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

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Abstract

The mathematical exploration of small assemblages of interacting species (community modules) has proven key to understand emergent properties of ecological communities. These models use differential equations to study pairwise relations between species. However, as community modules become more complex, one may wonder whether all potential interactions are effectively realized. Here, we use community modules to experimentally explore whether the number of trophic links among species increases as another aspect of complexity increases; i.e., the number of species that are known to feed on each other in pair-wise trials. To this aim, we use 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 alternative food, with the potential for (intraguild) predation and (apparent) competition to be expressed. Using a series of controls, we could assess whether the presence of one species affected the abundance 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 confronted in pairs do not necessarily occur when other components of the community are present. Consequently, food web complexity may be erroneously over-estimated in theoretical community modules that are parameterized based on pair-wise interactions observed when alternative prey is absent.

Introduction

Community ecology has traditionally viewed trophic interactions as linear chains, with an upper level controlling the densities of the level immediately below, generating a trophic cascade (Hairston *et al.* 1960; Oksanen *et al.* 1981; Carpenter *et al.* 1985). However, it is by 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 and the notion that widespread omnivory would 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). 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. stability) 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 exploitative 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 into intraguild predation 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 system stability, although this may depend on which species use refuges (Liu & Zhang 2013). Moreover, stage structure in the intraguild prey promotes stability, 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 stability is lower than that of a simple trophic chain. This lack of 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 theory of IGP and 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 affected stability (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 quality of the alternative food is high enough, then the intraguild predator switches to feeding on the alternative food, 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.

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

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

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

Material and Methods

All cultures and experiments were done in a climate chamber at 25±1ºC, 65±5% RH and 16:8h L:D (Light:Dark).

Mite cultures

Cultures of the predatory mite *E. stipulatus* were started in 2007 from ca. 300 individuals collected from avocado trees located in the experimental station of "La Mayora". Rearing units consisted of three bean plants (*Phaseolus vulgaris* L.) with 6-10 leaves, positioned vertically, with the stems in contact with sponges (*ca.* 30 x 20 x 5 cm) covered with cotton wool and a plastic sheet (27 x 17 cm), and placed inside water-containing trays (8 L, 42.5 x 26 x 7.5 cm). The plant roots were in contact with the water, and the aerial parts were touching each other, forming a tent-like three-dimensional structure, where individuals could easily walk from one plant to the other. Cotton threads were placed on the leaves, to serve as oviposition sites for the females. Mites were fed *ad libitum* twice a week with pollen of *Carpobrotus edulis* (cat´s claw) spread on leaves with a fine brush. *Euseius stipulatus* is able to develop and reproduce on this food source (Ferragut *et al.* 1987). Every three weeks, new rearings were made by transferring, leaves with mites and the cotton threads filled with eggs to a new unit. The culture was found to be contaminated a few 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 37ºC 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 << 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 << 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 << 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

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

Theoretical models exploring persistence in three-species communities with IGP find a limited parameter space for coexistence of IG-predator and IG-prey (e.g. Mylius *et al.* 2001), but field observations show that IGP is actually widespread (Polis 1991). Our results suggest that IGP in some systems might actually be occasional, as predators will tend to forage on the most profitable food, which generally is not the IG prey (Polis *et al.* 1989). In line with this, some natural systems have shown that communities with IGP actually show dynamics that are compatible with linear food chains, rather than with IGP (Borer *et al.* 2003). Therefore, predators may coexist because they rarely engage in IGP, and complexity may be over-estimated (Magalhães *et al.* 2005). This agrees with food web theory stating that weak trophic interaction promote the persistence of communities (May 1972; Paine 1992; McCann *et al.* 1998, among others). For example, Hiltunen *et al.* (2014) found long-term cycling dynamics when modelling a three-species planktonic food web with IGP, with 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 the higher the number of potential interacting species is, the weaker most of interactions among species become. Indeed, the structure of interactions among species in natural communities is characterized by many weak interactions and few strong interactions (Paine 1992; McCann *et al.* 1998), and such skewedness towards weak interactions is crucial to food web stability (Neutel *et al.* 2002; 2007; Montoya *et al.* 2009; Neutel & Thorne 2014). Because a specie's fundamental niche (all of its potential interactions) is unlikely to be realized at particular places or times, it is crucial to determine on which resources do 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 thus key to understanding these ecological networks and their persistence.

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

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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*			

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).
771
772 Figure 1. Mortality rates (average ± S.E.) of a) herbivore prey (*Oligonychus perseae* females)
773 and b) IG-prey (*Neoseiulus californicus* juveniles), and c) oviposition rates (average ± 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 ± S.E.) of a) herbivore prey (*Oligonychus perseae* females)
780 and b) IG-prey (*Euseius stipulatus* juveniles), and c) oviposition rates (average ± S.E.) of IG-
781 predators (*Neoseiulus califonicus* 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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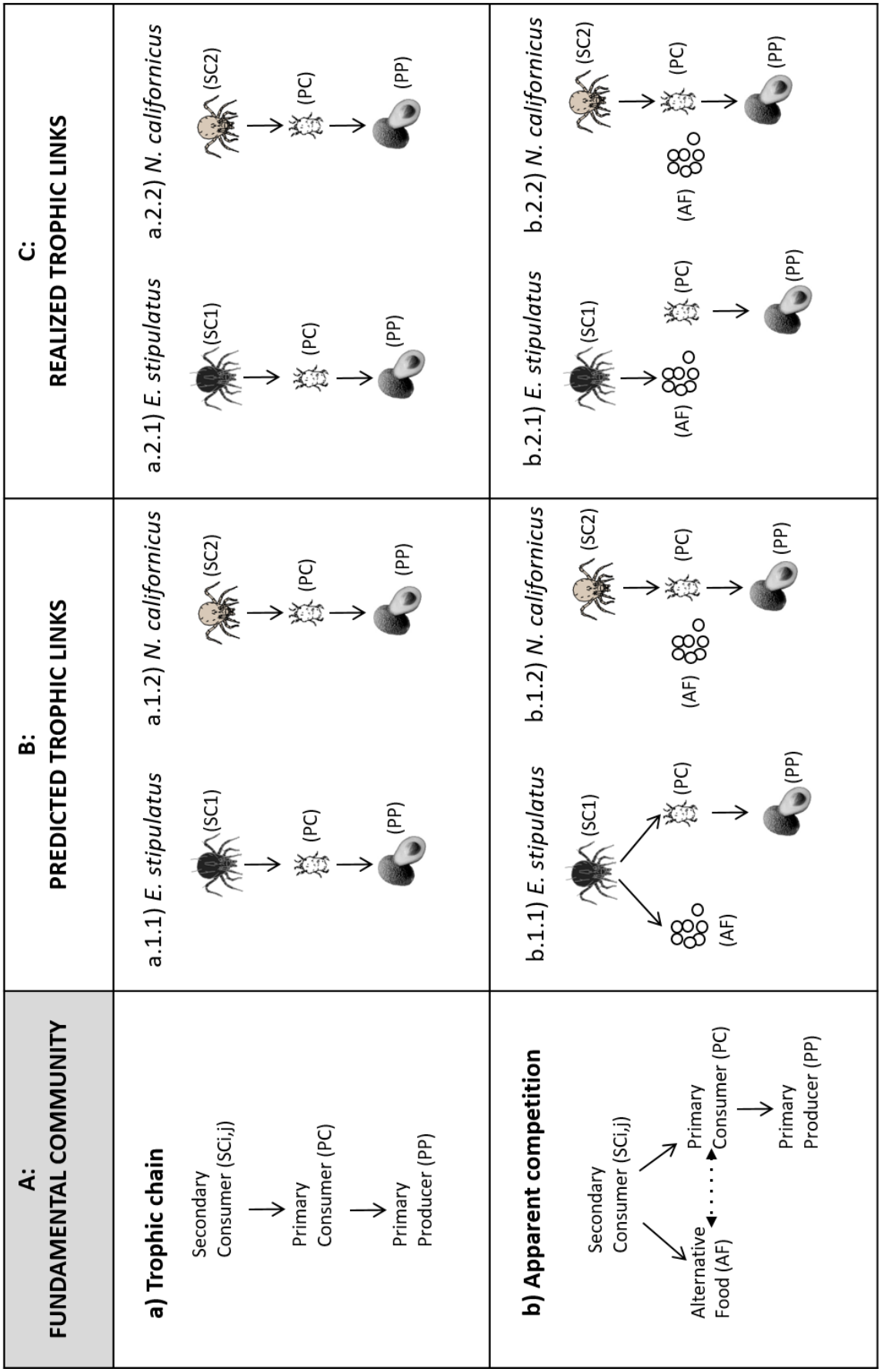
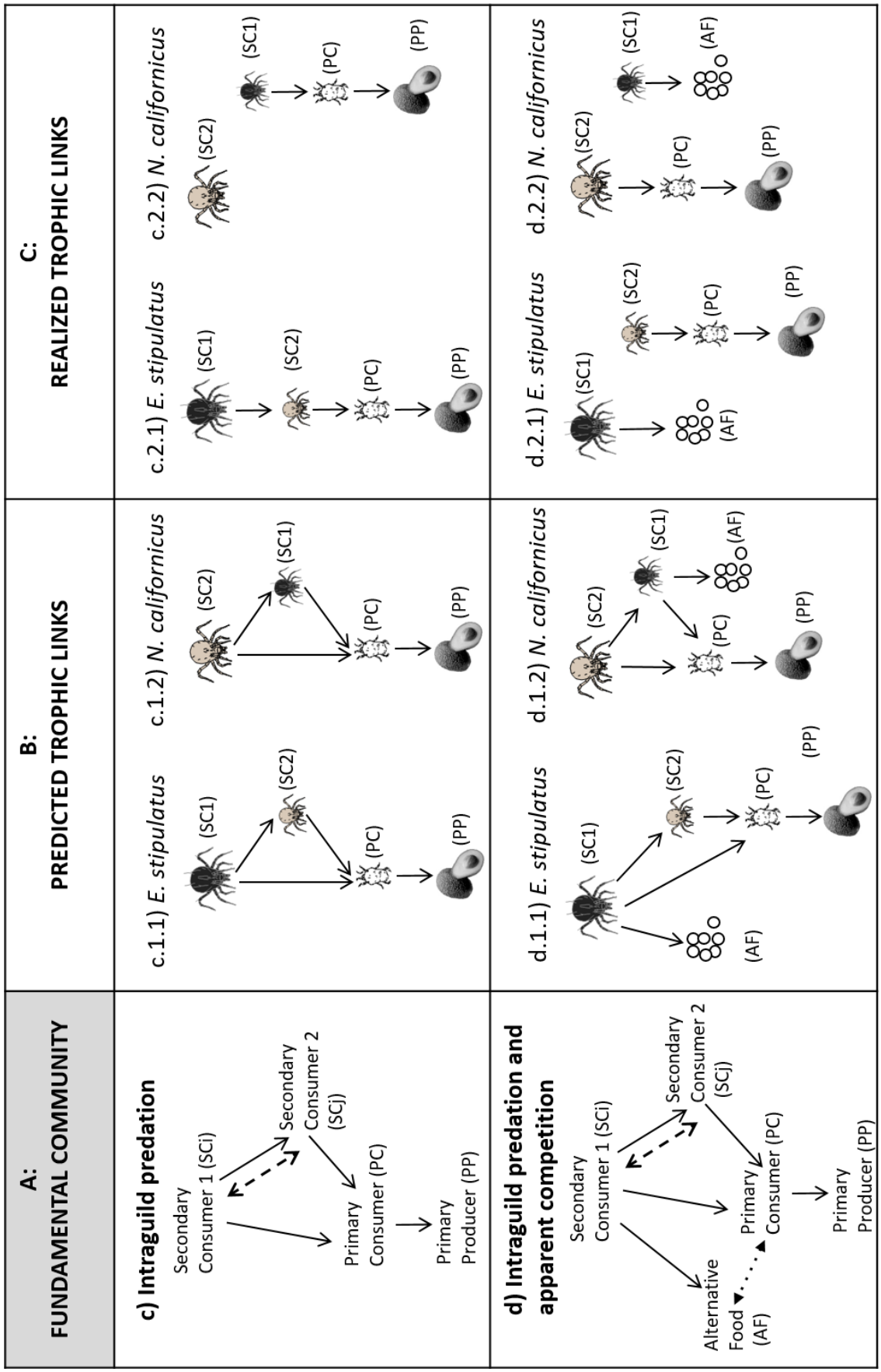
787 Box 1.


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
a.2.1) E. stipulatus
a.2.2) N. californicus
(SC1)
(SC2)
(PC)
(PP)
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
b.2.1) E. stipulatus
b.2.2) N. californicus
(AF)

Box 1 (cont.)


A:
FUNDAMENTAL COMMUNITY
B:
PREDICTED TROPHIC LINKS
C:
REALIZED TROPHIC LINKS
c) Intraguild predation
Secondary Consumer 1 (SCi)
Secondary Consumer 2 (SCj)
Primary Consumer (PC)
Primary Producer (PP)
c.1.1) E. stipulatus
c.1.2) N. californicus
c.2.1) E. stipulatus
c.2.2) N. californicus
(SC1)
(SC2)
(PC)
(PP)
d) Intraguild predation and apparent competition
Alternative Food (AF)
d.1.1) E. stipulatus
d.1.2) N. californicus
d.2.1) E. stipulatus
d.2.2) N. californicus
(AF)

789 Figure 1.

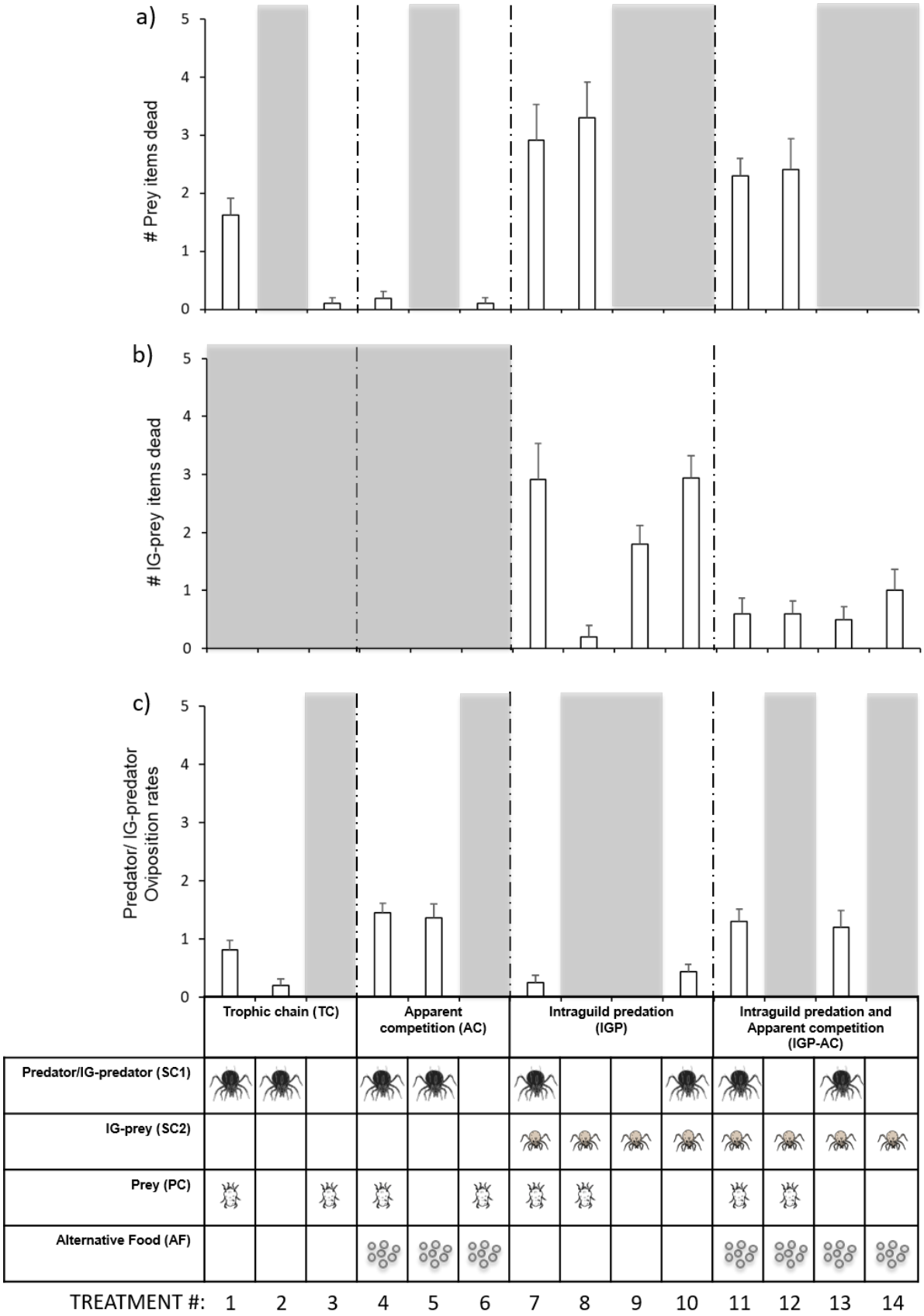


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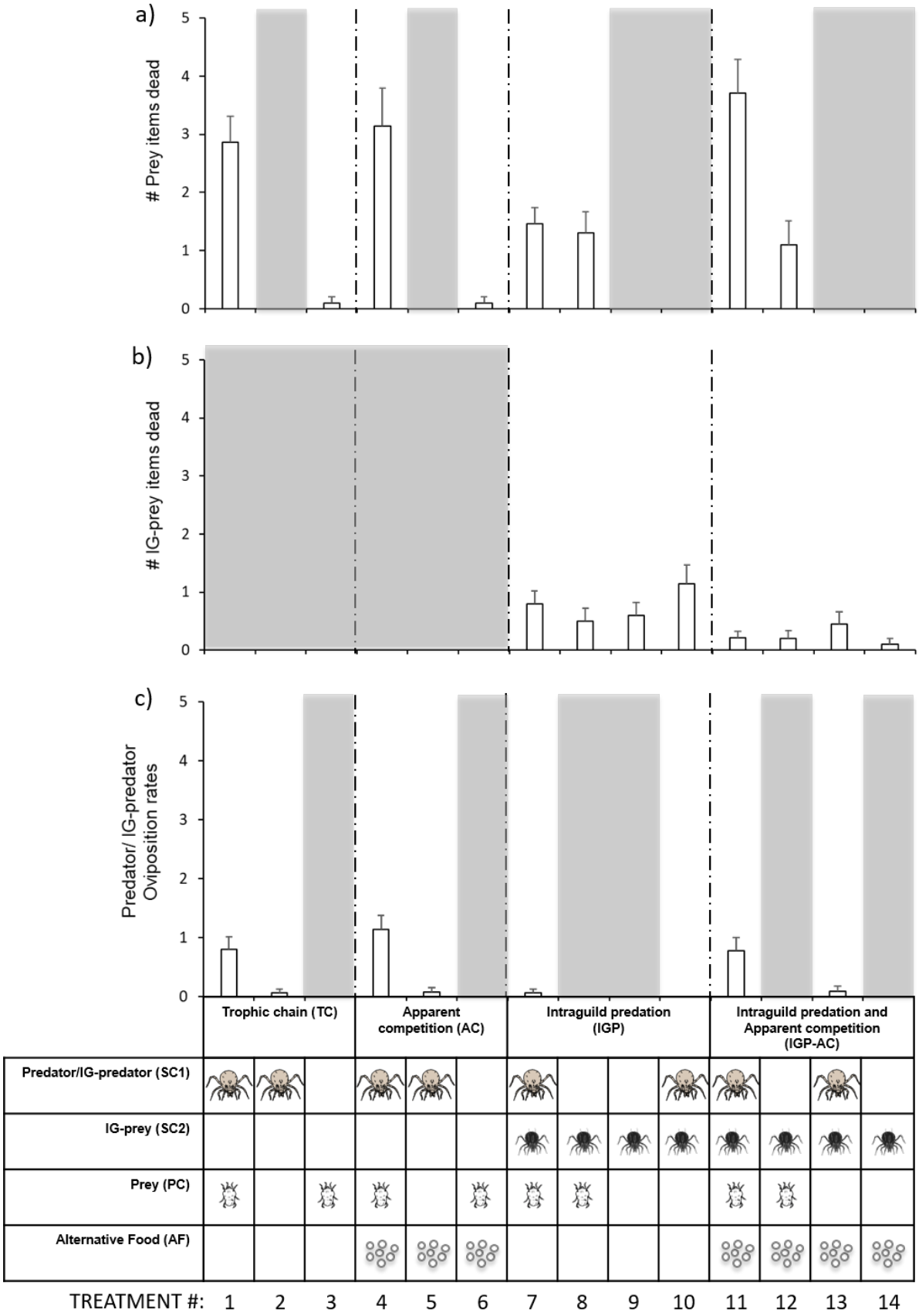
Figure 2.


a)
Prey items dead
b)
IG-prey items dead
c)
Predator/ IG-predator Oviposition rates
Trophic chain (TC)
Apparent competition (AC)
Intraguild predation (IGP)
Intraguild predation and Apparent competition (IGP-AC)
Predator/IG-predator (SC1)
IG-prey (SC2)
Prey (PC)
Alternative Food (AF)
TREATMENT #: 1 2 3 4 5 6 7 8 9 10 11 12 13 14