Peer Community In Ecology

Tell me what you've eaten, I'll tell you how much you'll eat (and be eaten)

Sara Magalhães and Raul Costa-Pereira based on reviews by Bastien Castagneyrol and 1 anonymous reviewer

Open Access

Published: 18 March 2020

A recommendation of:

Arnaud Sentis, Raphaël Bertram, Nathalie Dardenne, Jean-Christophe Simon, Alexandra Magro, Benoit Pujol, Etienne Danchin and Jean-Louis Hemptinne. **Intraspecific difference among herbivore lineages and their host-plant specialization drive the strength of trophic cascades** *(2020), bioRxiv, 722140, ver. 4 peer-reviewed by Peer Community in Ecology.* 10.1101/722140

Submitted: 02 August 2019, Recommended: 18 March 2020

Cite this recommendation as:

Sara Magalhães and Raul Costa-Pereira (2020) Tell me what you've eaten, I'll tell you how much you'll eat (and be eaten). *Peer Community in Ecology, 100047.* 10.24072/pci.ecology.100047

Tritrophic interactions have a central role in ecological theory and applications [1-3]. Particularly, systems comprised of plants, herbivores and predators have historically received wide attention given their ubiquity and economic importance [4]. Although

ecologists have long aimed to understand the forces that govern alternating ecological effects at successive trophic levels [5], several key open questions remain (at least partially) unanswered [6]. In particular, the analysis of complex food webs has questioned whether ecosystems can be viewed as a series of trophic chains [7,8]. Moreover, whether systems are mostly controlled by top-down (trophic cascades) or bottom-up processes remains an open question [6].

Traditionally, studies have addressed how species diversity at different food chain compartments affect the strength and direction of trophic cascades [9]. For example, many studies have tested whether biological control was more efficient with more than one species of natural enemies [10-12]. Much less attention has been given to the role of within-species variation in shaping trophic cascades [13]. In particular, whereas the impact of trait variation within species of plants or predators on successive trophic levels has been recently addressed [14,15], the impact of intraspecific herbivore variation is in its infancy (but see [16]). This is at odds with the resurgent acknowledgment of the importance of individual variation for several ecological processes operating at higher levels of biological organization [17]. Sources of variation within species can come in many flavours. In herbivores, striking ecological variation can be found among populations occurring on different host plants, which become genetically differentiated, thus forming host races [18,19]. Curiously, the impact of variation across host races on the strength of trophic cascades has, to date, not been explored. This is the gap that the manuscript by Sentis and colleagues [20] fills. They experimentally studied a curious tri-trophic system where the primary consumer, pea aphids, specializes in different plant hosts, creating intraspecific variation across biotypes. Interestingly, there is also ecological variation across lineages from the same biotype. The authors set up experimental food chains, where pea aphids from different lineages and biotypes were placed in their universal legume host (broad bean plants) and then exposed to a voracious but charming predator, ladybugs. The full factorial design of this experiment allowed the authors to measure vertical effects of intraspecific variation in herbivores on both plant productivity (top-down) and predator individual growth (bottom-up). The results nicely uncover the mechanisms by which intraspecific differences in herbivores precipitates vertical modulation in food chains. Herbivore lineage and host-plant

specialization shaped the strength of trophic cascades, but curiously these effects were not modulated by density-dependence. Further, ladybugs consuming pea aphids from different lineages and biotypes grew at distinct rates, revealing bottom-up effects of intraspecific variation in herbivores. These findings are novel and exciting for several reasons. First, they show how intraspecific variation in intermediate food chain compartments can simultaneously reverberate both top-down and bottom-up effects. Second, they bring an evolutionary facet to the understanding of trophic cascades, providing valuable insights on how genetically differentiated populations play particular ecological roles in food webs. Finally, Sentis and colleagues' findings [20] have critical implications well beyond their study systems. From an applied perspective, they provide an evident instance on how consumers' evolutionary specialization matters for their role in ecosystems processes (e.g. plant biomass production, predator conversion rate), which has key consequences for biological control initiatives and invasive species management. From a conceptual standpoint, their results ignite the still neglected value of intraspecific variation (driven by evolution) in modulating the functioning of food webs, which is a promising avenue for future theoretical and empirical studies.

References

[1] Price, P. W., Bouton, C. E., Gross, P., McPheron, B. A., Thompson, J. N., & Weis, A. E. (1980). Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. Annual review of Ecology and Systematics, 11(1), 41-65. doi: 10.1146/annurev.es.11.110180.000353 [2] Olff, H., Brown, V.K. & Drent, R.H. (1999). Herbivores: between plants and predators. Blackwell Science, Oxford. [3] Tscharntke, T. & Hawkins, B.A. (2002). Multitrophic level interactions. Cambridge University Press. doi: 10.1017/CBO9780511542190 [4] Agrawal, A. A. (2000). Mechanisms, ecological consequences and agricultural implications of tri-trophic interactions. Current opinion in plant biology, 3(4), 329-335. doi: 10.1016/S1369-5266(00)00089-3 [5] Pace, M. L., Cole, J. J., Carpenter, S. R., & Kitchell, J. F. (1999). Trophic cascades revealed in diverse ecosystems. Trends in ecology & evolution, 14(12), 483-488. doi: 10.1016/S0169-5347(99)01723-1 [6] Abdala-

Roberts, L., Puentes, A., Finke, D. L., Marquis, R. J., Montserrat, M., Poelman, E. H., ... & Mooney, K. (2019). Tri-trophic interactions: bridging species, communities and ecosystems. Ecology letters, 22(12), 2151-2167. doi: 10.1111/ele.13392 [7] Polis, G.A. & Winemiller, K.O. (1996). Food webs. Integration of patterns and dynamics. Chapmann & Hall, New York. doi: 10.1007/978-1-4615-7007-3 [8] Torres-Campos, I., Magalhães, S., Moya-Laraño, J., & Montserrat, M. (2020). The return of the trophic chain: Fundamental vs. realized interactions in a simple arthropod food web. Functional Ecology, 34(2), 521-533. doi: 10.1111/1365-2435.13470 [9] Polis, G. A., Sears, A. L., Huxel, G. R., Strong, D. R., & Maron, J. (2000). When is a trophic cascade a trophic cascade?. Trends in Ecology & Evolution, 15(11), 473-475. doi: 10.1016/S0169-5347(00)01971-6 [10] Sih, A., Englund, G., & Wooster, D. (1998). Emergent impacts of multiple predators on prey. Trends in ecology & evolution, 13(9), 350-355. doi: 10.1016/S0169-5347(98)01437-2 [11] Diehl, E., Sereda, E., Wolters, V., & Birkhofer, K. (2013). Effects of predator specialization, host plant and climate on biological control of aphids by natural enemies: a meta-analysis. Journal of Applied Ecology, 50(1), 262-270. doi: 10.1111/1365-2664.12032 [12] Snyder, W. E. (2019). Give predators a complement: conserving natural enemy biodiversity to improve biocontrol. Biological control, 135, 73-82. doi: 10.1016/j.biocontrol.2019.04.017 [13] Des Roches, S., Post, D. M., Turley, N. E., Bailey, J. K., Hendry, A. P., Kinnison, M. T., ... & Palkovacs, E. P. (2018). The ecological importance of intraspecific variation. Nature Ecology & Evolution, 2(1), 57-64. doi: 10.1038/s41559-017-0402-5 [14] Bustos-Segura, C., Poelman, E. H., Reichelt, M., Gershenzon, J., & Gols, R. (2017). Intraspecific chemical diversity among neighbouring plants correlates positively with plant size and herbivore load but negatively with herbivore damage. Ecology Letters, 20(1), 87-97. doi: 10.1111/ele.12713 [15] Start, D., & Gilbert, B. (2017). Predator personality structures prey communities and trophic cascades. Ecology letters, 20(3), 366-374. doi: 10.1111/ele.12735 [16] Turcotte, M. M., Reznick, D. N., & Daniel Hare, J. (2013). Experimental test of an eco-evolutionary dynamic feedback loop between evolution and population density in the green peach aphid. The American Naturalist, 181(S1), S46-S57. doi: 10.1086/668078 [17] Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., ... & Vasseur, D. A. (2011). Why intraspecific trait

variation matters in community ecology. Trends in ecology & evolution, 26(4), 183-192. doi: 10.1016/j.tree.2011.01.009 [18] Drès, M., & Mallet, J. (2002). Host races in plant–feeding insects and their importance in sympatric speciation. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 357(1420), 471-492. doi: 10.1098/rstb.2002.1059 [19] Magalhães, S., Forbes, M. R., Skoracka, A., Osakabe, M., Chevillon, C., & McCoy, K. D. (2007). Host race formation in the Acari. Experimental and Applied Acarology, 42(4), 225-238. doi: 10.1007/s10493-007-9091-0 [20] Sentis, A., Bertram, R., Dardenne, N., Simon, J.-C., Magro, A., Pujol, B., Danchin, E. and J.-L. Hemptinne (2020) Intraspecific difference among herbivore lineages and their host-plant specialization drive the strength of trophic cascades. bioRxiv, 722140, ver. 4 peer-reviewed and recommended by PCI Ecology. doi: 10.1101/722140

Revision round #2

2020-03-02

I am now ready to make a recommendation of this preprint. I urge the authors to perform the small modifications requested by the reviewers while I prepare my text! thanks sara

Preprint DOI: 10.1101/722140

Reviewed by anonymous reviewer, 2020-01-20 17:23

The authors have made substantial improvements that have clarified and improved their manuscript. Nice work.

The English usage is generally excellent - much better than my French would be, that is for certain. There are still errors, but that is up to the authors to work on and ask a colleague to correct (for example, several are found in the legend of Figure 2).

Whether stringing together nouns and using them as adjectives is easier to read than sentences with prepositions varies by language. In English, prepositions are

crucial to ease of understanding and clarify in the writing. For example see: https://www.plainlanguage.gov/guidelines/words/avoid-noun-strings/ The target audience for that webpage is bureaucrats who speak English as their mother tongue, so clearly, this is an issue among native speakers as well.

Alternatively, I recommend reading beautiful writing and modeling one's own after it. One of my favorite writers in the field of evolutionary biology is Graham Bell. He uses prepositions liberally.

Reviewed by Bastien Castagneyrol, 2020-02-18 11:20

Dear Sara, dear authors,

My apologizes for having been too long to re-read Sentis and colleagues' paper. The authors made a good job in addressing all the comments they received. The paper is clearer now and is surely ready to be recommended. I only have very minor comments. Best regards, Bastien

L84-87 -- "In other words, when consumers are efficient at consuming and converting their resources into new biomass, this translates in higher population growth rate that then strengthens the consumer impacts on the next lower trophic level when damages are proportional to population abundance. " I appreciate this sentence rewords the above explanation, but there are two little things that are not completely clear. "next lower trophic level" : is "lower" really necessary? I find it misleading. "damage": maybe precise "herbivore damage"?

L91 -- "the faster the herbivore growth" -- the previous sentence refers to population growth rate, here "herbivore" looks like individuals.

L92 -- Move "for instance" to L93: "For instance, the pea aphid...."

L253-254 -- Maybe "indicating that the effect of predators on plant biomass (i.e. trophic cascade strength) depended on aphid biotypes" is not necessary, because it has been explained in the method section.

L379 -- "fast growing lineages support larger predators than slow growing lineages" -- The phrasing is correct but odd. Would the other way round make it better: "Predators were larger on fast growing aphid lineages"?

L406 -- "It would be interesting to conduct a similar experiment on the three host plants (clover, alfalfa and broad bean) to investigate potential trade-offs in host-plant specialization and their consequences for predator traits and the strength of trophic cascades." It is a matter of taste but generally, I am not a big fan of "it would be interesting" if the sentence does not explain why. I mean, any question reserach question if interesting for us, crazy people. What makes a particular question particularly interesting in the context of a particular study is wht this study failed to address. Here, I would rather start the conclusion of this paragraph acknowledging that the results could have been different, should the aphids having been reared on their "hist" lineages, and that that "it would be interesting"...

OK, you can ignore thus very last comment.

Again, I like the paper :)

Author's reply:

Download author's reply (PDF file)

Revision round #1

2019-10-28
Dear authors,

First of all, I deeply apologize for having taken so long with this reviewing process. Most of the time was spent trying to find reviewers that would agree on reviewing, although I admit that part of the blame is on me too… In any case, we have received two reviews that I find very helpful. As you will see, both reviewers are overall very positive about your paper, but they also raise some very pertinent issues. I also liked this paper very much, it is very clearly written and the

experiments are elegant. However, I totally agree with the referees' comments and urge you to modify the article accordingly. I herewith state my main comments on the article (note that these are mostly the reviewers comments stated otherwise): - I agree with the second reviewer that stating "intraspecific variation drives trophic cascades" (cf. title) is misleading. But I see this from a different angle. In my opinion, to test whether intraspecific variation affect trophic cascades you would need to have treatments with more or less intraspecific variation. This was not the case. So you do show that there is intraspecific variation in the ability of aphids to modulate trophic cascades, but you don't show that the amount of variation matters. As the second reviewer, I still think your question is interesting, but it should be formulated in a less ambiguous fashion. - I also agree with the first reviewer that there is no clear reason to state that you are testing the role of "evolutionary divergence". First, I do not see evidence for the fact that alfafa lineages have diverged more from clover lineages than from each other. Indeed, there can be very distantly related lineages within the same host race. Second, I also think that lineages from different plants should be considered as a special case of different lineages in general. In particular, the statistical analysis should reflect this. That is, there should be one statistical model that includes lineage in general, and then specific planned comparisons to compare between host races in particular. I would say this is a more elegant way of analysing the data. - Finally, I agree with the first reviewer that assessing the effect of each lineage on the strength of the trophic cascade requires a specific test that was not performed, if I understand the stats well. That is, it is tested whether, for each lineage, there is a trophic cascade, but not whether these cascades differ in strength.

Minor comments - I found that the introduction could be a bit streamlined. In particular, you refer to intraspecific variation in the middle of the second, then in the end of the third paragraph. I would move the former (lines 60-62) to just before the latter. Also, you mention that the role of intraspecific variation for the occurrence of trophic cascades has been studied before. It would be nice to know in which way the current study adds to the available literature. From what I gathered with the references you cited (and check also Clegg 2018 Ecology and Weiss and Post 2013 Oikos) it should be relatively easy to single out your original

contribution. But this should be explicitly stated. - Line 83: change to “the faster their growth, the stronger the trophic cascade”. - Lines 381-388: basically, I guess that what you’re trying to say is that aphids from Clover may have a lower assimilation efficiency. That is, they eat more (thus impact more the plant) but their conversion into eggs is lower. Right? - In the Discussion, I think you need to come up with one or more explanations for the differences found between the effects of clover vs alfalfa trophic chains. For example, the fact that ladybeetles are bigger when fed on alfalfa aphids suggest that these are of better quality, which goes in line with my previous point. Also, the fact that alfalfa aphids reach higher densities on this plant (in absence of predators) suggest that there are better adapted than clover aphids. This should be discussed.

Preprint DOI: 10.1101/722140

Reviewed by Bastien Castagneyrol, 2019-10-01 18:38

Arnaud Sentis and colleagues addresses the effect of intraspecific variability in aphid population growth rate on the strength of tritrophic interactions. The paper is well written, well structured, and the study has been well conducted. I only have a few general comments.

I must say that I have been a bit surprised that intraspecific trait variability was actually strain-specific differences in population growth rates. Not that this questions the validity of the paper, but my feeling is that “intraspecific trait variability” is maybe too broad. “Trait” is generally defined at the individual level. Yet, here, “trait” is a “population” trait. This is a bit misleading, but maybe the individual- and population-levels are confounded when one look at aphids? I would be more comfortable if the paper was explicitly framed in terms of “population growth rate” at least in the ‘methods’ and ‘results’ sections. Or, at least, if the authors could add a couple of sentences discussing this issue in the ‘introduction’ and ‘discussion’ sections.

The introduction reads well, but I had to read the paragraph L71-85 twice to fully understand the research question. The sentences L77-85 are central to the paper, but how the authors jump from predator and herbivore efficiency to population growth rate and adaptive divergence is not completely clear. My feeling is that it

works quite well for aphids because the amount of damage to the plant is directly proportional to the number of aphids and their population growth rate, but it is not necessarily true for other herbivores (e.g., defoliators). I suggest to expand a bit this section to avoid any confusion. In particular, the effect of “adaptive divergence” (L98) on the strength of trophic cascades is not really well introduced. At least, I missed some information to fully get the point here.

The analyses look nice. I commend the authors for having managed to link the effect of predators on plants and on herbivores, and the other way round. Although the approach based on effect sizes is surely correct, it was not completely clear how treatment means were aggregated when calculating Rp and Ra (L172-183). I guess treatments means were aggregated at the lineage level (n = 6) and then at the biotype level (n = 3), but that was not clear. Please expand.

Related: another option would have consisted in using model coefficient parameters from (G)LMM. Because of the significant Predation × Lineage or Predation × Biotype interactions, the authors could have extracted treatment specific estimates and corresponding 95%CI instead of calculating raw means and CI. The advange of this approach is that would have accounted for the effects of the three time replicates and the effect of the 6 lineages when aggregating the data at the biotype level. But, again, to the best of my understanding, the analyses are correct at present.

None of the two biotypes were reared on their host plants. I wandered whether the results (notably, strength of the tritrophic interaction between the two biotypes) would have been the same on clover and alfalfa. Maybe the could be commented?

More specific comments L83 - “growth” should be “grow”? L111 – Do not start the sentence with “H.” L146 – fully spell “30” at the beginning of the sentence. L148 – Not sure what 1/3 of 20 replicates is ;-) L149-150 – In understand that this data was used to confirm that the abiotic environment was fairly constant, but this information is not used. Maybe the authors could simply comment on it, or drop it. L169 – There was no previous mention of lineage colour before. L206 – Results: please also report the variance component for the random effects in

(G)LMM (random factors and residuals) as it helps assessing the amount of variance explained by the fixed effects. L229-230 – I disagree. Letters above bars indicate that in the absence of predators, only one of the lineage differed from the others. 10TV and T734 were not different from T9005, LL01 or OX683 L262 - “Strongly” is a matter of appreciation. Maybe it is overstated. L269-270 – This statement about the dashed line could go to the figure caption. L274 – In the figure caption, here and elsewhere, it would help the reader labeling the y-axis as “Tritrophic interaction strength” or “Plant response to predation”, and the x-axis as “Aphid response to predation” L302-305 – “positively” is odd, because the strength of the predator effect increases as the value becomes more negative. L323 – Throughout the discussion, it would be nice to refer to the appropriate figures. Because there is quite a lot of results, it will greatly help the readers. L330 - “evolutionary divergence”: with only two biotypes, it is hard to generalize that much. Maybe tone down? L350-363 – I would have phrased this paragraph the other way round: (1) likely effect of population growth, (2) possible effect of other unmeasured traits.

Overall, I liked the paper. I hope that my comments will help. Best regards, Bastien

Reviewed by anonymous reviewer, 2019-10-13 23:50

The authors present some interesting experiments in which they use 3 genotypes of two different “biotypes” of aphids (specialized on different host plants) to evaluate the consequences of genetic variation for trophic cascades. They use a single host plant that both biotypes of aphids can feed on and measure how predation affects herbivore density and plant wet weight. They find that variation among aphid genotypes influences the magnitude of the effects of predation in reducing impacts of the herbivores on the plants.

The study makes a nice contribution. However, I do not find focusing on “evolutionary divergence” of the host races is not particularly useful. Really, what the authors have is intraspecific variation, period. There are presumably smaller differences among clones within host races, and larger differences among host races, but treating intraspecific variation and evolutionary divergence as two

separate things is a false dichotomy. Many might argue that the host races are actually different species.

The paper would make a stronger contribution if a means of quantitatively comparing the strength of trophic cascades is presented visually in a schematic graph in the introduction.

The authors should use “of” and “in” more to produce a paper that is easier to read. E.g. “the strength of trophic cascades” not “trophic cascade strength”. And “intraspecific variation in herbivore traits” not “herbivore intraspecific trait variation.”

Below are comments that came up in the course of reading the manuscript, some minor some more major.

When describing the statistics, the authors don’t explicitly define how they measure the strength of a trophic cascade, though they say that is what they are studying (e.g. their first “step”). Specifically in the section between line 155 and 164, what exactly would the results be that would tell you that one trophic cascade is stronger than another? the paper would be stronger if that were stated explicitly. The analyses focus plant and predator biomass and on aphid density (why not biomass?). However, it seems to me that to evaluate relative strength of a cascade, what is needed is not, for example, plant biomass alone, but first how much plant biomass changed relative to a control when predators were added, and second whether that amount change differs by aphid lineage. That is not mentioned as part of the analysis at all. In sum, it would be really helpful if the authors outlined clearly and quantitatively how the strength of a trophic cascade is measured, and how the strength of one cascade is compared to the strength of another cascade.

OK, now I see that starting on line 172 there is a definition of trophic cascade strength. So, the problem is rather that the first “step” of the statistical analysis needs to be re-written. Currently it says, “(1) investigate whether trophic cascade

strength differed among aphid lineages to test for the existence of intra-specific effects" but that is not at all what they describe in their first "step" of analyses.

I continue to hold that clearly defining, in the introduction, how the strength of a trophic cascade is measured and compared would make the paper stronger. In fact, as figure 2 is the way the test is actually done, if I understand correctly, it would be really useful to make a mock-up of that figure showing equal strength of trophic cascades, and what stronger or weaker cascades would look like in that plot space. Better yet would be to have a response variable (Y-axis) that IS "Strength of Trophic Cascade" or "Trophic Cascade Strength". (with the latter being fine for a figure, but really for the text the former should be used)

Lines 190-192 – it is a stretch to call population growth of aphids without predators measured over 10 days, during which density would have grown a lot, the instantaneous population growth rate. If, during that time, plant quality drops (as clearly it does given the results) there it cannot be considered an instantaneous rate.

line 210 –should read "two times heavier" or "twice as heavy" (not twice heavier)

Figure 1 would be better if the error bars were confidence intervals (e.g. 1.96*SE rather than just the SE)

Line 265 "Predator indirect effect" should read, "the indirect of predators"

Figure. 2. Relationship between the magnitude (log ratio ± 95% CI) of the predator effects on aphid density and on plant fresh biomass according to aphid lineage (a) and biotype (b) Would be more easily understandable (and would aid in interpreting the text the follows) if it read, "The relationship between the magnitude () of the direct effects of predators on herbivore density and the indirect effects of predators on fresh plant biomass by aphid lineage (a) and biotype (b)."

In general, avoid "predator effects" – instead use "effects of predators" Avoid "plant fresh biomass" and use fresh plant biomass" (or wet weight)

line 284 – change “predator indirect effects” to “indirect effects of predators” here and everywhere. Also, replace “lineage population growth rate” with “the population growth rate of the aphid lineage”

Line 302 would read better as “The effects of predators on aphid density () were [not was] positively associated with the population growth rate of the different aphid lineages.”

406 “variations” should read “variation” here and elsewhere in the paper (there were instances of it earlier than this line). Just like “information,” variation is used in the singular in almost all cases in English.

420 and 424 “cascade” should read “cascades”

426 – associated with (not to)

Author's reply:

Download author's reply (PDF file)