

1 **High-order interactions maintain or enhance structural robustness of a coffee agroecosystem**
2 **network**

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35 **Highlights**

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37 • The robustness of a coffee-associated ecological network is either increased or unaffected by the
38 incorporation of high order interactions.

39 • A method is proposed for representing high order interactions in ordinary networks.

40 • A method is proposed to measure the robustness of networks with high order interactions.

41 • High order interactions may promote the persistence of diverse ecosystems.

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44 **Abstract**

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46 The capacity of highly diverse systems to prevail has proven difficult to explain. In addition to
47 methodological issues, the inherent complexity of ecosystems and issues like multicausality, non-linearity
48 and context-specificity make it hard to establish general and unidirectional explanations. Nevertheless, in
49 recent years, high order interactions have been increasingly discussed as a mechanism that benefits the
50 functioning of highly diverse ecosystems and may add to the mechanisms that explain their persistence.
51 Until now, this idea has been explored by means of hypothetical simulated networks. Here, we test this
52 idea using an updated and empirically documented network for a coffee agroecosystem. We identify
53 potentially key nodes and measure network robustness in the face of node removal with and without
54 incorporation of high order interactions. We find that the system's robustness is either increased or
55 unaffected by the addition of high order interactions, in contrast with randomized counterparts with
56 similar structural characteristics. We also propose a method for representing networks with high order
57 interactions as ordinary graphs and a method for measuring their robustness.

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59 **Keywords**

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61 Ecological networks, robustness, high order interactions, species coexistence, coffee agroecosystems

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63 1. Introduction

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65 The link between an ecosystem's diversity, structure and functioning has long been debated in ecology.
66 Both empirical and theoretical studies have tried to decipher the nature of their relationship and the
67 factors that take part in shaping it. On the one hand, the existence of different definitions for these
68 features has contributed to the difficulty of the task, while on the other hand, an intrinsic complexity
69 stems from the very numerous elements, processes and scales that interact to give rise to these qualities
70 (Ives & Carpenter 2007). Early ideas on the topic focused on the notion of stability, and maintained that
71 diversity made ecosystems stable through species limiting each others' growth by predation or
72 competition (Odum 1953; MacArthur 1955; Elton 1958). These notions were dramatically challenged by
73 the work of Robert May (1972; 1973), who used linear stability analyses to show that communities
74 modelled as random networks lose local stability as the number of species, the number of interactions, or
75 their strength rise. These results caused commotion in the scientific community, as they seemed to
76 contradict the very real biodiversity found around the world. Since then, two main extensions have
77 helped reconcile theory with observation; mainly: the use of realistic community structures (Lawlor 1978;
78 Lawlor 1980) and the complementation of linear stability analyses with other methods to assess
79 ecosystem function from both a structural and a dynamical point of view like robustness, feasibility or
80 structural stability (Landi et al. 2018). It is now generally recognized that diversity tends to positively
81 correlate with some measures of ecosystem functioning, like stability, robustness or productivity.
82 Nevertheless, this does not mean that diversity is the direct driver of these traits, rather, it should be
83 regarded as an 'umbrella' indicator of many ecological mechanisms that are inherent to ecosystems and
84 that are the actual determinants of the diversity-function relationships (McCann 2000). Such mechanisms
85 and how they may favor the assembly and reproduction of highly diverse communities are now the focus
86 of many studies (Chesson 2000; Levine et al. 2017).

87 Different mechanisms have since been proposed to enable the coexistence of species in highly
88 diverse systems (Chesson 2000; Wright 2002; Adler et al. 2013; Levine et al. 2017). Recently,
89 high order interactions (HOI) have been proposed as a key mechanism for the persistence of
90 diverse communities (Bairey et al. 2016, Grilli et al. 2017). A HOI is the effect a species has *on*
91 *the interaction* between any other two species. The importance of this kind of interactions has
92 been recognized, as they are quite common: ecosystem engineering, predatory adaptive
93 behavior, changes in foraging, facilitation, mutualisms and many so-called trait-mediated effects
94 commonly involve HOIs (Beckerman et al. 1997; Werner & Peacor 2003; Holt & Barfield 2012;

95 Kéfi et al. 2012; Bairey et al. 2016). Bairey et al. (2016) computationally explored the role of
96 HOIs on the linear stability and feasibility of systems described as virtual random networks and
97 found that HOIs could indeed attenuate or even revert a negative relationship between the
98 number of species and stability.

99

100 While the findings of Bairey and coworkers (2016) and other recent theoretical work have
101 greatly contributed to our understanding of the relationship between HOIs and species
102 coexistence (Grilli et al., 2017; Singh & Baruah, 2020; Li et al., 2020), they rely on hypothetical
103 networks whose interactions are set randomly and do not represent known ecological
104 interactions, or on the assessment of some focal species (Mayfield & Stouffer, 2017). It thus
105 remains unclear how HOIs may affect the function of empirically-documented networks which,
106 arguably, capture some aspects of their structure and dynamics in a more faithful manner. There
107 are now some well-studied ecological and few agroecological networks that could help fill this
108 important gap (Scheffer 1997; Yoon et al. 2004; Fortuna et al. 2014; Perfecto and Vandermeer,
109 2015; López Martínez 2017). Agroecosystems cover around 40 % of the Earth's surface (Foley
110 et al. 2005), represent a substantial part of the world's biodiversity, and have just recently begun
111 to be analyzed from a network perspective (Bohan et al. 2013; López Martínez 2017). The
112 insights gained from such a system-level approach hold the potential to guide our actions around
113 major issues like autonomous pest control, disease outbreaks and biodiversity conservation in
114 agricultural landscapes (Vandermeer et al. 2010, 2018; Ramos et al. 2018).

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116 With this in mind, in the present study we updated and analyzed an empirically-based network
117 for a coffee agroecosystem in southern Mexico. This biodiverse agroecosystem has been studied
118 for about three decades and many of its species and interactions have been thoroughly described
119 (Perfecto & Vandermeer 2015). Importantly, different HOIs have been found to play a key role
120 in the dynamics of the main coffee pests and their natural enemies (Vandermeer et al. 2010;
121 Perfecto et al., 2021), motivating discussions on different formalisms to integrate HOIs to
122 ecological network analyses, which remain an underdeveloped area (Golubski et al. 2016;
123 Battiston et al., 2020). Thus, we analyzed the coffee agroecosystem network from a structural
124 perspective in order to investigate the effects of HOIs on the overall robustness of this system,
125 defined as its capacity to remain connected in the face of node removal representing species loss.

126 To this aim, we propose a method for representing networks with high order interactions as
127 ordinary graphs and a method for measuring their robustness which is a modification of
128 Piraveenan et al. (2013). Our work aims to contribute to the understanding of the mechanisms
129 underlying species coexistence in highly diverse systems, as well as to provide novel insights
130 that can inform management practices based on the biological understanding of agroecosystems.

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133 2. Methods

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135 2.1 Study site

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137 The study site is “Finca Irlanda”, a 320 ha coffee plantation situated on the highlands of El Soconusco,
138 Chiapas (158110 N, 928200 W; 900 masl). Precipitation in the region averages 4500 mm per year and the
139 vegetation type is seasonal tropical forest. Nevertheless, primary vegetation has been almost completely
140 replaced by coffee plantations with different management intensities, aside from some tiny fragments of
141 original forest kept in some farms. In Finca Irlanda, there is a portion of such original vegetation set aside
142 for conservation, while the management of the surrounding productive area involves keeping the shade
143 provided by native trees, which, among other practices, make it a highly biodiverse agroecosystem
144 (Perfecto and Vandermeer, 2015).

145 It is convenient to detail some parts of the complex ecological web found in the study site. There are four
146 main antagonists of coffee plants: the coffee leaf rust, *Hemileia vastatrix*, the coffee berry borer,
147 *Hypothenemus hampei* (see Figure 3d further), the coffee leaf miner, *Leucoptera coffeella*, and the coffee
148 green scale, *Coccus viridis* (Figure 3c). The last one keeps a spatially clustered mutualistic relationship
149 with ants of the *Azteca* genus (Figure 3e), which feed on the honeydew produced by the scales while
150 protecting them from being eaten by a lady beetle, *Azya orbigera*. Thanks to this protection, the scale
151 populations reach high levels within the clusters, which in turn increases their probability of being
152 infected by the white halo fungus, *Lecanicillium lecanii*, a fungus that is also capable of infesting the
153 coffee rust. By patrolling coffee plants where green scales feed, *Azteca* keeps other herbivores, like the
154 berry borer beetle or the leaf miner from establishing big populations on these plants. However, all the
155 effects that the *Azteca* ants have on the system are temporally inhibited by flies in the genus *Pseudacteon*
156 (Family: Phoridae), who are parasitoids of the *Azteca* ants, and that cause them to retrieve to their nests,
157 hide or dramatically reduce their movement whenever they sense a fly nearby. This inhibition of *Azteca*

158 leaves the scales and the coffee plants unprotected for a period of time, a lapse that has been proven to be
159 ecologically relevant and that for example, is enough for allowing *Azya orbiger*a to prey on the scales or
160 oviposit underneath them, ensuring nourishment for their future larvae (Liere & Larsen 2010;
161 Vandermeer et al. 2010).

162 The system here described exhibits different kinds of direct interactions like herbivory and parasitism, but
163 also numerous HOIs (Table S1). For example, *Azteca* ants exert a second order interaction when they
164 inhibit the predation interaction among *C. viridis* and *A. orbygera* by harrasing the latter, mostly without
165 harming it (Vandermeer & Perfecto 2006; Liere & Larsen 2010; Vandermeer et al. 2010). An example of
166 a third order interaction is the effect of the phorid flies, which by paralyzing or chasing away *Azteca* ants,
167 inhibit the second order interaction they exerted and thus enable the predation of *C. viridis* by *A. orbygera*
168 (Hsieh et al. 2012).

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170 2.2 Network inference

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172 We used a network approach to analyze the community under study. Species were represented as nodes
173 whose connections were defined by the ecological interactions among them. In order to define the
174 network's structure, we reviewed published information on this particular agroecosystem and integrated
175 it in a common database.

176 The reviewing process began with a book that collects over 20 years of research in the area (Perfecto &
177 Vandermeer 2015). All referenced papers that explained, observationally or experimentally, at least one
178 ecological interaction among a pair of species, were examined too. The type of interactions and the
179 direction of their effects were extracted, including qualitative information about their strength, whenever
180 available. If any of the papers in this first group made reference to other investigations in the area, those
181 were also revised. All the information was integrated in a database organized as follows: *transmitter*
182 *node* (e.g. *H. hampei*), *recipient node* (e.g. *Coffea*), *kind of interaction* (e.g. +/-), *description* (e.g.
183 females of *H. hampei* bore into the coffee berries to oviposit and their larvae feed from it) and *reference*
184 (listing of the articles that support the interaction). For HOIs, instead of a *recipient node*, a column was
185 added with the *recipient interaction* (e.g. the presence of *Azteca* prevents *H. hampei* from boring into the
186 coffee, inhibiting herbivory). Interactions that were uncertain, but suspected, were annotated but not
187 considered for the construction of the network. Finally, the network was compared with smaller versions
188 published previously and revised by experts.

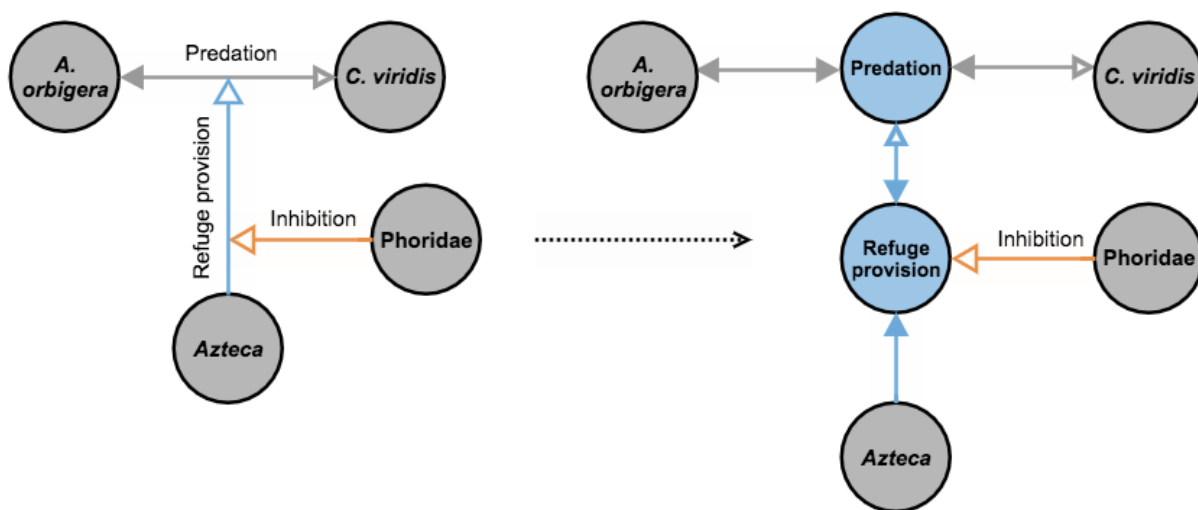
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190 2.3 Structure definition and general metrics

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192 The structure of the network was visualized with the software *Gephi 0.9.2*. Because network-related
193 methods only contemplate ensembles of nodes connected directly through edges (that is, first order
194 interactions), it is not possible to define a network with edges connecting to other edges, which is the
195 case of HOIs. For this reason, two versions of the network were created: the first one only captured the
196 nodes and their first order interactions; the second one included HOI modified interactions as artificial
197 pseudo-nodes, an artifact that allowed us to use the full force of network theory to analyze the system.
198 Topological analyses were conducted on both versions of the network in order to quantify the effect of
199 HOIs.

200 The transformation process of HOIs into pseudo-nodes is depicted in Figure 1. Basically, an edge that
201 was affected by a third node was labeled with a new pseudo-node (e. g. a pseudo-node named
202 ‘predation’), so the third node had now a simple edge connecting it to the new pseudo-node. The same
203 logic works for second, third or any higher order interactions. A similar procedure was suggested by
204 Newman (2018), where interactions involving more than two nodes are introduced by adding new nodes
205 belonging to a different category as part of a bipartite graph. This new node is connected by a single
206 edge to each original node. However, this procedure is limited as bipartite graphs do not account for
207 edges between nodes belonging to the same category.



208

209 Figure 1. Transformation process of second and third order interactions into pseudo-nodes. The grey
210 nodes represent biological taxa and the blue nodes are pseudo-nodes representing ecological
211 interactions which are modified by a HOI. First order edges are dark grey, second order edges
212 are blue and third order edges are orange. Filled arrows represent positive effects, and unfilled ones,
213 negative effects. For example, the predatory interaction between *A. orbigera* and *C. viridis* is turned into
214 a pseudo-node named *predation* in order to be modified by the refuge provision performed by *Azteca*, a
215 second order interaction. Likewise, this refuge provision is inhibited by the presence of phorids, so it is
216 turned into a second pseudo-node in order to be modified by the third order interaction performed by
217 *Phoridae*.

218 Once both versions on the network were obtained, standard network metrics were quantified to
219 characterize them: number of nodes, number of edges, mean degree, diameter, density, modularity
220 (using the Louvain algorithm), clustering coefficient, mean path length, and *sigma* and *omega* small
221 world coefficients (Humphries & Gurney 2008; Telesford et al. 2011). Afterwards, we analyzed node
222 relevance according to their centrality. For this, we used four commonly used metrics: degree, closeness
223 centrality, betweenness centrality, and eigenvector centrality. All calculations were made with the
224 software *Gephi 0.9.2*.

225

226 2.4 The effect of high order interactions on network robustness

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228 We conducted a robustness analysis for both versions of the network (with and without HOIs).
229 Robustness was measured by calculating the area under the curve that depicts the size of the biggest
230 connected component as nodes are removed one by one from the network (Kasthurirathna et al., 2013;
231 Piraveenan et al., 2013; Navarro Díaz 2015). This measure is compared with the area under the curve
232 traced by a complete graph, that is, a graph where every possible pair of nodes is connected by an edge.
233 Thus, following Equation 1, the relationship between these two areas gives us a measure of robustness
234 (for a full derivation of the equation see Piraveenan et al. (2013)).

$$235 \quad R_1 = \frac{A_g}{A_c} (\%) = \frac{200 \sum_{k=0}^N S_k - 100S_0}{N^2} \quad \dots \text{Equation 1}$$

236 Where A_g is the area under the curve of the evaluated graph and A_c that of the fully connected graph. S_k
237 is the size of the largest component after k nodes have been removed, S_0 denotes the initial largest

238 component size, and N is the network size. According to the above equation, for a fully connected
239 network of any size, the robustness coefficient (R) is always of 100% (taken from Kasthurirathna et al.,
240 2013).

241 For the empirical network that includes HOIs, only real nodes could be selected for removal, in order to
242 avoid the biologically meaningless action of removing pseudo-nodes. Following this logic, whenever a
243 node got selected for removal, any pseudo-node connected to it was also eliminated, since pseudo-nodes
244 lose their meaning once the species causing the higher order effect is eliminated. Because this
245 modification often resulted in the elimination of several nodes at the time, we modified equation 1 in
246 order to control for it. In the Piraveenan et al (2013) derivation, the area under the curve of the fully
247 connected graph assumes one node removal per step in the x axis. If we assume n node removal per step
248 (in order to control for pseudo-node removal in the evaluated graph), this area is $A_c = N^2/2n$ and the
249 robustness equation becomes:

$$250 \quad R_n = \frac{A_g}{A_c} (\%) = \frac{200n \sum_{k=0}^{N'} S_k - 100nS_0}{N^2} \quad \dots \text{Equation 2}$$

251 Where n is the average number of nodes removed at each step (1.54 in this network) and N' is the
252 number of real nodes in the network (N minus the number of pseudo-nodes) . Equation 1 is equivalent to
253 Equation 2 when $n=1$ and there are no pseudo-nodes.

254 Hence, we used equation 1 for the network without HOIs and equation 2 for the network with HOIs. For
255 each of these networks, two node removal methods were tested. With the first one, nodes were randomly
256 selected and removed one by one until removing them all. This was done 200 independent times and a
257 robustness average was obtained. The second method consisted of removing nodes by degree, from
258 highest to lowest.

259 The robustness of each network with each removal method was also compared with the average
260 robustness of 200 randomized but comparable networks, i.e. with the same number of nodes, average
261 degree or interaction density. Three types of random networks were used: totally random networks
262 (Erdős & Rényi 1960), small-world networks (Watts & Strogatz 1998) and scale-free networks
263 (Barabási & Albert 1999). The first model generates random networks from a set of nodes in which the
264 edges are independently created between any pair of nodes with a probability p . Because the structure of
265 ecological networks is far from being random, we also used small-world and scale-free networks, which
266 have been proved to share structural characteristics with many real world networks (Montoya & Solé
267 2002; Barabási & Bonabeau 2003). Small-world networks follow an algorithm that starts with a regular

268 lattice where each node is connected to its k closest neighbors, and where each edge is then re-connected
269 to a randomly chosen node with a certain probability, avoiding duplicates and self-loops. This
270 construction produces networks with a high clustering coefficient and short paths, two particularities that
271 have been found in many ecological webs (Montoya & Solé 2002). The last method builds networks
272 with a preferential attachment mechanism, where nodes are added sequentially such that each new node
273 is connected to a number m of existing nodes, where the probability to choose a node for connection is
274 proportional to the number of links that this node already has. This creates networks with power-law
275 degree distributions, another characteristic that has been widely found in ecological webs (Barabási &
276 Bonabeau 2003). For the Erdős Rényi method we used the values $N=34$ and $p=0.095$, and $N=22$ and
277 $p=0.145$ for networks representing cases with and without HOIs, respectively (where N is the number of
278 nodes of the empirical web and p is taken from their density). For the Watts-Strogatz method, we chose
279 $N=34$, $k=3$ and $p=0.5$, and $N=22$, $k=3$ and $p=0.5$ for networks representing cases with and without HOIs,
280 respectively (where k is the average degree of the empirical web and p was arbitrarily chosen). For the
281 Barabasi-Albert method we chose $N=34$ and $m=1$, and $N=22$ and $m=2$ for networks representing cases
282 with and without HOIs, respectively (where m is chosen so that the resulting average degree matches the
283 empirical average degree).

284 Because nodes in the empirical network with HOIs were removed along with their associated pseudo-
285 nodes as discussed above, the randomized versions of this network needed to emulate this process too.
286 This was done in the following way: First, we quantified the probability to remove a number n of
287 pseudo-nodes with each real node removal in 100 simulations of the empirical network with HOIs.
288 Then, in the randomized networks (composed of 34 nodes), a subset of 22 randomly chosen nodes was
289 defined to stand for the real nodes, while the remaining 12 nodes stood for the pseudo-nodes. At each
290 removal step, a node was removed (randomly or by degree as explained above) from the real nodes pool
291 alongside with n nodes from the pseudo-node pool, with n drawn from the probability distribution
292 derived from the mentioned simulations. Again, we used Equation 1 for calculating robustness of the
293 randomized versions of the network without HOIs and Equation 2 for the randomized versions of the
294 network with HOIs. With these numerical experiments we were able to compare, on the one hand, the
295 robustness of the two versions of our network, that is, with and without HOIs, and on the other hand,
296 each empirical robustness with their randomized analogues. Simulations were done with the library
297 NetworkX 2.5 (Hagberg et al. 2008) in *Python 3.7.1*. and ANOVA tests were performed in *RStudio*
298 *1.2.1335* (RStudio Team 2020). Scripts are publicly available at:
299 <https://github.com/laparcela/CoffeeNetworkStructure>

300

301 **3. Results**

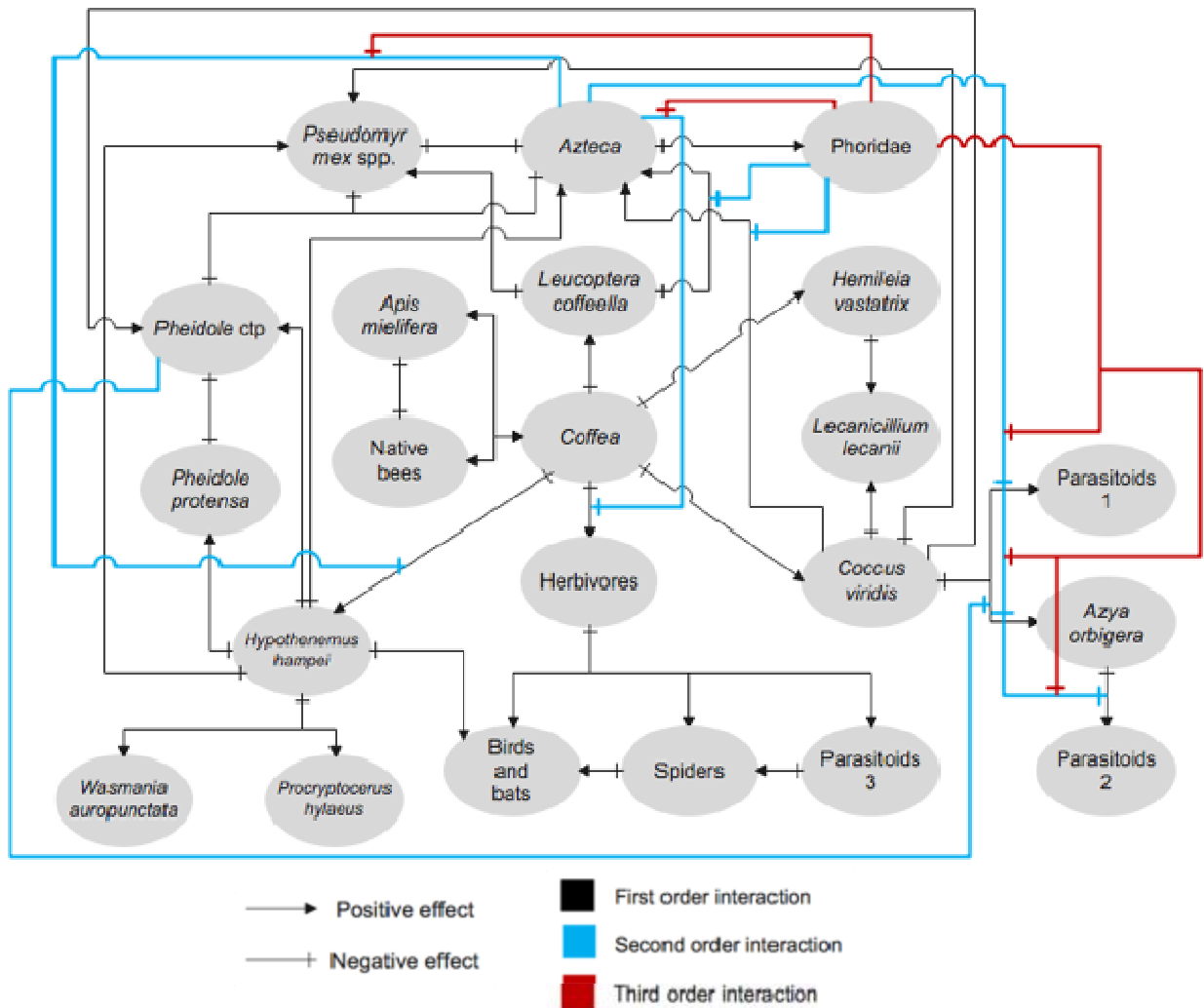
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303 3.1 Network inference

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305 From literature revision, 48 interactions between 22 nodes were established out of 44 scientific papers
 306 and books, all conducted in our study site (Figure 2). This information is organized in the supplementary
 307 material table S1.

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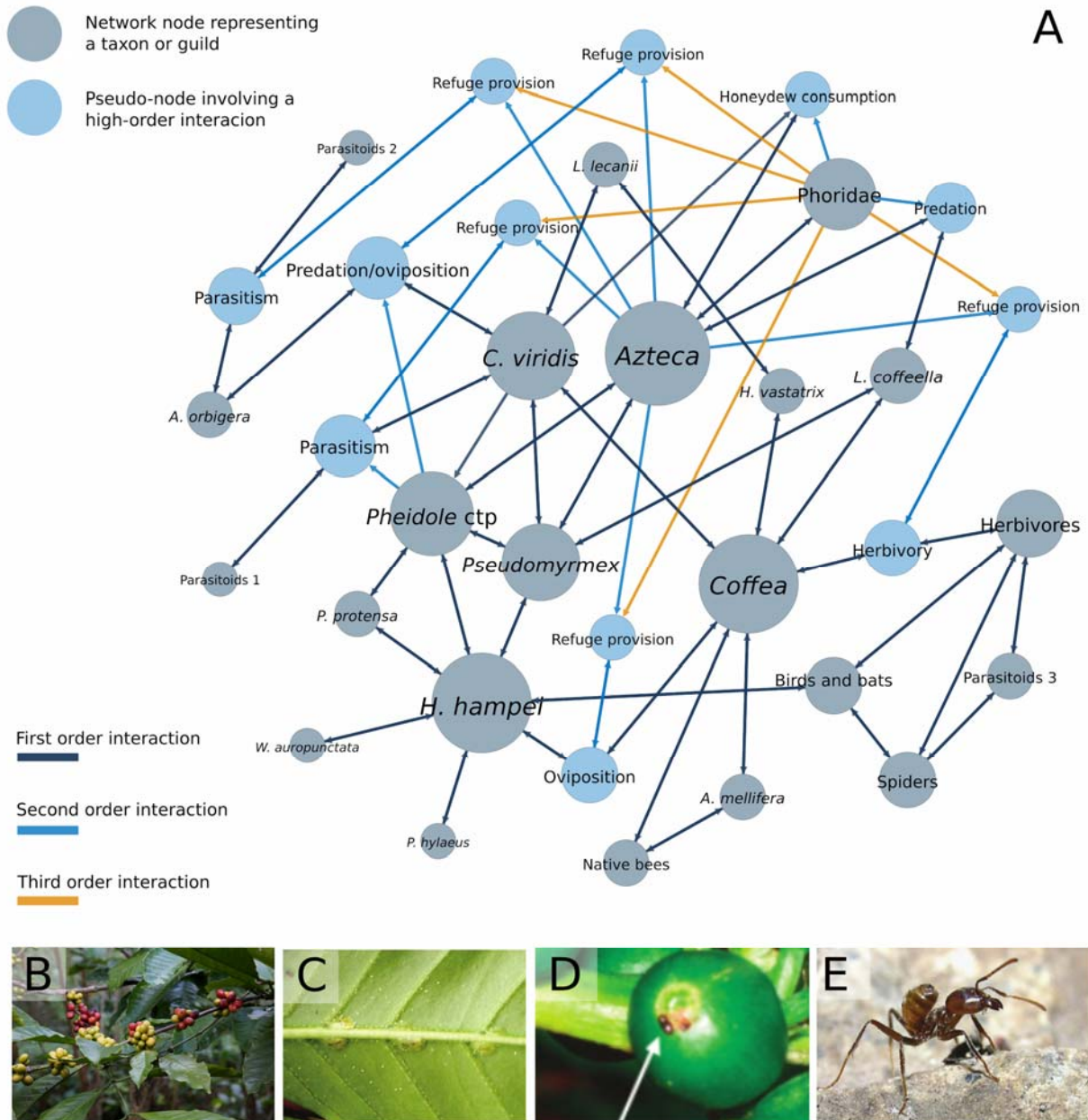
311 Figure 2. Complete network before transformation from HOIs to pseudo-nodes. Black lines are first order
 312 interactions, blue lines are second order interactions and red lines are third order interactions.

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314 3.2 Structure definition and general metrics

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316 Two versions of the web were obtained with *Gephi*, the first one containing only first order
 317 interactions and the second one after adding pseudo-nodes for HOIs (Figure 3).



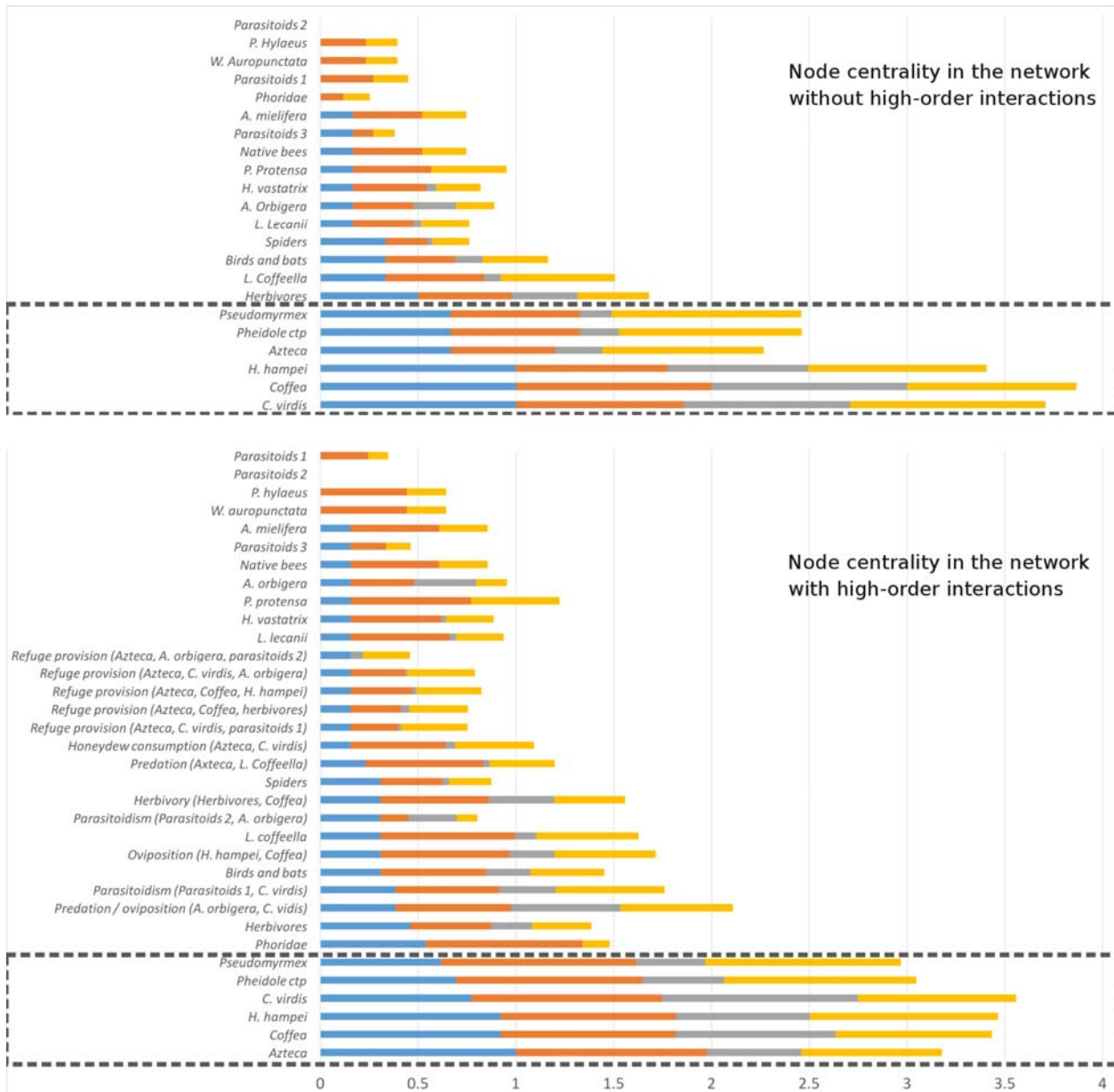
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319 Figure 3. A: Community network with first, second and third order interactions. Grey nodes
 320 represent biological taxa and blue nodes are pseudo-nodes representing ecological interactions
 321 which are subject to being modified by a HOI. Node size is determined by its degree. First order

322 edges are grey, second order edges are blue and third order edges are orange. B: Coffee plants
323 (*Coffea*). C: Coffee green scale (*Coccus viridis*), a potential pest in the system. D: Coffee berry borer
324 (*Hypothenemus hampei*), one of the main coffee pests, about to penetrate a coffee grain. E: *Azteca* ant, an
325 important regulator of this interaction network. Photographs: Wikimedia Commons by *Jmhullnot* at
326 <https://commons.wikimedia.org/wiki/File:CoffeeBerry.jpg> (B), John Vandermeer (C, D), Alex Wild (E)

327

328 Without HOIs, the network is composed of 22 nodes and 68 interactions, while incorporating
329 HOIs makes it a network of 34 nodes and 104 interactions. Both networks have an approximate
330 average degree of 3. Table S2 summarizes the general metrics obtained for both versions of the
331 network. Centrality analysis showed that *C. viridis*, *Coffea*, *H. hampei*, *Azteca*, *Pheidole ctp.* and
332 *Pseudomyrmex* spp are the nodes with the highest rankings in both networks and for different
333 centrality metrics (Figure 4).



334

335 Figure 4. Node centrality analysis for the network without HOIs (above) and with HOIs (below).

336 *C. viridis*, *Coffea*, *H. hampei*, *Azteca*, *Pheidole ctp* and *Pseudomyrmex* spp are the highest

337 ranking nodes in both networks.

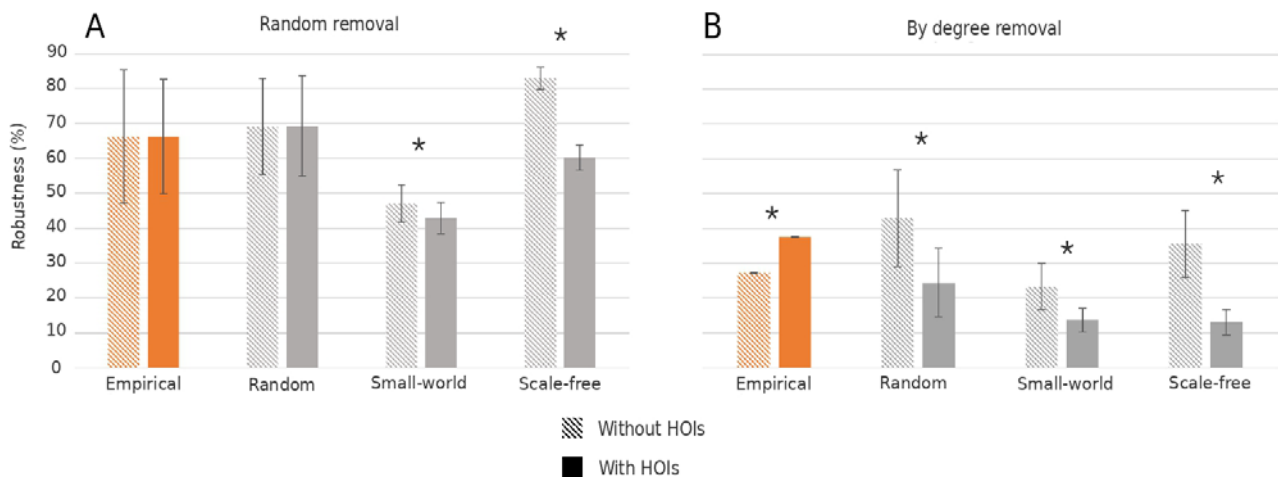
338 3.3 The effect of high order interactions on network robustness

339 Figure 5 presents the results of the robustness analyses for the empirical coffee networks with

340 and without HOIs, as well as the results for the three different types of randomized networks

341 with comparable structures. In the case of the empirical networks, the addition of HOIs did not

342 significantly change the network robustness under random node removal, but robustness
343 increased significantly under directed node removal. In contrast, for the three types of
344 randomized networks subject to the two node removal protocols, networks with comparable
345 structures to those with HOI addition significantly lost robustness, except for the completely
346 random networks (Erdos-Renyi) under random removal, which showed no significant changes.
347 Additionally, in the node removal by degree, taking HOIs into account made the empirical
348 network more robust than all its randomized counterparts. Statistical analyses can be found in the
349 table S3 of the Supplementary material. Because all randomized analogues of the network with
350 HOIs have the tendency to lose robustness, while the robustness of the actual empirical networks
351 is either unchanged or increased by HOIs, we can say that the effects observed in the empirical
352 networks are indeed a result of HOI addition and not of simply increasing the number of
353 interactions. Indeed, it seems that high order interactions favor robust network structures that
354 may enable the coexistence of diverse systems.



355

356 Figure 5. Robustness of the coffee-associated network, with and without HOIs, as well as
357 random, small-world and scale free networks with same n , mean degree and density. A: Under
358 random node removal, the empirical web (orange bars) and the totally random networks (grey,
359 left) are not significantly changed by the addition of HOIs; while small-world (grey, middle) and
360 scale-free networks (grey, right) lose robustness under HOI addition. B: When removing nodes
361 by degree, the empirical network (orange bars) is significantly more robust when HOIs are
362 added, while the three types of randomized networks (grey bars) lose robustness when their
363 structures are comparable to that with HOI addition.

364

365 **4. Discussion**

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367 We have integrated a vast set of empirical evidence into a coffee-associated network that includes both
368 simple and high order ecological interactions (Figure 3). This network has enabled us to test the role of
369 HOIs on the network's structural robustness for a system of great ecological and agricultural importance.
370 We find that the robustness of the coffee-associated network structure is unchanged or increased by HOI
371 addition, and random reconfigurations indicate that this effect is not simply due to edge addition (Figure
372 5). This goes in agreement with previous studies considering hypothetical networks and different
373 measures of system function like stability or feasibility, where the addition of simple interactions has
374 been found to negatively repercute on system function while HOI addition has a neutral or a positive
375 effect (May 1972; Bairey et al., 2016; Grilli et al., 2017; Singh & Baruah, 2020; Li et al., 2020).
376 Our results therefore support the idea that HOIs contribute to the maintenance of highly diverse
377 ecological communities.

378

379 In our study, the structural robustness of the network was evaluated with the change in size of the biggest
380 connected component as the nodes were gradually removed, at random or by targeting nodes of higher
381 degree first. This way of conceptualizing robustness assumes that the connection between network
382 components is related to the function and integrity of the system, implying that a fully connected network
383 can maintain its elements and overall functions better than a disaggregated or partially disconnected
384 network (Albert et al. 2000; Dekker & Colbert 2004; Piraveenan et al. 2013; Sheykhalil et al. 2020).
385 Indeed, previous work on the coffee agroecosystem for which the network under study has been
386 uncovered suggests that some agroecosystemic functions, such as pest control, rely on the dynamics of
387 the whole system and on the documented interactions taking place (Vandermeer et al. 2010). In the
388 particular case of agroecosystems, the integrity of the network, in other words the maintenance of its
389 diversity, is also likely to be associated to yield and yield stability in the face of diverse perturbations
390 (Gaudin et al. 2015; Manns & Martin 2018).

391

392 While the coffee-associated system was studied as an undirected network, the type and sign of its HOIs
393 could inform the mechanism through which HOIs affect the overall robustness. In ecological terms, the
394 HOIs considered in this network may act as buffers of the interactions they modify, thereby diminishing
395 their intensity. For example, refuge provisioning, where one species protects another from one or several
396 predators, may not only explain prey survival (which is important for maintaining the predator), but also
397 how predators avoid competitive exclusion. It is possible that these mechanisms, coupled with spatial and

398 temporal heterogeneity, may create the necessary conditions for coexistence. However, it is important to
399 bear in mind that individual HOIs may have effects in different directions. Specially in the case of
400 agroecosystems, where effects are measured also in terms of human-based values like productivity, the
401 effect of individual HOIs should not be universally assumed as positive. For instance, it has been shown
402 that the ant *Wasmannia auropunctata* can indirectly protect the coffee leaf miner against potential
403 predators, potentially limiting the effectiveness of biological control elements (Perfecto et al., 2021).

404

405 The structural analyses of the coffee-associated network also allowed us to identify nodes with high
406 centrality according to different metrics (Figure 4). Centrality has been used as an indicator of the role of
407 individual nodes in the overall dynamics of networks; in ecological networks, node centrality is thought
408 to reflect how a node contributes to the flow of energy and matter and ecosystem functioning. Highly
409 central nodes indirectly connect many other nodes in a network and act as ‘bridges’, a reason why
410 centrality has been amply used in the study of socio-ecosystems networks (Freeman, 1979; Raghavan
411 Unnithan et al., 2014; Lü et al., 2016; Horcea-Milcu et al., 2020; Arroyo-Lambaer et al., 2020). We
412 identified five nodes that systematically exhibited a high centrality, independently of the centrality
413 measure: *C. viridis*, *Coffea*, *H. hampei*, *Azteca*, *Pheidole* ctp. and *Pseudomyrmex* spp. This is in
414 agreement with the crucial role of the coffee plant in this agroecosystem, as well as the effect of its
415 potential pests and pest enemies in its growth and development (Vandermeer et al. 2010). However, at
416 this point we cannot rule out the possibility that the high centrality of these nodes is due to a bias in
417 sampling and research efforts. We are currently pursuing analyses that go beyond the study of the
418 network structure and that might help uncover the role of HOIs and highly central nodes on the dynamics
419 of populations on such a network.

420

421 To conclude, our results support the hypothesis that HOIs can contribute to the maintenance and
422 robustness of highly diverse ecological systems, and agroecological systems in particular. In agreement
423 with previous empirical and theoretical studies, our work points to the importance of agroecological
424 management and practices that are based on a deep ecological understanding of productive systems, as
425 well as to the importance of a high diversity of taxons and interactions for the robustness and functioning
426 of agroecosystems.

427

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778 8. Supplementary Material

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780 Table S1. Complete database containing all nodes and interactions included in the network, as well as references supporting them.

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	Source node	Receptor node	Receptor interaction	Type of interaction	Description	Reference
Order 1	<i>Azteca</i>	<i>Coccus viridis</i>	-	(+/-)	<i>Azteca</i> feeds on honeydew secreted by <i>C. viridis</i> .	Vandermeer & Perfecto 2006; Styrsky & Eubanks 2007
	<i>Azteca</i>	<i>Pseudomyrmex</i> spp	-	(-/-)	Competition, <i>Azteca</i> tends to win.	Vandermeer et al. 2010
	<i>Azteca</i>	<i>Leucoptera coffeella</i>	-	(+/-)	<i>Azteca</i> predaes <i>L. coffeella</i> , light and sporadic.	Vandermeer et al. 2002; Lomeli-Flores et al. 2009; Vandermeer et al. 2010
	<i>Azteca</i>	Phoridae	-	(-/+)	Phorids are parasitoids of <i>Azteca</i> ants, causing the death of attacked individuals and stoping <i>Azteca</i> from foraging when their presence is sensed.	Philpott 2005; Vandermeer et al. 2008; Mathis et al. 2011; Hsieh & Perfecto 2012
	<i>Azteca</i>	<i>Pheidole synanthropica</i>	-	(-/-)	Competition, <i>Azteca</i> tends to win.	Vandermeer et al. 2010
	<i>Azteca</i>	<i>Hypothenemus</i>	-	(+/-)	<i>Azteca</i> predaes on <i>H. hampei</i> .	Perfecto &

	<i>hampei</i>				Vandermeer 2006
Parasitoids 2	<i>Azya orbiger</i>	-	(+/-)	Parasitoids attack <i>A. orbiger</i> and cause their death.	Liere & Perfecto 2008; Vandermeer et al. 2010
<i>Azya orbiger</i>	<i>Coccus viridis</i>	-	(+/-)	<i>A. orbiger</i> uses <i>C. viridis</i> as food or oviposition place.	Liere & Perfecto 2008; Liere & Larsen 2010
Parasitoids 1	<i>Coccus viridis</i>	-	(+/-)	Parasitoid wasps attack <i>C. Viridis</i> .	Vandermeer et al. 2010
<i>Hypothenemus hampei</i>	<i>Pheidole synanthropica</i>	-	(-/+)	<i>Pheidole</i> ctp predate on <i>H. hampei</i> . They are able to replace <i>Azteca</i> on this function.	Philpott et al. 2012; Jiménez-Soto et al. 2013; Vandermeer & Perfecto 2015
<i>Hypothenemus hampei</i>	<i>Wasmania auropunctata</i>	-	(-/+)	<i>Wasmania</i> predate on <i>H. hampei</i> .	Gonthier et al. 2013; Vandermeer & Perfecto 2015
<i>Hypothenemus hampei</i>	<i>Pheidole protensa</i>	-	(-/+)	<i>P. protensa</i> predate on <i>H. hampei</i> when the coffee grain falls to the ground.	Armbrecht & Perfecto 2003; Vandermeer & Perfecto 2015
<i>Hypothenemus hampei</i>	<i>Coffea</i>	-	(+/-)	<i>H. hampei</i> penetrates coffee grains in order to oviposit.	Damon 2000; Gonthier et al. 2013; Vandermeer & Perfecto 2015
<i>Hypothenemus hampei</i>	<i>Pseudomyrmex</i> spp	-	(-/+)	<i>Pseudomyrmex</i> predate on <i>H. hampei</i> .	Larsen & Philpott 2010
<i>Hypothenemus</i>	<i>Procryptocerus</i>	-	(-/+)	<i>P. hylaeus</i> predate on <i>H. hampei</i> .	Vandermeer &

<i>hampei</i>	<i>hylaesus</i>				Perfecto 2015
<i>Coccus viridis</i>	<i>Coffea</i>	-	(+/-)	<i>C. viridis</i> feeds on coffee's fluids.	Bess 1958; Young 1982
<i>Coccus viridis</i>	<i>Pheidole synanthropica</i>	-	(0/+)	<i>P. synanthropica</i> has a mutualism with <i>C. viridis</i> like <i>Azteca</i> 's, but weaker. This interaction helps maintain small colonies of <i>C. viridis</i> that <i>Azteca</i> can later use to establish new nests.	Vandermeer et al. 2010
<i>Coccus viridis</i>	<i>Lecanicillium lecanii</i>	-	(-/+)	<i>L. lecanii</i> infects <i>C. viridis</i> causing its death. The probability of infection is densodependent.	Jackson et al. 2009
<i>Hemileia vastatrix</i>	<i>Lecanicillium lecanii</i>	-	(-/+)	<i>L. lecanii</i> infects <i>H. vastatrix</i> .	Vandermeer et al. 2009
<i>Hemileia vastatrix</i>	<i>Coffea</i>	-	(+/-)	<i>H. vastatrix</i> infects coffee.	Avelino et al. 2004
Birds and bats	Herbivores	-	(+/-)	Birds and bats predate on herbivores.	Perfecto et al. 2004; Kalka et al. 2008; Williams-Guillén et al. 2008; Johnson et al. 2010; Mooney et al. 2010
Birds and bats	Spiders	-	(+/-)	Birds and bats predate on spiders.	Philpott et al. 2004; Mooney et al. 2010

Spiders	Parasitoids 3	-	(+/-)	Spiders predate on parasitoids 3.	Ibarra-Núñez et al. 2001; Schoener et al. 2002
Parasitoids 3	Herbivores	-	(+/-)	Parasitoids 3 attack multiple herbivores.	Ibarra-Núñez et al. 2001; Schoener et al. 2002; Vandermeer & Perfecto 2015
Spiders	Herbivores	-	(+/-)	Spiders predate on multiple herbivores.	Hodge 1999; Schmitz & Sokol-Hessner 2002
Herbivores	<i>Coffea</i>	-	(+/-)	Multiple herbivores predate on coffee.	Vandermeer & Perfecto 2015
<i>Pheidole synanthropica</i>	<i>Pheidole protensa</i>	-	(-/-)	Competition. <i>P. protensa</i> tends to win.	Vandermeer et al. 2010
<i>Pheidole synanthropica</i>	<i>Pseudomyrmex</i> spp	-	(-/-)	Competition. <i>Pheidole</i> tends to win.	Vandermeer et al. 2010
Native bees	<i>Coffea</i>	-	(+/+)	Native bee diversity promotes pollination and heavier coffee grains.	Kremen et al. 2002; Klein et al. 2003; Klein et al. 2007
<i>Apis mellifera</i>	Native bees	-	(-/-)	<i>Apis mellifera</i> competes with native bees and dominates when there is a low diversity of native shrubs and trees.	Jha & Vandermeer 2009
<i>Leucoptera coffeella</i>	<i>Coffea</i>	-	(+/-)	<i>L. coffeella</i> oviposits on coffee leaves, harming coffee.	Fragoso et al. 2002; Lomeli-Flores et al.

						2009
	<i>Coccus viridis</i>	<i>Pseudomyrmex</i> spp	-	(-/+)	<i>Pseudomyrmex</i> predate on <i>C. viridis</i>	Vandermeer et al. 2010
	<i>Leucoptera coffeella</i>	<i>Pseudomyrmex</i> spp	-	(-/+)	<i>Pseudomyrmex</i> spp predate on <i>L. coffeella</i>	De la Mora et al. 2008
	Birds and bats	<i>Hypothenemus hampei</i>	-	(+/-)	Birds and bats predate on <i>H. hampei</i>	Johnson et al. 2010
Order 2	<i>Azteca</i>	-	<i>Azya</i> 's oviposition under <i>C. viridis</i> or <i>Azya</i> 's predation of <i>C. viridis</i> .	inhibition	<i>Azteca</i> 's protection stops <i>Azya</i> from predating on or ovipositing under <i>C. viridis</i> .	Vandermeer & Perfecto 2006; Liere & Larsen 2010; Vandermeer et al. 2010
	<i>Azteca</i>	-	Parasitoidism 2 of <i>Azya</i> .	inhibition	<i>Azteca</i> 's foraging on coffee plants scares off parasitoids that would otherwise attack <i>Azya orbigera</i> .	Liere & Perfecto 2008; Vandermeer et al. 2010
	<i>Azteca</i>	-	Parasitoidism 1 of <i>C. viridis</i> .	inhibition	<i>Azteca</i> 's protection stops parasitoid wasps from attacking <i>C. viridis</i> .	Vandermeer & Perfecto 2006; Vandermeer et al. 2010
	<i>Azteca</i>	-	General herbivory of coffee from multiple organisms.	inhibition	<i>Azteca</i> 's foraging on coffee plants scares off multiple herbivores.	Styrsky & Eubanks 2007; Vandermeer & Perfecto 2015
	<i>Azteca</i>	-	<i>H. hampei</i> 's penetration of	inhibition	<i>Azteca</i> grabs <i>H. hampei</i> and throws it off the coffee plants, generally without	Jiménez-Soto et al. 2013

			coffee grains.		harming it.	
	Phoridae	-	Mutualism between <i>Azteca</i> and <i>C. viridis</i>	inhibition	The presence of phorids paralyzes <i>Azteca</i> , stopping them from foraging on <i>C. viridis</i> honeydew.	Pardee & Philpott 2011
	Phoridae	-	Interaction between <i>Azteca</i> and <i>L. coffeella</i> .	inhibition	The presence of phorids paralyzes <i>Azteca</i> , stopping them from preying on <i>L. coffeella</i> .	Vandermeer & Perfecto 2015
	<i>Pheidole synanthropica</i>	-	<i>Azya</i> 's oviposition under <i>C. viridis</i> or <i>Azya</i> 's predation of <i>C. viridis</i> .	inhibition	<i>P. synanthropica</i> has a mutualism with <i>C. viridis</i> like <i>Azteca</i> 's, but weaker. This interaction helps maintain small colonies of <i>C. viridis</i> that <i>Azteca</i> can later use to establish new nests.	Vandermeer et al. 2010
	<i>Pheidole synanthropica</i>	-	Parasitoidism 1 of <i>C. viridis</i> .	inhibition	<i>P. synanthropica</i> has a mutualism with <i>C. viridis</i> like <i>Azteca</i> 's, but weaker. This interaction helps maintain small colonies of <i>C. viridis</i> that <i>Azteca</i> can later use to establish new nests.	Vandermeer et al. 2010
Order 3	Phoridae	-	<i>Azteca</i> 's inhibition of parasitoidism 1 of <i>C. viridis</i> . (2nd order interaction).	inhibition	The presence of phorids paralyzes <i>Azteca</i> , stopping them from inhibiting wasp parasitoidism of <i>C. viridis</i> .	Vandermeer & Perfecto 2015
	Phoridae	-	<i>Azteca</i> 's inhibition of coffee	inhibition	The presence of phorids paralyzes <i>Azteca</i> , stopping them from inhibiting	Vandermeer & Perfecto 2015

			herbivory from multiple organisms. (2nd order interaction).		herbivory of multiple organisms on coffee.	
Phoridae	-		<i>Azteca</i> 's inhibition of <i>H. hampei</i> 's penetration of coffee grains. (2nd order interaction).	inhibition	The presence of phorids paralyzes <i>Azteca</i> , stopping them from throwing <i>H. hampei</i> off coffee plants. Ants like <i>P. symplex</i> and <i>P. hylaeus</i> are able to replace this function.	Pardee & Philpott 2011; Philpott et al. 2012
Phoridae	-		<i>Azteca</i> 's inhibition of interaction between <i>Azya</i> and <i>C. viridis</i> . (2nd order interaction).	inhibition	The presence of phorids paralyzes <i>Azteca</i> , stopping them from protecting <i>C. viridis</i> from <i>A. orbigera</i> .	Hsieh et al. 2012
Phoridae	-		<i>Azteca</i> 's inhibition of parasitoidism 2 of <i>Azya orbigera</i> . (2nd order interaction).	inhibition	The presence of phorids paralyzes <i>Azteca</i> , stopping them from scaring off parasitoids of <i>A. orbigera</i> .	Vandermeer & Perfecto 2015

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Table S2. General metrics obtained for the network with and without HOIs.

	<i>Without HOIs</i>	<i>With HOIs</i>
Nodes	22	34
Edges	68	104
Average degree	3.091	3.059

Diameter	5	8
Density	0.147	0.093
Modularity	0.44 (5 modules)	0.45 (6 modules)
Clustering coefficient	0.334	0.261
Average path length	2.632	3.362
Small world coefficient (<i>sigma</i>)	1.36	1.4

Small world coefficient (<i>omega</i>)	0.33	0.51
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Table S3. ANOVA analyses for the robustness of all networks.

		Degrees of freedom	Sum of squares	Mean sum of squares	Statistic	<i>p</i> value	<i>eta</i> square	<i>omega</i> square	<i>epsilon</i> square
Random node removal	Empirical with HOIs vs without HOIs	1	0.019	0.019	0	0.994	0	-0.003	0

	Random with HOIS vs without HOIS	1	0.014	0.014	0.17	0.68	0	-0.002	-0.002
	Small-world with HOIS vs without HOIS	1	1774.66	1774.66	72.14	<0.001	0.153	0.151	0.426
	Scale-free with HOIS vs without HOIS	1	50986.63	50986.63	4463.04	<0.001	0.918	0.918	3.349
By degree node removal	Random with HOIS vs without HOIS	1	34281.86	34281.86	236.54	<0.001	0.373	0.371	0.771
	Small-world with HOIS vs without HOIS	1	9312.47	9312.47	333.91	<0.001	0.456	0.454	0.916

	Scale-free with HOIs vs without HOIs	1	50922.49	50922.49	964.08	<0.001	0.708	0.707	21022.325
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