

1 **The return of the trophic chain: fundamental vs realized interactions in a simple arthropod**  
2 **food web**

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18

19 **Abstract**

20 The mathematical exploration of small assemblages of interacting species (community  
21 modules) has proven key to understand emergent properties of ecological communities.  
22 These models use differential equations to study pairwise relations between species.  
23 However, as community modules become more complex, one may wonder whether all  
24 potential interactions are effectively realized. Here, we use community modules to  
25 experimentally explore whether the number of trophic links among species increases as  
26 another aspect of complexity increases, i.e., the number of species that are known to feed  
27 on each other in pair-wise trials. To this aim, we use a simple mite community present in  
28 avocado orchards (*Persea americana*), composed of two predators (*Euseius stipulatus* and  
29 *Neoseiulus californicus*), one herbivore as shared prey (*Oligonychus perseae*), and pollen of  
30 *Carpobrotus edulis* as alternative food, with the potential for (intraguild) predation and  
31 (apparent) competition to be expressed. Using a series of controls, we could assess whether  
32 the presence of one species affected the abundance of another, or its conversion of food  
33 into offspring. We found that increasing the number of potential interactions did not result  
34 in more complex realized community modules. Instead, all communities were reduced to  
35 one or two linear trophic chains. Our results show that trophic links assumed to occur when  
36 species are confronted in pairs do not necessarily occur when other components of the  
37 community are present. Consequently, food-web complexity may be erroneously over-  
38 estimated in theoretical community modules that are parameterized based on pair-wise  
39 interactions observed when alternative prey is absent. This suggests a  
40 need for empirical work to work in concert with theoretical to develop more realistic and predictive food-web models.

Elton 1927  
↑

## 41 Introduction

initially conceptualised

42 Community ecology has traditionally viewed trophic interactions as linear chains, with an  
43 upper level <sup>potentially</sup> controlling the densities of the level immediately below, <sup>thus</sup> generating a trophic  
44 cascade (Hairston *et al.* 1960; Oksanen *et al.* 1981; Carpenter *et al.* 1985). However, it is ~~now~~  
45 now accepted that most communities do not follow this pattern as organisms are imbedded  
46 in complex food webs, blurring the notion of a trophic guild and the notion that widespread  
47 omnivory <sup>might</sup> would destabilize food webs (Polis & Holt 1992; Polis & Strong 1996).

Sensu  
trophic  
coherence

48 Food webs can be decomposed into "community modules" (i.e. "small number of  
49 species (e.g. three to six) linked in a specified structure of interactions, Holt 1997). Among  
50 those, intraguild predation (IGP), in which two consumers (the intraguild predator and the  
51 intraguild prey, hereafter IG-predator and IG-prey) not only compete for a shared resource  
52 but also engage in predator-prey interactions (Polis *et al.* 1989), and apparent competition,  
53 in which two non-competing prey share a common predator (Holt 1977; 1997), are the most  
54 common (Bascompte & Melián 2005).

Might be  
good to  
briefly  
explain why  
modules and  
motifs are  
similar.

55 Whether and how often species engage in intraguild predation or apparent  
56 competition strongly affects the long-term persistence (i.e. stability) of communities. Theory  
57 predicts that intraguild predation destabilizes communities because it reduces the  
58 parameter space where coexistence of IG-predator, IG-prey and shared prey is possible  
59 (Holt & Polis 1997), compared to that of trophic chain models (Oksanen *et al.* 1981). In most  
60 models with intraguild predation the possibility of 3-species persistence requires the IG-prey  
61 to be superior to IG-predators at <sup>long</sup> exploitative competition for the shared resource (Holt  
62 1997; Mylius *et al.* 2001; Kondoh 2008, among others). Furthermore, the occurrence of  
63 intraguild predation leads to a less efficient control of the shared prey populations because  
64 the IG-prey's equilibrium abundance is expected to decline towards extinction with  
65 increasing productivity (Mylius *et al.* 2001). This is especially important in agricultural  
66 systems, inherently highly productive, in which the introduction of several biocontrol agents  
67 may in fact reduce pest control. Curiously, empirical studies, mostly stemming from such  
68 systems, show that variable effects of intraguild predation on populations of the shared  
69 prey (e.g., Rosenheim *et al.* 1995; Janssen *et al.* 2006; Vance-Chalcraft *et al.* 2007; Messelink  
70 & Janssen 2014).

defn  
Pimm  
1984  
temporal  
stability  
in  
community  
composition

71 Some factors may, however, reduce such instability by promoting species  
72 coexistence, which generally occurs when conditions under which predator-predator

73 interactions occur are constrained (reviewed in Novak 2013, appendix S1). For example, 3-  
74 species coexistence is enhanced if predators engage into intraguild predation only when IGP  
75 competition for the shared prey is high (Křivan 2000), or the shared prey is less profitable  
76 than the intraguild prey (Křivan & Diehl 2005). Other studies suggest that the inclusion of  
77 habitat structure (Janssen *et al.* 2007), inducible defences (Kratina *et al.* 2010; Nakazawa *et*  
78 *al.* 2010) or temporal refuges (Amarasekare 2008) increases system stability, although this  
79 may depend on which species use refuges (Liu & Zhang 2013). Moreover, stage structure in  
80 the intraguild prey promotes stability, either by providing a stage refuge (Mylius *et al.* 2001;  
81 Rudolf & Armstrong 2008) or by inducing ontogenetic niche shifts in the predator (Hin *et al.*  
82 2011). However, in all cases, the models still predict that overall stability is lower than that  
83 of a simple trophic chain. This lack of stability is corroborated by empirical laboratory  
84 studies (Diehl & Feißel 2000; Montserrat *et al.* 2008b), but runs counter <sup>to</sup> the ubiquity of  
85 intraguild predation and trophic level omnivory in natural systems (Bascompte & Melián  
86 2005; Gagnon *et al.* 2011).

IGP  
dimensional  
eg. Donohue  
*et al.* 2010  
Ecol. Lett  
see earlier  
comments.

87 Discrepancies between theory of IGP and data suggest that some assumptions of  
88 theoretical models are not met in natural systems. In an effort to bring IGP models closer to  
89 real systems, while maintaining mathematical tractability, researchers have tested how the  
90 incorporation of an alternative food source affected stability (Heithaus 2001; Daugherty *et*  
91 *al.* 2007; Holt & Huxel 2007; Rudolf 2007). The general prediction is that providing  
92 alternative food to the intraguild prey leads to wider parameter regions of species  
93 coexistence (Daugherty *et al.* 2007; Holt & Huxel 2007), even if competitive superiority of IG-  
94 prey is precluded (Faria & Costa 2010). Instead, alternative food for the intraguild predator  
95 destabilizes the community (Daugherty *et al.* 2007; Holt & Huxel 2007). However, in the  
96 latter case, if the quality of the alternative food is high enough, then the intraguild predator  
97 switches to feeding on the alternative food, whereas the intraguild prey feeds on the shared  
98 prey (Ibid.). This again promotes coexistence by bringing the community structure closer to  
99 two linear food chains.

100 At prevailing outcome of IGP theory is, thus, that domains for persistence of  
101 communities with IGP increase when the strength of intraguild predation decreases. Indeed,  
102 weak interactions have long been recognized to stabilize ecosystems, particularly.  
103 Indeed, by dampening oscillations between consumers and resources, these interactions  
104 decrease the probability of species extinctions (McCann *et al.* 1998), thus promoting

Empirical  
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the ecological (IAP repetitive)  
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see comment  
good.  
Weak interactions  
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Worth defining here? (i.e.) #ind consumed per hour or what?

105 community persistence (May 1972; Pimm & Lawton 1978; Paine 1992; McCann *et al.* 1998;  
106 Emmerson & Yearsley 2004; Neutel *et al.* 2007; Gellner & McCann 2012; 2016). ~~107~~ here we  
107 address whether the fundamental niches of species (with all their potential interactions) are  
108 always realized. Specifically, we explore how pairwise trophic interactions between species  
109 are modified by the inclusion of other species in a simple community. We focus on  
110 predation rate as it is an excellent proxy for trophic interaction strength, used both in  
111 modelling (e.g. the equivalent to the "catching efficiencies" in *Kuijper et al.* 2003) and in  
112 empirical work (*Wootton & Emmerson 2005; Novak & Wootton 2010; Novak 2013*).  
113 Measurements of other relevant non-trophic interactions, such as competition, would  
114 require experiments at the population and community level that are beyond the scope of  
115 this manuscript. Our baseline hypothesis is that increasing the number of species that are  
116 known to interact when no alternative food is available will increase the number of realized  
117 links in the more complex community (Box 1A). We mimicked different community modules  
118 (Sensu Holt 1997) of increasing complexity using a community composed of two predatory  
119 mite species as intraguild predators (*Euseius stipulatus* and *Neoseiulus californicus*, Acari:  
120 Phytoseiidae), one species of herbivore mite as the shared prey (*Oligonychus perseae*, Acari:  
121 Tetranychidae), and pollen (of several anemophilous species) as alternative food (*González-*  
122 *Fernández et al.* 2009), all of which occur in the leaves of crops of avocado plants (*Persea*  
123 *americana*) in Southeastern Spain. Previous pairwise experimental designs have shown that  
124 the interaction between *N. californicus* and *O. perseae* is stronger - i.e. predation rates are  
125 higher than that between *E. stipulatus* and this same prey (*González-Fernández et al.*  
126 2009). Moreover, pollen is an optimal food source for *E. stipulatus* but not for *N. californicus*  
127 (*Ferragut et al.* 1987; *González-Fernández et al.* 2009). Finally, *E. stipulatus* and *N.*  
128 *californicus* engage in size-dependent predator-prey interactions (*Abad-Moyano et al.*  
129 2010). This knowledge was used to build predictions on realized trophic links occurring in  
130 this system across community modules of increasing complexity (Box 1B). Specifically, we  
131 predict that: i) in "trophic chain" community configurations, both predator species will  
132 interact with the herbivore (Box 1B, a.1.1. and a.1.2.); ii) in "apparent competition"  
133 community configurations, only *E. stipulatus* will interact with both the herbivore and pollen  
134 (Box 1B, b.1.1. and b.1.2.); iii) in "intraguild predation" community configurations, both IG-  
135 predator species will interact with the IG-prey and the herbivore (Box 1B, c.1.1. and c.1.2.);  
136 and iv) in "Intraguild predation and apparent competition" community configurations, only

ecological

Eltonian niche  
Could be worth mentioning predator vis a vis Reviewer #2

hence New paragraph

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specify

hence

137 adults and juveniles of *E. stipulatus* will establish trophic links with pollen (Box 1B, d.1.1. and  
138 d.1.2.). These predictions were then tested through a series of experimental treatments to  
139 assess which interactions were realized within each community module, by measuring IG-  
140 prey/herbivore mortality and how <sup>consumption of prey</sup> predation translates into predator fecundity as a result of  
141 these interactions. Specifically, we examined a) whether (IG)predators feed on each prey  
142 type; b) whether predation of (IG)predators on one prey type is affected by the presence of  
143 the other; c) whether predation of (IG)predators on both prey, and of IG-prey on the  
144 herbivore, is affected by the presence of alternative food; d) whether the presence of  
145 alternative food affects predation of (IG)predators on the two types of prey when they are  
146 together; e) number of eggs produced by (IG)predators when feeding on each prey type;  
147 and f) whether egg-production is additive when (IG)predators have more than one food  
148 type available. ]

Could hypothetically (IG) predators (i.e., no.)

→ this could be difficult to establish if it equals more food (i.e., same result might be observed with more of one prey)

## 151 Material and Methods

152 All cultures and experiments were done in a climate chamber at  $25 \pm 1^\circ\text{C}$ ,  $65 \pm 5\%$  RH and  
153 16:8h L:D (Light:Dark).

### 154 Mite cultures

155 Cultures of the predatory mite *E. stipulatus* were started in 2007 from ca. 300 individuals  
156 collected from avocado trees located in the experimental station of "La Mayora". Rearing  
157 units consisted of three bean plants (*Phaseolus vulgaris* L.) with 6-10 leaves, positioned  
158 vertically, with the stems in contact with sponges (ca. 30 x 20 x 5 cm) covered with cotton  
159 wool and a plastic sheet (27 x 17 cm), and placed inside water-containing trays (8 L, 42.5 x  
160 26 x 7.5 cm). The plant roots were in contact with the water, and the aerial parts were  
161 touching each other, forming a tent-like three-dimensional structure, where individuals  
162 could easily walk from one plant to the other. Cotton threads were placed on the leaves, to  
163 serve as oviposition sites for the females. Mites were fed *ad libitum* twice a week with  
164 pollen of *Carpobrotus edulis* (cat's claw) spread on leaves with a fine brush. *Euseius*  
165 *stipulatus* is able to develop and reproduce on this food source (Ferragut *et al.* 1987). Every  
166 three weeks, new rearings were made by transferring, leaves with mites and the cotton  
167 threads filled with eggs to a new unit. The culture was found to be contaminated a few  
168 times with *Tyrophagus* spp., a detritivorous mite species. In such instances, instead of

169 moving entire leaves, adult *E. stipulatus* females (ca. 300) were collected individually and  
170 transferred to the new rearing unit.

171 The *N. californicus* population was obtained from Koppert Biological Systems S.L. in  
172 bottles of 1000 individuals (Spical®). Colonies were kept on detached bean leaves infested  
173 with *Tetranychus urticae* that were placed on top of inverted flower-pots (20 cm Ø) inside  
174 water-containing trays.

175 The herbivore *Oligonychus perseae* was not maintained in a laboratory culture due  
176 to technical difficulties in preserving detached avocado leaves. They were thus collected  
177 from the field on a regular basis from avocado orchards located in the experimental station  
178 of "La Mayora".

179 Pollen of *C. edulis* was obtained from flowers collected in the experimental station.  
180 Stamens dried in a stove at 37°C for 48h, then sieved (350 µm).

181

#### 182 *Community modules*

183 Experimental arenas to test the outcome of community modules have been described in

184 detail in Guzmán *et al.* (2016a). Briefly, a hole (6.5 cm Ø) was cut in a petri dish (9 cm Ø),

185 turned upside down and <sup>then</sup> filled with an avocado leaf disc (7.5 cm Ø), <sup>with</sup> the borders <sup>were</sup> glued  
186 to a clay ring. Inside the petri dish, wet cotton wool ensured enough humidity to keep

187 leaves turgid. Petri dishes were then sealed with parafilm®. To prevent individuals from

188 escaping, a ring of Tanglefoot® was applied along the outer margin of the leaf disc. Cohorts

189 of *E. stipulatus* were made by transferring with a fine brush 400 eggs from the rearings to 2-

190 3 bean leaves placed on top of sponges (30 x 20 x 5 cm, approx.) covered with cotton wool,

191 inside water-containing trays (3.5 L), and with pollen of *C. edulis* as food. Cohorts of *N.*

192 *californicus* were made by placing 100 females during 48 h on 2-3 bean leaves infested with

193 *Tetranychus urticae* in containers similar to those used for the cultures. 10-14 days after egg

194 hatching, gravid predator females were randomly taken from these cohorts, and starved for

195 16 h in experimental containers similar to those above. Starvation was done to standardize

196 hunger among individuals, and to ensure that egg production in tested females was not

197 obtained from food ingested prior to the experiment. Predator juveniles (2-3 days old since

198 hatching) were taken from the cohorts when needed. Arenas containing the herbivore were

199 done as follows: Ten females of *O. perseae* were let to build nests and lay eggs on

200 experimental arenas during 4 days. The number of nests and eggs per nest on each arena

201 was counted at the onset of the experiment. Pollen in arenas assigned to treatments with  
202 alternative food was supplied *ad libitum*, using a fine brush.

203 We performed experiments using two 'community blocks', depending on the identity  
204 of the top predator (*N. californicus* or *E. stipulatus*). Throughout the text, the identity of  
205 (IG)-predator and (IG)-prey will be indicated using the subscripts "ES" for *E. stipulatus* and  
206 "NC" for *N. californicus*. Increased complexity in each of the two community blocks was

207 mimicked through the combination of the presence / absence of 4 factors: predator/IG-  
208 predator, IG-prey, herbivore and alternative food. This resulted in the community modules

209 (Sensu Holt 1997) depicted in the X-axis of figures 1 and 2. These modules were: <sup>1. //</sup> Trophic  
210 chain: either one *E. stipulatus* or *N. californicus* female was introduced in arenas containing

211 10 females of *O. perseae* (treatment # 1 in Figs 1 and 2). Arenas containing either one *E.*  
212 *stipulatus* or one *N. californicus* female without herbivores (treatment # 2), and containing

213 10 *O. perseae* females without predators (treatment # 3) were done as controls for predator  
214 oviposition rate and prey natural mortality, respectively. <sup>2. //</sup> Apparent competition: arenas

215 consisted of one female of either *E. stipulatus* or *N. californicus*, 10 females of *O. perseae*,  
216 and pollen of *C. edulis* supplied *ad libitum* (treatment # 4). Similar arenas but without the

217 herbivores (treatment # 5) were made as controls for oviposition rates of predators on  
218 pollen only, and without the IG-predator (treatment # 6) to assess potential effects of pollen

219 on the survival of the herbivore. <sup>3. //</sup> Intraguild predation: Because IGP is usually associated with  
220 size differences between contestants, IG-predators and IG-prey consisted of adult females

221 and heterospecific juveniles, respectively. Arenas consisted of 10 *O. perseae* females, either  
222 one *E. stipulatus* or *N. californicus* female, acting as the IG-predators, and 10 heterospecific

223 juveniles, acting as the IG-prey (treatment # 7). <sup>4. //</sup> Additionally, control treatments were done  
224 to evaluate: the predation/mortality rate of *O. perseae* in the presence of IG-prey but not of

225 IG-predator (treatment # 8); the mortality rate of IG-prey in the absence of both IG-predator  
226 and prey (treatment # 9), and in the presence of IG-predator but not of herbivores

227 (treatment # 10). <sup>4. //</sup> Intraguild predation - Apparent competition: Arenas consisted of 10 *O.*  
228 *perseae* females, either one *E. stipulatus* or *N. californicus* female, acting as the IG-

229 predators, 10 heterospecific juveniles, acting as the IG-prey, and pollen of *C. edulis* as  
230 alternative food, supplied *ad libitum* (treatment # 11). Similar arenas to those above but i)

231 without IG-predators (treatment # 12), ii) without herbivores (treatment # 13), and iii)  
232 without IG-predators and herbivores (treatment # 14), were done to evaluate predation of

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233 IG-prey on the herbivore in the presence of pollen, predation of IG-predators on IG-prey in  
234 the presence of pollen, and mortality of IG-prey in the presence of pollen, respectively.

235 Twenty-four hours later, the number of dead herbivores/IG-prey  
236 (predation/mortality rate), and the number of eggs laid by predators/IG-predators  
237 (oviposition rate), were recorded. Each treatment was replicated between 10 to 18 times.

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238

### 239 *Data analyses*

240 Analyses were done separately for communities where either *E. stipulatus* or *N. californicus*  
241 acted as the top-predator. Predation rates on herbivores and on IG-prey, and rates of

242 oviposition of IG-predators, were analysed using Generalized Lineal Models (GLM) assuming

243 a Poisson distribution as the distribution of data is expected to be skewed towards low

244 rather than high numbers, and a Log-link function as no overdispersion of the data was

hyphen

245 detected. All the analyses were 3 full-factorial designs; the main factors that were included

246 in each analysis are explained below. We followed a backward elimination procedure as

247 follows: when the interaction among the three explanatory variables was not significant

248 (and the model had higher AIC), this interaction was removed from the model.

249 Subsequently, the same procedure was followed for second-order interactions. GLM

250 analyses were performed using the computer environment R (R Core Team 2017). After

251 significance of general models, additional software (package "contrast") was used to

252 perform planned comparisons to address specific questions (see Results). When specific sets

253 of data were used in multiple comparisons, their significance was corrected using the

254 sequential Bonferroni method.

255 Mortality of *O. perseae* females was analysed using data from treatments containing

256 this species. The model included the presence/absence of IG-predators, IG-prey and

257 alternative food as explanatory variables, as well as their interactions.

258 IG-prey mortality was analysed using data from treatments containing IG-prey (i.e.

259 predator juveniles). The full model included the presence/absence of the IG-predator, the

260 herbivore and alternative food as explanatory variables, as well as their interactions.

261 Oviposition rates were analysed using data from treatments containing IG-predators

262 (i.e., adult predators). The full model included the presence/absence of the herbivore, the IG

263 prey and alternative food as explanatory variables, as well as their interactions.

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265 **Results**

266 *Communities with E. stipulatus as the (IG-)predator*

267 Mortality rates of the herbivore were significantly affected by the interaction between the  
268 presence of IG-predator<sub>ES</sub> and IG-prey<sub>NC</sub> and between the presence of IG-prey<sub>NC</sub> and pollen  
269 (Table 1a). Indeed, <sup>more</sup> prey died ~~more~~ when IG-prey<sub>NC</sub> were together with the IG-predator<sub>ES</sub>  
270 than when the IG-predator<sub>ES</sub> was alone (Fig 1a, compare bar 1 to 7), but not <sup>more</sup> than when the  
271 IG-prey<sub>NC</sub> was alone (Fig 1a, compare bar 8 to bar 7). Also, the presence of pollen reduced  
272 herbivore mortality rates, but only in the absence of IG-prey<sub>NC</sub> (Fig 1a, compare bars 4 and 6  
273 to bars 11 and 12).

274 Mortality rates of the IG-prey<sub>NC</sub> were affected by all the double interactions except  
275 that between the herbivore and pollen (Table 1b). Indeed, the presence of the IG-predator<sub>ES</sub>  
276 increased the mortality of IG-prey<sub>NC</sub>, but only in the absence of pollen (Fig 1b, compare bars  
277 7 and 10 to bars 11 and 13). Similarly, the presence of herbivores reduced mortality rates of  
278 IG-prey<sub>NC</sub> when IG-predators<sub>ES</sub> were absent (Fig1b, compare bar 8 to 9), but not when they  
279 were present (Fig1b, compare bar 7 to 10).

280 Planned comparisons revealed a) that IG-predators<sub>ES</sub> preyed on *O. perseae* ( $t_{81} =$   
281  $2.74, P = 0.0076$ ; Fig 1a, compare bars 1 and 3) and marginally on the IG-prey<sub>NC</sub> ( $t_{80} = -2.01,$   
282  $P = 0.048$ , not significant after Bonferroni correction; Fig 1b, compare bar 9 to 10) when  
283 each prey was offered alone; b) that adding IG-prey<sub>NC</sub> increased mortality of *O. perseae* ( $t_{81}$   
284  $= -2.26, P = 0.026$ ; Fig 1a, compare bar 1 to 7), but adding *O. perseae* did not influence  
285 mortality of the IG-prey<sub>NC</sub> ( $t_{80} = -0.31, P = 0.755$ ; Fig 1b, compare bar 10 to 7); c) that the  
286 presence of pollen yielded a drastic reduction in predation of IG-predators<sub>ES</sub> on both the  
287 herbivore ( $t_{81} = 2.99, P = 0.0037$ ; Fig 1a, compare bar 1 to 4) and the IG-prey<sub>NC</sub> ( $t_{80} = 3.91, P$   
288  $\ll 0.001$ ; Fig 1b, compare bar 10 to 13); d) that when both prey were available, the  
289 presence of pollen did not affect herbivore mortality ( $t_{81} = 0.88, P = 0.379$ ; Fig 1a, compare  
290 bar 7 to 11), but did lead to lower IG-prey<sub>NC</sub> mortality ( $t_{80} = 3.58, P \ll 0.001$ ; Fig 1b,  
291 compare bar 7 to 11).

292 Oviposition rates of IG-predators<sub>ES</sub> were only affected by the presence of pollen  
293 (main factor Pollen, Table 1c). However, further planned comparisons revealed that while  
294 feeding on the herbivore yielded <sup>stimulated</sup> ~~some~~ egg production ( $t_{96} = 2.19, P = 0.021$ ; Fig 1c, compare  
295 bar 1 to 2), feeding on IG-prey<sub>NC</sub> did not ( $t_{96} = -1.13, P = 0.259$ ; Fig 1c, compare bar 10 to 2).

296

297 *Communities with N. californicus as the (IG-)predator*

298 Herbivore mortality was affected only by the interaction between IG-predator<sub>NC</sub> and IG-  
299 prey<sub>ES</sub> (Table 2a). Indeed, mortality of herbivores was drastically affected by the presence of  
300 IG-predators<sub>NC</sub> (Fig 2a, compare bar 1 to 3), but this effect was lesser in the presence of IG-  
301 prey<sub>ES</sub> (Fig 2a, compare bar 1 to 7). Mortality of IG-prey<sub>ES</sub> was only affected by the presence  
302 of pollen (Table 2b).

303 Paired comparisons revealed that a) IG-predators<sub>NC</sub> preyed on *O. perseae* ( $t_{90} = 3.32$ ,  
304  $P = 0.013$ ; Fig 2a, compare bar 3 to 1) but not on IG-prey<sub>ES</sub> ( $t_{86} = -1.35$ ,  $P = 0.182$ ; Fig 2b,  
305 compare bar 9 to 10), when each prey was offered alone; b) adding IG-prey<sub>ES</sub> reduced  
306 mortality of *O. perseae* ( $t_{90} = 2.56$ ,  $P = 0.012$ ; Fig 2a, compare bar 1 to 7), but adding *O.*  
307 *perseae* did not change mortality of the IG-prey<sub>ES</sub> ( $t_{86} = -0.93$ ,  $P = 0.353$ ; Fig 2b, compare bar  
308 10 to 7); c) the presence of pollen did not affect mortality of either *O. perseae* ( $t_{90} = -0.43$ ,  $P$   
309  $= 0.669$ ; Fig 2a, compare bar 1 to 4) or the IG-prey<sub>ES</sub> ( $t_{86} = 1.80$ ,  $P = 0.075$ ; Fig 2b, compare  
310 bar 10 to 13); d) when both types of prey were available, the presence of pollen led to a  
311 significant increase in mortality of *O. perseae* ( $t_{90} = -3.65$ ,  $P \ll 0.001$ ; Fig 2a, compare bar 7  
312 to 11), but a significant decrease of mortality in IG-prey<sub>ES</sub> ( $t_{86} = 2.04$ ,  $P = 0.044$ ; Fig 2b,  
313 compare bar 7 to 11).

314 Oviposition rates of IG-predators<sub>NC</sub> were affected by the main factor Herbivore and  
315 the interaction between the IG-prey<sub>ES</sub> and pollen (Table 2c). Indeed, paired comparisons  
316 revealed that e) eggs were produced when IG-predators<sub>NC</sub> were offered the herbivore alone  
317 ( $t_{104} = 2.45$ ,  $P = 0.016$ ; Fig 2c, compare bar 1 to 2), but not when they were on arenas with  
318 either the IG-prey<sub>ES</sub> ( $t_{104} = 0.01$ ,  $P = 0.992$ ; Fig 2c, compare bar 10 to 2) or pollen ( $t_{104} = -0.15$ ,  
319  $P = 0.884$ ; Fig 2c, compare bar 5 to 2) alone. Moreover, in the presence of the herbivore,  
320 rates of oviposition were not influenced by the presence of pollen ( $t_{104} = -0.93$ ,  $P = 0.352$ ; Fig  
321 2c, compare bar 1 to 4), but dramatically decreased in the presence of the IG-prey<sub>ES</sub> ( $t_{104} =$   
322  $2.39$ ,  $P = 0.019$ ; Fig 2c, compare bar 1 to 7). However, when pollen was added to the system  
323 with both prey types, IG-predators<sub>NC</sub> resumed oviposition to its maximum ( $t_{104} = -2.36$ ,  $P =$   
324  $0.020$ ; Fig 2c, compare bar 7 to 11).

325

## 326 Discussion

327 In this study, we tested the effect of community structure on the realized interactions  
328 within a community of predatory and herbivorous mites. Because in our system the

Sub-headings

329 intraguild predator is the largest individual within a pair (as in most systems), we created  
330 communities in which adults (IG-predators) belonged to one species and juveniles (IG-prey)  
331 to the other, then inverted the species-stage identity in another set of communities. We  
332 then measured predation and oviposition in communities with all possible combinations of  
333 the presence of shared prey, the IG-prey, the IG-predator and <sup>a</sup> alternative food. We show <sup>resource.</sup>  
334 that adding species to a community increases the number of potential trophic interactions,  
335 but not necessarily their occurrence. Indeed, despite the potential for module  
336 configurations of communities with apparent competition and intraguild predation, all  
337 modules could be described by linear food chains (Box 1C). <sup>in our study system.</sup> Add disclaimer.

fense  
ok  
here.

338 <sup>the</sup> In trophic chain configurations, although *N. californicus* killed more *O. perseae*  
339 females per day than *E. stipulatus*, oviposition rates were similar between predators. This is  
340 in line with the finding that *E. stipulatus* can only forage on mobile *O. perseae* mites when  
341 they wander outside nests, whereas *N. californicus* can penetrate inside nests and forage on  
342 all the individuals residing within (González-Fernández *et al.* 2009). This suggests that *E.*  
343 *stipulatus* is the most efficient predator converting prey into eggs, but that *N. californicus* is  
344 more efficient at reducing herbivore populations. Which of these strategies is best for  
345 biological control will depend on the ecological condition: if <sup>outbreaks</sup> bursts of prey are confined in  
346 time, it may be more efficient to select a biocontrol agent that feeds more, as in  
347 “inundative” biocontrol strategies, whereas controlling and keeping resident populations at  
348 low levels may be best achieved with a predator with a strong numerical response, as in  
349 “innoculative” biocontrol strategies (Van Driesche *et al.* 2007). Moreover, unlike *N.*  
350 *californicus*, *E. stipulatus* fed and oviposited on pollen. This may allow the latter to remain in  
351 the field for longer periods, as actually observed in field surveys (González-Fernández *et al.*  
352 2009). Such <sup>partitioning</sup> temporal segregation may facilitate the presence of the two predators in the  
353 same fields (Otto *et al.* 2008).

makes  
specific to  
this study.

strange  
phrase

354 Our results also revealed asymmetry in the intraguild predation between *E.*  
355 *stipulatus* and *N. californicus*, with adults of the former preying upon juveniles of the latter,  
356 but not the reverse. Because *N. californicus* is likely the best competitor for the shared prey  
357 (González-Fernández *et al.* 2009), coexistence between predators is thus possible in this  
358 system (Holt & Polis 1997). Yet, the simultaneous presence of the two predators is likely to  
359 have little effect upon the densities of the shared prey. Indeed, whereas adding  
360 *N. californicus* adult intraguild predators to an arena with *E. stipulatus* juveniles results in

niche  
partitioning

Justification of discussion? Probably ok.

361 higher shared prey densities as compared to the presence of *N. californicus* adults alone  
362 with the shared prey, the reverse is not true when adding adult *E. stipulatus* to an arena  
363 with juveniles *N. californicus*. Thus, the net effect of these interactions upon prey density is  
364 probably negligible. This is corroborated by field studies (Montserrat *et al.* 2013). However,  
365 the presence of alternative food (i.e. pollen) contributed to reduce trophic interactions  
366 between predator species resulting in community configurations that could enhance pest  
367 control. Thus, supplying alternative and preferred food to the IG-predator is probably  
368 detrimental to populations of *O. perseae*. Again, this finding is in line with field observations  
369 (Montserrat *et al.* 2013).

370 Food web ecology predicts that species of the highest trophic levels engage in  
371 trophic interactions on more than one food source when these are available. Here, we show  
372 that *E. stipulatus* acting as intraguild predators feeds on the herbivore, *O. perseae*, on the  
373 intraguild prey, *N. californicus*, and on the alternative food, pollen, when each of these are  
374 presented alone. However, in the presence of pollen *E. stipulatus* reduces predation rates  
375 on both prey species. This may be explained by the fact that pollen is the most profitable  
376 food for this species, as found here and in other studies (Ferragut *et al.* 1987; McMurtry &  
377 Croft 1997; Bouras & Papadoulis 2005; González-Fernández *et al.* 2009). Similarly, *N.*  
378 *californicus* adults and juveniles ceased foraging on other food sources in presence of the  
379 herbivores. These results suggest that realized interactions hinge on the presence of the  
380 most profitable food source. In presence of the optimal food source for each of the two  
381 secondary consumers, communities tended to ~~melt down to become~~ be reduced to two simple trophic  
382 chains. Indeed, in the most complex communities studied here, with all 5 species present,  
383 the presence of the optimal food originated the split of the community into two trophic  
384 chains, one with *E. stipulatus* feeding on pollen and the other with *N. californicus* feeding on  
385 the herbivore (Box 1 d), compare d.1.1. and d.1.2. with d.2.1. and d.2.2.).

386 Another factor that contributed to the linearization of the food web was that, when  
387 both the IG-prey and the shared prey were together, IG-predators<sub>ES</sub> preyed mainly on the  
388 IG-prey. Indeed, mortality of *O. perseae* in presence of the IG-prey, *N. californicus*, was not  
389 affected by the presence of the IG-predator *E. stipulatus*. Furthermore, mortality of IG-  
390 prey<sub>NC</sub> was significantly higher in treatments with presence of the IG-predator, compared to  
391 the control without them. This suggests that mortality in the herbivore was mainly inflicted  
392 by the IG-prey, *N. californicus*, and that the IG-predator *E. stipulatus* preyed preferentially

Optimal foraging theory?

source  
by optimal foraging theory

increased modularity  
stable but not necessarily best functioning  
also modularity

393 | on the IG-prey *N. californicus*. This could be explained by *E. stipulatus* having no access to *O.*  
394 | *perseae* eggs or females located inside the nests (Montserrat *et al.* 2008a; González-  
395 | Fernández *et al.* 2009), which leads to higher encounter rates between *E. stipulatus* and *N.*  
396 | *californicus* than between *E. stipulatus* and *O. perseae*. Indeed, *E. stipulatus* forages only on  
397 | mobile stages that wander outside nests (Montserrat *et al.* 2008a; González-Fernández *et al.*  
398 | 2009). *Neoseiulus californicus*, however, can penetrate *O. perseae* nests, and thus may feed  
399 | on them. Therefore, the realized community was that of a 4-level trophic chain (Box 1,  
400 | c.2.1.). In the other community block, when *N. californicus* acted as the IG-predator,  
401 | mortality of *O. perseae* females was similar in all communities with the IG-prey *E. stipulatus*  
402 | present, irrespective of the presence of IG-predators<sub>NC</sub>. Furthermore, mortality of IG-prey<sub>ES</sub>  
403 | did not differ between treatments with and without the IG-predator<sub>NC</sub>, indicating that *N.*  
404 | *californicus* females did not forage on *E. stipulatus* juveniles. These results suggest that, in  
405 | presence of IG-prey (juveniles of *E. stipulatus*), the IG-predator<sub>NC</sub> ceased to forage on either  
406 | herbivore or IG-prey, likely because IG-prey<sub>ES</sub> interferes with the foraging activities of IG-  
407 | predators<sub>NC</sub>. Thus, the realized community was that of a trophic chain composed of the IG-  
408 | prey, the herbivore and the plant, with the IG-predator not interacting at all (Box 1, c.2.2.).  
409 | This can be explained by IG-predators<sub>NC</sub> avoiding foraging on a patch where its offspring  
410 | (future) IG-predator is also there. In line with this, Abad-Moyano *et al.* (2010) reported that  
411 | the presence of *E. stipulatus* immatures exerted non-lethal IG-effects on *N. californicus*  
412 | females, causing daily oviposition to decrease over time despite the availability of the  
413 | shared prey was kept constant. In any case, here, the trophic links are again linear, with *N.*  
414 | *californicus* being excluded from the realized community (Box 1, c.2.2.). Together, our  
415 | results show that none of the complex communities was actually realized, they were all  
416 | trophic chains.

417 | By combining data of mortality and oviposition at different community structures,  
418 | we could define who eats whom in a simple food web. Although this approach is very  
419 | powerful, it does have its limitations. Indeed, it assumes additive effects of conversion  
420 | efficiencies of pairwise interactions. For example, if feeding on a prey item allows predators  
421 | to better convert the food provided by another prey, this cannot be detected in our  
422 | approach (i.e., indirect effects on conversion efficiency). Furthermore, it may be largely  
423 | unfeasible to extend this approach to more complex food webs, although it is becoming  
424 | clear that we need to know how food is transformed into predator offspring in order to fully

transfer efficiencies

425 understand food webs in nature (Neutel & Thorne 2014). Indeed, such full-factorial studies  
426 are extremely rare in the literature (but see Schmitz & Sokol-Hessner 2002; Otto *et al.*  
427 2008). *If would be good to introduce connectance as*  
428 *It is becoming increasingly clear that connectance, that is, the number of realized*  
429 interactions in a food web, is generally much lower than the number of potential  
430 interactions (Beckerman *et al.* 2006). Identifying trophic links in food webs, however, is not  
431 a simple task. Molecular methods are useful to process field data and they deliver reliable  
432 information on who eats whom, but such tools *currently* only provide semi-quantitative estimates of  
433 predation, and they are expensive (Birkhofer *et al.* 2017). Another possible approach to  
434 measure connectance is by observations in the field (Dunne *et al.* 2002; Tylianakis *et al.*  
435 2007; Carnicer *et al.* 2009; Lazzaro *et al.* 2009; Plein *et al.* 2013; Baiser *et al.* 2016; Lemos-  
436 Costa *et al.* 2016). Although this approach allows including a high number of species in the  
437 observations, it suffers from two main shortfalls: (a) it is generally only possible to  
438 undertake it in systems with two trophic levels in which one are primary producers (but see  
439 Bukovinszky *et al.* 2008; Neutel & Thorne 2014), or in systems where trophic interactions  
440 are detectable long after the actual events, as in parasitoid/host interactions or via the  
441 analysis of gut contents; and (b) it does not account for how foraging on a given resource  
442 translates into consumer offspring (but see Bukovinszky *et al.* 2008; Vázquez *et al.* 2015).  
443 Observations in controlled experimental settings, in contrast, deliver quantitative estimates  
444 of predation rates and concomitant offspring production, especially when trophic links, and  
445 their strength, are estimated by confronting pairs of species. Alternatively, modelling  
446 complex systems provide relative estimates on interaction strengths that go beyond pair-  
447 wise interactions (Moya-Laraño *et al.* 2012; Moya-Laraño *et al.* 2014). Yet, one-on-one  
448 approaches may ignore emergent indirect effects of having several species together  
449 (Wootton 1994; Dambacher & Ramos-Jiliberto 2007). For instance, *Cancer productus*, a crab  
450 native to the Northwest Pacific, consumes equal amounts of native oysters and of invasive  
451 drill oysters when each type of prey is offered alone, but when they are offered together  
452 crabs interact with the native oyster species only (Grason & Miner 2012). Therefore, if  
453 trophic links are not evaluated in presence of all species in the community, one may reach  
454 erroneous conclusions on the strength of the interaction (Guzmán *et al.* 2016b; Fonseca *et al.*  
455 *al.* 2017) and overestimate connectance in food webs. We show that all *our experimental* communities ended  
456 up becoming a sum of one or more trophic chains (Box 1C). Thus, the fundamental trophic

*a measure of food web complexity first - then go into 428*

*ie plant pollinator networks*

*preference prey switching + optimal foraging*

19 **Abstract**

20 The mathematical exploration of small assemblages of interacting species (community  
21 modules) has proven key to understand emergent properties of ecological communities.

22 These models use differential equations to study pairwise relations between species.

23 However, as community modules become more complex, one may wonder whether all  
24 potential interactions are effectively realized. Here, we use community modules to

25 experimentally explore whether the number of trophic links among species increases as  
26 another aspect of complexity increases, i.e., the number of species that are known to feed

27 on each other in pair-wise trials. To this aim, we use a simple mite community present in  
28 avocado orchards (*Persea americana*), composed of two predators (*Euseius stipulatus* and

29 *Neoseiulus californicus*), one herbivore as shared prey (*Oligonychus perseae*), and pollen of  
30 *Carpobrotus edulis* as alternative food, with the potential for (intraguild) predation and

31 (apparent) competition to be expressed. Using a series of controls, we could assess whether  
32 the presence of one species affected the abundance of another, or its conversion of food

33 into offspring. We found that increasing the number of potential interactions did not result  
34 in more complex realized community modules. Instead, all communities were reduced to

35 one or two linear trophic chains. Our results show that trophic links assumed to occur when  
36 species are confronted in pairs do not necessarily occur when other components of the

37 community are present. Consequently, food-web complexity may be erroneously over-  
38 estimated in theoretical community modules that are parameterized based on pair-wise

39 interactions observed when alternative prey is absent. This suggests a  
40 need for empirical work to work in concert with

theoretical approaches to develop more realistic and predictive food-web models.



Elton 1927  
↓

## 41 Introduction

initially conceptualised

42 Community ecology has traditionally viewed trophic interactions as linear chains, with an  
43 upper level <sup>potentially</sup> controlling the densities of the level immediately below, <sup>thus</sup> generating a trophic  
44 cascade (Hairston *et al.* 1960; Oksanen *et al.* 1981; Carpenter *et al.* 1985). However, it is ~~now~~  
45 now accepted that most communities do not follow this pattern as organisms are imbedded  
46 in complex food webs, blurring the notion of a trophic guild and the notion that widespread  
47 omnivory <sup>might</sup> would destabilize food webs (Polis & Holt 1992; Polis & Strong 1996).

sensu  
trophic  
coherence

48 Food webs can be decomposed into "community modules" (i.e. "small number of  
49 species (e.g. three to six) linked in a specified structure of interactions, Holt 1997). Among  
50 those, intraguild predation (IGP), in which two consumers (the intraguild predator and the  
51 intraguild prey, hereafter IG-predator and IG-prey) not only compete for a shared resource  
52 but also engage in predator-prey interactions (Polis *et al.* 1989), and apparent competition,  
53 in which two non-competing prey share a common predator (Holt 1977; 1997), are the most  
54 common (Bascompte & Melián 2005).

Might be  
good to  
briefly  
explain why  
modules and  
motifs are  
similar.

55 Whether and how often species engage in intraguild predation or apparent  
56 competition strongly affects the long-term persistence (i.e. stability) of communities. Theory  
57 predicts that intraguild predation destabilizes communities because it reduces the  
58 parameter space where coexistence of IG-predator, IG-prey and shared prey is possible  
59 (Holt & Polis 1997) compared to that of trophic chain models (Oksanen *et al.* 1981). In most  
60 models with intraguild predation the possibility of 3-species persistence requires the IG-prey  
61 to be superior to IG-predators at exploitative competition for the shared resource (Holt  
62 1997; Mylius *et al.* 2001; Kondoh 2008, among others). Furthermore, the occurrence of  
63 intraguild predation leads to a less efficient control of the shared prey populations because  
64 the IG-prey's equilibrium abundance is expected to decline towards extinction with  
65 increasing productivity (Mylius *et al.* 2001). This is especially important in agricultural  
66 systems, inherently highly productive, in which the introduction of several biocontrol agents  
67 may in fact reduce pest control. Curiously, empirical studies, mostly stemming from such  
68 systems, show that variable effects of intraguild predation on populations of the shared  
69 prey (e.g., Rosenheim *et al.* 1995; Janssen *et al.* 2006; Vance-Chalcraft *et al.* 2007; Messelink  
70 & Janssen 2014).

defn  
Pimm  
1984  
temporal  
stability  
in  
community  
composition

71 Some factors may, however, reduce such instability by promoting species  
72 coexistence, which generally occurs when conditions under which predator-predator

73 interactions occur are constrained (reviewed in Novak 2013, appendix S1). For example, 3-  
74 species coexistence is enhanced if predators engage into intraguild predation only when  
75 competition for the shared prey is high (Křivan 2000), or the shared prey is less profitable  
76 than the intraguild prey (Křivan & Diehl 2005). Other studies suggest that the inclusion of  
77 habitat structure (Janssen *et al.* 2007), inducible defences (Kratina *et al.* 2010; Nakazawa *et*  
78 *al.* 2010) or temporal refuges (Amarasekare 2008) increases system stability, although this  
79 may depend on which species use refuges (Liu & Zhang 2013). Moreover, stage structure in  
80 the intraguild prey promotes stability, either by providing a stage refuge (Mylius *et al.* 2001;  
81 Rudolf & Armstrong 2008) or by inducing ontogenetic niche shifts in the predator (Hin *et al.*  
82 2011). However, in all cases, the models still predict that overall stability is lower than that  
83 of a simple trophic chain. This lack of stability is corroborated by empirical laboratory  
84 studies (Diehl & Feiße 2000; Montserrat *et al.* 2008b), but runs counter <sup>to</sup> the ubiquity of  
85 intraguild predation and trophic level omnivory in natural systems (Bascompte & Melián  
86 2005; Gagnon *et al.* 2011).

IGP

dimensional  
eg. Donohue  
*et al.* 2010  
Ecol. Letters

see  
earlier  
comments.

^

87 Discrepancies between theory of IGP and <sup>empirical</sup> data suggest that some assumptions of  
88 theoretical models are not met in natural systems. In an effort to bring IGP models closer to  
89 real systems, while maintaining mathematical tractability, researchers have tested how the  
90 incorporation of an alternative food source affected <sup>stability</sup> stability (Heithaus 2001; Daugherty *et*  
91 *al.* 2007; Holt & Huxel 2007; Rudolf 2007). The general prediction is that providing  
92 alternative food to the intraguild prey leads to wider parameter regions of species  
93 coexistence (Daugherty *et al.* 2007; Holt & Huxel 2007), even if competitive superiority of IG-  
94 prey is precluded (Faria & Costa 2010). Instead, alternative food for the intraguild predator  
95 destabilizes the community (Daugherty *et al.* 2007; Holt & Huxel 2007). However, in the  
96 latter case, if the quality of the alternative food is high enough, then the intraguild predator  
97 <sup>may</sup> switches to feeding on the alternative food, whereas the intraguild prey feeds on the shared  
98 prey (ibid.). This again promotes coexistence by bringing the community structure closer to  
99 two linear food chains.

see  
comment.

^

100 the prevailing outcome of IGP theory is, thus, that domains for persistence of  
101 communities with IGP increase when the strength of intraguild predation decreases. Indeed,  
102 weak interactions have long been recognized to stabilize ecosystems, particularly.  
103 Indeed, by dampening oscillations between consumers and resources, these interactions  
104 decrease the probability of species extinctions (McCann *et al.* 1998), this promoting

good.  
Weak  
interactions  
thereby

Worth defining here? (i.e.) #ind consumed per hour or what?

105 community persistence (May 1972; Pimm & Lawton 1978; Paine 1992; McCann *et al.* 1998;  
106 Emmerson & Yearsley 2004; Neutel *et al.* 2007; Gellner & McCann 2012; 2016). ~~107~~ here we  
107 address whether the fundamental niches of species (with all their potential interactions) are  
108 always realized. Specifically, we explore how pairwise trophic interactions between species  
109 are modified by the inclusion of other species in a simple community. We focus on  
110 predation rate as it is an excellent proxy for trophic interaction strength, used both ~~in~~  
111 modelling (e.g. the equivalent to the "catching efficiencies" in Kuijper *et al.* 2003) and in  
112 empirical work (Wootton & Emmerson 2005; Novak & Wootton 2010; Novak 2013).  
113 Measurements of other relevant non-trophic interactions, such as competition, would  
114 require experiments at the population and community level that are beyond the scope of  
115 this manuscript. Our ~~baseline~~ <sup>core</sup> hypothesis ~~is~~ <sup>was</sup> that increasing the number of species that are  
116 known to interact when no alternative food is available will increase the number of realized  
117 links in the more complex community (Box 1A). We mimicked different community modules  
118 (Sensu Holt 1997) of increasing complexity using a community composed of two predatory  
119 mite species as intraguild predators (*Euseius stipulatus* and *Neoseiulus californicus*, Acari:  
120 Phytoseiidae), one species of herbivore mite as the shared prey (*Oligonychus perseae*, Acari:  
121 Tetranychidae), and pollen (of several anemophilous species) as alternative food (González-  
122 Fernández *et al.* 2009), all of which occur in the leaves of crops of avocado plants (*Persea*  
123 *americana*) in Southeastern Spain. Previous pairwise experimental designs have shown that  
124 the interaction between *N. californicus* and *O. perseae* is stronger (i.e. predation rates are  
125 higher) ~~than that between *E. stipulatus* and this same prey~~ (González-Fernández *et al.*  
126 2009). Moreover, pollen is an optimal food source for *E. stipulatus* but not for *N. californicus*  
127 (Ferragut *et al.* 1987; González-Fernández *et al.* 2009). Finally, *E. stipulatus* and *N.*  
128 *californicus* engage in size-dependent predator-prey interactions (Abad-Moyano *et al.*  
129 2010). This knowledge was used to build predictions on realized trophic links occurring in  
130 this system across community modules of increasing complexity (Box 1B). Specifically, we  
131 predict that: i) in "trophic chain" community configurations, both predator species will  
132 interact with the herbivore (Box 1B, a.1.1. and a.1.2.); ii) in "apparent competition"  
133 community configurations, only *E. stipulatus* will interact with both the herbivore and pollen  
134 (Box 1B, b.1.1. and b.1.2.); iii) in "intraguild predation" community configurations, both IG-  
135 predator species will interact with the IG-prey and the herbivore (Box 1B, c.1.1. and c.1.2.);  
136 and iv) in "Intraguild predation and apparent competition" community configurations, only

Ecological

research

Eltonian niche  
Could be worth mentioning predator vis a vis Respower #2

hence New Paragraph

brackets + comma  
specify

hence

137 adults and juveniles of *E. stipulatus* will establish trophic links with pollen (Box 1B, d.1.1. and  
138 d.1.2.). These predictions were then tested through a series of experimental treatments to  
139 assess which interactions were realized within each community module, by measuring IG-  
140 prey/herbivore mortality and how predation translates into predator fecundity as a result of  
141 these interactions. Specifically, we examined a) whether (IG)predators feed on each prey  
142 type; b) whether predation of (IG)predators on one prey type is affected by the presence of  
143 the other; c) whether predation of (IG)predators on both prey, and of IG-prey on the  
144 herbivore, is affected by the presence of alternative food; d) whether the presence of  
145 alternative food affects predation of (IG)predators on the two types of prey when they are  
146 together; e) number of eggs produced by (IG)predators when feeding on each prey type;  
147 and f) whether egg-production is additive when (IG)predators have more than one food  
148 type available.

Consumption of prey

Could hypenate (IG) predators (i.e., no.)

the reproductive output of

→ this could be difficult to establish if it equals more food (i.e., same result might be observed with more of one prey)

## 151 Material and Methods

152 All cultures and experiments were done in a climate chamber at  $25 \pm 1^\circ\text{C}$ ,  $65 \pm 5\%$  RH and  
153 16:8h L:D (Light:Dark).

### 154 Mite cultures

155 Cultures of the predatory mite *E. stipulatus* were started in 2007 from ca. 300 individuals  
156 collected from avocado trees located in the experimental station of "La Mayora". Rearing  
157 units consisted of three bean plants (*Phaseolus vulgaris* L.) with 6-10 leaves, positioned  
158 vertically, with the stems in contact with sponges (ca. 30 x 20 x 5 cm) covered with cotton  
159 wool and a plastic sheet (27 x 17 cm), and placed inside water-containing trays (8 L, 42.5 x  
160 26 x 7.5 cm). The plant roots were in contact with the water, and the aerial parts were  
161 touching each other, forming a tent-like three-dimensional structure, where individuals  
162 could easily walk from one plant to the other. Cotton threads were placed on the leaves, to  
163 serve as oviposition sites for the females. Mites were fed *ad libitum* twice a week with  
164 pollen of *Carpobrotus edulis* (cat's claw) spread on leaves with a fine brush. *Euseius*  
165 *stipulatus* is able to develop and reproduce on this food source (Ferragut *et al.* 1987). Every  
166 three weeks, new rearings were made by transferring, leaves with mites and the cotton  
167 threads filled with eggs to a new unit. The culture was found to be contaminated a few  
168 times with *Tyrophagus* spp., a detritivorous mite species. In such instances, instead of

169 moving entire leaves, adult *E. stipulatus* females (ca. 300) were collected individually and  
170 transferred to the new rearing unit.

171 The *N. californicus* population was obtained from Koppert Biological Systems S.L. in  
172 bottles of 1000 individuals (Spical®). Colonies were kept on detached bean leaves infested  
173 with *Tetranychus urticae* that were placed on top of inverted flower-pots (20 cm Ø) inside  
174 water-containing trays.

175 The herbivore *Oligonychus perseae* was not maintained in a laboratory culture due  
176 to technical difficulties in preserving detached avocado leaves. They were thus collected  
177 from the field on a regular basis from avocado orchards located in the experimental station  
178 of "La Mayora".

179 Pollen of *C. edulis* was obtained from flowers collected in the experimental station.  
180 Stamens dried in a stove at 37°C for 48h, then sieved (350 µm).

181

#### 182 *Community modules*

183 Experimental arenas to test the outcome of community modules have been described in  
184 detail in Guzmán *et al.* (2016a). Briefly, a hole (6.5 cm Ø) was cut in a petri dish (9 cm Ø),  
185 turned upside down and <sup>then</sup> filled with an avocado leaf disc (7.5 cm Ø), <sup>with</sup> the borders <sup>were</sup> glued  
186 to a clay ring. Inside the petri dish, wet cotton wool ensured enough humidity to keep  
187 leaves turgid. Petri dishes were then sealed with parafilm®. To prevent individuals from  
188 escaping, a ring of Tanglefoot® was applied along the outer margin of the leaf disc. Cohorts  
189 of *E. stipulatus* were made by transferring with a fine brush 400 eggs from the rearings to 2-  
190 3 bean leaves placed on top of sponges (30 x 20 x 5 cm, approx.) covered with cotton wool,  
191 inside water-containing trays (3.5 L), and with pollen of *C. edulis* as food. Cohorts of *N.*  
192 californicus were made by placing 100 females during 48 h on 2-3 bean leaves infested with  
193 *Tetranychus urticae* in containers similar to those used for the cultures. 10-14 days after egg  
194 hatching, gravid predator females were randomly taken from these cohorts, and starved for  
195 16 h in experimental containers similar to those above. Starvation was done to standardize  
196 hunger among individuals, and to ensure that egg production in tested females was not  
197 obtained from food ingested prior to the experiment. Predator juveniles (2-3 days old since  
198 hatching) were taken from the cohorts when needed. Arenas containing the herbivore were  
199 done as follows: Ten females of *O. perseae* were let to build nests and lay eggs on  
200 experimental arenas during 4 days. The number of nests and eggs per nest on each arena

201 was counted at the onset of the experiment. Pollen in arenas assigned to treatments with  
202 alternative food was supplied *ad libitum*, using a fine brush.

203 We performed experiments using two 'community blocks', depending on the identity  
204 of the top predator (*N. californicus* or *E. stipulatus*). Throughout the text, the identity of  
205 (IG)-predator and (IG)-prey will be indicated using the subscripts "ES" for *E. stipulatus* and  
206 "NC" for *N. californicus*. Increased complexity in each of the two community blocks was

207 mimicked through the combination of the presence / absence of 4 factors: predator/IG-  
208 predator, IG-prey, herbivore and alternative food. This resulted in the community modules  
209 (Sensu Holt 1997) depicted in the X-axis of figures 1 and 2. These modules were: <sup>1. //</sup> Trophic

210 chain: either one *E. stipulatus* or *N. californicus* female was introduced in arenas containing  
211 10 females of *O. perseae* (treatment # 1 in Figs 1 and 2). Arenas containing either one *E.*  
212 *stipulatus* or one *N. californicus* female without herbivores (treatment # 2), and containing  
213 10 *O. perseae* females without predators (treatment # 3) were done as controls for predator

214 oviposition rate and prey natural mortality, respectively. <sup>2. //</sup> Apparent competition: arenas  
215 consisted of one female of either *E. stipulatus* or *N. californicus*, 10 females of *O. perseae*,  
216 and pollen of *C. edulis* supplied *ad libitum* (treatment # 4). Similar arenas but without the  
217 herbivores (treatment # 5) were made as controls for oviposition rates of predators on

218 pollen only, and without the IG-predator (treatment # 6) to assess potential effects of pollen  
219 on the survival of the herbivore. <sup>3. //</sup> Intraguild predation: Because IGP is usually associated with  
220 size differences between contestants, IG-predators and IG-prey consisted of adult females  
221 and heterospecific juveniles, respectively. Arenas consisted of 10 *O. perseae* females, either

222 one *E. stipulatus* or *N. californicus* female, acting as the IG-predators, and 10 heterospecific  
223 juveniles, acting as the IG-prey (treatment # 7). Additionally, control treatments were done  
224 to evaluate: the predation/mortality rate of *O. perseae* in the presence of IG-prey but not of

225 IG-predator (treatment # 8); the mortality rate of IG-prey in the absence of both IG-predator  
226 and prey (treatment # 9), and in the presence of IG-predator but not of herbivores  
227 (treatment # 10). <sup>4. //</sup> Intraguild predation - Apparent competition: Arenas consisted of 10 *O.*  
228 *perseae* females, either one *E. stipulatus* or *N. californicus* female, acting as the IG-

229 predators, 10 heterospecific juveniles, acting as the IG-prey, and pollen of *C. edulis* as  
230 alternative food, supplied *ad libitum* (treatment # 11). Similar arenas to those above but i)  
231 without IG-predators (treatment # 12), ii) without herbivores (treatment # 13), and iii)  
232 without IG-predators and herbivores (treatment # 14), were done to evaluate predation of

break  
out  
into numbers  
1. Trophic chain  
2. etc...  
make  
text less  
dense

New  
Paragraph

233 IG-prey on the herbivore in the presence of pollen, predation of IG-predators on IG-prey in  
234 the presence of pollen, and mortality of IG-prey in the presence of pollen, respectively.

235 Twenty-four hours later, the number of dead herbivores/IG-prey  
236 (predation/mortality rate), and the number of eggs laid by predators/IG-predators  
237 (oviposition rate) were recorded. Each treatment was replicated between 10 to 18 times.

no comma

### 239 Data analyses

240 Analyses were done separately for communities where either *E. stipulatus* or *N. californicus*  
241 acted as the top-predator. Predation rates on herbivores and on IG-prey, and rates of  
242 oviposition of IG-predators, were analysed using Generalized Lineal Models (GLM) assuming  
243 a Poisson distribution as the distribution of data is expected to be skewed towards low  
244 rather than high numbers, and a Log-link function as no overdispersion of the data was  
245 detected. All the analyses were 3 full-factorial designs; the main factors that were included  
246 in each analysis are explained below. We followed a backward elimination procedure as  
247 follows: when the interaction among the three explanatory variables was not significant  
248 (and the model had higher AIC), this interaction was removed from the model.  
249 Subsequently, the same procedure was followed for second-order interactions. GLM  
250 analyses were performed using the computer environment R (R Core Team 2017). After  
251 significance of general models, additional software (package "contrast") was used to  
252 perform planned comparisons to address specific questions (see Results). When specific sets  
253 of data were used in multiple comparisons, their significance was corrected using the  
254 sequential Bonferroni method.

hyphen

what not AIC?

hyphen

255 Mortality of *O. perseae* females was analysed using data from treatments containing  
256 this species. The model included the presence/absence of IG-predators, IG-prey and  
257 alternative food as explanatory variables, as well as their interactions.

258 IG-prey mortality was analysed using data from treatments containing IG-prey (i.e.  
259 predator juveniles). The full model included the presence/absence of the IG-predator, the  
260 herbivore and alternative food as explanatory variables, as well as their interactions.

261 Oviposition rates were analysed using data from treatments containing IG-predators  
262 (i.e., adult predators). The full model included the presence/absence of the herbivore, the IG  
263 prey and alternative food as explanatory variables, as well as their interactions.

comma

264

265 **Results**

266 *Communities with E. stipulatus as the (IG-)predator*

267 Mortality rates of the herbivore were significantly affected by the interaction between the  
268 presence of IG-predator<sub>ES</sub> and IG-prey<sub>NC</sub> and between the presence of IG-prey<sub>NC</sub> and pollen  
269 (Table 1a). Indeed, <sup>more</sup> prey died <sup>all</sup> when IG-prey<sub>NC</sub> were together with the IG-predator<sub>ES</sub>  
270 than when the IG-predator<sub>ES</sub> was alone (Fig 1a, compare bar 1 to 7), but not <sup>more</sup> than when the  
271 IG-prey<sub>NC</sub> was alone (Fig 1a, compare bar 8 to bar 7). Also, the presence of pollen reduced  
272 herbivore mortality rates, but only in the absence of IG-prey<sub>NC</sub> (Fig 1a, compare bars 4 and 6  
273 to bars 11 and 12).

274 Mortality rates of the IG-prey<sub>NC</sub> were affected by all the double interactions except  
275 that between the herbivore and pollen (Table 1b). Indeed, the presence of the IG-predator<sub>ES</sub>  
276 increased the mortality of IG-prey<sub>NC</sub>, but only in the absence of pollen (Fig 1b, compare bars  
277 7 and 10 to bars 11 and 13). Similarly, the presence of herbivores reduced mortality rates of  
278 IG-prey<sub>NC</sub> when IG-predators<sub>ES</sub> were absent (Fig 1b, compare bar 8 to 9), but not when they  
279 were present (Fig 1b, compare bar 7 to 10).

280 Planned comparisons revealed a) that IG-predators<sub>ES</sub> preyed on *O. perseae* ( $t_{81} =$   
281  $2.74, P = 0.0076$ ; Fig 1a, compare bars 1 and 3) and marginally on the IG-prey<sub>NC</sub> ( $t_{80} = -2.01,$   
282  $P = 0.048$ , not significant after Bonferroni correction; Fig 1b, compare bar 9 to 10) when  
283 each prey was offered alone; b) that adding IG-prey<sub>NC</sub> increased mortality of *O. perseae* ( $t_{81}$   
284  $= -2.26, P = 0.026$ ; Fig 1a, compare bar 1 to 7), but adding *O. perseae* did not influence  
285 mortality of the IG-prey<sub>NC</sub> ( $t_{80} = -0.31, P = 0.755$ ; Fig 1b, compare bar 10 to 7); c) that the  
286 presence of pollen yielded a drastic reduction in predation of IG-predators<sub>ES</sub> on both the  
287 herbivore ( $t_{81} = 2.99, P = 0.0037$ ; Fig 1a, compare bar 1 to 4) and the IG-prey<sub>NC</sub> ( $t_{80} = 3.91, P$   
288  $\ll 0.001$ ; Fig 1b, compare bar 10 to 13); d) that when both prey were available, the  
289 presence of pollen did not affect herbivore mortality ( $t_{81} = 0.88, P = 0.379$ ; Fig 1a, compare  
290 bar 7 to 11), but did lead to lower IG-prey<sub>NC</sub> mortality ( $t_{80} = 3.58, P \ll 0.001$ ; Fig 1b,  
291 compare bar 7 to 11).

292 Oviposition rates of IG-predators<sub>ES</sub> were only affected by the presence of pollen  
293 (main factor Pollen, Table 1c). However, further planned comparisons revealed that while  
294 feeding on the herbivore yielded <sup>stimulated</sup> ~~some~~ egg production ( $t_{96} = 2.19, P = 0.021$ ; Fig 1c, compare <sup>change</sup>  
295 bar 1 to 2), feeding on IG-prey<sub>NC</sub> did not ( $t_{96} = -1.13, P = 0.259$ ; Fig 1c, compare bar 10 to 2).

296



297 *Communities with N. californicus as the (IG-)predator*

298 Herbivore mortality was affected only by the interaction between IG-predator<sub>NC</sub> and IG-  
299 prey<sub>ES</sub> (Table 2a). Indeed, mortality of herbivores was drastically affected by the presence of  
300 IG-predators<sub>NC</sub> (Fig 2a, compare bar 1 to 3), but this effect was lesser in the presence of IG-  
301 prey<sub>ES</sub> (Fig 2a, compare bar 1 to 7). Mortality of IG-prey<sub>ES</sub> was only affected by the presence  
302 of pollen (Table 2b).

303 Paired comparisons revealed that a) IG-predators<sub>NC</sub> preyed on *O. perseae* ( $t_{90} = 3.32$ ,  
304  $P = 0.013$ ; Fig 2a, compare bar 3 to 1) but not on IG-prey<sub>ES</sub> ( $t_{86} = -1.35$ ,  $P = 0.182$ ; Fig 2b,  
305 compare bar 9 to 10), when each prey was offered alone; b) adding IG-prey<sub>ES</sub> reduced  
306 mortality of *O. perseae* ( $t_{90} = 2.56$ ,  $P = 0.012$ ; Fig 2a, compare bar 1 to 7), but adding *O.*  
307 *perseae* did not change mortality of the IG-prey<sub>ES</sub> ( $t_{86} = -0.93$ ,  $P = 0.353$ ; Fig 2b, compare bar  
308 10 to 7); c) the presence of pollen did not affect mortality of either *O. perseae* ( $t_{90} = -0.43$ ,  $P$   
309  $= 0.669$ ; Fig 2a, compare bar 1 to 4) or the IG-prey<sub>ES</sub> ( $t_{86} = 1.80$ ,  $P = 0.075$ ; Fig 2b, compare  
310 bar 10 to 13); d) when both types of prey were available, the presence of pollen led to a  
311 significant increase in mortality of *O. perseae* ( $t_{90} = -3.65$ ,  $P \ll 0.001$ ; Fig 2a, compare bar 7  
312 to 11), but a significant decrease of mortality in IG-prey<sub>ES</sub> ( $t_{86} = 2.04$ ,  $P = 0.044$ ; Fig 2b,  
313 compare bar 7 to 11).

314 Oviposition rates of IG-predators<sub>NC</sub> were affected by the main factor Herbivore and  
315 the interaction between the IG-prey<sub>ES</sub> and pollen (Table 2c). Indeed, paired comparisons  
316 revealed that e) eggs were produced when IG-predators<sub>NC</sub> were offered the herbivore alone  
317 ( $t_{104} = 2.45$ ,  $P = 0.016$ ; Fig 2c, compare bar 1 to 2), but not when they were on arenas with  
318 either the IG-prey<sub>ES</sub> ( $t_{104} = 0.01$ ,  $P = 0.992$ ; Fig 2c, compare bar 10 to 2) or pollen ( $t_{104} = -0.15$ ,  
319  $P = 0.884$ ; Fig 2c, compare bar 5 to 2) alone. Moreover, in the presence of the herbivore,  
320 rates of oviposition were not influenced by the presence of pollen ( $t_{104} = -0.93$ ,  $P = 0.352$ ; Fig  
321 2c, compare bar 1 to 4), but dramatically decreased in the presence of the IG-prey<sub>ES</sub> ( $t_{104} =$   
322  $2.39$ ,  $P = 0.019$ ; Fig 2c, compare bar 1 to 7). However, when pollen was added to the system  
323 with both prey types, IG-predators<sub>NC</sub> resumed oviposition to its maximum ( $t_{104} = -2.36$ ,  $P =$   
324  $0.020$ ; Fig 2c, compare bar 7 to 11).

325

## 326 Discussion

327 In this study, we tested the effect of community structure on the realized interactions  
328 within a community of predatory and herbivorous mites. Because in our system the

## Sub-headings

329 intraguild predator is the largest individual within a pair (as in most systems), we created  
330 communities in which adults (IG-predators) belonged to one species and juveniles (IG-prey)  
331 to the other, then inverted the species-stage identity in another set of communities. We  
332 then measured predation and oviposition in communities with all possible combinations of  
333 the presence of shared prey, the IG-prey, the IG-predator and <sup>a</sup>alternative food. We show <sup>resource.</sup>  
334 that adding species to a community increases the number of potential trophic interactions,  
335 but not necessarily their occurrence. Indeed, despite the potential for module  
336 configurations of communities with apparent competition and intraguild predation, all  
337 modules could be described by linear food chains (Box 1C). <sup>in our study system.</sup> Add disclaimer.

338 <sup>the</sup>In trophic chain configurations, although *N. californicus* killed more *O. perseae*  
339 females per day than *E. stipulatus*, oviposition rates were similar between predators. This is <sup>makes</sup>  
340 in line with the finding that *E. stipulatus* can only forage on mobile *O. perseae* mites when <sup>specific to</sup>  
341 they wander outside nests, whereas *N. californicus* can penetrate inside nests and forage on <sup>this study.</sup>  
342 all the individuals residing within (González-Fernández *et al.* 2009). This suggests that *E.*  
343 *stipulatus* is the most efficient predator converting prey into eggs, but that *N. californicus* is <sup>strange</sup>  
344 more efficient at reducing herbivore populations. Which of these strategies is best for <sup>phrase</sup>  
345 biological control will depend on the ecological condition: if <sup>outbreaks</sup>bursts of prey are confined in  
346 time, it may be more efficient to select a biocontrol agent that feeds more, as in  
347 "inundative" biocontrol strategies, whereas controlling and keeping resident populations at  
348 low levels may be best achieved with a predator with a strong numerical response, as in  
349 "innoculative" biocontrol strategies (Van Driesche *et al.* 2007). Moreover, unlike *N.*  
350 *californicus*, *E. stipulatus* fed and oviposited on pollen. This may allow the latter to remain in  
351 the field for longer periods, as actually observed in field surveys (González-Fernández *et al.*  
352 2009). Such <sup>partitioning</sup>temporal segregation may facilitate the presence of the two predators in the <sup>niche</sup>  
353 same fields (Otto *et al.* 2008). <sup>partitioning</sup>

354 Our results also revealed asymmetry in the intraguild predation between *E.*  
355 *stipulatus* and *N. californicus*, with adults of the former preying upon juveniles of the latter,  
356 but not the reverse. Because *N. californicus* is likely the best competitor for the shared prey  
357 (González-Fernández *et al.* 2009), coexistence between predators is thus possible in this  
358 system (Holt & Polis 1997). Yet, the simultaneous presence of the two predators is likely to  
359 have little effect upon the densities of the shared prey. Indeed, whereas adding  
360 *N. californicus* adult intraguild predators to an arena with *E. stipulatus* juveniles results in

Structure of discussion? Probably ok. Lot

361 higher shared prey densities as compared to the presence of *N. californicus* adults alone  
362 with the shared prey, the reverse is not true when adding adult *E. stipulatus* to an arena  
363 with juveniles *N. californicus*. Thus, the net effect of these interactions upon prey density is  
364 probably negligible. This is corroborated by field studies (Montserrat *et al.* 2013). However,  
365 the presence of alternative food (i.e. pollen) contributed to reduce trophic interactions  
366 between predator species resulting in community configurations that could enhance pest  
367 control. Thus, supplying alternative and preferred food to the IG-predator is probably  
368 detrimental to populations of *O. perseae*. Again, this finding is in line with field observations  
369 (Montserrat *et al.* 2013).

370 Food web ecology predicts that species of the highest trophic levels engage in  
371 trophic interactions on more than one food source when these are available. Here, we show  
372 that *E. stipulatus* acting as intraguild predators feeds on the herbivore, *O. perseae*, on the  
373 intraguild prey, *N. californicus*, and on the alternative food, pollen, when each of these are  
374 presented alone. However, in the presence of pollen *E. stipulatus* reduces predation rates  
375 on both prey species. This may be explained by the fact that pollen is the most profitable  
376 food for this species, as found here and in other studies (Ferragut *et al.* 1987; McMurtry &  
377 Croft 1997; Bouras & Papadoulis 2005; González-Fernández *et al.* 2009). Similarly, *N.*  
378 *californicus* adults and juveniles ceased foraging on other food sources in presence of the  
379 herbivores. These results suggest that realized interactions hinge on the presence of the  
380 most profitable food source. In presence of the optimal food source for each of the two  
381 secondary consumers, communities tended to ~~melt down to become~~ be reduced to two simple trophic  
382 chains. Indeed, in the most complex communities studied here, with all 5 species present,  
383 the presence of the optimal food originated the split of the community into two trophic  
384 chains, one with *E. stipulatus* feeding on pollen and the other with *N. californicus* feeding on  
385 the herbivore (Box 1 d), compare d.1.1. and d.1.2. with d.2.1. and d.2.2.).

386 Another factor that contributed to the linearization of the food web was that, when  
387 both the IG-prey and the shared prey were together, IG-predators<sub>ES</sub> preyed mainly on the  
388 IG-prey. Indeed, mortality of *O. perseae* in presence of the IG-prey, *N. californicus*, was not  
389 affected by the presence of the IG-predator *E. stipulatus*. Furthermore, mortality of IG-  
390 prey<sub>NC</sub> was significantly higher in treatments with presence of the IG-predator, compared to  
391 the control without them. This suggests that mortality in the herbivore was mainly inflicted  
392 by the IG-prey, *N. californicus*, and that the IG-predator *E. stipulatus* preyed preferentially

Optimal foraging theory?

source, eg. optimal foraging theory.

increased modularity  
stable but not necessarily best functioning  
also modularity

393 | on the IG-prey *N. californicus*. This could be explained by *E. stipulatus* having no access to *O.*  
394 *perseae* eggs or females located inside the nests (Montserrat *et al.* 2008a; González-  
395 Fernández *et al.* 2009), which leads to higher encounter rates between *E. stipulatus* and *N.*  
396 *californicus* than between *E. stipulatus* and *O. perseae*. Indeed, *E. stipulatus* forages only on  
397 mobile stages that wander outside nests (Montserrat *et al.* 2008a; González-Fernández *et al.*  
398 2009). *Neoseiulus californicus*, however, can penetrate *O. perseae* nests, and thus may feed  
399 on them. Therefore, the realized community was that of a 4-level trophic chain (Box 1,  
400 c.2.1.). In the other community block, when *N. californicus* acted as the IG-predator,  
401 mortality of *O. perseae* females was similar in all communities with the IG-prey *E. stipulatus*  
402 present, irrespective of the presence of IG-predators<sub>NC</sub>. Furthermore, mortality of IG-prey<sub>ES</sub>  
403 did not differ between treatments with and without the IG-predator<sub>NC</sub>, indicating that *N.*  
404 *californicus* females did not forage on *E. stipulatus* juveniles. These results suggest that, in  
405 presence of IG-prey (juveniles of *E. stipulatus*), the IG-predator<sub>NC</sub> ceased to forage on either  
406 herbivore or IG-prey, likely because IG-prey<sub>ES</sub> interferes with the foraging activities of IG-  
407 predators<sub>NC</sub>. Thus, the realized community was that of a trophic chain composed of the IG-  
408 prey, the herbivore and the plant, with the IG-predator not interacting at all (Box 1, c.2.2.).  
409 This can be explained by IG-predators<sub>NC</sub> avoiding foraging on a patch where its offspring  
410 (future) IG-predator is also there. In line with this, Abad-Moyano *et al.* (2010) reported that  
411 the presence of *E. stipulatus* immatures exerted non-lethal IG-effects on *N. californicus*  
412 females, causing daily oviposition to decrease over time despite the availability of the  
413 shared prey was kept constant. In any case, here, the trophic links are again linear, with *N.*  
414 *californicus* being excluded from the realized community (Box 1, c.2.2.). Together, our  
415 results show that none of the complex communities was actually realized, they were all  
416 trophic chains.

417 | By combining data of mortality and oviposition at different community structures,  
418 we could <sup>define</sup> recover who eats whom in a simple food web. Although this approach is very  
419 powerful, it does have its limitations. Indeed, it assumes additive effects of conversion  
420 efficiencies of pairwise interactions. For example, if feeding on a prey item allows predators  
421 to better convert the food provided by another prey, this cannot be detected in our  
422 approach (i.e., indirect effects on conversion efficiency). Furthermore, it may be largely  
423 unfeasible to extend this approach to more complex food webs, although it is becoming  
424 clear that we need to know how food is transformed into predator offspring in order to fully

transfer efficiencies

425 understand food webs in nature (Neutel & Thorne 2014). Indeed, such full-factorial studies  
426 are extremely rare in the literature (but see Schmitz & Sokol-Hessner 2002; Otto *et al.*  
427 2008). *If would be good to introduce connectance as*  
428 *It is becoming increasingly clear that connectance, that is, the number of realized*  
429 interactions in a food web, is generally much lower than the number of potential  
430 interactions (Beckerman *et al.* 2006). Identifying trophic links in food webs, however, is not  
431 a simple task. Molecular methods are useful to process field data and they deliver reliable  
432 information on who eats whom, but such tools only provide semi-quantitative estimates of  
433 predation, and they are expensive (Birkhofer *et al.* 2017). Another possible approach to  
434 measure connectance is by observations in the field (Dunne *et al.* 2002; Tylianakis *et al.*  
435 2007; Carnicer *et al.* 2009; Lazzaro *et al.* 2009; Plein *et al.* 2013; Baiser *et al.* 2016; Lemos-  
436 Costa *et al.* 2016). Although this approach allows including a high number of species in the  
437 observations, it suffers from two main shortfalls: (a) it is generally only possible to  
438 undertake it in systems with two trophic levels in which one are primary producers (but see  
439 Bukovinszky *et al.* 2008; Neutel & Thorne 2014), or in systems where trophic interactions  
440 are detectable long after the actual events, as in parasitoid/host interactions or via the  
441 analysis of gut contents; and (b) it does not account for how foraging on a given resource  
442 translates into consumer offspring (but see Bukovinszky *et al.* 2008; Vázquez *et al.* 2015).  
443 Observations in controlled experimental settings, in contrast, deliver quantitative estimates  
444 of predation rates and concomitant offspring production, especially when trophic links, and  
445 their strength, are estimated by confronting pairs of species. Alternatively, modelling  
446 complex systems provide relative estimates on interaction strengths that go beyond pair-  
447 wise interactions (Moya-Laraño *et al.* 2012; Moya-Laraño *et al.* 2014). Yet, one-on-one  
448 approaches may ignore emergent indirect effects of having several species together  
449 (Wootton 1994; Dambacher & Ramos-Jiliberto 2007). For instance, *Cancer productus*, a crab  
450 native to the Northwest Pacific, consumes equal amounts of native oysters and of invasive  
451 drill oysters when each type of prey is offered alone, but when they are offered together  
452 crabs interact with the native oyster species only (Grason & Miner 2012). Therefore, if  
453 trophic links are not evaluated in presence of all species in the community, one may reach  
454 erroneous conclusions on the strength of the interaction (Guzmán *et al.* 2016b; Fonseca *et al.*  
455 *et al.* 2017) and overestimate connectance in food webs. We show that all communities ended  
456 up becoming a sum of one or more trophic chains (Box 1C). Thus, the fundamental trophic

*a measure of food-web complexity first - then go into 428*

*ie plant pollinator networks*

*preferences prey switching + optimal foraging*

457 niche of species in this system (i.e., the food items that the species is able to feed on) is  
458 larger than the realized one (i.e., the food items that the species feeds on when they are all  
459 present simultaneously – (Hutchinson 1961)). Therefore, our results suggest that some food  
460 webs may be less complex than previously thought in terms of the frequency and strength  
461 of IGP.

462 Theoretical models exploring persistence in three-species communities with IGP find  
463 a limited parameter space for coexistence of IG-predator and IG-prey (e.g. Mylius *et al.*  
464 2001), but field observations show that IGP is actually widespread (Polis 1991). Our results  
465 suggest that IGP in some systems might actually be occasional, as predators will tend to  
466 forage on the most profitable food, which generally is not the IG prey (Polis *et al.* 1989). In  
467 line with this, some natural systems have shown that communities with IGP actually show  
468 dynamics that are compatible with linear food chains, rather than with IGP (Borer *et al.*  
469 2003). Therefore, predators may coexist because they rarely engage in IGP, and complexity  
470 may be over-estimated (Magalhães *et al.* 2005). This agrees with food web theory stating  
471 that weak trophic interactions promote the persistence of communities (May 1972; Paine  
472 1992; McCann *et al.* 1998, among others). For example, Hiltunen *et al.* (2014) found long-  
473 term cycling dynamics when modelling a three-species planktonic food web with IGP, with  
474 interaction strength between IG-predator and IG-prey set to be much weaker to that  
475 between IG-predator and the shared resource. Our results suggest that the higher the  
476 number of potential interacting species is, the weaker most of interactions among species  
477 become.) Indeed, the structure of interactions among species in natural communities is  
478 characterized by many weak interactions and few strong interactions (Paine 1992; McCann  
479 *et al.* 1998), and such skewedness towards weak interactions is crucial to food web stability  
480 (Neutel *et al.* 2002; 2007; Montoya *et al.* 2009; Neutel & Thorne 2014). Because a species'  
481 fundamental niche (all of its potential interactions) is unlikely to be realized at particular  
482 places or times, it is crucial to determine on which resources do species in a community  
483 actually feed upon, and under what circumstances. Therefore, unravelling realized food  
484 webs, (i.e., interaction strengths across different nodes and trophic levels, including indirect  
485 effects) may be ~~the~~ key to understanding these ecological networks and their persistence.

489 **Acknowledgements**

490 The authors are indebted to Rosa María Sahún Logroño for her valuable help [in maintaining](#)  
491 [the experimental populations](#). This work was financed by the Spanish Ministry of Science  
492 and Innovation (CGL2015-66192-R and AGL2011-30538-C03-03). I.T.C. was recipient of a  
493 grant from the Spanish National Research Council (CSIC, ref: JAE-PRE 041). The animals used  
494 for the research of this publication are not test animals in the legal sense. The authors have  
495 no conflict of interest to declare.

496

497

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692 | Table 1. Results of Generalized Linear Models applied to a) herbivore mortality rates, b) IG-  
693 | prey (juveniles of *N. californicus*) mortality rates, and c) (IG-)predator (females of *E.*  
694 | *stipulatus*) oviposition rates. All the analyses were 3 full-factorial designs. When interactions  
695 | among the three explanatory variables were not significant, and if the new model yielded a  
696 | lower AIC, they were removed from the model. Subsequently, the same procedure was  
697 | followed for double interactions. These cases are shown in the table as NS\*.

a) Herbivore mortality rates	Estimate	Std. Error	z value	Pr(> z )
Intercept	-1.755	0.712	-2.466	0.014
IG-predator (1)	2.212	0.732	3.021	0.002
IG-prey (2)	2.932	0.729	4.023	<0.001
Pollen (3)	-1.851	0.609	-3.040	<0.001
IG-predator * IG-prey	-2.302	0.756	-3.047	0.002
IG-predator * Pollen	NS			
IG-prey * Pollen	1.573	0.639	2.466	.014
(1) * (2) * (3)	NS			
b) IG-prey mortality rates	Estimate	Std. Error	z value	Pr(> z )
Intercept	0.513	0.238	2.156	0.031
IG-predator (1)	0.591	0.273	2.163	0.030
Herbivore (2)	-1.624	0.496	-3.276	0.001
Pollen (3)	-0.392	0.359	-1.091	0.275
IG-predator * Herbivore	1.552	0.511	3.037	0.002
IG-predator * Pollen	-1.705	0.517	-3.300	<0.001
Herbivore * Pollen	0.749	0.520	1.439	0.150
(1) * (2) * (3)	NS			
c) IG-predator oviposition rates	Estimate	Std. Error	z value	Pr(> z )
Intercept	-0.843	0.245	-3.443	<0.001
IG-prey (1)	-0.194	0.220	-0.882	0.378
Herbivore (2)	0.220	0.216	1.018	0.308
Pollen (3)	1.104	0.235	4.703	<0.001
IG-prey * Herbivore	NS			
IG-prey * Pollen	NS			
Herbivore * Pollen	NS			
(1) * (2) * (3)	NS*			

Why not nested models?

724 | Table 2. Results of Generalized Linear Models applied to a) herbivore mortality rates, b) IG-  
 725 | prey (juveniles of *E. stipulatus*) mortality rates, and c) (IG-)predator (females of *N.*  
 726 | *californicus*) oviposition rates. All the analyses were 3 full-factorial designs. When  
 727 | interactions among the three explanatory variables were not significant, and if the new  
 728 | model yielded a lower AIC, they were removed from the model. Subsequently, the same  
 729 | procedure was followed for double interactions. These cases are shown in the table as NS\*.

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a) Herbivore mortality rates	Estimate	Std. Error	z value	Pr(> z )
Intercept	-1.954	0.722	-2.707	0.007
IG-predator (1)	2.997	0.729	4.109	<0.001
IG-prey (2)	2.184	0.746	2.927	0.003
Pollen (3)	-0.888	0.499	-1.782	0.075
IG-predator * IG-prey	-2.825	0.764	-3.699	<0.001
IG-predator * Pollen	0.999	0.460	2.175	0.030
IG-prey * Pollen	0.791	0.325	2.436	0.015
(1) * (2) * (3)	NS*			

b) IG-prey mortality rates	Estimate	Std. Error	z value	Pr(> z )
Intercept	-0.4855	0.3035	-1.600	0.110
IG-predator (1)	0.6150	0.3152	1.951	0.051
Herbivore (2)	-0.3174	0.2851	-1.114	0.265
Pollen (3)	-1.1505	0.3416	-3.368	<0.001
IG-predator * Herbivore	NS*			
IG-predator * Pollen	NS*			
Herbivore * Pollen	NS*			
(1) * (2) * (3)	NS*			

c) IG-predator oviposition rates	Estimate	Std. Error	z value	Pr(> z )
Intercept	-2.7430	0.6172	-4.444	<0.001
IG-prey (1)	-2.5550	1.0378	-2.462	0.014
Herbivore (2)	2.5174	0.5989	4.204	<0.001
Pollen (3)	0.3476	0.3685	0.943	0.346
IG-prey * Herbivore	NS*			
IG-prey * Pollen	2.2175	1.1041	2.008	0.045
Herbivore * Pollen	NS*			
(1) * (2) * (3)	NS*			

757 **Box 1. A: Fundamental community modules** included in this study. a) trophic chain, b)  
758 apparent competition, c) intraguild predation, and d) intraguild predation and apparent  
759 competition. From a) to d) the complexity of the community is increased via increasing the  
760 number of species and the number of interactions among them. **B: Predicted trophic links**  
761 that have been observed using pairwise experimental settings. **C: Realized trophic links**  
762 occurring across community modules of increasing complexity, obtained from the  
763 experiments presented here, where interactions are measured in the presence of other  
764 components of the community. SC stands for secondary consumer, PC for primary  
765 consumer, PP for primary producer, and AF for alternative food. SC1 and SC2 are phytoseiid  
766 predatory mites, i.e. *Euseius stipulatus* and *Neoseiulus californicus*, respectively, PC is the  
767 tetranychid herbivore mite *Oligonychus perseae*, AF is pollen of *Carpobrotus edulis*, and PP  
768 is the avocado *Persea americana*. Solid arrows indicate negative direct interactions (who  
769 eats whom), whereas dotted and dashed arrows in Box 1A indicate negative indirect  
770 interactions (apparent competition and competition).

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772 | Figure 1. Mortality rates (average  $\pm$  S.E.) of a) herbivore prey (*Oligonychus perseae* females)  
773 and b) IG-prey (*Neoseiulus californicus* juveniles), and c) oviposition rates (average  $\pm$  S.E.) of  
774 IG-predators (*Euseius stipulatus* females), in 14 different treatments defined by presence or  
775 absence of either IG-predators, IG-prey, herbivores or alternative food (pollen), depicted in  
776 the lower part of the figure, that mimicked four different community configurations and  
777 their respective controls.

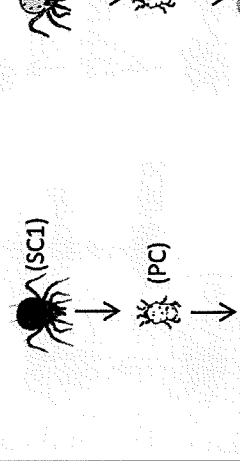
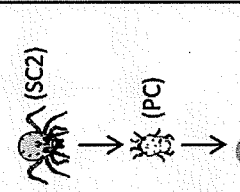
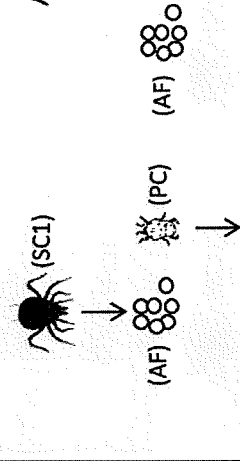
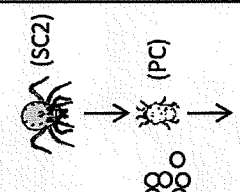
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779 | Figure 2. Mortality rates (average  $\pm$  S.E.) of a) herbivore prey (*Oligonychus perseae* females)  
780 and b) IG-prey (*Euseius stipulatus* juveniles), and c) oviposition rates (average  $\pm$  S.E.) of IG-  
781 predators (*Neoseiulus californicus* females), in 14 different treatments defined by presence  
782 or absence of either IG-predators, IG-prey, herbivores or alternative food (pollen), depicted  
783 in the lower part of the figure, that mimicked four different community configurations and  
784 their respective controls.

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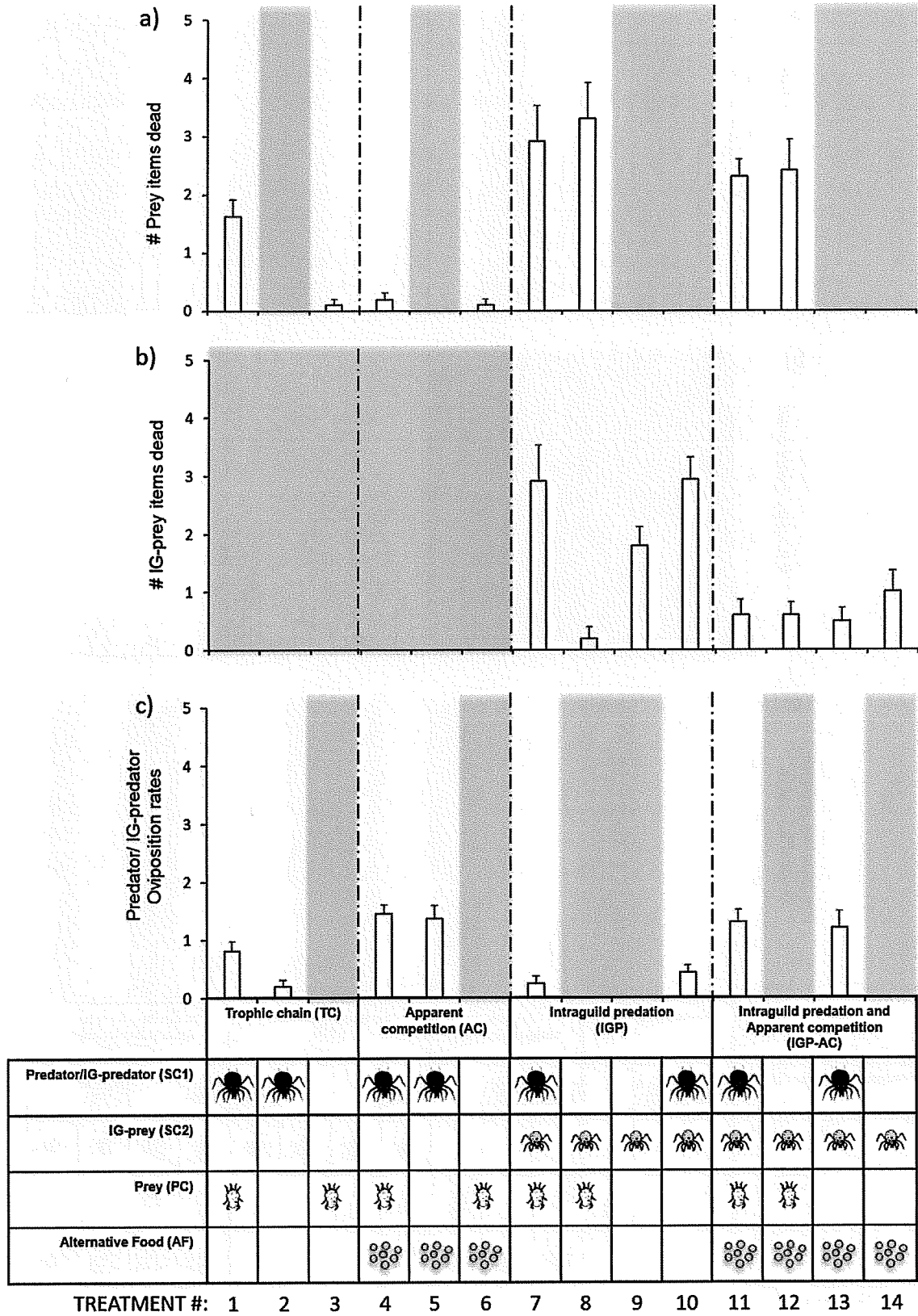


A: FUNDAMENTAL COMMUNITY	B: PREDICTED TROPHIC LINKS	C: REALIZED TROPHIC LINKS
<p><b>a) Trophic chain</b></p> <pre> graph TD     SC[Secondary Consumer (SC<sub>i,j</sub>)] --&gt; PC[Primary Consumer (PC)]     PC --&gt; PP[Primary Producer (PP)]                     </pre>	<p>a.1.1) <i>E. stipulatus</i>      a.1.2) <i>N. californicus</i></p> 	<p>a.2.1) <i>E. stipulatus</i>      a.2.2) <i>N. californicus</i></p> 
<p><b>b) Apparent competition</b></p> <pre> graph TD     SC[Secondary Consumer (SC<sub>i,j</sub>)] --&gt; PC[Primary Consumer (PC)]     SC --&gt; AF[Alternative Food (AF)]     PC --&gt; PP[Primary Producer (PP)]                     </pre>	<p>b.1.1) <i>E. stipulatus</i>      b.1.2) <i>N. californicus</i></p> 	<p>b.2.1) <i>E. stipulatus</i>      b.2.2) <i>N. californicus</i></p>  <p style="text-align: right; font-style: italic;">prey switching</p>

A: FUNDAMENTAL COMMUNITY	B: PREDICTED TROPHIC LINKS	C: REALIZED TROPHIC LINKS
<p><b>c) Intraguild predation</b></p> <pre> graph TD     SC1[Secondary Consumer 1 (SC1)] --&gt; PC[Primary Consumer (PC)]     SC1 -.-&gt; SC2[Secondary Consumer 2 (SC2)]     SC2 --&gt; PC     PC --&gt; PP[Primary Producer (PP)]         </pre>	<p>c.1.1) <i>E. stipulatus</i> (SC1) → (SC2) → (PC) → (PP)</p> <p>c.1.2) <i>N. californicus</i> (SC2) → (SC1) → (PC) → (PP)</p>	<p>c.2.1) <i>E. stipulatus</i> (SC1) → (SC2) → (PC) → (PP)</p> <p>c.2.2) <i>N. californicus</i> (SC2) → (SC1) → (PC) → (PP)</p>
<p><b>d) Intraguild predation and apparent competition</b></p> <pre> graph TD     SC1[Secondary Consumer 1 (SC1)] --&gt; AF[Alternative Food (AF)]     SC1 --&gt; PC[Primary Consumer (PC)]     SC1 --&gt; SC2[Secondary Consumer 2 (SC2)]     SC2 --&gt; PC     PC --&gt; PP[Primary Producer (PP)]         </pre>	<p>d.1.1) <i>E. stipulatus</i> (SC1) → (SC2) → (PC) → (PP)</p> <p>d.1.2) <i>N. californicus</i> (SC2) → (SC1) → (PC) → (PP)</p>	<p>d.2.1) <i>E. stipulatus</i> (SC1) → (SC2) → (PC) → (PP)</p> <p>d.2.2) <i>N. californicus</i> (SC2) → (SC1) → (PC) → (PP)</p>

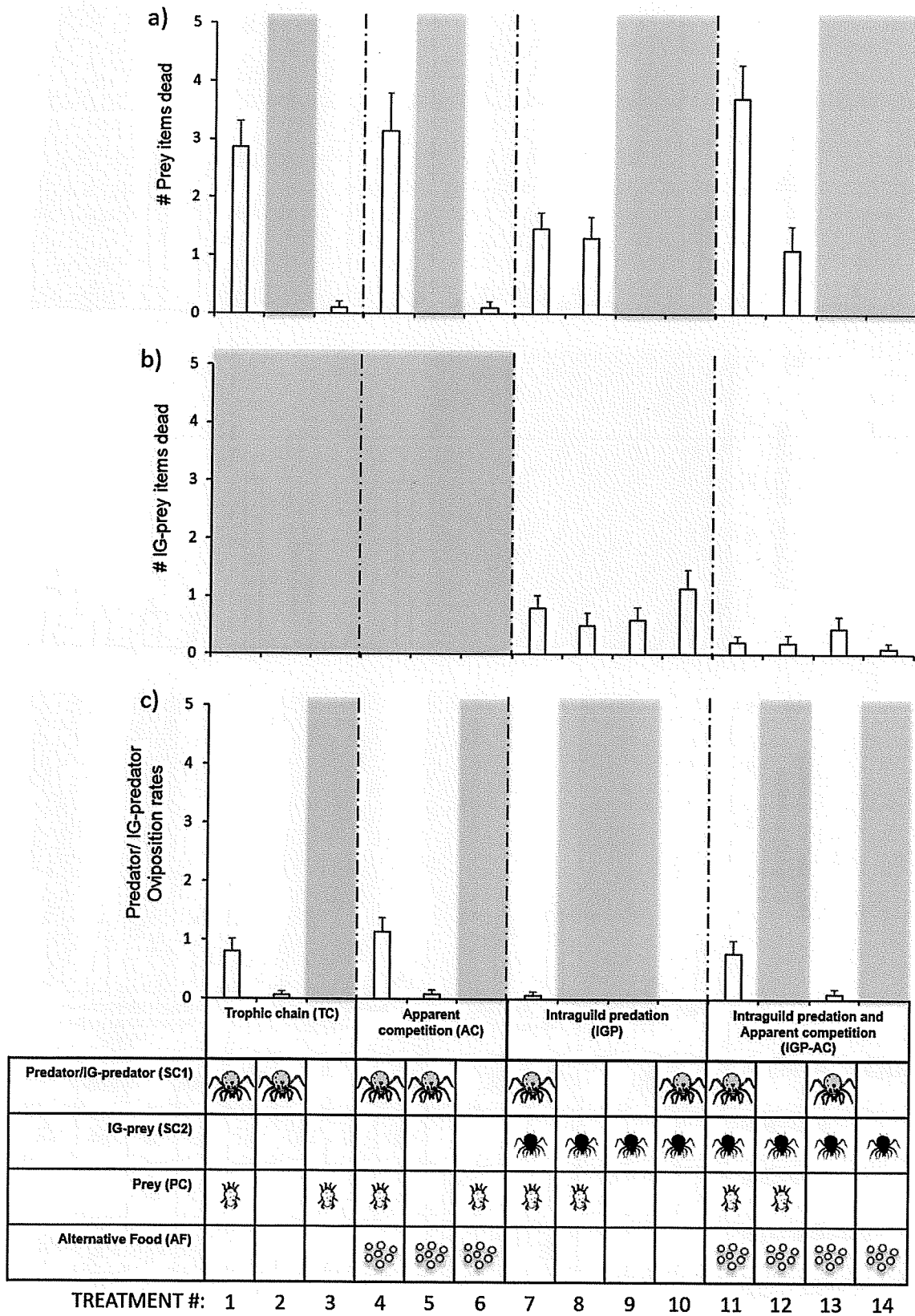
*Modularity*

789 Figure 1.



790

791 Figure 2.



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793