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 numbers of another, or its conversion of food into offspring. We found that increasing the number of potential interactions did not result in realized more complex 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 in terms of connectance may be erroneously over-estimated in theoretical community modules that are parameterized based on pair-wise interactions observed when alternative prey is not present.

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 (Holt 1997), and among those, intraguild predation, in which two consumers 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) are the most common (Bascompte & Melián 2005).

Whether and how often species engage in intraguild predation or apparent competition strongly affects community stability and composition. Indeed, theory predicts that intraguild predation destabilizes communities (Holt & Polis 1997). Some factors may, however, reduce such instability by promoting species coexistence, which generally occurs via a reduction in the strength of intraguild predation. For example, stability 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). The occurrence of intraguild predation is also expected to lead to a less efficient control of the shared prey populations (Mylius *et al.* 2001). This is especially important in biological control systems, in which the introduction of several biocontrol agents may in fact reduce pest

control. Curiously, empirical studies, mostly stemming from such systems, show that intraguild predation may have variable effects on populations of the shared prey (e.g., Rosenheim *et al.* 1995; Janssen *et al.* 2006; Vance-Chalcraft *et al.* 2007; Messelink & Janssen 2014). This discrepancy between theory and data suggests that some assumptions of theoretical models are not met in natural systems.

Models of intraguild predation consider that the intraguild predator, the intraguild prey and the shared prey form an isolated community module. Although this certainly increases the tractability of models and of their respective experimental tests, it is a significant simplification of real ecosystems. To bring models closer to real systems, while maintaining 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, whereas 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 (Daugherty *et al.* 2007; Holt & Huxel 2007). This again promotes coexistence, by bringing the community structure closer to two linear food chains. Therefore, it is crucial to determine on which resources do species in a community actually feed upon.

Here, we explore how pairwise interactions between species are modified by the inclusion of other species in a simple community. Our baseline hypothesis is that increasing an aspect of complexity in the community module, i.e., the richness of species that are known to interact when no alternative food is provided will increase the number of realized links in the more complex community (Box 1A). We mimicked different community modules 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 deposited on leaves) as alternative food (González-Fernández *et al.* 2009), all of which occur in the leaves of crops of avocado (*Persea americana*) in Southestern Spain. From pairwise experimental designs we know that predator-herbivore trophic interactions are stronger when *N. californicus* is the predator

than when it is *E. stipulatus* (González-Fernández et al. 2009); that pollen is an optimal food source for *E. stipulatus* but not for *N. californicus* (Ferragut et al. 1987; González-Fernández et al. 2009); and that *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 our system across community modules of increasing complexity (Box 1B), that is: *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 tested through a series of experimental treatments in which we assessed what interactions were realized within each community module, by measuring IG-prey/herbivore mortality and how predation translates into predator fecundity as a result of the interactions that were occurring. 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) yield egg production produced by feeding on each prey type in (IG)predators; 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

135 vertically, with the stems in contact with sponges (*ca.* 30 x 20 x 5 cm) covered with cotton
136 wool and a plastic sheet (27 x 17 cm), and placed inside water-containing trays (8 L, 42.5 x
137 26 x 7.5 cm). The plant roots were in contact with the water, and the aerial parts were
138 touching each other, forming a tent-like three-dimensional structure, where individuals
139 could easily walk from one plant to the other. Cotton threads were placed on the leaves, to
140 serve as oviposition sites for mite females. Mites were fed *ad libitum* twice a week with
141 pollen of *Carpobrotus edulis* (cat´s claw) spread on leaves with a fine brush. *Euseius*
142 *stipulatus* is able to develop and reproduce on this food source (Ferragut *et al.* 1987). Every
143 three weeks, new rearings were made by transferring, from old rearings to a new unit,
144 leaves with mites and the cotton threads filled with eggs. The culture was found to be
145 contaminated a few times with *Tyrophagus* spp., a detritivorous mite species. In such
146 instances, instead of moving entire leaves, adult *E. stipulatus* females (ca. 300) were
147 collected individually and transferred to the new rearing unit.
148 The *N. californicus* population was obtained from Koppert Biological Systems S.L. in
149 bottles of 1000 individuals (Spical®). Colonies were kept on detached bean leaves infested
150 with *Tetranychus urticae* that were placed on top of inverted flower-pots (20 cm Ø) inside
151 water-containing trays.
152 The herbivore *Oligonychus perseae* was not maintained in a laboratory culture due
153 to technical difficulties in maintaining detached avocado leaves. They were thus collected
154 from the field on a regular basis from avocado orchards located in the experimental station
155 of "La Mayora".
156 Pollen of *C. edulis* was obtained from flowers collected in the experimental station.
157 Stamens dried in a stove at 37ºC for 48h, then sieved (350 µm).
158
159 *Community modules*
160 Experimental arenas to test the outcome of community modules consisted of avocado leaf
161 discs placed in petri dishes with a circular hole in the middle, as described in Guzmán *et al.*
162 (2016a). Briefly, a hole (6.5 cm Ø) was cut in a petri dish (9 cm Ø) turned upside down and
163 filled with an avocado leaf disc (7.5 cm Ø), with the borders glued to a clay ring. Inside the
164 petri dish, wet cotton wool ensured enough humidity to keep leaves turgid. Petri dishes
165 were then sealed with parafilm®. To prevent individuals from escaping, a ring of Tanglefoot®
166 was applied along the outer margin of the leaf disc. Female and juvenile predators used in

167 the experiments were 10-14 and 2-3 days old since egg hatching, respectively. Cohorts of *E.*
168 *stipulatus* were made by transferring with a fine brush 400 eggs from the rearings to 2-3
169 bean leaves placed on top of sponges (30 x 20 x 5 cm, approx.) covered with cotton wool,
170 inside water-containing trays (3.5 L), and with pollen of *C. edulis* as food. Because it was
171 difficult to obtain eggs of *N. californicus* from the rearings, cohorts of this species were
172 made by transferring 100 females to 2-3 bean leaves infested with *Tetranychus urticae*
173 placed on containers similar to those used for the cultures. After allowing *N. californicus*
174 females to feed and oviposit for 48 h, they were removed with a fine brush. Before the
175 experiments, gravid predator females were randomly taken from the cohorts, and starved
176 for 16 h in experimental containers similar to those above. Starvation was done to
177 standardize hunger among individuals, and to ensure that egg production in tested females
178 was not obtained from food ingested prior to the experiment. Predator juveniles were taken
179 from the cohorts when needed. Arenas containing the herbivore were done as follows: Ten
180 females of *O. perseae* were let to build nests and lay eggs on experimental arenas during 4
181 days. The number of nests and eggs laid per nest on each arena was counted at the onset of
182 the experiment. Pollen in arenas assigned to treatments with alternative food was supplied
183 *ad libitum*, using a fine brush.

184 We performed experiments using two 'community blocks', depending on the identity
185 of the top predator (*N. californicus* or *E. stipulatus*). Increased complexity in each of the two
186 community blocks was mimicked through the combination of the presence / absence of 4
187 factors: predator/IG-predator, IG-prey, herbivore and alternative food. This resulted in the
188 community modules depicted in the X-axis of figures 1 and 2. These modules were: Trophic
189 chain: either one *E. stipulatus* or *N. californicus* female was introduced in arenas containing
190 10 females of *O. perseae* (treatment # 1 in Fig 1 and 2). Arenas containing either one *E.*
191 *stipulatus* or one *N. californicus* female without herbivores (treatment # 2), and containing
192 10 *O. perseae* females without predators (treatment # 3) were done as controls for predator
193 oviposition rate and prey natural mortality, respectively. Apparent competition: arenas
194 consisted of one female of either *E. stipulatus* or *N. californicus*, 10 females of *O. perseae*,
195 and pollen of *C. edulis* supplied *ad libitum* (treatment # 4). Similar arenas but without the
196 herbivores (treatment # 5) were made as controls for oviposition rates of predators on
197 pollen only, and without the IG-predator (treatment # 6) to assess potential effects of pollen
198 on the survival of the herbivore. Intraguild predation: Because IGP is usually associated with

size differences between contestants IG-predators and IG-prey consisted of adult females and heterospecific juveniles, respectively. Arenas consisted of 10 *O. perseae* females, either one *E. stipulatus* or *N. californicus* female, acting as the IG-predators, and 10 heterospecific juveniles, acting as the IG-prey (treatment # 7). Additionally, several control treatments were done to evaluate: the predation/mortality rate of *O. perseae* in the presence of IG-prey but not of IG-predator (treatment # 8); the mortality rate of IG-prey in the absence of both IG-predator and prey (treatment # 9), and in the presence of IG-predator but not of herbivores (treatment # 10). Intraguild predation - Apparent competition: Arenas consisted of 10 *O. perseae* females, either one *E. stipulatus* or *N. californicus* female, acting as the IG-predators, 10 heterospecific juveniles, acting as the IG-prey, and pollen of *C. edulis* as alternative food, supplied *ad libitum* (treatment # 11). Similar arenas to those above but i) without IG-predators (treatment # 12), ii) without herbivores (treatment # 13), and iii) without IG-predators and herbivores (treatment # 14), were done to evaluate predation of IG-prey on the herbivore in the presence of pollen, predation of IG-predators on IG-prey in the presence of pollen, and mortality of IG-prey in the presence of pollen, respectively.

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

Data analyses

Analyses were done separately for communities where either *E. stipulatus* or *N. californicus* acted as the top-predator. Mortality rates of herbivores and IG-prey, and rates of oviposition of IG-predators, were analysed using Generalized Lineal Models (GLM) assuming a Poisson distribution and a Log link function, as no overdispersion of the data was detected. All the analyses were 3 full-factorial designs (see below). We followed a backward elimination procedure as follows: when the interaction among the three explanatory variables was not significant (and the model had higher AIC), this interaction was removed from the model. Subsequently, the same procedure was followed for second order interactions. GLM analyses were performed using the computer environment R (R Core Team 2017). After significance of general models, additional software (package “contrast”) was used to perform planned comparisons to address specific questions (see Results). When

specific sets of data were used in multiple comparisons, their significance was corrected using the sequential Bonferroni method.

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

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

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

Results

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

Mortality rates of the herbivore and of the IG-prey were affected by all three main factors (Table 1a and b) except pollen in the case of the IG-prey (Table 1b), and all the double interactions except that between IG-predator and pollen, in the case of the herbivore (Table 1a), and that between the herbivore and pollen, in the case of the IG-prey (Table 1b). Planned comparisons revealed a) that *E. stipulatus* preyed on *O. perseae* (t_{81} = 2.74, P = 0.0076; Fig 1a, compare bars 1 and 3) and marginally on *N. californicus* juveniles (t_{80} = -2.01, P = 0.048, not significant after Bonferroni correction; Fig 1b, compare bar 9 to 10) when each prey was offered alone; b) that adding IG-prey increased mortality of *O. perseae* (t_{81} = -2.26, P = 0.026; Fig 1a, compare bar 1 to 7), but adding *O. perseae* did not influence mortality of the IG-prey (t_{80} = -0.31, P = 0.755; Fig 1b, compare bar 10 to 7); c) that the presence of pollen yielded a drastic reduction in predation of IG-predators on both the herbivore (t_{81} = 2.99, P = 0.0037; Fig 1a, compare bar 1 to 4) and the IG-prey (t_{80} = 3.91, $P \ll 0.001$; Fig 1b, compare bar 10 to 13); d) that when both prey were available, the presence of pollen did not affect herbivore mortality (t_{81} = 0.88, P = 0.379; Fig 1a, compare bar 7 to 11), but did lead to lower IG-prey mortality (t_{80} = 3.58, $P \ll 0.001$; Fig 1b, compare bar 7 to 11).

Oviposition rates of *E. stipulatus* were only affected by the presence of pollen (main factor Pollen, Table 1c). However, further planned comparisons revealed that while feeding

261 on the herbivore yielded some egg production (t_{96} = 2.19, P = 0.021; Fig 1c, compare bar 1 to
262 2), feeding on IG-prey did not (t_{96} = -1,13, P = 0.259; Fig 1c, compare bar 10 to 2).
263
264 *Communities with N. californicus as the (IG-)predator*
265 Herbivore mortality was affected by all second order interactions (Table 2a), and that of the
266 IG-prey (juveniles of *E. stipulatus*) was only affected by the presence of pollen (Table 2b).
267 Paired comparisons revealed that a) *N. californicus* preyed on *O. perseae* (t_{90} = 3.32, P =
268 0.013; Fig 2a, compare bar 3 to 1) but not on *E. stipulatus* juveniles (t_{86} = -1.35, P = 0.182; Fig
269 2b, compare bar 9 to 10), when each prey was offered alone; b) adding IG-prey reduced
270 mortality of *O. perseae* (t_{90} = 2.56, P = 0.012; Fig 2a, compare bar 1 to 7), but adding *O.*
271 *perseae* did not change mortality of the IG-prey (t_{86} = -0.93, P = 0.353; Fig 2b, compare bar
272 10 to 7); c) the presence of pollen did not affect mortality of either *O. perseae* (t_{90} = -0.43, P
273 = 0.669; Fig 2a, compare bar 1 to 4) or the IG-prey (t_{86} = 1.80, P = 0.075; Fig 2b, compare bar
274 10 to 13); d) when both types of prey were available, the presence of pollen led to a
275 significant increase in mortality of *O.perseae* (t_{90} = -3.65, P << 0.001; Fig 2a, compare bar 7
276 to 11), but a significant decrease of mortality in *E. stipulatus* juveniles (t_{86} = 2.04, P = 0.044;
277 Fig 2b, compare bar 7 to 11).
278 Oviposition rates of *N. californicus* were affected by the main factor Herbivore and
279 the interaction between the IG-prey and pollen (Table 2c). Indeed, paired comparisons
280 revealed that e) eggs were produced when *N. californicus* was offered the herbivore alone
281 (t_{104} = 2.45, P = 0.016; Fig 2c, compare bar 1 to 2), but not when they were on arenas with
282 either the IG-prey (t_{104} = 0.01, P = 0.992; Fig 2c, compare bar 10 to 2) or pollen (t_{104} = -0.15,
283 P = 0.884; Fig 2c, compare bar 5 to 2) alone. Moreover, in the presence of the herbivore,
284 rates of oviposition were not influenced by the presence of pollen (t_{104} = -0.93, P = 0.352; Fig
285 2c, compare bar 1 to 4), but dramatically decreased in the presence of the IG-prey (t_{104} =
286 2.39, P = 0.019; Fig 2c, compare bar 1 to 7). However, when pollen was added to the system
287 with both prey types, IG-predators resumed oviposition to its maximum (t_{104} = -2.36, P =
288 0.020; Fig 2c, compare bar 7 to 11).
289
290 **Discussion**
291 In this study, we tested the effect of community structure on the realized interactions
292 within a community of predatory and herbivorous mites. Because in our system the

293 intraguild predator is the largest individual within a pair (as in most systems), we created
294 communities in which adults belonged to one species and juveniles to the other, then
295 inverted the species-stage identity in another set of communities. We then measured
296 predation and oviposition in communities with all possible combinations of the presence of
297 shared prey, the intraguild prey, the intraguild predator and alternative food. We show that
298 adding species to a community increases the number of potential interactions, but not
299 necessarily their occurrence. Indeed, despite the potential for apparent competition and
300 intraguild predation in modules with several species, all modules could be described by
301 linear food chains (Box 1C).

302 Although *N. californicus* killed more *O. perseae* females per day, oviposition rates
303 were similar between predators. This is in line with the finding that *E. stipulatus* can only
304 forage on mobile *O. perseae* mites when they wander outside nests, whereas *N. californicus*
305 can penetrate inside nests and forage on all the individuals residing within (González-
306 Fernández *et al.* 2009). This suggests that *E. stipulatus* is the most efficient predator
307 converting prey into eggs, but that *N. californicus* is more efficient at reducing herbivore
308 populations. Which of these strategies is best for biological control will depend on the
309 ecological condition: if bursts of prey are confined in time, it may be more efficient to select
310 a biocontrol agent that feeds more, as in "inundative" biocontrol strategies, whereas
311 controlling and keeping resident populations at low levels may be best achieved with a
312 predator with a strong numerical response, as in "innoculative" biocontrol strategies (Van
313 Driesche *et al.* 2007).

314 Moreover, unlike *N. californicus*, *E. stipulatus* fed and oviposited on pollen. This may
315 allow the latter to remain in the field for longer periods, as actually observed in field surveys
316 (González-Fernández *et al.* 2009). Such temporal segregation may facilitate the presence of
317 the two predators in the same fields (Otto *et al.* 2008). Moreover, our results revealed
318 asymmetry in the intraguild predation between. *E. stipulatus* and *N. californicus*, with adults
319 of the latter preying upon juveniles of the latter, but not the reverse. Because *N. californicus*
320 is likely the best competitor for the shared prey (González-Fernández *et al.* 2009),
321 coexistence between predators is thus possible in this system (Holt & Polis 1997).

322 The simultaneous presence of the two predators is likely to have little effect upon
323 the densities of the shared prey. Indeed, whereas adding adults of *E. stipulatus* to an arena
324 with *N. californicus* juveniles results in higher prey densities as compared to the presence of

325 *N. californicus* alone, the reverse is not true when adding juveniles of *E. stipulatus* to an
326 arena with adult *N. californicus*. Thus, the net effect of these interactions upon prey density
327 is probably negligible. This is corroborated by field studies (Montserrat *et al.* 2013).
328 However, the presence of alternative food (i.e. pollen) contributed to reduce trophic
329 interactions between predator species resulting in community configurations that could
330 enhance pest control. Thus, supplying alternative and preferred food to the IG-predator is
331 probably detrimental to populations of *O. perseae*. Again, this finding mirrors field data
332 (Montserrat *et al.* 2013).

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

344 Food web ecology predicts that species of the highest trophic levels engage in
345 trophic interactions on more than one food source when these are available. Here, we show
346 that *E. stipulatus* feeds on the herbivore, *O. perseae*, on the intraguild prey, *N. californicus*,
347 and on the alternative food, pollen, when each of these are presented alone. However, in
348 the presence of pollen *E. stipulatus* reduces predation rates on both prey species. This may
349 be explained by the fact that pollen is the most profitable food for this species, as found
350 here and in other studies (Ferragut *et al.* 1987; McMurtry & Croft 1997; Bouras &
351 Papadoulis 2005; González-Fernández *et al.* 2009). Similarly, *N. californicus* adults and
352 juveniles ceased foraging on other food sources in presence of the herbivores. These results
353 suggest that realized interactions hinge on the presence of the most profitable food source.
354 In presence of the optimal food source for each of the two secondary consumers,
355 communities tended to melt down to become two simple trophic chains. Indeed, in the
356 most complex communities studied here, with all 5 species present, the presence of the

357 optimal food originated the split of the community into two trophic chains, one with *E.*
358 *stipulatus* feeding on pollen and the other with *N. californicus* feeding on the herbivore (Box
359 1 d), compare d.1.1. and d.1.2. with d.2.1. and d.2.2.).

360 Another factor that contributed to the linearization of the food web was that, when
361 both the IG-prey and the shared prey were together, *E. stipulatus* preyed mainly on the IG-
362 prey. Indeed, mortality of *O. perseae* in presence of the IG-prey, *N. californicus*, was not
363 affected by the presence of *E. stipulatus*. Furthermore, mortality of *N. californicus* juveniles
364 was significantly higher in treatments with presence of the IG-predator, compared to the
365 control without them. This suggests that mortality in the herbivore was mainly inflicted by
366 juveniles of *N. californicus*, and that *E. stipulatus* females preyed preferentially on juveniles
367 of *N. californicus*. This could be explained by *E. stipulatus* having no access to *O. perseae*
368 eggs or females located inside the nests (Montserrat *et al.* 2008a; González-Fernández *et al.*
369 2009), which leads to higher encounter rates between *E. stipulatus* and *N. californicus* than
370 between *E. stipulatus* and *O. perseae*. *Neoseiulus californicus* juveniles, however, can
371 penetrate *O. perseae* nests, and thus may feed on them. Therefore, the realized community
372 was that of a 4-level trophic chain (Box 1, c.2.1.). In the other community block, when *N.*
373 *californicus* acted as the IG-predator, mortality of *O. perseae* females was similar in all
374 communities with the IG-prey, irrespective of the presence of IG-predators. Furthermore,
375 mortality of IG-prey did not differ between treatments with and without the IG-predator,
376 indicating that *N. californicus* females did not forage on *E. stipulatus* juveniles. These results
377 suggest that, in presence of IG-prey (juveniles of *E. stipulatus*), the IG-predator ceased to
378 forage on either herbivore or IG-prey. Thus, the realized community was that of a trophic
379 chain composed of the IG-prey, the herbivore and the plant, with the IG-predator not
380 interacting at all (Box 1, c.2.2.). This can be explained by *N. californicus* females avoiding
381 foraging on a patch where its offspring (future) IG-predator is also there. In line with this,
382 Abad-Moyano *et al.* (2010) reported that the presence of *E. stipulatus* immatures exerted
383 non-lethal IG-effects on *N. californicus* females, causing daily oviposition to decrease over
384 time despite the availability of the shared prey was kept constant. In any case, here, the
385 trophic links are again linear, with *N. californicus* being excluded from the realized
386 community (Box 1, c.2.2.). Together, our results show that none of the complex
387 communities was actually realized, they were all trophic chains.

Our results presented may contribute to solving the paradox of stability in systems with intraguild predation. Indeed, theoretical models exploring persistence in three-species communities with IGP find a rather limited room 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). In line with this, Hiltunen *et al.* (2014) found long-term cycling dynamics when modelling a three-species planktonic food web, with interaction strength between IG-predator and IG-prey set to be much weaker to that between IG-predator and the shared resource.

It is becoming increasingly clear that connectance, that is, the number of realized interactions in a food web, 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 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 (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 in the direct study 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 experimental settings, in contrast, deliver quantitative estimates of predation rates and concomitant offspring production, especially when trophic links, and their strength, are estimated by confronting pairs of species. Alternatively, modelling complex systems provide relative estimates on interaction strengths that go beyond pair-

wise interactions (Moya-Laraño *et al.* 2012; Moya-Laraño *et al.* 2014). Yet, one-on-one approaches may ignore emergent indirect effects of having several species together (Wootton 1994; Dambacher & Ramos-Jiliberto 2007). For instance, *Cancer productus*, a crab native to the pacific Northwest, consumes equal amounts of native oysters and of invasive drill oysters when each type of prey is offered alone, but when they are offered together crabs interact with the native oyster species only (Grason & Miner 2012). Therefore, if trophic links are not evaluated in presence of all species in the community, one may reach erroneous conclusions on the strength of the interaction (Guzmán *et al.* 2016b; Fonseca *et al.* 2017) and overestimate connectance in food webs. In this work, through the addition of species we created a series of communities of increased number of species and increased number of potential interactions (links) among them, both direct (trophic) or indirect (competition, apparent competition). However, our experimental results revealed that all communities ended up becoming a sum of one or more trophic chains (Box 1C). These results are consistent with the idea that the fundamental trophic niche of a species (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)). Our results suggest that some food webs may be less complex than previously thought in terms on the frequency and strength of IGP. 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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Table 1. Results of Generalized Lineal Models applied to a) herbivore mortality rates, b) IG-prey (juveniles of *N. californicus*) mortality rates, and c) (IG-)predator (females of *E. stipulatus*) 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	-1.755	0.712	-2.466	0.014
IG-predator (1)	2.212	0.732	3.021	0.002
IG-prey (2)	2.932	0.729	4.023	<0.001
Pollen (3)	-1.851	0.609	-3.040	<0.001
IG-predator * IG-prey	-2.302	0.756	-3.047	0.002
IG-predator * Pollen	NS			
IG-prey * Pollen	1.573	0.639	2.466	.014
(1) * (2) * (3)	NS			

b)

IG-prey mortality rates	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	0.513	0.238	2.156	0.031
IG-predator (1)	0.591	0.273	2.163	0.030
Herbivore (2)	-1.624	0.496	-3.276	0.001
Pollen (3)	-0.392	0.359	-1.091	0.275
IG-predator * Herbivore	1.552	0.511	3.037	0.002
IG-predator * Pollen	-1.705	0.517	-3.300	<0.001
Herbivore * Pollen	0.749	0.520	1.439	0.150
(1) * (2) * (3)	NS			

c)

IG-predator oviposition rates	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	-0.843	0.245	-3.443	<0.001
IG-prey (1)	-0.194	0.220	-0.882	0.378
Herbivore (2)	0.220	0.216	1.018	0.308
Pollen (3)	1.104	0.235	4.703	<0.001
IG-prey * Herbivore	NS			
IG-prey * Pollen	NS			
Herbivore * Pollen	NS			
(1) * (2) * (3)	NS*			

Table 2. Results of Generalized Lineal 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.

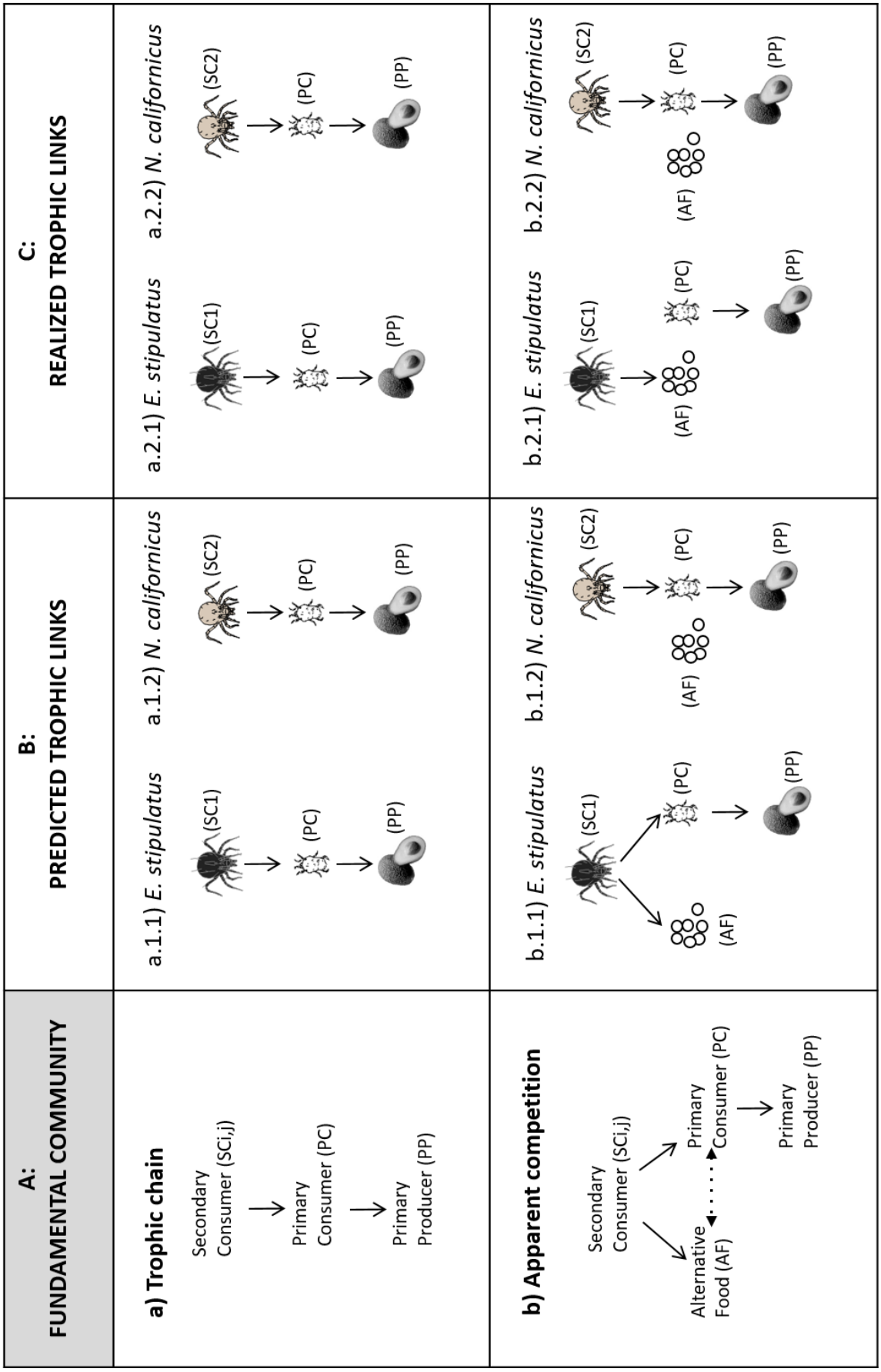
a) Herbivore mortality rates	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	-1.954	0.722	-2.707	0.007
IG-predator (1)	2.997	0.729	4.109	<0.001
IG-prey (2)	2.184	0.746	2.927	0.003
Pollen (3)	-0.888	0.499	-1.782	0.075
IG-predator * IG-prey	-2.825	0.764	-3.699	<0.001
IG-predator * Pollen	0.999	0.460	2.175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

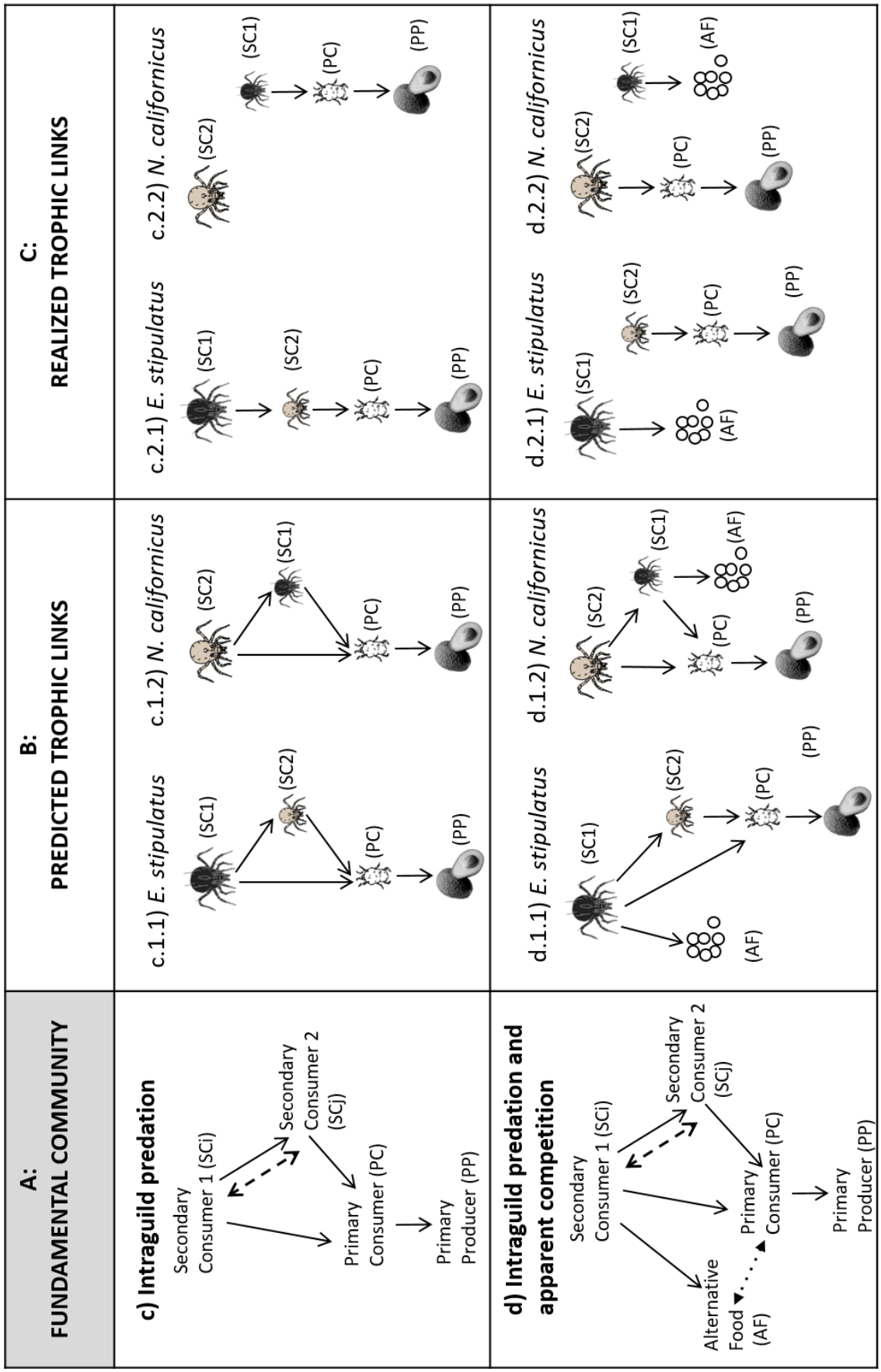
c) IG-predator oviposition rates	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	-2.7430	0.6172	-4.444	<0.001
IG-prey (1)	-2.5550	1.0378	-2.462	0.014
Herbivore (2)	2.5174	0.5989	4.204	<0.001
Pollen (3)	0.3476	0.3685	0.943	0.346
IG-prey * Herbivore	NS*			
IG-prey * Pollen	2.2175	1.1041	2.008	0.045
Herbivore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

685 Box 1. **A: Fundamental community modules** included in this study. a) trophic chain, b)
686 apparent competition, c) intraguild predation, and d) intraguild predation and apparent
687 competition. From a) to d) the complexity of the community is increased via increasing the
688 number of species and the number of interactions among them. **B: Predicted trophic links**
689 that have been observed using pairwise experimental settings**. C: Realized trophic links**
690 occurring across community modules of increasing complexity, obtained from the
691 experiments presented here, where interactions are measured in the presence of other
692 components of the community. SC stands for secondary consumer, PC for primary
693 consumer, PP for primary producer, and AF for alternative food. SC1 and SC2 are phytoseiid
694 predatory mites, i.e. *Euseius stipulatus* and *Neoseiulus californicus*, respectively, PC is the
695 tetranychid herbivore mite *Oligonychus perseae*, AF is pollen of *Carpobrotus edulis*, and PP
696 is the avocado *Persea americana*. Solid arrows indicate negative direct interactions (who
697 eats whom), whereas dotted and dashed arrows in Box 1A indicate negative indirect
698 interactions (apparent competition and competition).
699
700 Figure 1. Mortality rates (average ± S.E.) of a) herbivores (*Oligonychus perseae* females) and
701 b) IG-prey (*Neoseiulus californicus* juveniles), and c) oviposition rates (average ± S.E.) of IG-
702 predators (*Euseius stipulatus* females), in 14 different treatments defined by presence or
703 absence of either IG-predators, IG-prey, herbivores or alternative food (pollen), depicted in
704 the lower part of the figure, that mimicked four different community configurations and
705 their respective controls.
706
707 Figure 2. Mortality rates (average ± S.E.) of a) herbivores (*Oligonychus perseae* females) and
708 b) IG-prey (*Euseius stipulatus* juveniles), and c) oviposition rates (average ± S.E.) of IG-
709 predators (*Neoseiulus califonicus* females), in 14 different treatments defined by presence
710 or absence of either IG-predators, IG-prey, herbivores or alternative food (pollen), depicted
711 in the lower part of the figure, that mimicked four different community configurations and
712 their respective controls.
713
714

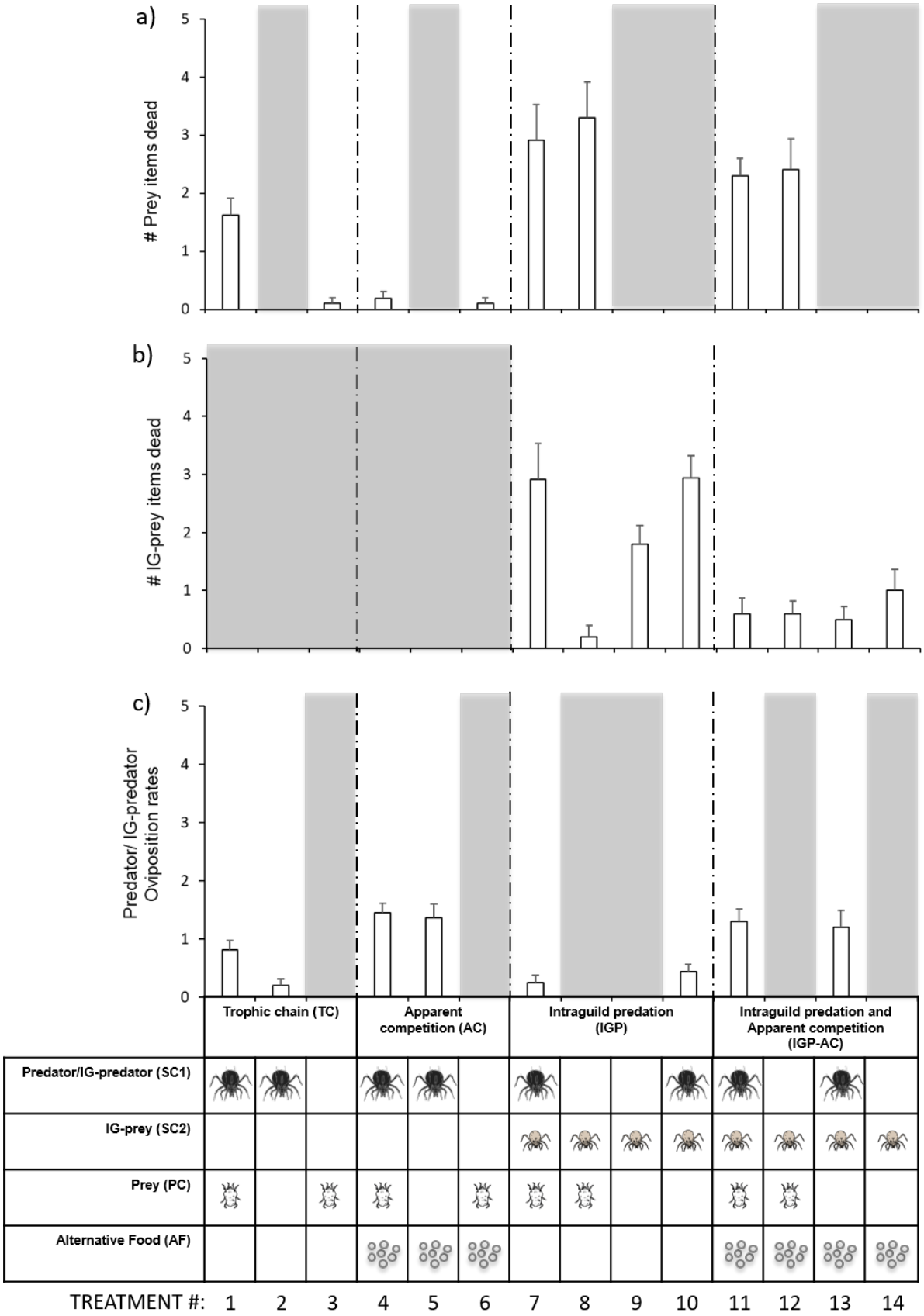
Box 1.


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)

716 Box 1 (cont.)

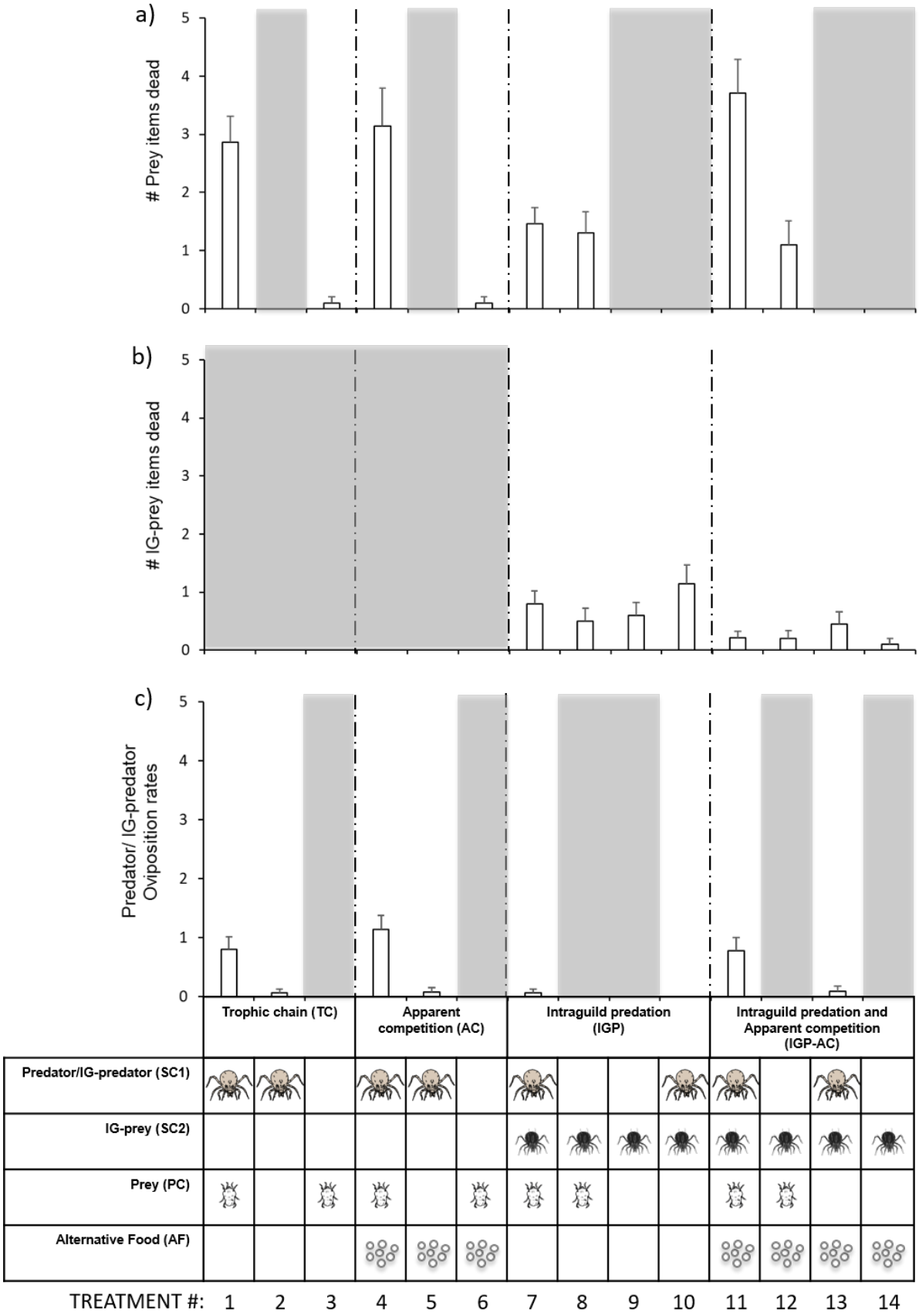


717 Figure 1.



718

719 Figure 2.



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721