

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

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1 **Plants emit an extraordinary diversity of chemicals, providing information about**
2 **their identity and mediating interactions with insects. However, most studies have**
3 **focused on a few model species in controlled environments, limiting our capacity to**
4 **understand plant-insect chemical communication in ecological communities. Here, by**
5 **integrating information theory with ecological and evolutionary theories, we show**
6 **that a stable information structure of plant volatile organic compounds (VOCs) can**
7 **emerge from a conflicting information process between plants and herbivores. We**
8 **corroborate this information arms-race theory with field data recording plant-VOC**
9 **associations and herbivore-plant interactions in a tropical dry forest. We reveal that**
10 **plant VOC redundancy and herbivore specialization can be explained by a conflicting**
11 **information transfer. Information-based communication approaches can increase our**
12 **understanding of species interactions across trophic levels.**

13 One-sentence summary: We find that a stable information structure of plant volatile organic
14 compounds can emerge from a conflicting information process between plants and herbivores in
15 ecological communities.

16 Chemical information is an ancient and ubiquitous channel to mediate species interactions (1)
17 (e.g., attracting or repelling individuals) and regarded as one of the main forces shaping
18 plant-herbivore interaction networks (2, 3). For example, insects have a large number of olfactory
19 receptors with high sensitivity for chemical signals (4, 5), which play essential roles in their
20 fundamental activities (6) including foraging (7) and oviposition (8). Chemically-mediated species
21 interactions are based on information transfer; which, we define simply as communication
22 regardless of the benefit to the emitter and receiver, following previous work (9). Indeed,
23 understanding the chemical communication between plants and herbivores has been an active
24 field of research (10–12), where the majority of work has focused on how a specific plant (or
25 genus) defends against herbivores directly by using chemical repellents (13) or by producing
26 stronger chemical defenses (14–16), or indirectly by emitting signals to attract herbivores’
27 enemies (e.g., predators or parasitoids) (17–22). So far, only a few descriptive studies (23, 24)
28 have begun to investigate this chemical communication at the community level. More critically,
29 little is known about how information transfer shapes species interactions. For example, it
30 remains unclear how plants code chemical information to deal with a diversity of potential
31 herbivores, and how herbivores decode such olfactory signals to distinguish among plants and
32 identify potential hosts. Even less is known about whether there is any general information
33 structure of plant-herbivore chemical communication, and how such structure can be maintained
34 under an ongoing chemical arms race between plants and herbivores.

35 Information theory (25), which provides a quantitative and scalable way to measure information
36 transfer, has already brought key insights about the structure and emergence of human
37 language (26) and can be extended to increase our understanding about the “chemical language”
38 in ecological communities (12, 27–29). Yet, such attempts have only been employed to study
39 chemical communication of a single plant species with its interacting insects (30). Here, we
40 employ information theory to study plant volatile organic compounds (VOCs) as a
41 communication channel forming plant-insect interaction networks (31). From an information
42 perspective, the relationship between a sender and a receiver (or speaker and hearer) determines
43 the nature of the signal transmission as well as the evolution of the information structure shaping
44 the communication pattern between individuals. That is, individuals can either provide clear
45 information that could be decoded easily or spurious information that could be difficult to decode.
46 Moreover, a conflicting or harmonious communication process between sender and receiver can be

47 modeled by the combinations of maximizing or minimizing uncertainty (or mutual information) of
48 the two parties, respectively (26).

49 Specifically, for a given communication system that is formalized by a matrix describing how a
50 vector of signals (S) is associated with a vector of objects (O), the clearness (or the spuriousness)
51 of the communication can be described by two important information measurements (25): First,
52 mutual information ($I(O, S)$) describes the amount of information that one can obtain about
53 objects by knowing the signals. Second, conditional entropy ($H(O|S)$) describes the uncertainty
54 of correctly identifying an object given that a specific signal has been observed (Ref. (32) provides
55 a detailed mathematical account of these expressions). Importantly, both mutual information and
56 conditional entropy represent the efficiency of the coding (and decoding) strategies and can be
57 related to the fitness of senders and receivers (26).

58 Tropical dry forests host a large number of interacting and co-evolving plant and butterfly species
59 and are regarded as biodiversity hotspots (33). Our field work was conducted in a tropical dry
60 forest of the Chamela-Cuixmala Biosphere Reserve (19° 22'-19° 39'N, 104° 56'-105° 10'W) in
61 Jalisco, Mexico. During the rainy season of 2018, we searched comprehensively for Lepidopteran
62 larvae on leaves of target plants in our transect plots and reared the larvae in the laboratory with
63 leaves collected from their host plant species to confirm their trophic interaction and identify the
64 herbivore species. Ref. (32) provides a detailed account of plants and insects, sampling, and
65 identification procedures. We constructed a qualitative (presence/absence) animal-plant (*AP*)
66 interaction matrix comprising 28 Lepidopteran herbivore species and 20 plant species. The *AP*
67 matrix was rather sparse (see Figure 1A, Table S1) with a median of 1 plant species per herbivore
68 (ranging from 1 to 9 plant species per herbivore).

69 Additionally, we sampled the headspace around leaves to retrieve VOCs from each of these plant
70 species. We were able to match 93 analytes from headspace samples to the NIST17 VOC library,
71 of which 56 were likely biogenic (from plants, or from plants and microbes), and 31 of these
72 biogenic VOCs could be identified by one or more abundant ions in an untargeted analysis. We
73 used single representative ions from these 31 VOCs for quantification. Ref. (32) provides a
74 detailed account of VOC sampling, identification, and quantification procedures. Figure 1B (and
75 Table S2) shows that, contrary to the *AP* matrix, the plant-VOC (*PV*) association matrix is
76 dense and erratic with a median of 28 VOCs per plant (ranging from 23 to 30 VOCs).

77 Importantly, the PV matrix provides information about plant-VOC associations, whereas the AV
78 matrix (mathematically defined by the matrix multiplication $AP \times PV$) provides information
79 about herbivore-VOC associations. These associations describe the patterns of plants emitting
80 information and herbivores receiving it, and thus represent plant coding and herbivore decoding
81 strategies. The AV matrix (Fig. 1C) is dense and weighted, indicating that individual VOCs are
82 associated with more than one herbivore. Note that to generate the herbivore-VOC association
83 (AV matrix) we assumed that if a herbivore can feed on a plant, it must be able to cope with
84 spatial and temporal variation in VOCs that are used to distinguish suitable hosts, despite the
85 effects of these VOCs on the herbivore (attract, deter, neutral). Altering either the PV or AP
86 matrix can change the herbivore-VOC associations (AV matrix).

87 We built the conceptual framework for our study based on a conflicting optimization process
88 between plants and herbivores (see Fig. 2). Specifically, we hypothesized that plants aim to
89 decrease the decoding efficiency of herbivores via changing plant-VOC associations (PV), whereas
90 herbivores aim to increase this efficiency via changing herbivore-plant interactions (AP).
91 Ecologically, the decoding strategy can be linked to the fitness of plants and herbivores. A high
92 decoding efficiency can increase the attack rates and decrease the fitness of plants. In contrast,
93 low efficiency can increase the searching time and decrease the fitness of herbivores (12). Formally,
94 we define the fitness relationships as $F_P = H(A|V) \in [0, 1]$ and $F_A = 1 - H(V|A) \in [0, 1]$,
95 respectively. That is, plant fitness is proportional to the conditional entropy (uncertainty)
96 between VOCs and herbivores, whereas herbivore fitness is negatively proportional to the
97 conditional entropy between herbivores and VOCs. Ref. (32) provides details on the calculations.

98 To track the evolutionary trajectory of the communication system between plants and herbivores
99 based on our hypothesis, we simulated the optimization process above in the following way. Plants
100 and herbivores can increase their fitness relationships (based on the AV matrix) via modifying
101 the interactions in the PV matrix and in the AP matrix, respectively (see Figure 2). These
102 modifications come from random mutations of a given number of elements in the PV and AP
103 matrices. We assumed equal mutation rate for each link (plant-VOC link or herbivore-plant link)
104 in the absence of any prior knowledge. Therefore, the number of random mutations that plants
105 and herbivores can have for each round were proportional to the number of all possible links (i.e.,
106 number of elements in PV and AP matrices). Mutations are only selected if they increase the
107 corresponding fitness relationships. To mimic a continuous arms race, we only allowed changes by

108 plants and herbivores in an alternating fashion (see Figure 2). Both the PV and AP matrices can
109 be initialized from any random configuration with the only restriction of matrix size. To make our
110 simulation as simple as possible, we assumed that plants can potentially emit any VOC and
111 herbivores can potentially eat any plant without any phylogenetic or physiological constraints.

112 We investigated the capacity of our hypothesized mechanism to explain both the (de)coding
113 strategies and the information structure of chemical communication between plants and
114 herbivores observed in the field. Specifically, we determined the ability of our model to explain
115 the conditional entropies $H(P|V)$, $H(A|P)$, and $H(A|V)$; which characterize the PV , AP , and
116 AV matrices, respectively. Then, we determined its ability to explain the observed fitness
117 relationships F_P and F_A . Note that conditional entropy by definition is the *average* entropy given
118 each specific signal (i.e., individual VOC in the case of $H(P|V)$ and $H(A|V)$). Furthermore, we
119 tested how accurately our model could generate the *cumulative* information structure given a
120 combination of VOCs by calculating the mutual information between plants and VOCs ($I(P, V)$)
121 and between herbivores and VOCs ($I(A, V)$) as a function of the number of VOCs.

122 Additionally, we compared our proposed optimization mechanism against the three following
123 alternative optimization mechanisms: The fitness relationships of plants and herbivores depend on
124 their capacity to (1) maximize uncertainty (i.e., $F_P = H(A|V)$ and $F_A = H(V|A)$), (2) minimize
125 uncertainty (i.e., $F_P = 1 - H(A|V)$ and $F_A = 1 - H(V|A)$), and (3) minimize and maximize
126 uncertainty (i.e., $F_P = 1 - H(A|V)$ and $F_A = H(V|A)$). We also ran all our simulations over
127 different initial conditions, ranging from highly specialized to highly generalized matrices. The
128 rationale for using these alternative mechanisms and initializations is to illustrate that potential
129 matches between our theoretical expectations and observed values are not just an artifact of
130 sample size, metrics, any given optimization process, or the high (low) connectivity observed in
131 the PV (AP) matrix. Ref. (32) provides all the details about these additional analyses.

132 Because sampling bias is an important concern in the majority of ecological studies (34), we
133 tested whether our results would be affected by the sampling effort in reporting species, by an
134 incomplete plant VOC profile, and by sampling the interaction network in a different year or
135 place. We found that all our results were qualitatively equivalent when using sub-samples from
136 the whole dataset (illustrating the scalability of our findings), changing the VOC profile from 31
137 to 52 by including potential undefined biogenic VOCs, and using information of plant-herbivore
138 interaction networks from previous years (from 2007-2017) (35). Ref. (32) provides all the details

139 about the robustness of our results to changes in community size, number of VOCs, and identity
140 and number of species interactions.

141 Figure 3 shows that the proposed, conflicting, information process is able to explain the coding
142 and decoding patterns observed in the field. In particular, Figure 3A shows that the conditional
143 entropies $H(P|V)$ (see triangles), $H(A|P)$ (see squares), and $H(A|V)$ (see circles) remain
144 bounded across the simulated time to values close to those observed (see dashed, dotted and solid
145 lines). Similarly, Figure 3B shows that the optimized fitness relationships of plants F_P (see +
146 symbols) and herbivores F_A (see \times symbols) quickly converge to a stable value close to that
147 observed (see solid lines). Importantly, Figure 3C shows that the alternative optimization
148 mechanisms are not able to explain all the patterns.

149 Additionally, Figure 4 shows that of our four tested models, only our proposed conflicting
150 optimization process can recover the information structure observed in the field. Recall that we
151 measured the cumulative information structure by the mutual information ($I(P, V)$ and $I(A, V)$),
152 where values closer to one imply that the presence or absence of a VOC (or a combination of
153 VOCs) gives more information or has higher probability to tell all the species apart. In fact, the
154 field data revealed that as few as 8 VOCs can tell all the plants apart and 15 VOCs can give 97%
155 information about herbivores (i.e., have 97% of probability to correctly tell all the herbivores
156 apart). Importantly, this structure was closely recovered by our proposed optimization
157 mechanism (9 VOCs yield all the information of plants, and 14 VOCs for 97% information of
158 herbivores, red lines). In contrast, the three alternative optimization mechanisms yield very
159 different information structures, where either a large number of VOCs would be needed to
160 uniquely identify species or the identification from VOCs would be less likely. For example, in the
161 case where both parties aim to maximize uncertainty (i.e., confuse their opponents as in a
162 mutually competitive relationship, blue lines), even by using the combination of all VOCs, it
163 would be impossible to tell all the species apart. All these results are robust to changes in
164 community size, number of VOCS, the identity and number of species interactions, and different
165 initial conditions (see Ref. (32) Fig. S1-S6).

166 While a few recent studies have begun to demonstrate chemical patterns associated with
167 plant-insect communities (24, 31, 36), our study proposes a plausible theoretical framework that
168 explains and recovers patterns of information transfer between plants and herbivores from
169 empirical data. Our work is hypothesis-driven and suggests that an information arms race

170 between plants and herbivores can drive plants to produce VOCs that are commonly shared by
171 other species, increasing the difficulty for herbivores to identify suitable plants and potentially
172 pressuring herbivores to specialize on a few plants (as the AP matrix shows in Fig. 1). Indeed,
173 previous studies have shown a substantial overlap among the VOCs emitted by different plant
174 species (31, 37, 38). However, functional roles of a large portion of plant VOCs have been
175 unexplained and overlooked because most mechanistic studies have focused on specific plant
176 species and on the ecological functions of only a few VOCs (12). Here, our information arms-race
177 theory suggests that these seemingly redundant VOCs play an important role in confusing
178 herbivores at the community level. Focusing on herbivore-plant interactions, herbivores are
179 commonly regarded as specialists (6), which was also recovered from our theory. In fact, it is
180 estimated that $< 10\%$ of all herbivores feed on plants that span more than 3 families (39).

181 Our findings further suggest that a conflicting information process drives the rapid accumulation
182 of information by adding VOCs (Fig. 4), contrary to other optimization processes. This provides
183 additional evidence for an arms-race process explaining the large diversity of VOCs in nature,
184 where herbivores have the evolutionary potential to quickly tell all plant species apart by making
185 use of the few most informative VOCs and plants can in-turn respond to this potential by adding
186 more VOCs to their profile. Interestingly, under the same process, herbivores themselves can also
187 be identified using a set of informative VOCs (Fig. 4B). This raises the question of how these
188 VOC profiles result in evolutionary trade-offs regulating the attraction of herbivores and their
189 predators and parasitoids (17, 18). Overall, our study suggests information-transfer processes are
190 key drivers of the formation and maintenance of species interactions across trophic levels.

191

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305 **Figure legends**

306 **Fig. 1. Field data on herbivore (animal)-plant interactions, plant-VOC associations,**
307 **and herbivore-VOC associations.** Panel **A**, each row and column represents one of the 28
308 insect herbivores and 20 plants sampled, respectively. Black and white squares show that a given
309 herbivore was, or was not observed feeding on a given plant, respectively. We refer to this as the
310 AP matrix and we use it to investigate the plant-herbivore interaction network. Panel **B**, each
311 row and column represent one of the 20 plants and 31 VOCs sampled, respectively. Black and
312 white squares show that a given VOC was present or absent in a given plant, respectively. We
313 refer to this as the PV matrix and we use it to investigate the coding strategy of plants. Panel **C**
314 shows the matrix of herbivore-VOC associations produced by the multiplication of the previous
315 two matrices ($AP \times PV$). Each row and column represents one of the 28 herbivores and 31 VOCs
316 associated, respectively. The darker the squares, the greater the frequency with which a given
317 herbivore is associated with a given VOC. We refer to this as the AV matrix and we use it to
318 investigate the decoding strategy of herbivores. See Ref. (32) Table S1-S2 for more information
319 about these matrices.

320 **Fig. 2. Conceptual diagram of the proposed, conflicting, information process**
321 **(information arms race) between plants and insect herbivores.** The coding strategy by
322 plants is characterized by the plant-VOC (PV) association matrix (green right box). The
323 animal-plant (AP) interaction matrix (blue left box) is used to infer how plants' codes are
324 decoded by herbivores. These matrices undergo mutations by changing any of their elements (e.g.,
325 red numbers): zeros and ones correspond to absence and presence, respectively. These mutations
326 will fixate only if the fitness relationship of the corresponding species increases. The fitness
327 relationship of species is defined by herbivores' decoding efficiency based in the communication
328 system, i.e., the AV matrix that results from the product of AP and PV matrices. Specifically,
329 we defined plant and herbivore fitness relationships by the expressions $F_P = H(A|V)$ and
330 $F_A = 1 - H(V|A)$, where $H(\cdot)$ corresponds to the conditional entropy. To increase this fitness
331 relationship, plants and herbivores go through an alternating optimization process, mimicking
332 their arms race. Main text and Ref. (32) provide details about this process.

333 **Fig. 3. Simulated results based on the information arms-race theory recover the**
334 **observed information structures in the field.** Panel **A** illustrates the simulation over 1000
335 time steps derived from our proposed optimization mechanism (information arms-race). The
336 simulation is randomly initialized. The circles, triangles and squares correspond to the conditional
337 entropies $H(A|V)$, $H(P|V)$ and $H(A|P)$, respectively. The solid, dotted and dashed lines stand
338 for the corresponding conditional entropies from field observations. For the same simulation, in
339 Panel **B**, the + and \times symbols correspond to the fitness relationships of plants (F_P) and
340 herbivores (F_A), respectively. The solid lines correspond to the field observations. Panel **C** shows
341 the summary of the observed and simulated values (*mean \pm s.d.*) based on the last 250 steps (the
342 rectangle window in Panel **A**) when reaching equilibrium for our proposed mechanism (in red;
343 plants aim to maximize, \max_A , and herbivores aim to minimize, \min_P , uncertainty of
344 information, see Fig. 2) and the corresponding ones for the three alternative mechanisms (in
345 green, yellow, and blue; the alternative combinations of the maximization and minimization).

346 **Fig. 4. Emergence of cumulative mutual information.** The figure shows the information
347 structure characterized by the cumulative mutual information of **A**) plants and VOCs, i.e.,
348 $I(P, V)$ and that of **B**) herbivores and VOCs, i.e., $I(A, V)$. The higher the value, the better that
349 the presence or absence of VOCs can identify plants. The cumulative mutual information is
350 calculated as a function of the number of VOCs. The black curve corresponds to the field
351 observation, whereas the colored curves correspond to the proposed (in red) and alternative
352 optimization mechanisms. Dashed lines correspond to the minimum number of VOCs that gives
353 the best mutual information according to the field data.

354 **Supplementary Materials**

355 science.sciencemag.org/content/XXX

356 Materials and Methods

357 Supplementary Text

358 Figs. S1-S6

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361 R scripts as zipped archives

362 References (*40-45*)

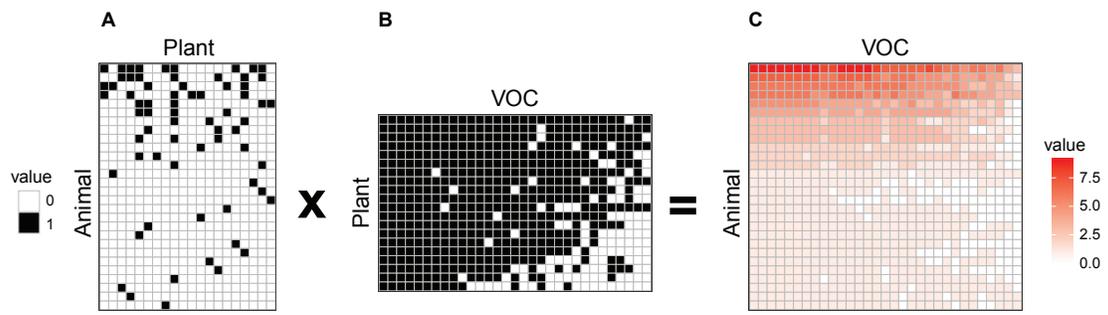


Fig. 1

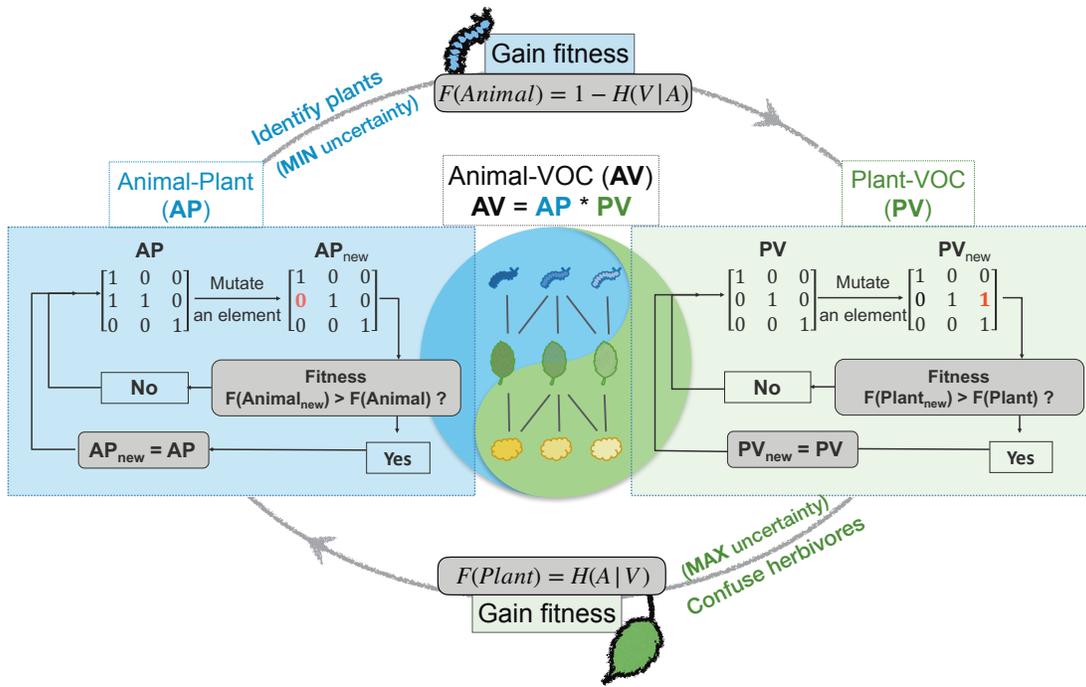


Fig. 2

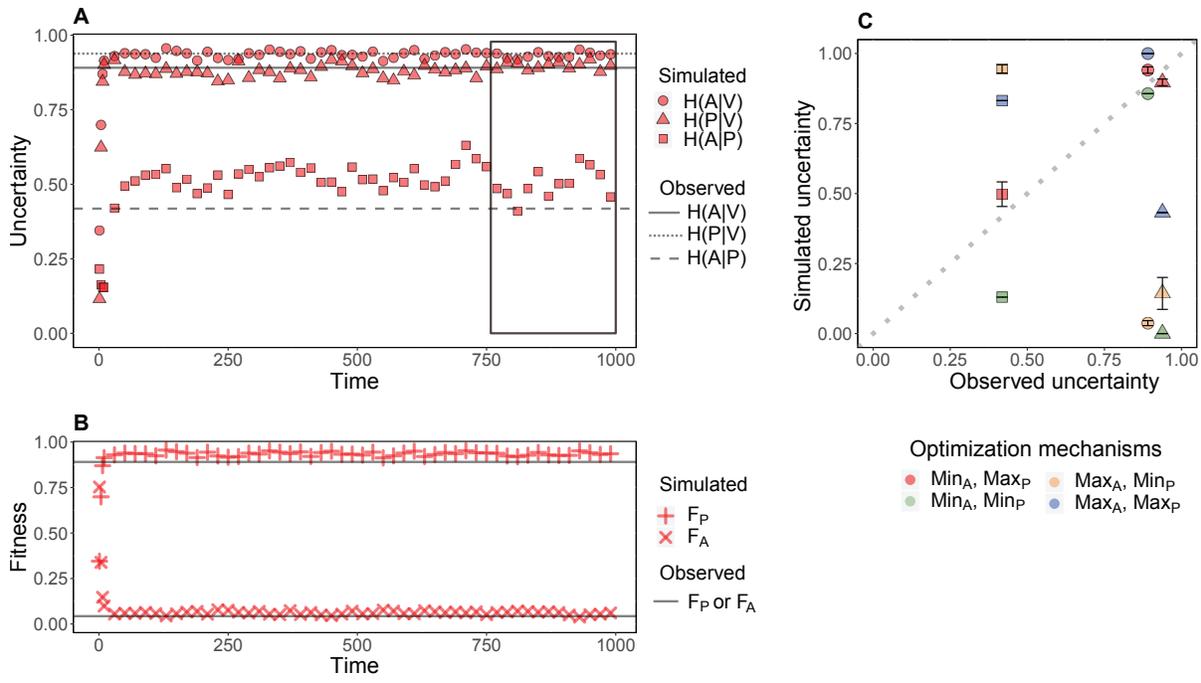


Fig. 3

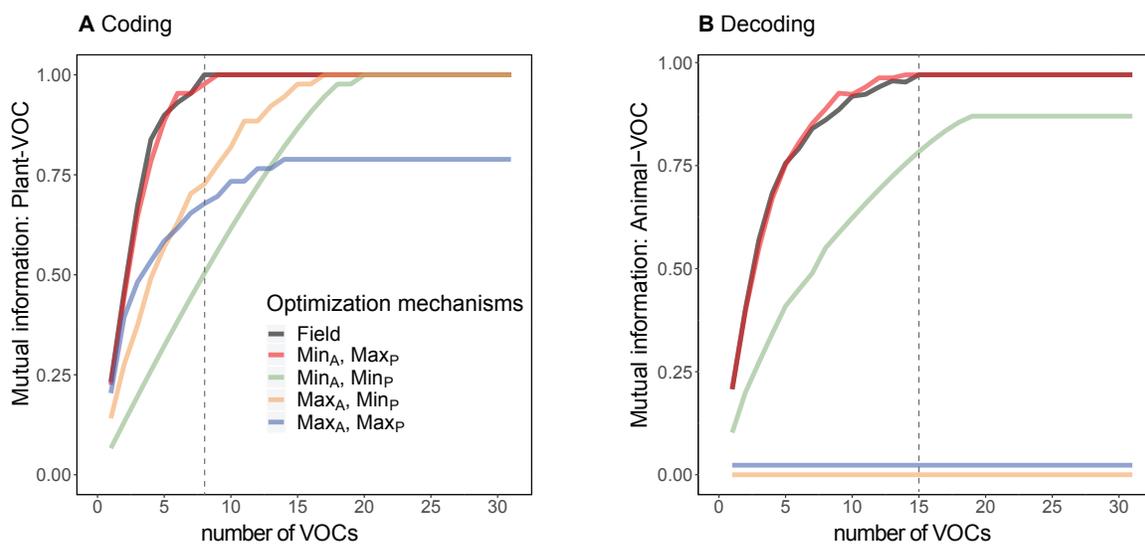


Fig. 4



Supplementary Materials for

Information Arms Race Explains Plant-herbivore Chemical Communication in Ecological Communities

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This PDF file includes:

Materials and Methods

- A. Field data
- B. Information theory
- C. Simulation and statistics
- D. Robustness tests concerning effects of sampling bias

Figs. S1 to S6

Tables S1 to S2

References

Other Supplementary Material for this manuscript includes the following:

Databases S1: Zu_etal_2020_Data_Archive.xlsx

R scripts as zipped archives: Zu_etal_2020_R_example.zip

(https://github.com/MITEcology/Science_Zu_et_al_2020)

Materials and Method

A Field data

Field site

The field data were collected in 2018 from a tropical dry forest located in the surroundings Chamela-Cuixmala Biosphere Reserve (19° 22'-19° 39'N, 104° 56'-105° 10'W) in Jalisco, Mexico. This site has been established for plant-herbivore network annual surveys during rainy seasons since 2007. Annual average precipitation during the past 12 years ranged from 523 to 1172 mm. There are three stages of secondary succession of the forest: mature (more than 50 years without anthropogenic perturbations), intermediate (approximately 20 years after being excluded and protected from cattle ranching use), and early (approximately 6 years after being excluded and protected). We targeted 20 tree species in plots belonging to the three stages (See Tables S1-S2 for a detailed list of species).

Construction of field plant-herbivore network

To sample herbivores within each plot, we established four transects of $2 \times 20\text{m}$ every 10m, in which we marked all the target tree species with diameter $\geq 1\text{cm}$ and height $\geq 50\text{cm}$. We searched for Lepidopteran larvae on all the leaves up to 3 meters of the target trees, and in the cases of taller trees, we randomly chose 3 branches per individual for searching. We conducted a monthly census during the four-month rainy season. We reared larvae to adulthood in the laboratory with leaves from the species on which they were found to confirm their trophic interaction. Lepidopterans were identified using traditional taxonomy complemented with molecular identification (we used the standard DNA barcoding for insects: cytochrome oxidase I, or COI, mitochondrial DNA) of operational taxonomic units (35, 40), especially for those cases in which adults failed to emerge. We edited sequences with Sequencher version 4.0.5 (Gene Codes) and aligned them manually based on their translated amino acids. All caterpillars and their host plants registered within the year in each plot were considered as a pooled community, hence we had a total of 29 herbivore species on the targeted plant species. Specific details on the sampling design, molecular identification and species identities can be found in Ref. (35)

Plant VOC collection and construction of plant-VOC network

We sampled the leaf headspace from three individuals each of the 20 target tree species that were sampled in the field from August 27th - 31st, 2018. We used polydimethylsiloxane (PDMS) tubing (provided by the Max Planck Institute for Chemical Ecology, Jena, Germany) following the method developed in Ref. (41). Specifically, we selected leaves with no or minimal damage and gently covered it with a cleaned Polyethylene terephthalate (PET) cup. A PET lid was also used to close the cup, with a hole allowing the petiole to penetrate. We punctured two holes (one at the bottom of the cup, one in the center of lid where the petiole went through) to avoid moisture accumulation. We placed five pieces of silicone tubing (each 5mm length, 1mm i.d. \times 1.8mm o.d.) in each cup and left these to equilibrate for 24 hours to avoid differences due primarily to daily dynamics of VOC emission. We set two to three air controls from empty cups for each successional stage plot and each round of VOC sampling. At the end of each sampling,

we removed the leaves from the cups and transferred the silicone tubing from each sample into a 1.5ml glass vial (Sigma-Aldrich Chemie GmbH, Munich, Germany), and screwed on the vial lid (with PTFE/silicone septum bonded, Sigma-Aldrich Chemie GmbH Munich, Germany). We stored samples in a -20°C freezer before transport to the Royal Botanic Gardens, Kew, London, UK for analysis.

To analyze the leaf VOC samples, we used an Agilent Technologies (Palo Alto, CA, USA, 7890A) gas chromatograph connected to an Agilent Technologies 5975C MSD mass spectrometer (GC-MS) coupled with a Markes International TD100 thermal desorption auto-sampler. We placed two silicone tubes from each sample into the sample tray and injected desorbed volatiles into the GC under a temperature program following Ref. (41). The GC was equipped with an Agilent Technologies DB-5 MS capillary column (30m length, 0.25mm diameter, $0.25\mu\text{m}$ film thickness). We set the temperature of the GC oven to 40°C (5min hold) and increased to 185°C at $5^{\circ}\text{C}/\text{min}$, then increased to 280°C at $30^{\circ}\text{C}/\text{min}$ (0.83min hold). We used helium as the carrier gas, with a constant flow of 40 cm/second.

To retrieve leaf VOC profiles, we used an untargeted analysis to screen all the peaks across all the samples in R (42) using the package XCMS as described in Qi et al. 2016 (43). We removed the typical contamination peaks, and then compared the analytes from headspace samples with the National Institute of Standards and Technologies NIST17 mass spectral library. The relative retention of different identified compounds was checked against that expected for a DB5 column. This allowed the assignment of 93 analytes (although did not distinguish enantiomers where they may have occurred e.g., (+) and (-) α -pinene) of which 56 were likely biogenic (from plants, or from plants and microbes), and 31 of the biogenic VOCs could be identified by one or more abundant ions (i.e., ions specific to the analyte and having at least 20% of the maximum relative intensity across the electron impact mass spectrum) in an untargeted analysis. Each VOC may be represented by a "fingerprint" of multiple m/z values. We chose one m/z value to represent one VOC. If we had used all m/z values for each VOC, this would have produced multiple peaks per VOC (redundant information) as well as different numbers of peaks for different VOCs. An alternative is to use the TIC (total ion chromatogram) but that is less specific and is inaccurate in cases where there is chromatographic overlap of VOCs, or of VOCs with contaminants (41). Then we generated qualitative data (1 for presence, 0 for absence) for each species by comparing the peaks in the samples to those in the air controls. Due to the variation of VOC emission within species, we regarded it to be 'presence' as long as one or more individual emitted the compound in a greater amount than in the air controls. The plant-animal interaction matrix as well as the plant-herbivore association matrix were constructed by pooling together the four plots sampled in our study. This was done in order to provide a better approximation to a community-wide pattern of communication.

We used the plant-VOC matrix with either 31 or 56 VOCs to test the robustness of our results to changes in the number of VOCs. In addition to the 20 target tree species that were used for the plant-VOC network in year 2018, we also randomly chose another 27 tree species in different succession stages and collected their VOCs. These 47 plants and their VOC patterns were used to test the robustness of our results to changes in species interaction networks from other years (2007-2017) (See below Section D *Robustness tests concerning effects of sampling bias*. Zu_etal_2020_Data_Archive.xlsx).

Note that in this study, we sampled plant VOCs in the field under natural conditions, reflecting an ecologically relevant chemical environment encountered by herbivores. Our data represent qualitative "snapshots" of VOCs likely including both constitute and induced VOCs. Additionally, we have taken a top-down perspective: if an herbivore can feed on a plant, it must be able to deal with the VOCs which the plant emits, despite the effect of each VOC on the herbivore (attract,

deter, neutral). Because insects are known to have a large number of olfactory receptors with high sensitivity, it should therefore be reasonable to assume that the insects in our community take into account plant VOCs across spatial and temporal variation when deciding where to feed. However, future work can explore the capacity of our theoretical work in understanding chemical communication and species interactions by including different sets of VOCs (e.g., constitute and induced VOCs), VOCs from different organs (e.g., from flowers, leaves and roots), and different sets of partners across trophic levels (e.g., pollinators, microbes, parasitoids and predators). Moreover, experimental work could be further conducted to determine which VOCs are relevant for which herbivores. This includes measuring VOC profiles under controlled conditions, e.g., measuring before and after herbivore damage, conducting behavioral assays using synthetic compounds, using different VOC concentrations and combinations, and measuring from a larger number of samples per species. There are many such published studies which could perhaps be analyzed using the framework we propose here. Similar experiments can be conducted repeatedly along time (seasons) to explore temporal dynamics of chemical communication between plants and insects.

B Information theory

For any binary $m \times n$ matrix, say object-signal (OS) matrix with m objects and n signals and each element os_{ij} ($i \in 1, 2, \dots, m, j \in 1, 2, \dots, n$) representing the presence $os_{ij} = 1$ or absence $os_{ij} = 0$ of an interaction (or association), we can calculate the conditional entropy as $H_n(O|S) = \sum_{j=1}^n P(S_j)H_n(O|S_j)$. Note that $H_n(O|S) \in (0, 1)$, where the higher the value, the higher the uncertainty (information needed) to know the outcome (identity) of an object given that a specific signal was observed. In this calculation, $P(S_j) = \frac{\sum_{i=1}^m os_{i,j}}{\sum_{i=1}^m \sum_{j=1}^n os_{i,j}}$ corresponds to the probability of having signal j given that signal was observed. Then, $H_n(O|S_j) = -\sum_{i=1}^m P(O_i|S_j)\log_n P(O_i|S_j)$, where $P(O_i|S_j) = \frac{os_{i,j}}{\sum_{i=1}^m os_{i,j}}$ corresponds to the probability of having object i given that signal j was observed.

We can also calculate the mutual information $I(O, S) = H_m(O) - H_n(O|S)$, where $H_n(O|S)$ is calculated as previously mentioned, and $H_m(O) = -\sum_{i=1}^m P(O_i)\log_n P(O_i)$. In our analysis, objects correspond to species and given that we generated qualitative matrices (with 0s and 1s), we did not use species abundances and considered $P(O_i) = \frac{1}{m}$. Note that $I(O, S) = I(S, O) \in (0, 1)$, where the higher the value, the greater the information (identity) that we can obtain about an object by knowing the presence or absence of a signal.

Similarly, to calculate the mutual information between an object and a library (combination) of signals, we constructed new matrices describing an object and a library (i.e., a OL matrix). For example, for a given library size (say 2) with a given set of signals (say S_1 and S_2), all the unique combinations of the library (e.g., (1,1), (1,0), (0,1), and (0,0)) would form the columns of the matrix and the objects form the rows. Then, we filled the elements of the OL matrix with either 1 or 0, depending on the presence or absence of the specific set of signals in the corresponding object. As the library size increases, the number of signal combinations exponentially increases, making potential analyses infeasible. For example, choosing a library size of 2 out of 50 will give 2,450 different combinations, whereas choosing a size of 5 out of 50 will give 10,593,800 different combinations. Therefore, for each library size, we used 5000 unique random combinations and then calculated the maximum mutual information we could obtain from these combinations to represent the situation with a best set of VOCs. We calculated the mutual information between herbivores and VOCs as a function of the VOC library size based on the herbivore-VOC (AV) matrix. Because the AV matrix is weighted, we first scaled the number of VOCs for each herbivore based on the total number of plants that a given herbivore interacts with. This produced a probability matrix representing the chance that a herbivore associates with each of the VOCs. Next, we created 30 replicates or realizations of binary AV matrices based on the corresponding probability for each interaction, mimicking the decoding process. Then, for each of these binary AV matrices, we calculated the mutual information the same way as stated before for the PV matrices. Then we calculated the median (due to the skewed distribution) mutual information based on these results from the 30 realizations.

C Simulations and statistics

To test the long-term behavior of the studied optimization mechanisms, we used three initial conditions for the AP and PV matrices. We defined the first initial condition by a matrix with highly specialized interactions. That is, each plant interacts with only one or maximum two (given the constraints imposed by the dimension of the matrices) herbivores and VOCs. The second initial condition was defined by a matrix with highly generalized interactions. That is, each plant interacts with all but one or maximum two herbivores and VOCs. The third initial condition was defined by randomly drawing values (1 or 0) with different probabilities. Note that the third condition is the only one generating different matrices, hence, we explore many different randomization and probability values. To control for confounding factors related to dimensionality, all the simulated matrices had the the same dimension as the observed matrices.

For each initial condition (matrices), we calculated the conditional entropy (for AP and PV) and the plant and animal fitness relationships ($F_P = H(A|V)$ and $F_A = 1 - H(V|A)$, where $AV = AP \times PV$). Then, the optimization mechanism began with herbivores, which were allowed to alter their interactions with plants (i.e., mutate 1 and 0 in the AP-matrix) to maximize their fitness relationships. Specifically, as shown in Figure 2, one element will mutate at each time, and a new fitness relationship will be calculated accordingly. The old matrix will remain if the new fitness relationship is smaller than the old value. Otherwise, the new matrix will fixate and will be used for the next mutation event. We assumed equal mutation rate for each link (plant-VOC link or herbivore-plant link) in the absence of any prior knowledge. Therefore, the number of random mutations that plants and herbivores can have for each round were proportional to the number of all possible links (i.e., number of elements in PV and AP matrices). However, different mutation rates for plants and herbivores mimicking unequal ability in combating in the arms-race can be further investigated. Here, the number of mutation events in herbivores is given by 20% of the total number of elements in the AP matrix. After this number of mutations, plants take a turn and maximize their fitness relationships by changing their association with VOCs (i.e., mutate elements in the PV matrix in the same fashion as described before). The number of mutation events in plants is also given by 20% of the total number of elements in the PV matrix. This alternated optimization scheme is repeated 1000 times. The number of mutations within each round does not change the pattern; it only changes the time to reach equilibrium (Fig. S1). Starting the optimization mechanism with plants or herbivores also does not affect the results.

To test whether the optimization mechanisms, starting from the simulated matrices, would converge to our field observations, we examined the long-term patterns of each simulated matrix. Specifically, we calculated conditional entropies and fitness relationships based on simulated matrices using the average values over the last 250 rounds of the simulated time series. The specific number of rounds did not change our results, but we used this number in order to provide a mean behavior over time. All the simulations and statistics were conducted with R version 3.5.2. (42).

D Robustness tests concerning effects of sampling bias

Sampling bias is an important concern in ecological studies (34). To test whether the sampling effort will affect our results, we conducted multiple paralleled analyses with different conditions: (1) community size, (2) number of VOCs, and (3) interaction network.

1. Community size: Will results be affected by a sub-sampling of the community? For this test, we used a subset of the plant-herbivore community (a specific plot with 8 plants and 16 herbivores instead of the entire pooled community as in the main text). We found that the results remain qualitatively equivalent regardless of community size, illustrating the scalability of our findings (Figure S2). We also performed simulations with many different sub-samples and they were all qualitatively equivalent to Figure S2.
2. Number of VOCs: Are our results affected by an incomplete plant VOC profile? Here, we were concerned about the potential effects of unidentified plant VOCs. For this test, we included 21 more undefined VOCs that were potential biogenic VOCs (see above Section *Construction of field leaf scent collection and plant-VOC network* under *A Field data*), and kept the interaction matrix unchanged. We found that the results still remain qualitatively equivalent (Figure S3, all VOC information see `Zu_etal_2020_Data_Archive.xlsx`).
3. Interaction network: Will results be affected by sampling the interaction network in a different place or year? To test this, we used information from previous years (from 2007-2017 using data from Ref. (44)) and repeated all our analyses. Specifically, using the pool of plant species and VOC information collected in 2018, we checked for those plant species present in a given previous year together with all their feeding herbivores present in such year to form yearly interaction matrices. This made both the identity and number of plant-herbivore interactions to change each year. Note that here we assumed that VOCs of a specific plant species in a specific plot remain qualitatively unchanged through these years. We found that the results remain qualitatively equivalent regardless of the identity and number of species interactions (Figures S4-S6, all interaction networks under analyses from previous years see `Zu_etal_2020_Data_Archive.xlsx`).

The robustness of these results is aligned with previous work (45) that has found no change of global network measures in the data despite large beta diversity along each year (turnovers of herbivores). This result further indicates that a community can be formed by different species, but the interaction patterns (and likely the mechanism to drive the interaction patterns) do not change at our level of resolution.

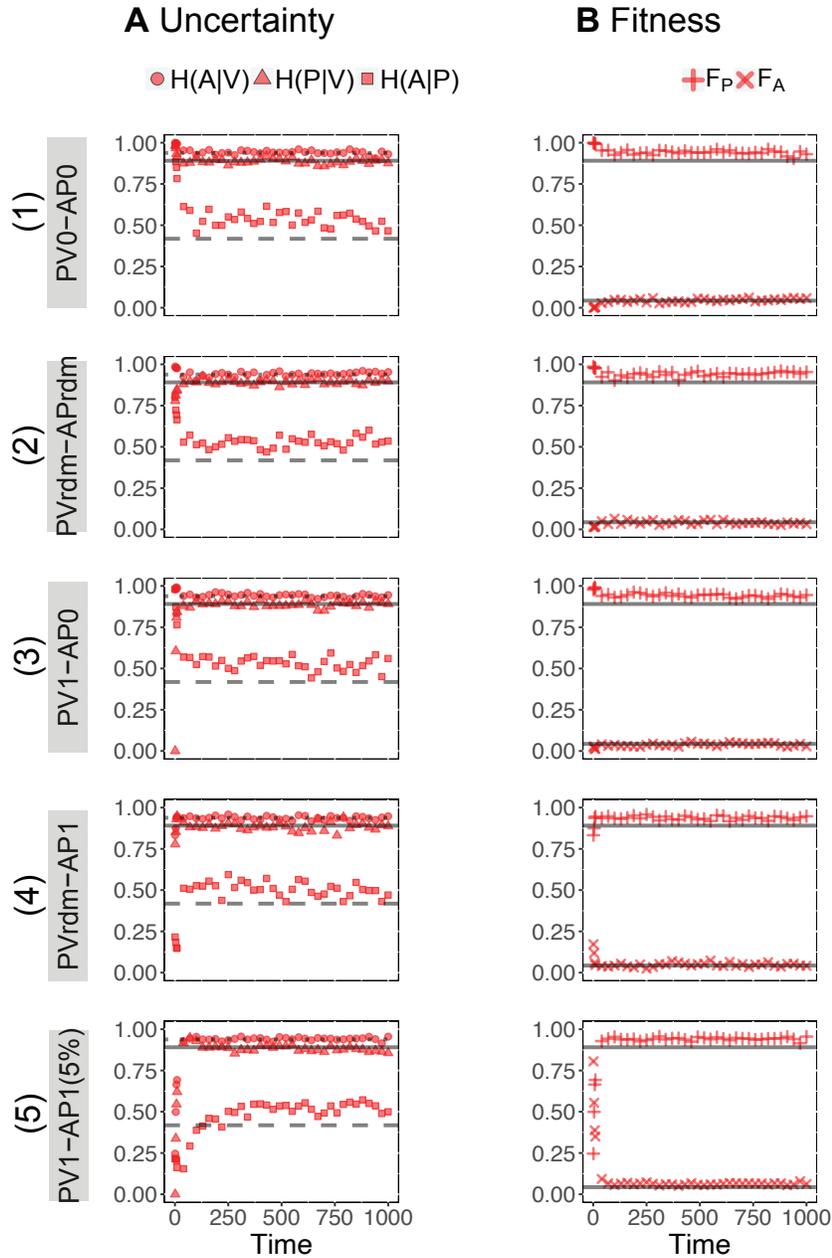
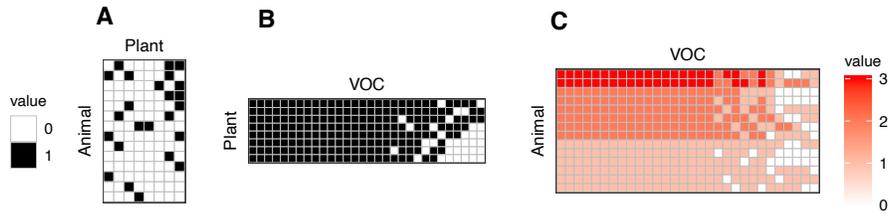
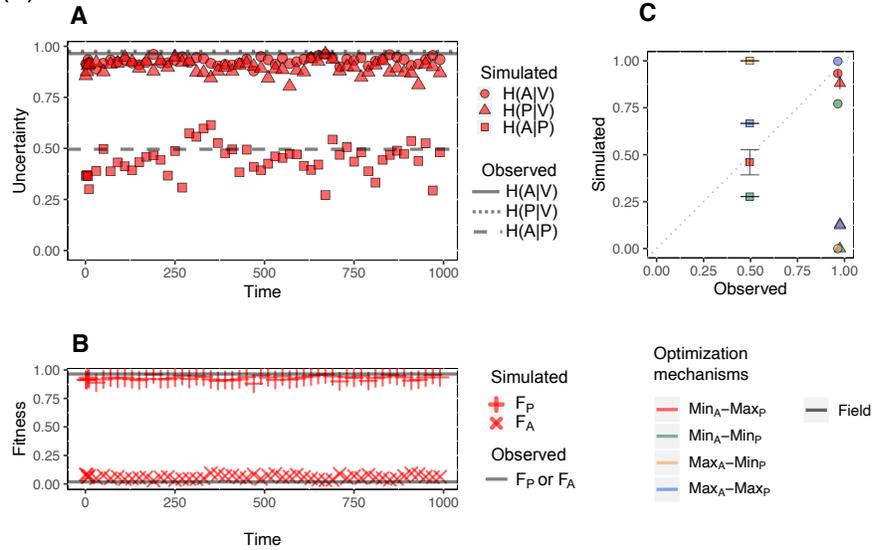


Figure S1: **Simulations from different starting matrices.** The simulations started from PV and AP matrices that are: (1) both generalized relationship matrices; (2) both random; (3) PV specialized and AP generalized; (4) PV random and AP specialized; (5) both specialized, and the element mutation rate is 5% of the total elements (instead of 20% for all the other cases). Panel **A** illustrates the uncertainty (conditional entropy) of the three matrices simulated over 1000 time steps derived from our proposed optimization mechanism. The circles, triangles and squares correspond to the conditional entropies $H(A|V)$, $H(P|V)$ and $H(A|P)$, respectively. The solid, dotted and dashed lines stand for to the corresponding conditional entropies from field observations. For the same simulation, in Panel **B**, the + and × symbols correspond to the fitness relationships of plants (F_P) and herbivores (F_A), respectively. The solid lines correspond to the field observations.

(1) Field observation



(2) Simulation results



(3) Emergence of cumulative mutual information

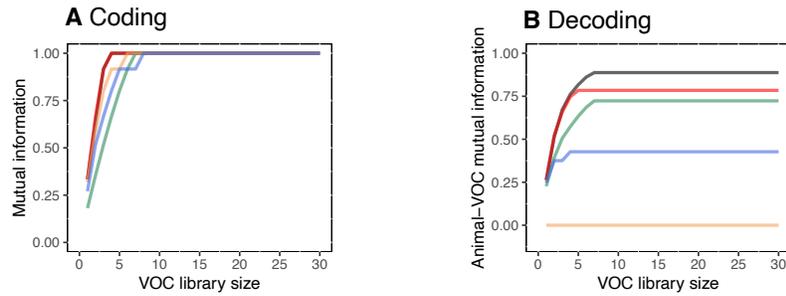
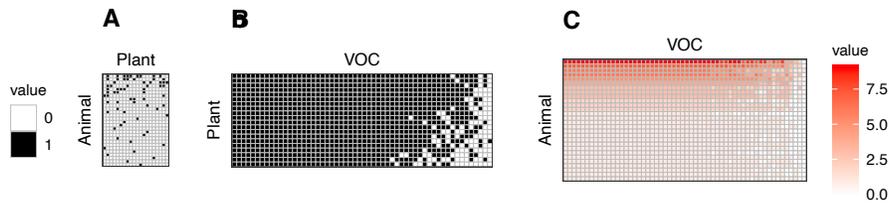
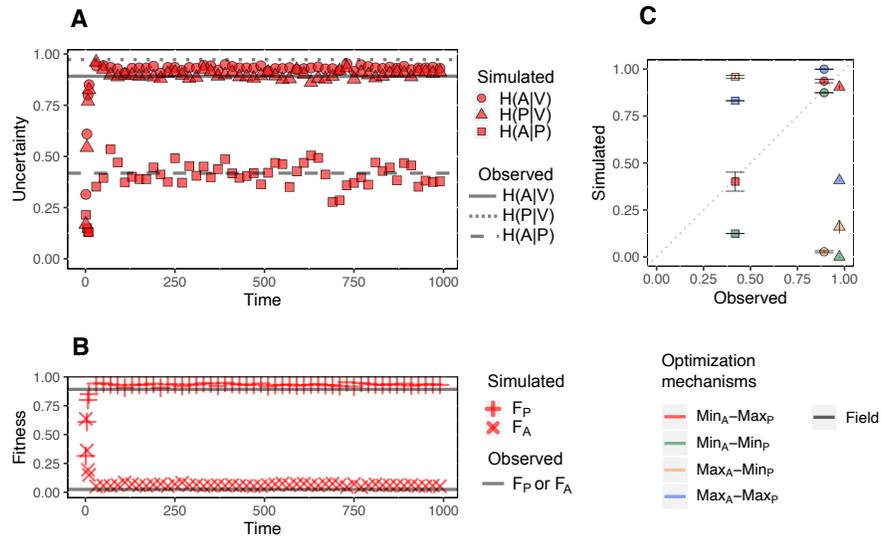


Figure S2: **Test with a subset of the plant-herbivore community.** This analysis corresponds to a subset of the community from year 2018. This includes 16 animal species, 8 plant species, and 30 VOCs. Here we have 30 VOCs instead of 31 because one VOC was emitted by none of the 8 plant species. For detailed figure captions see Figures 1, 3, and 4 in the main text.

(1) Field observation



(2) Simulation results



(3) Emergence of cumulative mutual information

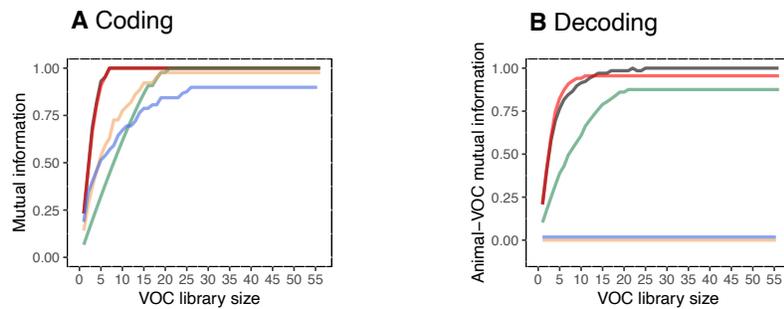
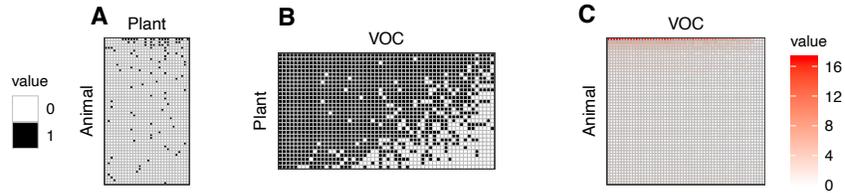
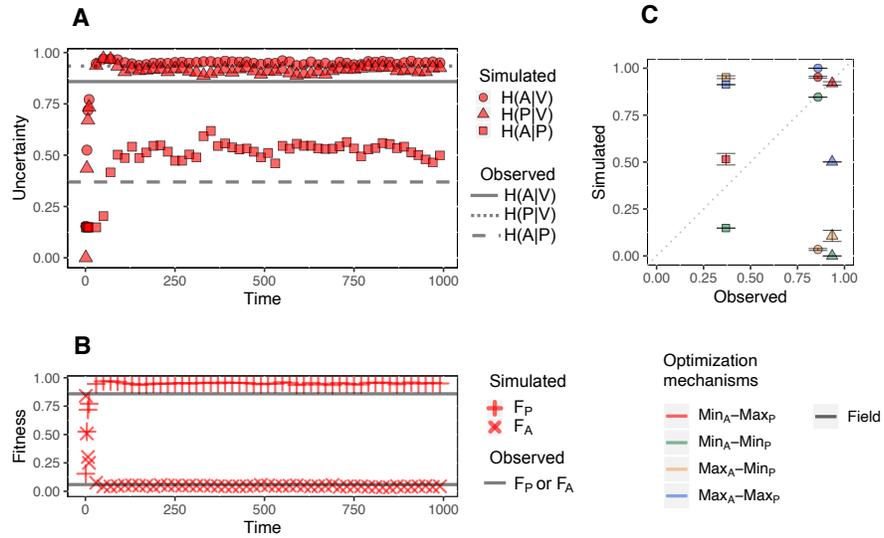


Figure S3: **Test with 56 VOCs**. Here we used 56 VOCs (instead of 31 VOCs as in the main text, which did not include biogenic VOCs). This corresponds to 28 animal species, 20 plant species, and 56 VOCs. For detailed figure captions see Figures 1, 3, and 4 in the main text.

(1) Field observation



(2) Simulation results



(3) Emergence of cumulative mutual information

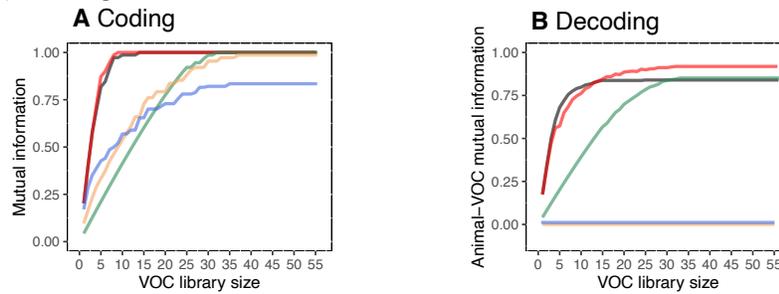
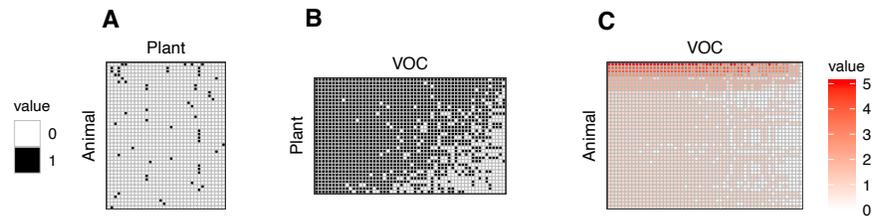
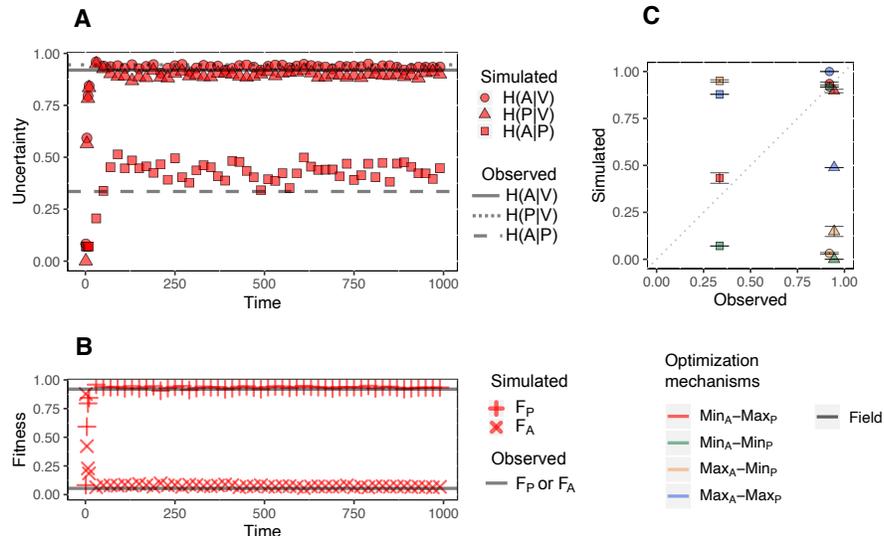


Figure S4: **Test with different network communities - year 2017.** We used the plant-herbivore interaction matrix sampled in the year 2017. This corresponds to 52 animal species, 30 plant species, and 56 VOCs. For detailed figure captions see Figures 1, 3, and 4 in the main text.

(1) Field observation



(2) Simulation results



(3) Emergence of cumulative mutual information

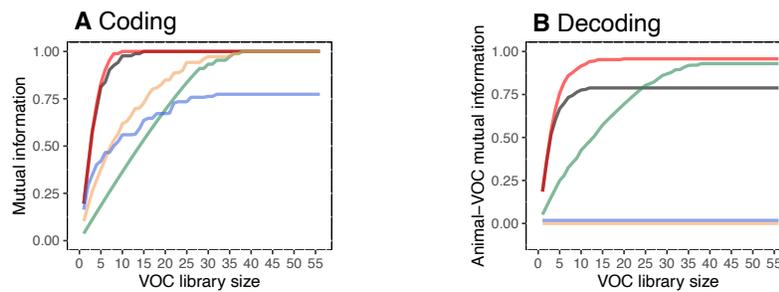


Figure S5: **Test with different network communities - year 2007.** We used the plant-herbivore interaction matrix sampled in the year 2007. This corresponds to 42 animal species, 34 plant species, and 56 VOCs. For detailed figure captions see Figures 1, 3, 4 in the main text.

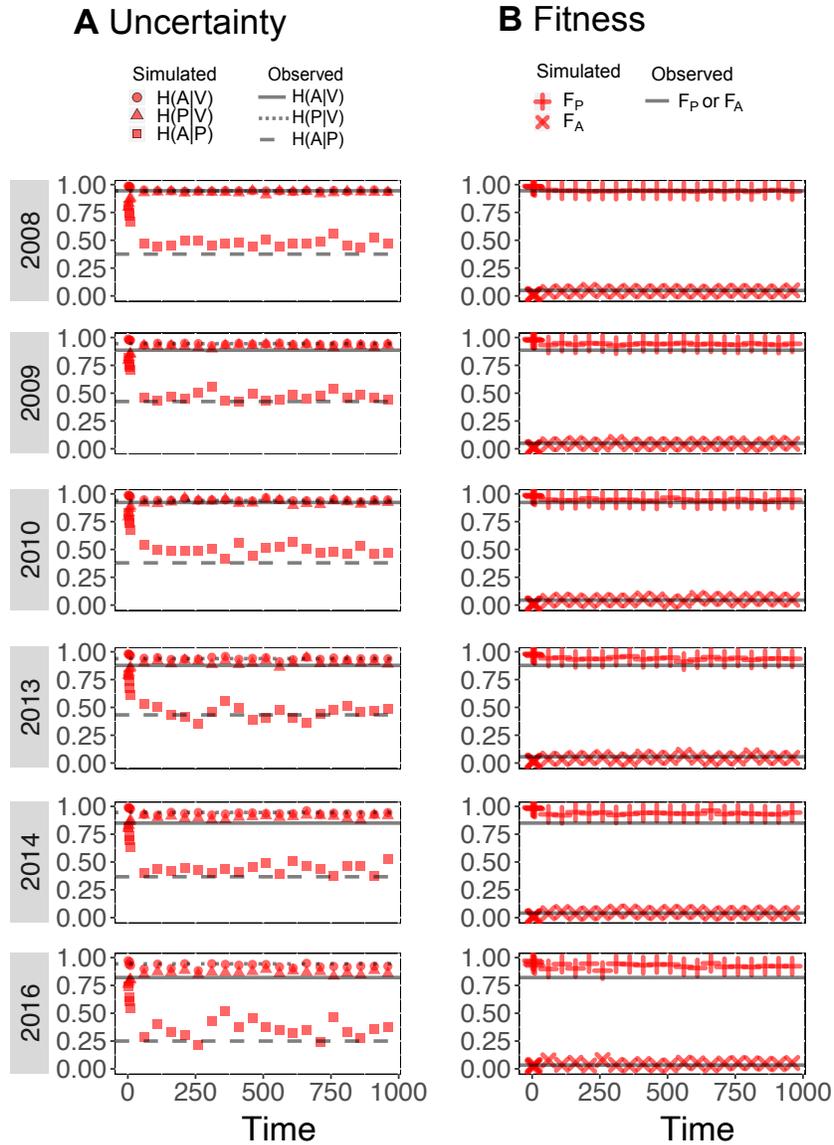


Figure S6: **Summary test with different network communities - years 2008-2016.** We used the plant-herbivore interaction matrix sampled in the years 2008-2016. The number of VOCs is 56 for all these years. Number of animal species (A) and number of plant species (P) in each year are: 2008 (75A-28P), 2009 (57A-25P), 2010 (63A-22P), 2013 (36A-20P), 2014 (37A-25P), 2016 (13A-14P). The year 2015 was not sampled due to bad weather conditions generated by Hurricane Patricia boege2019temporal. The years 2011 and 2012 are missing because no VOC information is available for the tree species sampled that year. For detailed figure captions see Figure 3 in the main text.

Table S1: Herbivore-plant interaction network. Data for Figure 1A in the main text.

Herbivore code	Herbivore species	Plant species		GUMA	COCA	CRRO	APPA	LELA	CANI	CACO	THPA	PICO	AYMI	MAAC	GYJA	HILA	ZAFA	DIAE	BUPA	RATE	STDO	SPPU	COTR	Sum	
		Plant code	Succession stage																						
O3	<i>Psychidae</i> sp1.			1	0	1	1	1	0	0	1	1	0	0	0	0	0	0	1	0	1	1	0	9	
O30	<i>Orgya</i> sp.			0	0	1	1	1	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	7	
O18	<i>Hypercompe</i> sp.			1	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	6	
O14	<i>Psychidae</i> sp2.			1	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	0	6	
O347	<i>Eudesmia menea</i>			0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	5
O24	<i>Wockia chewbacca</i>			0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	4	
O741	<i>Lepidoptera</i> sp1.			0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	3	
O44	<i>Misoria amra</i>			0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	3	
O161	<i>Dalcerides</i> sp1.			0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	3	
O69	<i>Diaphania jairusalis</i>			0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	2	
O752	<i>Lepidoptera</i> sp2.			0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
O718	<i>Erebinae</i> sp1.			0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	2	
O765	<i>Lepidoptera</i> sp4.			0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
O719	<i>Erebinae</i> sp2.			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	
O230	<i>Anacamptodes herse</i>			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
O190	<i>Cargida pyrtha</i>			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
O775	<i>Lepidoptera</i> sp3.			0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
O52	<i>Gonodonta pyrigo</i>			0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
O25	<i>Michaelophorus</i> sp.			0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
O1	<i>Dalcerides</i> sp2.			0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
O71	<i>Helia sueroides</i>			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
O768	<i>Deinopa biligula</i>			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
O341	<i>Perigonia ilus</i>			0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
O114	<i>Lophocampa citrina</i>			0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
O213	<i>Melipotis perpendicularis</i>			0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
O746	<i>Geometridae</i> sp1.			0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
O700	<i>Noctuidae</i> sp1.			0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
O96	<i>Syllepsis hortalis</i>			0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1

