

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

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9 compounds, plant-herbivore coevolution, coevolutionary arms-race

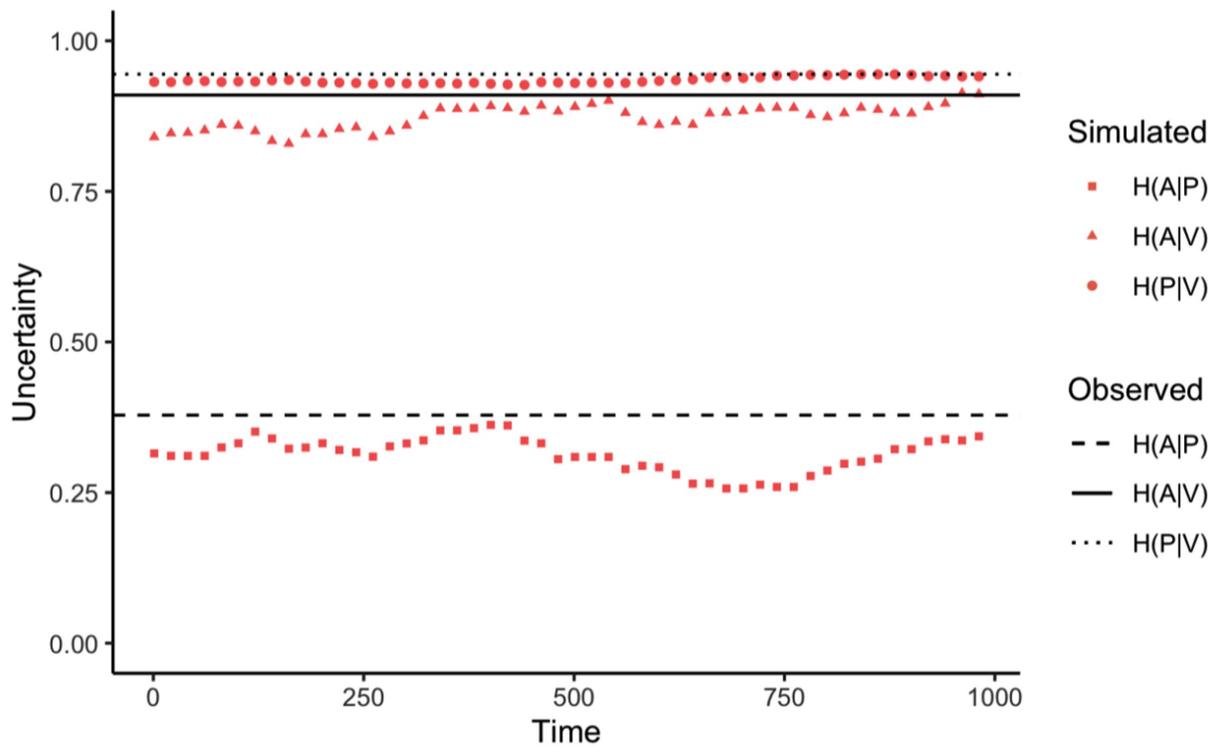
10 **Abstract:**

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

17 **Main Text:**

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

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



48

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

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

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

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

88 VOC redundancy and herbivore specialization can both be explained without invoking an  
89 implausible process of community selection. VOC redundancy for example can be explained as a  
90 simple product of the shared evolutionary history between plant species, combined with  
91 stabilizing selection for beneficial VOCs. While it seems plausible that chemical crypsis could  
92 play a role in the evolution of VOC redundancy (10), there is currently no reason to believe that  
93 this is a major function of chemical information transfer, much less the only function.  
94 Meanwhile, the "information processing hypothesis" – that herbivore specialization can arise  
95 from selection on insects to maximize host-finding efficiency – while plausible, is not original to  
96 the present work, being one of several widely discussed explanations of herbivore specialization  
97 (11–13).

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

104 
$$I(O; S) = \sum_o p(o) I(O = o; S) \quad 1$$

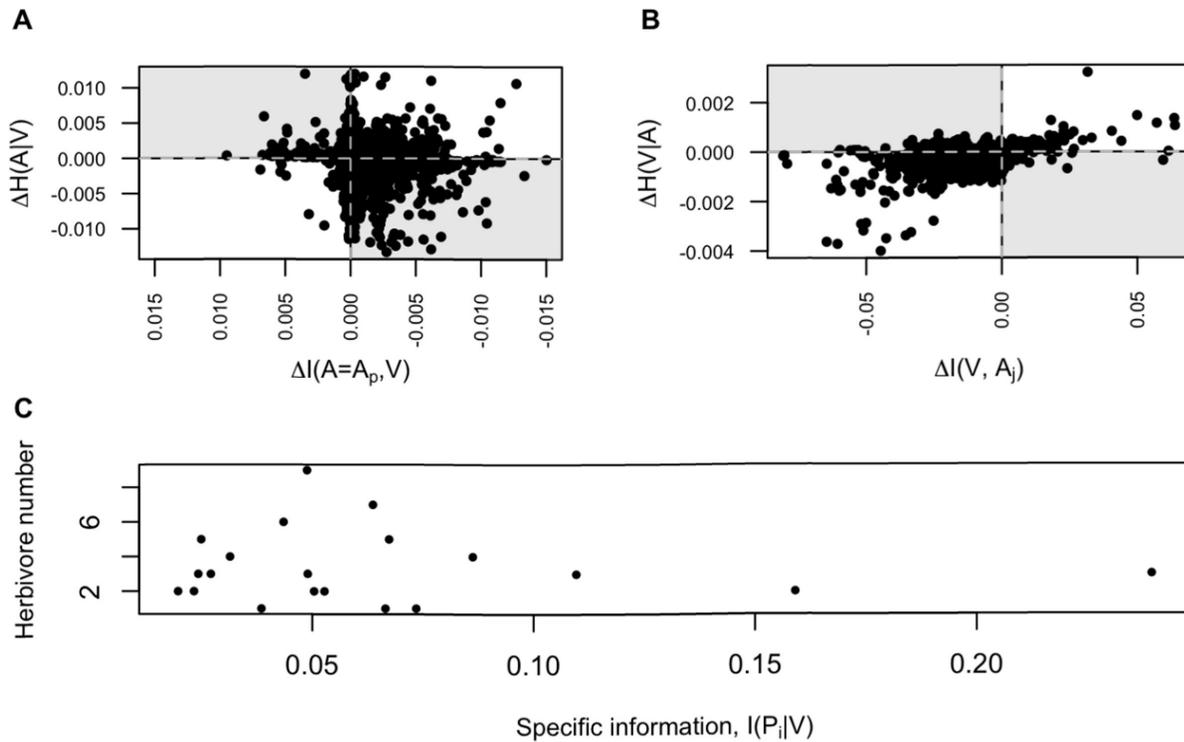
105 where the specific information,  $I(O = o; S)$  is a measure of the information associated with a  
106 particular outcome  $o$  of  $O$  (15, 16).

$$107 \quad I(O = o; S) = \sum_s p(s|o) \left[ \log \frac{p(o|s)}{p(o)} \right] \quad 2$$

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

$$109 \quad I(O = o; S) = \sum_s p(s|o) \left[ \log \frac{p(s|o)}{p(s)} \right] \quad 3$$

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



126

127 **Fig. 2** (A) Relationship between the fitness of the mutated plant species, calculated as  $1 -$   
 128  $I(A_p, V)$  and the community conditional entropy  $H(A|V)$ , where  $I(A_p, V)$  is calculated as the  
 129 weighted average of the specific information  $I(A = a, V)$  (Equation 3) for the set of herbivores  
 130 that interact with plant  $p$  ( $p = 0.81, R^2 \cong 0$ ). (B) Relationship between the “fitness” of the  
 131 mutated herbivore species, calculated as  $I(A_j, V)$ , and the community conditional entropy  
 132  $H(V|A)$ , where  $I(A = a_j, V)$  is the specific information of the mutated herbivore species with  
 133 respect to VOCs ( $p < 0.001, R^2 = 0.31$ ). (The shaded quadrants in A and B indicate areas  
 134 where the “community fitness” and the species-level fitness are of opposite sign, indicating that  
 135 a mutation would be selected in one model, where it would be eliminated in the other). (C)  
 136 Relationship between the specific information  $I(P_i|V)$  and the number of herbivores associated  
 137 with each plant species ( $p = 0.69, R^2 = 0.009$ ).

138

139

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 146 analyses is available on Zenodo (<https://doi.org/10.5281/zenodo.5523276>).

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148 **References and Notes:**

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188 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  
189 defined as the set of herbivores associated with plant  $p$ .