Peer Community In Zoology

Raise and fall of an invasive pest and consequences for native parasitoid communities

Stefaniya Kamenova based on reviews by Kévin Tougeron and Miguel González Ximénez de Embún

A recommendation of:

David Muru, Nicolas Borowiec, Marcel Thaon, Nicolas Ris, Madalina Ionela Viciriuc, Sylvie Warot, Elodie Vercken. **The open bar is closed: restructuration of a native parasitoid community following successful control of an invasive pest.** *(2020), bioRxiv, 2019.12.20.884908, ver. 6 peer-reviewed and recommended by Peer Community in Zoology.* 10.1101/2019.12.20.884908

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Host-parasitoid interactions have been the focus of extensive ecological research for decades. One the of the major reasons is the importance host-parasitoid interactions play for the biological control of crop pests. Parasitoids are the main natural regulators for a large number of economically important pest insects, and in many cases they could be the only viable crop protection strategy. Parasitoids are also integral part of complex food webs whose structure and diversity display large spatio-temporal variations [1-3]. With the increasing globalization of human activities, the generalized spread and establishment of invasive species is a major cause of disruption in local community and food web spatio-temporal dynamics. In particular, the deliberate introduction of non-native parasitoids as part of biological control programs, aiming the suppression of established, and also highly invasive crop pests, is a common practice with potentially significant, yet poorly understood effects on local food web dynamics (e.g. [4]).
In their study, Muru et al. [5] took advantage of an existing biological control program focusing on the Asian chestnut gall wasp *Dryocosmus kuriphilus*, an invasive (and highly damaging) pest of chestnut trees. The species is currently a successful invader in many geographic regions, including southern France, where local parasitoid communities failed to provide an adequate control since its widespread establishment in 2010 [6]. In response, the non-native parasitoid species *Torymus sinensis*, which is highly-specific to the Asian chestnut gall wasp, was massively released in commercial chestnut orchards across several regions in France and the island of Corsica. The pest population outbreak was successfully contained, and thanks to the vast amount of host-parasitoid interaction data collected as part of the program, the authors were able to explore the effects of the large fluctuations in Asian chestnut gall wasp natural abundances on native parasitoid

communities, immediately before, and up to five years following the introduction of its natural enemy *T. sinensis*.

Using co-occurrence and clustering analyses, Muru et al. [5] demonstrate that the invasion and the consecutive (efficient) control of the Asian chestnut gall wasp by the parasitoid *T. sinensis* have a significant impact on the structure of local parasitoid food webs. In particular, following decline in the Asian chestnut gall wasp's populations, native parasitoids markedly switched to alternative hosts, most likely due to their respectively higher relative abundances. This pattern seemed to be driven by the degree of generalism in native parasitoid species. Indeed, when its abundances were still relatively high, the Asian chestnut gall wasp was primarily attacked by species capable of exploiting a broad range of hosts, while at low population densities only specialist parasitoids such as *Mesolobus sericeus* were able to persist and compete with the non-native *T. sinensis*.

The current study is important for two major reasons. First, it underscores the value of long-term species interaction data in order to understand the dynamic nature of food webs, namely their structural flexibility in response to changes in the environment or, as in this case, large fluctuation in abundances of a major pest species. In this context, biological control programs could be a great source of data for exploring long-term, large-scale dynamics of species interactions, and their use in ecological studies deserves to be further emphasized. Second, the study adds to the increasing empirical evidence that mobile generalist foragers can display adaptive, frequency-dependent switching behaviour ([1], [7]), which has been suggested to act as a key stabilizing mechanism in food webs by buffering fluctuating population dynamics at larger spatial scales ([8- 10]).

However, the timing of such buffering seems important, especially in systems such as commercial chestnut orchards. Despite their capacity to adaptively switch their foraging behaviour, the response of the native parasitoid communities to the new, unfamiliar resource was not fast enough in order to contain the primary outbreak under an appropriate damage threshold, thus requiring the introduction of the more specialized parasitoid *T. sinensis*. Nevertheless, based on current ecological theory, results presented by Muru et al. [5] suggest that the response of native parasitoid community to fluctuating host dynamics – i.e. shifts in parasitoid foraging behaviour based on their traits – could be predictable. This is encouraging considering the growing impact of biological invasions and insect pest outbreaks, but also the need to implement efficient, yet sustainable strategies for crop protection. Future studies would show at what extent observations by Muru et al. [5] are generalizable over longer time periods or other model systems. Noticeably, better understanding about population dynamics and interactions with the broader community of hosts available across habitats should allow to fine-tune predictions about parasitoids' response to fluctuating resources.

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doi: 10.1101/2019.12.20.884908

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Revision round #3

2020-06-21
The authors have done fantastic work on integrating comments and changes into the manuscript, which reads now really well. Based on that I am ready to recommend its publication in PCI Entomology. Nevertheless, still quite some typos or omissions remain throughout the text - you can find my comments in the attached document. I propose that while I am working on my recommendation text, the authors use the time to integrate these last changes required. Additionally, I will ask them to make sure that:

1) Data is made available to readers after recommendation, either in the text or through an open data repository such as Zenodo (free), Dryad (to pay) or some other institutional repository. Data must be reusable, thus metadata or accompanying text must carefully describe the data;

2) Details on quantitative analyses (e.g., data treatment and statistical scripts in R, bioinformatic pipeline scripts, etc.) and details concerning simulations (scripts, codes) are made available to readers in the text, as appendices, or through an open data repository, such as Zenodo, Dryad or some other institutional repository. The scripts or codes must be carefully described so that they can be reused;

Also, please make sure to state that:

3) You have no financial conflict of interest relating to the article. The article must contain a "Conflict of interest disclosure" paragraph before the reference section containing this sentence: "The authors of this article declare that they have no financial conflict of interest with the content of this article.";

4) This disclosure has to be completed by a sentence indicating that some of the authors are PCI recommenders: “XY is one of the PCI Entomol recommenders.”

Preprint DOI: https://doi.org/10.1101/2019.12.20.884908

Author's reply:

Dear Stephanyia Kamenova,

We took into account all your final remarks (see our answers to your remarks in the attach document).

One of your remarks had us include a new small paragraph into the results section to address molecular results.

We figured that this small paragraph needs therefore to be reviewed before we can submit the final version of the article. That is why, and to speed up the process for this round of review, there will be no new version of the article uploaded in BiorXive. However, I will copy/paste said paragraphe here so that you can still review it. I will also attach the file with our answers to your remarks as usual.

The new Paragraph within the result section:

"Molecular-assisted species identification

The identification of individuals was realized in routine using morphological characters. The molecular characterization was however necessary for taxa in which a species' complex is known (for instance, in the Eupelmus genus – see Al Khatib et al. 2014 and 2016) or for which few information is available. As shown in the Figure S2, the COI sequenced (between 550 and 612pb) were informative enough to distinguish closely related species, as in the Sycophyla and Torymus genera. For some taxa (Aulogymnus arsames, Eurytoma setigera, Megastigmus dorsalis, Torymus affinis), the within molecular diversity may suggest the presence of sister species and/or a marked intraspecific variability."

Download author's reply (PDF file)

Revision round #2

2020-05-28
Dear all, My apology for the delayed reply. I took the time to go through your revised manuscript, which has been indeed improved in many ways. However, I feel that it still deserves additional work in terms of writing and organisation. I don't think it needs to go through a second round of reviews but I attach a list of issues that still seem to me important to be addressed. I hope that you will be able to take them into consideration. As I am not entirely an expert in this topic, I am very much open to argumentation but as you can see it is not the work and approaches in overall that are questioned but rather the quality of the information presented. Please find attached my comments here below and good luck with the revision.

Very much looking forward to see the final version of the paper!

Preprint DOI: https://doi.org/10.1101/2019.12.20.884908

Author's reply:

Download author's reply (PDF file)

Revision round #1

2020-02-16
Dear authors, After a first round of reviews, both the reviewers and I, agree that your paper has a great potential for addressing important scientific questions using a highly valuable dataset of host-parasitoid dynamics. Nevertheless, the manuscript will require a substantial amount of revision before it is accepted for publication. On top of some more specific remarks, the general criticisms revolve around the clarity of writings (especially regarding the Material & Methods and Results sections) and data analyses and interpretation. Additional effort will be required to better frame the scope of the study as well as the more specific questions/expectations.
We all provided numerous comments that we hope will help you throughout the revision. Please find all reviewers comments here below, and my own comments within the manuscript in attachment.
Good luck and looking forward to see your re-submission!

Preprint DOI: https://doi.org/10.1101/2019.12.20.884908

Reviewed by Kévin Tougeron, 2020-01-20 16:22

Review for PCI Ecology: preprint The open bar is closed: restructuration of a native parasitoid community following successful control of an invasive pest. By Muru et al.

General comments.
This paper is overall well written and deals with an important question in the context of biological invasions and community ecology. The introduction is clear and presents the state of the Art and the general context in a very concise manner. The material and methods and the result section were a bit more confusing. I have made some suggestion that could help improving the way information is displayed. The work is overall very descriptive and somehow lacks statistical evidences to fully support the results and to claim strong conclusions. For example, it should be interesting to mention that M. sericeus is statistically more present in semi-natural orchards than in other sites, and significantly more present in those sites than any other species at year 5. GLMs on relative abundances could be done to resolve this issue. Overall the result and discussion sections could be improved by adding more quantitative information into the manuscript. It should be kept in mind (and discussed) that with descriptive analyses such as PCAs or cluster analyses, one overabundant species may be driving the observed patterns. Conclusions should thus be made with caution and nuance.
Please add line numbers on the next version of the manuscript so it is easier to comment.
Please make sure the past tense is used in both the material and methods and the result sections.
Please double check the reference section as some reference are not lister properly.

Abstract.
I like the word “bonanza” but maybe a more common synonym would facilitate the reading.
First paragraph: Remove “the” before “patterns”
The authority Yasumatsu is given for Dryocosmus kuriphilus, please do the same (or remove it) for every species mentioned in the manuscript, for consistency
After reading the results, I would add “two alternative patterns were observed depending on the sampled site” or “on the sampled location”

Introduction
Page 2, 2nd paragraph: I would suggest replacing “invasive species” by “primary-consumer invasive species” to match the “top-consumer” mentioned at the beginning of the sentence.
I would replace “host range expansion” by another term because at first reading I immediately thought of geographic range expansion and it was a bit confusing. Maybe use the term “host spectrum” or any similar wording?
Page 3, “In other words…”: I guess this situation only happens when the native parasitoid community has been facing the exotic pest for a short time? If native parasitoids have time to get used and to adapt to the exotic pest, the introduction of the exotic parasitoid is unlikely to have huge effects on native parasitoid communities. Is there any reference in the literature on this time factor? When native parasitoids are displaced from their native hosts to an invasive one, aren’t they becoming as efficient and as specialized on this exotic host than the invasive parasitoid? Is the introduced parasitoid in all or most cases a superior competitor?
Page 3, last paragraph: please add “:” between “Hymenoptera” and “Cynipidae”
You mention apiculture. Is it because of honey produced from chestnut trees? I am just curious, no need to precise in the manuscript.
I would replace the second to last sentence by: “Torymus sinensis has been proven established in France with fast and significant impacts on the targeted pest in the subsequent years (Borowiec et al 2018).”

Material and methods
Page 3, first paragraph of the methods, line 2: write “Torymus” in full at the beginning of the sentence
Figure 1: Please precise in the figure caption what you mean by “agricultural” and “semi-natural” habitats. It would be worth mentioning it also in the main text (or refer to another study describing it)
Page 4: Please replace “10” by “Ten” at the beginning o the sentence

On the random selection method: precise how it was done? Only twigs with at least one gall were selected, or was it totally random?
Page 5: Please add more details on the identification process (especially for barcoding).
Why were the galls in boxes placed outdoor? Was it necessary for complete development of the wasps?
Askew and Thuroczy: incomplete reference
Please write the nine native parasitoid species and their characteristics in a sentence or in a table, not using a bullet list. I suggest a clear table presenting the species, its degree of specialization and the ad hoc references.
It can be a bit tricky to understand how the C-score works for those who have never used such metric. Maybe just add a short example of what it means to have a low (aggregative) or high (segregative) C-score in terms of species interactions within a community?
Page 6: Does pheatmap uses relative abundances of each species or absolute abundance values? It is of first importance to interpret the results. For example, M. sericeus could be more abundant than other species in Corsica, but the interpretation of the results could change a bit if we use relative abundances.
More informative metrics on community structure and composition could for instance be added to support the results from the PCA and the heatmap. Authors could for instance use metrics from the packages codyn or bipartite in R to describe how each parasitoid species interact with the exotic host (relative abundances, …). But maybe it is impossible to assess in communities where only one host species was monitored.

Results
Figure 2: The y scale for infestation by D. kuriphilus has to match the scale provided in Table 1. It should go from 1 to 5 if I understand correctly.
Please also add details in the figure caption. I do not understand what each point stands for. Is each point representing a field replicate? In that case there should be 26 points per year per species. If some points are confounded, it should be stated in the caption to clarify this matter. Are the lines and points in bold representing mean values? If so, standard errors should also be supplied, either to the text or in the figure itself.
Is it possible to provide numbers on the rate of infestation level decrease of D. kuriphilus? And on the rate of increase in the introduced parasitoid?
"The concomitance between…": This is already discussion. Please remove from the result section.
Page 8: Is it possible to provide the relative abundance of each species, in % of the total number of parasitoid species, in addition to the absolute numbers that are already provided?
Figure 3: I understand this was done for space issues, but the figure should be placed after the paragraph "Co-occurrence null model analyses" describing it.
The paragraph "Co-occurrence null model analyses" has to explain the results to the readers in biological terms. The description of the figure has already been done in the figure caption. Therefore, "The higher the observed value compared to the simulated values, the more the community is structured by exclusion patterns. Conversely, the lower the observed value, the more the community structure relies on association patterns." should be in the figure caption and "Here, a clear trend is observed towards an overall exclusion which seems to appear around the third year of the survey." should appear in the description paragraph.
Please also provide directly in the text statistical results for the C-score values analyses: confidence intervals 95%, the observed value and any p-value that could have been calculated from the permutation tests done to simulate C-values.
Figure 4 caption: What do the numbers represent for M. sericeus on the figure? Values of the heatmap scale depending on the species' abundances and occurrences? Please precise.
Figure 5 and 6: Same issue as for Fig 3, the figure should be placed after the paragraph "Role of the environment" describing it. I would suggest combining both figures into one using the biplot function of the package factoextra (may also work with FactoMineR). Also, please precise how the ellipses were calculated (what is the confidence interval around the barycenter).
Figure 7: This figure does not bring much more information that what is already provided in the text and by the PCA. I suggest removing it or placing it in supplementary material. Adding the text that is currently present in the discussion would also work: "five continental sites (i.e. ArdX6, Dro3, Ard1T, Ard4, Ard1;

assigned with stars in Figure 4) also exhibits a less marked but similar increase of M. sericeus, four of them being in semi-natural landscapes (Figure 1)."

Discussion
Paragraph 2: Is there any evidence of native parasitoids shifting hosts after introduction of the exotic parasitoid (e.g. on other Cynipidae)? I see this question is raised on the second to last paragraph, so maybe it is worth to merge these two paragraphs here.
M. sericeus seems to be a specialist. Did the authors try to redo the analysis (heatmap and PCA) by removing this species from the dataset? I am not implying this is the way results should be presented, but that this species seems to drive everything in the cluster analysis and in the PCA, so by removing it we could see what happens with the other 8 native parasitoid species. The problem with analyses presented in Figures 4 to 6 is that they are relative comparisons (i.e. a species is more abundant or occurs more frequently than others), so it is sometime tricky to see a clear pattern. Other 8 species can be masked/hidden by the effect of M. sericeus in the analyses.
Paragraph 3: I think the survey would really benefit from an analysis on parasitoid relative abundances depending either on the site (continental vs. island) or the habitat (agricultural vs. semi-natural). It could be easily done using GLMs because of the numerous replication points in the study, and it would allow answering the issue raised by the authors at the end of Page 12
Is anything expected in the context of climate-change and biological invasions in southern France? I am thinking about new geographic range shifts, phenology shifts and mis-synchrony between hosts and parasitoids (and host plants) that could happen within these communities. I think it could be interesting to add a few sentences on these matters without being too speculative because it is not the core aim of this survey.

Download the review (PDF file)

Reviewed by Miguel González Ximénez de Embún, 2020-02-11 00:08

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Author's reply:

Thank you for the great review of our article you provided. We have done our best to take into account everything the reviewers noticed. We have improved the paper all the way through and hope the reviewers will be satisfied with it.

In a nutshell: We added the recommended literature to the introduction and reworked the transitions for a easier reading and, we hope, increased clarity. We added a substantial amount of explications within the method sections and added a section talking about our sampling effort. We added new analyses without M. sericeus to see if its impact was covering an impact on some other species. We reworked most of our illustration. Now the heat map is a lot more explicit and PCA figures were merged into a single one. The discussion has had the most rework: literature has been added, text was restructured to be more comprehensive.

Of course the changes we made are not limited to what is above. Commentaries were numerous and we tried to take them all into account.

We hope the revision will reach expectations of the reviewers.