

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](#).

40

41 Introduction

42 Community ecology has traditionally viewed trophic interactions as linear chains, with an
43 upper level controlling the densities of the level immediately below, generating a trophic
44 cascade (Hairston *et al.* 1960; Oksanen *et al.* 1981; Carpenter *et al.* 1985). However, it is by
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 would destabilize food webs (Polis & Holt 1992; Polis & Strong 1996).

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).

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).

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 & Feißel 2000; Montserrat *et al.* 2008b), but runs counter the ubiquity of
85 intraguild predation and trophic level omnivory in natural systems (Bascompte & Melián
86 2005; Gagnon *et al.* 2011).

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 A 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 long recognized to stabilize ecosystems, particularly.
103 Indeed, by dampening oscillations between consumers and resources, these interactions
104 decrease the probability of species extinction (McCann *et al.* 1998), thus promoting

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](#)). In 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

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.

149

150

151 **Material and Methods**

152 All cultures and experiments were done in a climate chamber at 25±1°C, 65±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 filled with an avocado leaf disc (7.5 cm Ø), with the borders 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: 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. 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. 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). 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

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.

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
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.

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_{ES} and IG-prey_{NC} and between the presence of IG-prey_{NC} and pollen
269 (Table 1a). Indeed, prey died more when IG-prey_{NC} were together with the IG-predator_{ES}
270 than when the IG-predator_{ES} was alone (Fig 1a, compare bar 1 to 7), but not than when the
271 IG-prey_{NC} 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_{NC} (Fig 1a, compare bars 4 and 6
273 to bars 11 and 12).

274 Mortality rates of the IG-prey_{NC} were affected by all the double interactions except
275 that between the herbivore and pollen (Table 1b). Indeed, the presence of the IG-predator_{ES}
276 increased the mortality of IG-prey_{NC}, 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_{NC} when IG-predators_{ES} 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_{ES} 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_{NC} ($t_{80} = -2.01,$
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_{NC} 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_{NC} ($t_{80} = -0.31, P = 0.755$; Fig 1b, compare bar 10 to 7); c) that the
286 presence of pollen yielded a drastic reduction in predation of IG-predators_{ES} on both the
287 herbivore ($t_{81} = 2.99, P = 0.0037$; Fig 1a, compare bar 1 to 4) and the IG-prey_{NC} ($t_{80} = 3.91, P$
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_{NC} mortality ($t_{80} = 3.58, P \ll 0.001$; Fig 1b,
291 compare bar 7 to 11).

292 Oviposition rates of IG-predators_{ES} 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 some egg production ($t_{96} = 2.19, P = 0.021$; Fig 1c, compare
295 bar 1 to 2), feeding on IG-prey_{NC} 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_{NC} and IG-
299 prey_{ES} (Table 2a). Indeed, mortality of herbivores was drastically affected by the presence of
300 IG-predators_{NC} (Fig 2a, compare bar 1 to 3), but this effect was lesser in the presence of IG-
301 prey_{ES} (Fig 2a, compare bar 1 to 7). Mortality of IG-prey_{ES} was only affected by the presence
302 of pollen (Table 2b).

303 Paired comparisons revealed that a) IG-predators_{NC} preyed on *O. perseae* ($t_{90} = 3.32$,
304 $P = 0.013$; Fig 2a, compare bar 3 to 1) but not on IG-prey_{ES} ($t_{86} = -1.35$, $P = 0.182$; Fig 2b,
305 compare bar 9 to 10), when each prey was offered alone; b) adding IG-prey_{ES} 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_{ES} ($t_{86} = -0.93$, $P = 0.353$; 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_{ES} ($t_{86} = 1.80$, $P = 0.075$; 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_{ES} ($t_{86} = 2.04$, $P = 0.044$; Fig 2b,
313 compare bar 7 to 11).

314 Oviposition rates of IG-predators_{NC} were affected by the main factor Herbivore and
315 the interaction between the IG-prey_{ES} and pollen (Table 2c). Indeed, paired comparisons
316 revealed that e) eggs were produced when IG-predators_{NC} 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_{ES} ($t_{104} = 0.01$, $P = 0.992$; 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_{ES} ($t_{104} =$
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_{NC} 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

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 alternative food. We show
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).

338 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 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 temporal segregation may facilitate the presence of the two predators in the
353 same fields (Otto *et al.* 2008).

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

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 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_{ES} 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_{NC} 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

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_{NC}. Furthermore, mortality of IG-prey_{ES}
403 | did not differ between treatments with and without the IG-predator_{NC}, 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_{NC} ceased to forage on either
406 | herbivore or IG-prey, likely because IG-prey_{ES} interferes with the foraging activities of IG-
407 | predators_{NC}. 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_{NC} 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 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

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).

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*
455 *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

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 on 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 interaction 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 specie's](#)
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 thus key to understanding these ecological networks and their persistence.

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488 |

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691

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*.

698	a)	Herbivore mortality rates	Estimate	Std. Error	z value	Pr(> z)
699		Intercept	-1.755	0.712	-2.466	0.014
700		IG-predator (1)	2.212	0.732	3.021	0.002
701		IG-prey (2)	2.932	0.729	4.023	<0.001
702		Pollen (3)	-1.851	0.609	-3.040	<0.001
703		IG-predator * IG-prey	-2.302	0.756	-3.047	0.002
704		IG-predator * Pollen	NS			
705		IG-prey * Pollen	1.573	0.639	2.466	.014
706		(1) * (2) * (3)	NS			
707	b)	IG-prey mortality rates	Estimate	Std. Error	z value	Pr(> z)
708		Intercept	0.513	0.238	2.156	0.031
709		IG-predator (1)	0.591	0.273	2.163	0.030
710		Herbivore (2)	-1.624	0.496	-3.276	0.001
711		Pollen (3)	-0.392	0.359	-1.091	0.275
712		IG-predator * Herbivore	1.552	0.511	3.037	0.002
713		IG-predator * Pollen	-1.705	0.517	-3.300	<0.001
714		Herbivore * Pollen	0.749	0.520	1.439	0.150
715		(1) * (2) * (3)	NS			
716	c)	IG-predator oviposition rates	Estimate	Std. Error	z value	Pr(> z)
717		Intercept	-0.843	0.245	-3.443	<0.001
718		IG-prey (1)	-0.194	0.220	-0.882	0.378
719		Herbivore (2)	0.220	0.216	1.018	0.308
720		Pollen (3)	1.104	0.235	4.703	<0.001
721		IG-prey * Herbivore	NS			
722		IG-prey * Pollen	NS			
723		Herbivore * Pollen	NS			
		(1) * (2) * (3)	NS*			

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*.

730	a)	Herbivore mortality rates	Estimate	Std. Error	z value	Pr(> z)
731		Intercept	-1.954	0.722	-2.707	0.007
732		IG-predator (1)	2.997	0.729	4.109	<0.001
733		IG-prey (2)	2.184	0.746	2.927	0.003
734		Pollen (3)	-0.888	0.499	-1.782	0.075
735		IG-predator * IG-prey	-2.825	0.764	-3.699	<0.001
736		IG-predator * Pollen	0.999	0.460	2.175	0.030
737		IG-prey * Pollen	0.791	0.325	2.436	0.015
738		(1) * (2) * (3)	NS*			
739	b)	IG-prey mortality rates	Estimate	Std. Error	z value	Pr(> z)
740		Intercept	-0.4855	0.3035	-1.600	0.110
741		IG-predator (1)	0.6150	0.3152	1.951	0.051
742		Herbivore (2)	-0.3174	0.2851	-1.114	0.265
743		Pollen (3)	-1.1505	0.3416	-3.368	<0.001
744		IG-predator * Herbivore	NS*			
745		IG-predator * Pollen	NS*			
746		Herbivore * Pollen	NS*			
747		(1) * (2) * (3)	NS*			
748	c)	IG-predator oviposition rates	Estimate	Std. Error	z value	Pr(> z)
749		Intercept	-2.7430	0.6172	-4.444	<0.001
750		IG-prey (1)	-2.5550	1.0378	-2.462	0.014
751		Herbivore (2)	2.5174	0.5989	4.204	<0.001
752		Pollen (3)	0.3476	0.3685	0.943	0.346
753		IG-prey * Herbivore	NS*			
754		IG-prey * Pollen	2.2175	1.1041	2.008	0.045
755		Herbivore * Pollen	NS*			
756		(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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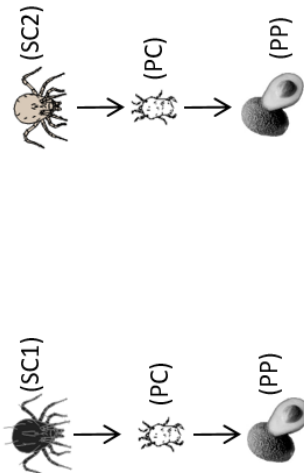
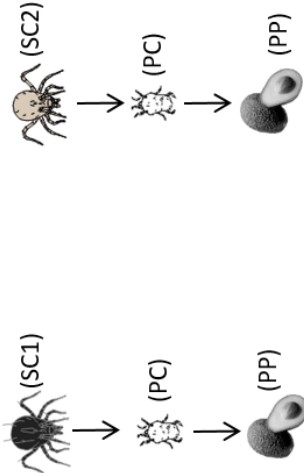
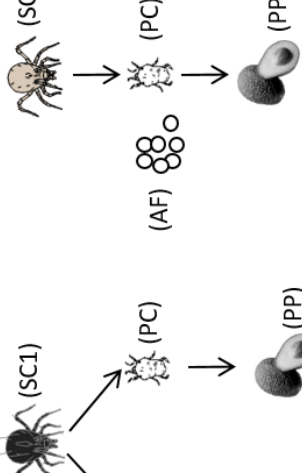
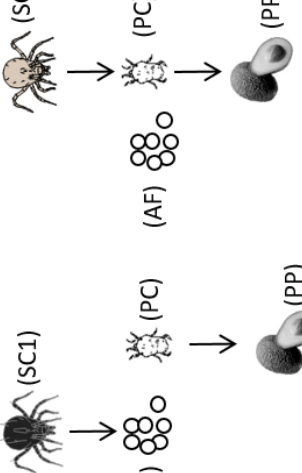
772 | Figure 1. Mortality rates (average \pm S.E.) of a) herbivore **prey** (*Oligonychus perseae* females)
773 and b) IG-prey (*Neoseiulus californicus* juveniles), and c) oviposition rates (average \pm S.E.) of
774 IG-predators (*Euseius stipulatus* females), in 14 different treatments defined by presence 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.

778

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.

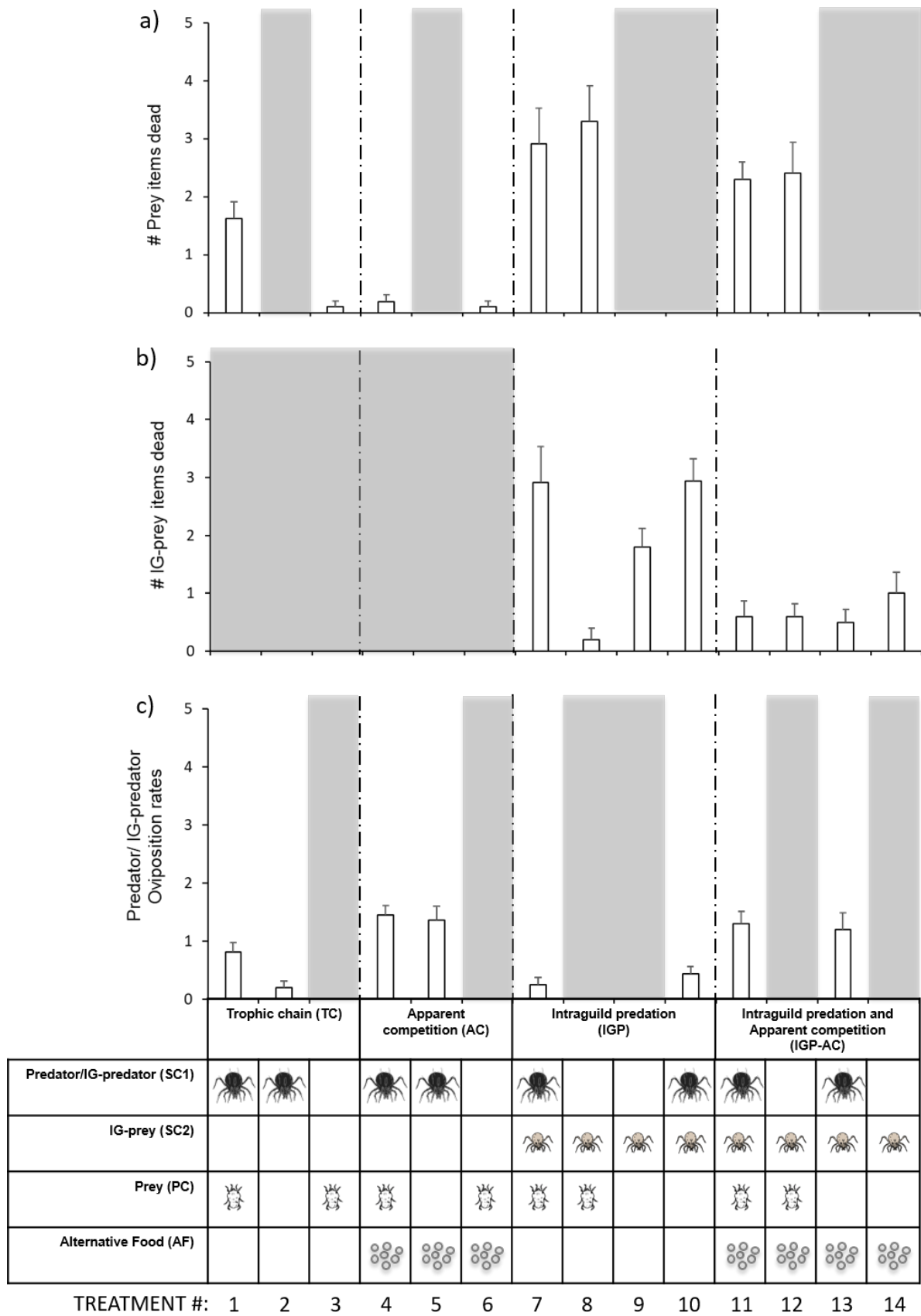
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<p>A: FUNDAMENTAL COMMUNITY</p>	<p>B: PREDICTED TROPHIC LINKS</p>	<p>C: REALIZED TROPHIC LINKS</p>
<p>a) Trophic chain</p> <pre> graph TD SC[Secondary Consumer (SC_{i,j})] --> PC[Primary Consumer (PC)] PC --> PP[Primary Producer (PP)] </pre>	<p>a.1.1) <i>E. stipulatus</i> (SC1) → (PC) → (PP)</p> <p>a.1.2) <i>N. californicus</i> (SC2) → (PC) → (PP)</p> 	<p>a.2.1) <i>E. stipulatus</i> (SC1) → (PC) → (PP)</p> <p>a.2.2) <i>N. californicus</i> (SC2) → (PC) → (PP)</p> 
<p>b) Apparent competition</p> <pre> graph TD SC[Secondary Consumer (SC_{i,j})] --> PC[Primary Consumer (PC)] SC --> AF[Alternative Food (AF)] PC --> PP[Primary Producer (PP)] </pre>	<p>b.1.1) <i>E. stipulatus</i> (SC1) → (PC) → (PP)</p> <p>b.1.2) <i>N. californicus</i> (SC2) → (PC) → (PP)</p> 	<p>b.2.1) <i>E. stipulatus</i> (SC1) → (AF) → (PC) → (PP)</p> <p>b.2.2) <i>N. californicus</i> (SC2) → (PC) → (PP)</p> 

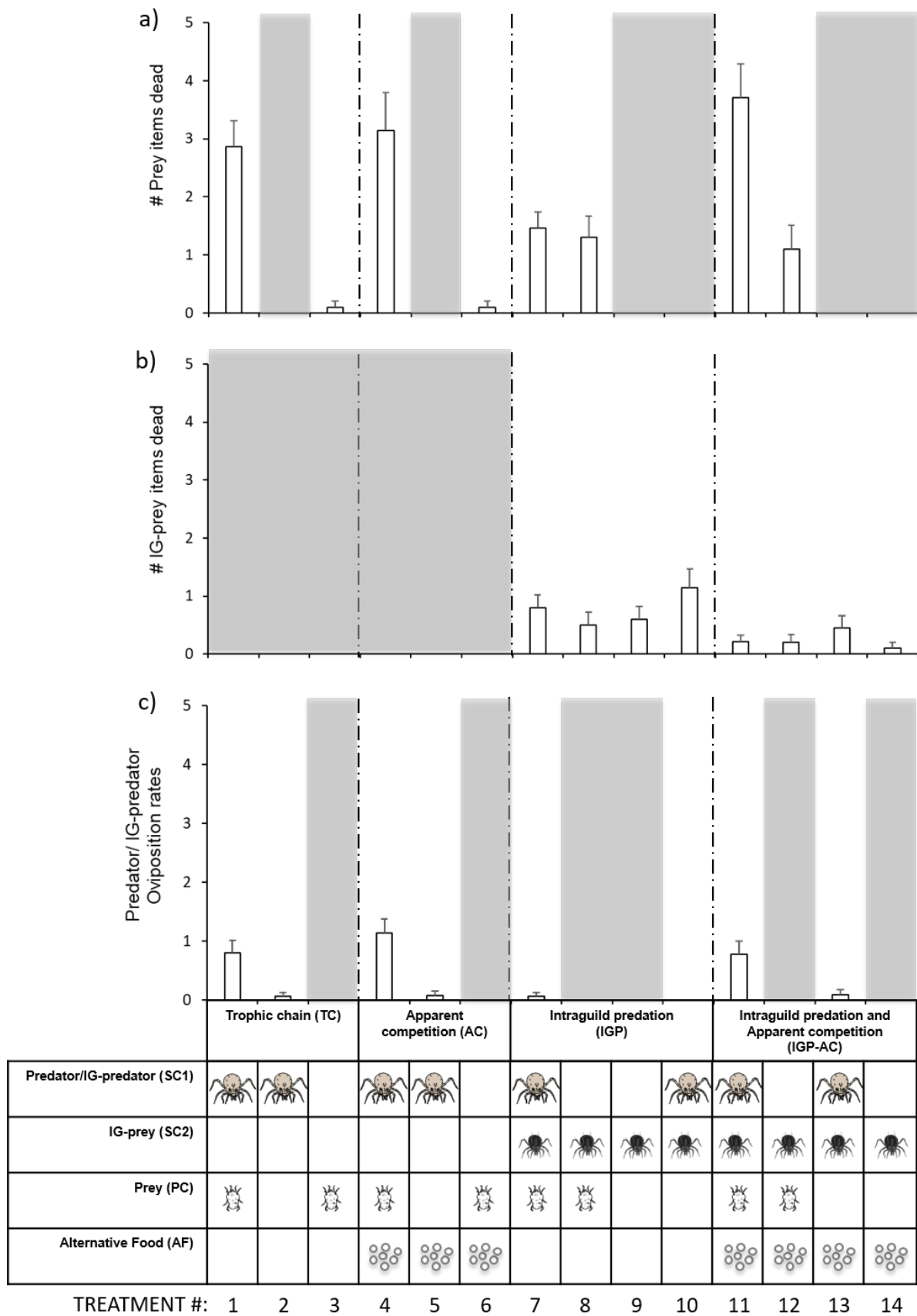
A: FUNDAMENTAL COMMUNITY	B: PREDICTED TROPHIC LINKS	C: REALIZED TROPHIC LINKS
<p>c) Intraguild predation</p>	<p>c.1.1) <i>E. stipulatus</i> (SC1) → (SC2) → (PC) → (PP)</p> <p>c.1.2) <i>N. californicus</i> (SC2) → (SC1) → (PC) → (PP)</p>	<p>c.2.1) <i>E. stipulatus</i> (SC1) → (SC2) → (PC) → (PP)</p> <p>c.2.2) <i>N. californicus</i> (SC2) → (PC) → (PP)</p>
<p>d) Intraguild predation and apparent competition</p>	<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) → (PC) → (PP)</p> <p>d.2.2) <i>N. californicus</i> (SC2) → (PC) → (PP)</p>

789 Figure 1.



790

791 Figure 2.



792

793