**Response to Reviewers’ Comments**

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**Title of Article**: A predator in need is a predator indeed: generalist arthropod predators function as pest specialists at the late growth stage of rice

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**Associate Editor's Comments to the Author(s):**

**Comment 1** > Although the reviewers recognized that the work represents a large body of field work under realistic conditions, the study does not advance in the field as similar findings have been shown before by the authors (Hsu et al. 2021), and the core conclusion is similar to that presented by Settle et al. (1996).  
**Response** > There are several distinctions between this manuscript and our previous article: (1) We presented three years instead of one year of stable isotope results in this manuscript to support our statements. (2) We further separated GAPs into two main predator groups (spiders and ladybeetles) and showed that they had different dietary patterns over the crop season. (3) We examined the relationship between surrounding landscape and diet composition of GAPs, which we did not do in our previous article. Although part of the results have been previously shown, this manuscript provides a more complete picture of GAPs’ diet and therefore it should help improve our understanding of predator-prey trophic dynamics in rice agroecosystem.

Both Settle et al. (1999) and our study examine the patterns of generalist arthropod predator-prey trophic interactions over the crop season in rice farms. However, the ecological question addressed in this manuscript is different from that in Settle et al. (1999): Settle et al. (1999) focuses on the *densities* of predators and prey, whereas our study focuses on the *pest consumption* by predators. Therefore, despite having similar temporal trends, this study does not merely mirror Settle et al. (1999) but indeed reveals another aspect of predator-prey trophic interactions in rice farms that can complement their results.

**Reviewer 1's Comments to the Author(s):**

**Comment 1** > This is a substantial stable isotope study in multiple rice fields, showing marked diet shifts of generalist predators (mostly spiders) from detritivore to herbivore prey over the cropping season. Such diet shifts have long been expected, but were to my knowledge not previously found in this clarity. Remarkably, the pattern is even consistent over the three years of study. Unfortunately, much of the originality of the work is already contained in a previous publication (Hsu et al. 2021) that is based on data from one out of the three years presented in the current manuscript. Since the diet shift is already published, I would mention this more explicitly in the introduction and focus the current manuscript more strongly on the consistence over years, and possibly on other not yet published aspects.

One general point is that high proportions of pests in predator diets do not necessarily imply effective population regulation below economic damage thresholds. Predators may switch to pests too late after the build-up of damaging infestation levels, and/or not reach sufficient top-down effects (consumption rates plus non-consumptive effects) to prevent pest damage. Both can apply even if the predator diet is 100% pest at some point. Thus, additional evidence is needed to conclude about pest control, such as experimental manipulation of predator densities in the field or carefully parameterized predator-prey models. This limitation is briefly covered in the discussion, but should be reflected throughout the text.

**Response** > I agree with the reviewer’s comments that we may want to emphasize more the consistence of GAPs’ diet over years and other new findings not presented in our previous paper. Though I am not sure if we should “explicitly” mention our previous findings in the introduction as this might alter our current structure (If we decide to do so, it seems that we can make some changes in the third paragraph).

Regarding the second point the reviewer raised, I think we do clarify the distinction between per capita pest consumption and suppression of pest populations in the potential caveats of the study. I feel that it is not necessary to mention this throughout the text. Nonetheless, I think we can elaborate on this caveat as follows (Line 376-377): *“future work may require complementing stable isotope analysis with observations of predator and pest populations as well as experimental manipulations of predator densities in the field.”*

*Abstract*

**Comment 2** > L27: Avoid parentheses in the abstract.

**Response** > Yes, I agree that we can remove the parentheses.

**Comment 3** > L30: Again remove parentheses. As the crop stage effect is already mentioned under (a), (c) should describe the farming type effect more concretely (without parentheses), e.g. “Consumption of rice pests was XY% higher in conventional than in organic fields.”

**Response** > Yes, I agree that we can be more specific about the pest consumption in organic and conventional farms. Maybe revise the sentence as follows:

“c) Pest consumption by GAPs varied with farm type, with consumption on average 13% higher in conventional than in organic farms over the three study years.”

**Comment 4 >** L33: Can you give more information how generalist predators should be incorporated into pest management? How can their densities be increased? The last sentence should not overstate – sustainable agriculture is more than pest management with generalist predators. Better concentrate on what you can specifically expect from generalist predators. E.g. natural suppression of pest insects with no need for chemical control. This may contribute to the sustainability of rice production. But see above for the difference between high pest consumption and natural pest control.

**Response >** Thanks for the suggestions. Perhaps we can modify our last point as follows:

*“This study reveals the potential that generalist predators may produce a stable, predictable top-down effect on pests. Therefore, incorporating these ubiquitous predators in pest management by boosting their field densities will likely enhance natural biological control and help achieve the goal of sustainable agriculture.”*

**Comment 5 >** L89: Some more detail should be given. According to Bengtsson, detritivores and predators, but not herbivores, have higher densities in organic farming. As the reference is from 2005, the literature should be reviewed for possible new information on these patterns, with special focus on rice. Having more predators at constant pest densities will likely increase, not reduce, pest consumption in organic farming, unless predators switch to alternative prey. Only per capita pest consumption can be expected to decrease even in the absence of switching.

**Response >** I have revised the sentence a bit and added a recent meta-analysis comparing arthropod diversity in organic and conventional farms:

Original: *“In general, compared to conventional farming, organic farming promotes arthropod diversity (both pest and alternative prey), potentially lowering the pest consumption by generalist predators.”*

*Revised: “Studies have shown that organic farming promotes arthropod abundance and diversity (Bengtsson et al. 2005, Lichtenberg et al. 2017), which could potentially lower pest consumption by generalist predators if they shift their diets toward alternative prey.”*

Reference (actually we have already cited this paper [ref No. 30] in our manuscript in other place):

Lichtenberg, E. M., Kennedy, C. M., Kremen, C., Batary, P., Berendse, F., Bommarco, R., ... & Crowder, D. W. (2017). A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. Global change biology, 23(11), 4946-4957.

*Introduction*

**Comment 6 >** All essential information is given in L40-102. L103-127 repeats the study aims and summarizes the methods and findings, which is not necessary for this journal. This section should be removed. Some information on the isotope method and possibly on the study organisms may be included earlier in the introduction, instead.

**Response >** Yes, I agree that a lot of information in the last paragraph of introduction is not necessary. The Nature journals we originally targeted have a special format for the last introduction paragraph. Since now we are submitting to standard journals, I think we can probably remove the results and conclusions there. Below is the revision I suggest:

*“To address these three knowledge gaps, we sampled generalist arthropod predators (GAPs) and their prey in sub-tropical organic and conventional rice farms over the rice growth season from 2017 to 2019 and applied stable isotope analysis to 1) quantify the diet composition of GAPs (ladybeetles and spiders) at each major crop stage, 2) examine the consistency of pest consumption by GAPs over years, and 3) investigate how various abiotic and biotic factors (farm type, crop stage, percent forest cover, and the relative abundance of pests in the field) may affect pest composition by GAPs. Filling these gaps will provide insights for applying GAPs in biocontrol programs. Additionally, stable isotope analysis has been widely applied in ecology to infer predator-prey trophic interactions and estimate the proportion contribution of different prey sources to predators’ diets 31-33. This quantification method has an advantage over other “snap-shot” techniques (e.g., field observations and molecular gut content analysis) as it reflects the accumulated prey consumption in predators’ diets 34 and thus this approach is suitable for the purpose of this study.”*

*Methods*

**Comment 7 >** L132: geographic coordinates missing.

**Response >** There are two options for this (either one is fine):

1. Simply provide the geographic coordinates in the text (longitude range: 120.656-120.721 °E; latitude range: 24.364-24.489 °N).
2. Provide a table in the Appendix S1 summarizing the basic information of the study farms (this will be the new Appendix S1: Table S1).

Table S1. The geographic coordinates, farm size, and the percent forest cover of the study farms

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Farm type | Farm ID | Longitude (°E) | Latitude (°N) | Farm size (ha) (not sure if we have the data) | Percent forest cover (%)\* |
| Organic | MO-1 | 24.412 | 120.716 |  | 44.1 |
|  | MO-2 | 24.406 | 120.722 |  | 58.4 |
|  | MO-3 | 24.422 | 120.690 |  | 30.9 |
|  | LO-1 | 24.381 | 120.705 |  | 39.0 |
|  | LO-2 | 24.364 | 120.708 |  | 19.1 |
|  | LO-3 | 24.369 | 120.705 |  | 13.2 |
|  | SO-1 | 24.459 | 120.656 |  | 5.1 |
| Conventional | MC-1 | 24.411 | 120.716 |  | 47.7 |
|  | MC-2 | 24.407 | 120.722 |  | 57.1 |
|  | MC-3 | 24.421 | 120.689 |  | 27.3 |
|  | LC-1 | 24.378 | 120.697 |  | 0.4 |
|  | LC-2 | 24.364 | 120.708 |  | 19.6 |
|  | LC-3 | 24.370 | 120.709 |  | 36.5 |
|  | SC-1 | 24.458 | 120.657 |  | 8.6 |

\* The percent forest cover was estimated within a 1-km radius circular buffer around each farm.

*Results*

**Comment 8 >** In addition to the number of potential prey, also the abundance of the different predators over the season should be given, because in addition to diet composition, the ratio between predator and prey densities is crucial for top-down effects. It is also interesting to what degree densities of the different predators increase in the fields with increasing herbivore densities (strong increase expected for ladybeetles, less for spiders).

**Response >** I have made a new figure showing the abundance of spiders and ladybeetles over the crop season in organic and conventional farms in the three study years. We can include it in the Appendix S1 (but I am not sure where to put this in the main text).

abd_predator.tiff

Figure Sx. The number of spider and ladybeetle individuals (mean ± SE) in the sweep-net samples in organic and conventional rice farms over crop stages during the three study years. The numbers of individuals were averaged across the replicate farms.

**Comment 9 >** L305: Some care should be taken regarding foraging mode and the diversity of spiders sampled. Tetragnathidae can be either orb web builders (e.g. Tetragnatha) or active hunting (Pachygnatha). Do you know what you had in your samples? Some spiders (e.g. Clubionidae) are active hunters.

**Response >** I think we can directly write the species name there (*Tetragnatha maxillosa*).

**Comment 10 >** L306: This statement should be stronger – the catch of aerial webs is very strongly expected to reflect prey abundance – it is a classical example of type I functional response.

**Response >** Yes, the diet compositions of orb-weavers are largely determined by the relative abundance of prey species in the habitat compared to active hunters. However, there are many potential factors that might affect the actual prey captured on the webs, which can cause their diet compositions to deviate from the relative prey abundance. Therefore, I think it would be better not to put it too strongly. Perhaps we can modify the sentence as this: *“The diet composition of these predators are largely influenced by prey abundance.”*

**Comment 11 >** L309: What rice pests did you sample? If it was aphids, this is something clearly preferred by many ladybeetles.

**Response >** The pest herbivores were mostly plant hoppers, leafhoppers, and stinkbugs.

*Discussion*

**Comment 12 >** The authors discuss the increase in herbivore densities attracting predation by GAPs. However, there seems to be also a marked decline in the availability of detritivore prey. What could be the reason(s) for the decline in detritivores? Is it dry condition during the later cropping stages? It would be good to have some information on this.

**Response >** Maybe we can add a bit of information to our discussion, perhaps in the last sentence of the second paragraph:

***“****This could be because of a higher herbivore (pest) density at late crop stages, as indicated by a correlation between rice herbivore consumption and crop stage (see* Factors associated with pest consumption by predators*), along with a drastic decline in alternative prey (detritivore) abundance due to drainage of rice farms.”*

*Conclusions*

**Comment 13 >** It would be good to focus more on what can be concluded from the current work, less background and results.

**Response >** I think we can add a bit of information before the last sentence in the conclusions (Line 395):

*“Therefore, boosting the field densities of these predators will likely enhance natural biological control. As sustainable agriculture has become more important than ever in human history, incorporating the ubiquitous generalist predators into pest management will open a promising avenue towards this goal.”*

**Reviewer 2's Comments to the Author(s):**

Hsu et al. use stable isotope analysis to measure the proportion of generalist predator prey that is herbivorous versus detritus feeding through the growing season, in rice crops. The proportion of herbivorous prey generally increases through the growing season, leading the authors to conclude that the biocontrol effectiveness of the generalist predators also increases. This pattern held for both organic and conventional farms. It is a strength of the study that the work is done in rice fields across multiple years and two farming systems, such that they are tracking the feeding patterns of the generalist predators under entirely natural conditions. I do have a few concerns:

**Comment 1** > In the abstract, the authors conclude that their generalists “produce a stable, predictable top-down effect on pests”. They have shown that the predators are feeding on herbivores, but we do not really know that these are the key pests that are limiting production at the times when predators are feeding most heavily on the herbivores. So, the link between consumption and pest control is not certain.

**Response** > Given that pest densities were the highest during later crop season when the rice plants were flowering and fruiting, and that the pest consumption by predators was also the highest during this period, there is a high potential that these predators can exert top-down regulation on pests. That said, I agree that more experiments are needed to test whether such pest consumption is critical for crop production.

**Comment 2 >** The Introduction begins quite broadly, starting with the earliest days of biocontrol. It might be more effective to somewhat “narrow the funnel” of where this study fits in the literature – what specific questions about generalist predators and biocontrol, beyond whether they have any benefit at all – does this study address? I suggest that the first paragraph of the Intro might be deleted.

**Response >** I think we can either keep the fist paragraph or delete/modify it. I don’t have any strong preference.

**Comment 3 >** It seems a bit of a stretch to conclude that “generalist predators may function as specialist predators of pests at late crop stages (when pests are abundant)”. The stable isotopes are identifying broad trophic position of prey, which of course might still include many many different species. The results seem consistent with the predators simply sampling whatever prey are available, which seems like the definition of a generalist.

**Response >** Of course GAPs still fed on multiple prey items at later crop stages, but most of the prey were pest herbivores, and thus I think it is fair to state that these predators function like a temporary specialist of pest herbivores (as a prey guild) during later season.

**Comment 4 >** I wondered if arthropod communities in the rice fields were impacted by surrounding landscapes. Of course, if the prey communities did not differ across landscapes then there would not be an expectation for feeding patterns among predators to differ. Likewise, it would be helpful to know how prey communities differed between organic and conventional fields, when seeking to understand why feeding patterns might (or might not) differ between the two farming systems.

**Response >** Yes, prey community compositions may influence the diet composition of generalist predators. However, our study focuses on trophic guilds rather individual species, and we did provide information of the relative abundance of different prey guilds in organic and conventional farms (Fig. 3). We also have a table for the relative abundance of different rice herbivore genera at flowering and ripening stages in the three study years, although the samples are pooled across the two farm types (Fig. S3). I think we can further split this table by farm type:

Table S3. The relative abundance of the major families/genera in rice herbivore guild at the flowering and ripening stages in the three study years. Samples were pooled across the replicate organic and conventional farms, respectively.

(a) Flowering stage

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Family/Genus | Year 2017 | | Year 2018 | | Year 2019 | |
|  | Organic | Conventional | Organic | Conventional | Organic | Conventional |
| Cicadellidae/*Nephotettix* | 6.70% | 8.30% | 28.10% | 17.70% | 63.90% | 73.70% |
| Delphacidae/*Nilaparvata* | 84.80% | 90.40% | 65.50% | 77.30% | 29.90% | 22.10% |
| Lygaeidae/*Pachybrachius* | *NA* | *NA* | 1.70% | *NA* | 2.10% | 0.80% |
| Pentatomidae/*Scotinophara* | 1% | 0.60% | 1.70% | 4% | 1.50% | 0.30% |
| Others | 7.60% | 0.60% | 3% | 1.10% | 2.50% | 3.10% |
| *Total* | 100% | 100% | 100% | 100% | 100% | 100% |

(b) Ripening stage

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Family/Genus | Year 2017 | | Year 2018 | | Year 2019 | |
|  | Organic | Conventional | Organic | Conventional | Organic | Conventional |
| Cicadellidae/*Nephotettix* | 62.10% | 71.70% | 72% | 78.20% | 57% | 92.70% |
| Delphacidae/*Nilaparvata* | 34.50% | 27.20% | 15.30% | 11.20% | 12.40% | 4% |
| Lygaeidae/*Pachybrachius* | *NA* | *NA* | *NA* | 0.50% | 15.10% | 0.30% |
| Pentatomidae/*Scotinophara* | 3.40% | 1.10% | 11.40% | 9.20% | 10.20% | 2.50% |
| Others | *NA* | *NA* | 1.30% | 1% | 5.20% | 0.60% |
| *Total* | 100% | 100% | 100% | 100% | 100% | 100% |

**Comment 5 >** Overall, the paper is exceptionally well written and clear, and represents a large body of field work under realistic conditions. Yet, the core conclusion, that generalist predators eat more detritivores early and more herbivores late, is essentially the same take-home message as the classic Settle et al. (1996) Ecology paper. I agree with the authors that greater information on specific prey species being consumed and the impacts of this feeding on arthropod abundance and plant biomass/productivity, including consumption of other predator species, using molecular gut content analysis or manipulative field experiments, would help flesh out this study and make a bigger step forward.

**Response >** Both Settle et al. (1999) and our study examine the patterns of generalist arthropod predator-prey trophic interactions over the crop season in rice farms, but the ecological questions are different: Settle et al. (1999) focuses on the *densities* of predators and prey, whereas we focus on the *pest consumption* by predators. Therefore, despite having similar temporal trends, I think our study does not merely mirror Settle et al. (1999) but indeed reveals another aspect of predator-prey trophic interactions in rice farms that can complement their results.

Our study shows high per capita pest consumption by predators at later crop stages, which could contribute to an effective top-down control on pests. That said, I agree that more experiments are needed to clarify the link between pest consumption, pest populations, and crop production.