Peer Community In
Ecology

From deserts to avocado orchards - understanding realized trophic interactions in communities

Francis John Burdon *based on peer reviews by* ***Owen Petchey*** *and 2 anonymous reviewers*

Inmaculada Torres-Campos, Sara Magalhães, Jordi Moya-Laraño, Marta Montserrat (2018) The return of the trophic chain: fundamental vs realized interactions in a simple arthropod food web. bioRxiv, ver. 1, peer-reviewed and recommended by Peer Community in Ecology. https://doi.org/10.1101/324178

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The late eminent ecologist Gary Polis once stated that “most catalogued food-webs are oversimplified caricatures of actual communities” and are “grossly incomplete representations of communities in terms of both diversity and trophic connections.” Not content with that damning indictment, he went further by railing that “theorists are trying to explain phenomena that do not exist” [1]. The latter critique might have been push back for Robert May´s ground-breaking but ultimately flawed research on the relationship between food-web complexity and stability [2]. Polis was a brilliant ecologist, and his thinking was clearly influenced by his experiences researching desert food webs. Those food webs possess an uncommon combination of properties, such as frequent omnivory, cannibalism, and looping; high linkage density (L/S); and a nearly complete absence of apex consumers, since few species completely lack predators or parasites [3]. During my PhD studies, I was lucky enough to visit Joshua Tree National Park on the way to a conference in New England, and I could immediately see the problems posed by desert ecosystems. At the time, I was ruminating on the “harsh-benign” hypothesis [4], which predicts that the relative importance of abiotic and biotic forces should vary with changes in local environmental conditions (from harsh to benign). Specifically, in more “harsh” environments, abiotic factors should determine community composition whilst weakening the influence of biotic interactions. However, in the harsh desert environment I saw first-hand evidence that species interactions were not diminished; if anything, they were strengthened. Teddy-bear chollas possessed murderously sharp defenses to protect precious water, creosote bushes engaged in belowground “chemical warfare” (allelopathy) to deter potential competitors, and rampant cannibalism amongst scorpions drove temporal and spatial ontogenetic niche partitioning. Life in the desert was hard, but you couldn´t expect your competition to go easy on you. If that experience colored my thinking about nature's reaction to a capricious environment, then the seminal work by Robert Paine on the marine rocky shore helped further cement the importance of biotic interactions. The insights provided by Paine [5] brings us closer to the research reported in the preprint "The return of the trophic chain: fundamental vs realized interactions in a simple arthropod food web" [6], given that the authors in that study hold the environment constant and test the interactions between different permutations of a simple community. Paine [5] was able to elegantly demonstrate using the chief protagonist *Pisaster ochraceus* (a predatory echinoderm also known as the purple sea star) that a keystone consumer could exert strong top-down control that radically reshaped the interactions amongst other community members. What was special about this study was that the presence of *Pisaster* promoted species diversity by altering competition for space by sedentary species, providing a rare example of an ecological network experiment combining trophic and non-trophic interactions. Whilst there are increasing efforts to describe these interactions (e.g., competition and facilitation) in multiplex networks [7], the authors of "The return of the trophic chain: fundamental vs realized interactions in a simple arthropod food web" [6] have avoided strictly competitive interactions for the sake of simplicity. They do focus on two trophic forms of competition, namely intraguild predation and apparent competition. These two interaction motifs, along with prey switching are relevant to my own research on the influence of cross-ecosystem prey subsidies to receiving food webs [8]. In particular, the apparent competition motif may be particularly important in the context of emergent adult aquatic insects as prey subsidies to terrestrial consumers. This was demonstrated by Henschel et al. [9] where the abundances of emergent adult aquatic midges in riparian fields adjacent to a large river helped stimulate higher abundances of spiders and lower abundances of herbivorous leafhoppers, leading to a trophic cascade. The aquatic insects had a bottom-up effect on spiders and this subsidy facilitated a top-down effect that cascaded from spiders to leafhoppers to plants. The apparent competition motif becomes relevant because the aquatic midges exerted a negative indirect effect on leafhoppers mediated through their common arachnid predators. In the preprint "The return of the trophic chain: fundamental vs realized interactions in a simple arthropod food web" [6], the authors have described different permutations of a simple mite community present in avocado orchards (*Persea americana*). This community comprises of two predators (*Euseius stipulatus* and *Neoseiulus californicus*), one herbivore as shared prey (*Oligonychus perseae*), and pollen of *Carpobrotus edulis* as alternative food resource, with the potential for the intraguild predation and apparent competition interaction motifs to be expressed. The authors determined that these motifs should be realized based off pairwise feeding trials. It is common for food-web researchers to depict potential food webs, which contain all species sampled and all potential trophic links based on laboratory feeding trials (as demonstrated here) or from observational data and literature reviews [10]. In reality, not all these potential feeding links are realized because species may partition space and time, thus driving alternative food-web architectures. In "The return of the trophic chain: fundamental vs realized interactions in a simple arthropod food web" [6], the authors are able to show that placing species in combinations that should yield more complex interaction motifs based off pairwise feeding trials fails to deliver – the predators revert to their preferred prey resulting in modular and simple trophic chains to be expressed. Whilst these realized interaction motifs may be stable, there might also be a tradeoff with function by yielding less top-down control than desirable when considering the potential for ecosystem services such as pest management. These are valuable insights, although it should be noted that here the fundamental niche is described in a strictly Eltonian sense as a trophic role [11]. Adding additional niche dimensions (sensu [12]), such as a thermal gradient could alter the observed interactions, although it might be possible to explain these contingencies through metabolic and optimal foraging theory combined with species traits. Nonetheless, the results of these experiments further demonstrate the need for ecologists to cross-validate theory with empirical approaches to develop more realistic and predictive food-web models, lest they invoke the wrath of Gary Polis´ ghost by "trying to explain phenomena that do not exist".

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Reviews

Evaluation round #3

DOI or URL of the preprint: **10.1101/324178**
Version of the preprint: 3

Authors' reply, 14 December 2018

Decision by **Francis John Burdon**, posted 12 December 2018

Revise and resubmit draft for the preprint titled "The return of the trophic chain: fundamental vs realized interactions in a simple arthropod food web"

Dear Marta (and co-Authors),

Thank you for resubmitting the minor revisions so promptly. I appreciate you hearing the majority of my and the Reviewers concerns. However, I feel that we should resolve the issue of "niche", which I believe is an important conceptual element underpinning your study.

In your response, you stated: "Our paper does not concern the concept of niche." With respect, this statement is incorrect. I can list four instances where "niche" is mentioned.

L85 "ontogenetic niche shifts" – here meant in the Eltonian sense (i.e., trophic role) as a predator shifts its dietary preference ontogenetically.

L360 "temporal niche partitioning" – here again meant primarily in the Eltonian sense, although if one considers time and space as niche dimensions then this also invokes Hutchinson's "n-dimensional hypervolume".

L468-471 "fundamental trophic niche" – this is an important statement of the key concept underpinning the paper i.e., trophic roles can be fundamental, but may differ in realization depending on the biotic context. Here this is linked to Hutchinson (see 1957 reference below), but I believe it would be better if Elton (1927) were too acknowledged by explicitly outlining this conceptual framework in the introduction (see Practical action #3 below).

L492 "fundamental niche" – as defined above (but here I think it would be better to continue with the use of "fundamental trophic niche" for consistency and clarity).

Why do I say this? Elton defined a species "niche" as the sum of all the interactions (especially trophic) that link it to other species in an ecosystem (Elton 1927). Leibold (1995) has summed up this perspective as the following: the Eltonian niche represents the overall trophic role of that species. I believe the Eltonian trophic niche can be applied with Hutchinson's fundamental and realized niche concepts, so there is no real disagreement other than needing to establish this conceptual framework in the introduction (as previously done, albeit without this nuance).

The important difference is that your study system holds environmental variability constant (i.e., other niche dimensions) and just focuses on the trophic niche (i.e., the trophic role of each species). If you were to add a temperature gradient to the study system, then this would constitute another niche dimension more consistent with Hutchinson's broader definition. There are also some interesting aspects involving niche (trophic) and fitness characteristics in your study, but I would focus on the main story by resolving the issue outlined above.

As a side note: part of this disagreement may stem from your justified avoidance of direct competition (L118), and the over-emphasis that Hutchinson placed on competition for resources driving much of niche ecology (see Chase and Leibold 2003, p.11).

Moving forward, for practical actions I recommend:

1. Using "fundamental trophic niche" (and "realized trophic niche") in the MS to make it very explicit how the niche concept is applied (i.e., L492).

2. Reword L110-111 "However, it remains unclear how the addition of species into a community alters all other trophic interactions in the network (e.g., Bascompte et al 2006)." The way this was previously worded sounded like an invasion (i.e., species introduction), which isn´t really the same as the study system where these species have co-evolved.

3. Adding the following text at L112 “To address this question, we have considered if the fundamental trophic niches of species (i.e., with all their potential interactions; Elton 1927) are always realized (Hutchinson 1957). Specifically, we explore how pairwise trophic interactions between species are modified by the inclusion of other species in a simple community. We focus on....”
4. Rewording L468-471 to something along the lines of “Thus, the fundamental trophic niche of species in this system (i.e., the food items that species are potentially able to feed on) is larger than the realized trophic niche (i.e., the food items that species actually feed on when present in combinations exceeding the individual pairwise interactions).”

I don´t want to seem like a pedant about this issue, especially since I mostly agree with how you have applied it in the MS. But it would be really good if this minor issue of definition and interpretation were cleared up so I can proceed with the recommendation.

Sincerely,

Dr. Francis J. Burdon

Literature mentioned above:

Bascompte, J., Jordano, P. & Olesen, J.M. 2006) Asymmetric co-evolutionary networks facilitate biodiversity maintenance. Science, 312, 431–433.

Chase, J. M. & Leibold. M. A. 2003. Ecological Niches: Linking Classical and Contemporary Approaches. University of Chicago Press, IL, USA

Elton, C. S. 1927. Animal Ecology. Sidgwick and Jackson, London, UK.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22: 415–427.

Leibold, M. A. 1995. The niche concept revisited: mechanistic models and community context. Ecology 76: 1371–1382

Evaluation round #2

DOI or URL of the preprint: **10.1101/324178**

Version of the preprint: 2

Authors’ reply, 11 December 2018

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Decision by **Francis John Burdon**, posted 06 December 2018

Revise and resubmit draft for the preprint titled ”The return of the trophic chain: fundamental vs realized interactions in a simple arthropod food web”

Dear Authors,

Thank you very much for resubmitting your revised manuscript on this interesting study. I have now read through your responses to the reviewers and the amended version of the manuscript. I appreciate the further consideration of weak interactions in the Introduction and Discussion. Whilst I can see that you have met the vast majority of the reviewers concerns, there remain some minor edits that should be made before I submit my recommendation. I have attached an annotated version with suggested changes. However, below I have highlighted some of the more important minor edits that would in my mind help “polish” the final version.

Sincerely, Dr. Francis J. Burdon

Minor comments

L20-40. I have suggested some changes to the abstract that would help make this summary “pop” a bit more. See scan of the annotated MS for further information. As the first key pt. I would reword the opening sentence to “The mathematical theory describing small assemblages of interacting species (community modules or motifs) has proven to be essential to understanding the emergent properties of ecological communities.” As another key pt., it might be good to finish with a statement indicating the path forward E.g., “This further suggests a need for empirical research to work in concert with theoretical approaches to develop more realistic and predictive food-web models.”

L42. Reviewer 2 suggested that you could reference the seminal work of Charles Elton. I have suggested that you could cite Elton 1927 (“Animal Ecology”) in this first sentence. I would reword this opening statement to “Community ecology initially conceptualized trophic interactions as linear chains (Elton 1927), with an upper trophic level potentially controlling the densities of the level immediately below, thus generating a trophic cascade (HSS..., etc.).

L46. “blurring the notion of a trophic guild (sensu trophic coherence)...”

L48. I appreciate that you have defined “community modules” in response to the comments by Reviewer 3. However, I wondered if it might be good to briefly explain how these are similar to “motifs” (since that is a major feature of ecological network analysis). E.g., “Our community modules are similar to network motifs studied in previous research (e.g., Bascompte and Melian 2005, Prill et al. 2005, Stouffer et al. 2007).”

L56. Reviewer 3 was concerned that the stability concept was used loosely, and I tend to agree. I would go further with defining “persistence” E.g., “temporal stability in community composition” (Pimm 1984 Nature). I would also check if stability as a general concept versus a particular dimension (sensu Donohue et al. 2010 Ecol. Letters) is correctly used in the Intro and Discussion (e.g., L78, L80, L82, L83). I wouldn´t get bogged down in semantics, but some clarity might be good if there is some underlying nuance missed with the ideas presented here.

L106-108. Reviewer 2 was concerned that the niche concept might need further elaboration. Here it might be good to indicate that you are considering the niche in the Eltonian sense E.g., ”The ’niche’ of an animal means its place in the biotic environment, its relations to food and enemies.” (Elton 1927). You then apply the Hutchinsonian concepts of fundamental and realized roles to the Eltonian niche (i.e., fundamental and realized trophic roles). I don´t think this needs to be long-winded or overly complicated, but some “hat-tipping” here would satisfy the concerns of Reviewer 2.

L115. New paragraph.

L147. I wonder if it is worth mentioning Hypothesis (f) at all here – it seems nice to know, but not need to know. It could be considered in the Discussion, but I am concerned that you don´t have the ability to test this adequately – I.e., it could be difficult to establish if adding prey type also increases the amount of food available (i.e., the same result might be observed by adding more of one prey type – depending on the functional response, etc.).

L209-234. I would break the community modules up into numbered points to help make the text less dense in this section.

L327-485. I wondered if the Discussion would not benefit from some sub-headings (e.g., L338-416 seems to mostly discuss the actual results in context of the study systems, whereas L417-485 focuses more on the contribution of the results to food-web theory). Those sections could have sub-heading to help guide the reader.

L337. Add disclaimer “...all modules could be described by linear food chains in our study system.”

L345. “bursts” = “outbreaks”

L352. “temporal segregation” = “temporal partitioning” (keeps it consistent with niche concepts).

L370. I would be more specific here “Food web ecology” = “Optimal foraging theory” E.g. Pulliam 1974 The American Naturalist.

L381. “...communities tended to be reduced to two simple trophic chains,...”

L428. It would be good to define connectance more specifically as a measure of food-web complexity before making the point that it is general a lot lower than the number of potential interactions. E.g., “Connectance is a fundamental measure of food-web complexity which 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 total number of potential interactions (Beckerman et al. 2006).”

L438. Could be good to explicitly give plant-pollinator networks as an example here.

L476. Reword. E.g., “Our results suggest that increasing the number of potentially interacting species results in the majority of species interactions becoming weaker.” **Download recommender’s annotations**

Evaluation round #1

DOI or URL of the preprint: **10.1101/324178**

Version of the preprint: 1

Authors’ reply, 30 October 2018

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Decision by **Francis John Burdon**, posted 30 October 2018

Revision needed

Dear authors,

Thank you for submitting your preprint to PCI Ecology. Three expert reviewers have commented on your manuscript, and you will find their reports below. Although R1 was positive about your research, there were no suggestions of ways to improve the manuscript. In contrast, whilst R2 and R3 appreciated aspects of the study, they were more critical of your work.

R2 emphasized that the Introduction and Discussion needs a more nuanced and measured approach, with greater attention given to the published theoretical studies that consider the role of weak interactions and their contribution to network stability.

R3 thought that you should clarify how interactions are defined and measured in the study, and if these observations are sufficient for the conclusions made. R3 was also concerned about invoking apparent competition, when the experiments seemingly fail to meet all criteria stated in the definition provided by Holt and Bonsall (2017). While I can see that these interpretations are potentially too narrow, the authors will need to justify how their experimental system is useful for drawing inferences about interaction frequencies (cf. strengths) and apparent competition.

Both R2 and R3 struggled at times to follow the results, and in particular which mite serves as the intraguild predator or prey (see also R3 comments about ´predator juveniles´). The authors will need to ensure all terminology used is consistent and well-explained throughout the manuscript.

Therefore, I would like to invite the authors to submit a revised manuscript before a decision is made about a recommendation.

Best regards, Dr. Francis Burdon

Reviewers Comments

Reviewer 1

In this experimental study of effects of community structure on interactions among predatory and herbivorous mites, there was strong and frequent evidence that interactions that occurred when only pairs of species were present did not occur when other species were also present.

Evidence was from factorial experimental manipulations of species presence/absence showing frequent strong two-way interactions in the effect of species presence/absence on predation/mortality rates.

As the Discussion points out, these results, if generalizable to other and more complex food webs, would imply that the food web structure predicted from knowledge of interactions from pairwise trials would/could predict a more connected food web than would be realised. Furthermore, and again as pointed out in the Discussion, observations of interactions in the field will be more important than previously thought, and models that can predict the community context-dependence of pairwise interaction strengths might be preferable.

The information in the manuscript was clearly presented, conclusions were supported by the results, and the methods were appropriate to produce the results. The Introduction and Discussion were appropriate.

Reviewer 2

The authors conducted a series of arena-based tests to determine which feeding links occur when various combinations of 5 species are placed together. They found that, in general, intraguild predation links between two mite species are weak to nonexistent. The major dynamics of this system therefore tend to resolve into one or more food chains rather than omnivory motifs.

The testing seems to have been well done and comprehensive; my only major comment for the methods and results sections is that it can be difficult to keep track of which results are being described (in particular, which mite is serving as the IG predator and prey). The authors can likely resolve this by adding subheadings or something along that line.

One minor comment about tables 1-2: there seems to be a typo of Generalized Lineal Models. This should almost certainly be Generalized Linear Models.

The simple and intuitive hypothesis tested (i.e., predators with the choice of two food items will tend to consume the preferred prey rather than both prey) and the thoroughly documented results are, unfortunately, rather weakened by the introduction and discussion.

The introduction dismisses some very early work on food webs (e.g., Elton, 1927) to suggest an exclusive focus on linear chains, and then builds up quite a straw man by saying that intraguild predation/omnivory are expected to destabilize food webs. This was indeed the early expectation, but more recent tests have shown that weak links in omnivory/intraguild predation modules can increase stability (e.g., McCann et. al, 1998). Omitting this research makes the introduction read as overly dismissive of prior work and, to me, risks biasing readers against this manuscript. I strongly suggest that the authors carefully revise the introduction to include more recent theoretical tests of omnivory/intraguild predation effects on stability and to make clear that, despite this theoretical work, it is often assumed that all links in empirical webs are equally strong. This then leads naturally to the idea that a species' fundamental niche (all of its potential interactions) are unlikely to be realised at a particular place/time. Lines 56-63 give many excellent examples of how potential interactions may not always occur despite forming part of the food web at large.

The discussion has similar problems with over-simplification and loses the "fundamental vs. realised" thread almost completely. The authors seem to assume that, because predators tend to take only the preferred prey when both are offered together, predators in a field system will only ever take the preferred prey. This disregards the likely case that prey availability will vary such that, over its lifetime, an intraguild predator will indeed act as an omnivore. There is an interesting discussion to be had about how best to consider the different strengths of interaction between omnivory motifs (particularly stage-structured omnivory, as in this system), but this is largely skipped in the present manuscript. I particularly missed a discussion of weak interactions given the weight the authors place upon stability in the introduction. The author's discussion of different biocontrol strategies might offer a good place to include this: if occasional intraguild predation among mites occurs when aphids are scarce, might this allow both mite species to persist and provide better biocontrol? The authors could also incorporate theoretical work showing that weak interactions tend to stabilize food webs in order to tie their findings of weak IGP back to the stability theme in the introduction.

Finally, both sections vastly over-state the "complexity" of the study system (5 species is certainly more complex than a pairwise system but is unlikely to accurately represent the hundreds-thousands of species in a real food web). Testing all combinations of species will therefore be impossible in many systems, and the authors' findings from a small and tightly-controlled system may not generalize to larger systems with varying abundances and densities of potential prey. I would therefore suggest that the authors soften their general claims and try to add more nuance to their discussion.

To sum up, I think the authors have conducted a well-done and important test of the strength of different feeding links in a system where intraguild predation is possible. The introduction and discussion are a little over-blown and tend to over-simplify the results, and this risks reducing the potential uptake of these results.

I suggest the authors carefully revise the introduction and discussion before submitting the manuscript for publication, being careful to look for recent theoretical tests of different intraguild predation strengths. My impression is that this work is generally in agreement with the authors' results (i.e., stable systems tend to have weak IGP), so including it would help to reduce the somewhat combative tone of the manuscript.

Speaking as a theoretical ecologist: we are aware that not all interactions occur with equal frequency and that occurrence of many interactions is contingent upon the sets of species present. Strong data on interaction frequencies (especially with respect to contingencies) is, however, almost always lacking. This is the root of the simplifying assumption of constant interaction frequencies. Studies like this one are an important step towards providing this information and so I hope that the authors will adjust the manuscript for a broader audience.

Reviewer 3

The ms 'The return of the trophic chain: fundamental vs realized interactions in a simple arthropod food web' proposes an interesting idea of how increasing the number of species in a community might not necessarily increase the number of interactions.

Unfortunately, I don't think this can be tested with the experiment presented here, as the actual occurrence or frequency of inter-specific interactions was not measured, but rather the authors present results on whether the presence of one species affects the mortality and oviposition of another species. I also wonder if testing for apparent competition is legitimate when the authors only have 1 individual of the top predator and such a short time scale. As Holt and Bonsall mentioned in their Apparent Competition paper (Annual Review of Ecology, Evolution, and Systematics 2017), 'the qualitative assumptions leading to apparent competition are that an increase in the abundance of each prey benefits the predator, boosting its numbers, and that an increase in predator numbers then harms each prey'.

I do think that the experiment was well designed for testing changes in mortality and oviposition rates under different combination of species, and I really appreciate all the different control treatments performed.

There are several points within the manuscript that need to be clarified:

Introduction - It would be useful to clearly define here what the authors mean by modules, as this term can have many interpretations in ecology.

Similarly, stability can have multiple definitions, so the authors should clarify what they mean exactly by this term. Also, do all those studies mentioned (L55-67) use the same 'stability' measure? It would be useful to clarify this point.

In L95 the idea of a ´more complex´ community is introduced, but the author's haven´t explained well what they mean by this.

L102: What do the authors mean by interactions are stronger? More frequent? Methods

L214-216: I interpreted the results as the number of dead herbivores was estimated based on the number of herbivores that remained alive at the end of the experiment. The authors should clarify this.

In the Data analyses section, it would be useful to clearly explain what each interaction term means, i.e. why were they used? What would the interaction terms tell me if they were significantly positive or negative? What would a three interaction term mean?

In this subsection the authors also mention 'rates of oviposition'. What exactly do they mean by this? Abundance of eggs laid per female?

Also, why did the authors use a Poisson distribution? Wouldn't it be better to use a binomial distribution for assessing rates (i.e., number of dead individuals vs. number of survivors)?

L223-226: The authors haven't mentioned how the model is specified or that it has an interaction term, so they should move the model selection part after they describe the model.

L235: I found the term ‘predator juveniles’ confusing. Are the authors referring to IG-prey that were juveniles?

L238: Please clarify if that is oviposition rates of IG-predators.

Results

L244: Please clarify which were the ‘main factors´ referred to here. I think that readers would have problems understanding from the text what is described here without looking at the table.

L248-259: This sentence is long and difficult to follow. Please revise.

L248-251: Isn’t this the same as what the glm tells us? I didn’t understand why the authors used planned comparisons when they did their glm´s already, as both seem to answer the same questions.

L252-253: ‘adding O. perseae did not influence mortality of the IG-prey’ but the glm indicates the opposite (Table 1b, IG-predator x herbivore interaction).

L254: ‘predation of IG-predators’, use the same term as used in the Figures so that it’s easier to follow.

L259: Since the authors reared E. stipulatus on pollen of C. edulis, could there already be a preference for this food type by E. stipulatus? Ideally these consumers would have been fed something different to the resources used in the experiment.

L267-268: Again, how is this different from the author’s glm results and why do they then need both analyses?

L283: ‘bar 5’, according to the author’s figure there was oviposition.

Discussion

The results presented by the authors are about changes in mortality and oviposition rates when species are added, not whether an interaction occurred or not, so I would modify the discussion according to this.

L299: ‘But not necessarily their occurrence’. The authors haven´t observed whether an interaction occur, but rather the consequences of adding species on mortality and oviposition rates.

L299-301: If so, how do the authors explain the significant interaction terms in their glm´s?

L302: ‘N. californicus killed more O. perseae females per day’ than... Please elaborate.

L319: Please revise this sentence. Also, there were IG-prey dead in both treatments with both IG-predator species (treatment number 10).

L319-321: And also because E. stipulatus can feed on something else (pollen), otherwise E. stipulatus could be outcompeted.

L323-325: This doesn’t match with treatments 7 and 8 (Fig. 1). The number of prey items dead is equal.

L348: I wonder if this is because the authors reared them with pollen and whether this could have had an effect on the feeding preferences of these invertebrates.

L352: According to the authors treatment 11 (Fig. 2b) there were IG-prey items dead. Please explain.

L360-361: But there were no differences between treatment 11 and 12 in Fig 1b (number of IG-prey dead)? Please explain.

L367-370: But wasn’t O. perseae accessible to E. stipulatus? If it wasn’t accessible, then the experimental design may be flawed, thus hindering the author’s ability to invoke apparent competition here.

L377-378: This doesn’t make sense to me. Why would the predator stop feeding?

Tables: What does the * mean in the tables?

Figures: 1 and 2 a) sometimes the authors say prey, others herbivores, others O. perseae. It would be better to use one term throughout the entire ms. Also, what do the authors mean by ‘items’? Is this individuals? Please clarify.

Reviewed by **Owen Petchey**, 28 May 2018

In this experimental study of effects of community structure on interactions among predatory and herbivorous mites, there was strong and frequent evidence that interactions that occurred when only pairs of species were present did not occur when other species were also present. Evidence was from factorial experimental manipulations of species presence/absence showing frequent strong two-way interactions in the effect of species presence/absence on predation/mortality rates. As the Discussion points out, these results, if generalizable to other and more complex food webs, would imply that the food web structure predicted from knowledge of interactions from pairwise trials would/could predict a more connected food web than would be realised. Furthermore, and again as pointed out in the Discussion, observations of interactions in the field will be more important than previously thought, and models that can predict the community context-dependence of pairwise interaction strengths might be preferable.

The information in the manuscript was clearly presented, conclusions were supported by the results, and the methods were appropriate to produce the results. The Introduction and Discussion were appropriate.

Reviewed by anonymous reviewer 2, 15 June 2018

The ms 'The return of the trophic chain: fundamental vs realized interactions in a simple arthropod food web' proposes an interesting idea of how increasing the number of species in a community might not necessarily increase the number of interactions. Unfortunately, I don't think this can be tested with the experiment presented here, as the actual occurrence or frequency of inter-specific interactions was not measured, but rather the authors present results on whether the presence of one species affects the mortality and oviposition of another species. I also wonder if testing for apparent competition is legitimate when you only have 1 individual of the top predator and such a short time scale. As Holt and Bonsall mentioned in their Apparent Competition paper (Annual Review of Ecology, Evolution, and Systematics 2017), 'the qualitative assumptions leading to apparent competition are that an increase in the abundance of each prey benefits the predator, boosting its numbers, and that an increase in predator numbers then harms each prey'.

I do think that the experiment was well design for testing changes in mortality and oviposition rates under different combination of species, and I really appreciate all the different control treatments performed. There are several points along the manuscript that need to be clarified.

Introduction - It might be a good idea to clearly define what do you mean by modules, as this term can have many interpretations in ecology. Similarly, stability can have multiple definitions, so you should clarify what do you mean by this term. Also, do all those studies you mention (L55-67) used the same 'stability' measure? - In L95 you introduce the idea of a more complex community, but you don't actually define what do you mean by this. - L102: what do you mean by interactions are stronger? More frequent?

Methods - L214-216: I assumed the number of dead herbivores was estimated based on the number of herbivores that remained alive at the end of the experiment. You should clarify this. - In your Data analyses section it would be useful to clearly explain what each interaction term mean, i.e. why did you include them. What would the interaction terms tell me if they were significantly positive or negative? What would a three interaction term mean? In this subsection you also mention 'rates of oviposition'. What do you mean by this? Abundance of eggs laid per female? Also, why did you used a Poisson distribution? wouldn't be better to use a binomial distribution for assessing rates (i.e. number of dead individuals vs. number of survivors)? - L223-226: you haven't mentioned how the model is or that it has an interaction term, so you should move this model selection part after you describe the model. - L235: 'predator juveniles' is confusing. Are you referring to your IG-prey that were juveniles? - L238: clarify that is oviposition rates of IG-predators.

Results - L244: clarify which were the 'main factors' you are referring to here. The reader should be able to understand from the text what do you want to say without having to look at the table. - L248-259: This sentence is too long and hard to follow. - L248-251: Isn't this the same as what the glm tells you? I didn't understand why you used planned comparisons when you did glms already, as both seem to answer the same questions. - L252-253: 'adding O. perseae did not influence mortality of the IG-prey' but the glm tells you the opposite (Table 1b, IG-predator x herbivore interaction). - L254: 'predation of IG-predators', use the same term as in the Figures so that it's easier to follow. - L259: since you reared your E. stipulatus on pollen of C. edulis, could there already be a preference for this food type by E. stipulatus? Ideally you should have fed them on something different to the resources you're using in your experiment. - L267-268: again, how is this different from your glm results and why do you need both analyses? - L283: 'bar 5', according to your figure there was oviposition.

Discussion Your results are about changes in mortality and oviposition rates when species are added, not whether an interaction occurred or not, so I would modify the discussion according to this. - L299: 'but not necessarily their occurrence'. You actually didn't observe whether an interaction occur, but rather the consequences of adding species on mortality and oviposition rates. - L299-301: If so, how do you explain the significant interaction terms in your glms? - L302: 'N. californicus killed more O. perseae females per day' THAN... - L319: revise this sentence. Also, there were IG-prey dead in both treatments with both IG-predator species (treatment number 10). - L319-321: and also because E. stipulatus can feed on something else (pollen), otherwise E. stipulatus could be outcompeted. - L323-325: This doesn't match with treatments 7 and 8 (Fig. 1). The number of prey items dead is equal. - L348: I wonder if this is because you reared them with pollen and whether this could have had an effect on their feeding preferences. - L352: according to your treatment 11 (Fig. 2b) there were IG-prey items dead. - L360-361: but there were no differences between treatment 11 and 12 om Fig 1b (number of IG-prey dead)? - L367-370: but wasn't O. perseae accessible to E. stipulatus?? If it wasn't accessible, then the experiment wasn't well design and you can't really say anything about apparent competition. - L377-378: this doesn't make sense. Why would the predator stop feeding?

Tables: what do the * mean in the tables? Figures: 1 and 2 a) sometimes you say prey, others herbivores, others O. perseae. It would be better to use one term along the entire ms. Also, what do you mean by 'items'? Individuals??

Reviewed by anonymous reviewer 1, 29 June 2018

The authors conducted a series of arena-based tests to determine which feeding links occur when various combinations of 5 species are placed together. They found that, in general, intraguild predation links between two mite species are weak to nonexistent. The major dynamics of this system therefore tend to resolve into one or more food chains rather than omnivory motifs. The testing seems to have been well done and comprehensive; my only major comment for the methods and results sections is that it can be difficult to keep track of which results are being described (in particular, which mite is serving as the IG predator and prey). The authors can likely resolve this by adding subheadings or something along that line. One minor comment about tables 1-2: there seems to be a typo of Generalized Lineal Models. This should almost certainly be Generalized Linear Models.

The simple and intuitive hypothesis tested (i.e., predators with the choice of two food items will tend to consume the preferred prey rather than both prey) and the thoroughly documented results are, unfortunately, rather weakened by the introduction and discussion. The introduction dismisses some very early work on food webs (e.g., Elton, 1927) to suggest an exclusive focus on linear chains, and then builds up quite a straw man by saying that intraguild predation/omnivory are expected to destabilize food webs. This was indeed the early expectation, but more recent tests have shown that weak links in omnivory/intraguild predation modules can increase stability (e.g., McCann et. al, 1998). Omitting this research makes the introduction read as overly dismissive of prior work and, to me, risks biasing readers against this manuscript. I strongly suggest that the authors carefully revise the introduction to include more recent theoretical tests of omnivory/intraguild predation effects on stability and to make clear that, despite this theoretical work, it is often assumed that all links in empirical webs are equally strong. This then leads naturally to the idea that a species' fundamental niche (all of its potential interactions) are unlikely to be realised at a particular place/time. Lines 56-63 give many excellent examples of how potential interactions may not always occur despite forming part of the food web at large.

The discussion has similar problems with over-simplification and loses the "fundamental vs. realised" thread almost completely. The authors seem to assume that, because predators tend to take only the preferred prey when both are offered together, predators in a field system will only ever take the preferred prey. This disregards the likely case that prey availability will vary such that, over its lifetime, an intraguild predator will indeed act as an omnivore. There is an interesting discussion to be had about how best to consider the different strengths of interaction between omnivory motifs (particularly stage-structured omnivory, as in this system), but this is largely skipped in the present manuscript. I particularly missed a discussion of weak interactions given the weight the authors place upon stability in the introduction. The author's discussion of different biocontrol strategies might offer a good place to include this: if occasional intraguild predation among mites occurs when aphids are scarce, might this allow both mite species to persist and provide better biocontrol? The authors could also incorporate theoretical work showing that weak interactions tend to stabilize food webs in order to tie their findings of weak IGP back to the stability theme in the introduction.

Finally, both sections vastly over-state the ”complexity” of the study system (5 species is certainly more complex than a pairwise system but is unlikely to accurately represent the hundreds-thousands of species in a real food web). Testing all combinations of species will therefore be impossible in many systems, and the authors' findings from a small and tightly-controlled system may not generalize to larger systems with varying abundances and densities of potential prey. I would therefore suggest that the authors soften their general claims and try to add more nuance to their discussion.

To sum up, I think the authors have conducted a well-done and important test of the strength of different feeding links in a system where intraguild predation is possible. The introduction and discussion are a little over-blown and tend to over-simplify the results, and this risks reducing the potential uptake of these results. I suggest the authors carefully revise the introduction and discussion before submitting the manuscript for publication, being careful to look for recent theoretical tests of different intraguild predation strengths. My impression is that this work is generally in agreement with the authors' results (i.e., stable systems tend to have weak IGP), so including it would help to reduce the somewhat combative tone of the manuscript. Speaking as a theoretical ecologist: we are aware that not all interactions occur with equal frequency and that occurrence of many interactions is contingent upon the sets of species present. Strong data on interaction frequencies (especially with respect to contingencies) is, however, almost always lacking. This is the root of the simplifying assumption of constant interaction frequencies. Studies like this one are an important step towards providing this information and so I hope that the authors will adjust the manuscript for a broader audience.