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

Inmaculada Torres-Campos[1,4], Sara Magalhães[2], Jordi Moya-Laraño[3], Marta Montserrat[1]

[1]Instituto de Hortofruticultura Subtropical y Mediterránea "La Mayora", Universidad de Málaga, Consejo Superior de Investigaciones Científicas (IHSM-UMA-CSIC), Avda Dr. Weinberg s/n, Algarrobo-Costa, 29750 Málaga, Spain.

[2]cE3c: Centre for Ecology, Evolution and Environmental Changes, Faculdade de Ciências, Universidade de Lisboa, Campo Grande, Edifício C2, 1749-016 Lisboa, Portugal.

[3]Estación Experimental de Zonas Áridas – CSIC, Carretera de Sacramento s/n, La Cañada de San Urbano, 04120 Almería, Spain.

[4]Current address: Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94240, 1090 GE Amsterdam, The Netherlands.

Abstract

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

Introduction

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

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

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

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

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

resources, thereby decreasing the probability of species extinctions (McCann *et al.* 1998), and 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). However, it is as yet unclear how the introduction of a species into a community affects the interaction among all species in that community.

Here, 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* (in here, number of individuals consumed per day) as it is an excellent proxy for trophic interaction strength, and is used both in ecological modelling (e.g. the equivalent to the "catching efficiencies" in Kuijper *et al.* 2003) and in empirical research (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 core hypothesis was 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 predicted 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

139 (Box 1B, b.1.1. and b.1.2.); *iii*) in "intraguild predation" community configurations, both IG-
140 predator species will interact with the IG-prey and the herbivore (Box 1B, c.1.1. and c.1.2.);
141 and iv) in "Intraguild predation and apparent competition" community configurations, only
142 adults and juveniles of *E. stipulatus* will establish trophic links with pollen (Box 1B, d.1.1. and
143 d.1.2.). These predictions were then tested through a series of experimental treatments to
144 assess which interactions were realized within each community module, by measuring IG-
145 prey/herbivore mortality and how consumption of prey translates into predator fecundity as
146 a result of these interactions. Specifically, we examined a) whether (IG-)predators feed on
147 each prey type; b) whether predation of (IG-)predators on one prey type is affected by the
148 presence of the other; c) whether predation of (IG-)predators on both prey, and of IG-prey
149 on the herbivore, is affected by the presence of alternative food; d) whether the presence of
150 alternative food affects predation of (IG-)predators on the two types of prey when they are
151 together; e) number of eggs produced by (IG-)predators when feeding on each prey type;
152 and f) whether egg-production is additive when (IG-)predators have more than one food
153 type available.
154
155
156 **Material and Methods**
157 All cultures and experiments were done in a climate chamber at 25±1ºC, 65±5% RH and
158 16:8h L:D (Light:Dark).
159 *Mite cultures*
160 Cultures of the predatory mite *E. stipulatus* were started in 2007 from ca. 300 individuals
161 collected from avocado trees located in the experimental station of "La Mayora". Rearing
162 units consisted of three bean plants (*Phaseolus vulgaris* L.) with 6-10 leaves, positioned
163 vertically, with the stems in contact with sponges (*ca.* 30 x 20 x 5 cm) covered with cotton
164 wool and a plastic sheet (27 x 17 cm), and placed inside water-containing trays (8 L, 42.5 x
165 26 x 7.5 cm). The plant roots were in contact with the water, and the aerial parts were
166 touching each other, forming a tent-like three-dimensional structure, where individuals
167 could easily walk from one plant to the other. Cotton threads were placed on the leaves, to
168 serve as oviposition sites for the females. Mites were fed *ad libitum* twice a week with
169 pollen of *Carpobrotus edulis* (cat´s claw) spread on leaves with a fine brush. *Euseius*
170 *stipulatus* is able to develop and reproduce on this food source (Ferragut *et al.* 1987). Every

171 three weeks, new rearings were made by transferring, leaves with mites and the cotton
172 threads filled with eggs to a new unit. The culture was found to be contaminated a few
173 times with *Tyrophagus* spp., a detritivorous mite species. In such instances, instead of
174 moving entire leaves, adult *E. stipulatus* females (ca. 300) were collected individually and
175 transferred to the new rearing unit.

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

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

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

186

187 *Community modules*

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

203 hatching) were taken from the cohorts when needed. Arenas containing the herbivore were
204 done as follows: Ten females of *O. perseae* were let to build nests and lay eggs on
205 experimental arenas during 4 days. The number of nests and eggs per nest on each arena
206 was counted at the onset of the experiment. Pollen in arenas assigned to treatments with
207 alternative food was supplied *ad libitum*, using a fine brush.

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

235 prey, and pollen of *C. edulis* as alternative food, supplied *ad libitum* (treatment # 11). Similar
236 arenas to those above but i) without IG-predators (treatment # 12), ii) without herbivores
237 (treatment # 13), and iii) without IG-predators and herbivores (treatment # 14), were done
238 to evaluate predation of IG-prey on the herbivore in the presence of pollen, predation of IG-
239 predators on IG-prey in the presence of pollen, and mortality of IG-prey in the presence of
240 pollen, respectively.

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

244

245 *Data analyses*

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

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

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

267 Oviposition rates were analysed using data from treatments containing IG-predators
268 (i.e., adult predators). The full model included the presence/absence of the herbivore, the
269 IG prey and alternative food as explanatory variables, as well as their interactions.
270
271 **Results**
272 *Communities with E. stipulatus as the (IG-)predator*
273 Mortality rates of the herbivore were significantly affected by the interaction between the
274 presence of IG-predator$_{ES}$ and IG-prey$_{NC}$ and between the presence of IG-prey$_{NC}$ and pollen
275 (Table 1a). Indeed, more prey died when IG-prey$_{NC}$ were together with the IG-predator$_{ES}$
276 than when the IG-predator$_{ES}$ was alone (Fig 1a, compare bar 1 to 7), but not more than
277 when the IG-prey$_{NC}$ was alone (Fig 1a, compare bar 8 to bar 7). Also, the presence of pollen
278 reduced herbivore mortality rates, but only in the absence of IG-prey$_{NC}$ (Fig 1a, compare
279 bars 4 and 6 to bars 11 and 12).
280 Mortality rates of the IG-prey$_{NC}$ were affected by all the double interactions except
281 that between the herbivore and pollen (Table 1b). Indeed, the presence of the IG-predator$_{ES}$
282 increased the mortality of IG-prey$_{NC}$, but only in the absence of pollen (Fig 1b, compare bars
283 7 and 10 to bars 11 and 13). Similarly, the presence of herbivores reduced mortality rates of
284 IG-prey$_{NC}$ when IG-predators$_{ES}$ were absent (Fig1b, compare bar 8 to 9), but not when they
285 were present (Fig1b, compare bar 7 to 10).
286 Planned comparisons revealed a) that IG-predators$_{ES}$ preyed on *O. perseae* (t_{81} =
287 2.74, P = 0.0076; Fig 1a, compare bars 1 and 3) and marginally on the IG-prey$_{NC}$ (t_{80} = -2.01,
288 P = 0.048, not significant after Bonferroni correction; Fig 1b, compare bar 9 to 10) when
289 each prey was offered alone; b) that adding IG-prey$_{NC}$ increased mortality of *O. perseae* (t_{81}
290 = -2.26, P = 0.026; Fig 1a, compare bar 1 to 7), but adding *O. perseae* did not influence
291 mortality of the IG-prey$_{NC}$ (t_{80} = -0.31, P = 0.755; Fig 1b, compare bar 10 to 7); c) that the
292 presence of pollen yielded a drastic reduction in predation of IG-predators$_{ES}$ on both the
293 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
294 << 0.001; Fig 1b, compare bar 10 to 13); d) that when both prey were available, the
295 presence of pollen did not affect herbivore mortality (t_{81} = 0.88, P = 0.379; Fig 1a, compare
296 bar 7 to 11), but did lead to lower IG-prey$_{NC}$ mortality (t_{80} = 3.58, P << 0.001; Fig 1b,
297 compare bar 7 to 11).

298 Oviposition rates of IG-predators$_{ES}$ were only affected by the presence of pollen
299 (main factor Pollen, Table 1c). However, further planned comparisons revealed that while
300 feeding on the herbivore stimulated egg production (t_{96} = 2.19, P = 0.021; Fig 1c, compare
301 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).
302
303 *Communities with N. californicus as the (IG-)predator*
304 Herbivore mortality was affected only by the interaction between IG-predator$_{NC}$ and IG-
305 prey$_{ES}$ (Table 2a). Indeed, mortality of herbivores was drastically affected by the presence of
306 IG-predators$_{NC}$ (Fig 2a, compare bar 1 to 3), but this effect was lesser in the presence of IG-
307 prey$_{ES}$ (Fig 2a, compare bar 1 to 7). Mortality of IG-prey$_{ES}$ was only affected by the presence
308 of pollen (Table 2b).
309 Paired comparisons revealed that a) IG-predators$_{NC}$ preyed on *O. perseae* (t_{90} = 3.32,
310 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,
311 compare bar 9 to 10), when each prey was offered alone; b) adding IG-prey$_{ES}$ reduced
312 mortality of *O. perseae* (t_{90} = 2.56, P = 0.012; Fig 2a, compare bar 1 to 7), but adding *O.*
313 *perseae* did not change mortality of the IG-prey$_{ES}$ (t_{86} = -0.93, P = 0.353; Fig 2b, compare bar
314 10 to 7); c) the presence of pollen did not affect mortality of either *O. perseae* (t_{90} = -0.43, P
315 = 0.669; Fig 2a, compare bar 1 to 4) or the IG-prey$_{ES}$ (t_{86} = 1.80, P = 0.075; Fig 2b, compare
316 bar 10 to 13); d) when both types of prey were available, the presence of pollen led to a
317 significant increase in mortality of *O.perseae* (t_{90} = -3.65, P << 0.001; Fig 2a, compare bar 7
318 to 11), but a significant decrease of mortality in IG-prey$_{ES}$ (t_{86} = 2.04, P = 0.044; Fig 2b,
319 compare bar 7 to 11).
320 Oviposition rates of IG-predators$_{NC}$ were affected by the main factor Herbivore and
321 the interaction between the IG-prey$_{ES}$ and pollen (Table 2c). Indeed, paired comparisons
322 revealed that e) eggs were produced when IG-predators$_{NC}$ were offered the herbivore alone
323 (t_{104} = 2.45, P = 0.016; Fig 2c, compare bar 1 to 2), but not when they were on arenas with
324 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,
325 P = 0.884; Fig 2c, compare bar 5 to 2) alone. Moreover, in the presence of the herbivore,
326 rates of oviposition were not influenced by the presence of pollen (t_{104} = -0.93, P = 0.352; Fig
327 2c, compare bar 1 to 4), but dramatically decreased in the presence of the IG-prey$_{ES}$ (t_{104} =
328 2.39, P = 0.019; Fig 2c, compare bar 1 to 7). However, when pollen was added to the system

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

360 2009). Such temporal niche partitioning may facilitate the presence of the two predators in
361 the same fields (Otto *et al.* 2008).

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

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

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

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

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

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

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

455 experimental settings, in contrast, deliver quantitative estimates of predation rates and
456 concomitant offspring production, especially when trophic links, and their strength, are
457 estimated by confronting pairs of species. Alternatively, modelling complex systems provide
458 relative estimates on interaction strengths that go beyond pair-wise interactions (Moya-
459 Laraño *et al.* 2012; Moya-Laraño *et al.* 2014). Yet, one-on-one approaches may ignore
460 emergent indirect effects of having several species together (Wootton 1994; Dambacher &
461 Ramos-Jiliberto 2007). For instance, *Cancer productus*, a crab native to the Northwest
462 Pacific, consumes equal amounts of native oysters and of invasive drill oysters when each
463 type of prey is offered alone, but when they are offered together crabs interact with the
464 native oyster species only (Grason & Miner 2012). Therefore, if trophic links are not
465 evaluated in presence of all species in the community, one may reach erroneous conclusions
466 on the strength of the interaction (Guzmán *et al.* 2016b; Fonseca *et al.* 2017) and
467 overestimate connectance in food webs. We show that all communities ended up becoming
468 a sum of one or more trophic chains (Box 1C). Thus, the fundamental trophic niche of
469 species in this system (i.e., the food items that the species is able to feed on) is larger than
470 the realized one (i.e., the food items that the species feeds on when they are all present
471 simultaneously – (Hutchinson 1961)). Therefore, our results suggest that some food webs
472 may be less complex than previously thought in terms of the frequency and strength of IGP.
473 Theoretical models exploring persistence in three-species communities with IGP find
474 a limited parameter space for coexistence of IG-predator and IG-prey (e.g. Mylius *et al.*
475 2001), but field observations show that IGP is actually widespread (Polis 1991). Our results
476 suggest that IGP in some systems might actually be occasional, as predators will tend to
477 forage on the most profitable food, which generally is not the IG prey (Polis *et al.* 1989). In
478 line with this, some natural systems have shown that communities with IGP actually show
479 dynamics that are compatible with linear food chains, rather than with IGP (Borer *et al.*
480 2003). Therefore, predators may coexist because they rarely engage in IGP, and complexity
481 may be over-estimated (Magalhães *et al.* 2005). This agrees with food web theory stating
482 that weak trophic interactions promote the persistence of communities (May 1972; Paine
483 1992; McCann *et al.* 1998, among others). For example, Hiltunen *et al.* (2014) found long-
484 term cycling dynamics when modelling a three-species planktonic food web with IGP, with
485 interaction strength between IG-predator and IG-prey set to be much weaker to that
486 between IG-predator and the shared resource. Our results suggest that increasing the

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

Acknowledgements

The authors deeply thank Francis J. Burdon and two anonymous reviewers of PCI Ecology for significantly improving the quality of the manuscript with their contributions. We are indebted to Rosa María Sahún Logroño for her valuable help in maintaining the experimental populations. This work was financed by the Spanish Ministry of Science and Innovation (CGL2015-66192-R and AGL2011-30538-C03-03). I.T.C. was recipient of a grant from the Spanish National Research Council (CSIC, ref: JAE-PRE 041). The animals used for the research of this publication are not test animals in the legal sense. The authors have no conflict of interest to declare.

References

Abad-Moyano, R., Urbaneja, A. & Schausberger, P. (2010). Intraguild interactions between *Euseius stipulatus* and the candidate biocontrol agents of *Tetranychus urticae* in Spanish clementine orchards: *Phytoseiulus persimilis* and *Neoseiulus californicus*. *Experimental and Applied Acarology*, 50, 23-34.

Amarasekare, P. (2008). Coexistence of intraguild predators and prey in resource-rich environments. *Ecology*, 89, 2786-2797.

Baiser, B., Elhesha, R. & Kahveci, T. (2016). Motifs in the assembly of food web networks. *Oikos*, 125, 480-491.

Bascompte, J. & Melián, C.J. (2005). Simple trophic modules for complex food webs. *Ecology*, 86, 2868-2873.

Beckerman, A.P., Petchey, O.L. & Warren, P.H. (2006). Foraging biology predicts food web complexity. *Proceedings of the National Academy of Sciences*, 103, 13745-13749.

Birkhofer, K., Bylund, H., Dalin, P., Ferlian, O., Gagic, V., Hambäck, P.A. *et al.* (2017). Methods to identify the prey of invertebrate predators in terrestrial field studies. *Ecology and Evolution*, 7, 1942-1953.

Borer, E.T., Briggs, C.J., Murdoch, W.W. & Swarbrick, S.L. (2003). Testing intraguild predation theory in a field system: does numerical dominance shift along a gradient of productivity? *Ecology Letters*, 6, 929-935.

Bouras, S.L. & Papadoulis, G.T. (2005). Influence of selected fruit tree pollen on life history of *Euseius stipulatus* (Acari: Phytoseiidae). *Experimental and Applied Acarology*, 36, 1-14.

Bukovinszky, T., van Veen, F.F., Jongema, Y. & Dicke, M. (2008). Direct and indirect effects of resource quality on food web structure. *Science*, 319, 804-807.

Carnicer, J., Jordano, P. & Melián, C.J. (2009). The temporal dynamics of resource use by frugivorous birds: a network approach. *Ecology*, 90, 1958-1970.

Carpenter, S.R., Kitchell, J.F. & Hodgson, J.R. (1985). Cascading trophic interactions and lake productivity. *BioScience*, 35, 634-639.

Dambacher, J.M. & Ramos-Jiliberto, R. (2007). Understanding and predicting effects of modified interactions through a qualitative analysis of community structure. *The Quarterly Review of Biology*, 82, 227-250.

Daugherty, M.P., Harmon, J.P. & Briggs, C.J. (2007). Trophic supplements to intraguild predation. *Oikos*, 116, 662-677.

Diehl, S. & Feißel, M. (2000). Effects of enrichment on three-level food chains with omnivory. *The American Naturalist*, 155, 200-218.

Dunne, J.A., Williams, R.J. & Martinez, N.D. (2002). Food-web structure and network theory: the role of connectance and size. *Proceedings of the National Academy of Sciences*, 99, 12917-12922.

Elton, C.(1927) Animal Ecology. Sidgwick and Jackson, London. Reprinted several times, e.g. 2001 by The University of Chicago Press, ISBN 0-226-20639-4

Emmerson, M. & Yearsley, J.M. (2004). Weak interactions, omnivory and emergent food-web properties. *Proceedings of the Royal Society of London B: Biological Sciences*, 271, 397-405.

Faria, L.D.B. & Costa, M.I.S. (2010). Omnivorous food web, prey preference and allochthonous nutrient input. *Ecological Complexity*, 7, 107-114.

Ferragut, F., Garcia-Mari, F., Costa-Comelles, J. & Laborda, R. (1987). Influence of food and temperature on development and oviposition of *Euseius stipulatus* and *Typhlodromus phialatus* (Acari: Phytoseiidae). *Experimental and Applied Acarology*, 3, 317-329.

Fonseca, M.M., Montserrat, M., Guzmán, C., Torres-Campos, I., Pallini, A. & Janssen, A. (2017). How to evaluate the potential occurrence of intraguild predation. *Experimental and Applied Acarology*, 72, 103-114.

Gagnon, A.E., Heimpel, G.E. & Brodeur, J. (2011). The ubiquity of intraguild predation among predatory arthropods. *PLoS ONE*, 6, e28061.

Gellner, G. & McCann, K. (2012). Reconciling the omnivory-stability debate. *The American Naturalist*, 179, 22-37.

Gellner, G. & McCann, K.S. (2016). Consistent role of weak and strong interactions in high-and low-diversity trophic food webs. *Nature communications*, 7, 11180.

González-Fernández, J., De la Peña, F., Hormaza, J.I., Boyero, J., Vela, J., Wong, E. *et al.* (2009). Alternative food improves the combined effect of an omnivore and a predator on biological pest control. A case study in avocado orchards. *Bulletin of Entomological Research*, 99, 433-444.

Grason, E.W. & Miner, B.G. (2012). Preference alters consumptive effects of predators: top-down effects of a native crab on a system of native and introduced prey. *PloS ONE*, 7, e51322.

Guzmán, C., Aguilar-Fenollosa, E., Sahún, R.M., Boyero, J.R., Vela, J.M., Wong, E. *et al.* (2016a). Temperature-specific competition in predatory mites: Implications for biological pest control in a changing climate. *Agriculture, Ecosystems and Environment*, 216, 89-97.

Guzmán, C., Sahún, R. & Montserrat, M. (2016b). Intraguild predation between phytoseiid mite species might not be so common. *Experimental and Applied Acarology*, 68, 441-453.

Hairston, N.G., Smith, F.E. & Slobodkin, L.B. (1960). Community structure, population control, and competition. *The American Naturalist*, 94, 421-425.

Heithaus, M.R. (2001). Habitat selection by predators and prey in communities with asymmetrical intraguild predation. *Oikos*, 92, 542-554.

Hiltunen, T., Ellner, S.P., Hooker, G., Jones, L.E. & Hairston Jr, N.G. (2014). Eco-evolutionary dynamics in a three-species food web with intraguild predation: intriguingly complex. In: *Advances in Ecological Research*. Elsevier, pp. 41-73.

Hin, V., Schellekens, T., Persson, L. & de Roos, A.M. (2011). Coexistence of predator and prey in intraguild predation systems with ontogenetic niche shifts. *The American Naturalist*, 178, 701-714.

Holt, R.D. (1977). Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology*, 12, 197-229.

Holt, R.D. (1997). Community modules. In: *Multitrophic interactions in Terrestrial Systems* (eds. Gange, A & Brown, V). Blackwell Science London, UK, pp. 333-350.

Holt, R.D. & Huxel, G.R. (2007). Alternative prey and the dynamics of intraguild predation: theoretical perspectives. *Ecology*, 88, 2706-2712.

Holt, R.D. & Polis, G.A. (1997). A theoretical framework for intraguild predation. *The American Naturalist*, 149, 745-764.

Hutchinson, G.E. (1961). The paradox of the plankton. *The American Naturalist*, 95, 137-145.

Janssen, A., Montserrat, M., HilleRisLambers, R., Roos, A.M., Pallini, A. & Sabelis, M.W. (2006). Intraguild predation usually does not disrupt biological control. In: *Trophic and Guild in Biological Interactions Control* (eds. Brodeur, J & Boivin, G). Springer Netherlands Dordrecht, pp. 21-44.

Janssen, A., Sabelis, M.W., Magalha es, S., Montserrat, M. & van der Hammen, T. (2007). Habitat structure affects intraguild predation. *Ecology*, 88, 2713-2719.

Johnson, S., Domínguez-García, V., Donetti, L. & Muñoz, M. A. Trophic coherence determines food-web stability. Proc.Natl. Acad. Sci. 111, 17923–17928.

Kondoh, M. (2008). Building trophic modules into a persistent food web. *Proceedings of the National Academy of Sciences*, 105, 16631-16635.

Kratina, P., Hammill, E. & Anholt, B.R. (2010). Stronger inducible defences enhance persistence of intraguild prey. *Journal of Animal Ecology*, 79, 993-999.

Křivan, V. (2000). Optimal intraguild foraging and population stability. *Theoretical Population Biology*, 58, 79-94.

Křivan, V. & Diehl, S. (2005). Adaptive omnivory and species coexistence in tri-trophic food webs. *Theoretical Population Biology*, 67, 85-99.

Kuijper, L.D., Kooi, B.W., Zonneveld, C. & Kooijman, S.A. (2003). Omnivory and food web dynamics. *Ecological Modelling*, 163, 19-32.

Lazzaro, X., Lacroix, G., Gauzens, B., Gignoux, J. & Legendre, S. (2009). Predator foraging behaviour drives food-web topological structure. *Journal of Animal Ecology*, 78, 1307-1317.

Lemos-Costa, P., Pires, M.M., Araújo, M.S., Aguiar, M.A. & Guimarães, P.R. (2016). Network analyses support the role of prey preferences in shaping resource use patterns within five animal populations. *Oikos*, 125, 492-501.

Liu, Z. & Zhang, F. (2013). Species coexistence of communities with intraguild predation: The role of refuges used by the resource and the intraguild prey. *Biosystems*, 114, 25-30.

Magalhães, S., Tudorache, C., Montserrat, M., Van Maanen, R., Sabelis, M.W. & Janssen, A. (2005). Diet of intraguild predators affects antipredator behavior in intraguild prey. *Behavioral Ecology*, 16, 364-370.

May, R.M. (1972). Will a large complex system be stable? *Nature*, 238, 413.

McCann, K., Hastings, A. & Huxel, G.R. (1998). Weak trophic interactions and the balance of nature. *Nature*, 395, 794.

McMurtry, J. & Croft, B. (1997). Life-styles of phytoseiid mites and their roles in biological control. *Annual Review of Entomology*, 42, 291-321.

Messelink, G.J. & Janssen, A. (2014). Increased control of thrips and aphids in greenhouses with two species of generalist predatory bugs involved in intraguild predation. *Biological Control*, 79, 1-7.

Montoya, J., Woodward, G., Emmerson, M.C. & Solé, R.V. (2009). Press perturbations and indirect effects in real food webs. *Ecology*, 90, 2426-2433.

Montserrat, M., de la Peña, F., Hormaza, J. & González-Fernández, J. (2008a). How do *Neoseiulus californicus* (Acari: Phytoseiidae) females penetrate densely webbed spider mite nests? *Experimental and Applied Acarology*, 44, 101-106.

Montserrat, M., Guzmán, C., Sahún, R., Belda, J. & Hormaza, J. (2013). Pollen supply promotes, but high temperatures demote, predatory mite abundance in avocado orchards. *Agriculture, Ecosystems & Environment*, 164, 155-161.

Montserrat, M., Magalhães, S., Sabelis, M.W., De Roos, A.M. & Janssen, A. (2008b). Patterns of exclusion in an intraguild predator–prey system depend on initial conditions. *Journal of Animal Ecology*, 77, 624-630.

Moya-Laraño, J., Bilbao-Castro, J.R., Barrionuevo, G., Ruiz-Lupión, D., Casado, L.G., Montserrat, M. *et al.* (2014). Eco-evolutionary spatial dynamics: rapid evolution and isolation explain food web persistence. *Advances in Ecological Research*, 50, 75-144.

Moya-Laraño, J., Verdeny-Vilalta, O., Rowntree, J., Melguizo-Ruiz, N., Montserrat, M. & Laiolo, P. (2012). Climate Change and Eco-Evolutionary Dynamics in Food Webs. *Advances in Ecological Research*, 47, 1-80.

Mylius, S.D., Klumpers, K., de Roos, A.M. & Persson, L. (2001). Impact of intraguild predation and stage structure on simple communities along a productivity gradient. *The American Naturalist*, 158, 259-276.

Nakazawa, T., Miki, T. & Namba, T. (2010). Influence of predator-specific defense adaptation on intraguild predation. *Oikos*, 119, 418-427.

Neutel, A.M., Heesterbeek, J.A. & de Ruiter, P.C. (2002). Stability in real food webs: weak links in long loops. *Science*, 296, 1120-1123.

Neutel, A.M., Heesterbeek, J.A., Van de Koppel, J., Hoenderboom, G., Vos, A., Kaldeway, C. *et al.* (2007). Reconciling complexity with stability in naturally assembling food webs. *Nature*, 449, 599.

Neutel, A.M. & Thorne, M.A. (2014). Interaction strengths in balanced carbon cycles and the absence of a relation between ecosystem complexity and stability. *Ecology letters*, 17, 651-661.

Novak, M. (2013). Trophic omnivory across a productivity gradient: intraguild predation theory and the structure and strength of species interactions. *Proceedings of the Royal Society of London B: Biological Sciences*, 280, 20131415.

Novak, M. & Wootton, J.T. (2010). Using experimental indices to quantify the strength of species interactions. *Oikos*, 119, 1057-1063.

Oksanen, L., Fretwell, S.D., Arruda, J. & Niemela, P. (1981). Exploitation ecosystems in gradients of primary productivity. *The American Naturalist*, 118:2, 240-261.

Otto, S.B., Berlow, E.L., Rank, N.E., Smiley, J. & Brose, U. (2008). Predator diversity and identity drive interaction strength and trophic cascades in a food web. *Ecology*, 89, 134-144.

Paine, R.T. (1992). Food-web analysis through field measurement of per capita interaction strength. *Nature*, 355, 73.

Pimm , S. L. (1984). Complexity and stability of ecosytems. Nature, 307, 321-326.

Pimm, S.L. & Lawton, J. (1978). On feeding on more than one trophic level. *Nature*, 275, 542-544.

Plein, M., Längsfeld, L., Neuschulz, E.L., Schultheiß, C., Ingmann, L., Töpfer, T. *et al.* (2013). Constant properties of plant–frugivore networks despite fluctuations in fruit and bird communities in space and time. *Ecology*, 94, 1296-1306.

Polis, G.A. (1991). Complex trophic interactions in deserts: an empirical critique of food-web theory. *The American naturalist*, 138, 123-155.

Polis, G.A. & Holt, R.D. (1992). Intraguild predation: the dynamics of complex trophic interactions. *Trends in Ecology & Evolution*, 7, 151-154.

Polis, G.A., Myers, C.A. & Holt, R.D. (1989). The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics*, 20, 297-330.

Polis, G.A. & Strong, D.R. (1996). Food web complexity and community dynamics. *The American Naturalist*, 147, 813-846.

Prill R.J., Iglesias P.A., Levchenko A. (2005). Dynamic properties of network motifs contribute to network organization. PLOS BIOLOGY, 3: 1881-1892.

Pulliam H.R. (1974). On the thory of optimal diets. American Naturalist, 108: 59-74.

R Core Team (2017). R: A Language and Environment for Statistical Computing. https://www.R-project.org/

Rosenheim, J.A., Kaya, H., Ehler, L., Marois, J.J. & Jaffee, B. (1995). Intraguild predation among biological-control agents: theory and evidence. *Biological Control*, 5, 303-335.

Rudolf, V.H. (2007). The interaction of cannibalism and omnivory: consequences for community dynamics. *Ecology*, 88, 2697-2705.

Rudolf, V.H.W. & Armstrong, J. (2008). Emergent impacts of cannibalism and size refuges in prey on intraguild predation systems. *Oecologia*, 157, 675-686.

Schmitz, O.J. & Sokol-Hessner, L. (2002). Linearity in the aggregate effects of multiple predators in a food web. *Ecology Letters*, 5, 168-172.

Tylianakis, J.M., Tscharntke, T. & Lewis, O.T. (2007). Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature*, 445, 202.

Van Driesche, R., Hoddle, M. & Center, T.D. (2007). Control de plagas y malezas por enemigas naturales. US Department of Agriculture, US Forest Service, Forest Health Technology Enterprise Team.

Vance-Chalcraft, H.D., Rosenheim, J.A., Vonesh, J.R., Osenberg, C.W. & Sih, A. (2007). The influence of intraguild predation on prey suppression and prey release: a meta-analysis. *Ecology*, 88, 2689-2696.

Vázquez, D.P., Ramos-Jiliberto, R., Urbani, P. & Valdovinos, F.S. (2015). A conceptual framework for studying the strength of plant–animal mutualistic interactions. *Ecology letters*, 18, 385-400.

Wootton, J.T. (1994). Putting the pieces together: testing the independence of interactions among organisms. *Ecology*, 75, 1544-1551.

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

Table 1. Results of Generalized Linear 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*			

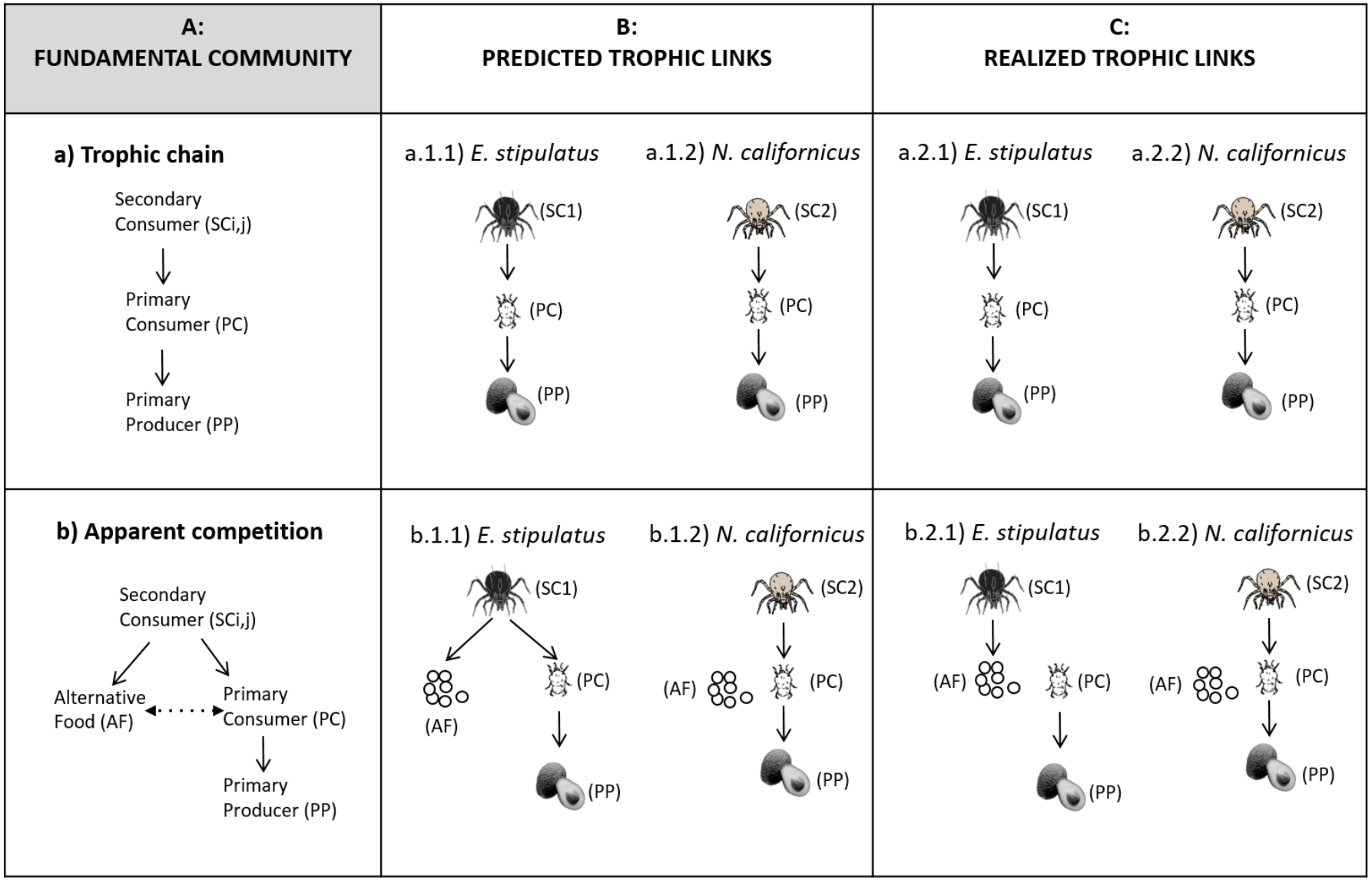
Table 2. Results of Generalized Linear Models applied to a) herbivore mortality rates, b) IG-prey (juveniles of *E. stipulatus*) mortality rates, and c) (IG-)predator (females of *N. californicus*) oviposition rates. All the analyses were 3 full-factorial designs. When interactions among the three explanatory 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*			

778 Box 1. **A: Fundamental community modules** included in this study. a) trophic chain, b)
779 apparent competition, c) intraguild predation, and d) intraguild predation and apparent
780 competition. From a) to d) the complexity of the community is increased via increasing the
781 number of species and the number of interactions among them. **B: Predicted trophic links**
782 that have been observed using pairwise experimental settings**. C: Realized trophic links**
783 occurring across community modules of increasing complexity, obtained from the
784 experiments presented here, where interactions are measured in the presence of other
785 components of the community. SC stands for secondary consumer, PC for primary
786 consumer, PP for primary producer, and AF for alternative food. SC1 and SC2 are phytoseiid
787 predatory mites, i.e. *Euseius stipulatus* and *Neoseiulus californicus*, respectively, PC is the
788 tetranychid herbivore mite *Oligonychus perseae*, AF is pollen of *Carpobrotus edulis*, and PP
789 is the avocado *Persea americana*. Solid arrows indicate negative direct interactions (who
790 eats whom), whereas dotted and dashed arrows in Box 1A indicate negative indirect
791 interactions (apparent competition and competition).
792
793 Figure 1. Mortality rates (average ± S.E.) of a) herbivore prey (*Oligonychus perseae* females)
794 and b) IG-prey (*Neoseiulus californicus* juveniles), and c) oviposition rates (average ± S.E.) of
795 IG-predators (*Euseius stipulatus* females), in 14 different treatments defined by presence or
796 absence of either IG-predators, IG-prey, herbivores or alternative food (pollen), depicted in
797 the lower part of the figure, that mimicked four different community configurations and
798 their respective controls.
799
800 Figure 2. Mortality rates (average ± S.E.) of a) herbivore prey (*Oligonychus perseae* females)
801 and b) IG-prey (*Euseius stipulatus* juveniles), and c) oviposition rates (average ± S.E.) of IG-
802 predators (*Neoseiulus califonicus* females), in 14 different treatments defined by presence
803 or absence of either IG-predators, IG-prey, herbivores or alternative food (pollen), depicted
804 in the lower part of the figure, that mimicked four different community configurations and
805 their respective controls.
806
807


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
(SC1)
(SC2)
(AF)
(PC)
(PP)

809 Box 1 (cont.)

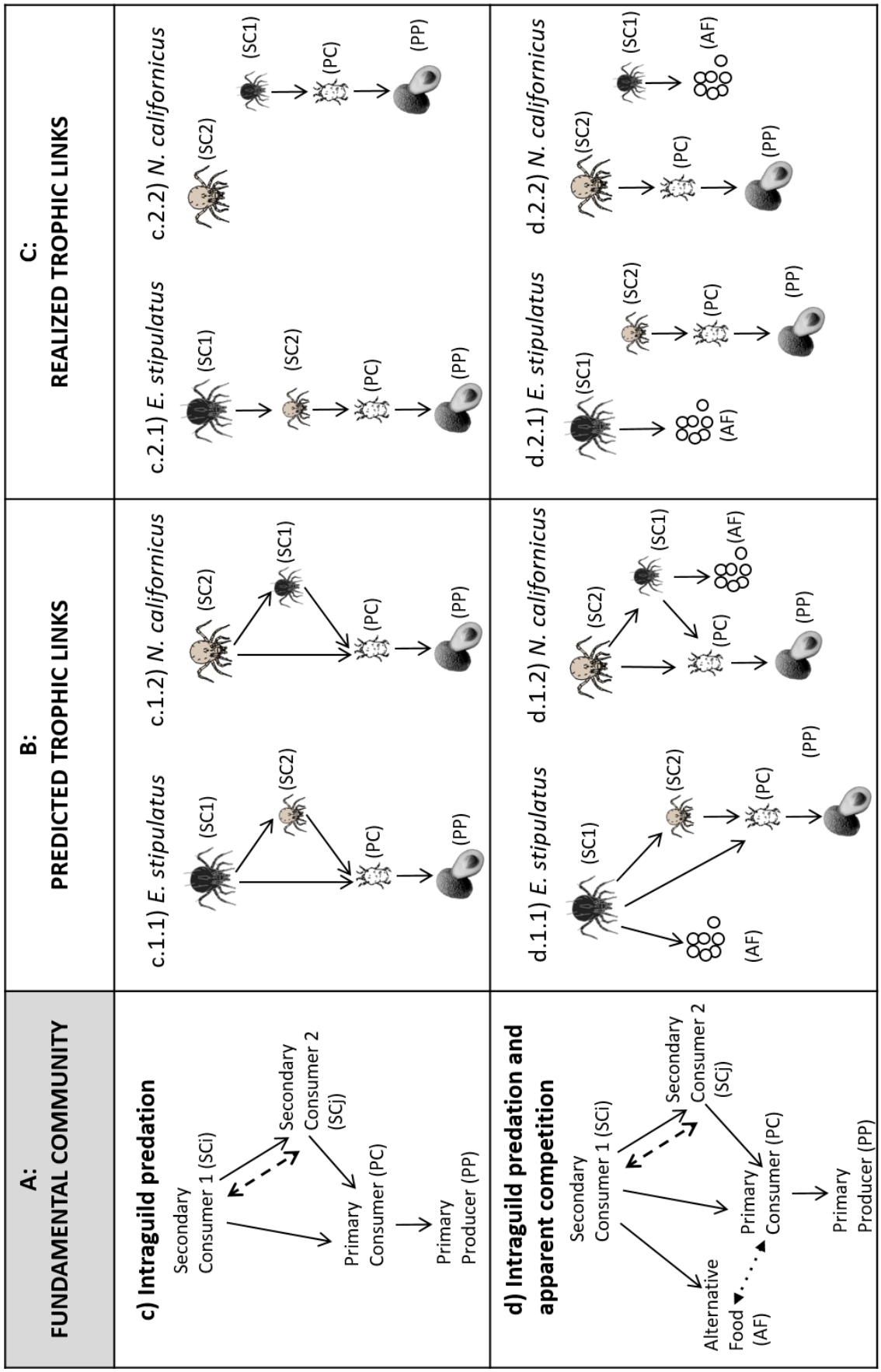


Figure 1.

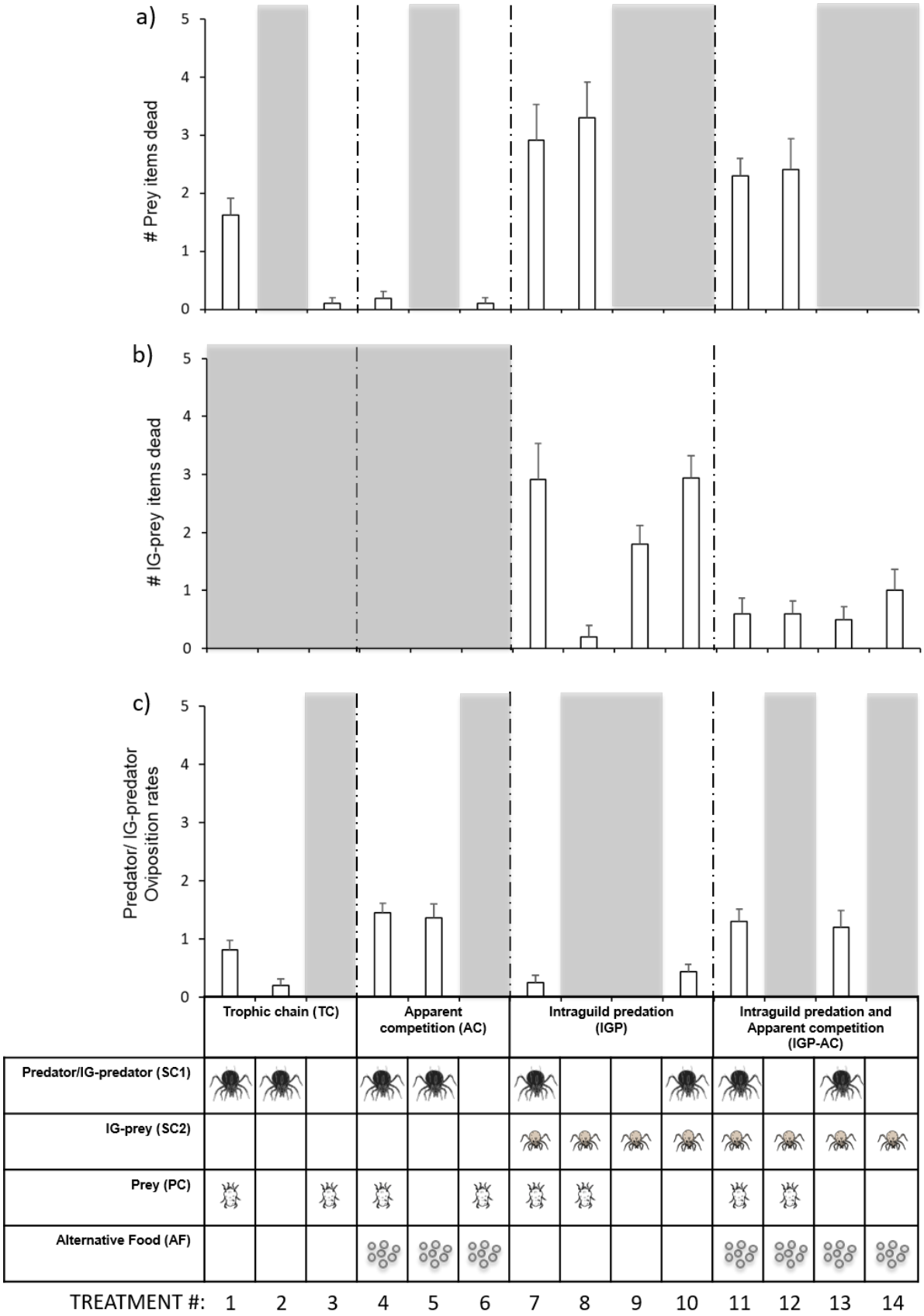
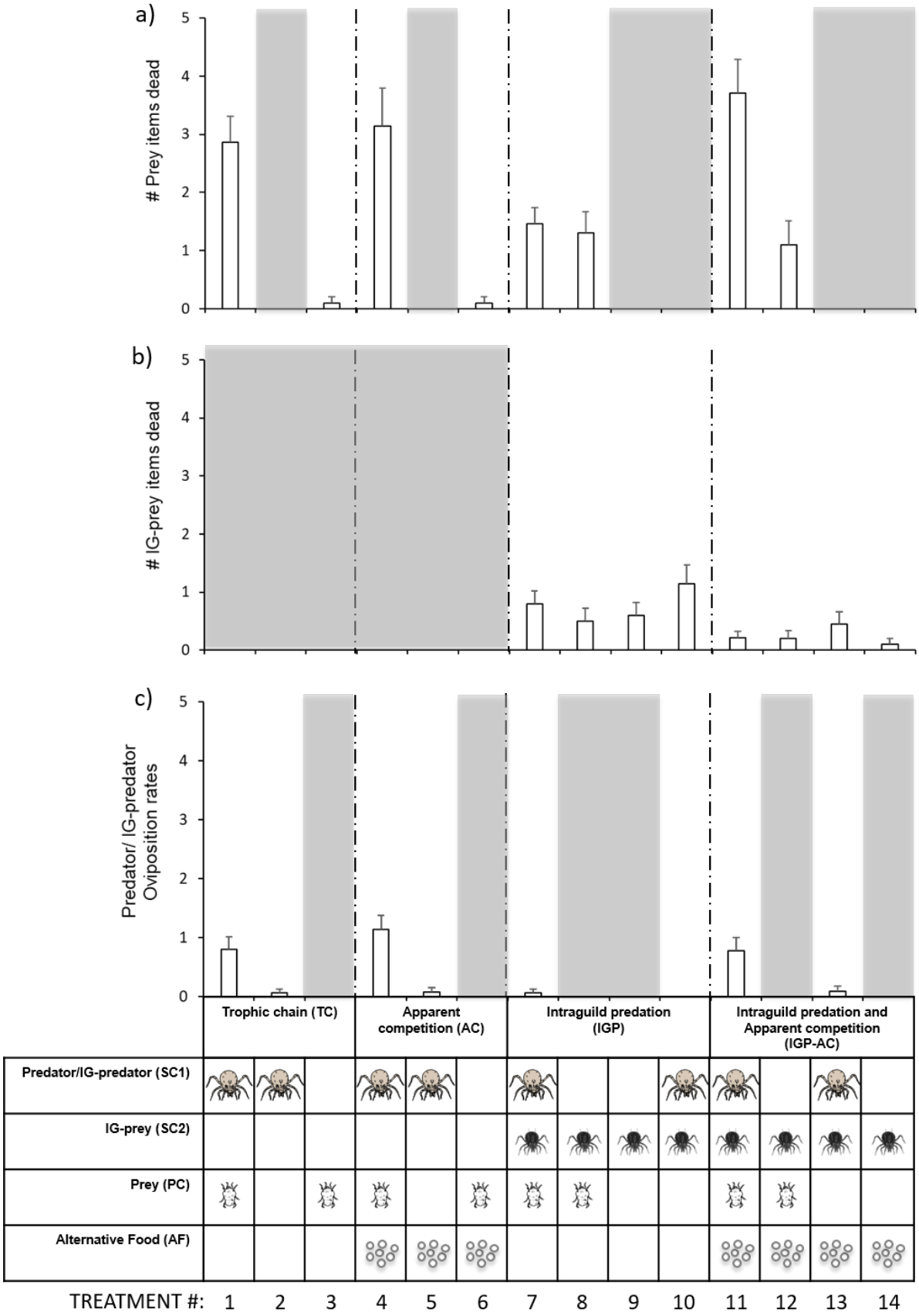

a)
Prey items dead
b)
IG-prey items dead
c)
Predator/ IG-predator Oviposition rates
Trophic chain (TC)
Apparent competition (AC)
Intraguild predation (IGP)
Intraguild predation and Apparent competition (IGP-AC)
Predator/IG-predator (SC1)
IG-prey (SC2)
Prey (PC)
Alternative Food (AF)
TREATMENT #: 1 2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

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