of values converge quite closely. This result is not surprising however, since the model assumes that plant and herbivore evolution is directed toward the optimization of precisely these indices ($H(A|V)$ and $1-H(V|A)$ respectively). The use of these indices as “fitness” proxies is also problematic because they are community-level averages and are thus identical for all plant and herbivore species at any given time. The resulting model thus implies that all plant species in the community somehow evolve cooperatively to minimize $H(A|V)$, a possibility which appears to conflict with basic evolutionary principles.

Here we show that a null model parameterized by the observed frequency of links in the plant-herbivore and plant-volatile networks reproduces the “information structure” deduced from the field data equally as well as the proposed model while relying on fewer problematic assumptions (Fig. 1). The null model demonstrates that the proposed information theoretical indices can be explained solely on the basis of network connectedness, such that any model generating the observed connectedness values will produce similar entropies. In other words, any mechanism generating moderate VOC redundancy combined with insect dietary specialization would be sufficient to reproduce the patterns observed by the authors. Since an information arms race is not a unique explanation for the observed pattern, we must assess the hypothesis on its merits relative to other plausible explanations and on the validity of its core assumptions.

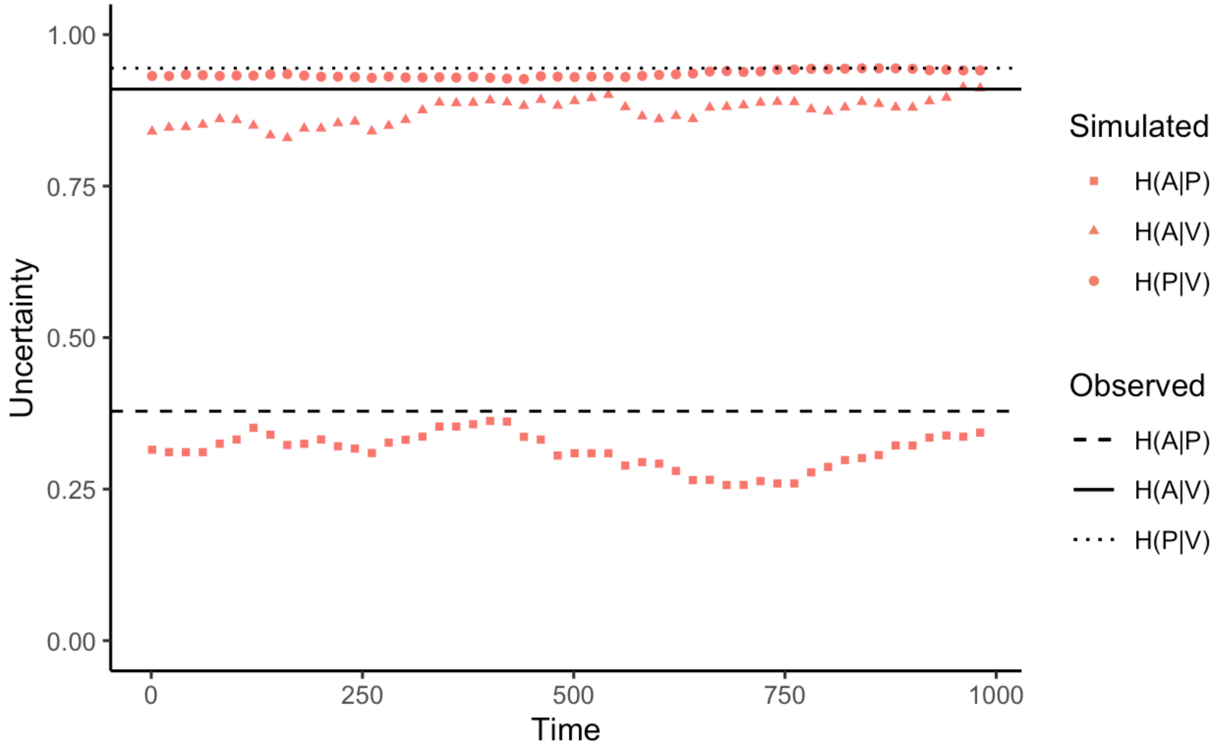

Fig. 1 *Simulation of neutrally evolving plant-herbivore community, where the connectedness of the PV and AP matrices is parameterized using frequencies estimated from the field data. We estimate that plant-volatile links occur with a probability of 0.8 and plant-herbivore links occur with a probability of 0.1. Observed entropies plotted as horizontal lines are mean values from three years of data reported by Zu et al. (Compare with figure 3A in Zu et al 2020).*

We take issue with several key assumptions of the proposed model: 1) that the proposed information theoretical metrics are a suitable proxy for fitness, 2) that plant VOC profiles are shaped primarily by "selection” on community conditional entropies, 3) that plants have no phylogenetic constraints on VOC production, and 4) that herbivores have no physiological constraints on diet (*1*). Together, these assumptions create a highly misleading picture, precluding the consideration of most plausible alternatives concerning the functions of chemical information. While the authors consider several alternative models, all proposed models assume the existence of a relationship between fitness and the conditional entropies H(A|V) and H(V|A), which represent the average uncertainty about the distribution of herbivores with respect to the

VOC composition of their host plants. Conceptually, the use of average conditional entropies as fitness proxies is problematic, since it implies that plant VOC profiles are maintained primarily by hierarchical selection at the community-level. This assumption contradicts most mainstream evolutionary thinking, even by advocates of an extended synthesis (*2*). Moreover, a model based on this assumption cannot explain the differential survival of individuals or species (i.e. evolution by natural selection), since all plant species are assumed to have identical fitness. Most importantly, it also assumes that plants somehow share a common interest in confusing all herbivores in the community, ignoring the fact that plants compete with one another. While it is plausible that plants may share a common interest in confusing shared herbivores, there is no reason to think that plants will benefit from confusing herbivores that eat only their competitors. In many cases it may instead be beneficial to advertise one's toxicity (chemical aposematism) or to hide behind the information of a neighbor (associational resistance) (*3*, *4*). Finally, it is difficult to imagine how the validity of these assumptions could be tested empirically, since "community fitness" cannot be measured for comparison with the proposed information theoretical indices.

By uncoupling insect diet from metabolism, the model also neglects to consider the obvious (and well-supported) hypothesis that plant VOCs may be directly repellent to herbivores, either because they are toxic, or because they encode information about other unsavory metabolites in the emitter (*5*). Consequently, the authors restrict themselves to the assumption that plant insect-coevolution should lead to the homogenization of plant chemistry rather than promoting diversification as is commonly assumed (*6*, *7*) Empirical studies have generally found that chemical similarity is associated with increased herbivory (*8*, *9*), contrary to the main prediction of the information arms race hypothesis. At the same time, the model fails to explain why plants should produce VOCs at all, since they could presumably induce equal confusion (at less metabolic cost) by abstaining from VOC production altogether.

VOC redundancy and herbivore specialization can both be explained without invoking an implausible process of community selection. VOC redundancy for example can be explained as a simple product of the shared evolutionary history between plant species, combined with stabilizing selection for beneficial VOCs. While it seems plausible that chemical crypsis could play a role in the evolution of VOC redundancy (*10*), there is currently no reason to believe that this is a major function of chemical information transfer, much less the only function. Meanwhile, the "information processing hypothesis" – that herbivore specialization can arise from selection on insects to maximize host-finding efficiency – while plausible, is not original to the present work, being one of several widely discussed explanations of herbivore specialization (*11–13*).

In order to test the model's key assumption that herbivore and plant fitness are related to the information provided by VOCs about host suitability, it is necessary to have species- or individual- level indices of volatile information. If VOC redundancy benefits plants by reducing their apparency (*14*), it follows that plants with more distinctive VOC profiles should be exposed to greater damage from herbivores. Accordingly, the mutual information can be decomposed into:

$$I(O;S) = \sum_{o} p\,(o) I(O = o; S) \tag{1}$$

where the specific information, $I(O = o; S)$ is a measure of the information associated with a particular outcome o of O (*15*, *16*).

$$I(O = o; S) = \sum_{s} p\,(s|o)\left[\log\frac{p(o|s)}{p(o)}\right] \qquad 2$$

According to Bayes Theorem, the specific information can then be rewritten as:

$$I(O = o; S) = \sum_{s} p\,(s|o)\left[\log\frac{p(s|o)}{p(s)}\right] \qquad 3$$

We constructed a model substituting this specific conditional information (Equation 3) for the average conditional information proposed by Zu *et al* (*1*) as a proxy for fitness. Specifically, plant fitness was equated with $1 - I(A_p, V)$,[17] and herbivore fitness with $I(V, A_j)$. This alternative model demonstrates that the "fitness" of individual species does not always align with the "fitness" of the community, leading to nonsensical results, such as the fixation of mutations that increase the "fitness" of the community at the expense of the affected species [Figs. 2A & B]. Thus, the concept of community fitness defined by Zu seems incongruous with basic evolutionary principles. We also show that there is no relationship between $I(P_i, V)$ and the number of herbivores associated with a particular plant species, suggesting that volatile information may not be a major determinant of plant resistance to herbivory [Fig. 2C]. While it would be better to regress $I(P_i, V)$ against actual herbivore damage levels, we use the number of herbivores associated with a given plant as a loose proxy for fitness, since data on herbivore damage was not available. While the general approach of integrating information theory with ecological and evolutionary theory is exciting, we wish to emphasize that attempts to integrate information theoretic indices with evolutionary theory must be rigorously tested to ensure that the field moves forward on firm empirical footing.

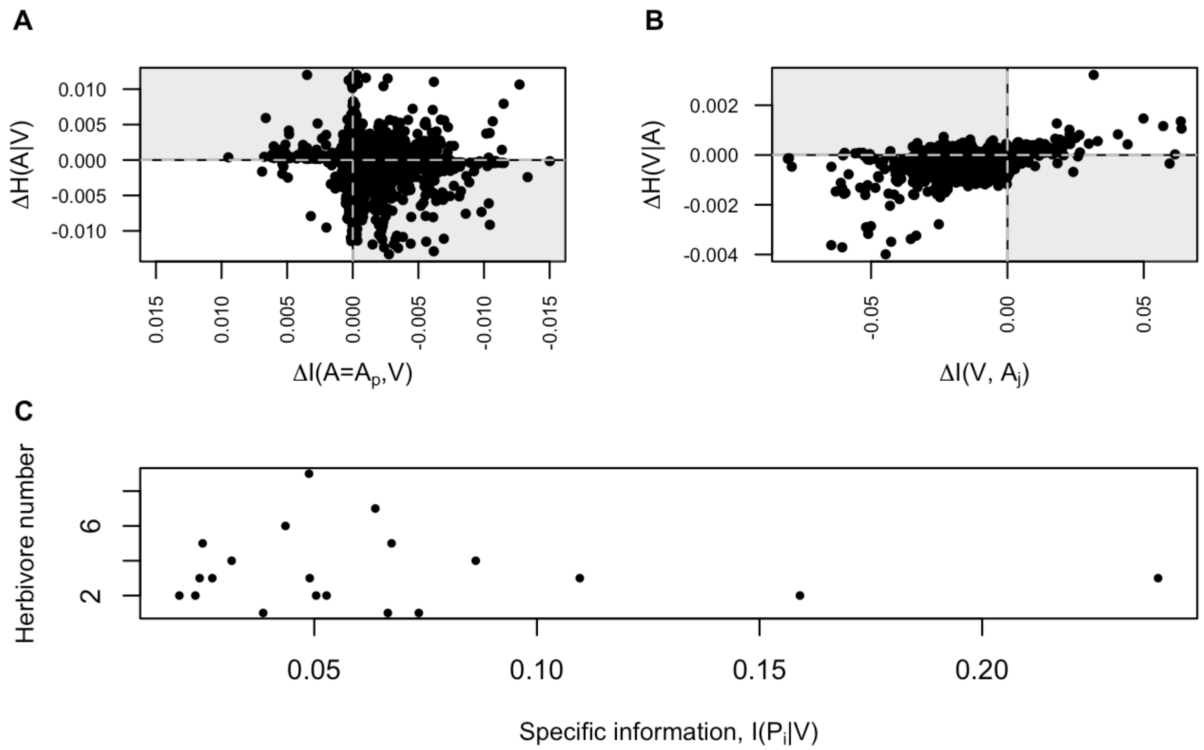

Fig. 2 *(A) Relationship between the fitness of the mutated plant species, calculated as* $1 - I(A_p, V)$ *and the community conditional entropy H(A|V), where* $I(A_p, V)$ *is calculated as the weighted average of the specific information* $I(A = a, V)$ *(Equation 3) for the set of herbivores that interact with plant p (*$p < 0.001, R^2 = 0.021$*). (B) Relationship between the "fitness" of the mutated herbivore species, calculated as* $I(A_j, V)$*, and the community conditional entropy H(V|A), where* $I(A = a_j, V)$ *is the specific information of the mutated herbivore species with respect to VOCs (*$p < 0.001, R^2 = 0.46$*). (The shaded quadrants in A and B indicate areas where the "community fitness" and the species-level fitness are of opposite sign, indicating that a mutation would be selected in one model, where it would be eliminated in the other). (C) Relationship between the specific information* $I(P_i|V)$ *and the number of herbivores associated with each plant species (*$p = 0.86, R^2 = 0.0018$*).*

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17. We define $I(A_p, V)$ as the weighted average of $I(A = a, V)$ taken over the set of herbivores associated with a particular plant, p, such that $I(A_p, V) = \sum_i^{A_p} p\,(a_i) I(A = a_i; V)$, where A_p is defined as the set of herbivores associated with plant p.