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 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 Southwestern 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±1°C, 65±5% RH and 16:8h L:D (Light:Dark).

**Mite cultures**

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

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

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

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

**Community modules**

Experimental arenas to test the outcome of community modules consisted of avocado leaf discs placed in petri dishes with a circular hole in the middle, as described in Guzmán *et al.* (2016a). Briefly, a hole (6.5 cm Ø) was cut in a petri dish (9 cm Ø) turned upside down and filled with an avocado leaf disc (7.5 cm Ø), with the borders glued to a clay ring. Inside the petri dish, wet cotton wool ensured enough humidity to keep leaves turgid. Petri dishes were then sealed with parafilm®. To prevent individuals from escaping, a ring of Tanglefoot® was applied along the outer margin of the leaf disc. Female and juvenile predators used in
the experiments were 10-14 and 2-3 days old since egg hatching, respectively. Cohorts of *E. stipulatus* were made by transferring with a fine brush 400 eggs from the rearings to 2-3 bean leaves placed on top of sponges (30 x 20 x 5 cm, approx.) covered with cotton wool, inside water-containing trays (3.5 L), and with pollen of *C. edulis* as food. Because it was difficult to obtain eggs of *N. californicus* from the rearings, cohorts of this species were made by transferring 100 females to 2-3 bean leaves infested with *Tetranychus urticae* placed on containers similar to those used for the cultures. After allowing *N. californicus* females to feed and oviposit for 48 h, they were removed with a fine brush. Before the experiments, gravid predator females were randomly taken from the cohorts, and starved for 16 h in experimental containers similar to those above. Starvation was done to standardize hunger among individuals, and to ensure that egg production in tested females was not obtained from food ingested prior to the experiment. Predator juveniles were taken from the cohorts when needed. Arenas containing the herbivore were done as follows: Ten females of *O. perseae* were let to build nests and lay eggs on experimental arenas during 4 days. The number of nests and eggs laid per nest on each arena was counted at the onset of the experiment. Pollen in arenas assigned to treatments with alternative food was supplied *ad libitum*, using a fine brush.

We performed experiments using two ‘community blocks’, depending on the identity of the top predator (*N. californicus* or *E. stipulatus*). Increased complexity in each of the two community blocks was mimicked through the combination of the presence / absence of 4 factors: predator/IG-predator, IG-prey, herbivore and alternative food. This resulted in the community modules depicted in the X-axis of figures 1 and 2. These modules were: **Trophic chain**: either one *E. stipulatus* or *N. californicus* female was introduced in arenas containing 10 females of *O. perseae* (treatment # 1 in Fig 1 and 2). Arenas containing either one *E. stipulatus* or one *N. californicus* female without herbivores (treatment # 2), and containing 10 *O. perseae* females without predators (treatment # 3) were done as controls for predator oviposition rate and prey natural mortality, respectively. **Apparent competition**: arenas consisted of one female of either *E. stipulatus* or *N. californicus*, 10 females of *O. perseae*, and pollen of *C. edulis* supplied *ad libitum* (treatment # 4). Similar arenas but without the herbivores (treatment # 5) were made as controls for oviposition rates of predators on pollen only, and without the IG-predator (treatment # 6) to assess potential effects of pollen 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. persea* 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* preyped on *O. persea* (*t* = 2.74, *P* = 0.0076; Fig 1a, compare bars 1 and 3) and marginally on *N. californicus* juveniles (*t* = -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. persea* (*t* = 2.26, *P* = 0.026; Fig 1a, compare bar 1 to 7), but adding *O. persea* did not influence mortality of the IG-prey (*t* = -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* = 2.99, *P* = 0.0037; Fig 1a, compare bar 1 to 4) and the IG-prey (*t* = 3.91, *P* << 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* = 0.88, *P* = 0.379; Fig 1a, compare bar 7 to 11), but did lead to lower IG-prey mortality (*t* = 3.58, *P* << 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
on the herbivore yielded some egg production ($t_{96} = 2.19, P = 0.021$; Fig 1c, compare bar 1 to 2), feeding on IG-prey did not ($t_{96} = -1.13, P = 0.259$; Fig 1c, compare bar 10 to 2).

Communities with *N. californicus* as the (IG-)predator

Herbivore mortality was affected by all second order interactions (Table 2a), and that of the IG-prey (juveniles of *E. stipulatus*) was only affected by the presence of pollen (Table 2b). Paired comparisons revealed that a) *N. californicus* preyed on *O. perseae* ($t_{90} = 3.32, P = 0.013$; Fig 2a, compare bar 3 to 1) but not on *E. stipulatus* juveniles ($t_{86} = -1.35, P = 0.182$; Fig 2b, compare bar 9 to 10), when each prey was offered alone; b) adding IG-prey reduced mortality of *O. perseae* ($t_{90} = 2.56, P = 0.012$; Fig 2a, compare bar 1 to 7), but adding *O. perseae* did not change mortality of the IG-prey ($t_{86} = -0.93, P = 0.353$; Fig 2b, compare bar 10 to 7); c) the presence of pollen did not affect mortality of either *O. perseae* ($t_{90} = -0.43, P = 0.669$; Fig 2a, compare bar 1 to 4) or the IG-prey ($t_{86} = 1.80, P = 0.075$; Fig 2b, compare bar 10 to 13); d) when both types of prey were available, the presence of pollen led to a significant increase in mortality of *O. perseae* ($t_{90} = -3.65, P << 0.001$; Fig 2a, compare bar 7 to 11), but a significant decrease of mortality in *E. stipulatus* juveniles ($t_{86} = 2.04, P = 0.044$; Fig 2b, compare bar 7 to 11).

Oviposition rates of *N. californicus* were affected by the main factor Herbivore and the interaction between the IG-prey and pollen (Table 2c). Indeed, paired comparisons revealed that e) eggs were produced when *N. californicus* was offered the herbivore alone ($t_{104} = 2.45, P = 0.016$; Fig 2c, compare bar 1 to 2), but not when they were on arenas with either the IG-prey ($t_{104} = 0.01, P = 0.992$; Fig 2c, compare bar 10 to 2) or pollen ($t_{104} = -0.15, P = 0.884$; Fig 2c, compare bar 5 to 2) alone. Moreover, in the presence of the herbivore, rates of oviposition were not influenced by the presence of pollen ($t_{104} = -0.93, P = 0.352$; Fig 2c, compare bar 1 to 4), but dramatically decreased in the presence of the IG-prey ($t_{104} = 2.39, P = 0.019$; Fig 2c, compare bar 1 to 7). However, when pollen was added to the system with both prey types, IG-predators resumed oviposition to its maximum ($t_{104} = -2.36, P = 0.020$; Fig 2c, compare bar 7 to 11).

Discussion

In this study, we tested the effect of community structure on the realized interactions within a community of predatory and herbivorous mites. Because in our system the
intraguild predator is the largest individual within a pair (as in most systems), we created communities in which adults belonged to one species and juveniles to the other, then inverted the species-stage identity in another set of communities. We then measured predation and oviposition in communities with all possible combinations of the presence of shared prey, the intraguild prey, the intraguild predator and alternative food. We show that adding species to a community increases the number of potential interactions, but not necessarily their occurrence. Indeed, despite the potential for apparent competition and intraguild predation in modules with several species, all modules could be described by linear food chains (Box 1C).

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

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

The simultaneous presence of the two predators is likely to have little effect upon the densities of the shared prey. Indeed, whereas adding adults of *E. stipulatus* to an arena with *N. californicus* juveniles results in higher prey densities as compared to the presence of
*N. californicus* alone, the reverse is not true when adding juveniles of *E. stipulatus* to an arena with adult *N. californicus*. Thus, the net effect of these interactions upon prey density is probably negligible. This is corroborated by field studies (Montserrat et al. 2013). However, the presence of alternative food (i.e. pollen) contributed to reduce trophic interactions between predator species resulting in community configurations that could enhance pest control. Thus, supplying alternative and preferred food to the IG-predator is probably detrimental to populations of *O. perseae*. Again, this finding mirrors field data (Montserrat et al. 2013).

By combining data of mortality and oviposition at different community structures, we could recover who eats whom in a relatively complex food web. Although this approach is very 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).

Food web ecology predicts that species of the highest trophic levels engage in trophic interactions on more than one food source when these are available. Here, we show that *E. stipulatus* feeds on the herbivore, *O. perseae*, on the intraguild prey, *N. californicus*, and on the alternative food, pollen, when each of these are presented alone. However, in the presence of pollen *E. stipulatus* reduces predation rates on both prey species. This may be explained by the fact that pollen is the most profitable food for this species, as found here and in other studies (Ferragut et al. 1987; McMurtry & Croft 1997; Bouras & Papadoulis 2005; González-Fernández et al. 2009). Similarly, *N. californicus* adults and juveniles ceased foraging on other food sources in presence of the herbivores. These results suggest that realized interactions hinge on the presence of the most profitable food source.

In presence of the optimal food source for each of the two secondary consumers, communities tended to melt down to become two simple trophic chains. Indeed, in the most complex communities studied here, with all 5 species present, the presence of the
optimal food originated the split of the community into two trophic chains, one with *E. stipulatus* feeding on pollen and the other with *N. californicus* feeding on the herbivore (Box 1 d), compare d.1.1. and d.1.2. with d.2.1. and d.2.2.).

Another factor that contributed to the linearization of the food web was that, when both the IG-prey and the shared prey were together, *E. stipulatus* preyed mainly on the IG-prey. Indeed, mortality of *O. perseae* in presence of the IG-prey, *N. californicus*, was not affected by the presence of *E. stipulatus*. Furthermore, mortality of *N. californicus* juveniles was significantly higher in treatments with presence of the IG-predator, compared to the control without them. This suggests that mortality in the herbivore was mainly inflicted by juveniles of *N. californicus*, and that *E. stipulatus* females preyed preferentially on juveniles of *N. californicus*. This could be explained by *E. stipulatus* having no access to *O. perseae* eggs or females located inside the nests (Montserrat et al. 2008a; González-Fernández et al. 2009), which leads to higher encounter rates between *E. stipulatus* and *N. californicus* than between *E. stipulatus* and *O. perseae*. *Neoseiulus californicus* juveniles, however, can penetrate *O. perseae* nests, and thus may feed on them. Therefore, the realized community was that of a 4-level trophic chain (Box 1, c.2.1.). In the other community block, when *N. californicus* acted as the IG-predator, mortality of *O. perseae* females was similar in all communities with the IG-prey, irrespective of the presence of IG-predators. Furthermore, mortality of IG-prey did not differ between treatments with and without the IG-predator, indicating that *N. californicus* females did not forage on *E. stipulatus* juveniles. These results suggest that, in presence of IG-prey (juveniles of *E. stipulatus*), the IG-predator ceased to forage on either herbivore or IG-prey. Thus, the realized community was that of a trophic chain composed of the IG-prey, the herbivore and the plant, with the IG-predator not interacting at all (Box 1, c.2.2.). This can be explained by *N. californicus* females avoiding foraging on a patch where its offspring (future) IG-predator is also there. In line with this, Abad-Moyano et al. (2010) reported that the presence of *E. stipulatus* immatures exerted non-lethal IG-effects on *N. californicus* females, causing daily oviposition to decrease over time despite the availability of the shared prey was kept constant. In any case, here, the trophic links are again linear, with *N. 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.
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)                |          |            |         |          |

### 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*      |            |         |          |
Box 1. **Fundamental community modules** included in this study. a) trophic chain, b) apparent competition, c) intraguild predation, and d) intraguild predation and apparent competition. From a) to d) the complexity of the community is increased via increasing the number of species and the number of interactions among them. **B: Predicted trophic links** that have been observed using pairwise experimental settings. **C: Realized trophic links** occurring across community modules of increasing complexity, obtained from the experiments presented here, where interactions are measured in the presence of other components of the community. SC stands for secondary consumer, PC for primary consumer, PP for primary producer, and AF for alternative food. SC1 and SC2 are phytoseiid predatory mites, i.e. *Euseius stipulatus* and *Neoseiulus californicus*, respectively, PC is the tetranychid herbivore mite *Oligonychus perseae*, AF is pollen of *Carpobrotus edulis*, and PP is the avocado *Persea americana*. Solid arrows indicate negative direct interactions (who eats whom), whereas dotted and dashed arrows in Box 1A indicate negative indirect interactions (apparent competition and competition).

Figure 1. Mortality rates (average ± S.E.) of a) herbivores (*Oligonychus perseae* females) and b) IG-prey (*Neoseiulus californicus* juveniles), and c) oviposition rates (average ± S.E.) of IG-predators (*Euseius stipulatus* females), in 14 different treatments defined by presence or absence of either IG-predators, IG-prey, herbivores or alternative food (pollen), depicted in the lower part of the figure, that mimicked four different community configurations and their respective controls.

Figure 2. Mortality rates (average ± S.E.) of a) herbivores (*Oligonychus perseae* females) and b) IG-prey (*Euseius stipulatus* juveniles), and c) oviposition rates (average ± S.E.) of IG-predators (*Neoseiulus californicus* females), in 14 different treatments defined by presence or absence of either IG-predators, IG-prey, herbivores or alternative food (pollen), depicted in the lower part of the figure, that mimicked four different community configurations and their respective controls.
| **A:** FUNDAMENTAL COMMUNITY | **B:** PREDICTED TROPHIC LINKS | **C:** REALIZED TROPHIC LINKS |
|-------------------------------|-------------------------------|-------------------------------|
| **a) Trophic chain**         | **a.1.1) *E. stipulatus***     | **a.2.1) *E. stipulatus***     |
| Secondary Consumer (SCI,j)   | (SC1)                          | (SC1)                          |
| ↓                            | (PC)                           | (PC)                           |
| Primary Consumer (PC)        | (PP)                           | (PP)                           |
| **a.1.2) *N. californicus***  | (SC2)                          | (SC2)                          |
| **a.2.2) *N. californicus***  |                                |                                |
| **b) Apparent competition**  | **b.1.1) *E. stipulatus***     | **b.2.1) *E. stipulatus***     |
| Secondary Consumer (SCI,j)   | (SC1)                          | (SC1)                          |
| ↓                            | (PC)                           | (PC)                           |
| Alternative Food (AF)        | (AF)                           | (AF)                           |
| ↓                            | (PC)                           | (PC)                           |
| Primary Consumer (PC)        | (PP)                           | (PP)                           |
| **b.1.2) *N. californicus***  | (SC2)                          | (SC2)                          |
| **b.2.2) *N. californicus***  |                                |                                |
A: FUNDAMENTAL COMMUNITY

c) Intraguild predation
Secondary Consumer 1 (SCI) → Secondary Consumer 2 (SCI) → Primary Consumer (PC) → Primary Producer (PP)

d) Intraguild predation and apparent competition
Secondary Consumer 1 (SCI) → Secondary Consumer 2 (SCI) → Primary Consumer (PC) → Primary Producer (PP)

B: PREDICTED TROPHIC LINKS

c.1.1) E. stipulatus
(S1C) → (S2C) → (PC) → (PP)

c.1.2) N. californicus
(S1C) → (S2C) → (PC) → (PP)

c.2.1) E. stipulatus
(S1C) → (PC) → (PP)

c.2.2) N. californicus
(S2C) → (PC) → (PP)

C: REALIZED TROPHIC LINKS

c.2.1) E. stipulatus
(S1C) → (PC) → (PP)

c.2.2) N. californicus
(S2C) → (PC) → (PP)
Figure 1.

(a) # Prey items dead

(b) # IG-prey items dead

(c) Predator / IG-predator Opposition rates

| Predator/IG-predator (SC1) | Trophic chain (TC) | Apparent competition (AC) | Intraguild predation (IGP) | Intraguild predation and Apparent competition (IGP-AC) |
|----------------------------|---------------------|--------------------------|----------------------------|--------------------------------------------------|
|                            |                     |                          |                            |                                                  |

| IG-prey (SC2)              |                     |                          |                            |                                                  |
|                            |                     |                          |                            |                                                  |

| Prey (PC)                  |                     |                          |                            |                                                  |
|                            |                     |                          |                            |                                                  |

| Alternative Food (AF)      |                     |                          |                            |                                                  |
|                            |                     |                          |                            |                                                  |

TREATMENT #: 1 2 3 4 5 6 7 8 9 10 11 12 13 14
