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

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Abstract

The mathematical theory describing small assemblages of interacting species (community modules or motifs) has proved to be essential in understanding the emergent properties of ecological communities. These models use differential equations to study pairwise interactions between species. However, as community modules become more complex, it is not certain that all potential interactions will be effectively realized. Here, we use community modules to experimentally explore whether the number of trophic links among species scales with community complexity (i.e., by adding species known to feed on each other from pair-wise trials). To investigate this question, we used a simple mite community present in avocado orchards (*Persea americana*), composed of two predators (*Euseius stipulatus* and *Neoseiulus californicus*), one herbivore as shared prey (*Oligonychus perseae*), and pollen of *Carpobrotus edulis* as an alternative food resource. These configurations enabled the potential for (intraguild) predation and (apparent) competition to be expressed. Using a series of controls, we assessed whether the presence of one species affected the survival of another, or its conversion of food into offspring). We found that increasing the number of potential interactions did not result in more complex realized community modules. Instead, all communities were reduced to one or two linear trophic chains. Our results show that trophic links assumed to occur when species are assembled in pairs do not necessarily occur when other components of the community are present. Consequently, food-web structure may be unrealistic in theoretical community modules that are parameterized based on pair-wise interactions observed when alternative prey is absent. This further suggests the need for empirical research to work in concert with theoretical approaches to develop more realistic and predictive food-web models.

Introduction

Community ecology initially conceptualized trophic interactions as linear chains (Elton 1927), with an upper level potentially controlling the densities of the level immediately below, thus generating a trophic cascade (Hairston *et al.* 1960; Oksanen *et al.* 1981; Carpenter *et al.* 1985). However, it is now accepted that most communities do not follow this pattern as organisms are imbedded in complex food webs, blurring the notion of a trophic guild (*sensu* trophic coherence, Johnson et al. 2014) and the notion that widespread omnivory destabilize food webs (Polis & Holt 1992; Polis & Strong 1996).

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

Whether and how often species engage in intraguild predation or apparent competition strongly affects the long-term persistence (i.e. "temporal stability in community composition", Pimm 1984) of communities. Theory predicts that intraguild predation destabilizes communities because it reduces the parameter space where coexistence of IG-predator, IG-prey and shared prey is possible (Holt & Polis 1997), compared to that of trophic chain models (Oksanen *et al.* 1981). In most models with intraguild predation the possibility of 3-species persistence requires the IG-prey to be superior to IG-predators at exploitation competition for the shared resource (Holt 1997; Mylius *et al.* 2001; Kondoh 2008, among others). Furthermore, the occurrence of intraguild predation leads to a less efficient control of the shared prey populations because the IG-prey's equilibrium abundance is expected to decline towards extinction with increasing productivity (Mylius *et al.* 2001). This is especially important in agricultural systems, inherently highly productive, in which the introduction of several biocontrol agents may in fact reduce pest control. Curiously, empirical studies, mostly stemming from such systems, show that variable effects of intraguild predation on populations of the shared prey (e.g., Rosenheim *et al.* 1995; Janssen *et al.* 2006; Vance-Chalcraft *et al.* 2007; Messelink & Janssen 2014).

Some factors may, however, reduce such instability by promoting species coexistence, which generally occurs when conditions under which predator-predator interactions occur are constrained (reviewed in Novak 2013, appendix S1). For example, 3-species coexistence is enhanced if predators engage in IGP only when competition for the shared prey is high (Křivan 2000), or the shared prey is less profitable than the intraguild prey (Křivan & Diehl 2005). Other studies suggest that the inclusion of habitat structure (Janssen *et al.* 2007), inducible defences (Kratina *et al.* 2010; Nakazawa *et al.* 2010) or temporal refuges (Amarasekare 2008) increases the persistence of IGP communities, although this may depend on which species use refuges (Liu & Zhang 2013). Moreover, stage structure in the intraguild prey promotes 3-species coexistence, either by providing a stage refuge (Mylius *et al.* 2001; Rudolf & Armstrong 2008) or by inducing ontogenetic niche shifts in the predator (Hin *et al.* 2011). However, in all cases, the models still predict that overall community persistence is lower than that of a simple trophic chain. This lack of temporal stability is corroborated by empirical laboratory studies (Diehl & Feißel 2000; Montserrat *et al.* 2008b), but runs counter the ubiquity of intraguild predation and trophic level omnivory in natural systems (Bascompte & Melián 2005; Gagnon *et al.* 2011).

Discrepancies between IGP theory and empirical data suggest that some assumptions of theoretical models are not met in natural systems. In an effort to bring IGP models closer to real systems, while maintaining mathematical tractability, researchers have tested how the incorporation of an alternative food source affects the persistence of IGP communities (Heithaus 2001; Daugherty *et al.* 2007; Holt & Huxel 2007; Rudolf 2007). The general prediction is that providing alternative food to the intraguild prey leads to wider parameter regions of species coexistence (Daugherty *et al.* 2007; Holt & Huxel 2007), even if competitive superiority of IG-prey is precluded (Faria & Costa 2010). Instead, alternative food for the intraguild predator destabilizes the community (Daugherty *et al.* 2007; Holt & Huxel 2007). However, in the latter case, if the alternative food quality is high, then the intraguild predator may switch to feeding on the alternative resource, whereas the intraguild prey feeds on the shared prey (Ibid.). This again promotes coexistence by bringing the community structure closer to two linear food chains. Thus, a prevailing outcome of the ecological theory is that domains for persistence of communities with IGP increase when the strength of intraguild predation decreases. Indeed, weak interactions have long been recognized to stabilize ecosystems by dampening oscillations between consumers and

107 resources, thereby decreasing the probability of species extinctions (McCann *et al.* 1998),
108 and thus promoting community persistence (May 1972; Pimm & Lawton 1978; Paine 1992;
109 McCann *et al.* 1998; Emmerson & Yearsley 2004; Neutel *et al.* 2007; Gellner & McCann
110 2012; 2016). However, it remains unclear how the addition of species into a community
111 alters all other trophic interactions in the network (e.g., Bascompte et al 2006).

112 To address this question, we have considered if the fundamental trophic niches of
113 species (i.e., with all their potential interactions; Elton 1927) are always realized (Hutchinson
114 1957). Specifically, we explore how pairwise trophic interactions between species are
115 modified by the inclusion of other species in a simple community. We focus on *predation*
116 *rate* (in here, number of individuals consumed per day) as it is an excellent proxy for trophic
117 interaction strength, and is used both in ecological modelling (e.g. the equivalent to the
118 "catching efficiencies" in Kuijper *et al.* 2003) and in empirical research (Wootton &
119 Emmerson 2005; Novak & Wootton 2010; Novak 2013). Measurements of other relevant
120 non-trophic interactions, such as *competition*, would require experiments at the population
121 and community level that are beyond the scope of this manuscript.

122 Our core hypothesis was that increasing the number of species that are known to
123 interact when no alternative food is available will increase the number of realized links in
124 the more complex community (Box 1A). We mimicked different community modules (Sensu
125 Holt 1997) of increasing complexity using a community composed of two predatory mite
126 species as intraguild predators (*Euseius stipulatus* and *Neoseiulus californicus*, Acari:
127 Phytoseiidae), one species of herbivore mite as the shared prey (*Oligonychus perseae*, Acari:
128 Tetranychidae), and pollen (of several anemophilous species) as alternative food (González-
129 Fernández *et al.* 2009), all of which occur in the leaves of crops of avocado plants (*Persea*
130 *americana*) in Southestern Spain. Previous pairwise experimental designs have shown that
131 the interaction between *N. californicus* and *O. perseae* is stronger (i.e., predation rates are
132 higher) than that between *E. stipulatus* and this same prey (González-Fernández et al. 2009).
133 Moreover, pollen is an optimal food source for *E. stipulatus* but not for *N. californicus*
134 (Ferragut et al. 1987; González-Fernández et al. 2009). Finally, *E. stipulatus* and *N.*
135 *californicus* engage in size-dependent predator-prey interactions (Abad-Moyano *et al.*
136 2010). This knowledge was used to build predictions on realized trophic links occurring in
137 this system across community modules of increasing complexity (Box 1B). Specifically, we
138 predicted that: *i*) in "trophic chain" community configurations, both predator species will

139 interact with the herbivore (Box 1B, a.1.1. and a.1.2.); *ii*) in "apparent competition"
140 community configurations, only *E. stipulatus* will interact with both the herbivore and pollen
141 (Box 1B, b.1.1. and b.1.2.); *iii*) in "intraguild predation" community configurations, both IG-
142 predator species will interact with the IG-prey and the herbivore (Box 1B, c.1.1. and c.1.2.);
143 and iv) in "Intraguild predation and apparent competition" community configurations, only
144 adults and juveniles of *E. stipulatus* will establish trophic links with pollen (Box 1B, d.1.1. and
145 d.1.2.). These predictions were then tested through a series of experimental treatments to
146 assess which interactions were realized within each community module, by measuring IG-
147 prey/herbivore mortality and how consumption of prey translates into predator fecundity as
148 a result of these interactions. Specifically, we examined a) whether (IG-)predators feed on
149 each prey type; b) whether predation of (IG-)predators on one prey type is affected by the
150 presence of the other; c) whether predation of (IG-)predators on both prey, and of IG-prey
151 on the herbivore, is affected by the presence of alternative food; d) whether the presence of
152 alternative food affects predation of (IG-)predators on the two types of prey when they are
153 together; e) number of eggs produced by (IG-)predators when feeding on each prey type;
154 and f) whether egg-production is additive when (IG-)predators have more than one food
155 type available.
156
157
158 **Material and Methods**
159 All cultures and experiments were done in a climate chamber at 25±1ºC, 65±5% RH and
160 16:8h L:D (Light:Dark).
161 *Mite cultures*
162 Cultures of the predatory mite *E. stipulatus* were started in 2007 from ca. 300 individuals
163 collected from avocado trees located in the experimental station of "La Mayora". Rearing
164 units consisted of three bean plants (*Phaseolus vulgaris* L.) with 6-10 leaves, positioned
165 vertically, with the stems in contact with sponges (*ca.* 30 x 20 x 5 cm) covered with cotton
166 wool and a plastic sheet (27 x 17 cm), and placed inside water-containing trays (8 L, 42.5 x
167 26 x 7.5 cm). The plant roots were in contact with the water, and the aerial parts were
168 touching each other, forming a tent-like three-dimensional structure, where individuals
169 could easily walk from one plant to the other. Cotton threads were placed on the leaves, to
170 serve as oviposition sites for the females. Mites were fed *ad libitum* twice a week with

171 pollen of *Carpobrotus edulis* (cat´s claw) spread on leaves with a fine brush. *Euseius*
172 *stipulatus* is able to develop and reproduce on this food source (Ferragut *et al.* 1987). Every
173 three weeks, new rearings were made by transferring, leaves with mites and the cotton
174 threads filled with eggs to a new unit. The culture was found to be contaminated a few
175 times with *Tyrophagus* spp., a detritivorous mite species. In such instances, instead of
176 moving entire leaves, adult *E. stipulatus* females (ca. 300) were collected individually and
177 transferred to the new rearing unit.

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

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

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

188

189 *Community modules*

190 Experimental arenas to test the outcome of community modules have been described in
191 detail in Guzmán *et al.* (2016a). Briefly, a hole (6.5 cm Ø) was cut in a petri dish (9 cm Ø),
192 turned upside down, and then filled with an avocado leaf disc (7.5 cm Ø). The borders were
193 glued to a clay ring. Inside the petri dish, wet cotton wool ensured enough humidity to keep
194 leaves turgid. Petri dishes were then sealed with parafilm®. To prevent individuals from
195 escaping, a ring of Tanglefoot® was applied along the outer margin of the leaf disc. Cohorts
196 of *E. stipulatus* were made by transferring with a fine brush 400 eggs from the rearings to 2-
197 3 bean leaves placed on top of sponges (30 x 20 x 5 cm, approx.) covered with cotton wool,
198 inside water-containing trays (3.5 L), and with pollen of *C. edulis* as food. Cohorts of *N.*
199 *californicus* were made by placing 100 females during 48 h on 2-3 bean leaves infested with
200 *Tetranychus urticae* in containers similar to those used for the cultures. 10-14 days after egg
201 hatching, gravid predator females were randomly taken from these cohorts, and starved for
202 16 h in experimental containers similar to those above. Starvation was done to standardize

203 hunger among individuals, and to ensure that egg production in tested females was not
204 obtained from food ingested prior to the experiment. Predator juveniles (2-3 days old since
205 hatching) were taken from the cohorts when needed. Arenas containing the herbivore were
206 done as follows: Ten females of *O. perseae* were let to build nests and lay eggs on
207 experimental arenas during 4 days. The number of nests and eggs per nest on each arena
208 was counted at the onset of the experiment. Pollen in arenas assigned to treatments with
209 alternative food was supplied *ad libitum*, using a fine brush.

210 We performed experiments using two 'community blocks', depending on the identity
211 of the top predator (*N. californicus* or *E. stipulatus*). Throughout the text, the identity of
212 (IG)-predator and (IG)-prey will be indicated using the subscripts "ES" for *E. stipulatus* and
213 "NC" for *N. californicus*. Increased complexity in each of the two community blocks was
214 mimicked through the combination of the presence / absence of 4 factors: predator/IG-
215 predator, IG-prey, herbivore and alternative food. This resulted in the community modules
216 (Sensu Holt 1997) depicted in the X-axis of figures 1 and 2. These modules were: 1. Trophic
217 chain: either one *E. stipulatus* or *N. californicus* female was introduced in arenas containing
218 10 females of *O. perseae* (treatment # 1 in Figs 1 and 2). Arenas containing either one *E.*
219 *stipulatus* or one *N. californicus* female without herbivores (treatment # 2), and containing
220 10 *O. perseae* females without predators (treatment # 3) were done as controls for predator
221 oviposition rate and prey natural mortality, respectively. 2. Apparent competition: arenas
222 consisted of one female of either *E. stipulatus* or *N. californicus*, 10 females of *O. perseae*,
223 and pollen of *C. edulis* supplied *ad libitum* (treatment # 4). Similar arenas but without the
224 herbivores (treatment # 5) were made as controls for oviposition rates of predators on
225 pollen only, and without the IG-predator (treatment # 6) to assess potential effects of pollen
226 on the survival of the herbivore. 3. Intraguild predation: Because IGP is usually associated
227 with size differences between contestants, IG-predators and IG-prey consisted of adult
228 females and heterospecific juveniles, respectively. Arenas consisted of 10 *O. perseae*
229 females, either one *E. stipulatus* or *N. californicus* female, acting as the IG-predators, and 10
230 heterospecific juveniles, acting as the IG-prey (treatment # 7). Additionally, control
231 treatments were done to evaluate: the predation/mortality rate of *O. perseae* in the
232 presence of IG-prey but not of IG-predator (treatment # 8); the mortality rate of IG-prey in
233 the absence of both IG-predator and prey (treatment # 9), and in the presence of IG-
234 predator but not of herbivores (treatment # 10). 4. Intraguild predation - Apparent

235 competition: Arenas consisted of 10 *O. perseae* females, either one *E. stipulatus* or *N.*
236 *californicus* female, acting as the IG-predators, 10 heterospecific juveniles, acting as the IG-
237 prey, and pollen of *C. edulis* as alternative food, supplied *ad libitum* (treatment # 11). Similar
238 arenas to those above but i) without IG-predators (treatment # 12), ii) without herbivores
239 (treatment # 13), and iii) without IG-predators and herbivores (treatment # 14), were done
240 to evaluate predation of IG-prey on the herbivore in the presence of pollen, predation of IG-
241 predators on IG-prey in the presence of pollen, and mortality of IG-prey in the presence of
242 pollen, respectively.
243 Twenty-four hours later, the number of dead herbivores/IG-prey
244 (predation/mortality rate), and the number of eggs laid by predators/IG-predators
245 (oviposition rate) were recorded. Each treatment was replicated between 10 to 18 times.
246
247 *Data analyses*
248 Analyses were done separately for communities where either *E. stipulatus* or *N. californicus*
249 acted as the top-predator. Predation rates on herbivores and on IG-prey, and rates of
250 oviposition of IG-predators, were analysed using Generalized Lineal Models (GLM) assuming
251 a Poisson distribution as the distribution of data is expected to be skewed towards low
252 rather than high numbers, and a Log-link function as no overdispersion of the data was
253 detected. All the analyses were 3 full-factorial designs; the main factors that were included
254 in each analysis are explained below. We followed a backward elimination procedure as
255 follows: when the interaction among the three explanatory variables was not significant
256 (and the model had higher AIC), this interaction was removed from the model.
257 Subsequently, the same procedure was followed for second-order interactions. GLM
258 analyses were performed using the computer environment R (R Core Team 2017). After
259 significance of general models, additional software (package "contrast") was used to
260 perform planned comparisons to address specific questions (see Results). When specific sets
261 of data were used in multiple comparisons, their significance was corrected using the
262 sequential Bonferroni method.
263 Mortality of *O. perseae* females was analysed using data from treatments containing
264 this species. The model included the presence/absence of IG-predators, IG-prey and
265 alternative food as explanatory variables, as well as their interactions.

266 IG-prey mortality was analysed using data from treatments containing IG-prey (i.e.
267 predator juveniles). The full model included the presence/absence of the IG-predator, the
268 herbivore and alternative food as explanatory variables, as well as their interactions.
269 Oviposition rates were analysed using data from treatments containing IG-predators
270 (i.e., adult predators). The full model included the presence/absence of the herbivore, the
271 IG prey and alternative food as explanatory variables, as well as their interactions.
272
273 **Results**
274 *Communities with E. stipulatus as the (IG-)predator*
275 Mortality rates of the herbivore were significantly affected by the interaction between the
276 presence of IG-predator$_{ES}$ and IG-prey$_{NC}$ and between the presence of IG-prey$_{NC}$ and pollen
277 (Table 1a). Indeed, more prey died when IG-prey$_{NC}$ were together with the IG-predator$_{ES}$
278 than when the IG-predator$_{ES}$ was alone (Fig 1a, compare bar 1 to 7), but not more than
279 when the IG-prey$_{NC}$ was alone (Fig 1a, compare bar 8 to bar 7). Also, the presence of pollen
280 reduced herbivore mortality rates, but only in the absence of IG-prey$_{NC}$ (Fig 1a, compare
281 bars 4 and 6 to bars 11 and 12).
282 Mortality rates of the IG-prey$_{NC}$ were affected by all the double interactions except
283 that between the herbivore and pollen (Table 1b). Indeed, the presence of the IG-predator$_{ES}$
284 increased the mortality of IG-prey$_{NC}$, but only in the absence of pollen (Fig 1b, compare bars
285 7 and 10 to bars 11 and 13). Similarly, the presence of herbivores reduced mortality rates of
286 IG-prey$_{NC}$ when IG-predators$_{ES}$ were absent (Fig1b, compare bar 8 to 9), but not when they
287 were present (Fig1b, compare bar 7 to 10).
288 Planned comparisons revealed a) that IG-predators$_{ES}$ preyed on *O. perseae* (t_{81} =
289 2.74, P = 0.0076; Fig 1a, compare bars 1 and 3) and marginally on the IG-prey$_{NC}$ (t_{80} = -2.01,
290 P = 0.048, not significant after Bonferroni correction; Fig 1b, compare bar 9 to 10) when
291 each prey was offered alone; b) that adding IG-prey$_{NC}$ increased mortality of *O. perseae* (t_{81}
292 = -2.26, P = 0.026; Fig 1a, compare bar 1 to 7), but adding *O. perseae* did not influence
293 mortality of the IG-prey$_{NC}$ (t_{80} = -0.31, P = 0.755; Fig 1b, compare bar 10 to 7); c) that the
294 presence of pollen yielded a drastic reduction in predation of IG-predators$_{ES}$ on both the
295 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
296 << 0.001; Fig 1b, compare bar 10 to 13); d) that when both prey were available, the
297 presence of pollen did not affect herbivore mortality (t_{81} = 0.88, P = 0.379; Fig 1a, compare

298 bar 7 to 11), but did lead to lower IG-prey$_{NC}$ mortality (t_{80} = 3.58, P << 0.001; Fig 1b,
299 compare bar 7 to 11).
300 Oviposition rates of IG-predators$_{ES}$ were only affected by the presence of pollen
301 (main factor Pollen, Table 1c). However, further planned comparisons revealed that while
302 feeding on the herbivore stimulated egg production (t_{96} = 2.19, P = 0.021; Fig 1c, compare
303 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).
304
305 *Communities with N. californicus as the (IG-)predator*
306 Herbivore mortality was affected only by the interaction between IG-predator$_{NC}$ and IG-
307 prey$_{ES}$ (Table 2a). Indeed, mortality of herbivores was drastically affected by the presence of
308 IG-predators$_{NC}$ (Fig 2a, compare bar 1 to 3), but this effect was lesser in the presence of IG-
309 prey$_{ES}$ (Fig 2a, compare bar 1 to 7). Mortality of IG-prey$_{ES}$ was only affected by the presence
310 of pollen (Table 2b).
311 Paired comparisons revealed that a) IG-predators$_{NC}$ preyed on *O. perseae* (t_{90} = 3.32,
312 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,
313 compare bar 9 to 10), when each prey was offered alone; b) adding IG-prey$_{ES}$ reduced
314 mortality of *O. perseae* (t_{90} = 2.56, P = 0.012; Fig 2a, compare bar 1 to 7), but adding *O.*
315 *perseae* did not change mortality of the IG-prey$_{ES}$ (t_{86} = -0.93, P = 0.353; Fig 2b, compare bar
316 10 to 7); c) the presence of pollen did not affect mortality of either *O. perseae* (t_{90} = -0.43, P
317 = 0.669; Fig 2a, compare bar 1 to 4) or the IG-prey$_{ES}$ (t_{86} = 1.80, P = 0.075; Fig 2b, compare
318 bar 10 to 13); d) when both types of prey were available, the presence of pollen led to a
319 significant increase in mortality of *O.perseae* (t_{90} = -3.65, P << 0.001; Fig 2a, compare bar 7
320 to 11), but a significant decrease of mortality in IG-prey$_{ES}$ (t_{86} = 2.04, P = 0.044; Fig 2b,
321 compare bar 7 to 11).
322 Oviposition rates of IG-predators$_{NC}$ were affected by the main factor Herbivore and
323 the interaction between the IG-prey$_{ES}$ and pollen (Table 2c). Indeed, paired comparisons
324 revealed that e) eggs were produced when IG-predators$_{NC}$ were offered the herbivore alone
325 (t_{104} = 2.45, P = 0.016; Fig 2c, compare bar 1 to 2), but not when they were on arenas with
326 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,
327 P = 0.884; Fig 2c, compare bar 5 to 2) alone. Moreover, in the presence of the herbivore,
328 rates of oviposition were not influenced by the presence of pollen (t_{104} = -0.93, P = 0.352; Fig
329 2c, compare bar 1 to 4), but dramatically decreased in the presence of the IG-prey$_{ES}$ (t_{104} =

330 2.39, P = 0.019; Fig 2c, compare bar 1 to 7). However, when pollen was added to the system
331 with both prey types, IG-predators$_{NC}$ resumed oviposition to its maximum (t_{104} = -2.36, P =
332 0.020; Fig 2c, compare bar 7 to 11).
333
334 **Discussion**
335 In this study, we tested the effect of community structure on the realized interactions
336 within a community of predatory and herbivorous mites. Because in our system the
337 intraguild predator is the largest individual within a pair (as in most systems), we created
338 communities in which adults (IG-predators) belonged to one species and juveniles (IG-prey)
339 to the other, then inverted the species-stage identity in another set of communities. We
340 then measured predation and oviposition in communities with all possible combinations of
341 the presence of shared prey, the IG-prey, the IG-predator and an alternative food resource.
342 We show that adding species to a community increases the number of potential trophic
343 interactions, but not necessarily their occurrence. Indeed, despite the potential for module
344 configurations of communities with apparent competition and intraguild predation, all
345 modules could be described by linear food chains in our system (Box 1C).
346
347 **Basic properties of the system and implications for biocontrol**
348 In the trophic chain configurations, although *N. californicus* killed more *O. perseae*
349 females per day than *E. stipulatus*, oviposition rates were similar between predators. This is
350 in line with the finding that *E. stipulatus* can only forage on mobile *O. perseae* mites when
351 they wander outside nests, whereas *N. californicus* can penetrate inside nests and forage on
352 all the individuals residing within (González-Fernández *et al.* 2009). This suggests that *E.*
353 *stipulatus* is the most efficient predator converting food into eggs, but that *N. californicus* is
354 more efficient at reducing herbivore populations. Which of these strategies is best for
355 biological control will depend on the ecological condition: if outbreaks of prey are confined
356 in time, it may be more efficient to select a biocontrol agent that feeds more, as in
357 "inundative" biocontrol strategies, whereas controlling and keeping resident populations at
358 low levels may be best achieved with a predator with a strong numerical response, as in
359 "innoculative" biocontrol strategies (Van Driesche *et al.* 2007). Moreover, unlike *N.*
360 *californicus*, *E. stipulatus* fed and oviposited on pollen. This may allow the latter to remain in
361 the field for longer periods, as actually observed in field surveys (González-Fernández *et al.*

362 2009). Such temporal niche partitioning may facilitate the presence of the two predators in
363 the same fields (Otto *et al.* 2008).

364 Our results also revealed asymmetry in the intraguild predation between *E.*
365 *stipulatus* and *N. californicus*, with adults of the former preying upon juveniles of the latter,
366 but not the reverse. Because *N. californicus* is likely the best competitor for the shared prey
367 (González-Fernández *et al.* 2009), coexistence between predators is thus possible in this
368 system (Holt & Polis 1997). Yet, the simultaneous presence of the two predators is likely to
369 have little effect upon the densities of the shared prey. Indeed, whereas adding
370 *N.californicus* adult intraguild predators to an arena with *E. stipulatus* juveniles results in
371 higher shared prey densities as compared to the presence of *N. californicus* adults alone
372 with the shared prey, the reverse is not true when adding adult *E. stipulatus* to an arena
373 with juveniles *N. californicus*. Thus, the net effect of these interactions upon prey density is
374 probably negligible. This is corroborated by field studies (Montserrat *et al.* 2013). However,
375 the presence of alternative food (i.e. pollen) contributed to reduce trophic interactions
376 between predator species resulting in community configurations that could enhance pest
377 control. Thus, supplying alternative and preferred food to the IG-predator is probably
378 detrimental to populations of *O. perseae*. Again, this finding is in line with field observations
379 (Montserrat *et al.* 2013).

380 Optimal foraging theory predicts that species engage in trophic interactions on more
381 than one food source when these are available (Pulliam 1974). Here, we show that *E.*
382 *stipulatus* acting as intraguild predators feeds on the herbivore, *O. perseae*, on the intraguild
383 prey, *N. californicus*, and on the alternative food, pollen, when each of these are presented
384 alone. However, in the presence of pollen *E. stipulatus* reduces predation rates on both prey
385 species. This may be explained by the fact that pollen is the most profitable food for this
386 species, as found here and in other studies (Ferragut *et al.* 1987; McMurtry & Croft 1997;
387 Bouras & Papadoulis 2005; González-Fernández *et al.* 2009). Similarly, *N. californicus* adults
388 and juveniles ceased foraging on other food sources in presence of the herbivores. These
389 results suggest that realized interactions hinge on the presence of the most profitable food
390 source. In presence of the optimal food source for each of the two secondary consumers,
391 communities tended to be reduced to two simple trophic chains. Indeed, in the most
392 complex communities studied here, with all 5 species present, the presence of the optimal
393 food originated the split of the community into two trophic chains, one with *E. stipulatus*

394 feeding on pollen and the other with *N. californicus* feeding on the herbivore (Box 1 d),
395 compare d.1.1. and d.1.2. with d.2.1. and d.2.2.).
396 Another factor that contributed to the linearization of the food web was that, when
397 both the IG-prey and the shared prey were together, IG-predators$_{ES}$ preyed mainly on the
398 IG-prey. Indeed, mortality of *O. perseae* in presence of the IG-prey, *N. californicus*, was not
399 affected by the presence of the IG-predator *E. stipulatus*. Furthermore, mortality of IG-
400 prey$_{NC}$ was significantly higher in treatments with presence of the IG-predator, compared to
401 the control without them. This suggests that mortality in the herbivore was mainly inflicted
402 by the IG-prey, *N. californicus*, and that the IG-predator *E. stipulatus* preyed preferentially
403 on the IG-prey *N. californicus*. This could be explained by *E. stipulatus* having no access to *O.*
404 *perseae* eggs or females located inside the nests (Montserrat *et al.* 2008a; González-
405 Fernández *et al.* 2009), which leads to higher encounter rates between *E. stipulatus* and *N.*
406 *californicus* than between *E. stipulatus* and *O. perseae*. Indeed, *E. stipulatus* forages only on
407 mobile stages that wander outside nests (Montserrat *et al.* 2008a; González-Fernández *et al.*
408 2009). *Neoseiulus californicus*, however, can penetrate *O. perseae* nests, and thus may feed
409 on them. Therefore, the realized community was that of a 4-level trophic chain (Box 1,
410 c.2.1.). In the other community block, when *N. californicus* acted as the IG-predator,
411 mortality of *O. perseae* females was similar in all communities with the IG-prey *E. stipulatus*
412 present, irrespective of the presence of IG-predators$_{NC}$. Furthermore, mortality of IG-prey$_{ES}$
413 did not differ between treatments with and without the IG-predator$_{NC}$, indicating that *N.*
414 *californicus* females did not forage on *E. stipulatus* juveniles. These results suggest that, in
415 presence of IG-prey (juveniles of *E. stipulatus*), the IG-predator$_{NC}$ ceased to forage on either
416 herbivore or IG-prey, likely because IG-prey$_{ES}$ interferes with the foraging activities of IG-
417 predators$_{NC}$. Thus, the realized community was that of a trophic chain composed of the IG-
418 prey, the herbivore and the plant, with the IG-predator not interacting at all (Box 1, c.2.2.).
419 This can be explained by IG-predators$_{NC}$ avoiding foraging on a patch where its offspring
420 (future) IG-predator is also there. In line with this, Abad-Moyano *et al.* (2010) reported that
421 the presence of *E. stipulatus* immatures exerted non-lethal IG-effects on *N. californicus*
422 females, causing daily oviposition to decrease over time despite the availability of the
423 shared prey was kept constant. In any case, here, the trophic links are again linear, with *N.*
424 *californicus* being excluded from the realized community (Box 1, c.2.2.). Together, our

results show that none of the complex communities was actually realized, they were all trophic chains.

The return of the trophic chain: **Fundamental vs realized trophic interactions**

By combining data of mortality and oviposition at different community structures, we could determine who eats whom in a simple food web. Although this approach is powerful, it does have its limitations. Indeed, it assumes additive effects of conversion efficiencies of pairwise interactions. For example, if feeding on a prey item allows predators to better convert the food provided by another prey, this cannot be detected in our approach (i.e., indirect effects on conversion efficiency). Furthermore, it may be largely unfeasible to extend this approach to more complex food webs, although it is becoming clear that we need to know how food is transformed into predator offspring in order to fully understand food webs in nature (Neutel & Thorne 2014). Indeed, such full-factorial studies are extremely rare in the literature (but see Schmitz & Sokol-Hessner 2002; Otto *et al.* 2008).

Connectance is a fundamental measure of food-web complexity that describes the proportion of realized interactions amongst all possible ones (May 1972). It is becoming increasingly evident that connectance is generally much lower than the number of potential interactions (Beckerman *et al.* 2006). Identifying trophic links in food webs, however, is not a simple task. Molecular methods are useful to process field data and they deliver reliable information on who eats whom, but such tools currently only provide semi-quantitative estimates of predation, and they are expensive (Birkhofer *et al.* 2017). Another possible approach to measure connectance is by observations in the field (Dunne *et al.* 2002; Tylianakis *et al.* 2007; Carnicer *et al.* 2009; Lazzaro *et al.* 2009; Plein *et al.* 2013; Baiser *et al.* 2016; Lemos-Costa *et al.* 2016). Although this approach allows including a high number of species in the observations, it suffers from two main shortfalls: (a) it is generally only possible to undertake it in systems with two trophic levels in which one are primary producers, for example in plant pollinator networks (but see Bukovinszky *et al.* 2008; Neutel & Thorne 2014), or in systems where trophic interactions are detectable long after the actual events, as in parasitoid/host interactions or via the analysis of gut contents; and (b) it does not account for how foraging on a given resource translates into consumer offspring (but see Bukovinszky *et al.* 2008; Vázquez *et al.* 2015). Observations in controlled

457 experimental settings, in contrast, deliver quantitative estimates of predation rates and
458 concomitant offspring production, especially when trophic links, and their strength, are
459 estimated by confronting pairs of species. Alternatively, modelling complex systems provide
460 relative estimates on interaction strengths that go beyond pair-wise interactions (Moya-
461 Laraño *et al.* 2012; Moya-Laraño *et al.* 2014). Yet, one-on-one approaches may ignore
462 emergent indirect effects of having several species together (Wootton 1994; Dambacher &
463 Ramos-Jiliberto 2007). For instance, *Cancer productus*, a crab native to the Northwest
464 Pacific, consumes equal amounts of native oysters and of invasive drill oysters when each
465 type of prey is offered alone, but when they are offered together crabs interact with the
466 native oyster species only (Grason & Miner 2012). Therefore, if trophic links are not
467 evaluated in presence of all species in the community, one may reach erroneous conclusions
468 on the strength of the interaction (Guzmán *et al.* 2016b; Fonseca *et al.* 2017) and
469 overestimate connectance in food webs. We show that all communities ended up becoming
470 a sum of one or more trophic chains (Box 1C). Thus, the fundamental trophic niche of
471 species in this system (i.e., the food items that species are potentially able to feed on) is
472 larger than the realized trophic niche (i.e., the food items that species actually feed on when
473 present in combinations exceeding the individual pairwise interactions (Hutchinson 1961)).
474 Therefore, our results suggest that some food webs may be less complex than previously
475 thought in terms of the frequency and strength of IGP.

476 Theoretical models exploring persistence in three-species communities with IGP find
477 a limited parameter space for coexistence of IG-predator and IG-prey (e.g. Mylius *et al.*
478 2001), but field observations show that IGP is actually widespread (Polis 1991). Our results
479 suggest that IGP in some systems might actually be occasional, as predators will tend to
480 forage on the most profitable food, which generally is not the IG prey (Polis *et al.* 1989). In
481 line with this, some natural systems have shown that communities with IGP actually show
482 dynamics that are compatible with linear food chains, rather than with IGP (Borer *et al.*
483 2003). Therefore, predators may coexist because they rarely engage in IGP, and complexity
484 may be over-estimated (Magalhães *et al.* 2005). This agrees with food web theory stating
485 that weak trophic interactions promote the persistence of communities (May 1972; Paine
486 1992; McCann *et al.* 1998, among others). For example, Hiltunen *et al.* (2014) found long-
487 term cycling dynamics when modelling a three-species planktonic food web with IGP, with
488 interaction strength between IG-predator and IG-prey set to be much weaker to that

between IG-predator and the shared resource. Our results suggest that increasing the number of potentially interacting species results in most species interactions becoming weaker. Indeed, the structure of interactions among species in natural communities is characterized by many weak and few strong interactions (Paine 1992; McCann *et al.* 1998), and such skewedness towards weak interactions is crucial to food web persistence (Neutel *et al.* 2002; 2007; Montoya *et al.* 2009; Neutel & Thorne 2014). Because a species' fundamental trophic niche (all of its potential interactions) is unlikely to be realized at a particular place or time, it is crucial to determine the resources which species in a community actually feed upon, and under what circumstances. Therefore, unravelling realized food webs, (i.e., interaction strengths across different nodes and trophic levels, including indirect effects) may be key to understanding these ecological networks and their persistence.

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Wootton, J.T. & Emmerson, M. (2005). Measurement of interaction strength in nature. *Annual Review of Ecology, Evolution, and Systematics*, 36, 419-444.

720 Table 1. Results of Generalized Linear Models applied to a) herbivore mortality rates, b) IG-
721 prey (juveniles of *N. californicus*) mortality rates, and c) (IG-)predator (females of *E.*
722 *stipulatus*) oviposition rates. All the analyses were 3 full-factorial designs. When interactions
723 among the three explanatory variables were not significant, and if the new model yielded a
724 lower AIC, they were removed from the model. Subsequently, the same procedure was
725 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	-1.755	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			

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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			

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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*			

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Table 2. Results of Generalized Linear Models applied to a) herbivore mortality rates, b) IG-prey (juveniles of *E. stipulatus*) mortality rates, and c) (IG-)predator (females of *N. californicus*) oviposition rates. All the analyses were 3 full-factorial designs. When interactions among the three explanatory variables were not significant, and if the new model yielded a lower AIC, they were removed from the model. Subsequently, the same procedure was 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	-1.954	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*			

785 Box 1. **A: Fundamental community modules** included in this study. a) trophic chain, b)
786 apparent competition, c) intraguild predation, and d) intraguild predation and apparent
787 competition. From a) to d) the complexity of the community is increased via increasing the
788 number of species and the number of interactions among them. **B: Predicted trophic links**
789 that have been observed using pairwise experimental settings**. C: Realized trophic links**
790 occurring across community modules of increasing complexity, obtained from the
791 experiments presented here, where interactions are measured in the presence of other
792 components of the community. SC stands for secondary consumer, PC for primary
793 consumer, PP for primary producer, and AF for alternative food. SC1 and SC2 are phytoseiid
794 predatory mites, i.e. *Euseius stipulatus* and *Neoseiulus californicus*, respectively, PC is the
795 tetranychid herbivore mite *Oligonychus perseae*, AF is pollen of *Carpobrotus edulis*, and PP
796 is the avocado *Persea americana*. Solid arrows indicate negative direct interactions (who
797 eats whom), whereas dotted and dashed arrows in Box 1A indicate negative indirect
798 interactions (apparent competition and competition).
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800 Figure 1. Mortality rates (average ± S.E.) of a) herbivore prey (*Oligonychus perseae* females)
801 and b) IG-prey (*Neoseiulus californicus* juveniles), and c) oviposition rates (average ± S.E.) of
802 IG-predators (*Euseius stipulatus* females), in 14 different treatments defined by presence or
803 absence of either IG-predators, IG-prey, herbivores or alternative food (pollen), depicted in
804 the lower part of the figure, that mimicked four different community configurations and
805 their respective controls.
806
807 Figure 2. Mortality rates (average ± S.E.) of a) herbivore prey (*Oligonychus perseae* females)
808 and b) IG-prey (*Euseius stipulatus* juveniles), and c) oviposition rates (average ± S.E.) of IG-
809 predators (*Neoseiulus califonicus* females), in 14 different treatments defined by presence
810 or absence of either IG-predators, IG-prey, herbivores or alternative food (pollen), depicted
811 in the lower part of the figure, that mimicked four different community configurations and
812 their respective controls.
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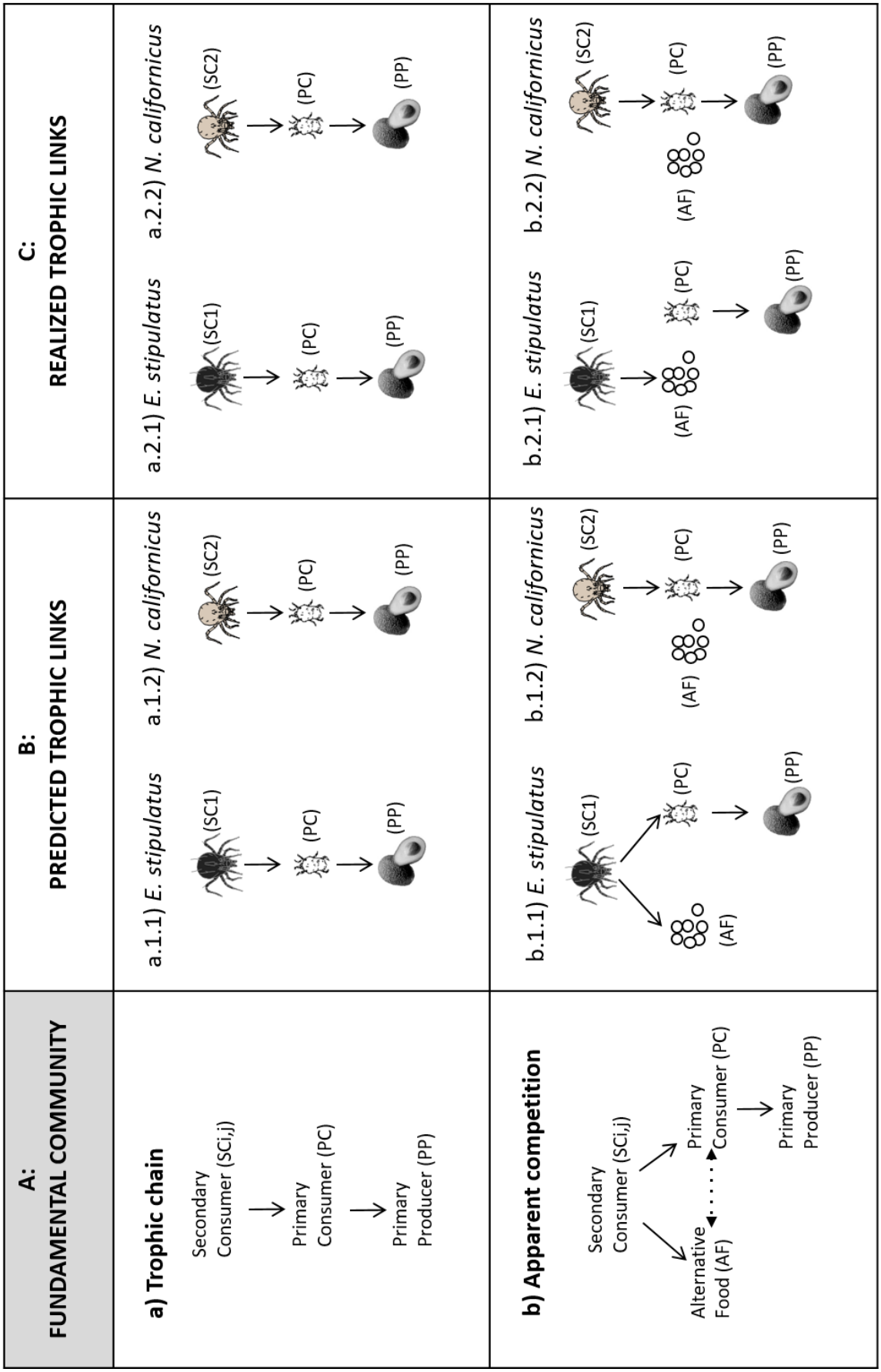
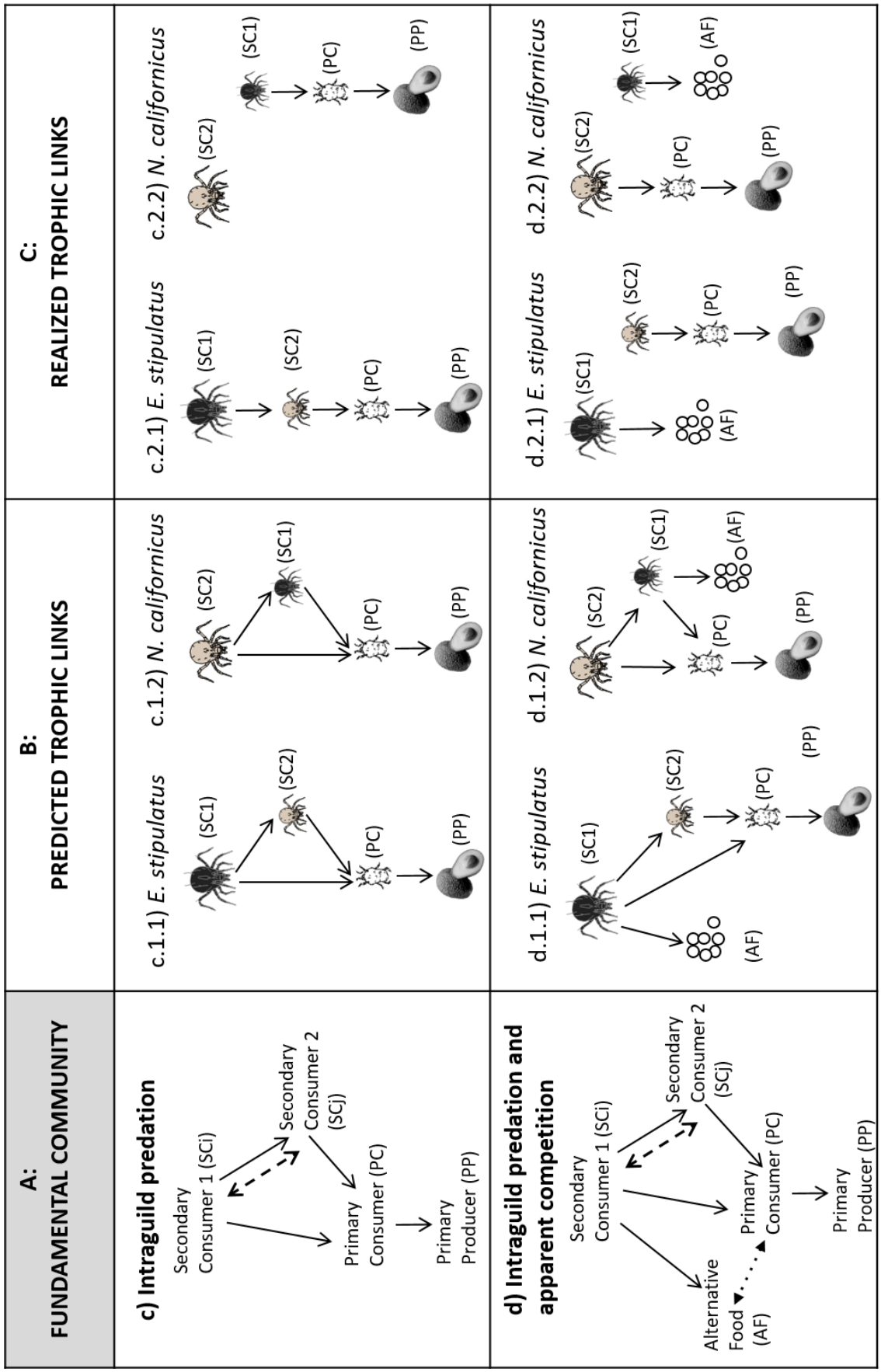
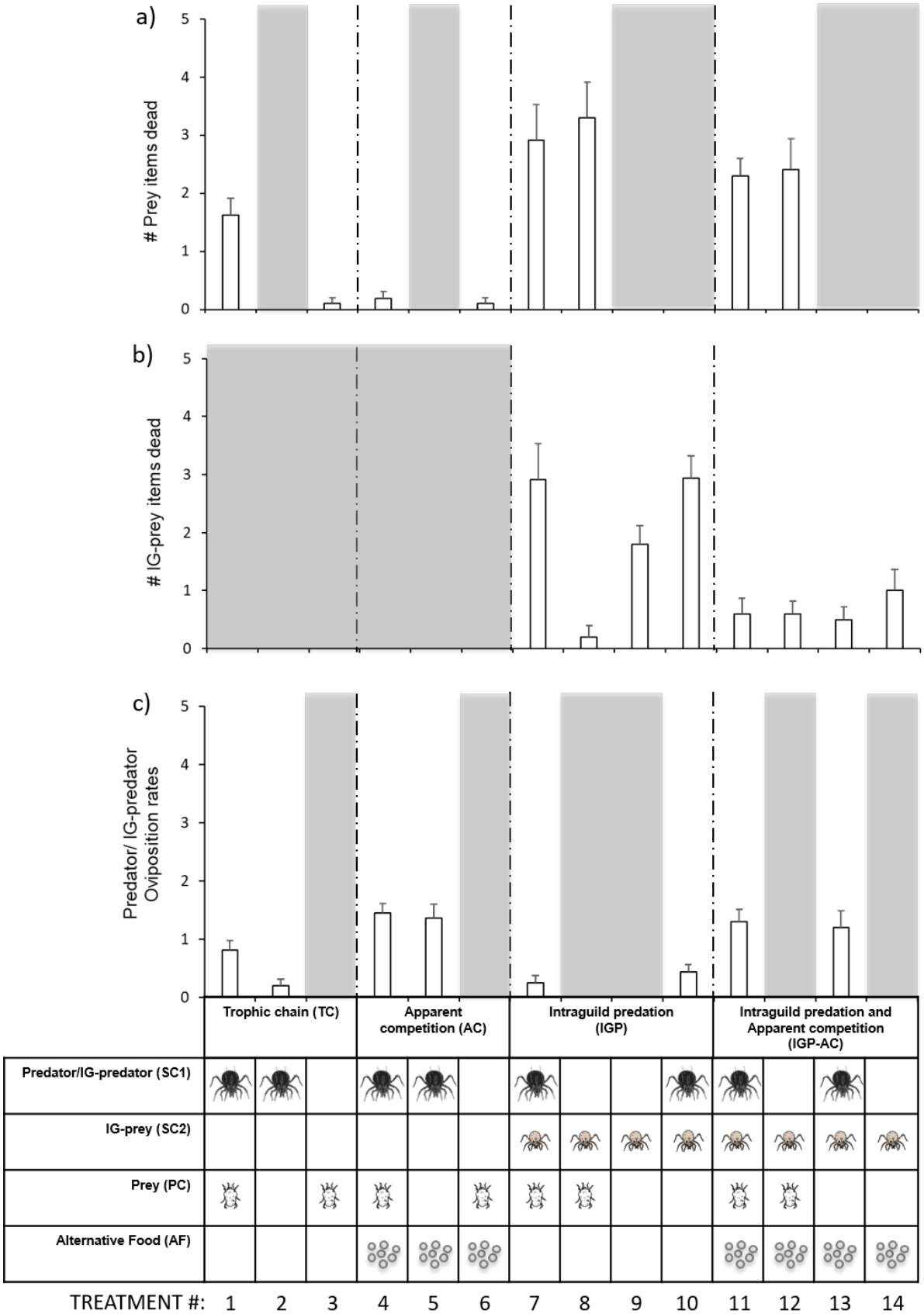
815 Box 1.


A:
FUNDAMENTAL COMMUNITY
B:
PREDICTED TROPHIC LINKS
C:
REALIZED TROPHIC LINKS
a) Trophic chain
Secondary Consumer (SCi,j)
Primary Consumer (PC)
Primary Producer (PP)
a.1.1) E. stipulatus
a.1.2) N. californicus
(SC1)
(SC2)
(PC)
(PP)
a.2.1) E. stipulatus
a.2.2) N. californicus
b) Apparent competition
Secondary Consumer (SCi,j)
Alternative Food (AF)
Primary Consumer (PC)
Primary Producer (PP)
b.1.1) E. stipulatus
b.1.2) N. californicus
(AF)
b.2.1) E. stipulatus
b.2.2) N. californicus

816 Box 1 (cont.)



817 Figure 1.



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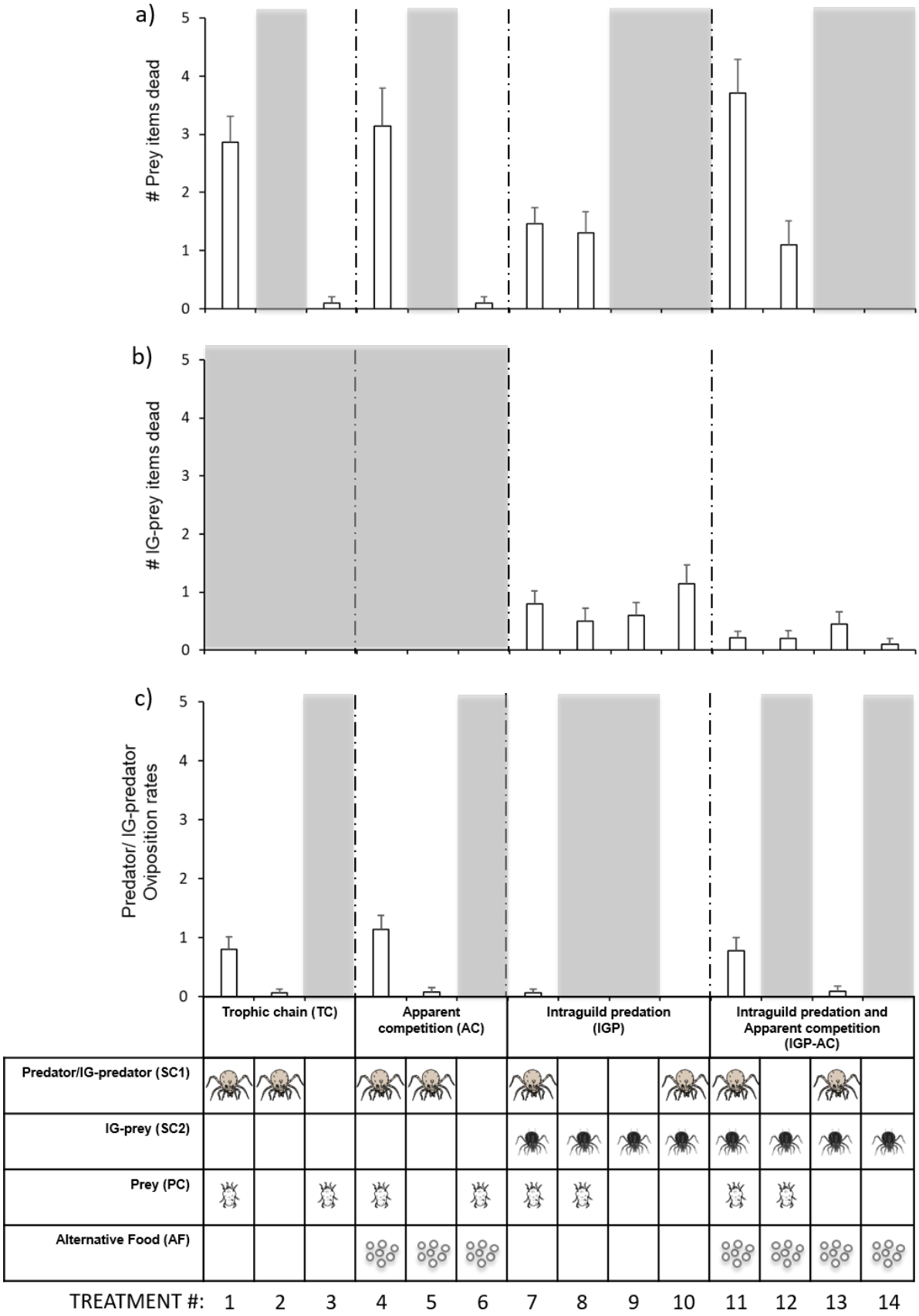
819 Figure 2.



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