**Title**

* Combine both?
* A predator in need is a predator indeed (add sustainable?)
* Generalist arthropod predators function as reliable pest specialists during critical stages of rice production

**Abstract**

* implications for the continuation of life on Earth, long-term solutions to environmental crisis
* Agriculture and food security, biodiversity, ecosystem service, health and environment, water pollution
* NS facilitates a cross-disciplinary dialogue around sustainability issues, and narrow the gap between research and policy making
* Introduction + Results + Discussion 4344 words currently > cut to 3500 (e.g., transfer citations to numbers)
* 3 years of field data, over 1,000 stable isotope samples
* This study aims to help fill the three aforementioned knowledge gaps by quantifying generalist predators’ diet composition, examining their consistency in pest consumption, and investigating how local abiotic and biotic factors affect the diet composition in rice system.
* Biocontrol, using natural enemies for pest control, has a long history in agriculture. There has been a surge of interest in biocontrol in the Anthropocene because of its potential as an important tool for sustainable agriculture.
* To evaluate the role of generalist arthropod predators (GAPs, ubiquitous in nature) as biocontrol agents, we used stable isotope analysis to quantify their diet composition in organic and conventional rice farms over crop stages in three consecutive years.
* We found that the proportion of rice pests in GAP’s diet increased toward late crop stages and reached 79-95% at the ripening stage consistently over three years (with different climatic conditions) in both organic and conventional farms. This high percentage and consistency indicates that GAP could function as effective specialist in pest management during the critical period in crop fruiting.
* The results provide strong support to applying GAP in biocontrol programs for sustainable agriculture.

**Introduction**

Using natural arthropod enemies for pest control has a long history in agriculture. For example, the earliest record of biocontrol was documented in the book *Plants of the Southern Regions* (*ca.* 304 A.D.) that people in Southern China sold ants and their nests (attached to branches) in market to control citrus insect pests 1. With the advent of new technologies in the past century, synthetic pesticides have become the main method to control pests in agriculture. However, this comes at a cost, such as posing risks to people, reducing biodiversity (e.g., decline in top predators) and hampering ecosystem functions (e.g., decline in pollinator service) 2,3. As agriculture has become the largest land use type worldwide and a major driver for global biodiversity crisis and environmental degradation in Anthropocene 4, a shift from synthetic pesticides to environmental-friendly practices (e.g., biocontrol) is urgently needed to make agriculture more sustainable 5. For example, the European Commission has recently announced its plan to reduce the use of chemical pesticides in European Union’s agricultural systems by 50% by 2030 6. To achieve this ambitious sustainability goal, biocontrol by enemies has been considered as a key approach and therefore regained its importance in modern agriculture.

The natural enemies for pest control can be classified into two major groups based on their prey range—specialist and generalist predators. While specialist predators (e.g., parasitoid wasps) have been widely advocated in agriculture because they target specific pest species and produce less undesirable non-target effects 7, generalist predators (e.g., spiders) have been increasingly appreciated for their conspicuous existence and consistent biocontrol effect on pests 7-10. For example, generalist predators were commonly reported in various agro-ecosystems and significantly reduced pest abundances in about 75% cases of 181 field manipulative studies 8. Moreover, a meta-analysis suggests that generalist predators may exert stronger biocontrol effects on pest populations over time compared to specialists 7.

While the value of generalist predators has been increasingly appreciated, a few fundamental knowledge gaps need to be filled to validate their biocontrol potential and the underlying mechanisms in agro-ecosystems. For example, although studies have qualitatively analyzed generalist predators’ diet (e.g., using molecular gut content analysis to identify prey species) 11-13, very few have quantified these predators’ diet compositions over growth season in the field *(knowledge gap 1)* 10. Quantifying the diet composition will provide critical information to address the concern that generalist predators may switch their diet from pests to alternative prey and thus weakens pest control 9. If generalist predators consume a high proportion of pests in their diet in field conditions with the presence of alternative prey, the result may help end a long debate on whether generalist predators serve well as biocontrol agents 8,9,14. Moreover, to assess the reliability of these predators as biocontrol agents in agriculture, it is important to examine their consistency in pest consumption over years in the field, although this information is lacking *(knowledge gap 2)*. Given that dynamics in population density or species compositions commonly occur in agro-ecosystems 15,16, a consistently high pest consumption by generalist predators over years, if it occurs, will provide strong support for applying these predators in pest management programs.

To better understand the underlying mechanisms for the biocontrol effect of generalist predators, we also need to examine how various abiotic and biotic factors affect the diet compositions of generalist predators in agro-ecosystems *(knowledge gap 3)*. First, arthropod community composition (e.g., pest vs. alternative prey density) may vary with crop stages over the growth season and affect predator-prey trophic interactions 17. Therefore, we should examine how crop stage affects the pest consumption by generalist predators in order to understand whether the role of these predators as biocontrol agents varies within a growth season. Second, we should examine whether farming practices (e.g., organic and conventional) influence the diet compositions of predators (e.g., pest consumption) 18. This will demonstrate whether generalist predators provide different biocontrol values in different farm types. In general, compared to conventional farming, organic farming promotes arthropod diversity (both pest and alternative prey) 19, potentially lowering the pest consumption by generalist predators 10. In contrast, the application of synthetic chemicals in conventional farms may promote pest abundance 16,20-22, potentially leading to higher pest consumption in predators’ diet. Third, we should investigate the relationship between the relative prey abundance and predators’ diet composition. This will clarify whether pest abundance or predator preference mainly explains the pest consumption by predators 17 23-25. Lastly, we should examine how surrounding vegetation (e.g., forest cover) affects the diet composition of generalist predators. While surrounding vegetation reportedly affected arthropod diversity and predator-prey interactions in agro-ecosystems 26-30, its effect on predators’ diet compositions is unclear. Understanding this will provide insights for managing agricultural landscape and promoting biocontrol services by generalist predators.

To address the aforementioned knowledge gaps, this study aims to 1) quantify the diet composition of generalist predators, 2) examine the predators’ consistency in pest consumption over years, and 3) investigate how abiotic and biotic factors affect these predators’ diet composition. Filling these gaps will provide insights for applying generalist predators in biocontrol programs. Specifically, this study sampled arthropod prey and generalist arthropod predators (GAPs) in sub-tropical organic and conventional rice farms over rice growth season (seedling, tillering, flowering, and ripening stages) in Miaoli County, Taiwan from 2017 to 2019. The objectives of this study were to (1) quantify the diet compositions of GAPs (ladybeetles and spiders) at each rice stage using stable isotope analysis (δ13C and δ15N), (2) examine GAPs’ consistency in pest consumption over years (i.e., the proportion of rice pests in GAPs’ diet in 2017-2019), and (3) investigate how local abiotic and biotic factors (e.g., farm type, crop stage, percent forest cover, and the relative abundance of pests in the field) may affect pest consumption by GAPs. Stable isotope analysis has been widely applied in ecological studies to infer predator-prey trophic interactions and estimate the proportion contribution of different prey sources to predators’ diet 31-33. This quantification method reflects accumulated prey consumption in predators’ diet, which may not be achieved by some “snap-shot” techniques (e.g., field observations and molecular gut content analysis) 34. We find that predators (GAPs) consumed a high proportion of rice pests in their diet at late crop stages (e.g., from 23-47% at the tillering stage to 79-95% at the ripening stage in all rice farms during 2017-2019). Such high pest consumption patterns were similar across the three study years, suggesting that i) generalist predators’ top-down control of pest are consistent over years, and ii) generalist predators may function as “specialist predators” of pests at late crop stages (when pests are abundant). Moreover, predators in conventional farms consumed higher proportion of rice pests than those in organic farms. By quantifying diet composition over crop stages and years, our study lends strong support to applying generalist predators as biocontrol agents in agro-ecosystems (e.g., high pest consumption regardless of organic and conventional rice farms). To promote sustainable agriculture, we encourage studies to investigate if generalist predators may commonly function as “specialist predators” of crop pests in various agro-ecosystems.

**Materials and Methods**

*Study system and sample collection*

We collected terrestrial arthropods in organic and conventional rice farms in subtropical Taiwan (latitude and longitude ranges) from 2017 to 2019 (three farms each in 2017 and seven farms each in 2018 and 2019). These farms, averaged at 0.2 hectares, were irrigated with surface water . The organic farms were managed with organic fertilizers (manure; 2-3 applications/crop season) and natural pesticides (tea saponins; 1 application/crop season). The conventional farms were managed with synthetic nitrogen fertilizers (2-3 applications/crop season) and organophosphate pesticides (1 application/crop season). At each major rice crop stages (seedling, tillering, flowering, and ripening stage) during the growing season (April - July) in each study year, we collected arthropod samples by sweep-netting (36 cm in diameter with a mesh size of 0.2 × 0.2 mm) the crop canopy 60 times along the farm ridges. Samples were sealed in bags without chemical preservatives, iced, and transferred to refrigerator (−20ºC) in the laboratory. We identified and counted arthropods under a dissecting scope to the lowest possible taxonomic level. Main orders, families, and genera have been documented in Hsu et al. 10.

*Stable isotope analysis of arthropod samples*

After identification, arthropod samples were prepared for stable isotope analysis. First, samples were oven dried (50ºC) for one week, ground, and weighed into individual tin capsules (5 × 9 mm). If necessary, several conspecifics would be pooled into a capsule to meet the minimum weight required for stable isotope analysis (i.e., 2 mg in this study). Stable isotope analysis was conducted at the UC Davis Stable Isotope Facility using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). The standards for carbon and nitrogen stable isotope ratios were Vienna PeeDee Beleminte and atmospheric N2, respectively. The results of our samples were expressed in per mil (‰) relative to the aforementioned international standards (δ13C and δ15N).

*Arthropod trophic guild assignment*

A trophic guild represents a group of species using similar resources and forms a basic component of food webs (Root 1967, Hawkins and Macmahon 1989). The concept has been proved to be practical in current ecology because it condenses broad taxonomic information into distinct functional groups in communities 35. In this study, we classified arthropod samples into four trophic guilds based on their dietary information and isotope signatures 10: (1) “Predators” consisted of spiders and ladybeetles, which are the primary GAPs inhabiting rice farms. (2) “Rice herbivores” consisted of major rice pests, including planthoppers, leafhoppers, and stink bugs. (3) “Tourist herbivores” consisted of herbivorous species without direct trophic association with rice plants, including some grasshoppers and leaf beetles. (4) “Detritivores” consisted of arthropods that feed on decaying organic material or plankton, including various midge and fly species. The arthropod families/genera in each trophic guild is detailed in Appendix S1: Table S1. This study focused on the trophic interactions between generalist predators and their prey sources and therefore did not consider less abundant trophic guilds (e.g., parasitoids) in subsequent analyses.

*Data analyses*

To quantify the diet compositions of predators, we constructed a Bayesian stable isotope mixing model using the R MixSIAR package 36 to estimate the proportions of different prey sources (i.e., the three prey guilds including rice herbivores, tourist herbivores, and detritivores) in predators’ diet. In the mixing model, individual farm-year combination and crop stage were included as fixed effects for predator isotope data to examine their effects on predators’ diet composition; isotope data for the three prey guilds were pooled respectively to generate fixed source values due to their high mobility across farms 37,38. Isotope data at the seedling stage for the three study years were omitted from the analysis due to insufficient sample sizes for model estimation. To improve our model estimates, carbon and nitrogen concentration dependencies as well as the residual/process errors were incorporated 39,40. Trophic discrimination factors (TDFs) were estimated from the diet-dependent discrimination equation proposed by Caut, et al. 41. We ran three Markov Chain Monte Carlo (MCMC) chains, each with 50,000 iterations and a burn-in number of 25,000, along with a non-informative Dirichlet prior. Chain convergence was assessed via Gelman-Rubin and Geweke diagnostics. Bayesian posterior mean estimates of diet compositions (for each farm-year-stage combination) were extracted for further analysis.

To examine how local abiotic and biotic factors (e.g., farm type, crop stage, percent forest cover, and the relative abundance of pests in the field) may affect the pest consumption by GAPs, we first fit beta regression models with year, farm type, crop stage, percent forest cover, and the relative abundance of rice herbivores as fixed effects without interactions and the proportion of rice herbivores consumed in predators’ diet as the response variable using the R betareg package 42. We then refit the first model by adding the interaction terms among all the significant factors to create the final model. Model parameters were estimated using maximum likelihood, and their significance was analyzed by a two-way ANOVA (type II test) using the “Anova” function in the R car package 43. Tukey’s post-hoc tests were performed for the significant factors using the “cld” function in the R emmeans package 44. Note that the percent forest cover around each study farm was estimated from Google Earth images by manually delimiting the forested areas within a 1-km radius circular buffer surrounding the farm and computing the fraction of these areas in the buffer zone. Because spiders and ladybeetles were the most abundant generalist predator groups in our study system and exhibited distinct foraging behavior (e.g., sit-and-wait vs. active hunting), we also performed all the aforementioned analyses separately for each of the two predator groups. All analyses were conducted in R version 4.0.3 45.

**Results**

*Diet compositions of predators in rice farms*

Across organic and conventional farms during 2017-2019, the proportion of rice herbivores in all predators’ diet increased over the course of the crop season from 23-47% at the tillering stage to 79-95% at the ripening stage; the proportion of detritivores in predators’ diet decreased from 38-59% at the tillering stage to 1-2% at the ripening stage; the proportion of tourist herbivores in predators’ diet also decreased from 15-22% at the tillering stage to 4-19% at the ripening stage (Fig. 1a; Appendix S1: Table S2).

Regarding individual predator groups, spiders and ladybeetles showed a marked difference in their diet compositions over crop stages during 2017-2019. Across organic and conventional farms, spiders consumed a higher proportion of detritivores (33-55%) in their diet in the beginning of crop season (tillering stage) and substantially increased the consumption on rice herbivores to 78-94% in late crop season (ripening stage) (Fig. 1b; Appendix S1: Table S2). In contrast, ladybeetles in both organic and conventional farms consumed a low proportion of detritivores (≤ 17%) and a steadily high proportion of rice herbivores (≥ 74%) in their diet throughout the crop season (Fig. 1c; Appendix S1: Table S2). For both predator groups, tourist herbivores generally did not constitute an important prey source and contributed less than 33% to the predators’ diet (Fig. 1b, c; Appendix S1: Table S2).

*Patterns of rice herbivore consumption by predators*

We further analyzed rice herbivore consumption by GAPs since these herbivores are the main pests of concern. The patterns of rice herbivore consumption by all predators in organic and conventional rice farms were generally similar across the three study years, suggesting consistency in GAPs’ feeding habits (Fig. 2). The consistency in herbivore consumption over years was also revealed by our beta regression model, which indicated that the proportion of rice herbivores consumed in all predators’ diet did not vary across years (*χ*2 = 1.99, *P* = 0.37; Table 1).

Interestingly, spiders and ladybeetles exhibited distinct within-season patterns of rice herbivore consumption. For spiders in organic and conventional farms, the proportion of rice herbivores in their diet increased toward later crop season, ranging from 20-48% (tillering) to 78-94% (ripening) (Fig. 2b; Appendix S1: Table S2), whereas for ladybeetles in organic and conventional farms, the proportion of rice herbivores in their diet remained relatively stable throughout the season, ranging from 74-85% (tilling) to 93-95% (ripening) (Fig. 2c; Appendix S1: Table S2).

*Factors associated with rice herbivore consumption by predators*

The proportion of rice herbivores consumed in GAPs’ diet differed between organic and conventional farms (All predators: *χ*2 = 15.98, *P* < 0.001; Spiders: *χ*2 = 13.38, *P* < 0.001; Ladybeetles: *χ*2 = 6.70, *P* = 0.001; Table 1). In particular, all predators in conventional farms consumed a higher proportion of rice herbivores in the diet compared with predators in organic farms (Tukey’s post-hoc test, *P* < 0.05; Table 2), although there was an interactive effect of farm type and year on spiders’ diet composition (*χ*2 = 7.64, *P* = 0.02; Table 2).

The proportion of rice herbivores consumed in GAPs’ diet also differed among crop stages (All predators: *χ*2 = 227.93, *P* < 0.001; Spiders: *χ*2 = 115.43, *P* < 0.001; Ladybeetles: *χ*2 = 152.60, *P* < 0.001; Table 1). Specifically, GAPs consumed higher proportions of rice herbivores in their diet at the flowering and/or ripening stage than they did at the tillering stage (Tukey’s post-hoc test, *P* < 0.05; Table 3).

Contrary to previous studies showing the importance of surrounding landscape in determining arthropod community structure and pest control by predators 46 , but see Karp, et al. 47, the proportion of rice herbivores consumed in GAPs’ diet was not associated with the percent forest cover within a 1-km radius buffer surrounding the study farms (All predators: *χ*2 = 0.30, *P* = 0.58; Spiders: *χ*2 = 1.28, *P* = 0.26; Ladybeetles: *χ*2 = 0.77, *P* = 0.38; Table 1). Furthermore, the proportion of rice herbivores consumed was not associated with the relative abundance of rice herbivores in the field (All predators: *χ*2 = 0.36, *P* = 0.55; Spiders: *χ*2 = 1.38, *P* = 0.24; Ladybeetles: *χ*2 = 0.93, *P* = 0.33; Table 1).

Table 1. Analysis of deviance (type II test) for the beta regression models fitted to data for all predators, spiders, and ladybeetles. The results were obtained from the Anova() function in the R “car” package 43. For each model, interactions were tested only between significant factors.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Model | Factor | *d.f.* | *χ*2 | *P* |
| All predators | Year | 2 | 1.99 | 0.37 |
|  | Farm type | 1 | 15.98 | < 0.001 |
|  | Crop stage | 2 | 227.93 | < 0.001 |
|  | Percent forest cover | 1 | 0.30 | 0.58 |
|  | Relative abundance of rice herbivores | 1 | 0.36 | 0.55 |
|  | Farm type × Crop stage | 2 | 2.06 | 0.36 |
| Spiders | Year | 2 | 7.92 | 0.02 |
|  | Farm type | 1 | 13.38 | < 0.001 |
|  | Crop stage | 2 | 115.43 | < 0.001 |
|  | Percent forest cover | 1 | 1.28 | 0.26 |
|  | Relative abundance of rice herbivores | 1 | 1.38 | 0.24 |
|  | Year × Farm type | 2 | 7.64 | 0.02 |
|  | Year × Crop stage | 4 | 0.99 | 0.91 |
|  | Farm type × Crop stage | 2 | 1.12 | 0.57 |
|  | Year × Farm type × Crop stage | 4 | 0.44 | 0.98 |
| Ladybeetles | Year | 2 | 13.20 | 0.001 |
|  | Farm type | 1 | 6.70 | 0.001 |
|  | Crop stage | 2 | 152.60 | < 0.001 |
|  | Percent forest cover | 1 | 0.77 | 0.38 |
|  | Relative abundance of rice herbivores | 1 | 0.93 | 0.33 |
|  | Year × Farm type | 2 | 5.78 | 0.06 |
|  | Year × Crop stage | 4 | 6.80 | 0.15 |
|  | Farm type × Crop stage | 2 | 1.95 | 0.38 |
|  | Year × Farm type × Crop stage | 4 | 2.37 | 0.67 |

Table 2. Tukey’s post-hoc tests comparing the proportion of rice herbivores consumed in the diet of predators in organic and conventional rice farms. The tests were performed using the function cld() from the R “multcomp” package 48. Different superscript letters indicate significant differences in the means (α = 0.05) within each model.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Model | Farm type | Mean (± SE) | Lower 2.5% | Upper 2.5% |
| All predators | Organic | 0.66a (± 0.015) | 0.63 | 0.69 |
|  | Conventional | 0.73b (± 0.014) | 0.70 | 0.76 |
| Spiders | Organic | 0.64a (± 0.020) | 0.60 | 0.68 |
|  | Conventional | 0.73b (± 0.019) | 0.69 | 0.77 |
| Ladybeetles | Organic | 0.86a (± 0.007) | 0.85 | 0.87 |
|  | Conventional | 0.88b (± 0.005) | 0.87 | 0.89 |

Table 3. Tukey’s post-hoc tests comparing the proportion of rice herbivores consumed in the diet of predators at three crop stages (tillering, flowering, and ripening stage). The tests were performed using the function cld() from the R “multcomp” package 48. Different superscript letters indicate significant differences in the means (α = 0.05) within each model.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Model | Crop stage | Mean (± SE) | Lower 2.5% | Upper 2.5% |
| All predators | Tillering | 0.32a (± 0.029) | 0.27 | 0.38 |
|  | Flowering | 0.84b (± 0.016) | 0.81 | 0.87 |
|  | Ripening | 0.92c (± 0.013) | 0.90 | 0.95 |
| Spiders | Tillering | 0.35a (± 0.036) | 0.28 | 0.42 |
|  | Flowering | 0.82b (± 0.021) | 0.78 | 0.86 |
|  | Ripening | 0.89b (± 0.024) | 0.84 | 0.93 |
| Ladybeetles | Tillering | 0.82a (± 0.012) | 0.80 | 0.85 |
|  | Flowering | 0.85a (± 0.007) | 0.84 | 0.87 |
|  | Ripening | 0.94b (± 0.004) | 0.93 | 0.95 |

Diet_proportion.tiff

Figure 1. The proportions (mean ± SE) of prey sources (rice herbivores, tourist herbivores, detritivores) consumed in predators’ diet in organic and conventional rice farms over crop stages: (a) all predators as a whole feeding guild, (b) spiders, and (c) ladybeetles. The proportions are the posterior mean estimates from the Bayesian stable isotope mixing models averaged over all replicate farms and across three study years.

Rice_herb_consumption.tiff

Figure 2. The proportion of rice herbivores consumed in the diet of predators in organic and conventional rice farms over crop stages in the three study years: (a) all predators as a whole feeding guild, (b) spiders, and (c) ladybeetles. The proportions are the posterior mean estimates from the Bayesian stable isotope mixing models.

Rel_abd.tiff

Figure 3. The relative abundances of prey sources in organic and conventional rice farms over crop stages in the three study years. The relative abundances were determined from the sweep-net samples pooled across the replicate farms.

**Discussion**

To echo with the global demand for environmentally friendly practices in agriculture, we investigated the potential of GAPs as biocontrol agents in agro-ecosystems. Specifically, we used stable isotopes to examine the diet compositions of GAPs in organic and conventional rice farms during the crop season in three consecutive years. Our main results include the following: 1) Across the three study years, GAPs’ consumption on rice herbivores increased in both organic and conventional farms over the crop season, from 23-47% at the tillering stage to 79-95% at the ripening stage (Fig. 1a). The high percentage at the ripening stage indicates that GAPs could function as specialists in pest management when things matter (late crop stages). Interestingly, rice herbivore consumption by spiders increased gradually toward later crop season (Fig. 2b), whereas the consumption by ladybeetles remained stable throughout the season (Fig. 2c). 2) Our results revealed similar among-year patterns in rice herbivore consumption by GAPs in organic and conventional rice farms, suggesting a consistency in their feeding habits and biocontrol value (Fig. 2; Table 1). 3) The proportion of rice herbivores consumed in GAPs’ diet varied with farm types and crop stages (e.g., higher in conventional farms and flowering/ripening stages). However, contrary to previous studies, pest consumption by GAPs was not associated with surrounding landscape (e.g., percent forest cover) or the relative abundance of rice herbivores in the field (Table 1). We discuss in the following a) the within-season and among-year patterns in the diet compositions of GAPs, b) the effects of various abiotic and biotic factors on pest consumption by GAPs, and c) the potential caveats of this study. We finish by highlighting the implications of our results for agricultural management.

*Generalist predators function as specialists at late crop stages (or when things matter)*

As the world seeks to transform from synthetic pesticides to environmental-friendly practices in agriculture, biocontrol, a farming practice with a long history, has regained its significance as a promising solution. To address the concern of using GAPs as biocontrol agents (i.e., potentially switching diet between pests and alternative prey), this study quantified their diet compositions and revealed their high pest consumption at late crop stages consistently over three years of sampling. In other words, these generalist predators actually functioned as specialist predators of pests, providing strong support for their application in sustainable pest management. Specifically, across the three study years, GAPs in both organic and conventional farms consumed an increasing proportion of rice herbivores over the crop season, reaching over 79% in predators’ diet at the ripening stage, whereas the proportions of alternative prey (detritivores and tourist herbivores) in their diet gradually decreased to less than 21% at the ripening stage (Fig. 1; Appendix S1: Table S2). The increase in rice herbivore consumption over time suggests that the biocontrol potential of predators increases toward the late crop stages and peaks when things matter most to crop production. Note that generalist predators have been reported to opportunistically exploit a wide range of prey items 49-51 , yet our results from stable isotope analysis provide a novel aspect of their functional role—generalists in agro-ecosystem may become specialists during later crop season. This could be because of a higher herbivore (pest) density at late crop stages, and our analysis indeed suggested a significant correlation between rice herbivore consumption and crop stage (see the section *Factors associated with pest consumption by predators*).

While our generalist predators consumed a high proportion of pests at late crop stages, the two main predator groups in our study system, spiders and ladybeetles (Table S1), exhibited distinct dietary patterns over the crop season (Fig. 1; Fig. 2). Specifically, pest consumption by spiders increased substantially, but pest consumption by ladybeetles remained stable over the season (Fig. 2b vs. 2c). Such distinct patterns may be due to the difference in their foraging modes—sit-and-wait (spiders) vs. actively hunting (ladybeetles), which could largely affect prey capture and thus diet compositions 52-54. For example, long-jawed orb-weavers (Tetragnathidae), the most abundant family in our spider samples, are sit-and-wait predators and encounter prey in a passive manner. Therefore, its diet compositions may be associated with the relative abundances of the prey items in close proximity 52. This explanation is consistent with our findings that the proportions of different prey sources consumed in spiders’ diets corresponded to the relative abundances of these sources in the field (Fig. 1b; Fig. 3), although our later analysis suggested crop stage, instead of pest relative abundances, as a better predictor for pest consumption by predators (see the section for *Factors associated with pest consumption by predators*). In contrast, ladybeetles are actively hunting predators and may preferentially feed on rice herbivores, resulting in stable pest consumption over time (Fig. 1c; Fig. 2c; Fig. 3). Since predator foraging modes play a key role in mediating predator-prey-plant interactions 55, we suggest future studies examine different assemblages of sit-and-wait vs. actively hunting predators in field conditions to reveal the most efficient pest control practices over the whole crop season.

*Generalists exhibit consistent pest consumption patterns over years*

Ideal biocontrol agents provide consistent top-down control on pests under variable environmental conditions (abiotic and biotic factors). In our case, GAPs (both spiders and ladybeetles) showed consistent patterns in pest consumption across years (e.g., similar seasonal trends in pest consumption and high consumption at late crop stages in all three years) (Fig. 2), despite the variations in the environmental conditions during our study years (details below). This further suggests that GAPs can be a predictable, valuable tool for pest control in sustainable agriculture. Specifically, regarding the abiotic factors, the daily mean temperature, particularly during the early crop season (from April to June), varied substantially among years (Appendix S1: Fig. S2a). The daily precipitation patterns also fluctuated over the three study years, with multiple high precipitation events in 2017, overall low precipitation in 2018, and relatively even precipitation in 2019 (Appendix S1: Fig. S2b). Regarding the biotic factors, the compositions of rice herbivores at the flowering and ripening stage differed substantially among the three years, in particular the two most dominant groups: leafhoppers (Cicadellidae/*Nephotettix*) and planthoppers (Delphacidae/*Nilaparvata*) (Appendix S1: Table S3). Although abiotic and biotic factors varied substantially over years in our study, pest consumption by GAPs generally remained stable, different from studies where pest consumption by GAPs was largely influenced by abiotic or biotic factors 56,57. Our finding of this consistency in GAPs’ functional role suggests GAPs as a promising tool that agricultural practitioners can apply to pest management.

*Factors associated with pest consumption by predators*

The proportion of rice pest consumed in GAPs’ diets differed between farm types and among crop stages but was not associated with the percent forest cover surrounding the farms or the relative abundance of rice herbivores in the field (Table 1). Overall, GAPs in conventional farms consumed a higher proportion of rice pests in their diet compared with those in organic farms did (Table 2). One explanation is that organic farming may promote arthropod diversity in the farms and therefore distract predators from feeding on target species (e.g., pests) 19,30,58. Another possible explanation for the higher proportion of pest consumption by predators in conventional than organic farms is that pest densities may be higher in conventional farms 59, thus leading to higher encounter rates and consumption percentage of pests in predators’ diet. Regardless of the explanations and mechanisms, our results highlight the important but overlooked biocontrol value of GAPs in conventional farming systems.

Besides farming practice, crop stage affected pest consumption as well. Specifically, pest consumption by GAPs increased from early (tillering) to late (ripening) stage (Fig. 2; Table 3), consistent with previous studies where predators consumed increasing pests in their diet over the crop season 10,17. The underlying mechanism in our study may be related to the low pest density at early crop stage (Fig. 2). As a result, the proportion of pests consumed by predators was relatively low. However, through the development of rice plants, pest populations increased and predominated at the ripening stage (Fig. 2), leading to high pest consumption by predators during this period. These findings indicate a higher biocontrol value of predators during later crop season, when the crop production is most vulnerable to pest damage. Therefore, farm management (e.g., chemical applications) that could potentially harm predator populations should be minimized during later season to maintain healthy populations of predators and the associated ecosystem services in the field.

While habitat structure (e.g., surrounding vegetation) critically affects predator abundance and diversity, its effect on predators’ diet composition remains to be investigated. Habitat structure governs the trophic dynamics of terrestrial arthropods 27. For example, higher complexity in surrounding vegetation could promote the abundance and diversity of predators by facilitating access to various prey resources and providing refuge for predators to avoid intra-guild predation 26,60,61. Higher complexity in surrounding vegetation, however, does not seem to affect predators’ diet compositions, at least based on our results of the pest consumption by predators (Table 1). This might be because the prey species in our study system were mostly associated with rice plants, and therefore the nearby forest vegetation may not significantly alter prey availability to predators, in accordance with a meta-analysis study showing no changes in the densities of potential prey (e.g., crop herbivores) in agricultural fields in response to different levels of habitat complexity 60. Taken together, although vegetation itself may not directly affect predators’ diet compositions, increasing vegetation complexity could still benefit pest control through enhancing the density and diversity of predators, whose pest consumption remains relatively stable regardless of the surrounding vegetation.

Surprisingly, although the diet compositions of generalist predators are largely influenced by prey availability in the field 10,25,62, our beta regression model suggests that the relative abundance of rice herbivores in the farms had no effect on the proportion of these herbivores consumed in GAPs’ diet (Table 1). An explanation for this is that the relative abundance of rice herbivores was highly correlated with crop stage, which was also included as a factor in our model (Fig. 3). In fact, our model did reveal a significant effect of crop stage on pest consumption (Table 1). As a result, the relative abundance of rice herbivores appeared to have no effect since most of the variation may have been explained by crop stage, a broader factor that is associated with various covariates (e.g., rice plant height). To shed light on the potential mechanisms underlying the foraging patterns of predators, we encourage further experiments, both observational and manipulative, to clarify the link between prey availability and diet compositions of generalist predators in the field.

*Potential caveats of this study*

Our study demonstrates the high consumption of rice pests by GAPs in the field over three consecutive years and examines the factors that may influence GAPs’ dietary patterns, providing evidence for the biocontrol potential of these predators. Nonetheless, some potential caveats may exist. First, high consumption of rice pests in GAPs’ diet does not necessarily imply a strong suppression of pest populations in the farms, as the population dynamics of pests depend on not only the per capita effect of predators but also predator density and diversity in the field 46,63,64. The effectiveness of biocontrol should be realized in the context of pest density. Therefore, future work would require complementing stable isotope analysis with field observations of predator and pest populations to unveil the connection between the per capita pest consumption and the overall pest dynamics. Second, while some cases of intra-guild predation among predators impacted the pest control by GAPs 9,65, intra-guild predation was not accounted for in our diet composition analysis as it remains a challenge for stable isotope mixing models 10. We, however, argue that this may not be a major concern in our study for two reasons: a) Intra-guild predation pressure can be substantially relaxed with increasing habitat (vegetation) complexity 66,67. Such effect likely occurred in our study system, where the rice plants grew rapidly and formed dense clumps throughout the crop season; b) Intra-guild predation may only play a minor role in affecting predator-prey interaction in the field 68,69. That being said, we caution that our diet estimates of predators (without predator-predator interference) might not apply to systems where intra-guild predation prevails.

*Conclusions*

While biocontrol has been recognized as an important tool to reach sustainable agriculture, whether generalist predators can serve as effective biocontrol agents in pest management remains unclear. Our study helps solve this long-standing puzzle by quantifying the diet compositions of GAPs and identifying the underlying mechanisms for enemy-pest interactions in rice farms over three consecutive years. The results show a high proportion of rice pests in the diet of GAPs in both organic and conventional farms (e.g., 79-95% at the ripening stage), suggesting that these generalist predators function as “specialist predators” at late crop stages (when rice plants are fruiting and pests are abundant). The high pest consumption remains consistent across years regardless of climatic conditions, providing convincing evidence that generalist predators are capable of producing stable top-down effect on pests. As sustainable agriculture has become more important than ever in human history, incorporating generalist predators, which are ubiquitous in nature, into pest management will open a promising avenue towards this goal.

**Acknowledgement**

We thank Miaoli District Agricultural Research and Extension Station for providing field assistance and logistic support. This study was funded by Council of Agriculture, R.O.C. (project number)

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**Appendix S1**

**Table S1**. The taxonomic information and trophic guilds of the arthropod samples in the three study years.

(a) Year 2017

|  |  |  |
| --- | --- | --- |
| Trophic guild | Order | Family/Genus |
| Predators | Araneae | Araneidae |
|  | Araneae | Clubionidae |
|  | Araneae | Oxyopidae |
|  | Araneae | Tetragnathidae |
|  | Araneae | Thomisidae |
|  | Coleoptera | Carabidae |
|  | Coleoptera | Coccinellidae |
| Rice herbivores | Hemiptera | Cicadellidae/*Nephotettix* |
|  | Hemiptera | Delphacidae/*Nilaparvata* |
|  | Hemiptera | Lygaeidae/*Pachybrachius* |
|  | Hemiptera | Pentatomidae/*Scotinophara* |
|  | Lepidoptera | Hesperiidae |
|  | Lepidoptera | Pyralidae |
|  | Lepidoptera | Nymphalidae |
|  | Orthoptera | Pyrgomorphidae/*Atractomorpha* |
| Tourist herbivores | Coleoptera | Chrysomelidae |
|  | Orthoptera | Acrididae |
| Detritivores | Diptera | Chironomidae |
|  | Diptera | Chloropidae |
|  | Diptera | Ephydridae |
|  | Diptera | Muscidae |
|  | Diptera | Sphaeroceridae |
|  | Diptera | Stratiomyidae |
|  | Diptera | Tephritidae |
|  | Orthoptera | Tetrigidae |

(b) Year 2018

|  |  |  |
| --- | --- | --- |
| Trophic guild | Order | Family/Genus |
| Predators | Araneae | Araneidae |
|  | Araneae | Clubionidae |
|  | Araneae | Oxyopidae |
|  | Araneae | Tetragnathidae |
|  | Araneae | Thomisidae |
|  | Coleoptera | Coccinellidae |
| Rice herbivores | Hemiptera | Alydidae/*Leptocorisa* |
|  | Hemiptera | Cicadellidae/*Nephotettix* |
|  | Hemiptera | Delphacidae/*Nilaparvata* |
|  | Hemiptera | Lygaeidae/*Pachybrachius* |
|  | Hemiptera | Pentatomidae/*Scotinophara* |
|  | Lepidoptera | Hesperiidae |
|  | Lepidoptera | Pyralidae |
|  | Orthoptera | Pyrgomorphidae/*Atractomorpha* |
| Tourist herbivores | Coleoptera | Chrysomelidae |
|  | Orthoptera | Acrididae |
| Detritivores | Diptera | Chironomidae |
|  | Diptera | Chloropidae |
|  | Diptera | Ephydridae |
|  | Diptera | Muscidae |
|  | Diptera | Sciomyzidae |
|  | Diptera | Stratiomyidae |
|  | Orthoptera | Tetrigidae |

(c) Year 2019

|  |  |  |
| --- | --- | --- |
| Trophic guild | Order | Family/Genus |
| Predators | Araneae | Araneidae |
|  | Araneae | Clubionidae |
|  | Araneae | Oxyopidae |
|  | Araneae | Tetragnathidae |
|  | Araneae | Thomisidae |
|  | Coleoptera | Coccinellidae |
| Rice herbivores | Diptera | Agromyzidae |
|  | Hemiptera | Alydidae/*Leptocorisa* |
|  | Hemiptera | Cicadellidae/*Nephotettix* |
|  | Hemiptera | Coreidae |
|  | Hemiptera | Delphacidae/*Nilaparvata* |
|  | Hemiptera | Lygaeidae/*Pachybrachius* |
|  | Hemiptera | Miridae |
|  | Hemiptera | Pentatomidae/*Scotinophara* |
|  | Hemiptera | Ricaniidae |
|  | Lepidoptera | Hesperiidae |
|  | Lepidoptera | Nymphalidae |
|  | Lepidoptera | Pyralidae |
|  | Orthoptera | Pyrgomorphidae/*Atractomorpha* |
| Tourist herbivores | Coleoptera | Chrysomelidae |
|  | Orthoptera | Acrididae |
| Detritivores | Diptera | Calliphoridae |
|  | Diptera | Chironomidae |
|  | Diptera | Chloropidae |
|  | Diptera | Ephydridae |
|  | Diptera | Lauxaniidae |
|  | Diptera | Muscidae |
|  | Diptera | Phoridae |
|  | Diptera | Platystomatidae |
|  | Diptera | Sarcophagidae |
|  | Diptera | Sciomyzidae |
|  | Diptera | Sphaeroceridae |
|  | Diptera | Stratiomyidae |
|  | Diptera | Tephritidae |
|  | Orthoptera | Tetrigidae |
|  | Orthoptera | Tridactylidae |

**Table S2.** The proportions (mean ± SE) of prey sources (rice herbivores, tourist herbivores, detritivores) consumed in predators’ diet in organic and conventional rice farms over crop stages in each study year. *n* represents the number of replicate farms for the diet estimation. (Note that the differences in *n* within the same study year were due to the absence of predators in the sweep-net samples in some replicate farms.)

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Year | Farm type | Crop stage | Predator | Source | | | *n* |
| Rice herbivore | Tourist herbivore | Detritivore |
| 2017 | Organic | Tillering | All | 0.27 ± 0.08 | 0.19 ± 0.05 | 0.54 ± 0.12 | 3 |
|  |  |  | Spider | 0.21 ± 0.13 | 0.33 ± 0.16 | 0.46 ± 0.18 | 3 |
|  |  |  | Ladybeetle | 0.74 | 0.09 | 0.17 | 1 |
|  |  | Flowering | All | 0.82 ± 0.04 | 0.13 ± 0.04 | 0.05 ± 0.03 | 3 |
|  |  |  | Spider | 0.69 ± 0.15 | 0.25 ± 0.15 | 0.06 ± 0.04 | 3 |
|  |  |  | Ladybeetle | 0.79 | 0.09 | 0.12 | 1 |
|  |  | Ripening | All | 0.92 ± 0.02 | 0.07 ± 0.02 | 0.02 ± 0.01 | 3 |
|  |  |  | Spider | 0.78 ± 0.12 | 0.19 ± 0.12 | 0.03 ± 0.02 | 3 |
|  |  |  | Ladybeetle | 0.93 ± 0.01 | 0.04 ± 0.01 | 0.03 ± 0.01 | 3 |
|  | Conventional | Tillering | All | 0.23 ± 0.01 | 0.17 ± 0.05 | 0.59 ± 0.05 | 3 |
|  |  |  | Spider | 0.25 ± 0.01 | 0.2 ± 0.06 | 0.55 ± 0.08 | 3 |
|  |  |  | Ladybeetle | 0.80 | 0.08 | 0.12 | 1 |
|  |  | Flowering | All | 0.83 ± 0.03 | 0.12 ± 0.03 | 0.05 ± 0.01 | 3 |
|  |  |  | Spider | 0.85 ± 0.02 | 0.11 ± 0.03 | 0.04 ± 0.01 | 3 |
|  |  |  | Ladybeetle | 0.88 ± 0.02 | 0.06 ± 0.01 | 0.06 ± 0.01 | 2 |
|  |  | Ripening | All | 0.92 ± 0.02 | 0.06 ± 0.02 | 0.02 ± 0.01 | 3 |
|  |  |  | Spider | 0.91 ± 0.01 | 0.07 ± 0.02 | 0.02 ± 0.01 | 3 |
|  |  |  | Ladybeetle | 0.95 ± 0.01 | 0.04 ± 0.01 | 0.02 ± 0.01 | 2 |
| 2018 | Organic | Tillering | All | 0.23 ± 0.03 | 0.22 ± 0.05 | 0.55 ± 0.06 | 7 |
|  |  |  | Spider | 0.20 ± 0.02 | 0.28 ± 0.07 | 0.52 ± 0.07 | 7 |
|  |  |  | Ladybeetle | 0.81 ± 0.02 | 0.08 ± 0.01 | 0.11 ± 0.01 | 6 |
|  |  | Flowering | All | 0.75 ± 0.04 | 0.17 ± 0.04 | 0.07 ± 0.02 | 6 |
|  |  |  | Spider | 0.73 ± 0.07 | 0.20 ± 0.07 | 0.08 ± 0.04 | 5 |
|  |  |  | Ladybeetle | 0.82 ± 0.01 | 0.09 ± 0.01 | 0.09 ± 0.01 | 3 |
|  |  | Ripening | All | 0.92 ± 0.02 | 0.05 ± 0.01 | 0.02 ± 0.01 | 5 |
|  |  |  | Spider | 0.85 ± 0.04 | 0.11 ± 0.03 | 0.05 ± 0.03 | 4 |
|  |  |  | Ladybeetle | 0.94 ± 0.01 | 0.04 ± 0.01 | 0.02 ± 0.01 | 5 |
|  | Conventional | Tillering | All | 0.47 ± 0.07 | 0.15 ± 0.02 | 0.38 ± 0.05 | 7 |
|  |  |  | Spider | 0.48 ± 0.10 | 0.19 ± 0.03 | 0.33 ± 0.08 | 7 |
|  |  |  | Ladybeetle | 0.83 ± 0.02 | 0.07 ± 0.01 | 0.10 ± 0.01 | 4 |
|  |  | Flowering | All | 0.90 ± 0.03 | 0.07 ± 0.02 | 0.02 ± 0.01 | 6 |
|  |  |  | Spider | 0.87 ± 0.06 | 0.10 ± 0.04 | 0.03 ± 0.02 | 6 |
|  |  |  | Ladybeetle | 0.86 ± 0.03 | 0.07 ± 0.01 | 0.07 ± 0.02 | 2 |
|  |  | Ripening | All | 0.95 ± 0.01 | 0.04 ± 0.01 | 0.01 ± 0.01 | 7 |
|  |  |  | Spider | 0.93 ± 0.05 | 0.06 ± 0.04 | 0.01 ± 0.01 | 2 |
|  |  |  | Ladybeetle | 0.94 ± 0.01 | 0.04 ± 0.01 | 0.02 ± 0.01 | 5 |
| 2019 | Organic | Tillering | All | 0.25 ± 0.08 | 0.19 ± 0.06 | 0.55 ± 0.06 | 7 |
|  |  |  | Spider | 0.31 ± 0.10 | 0.15 ± 0.06 | 0.54 ± 0.09 | 7 |
|  |  |  | Ladybeetle | 0.85 ± 0.04 | 0.08 ± 0.01 | 0.07 ± 0.03 | 3 |
|  |  | Flowering | All | 0.74 ± 0.12 | 0.20 ± 0.11 | 0.06 ± 0.01 | 7 |
|  |  |  | Spider | 0.77 ± 0.15 | 0.18 ± 0.14 | 0.05 ± 0.02 | 6 |
|  |  |  | Ladybeetle | 0.87 ± 0.02 | 0.07 ± 0.01 | 0.06 ± 0.02 | 3 |
|  |  | Ripening | All | 0.79 ± 0.16 | 0.19 ± 0.16 | 0.02 ± 0.01 | 5 |
|  |  |  | Spider | 0.78 ± 0.17 | 0.19 ± 0.16 | 0.03 ± 0.01 | 5 |
|  |  |  | Ladybeetle | 0.94 ± 0.01 | 0.04 ± 0.01 | 0.02 ± 0.01 | 5 |
|  | Conventional | Tillering | All | 0.37 ± 0.04 | 0.17 ± 0.04 | 0.46 ± 0.06 | 7 |
|  |  |  | Spider | 0.41 ± 0.06 | 0.17 ± 0.05 | 0.42 ± 0.08 | 7 |
|  |  |  | Ladybeetle | 0.84 ± 0.01 | 0.07 ± 0.01 | 0.09 ± 0.01 | 2 |
|  |  | Flowering | All | 0.89 ± 0.02 | 0.08 ± 0.02 | 0.03 ± 0.01 | 7 |
|  |  |  | Spider | 0.91 ± 0.02 | 0.06 ± 0.02 | 0.02 ± 0.01 | 7 |
|  |  |  | Ladybeetle | 0.89 ± 0.01 | 0.06 ± 0.01 | 0.05 ± 0.01 | 6 |
|  |  | Ripening | All | 0.95 ± 0.01 | 0.05 ± 0.01 | 0.01 ± 0.01 | 5 |
|  |  |  | Spider | 0.94 ± 0.02 | 0.05 ± 0.02 | 0.01 ± 0.01 | 5 |
|  |  |  | Ladybeetle | 0.95 ± 0.01 | 0.04 ± 0.01 | 0.02 ± 0.01 | 3 |

**Table S3.** The relative abundances of the major families/genera in rice herbivore guild at the flowering and ripening stage in the three study years. Samples were pooled across the replicate farms.

(a) Flowering stage

|  |  |  |  |
| --- | --- | --- | --- |
| Family/Genus | Year 2017 | Year 2018 | Year 2019 |
| Cicadellidae/*Nephotettix* | 7.6% | 22.5% | 69.7% |
| Delphacidae/*Nilaparvata* | 88.2% | 71.9% | 25.4% |
| Lygaeidae/*Pachybrachius* | *NA* | 0.8% | 1.3% |
| Pentatomidae/*Scotinophara* | 0.8% | 2.9% | 0.8% |
| Others | 3.4% | 1.9% | 2.8% |
| *Total* | 100% | 100% | 100% |

(b) Ripening stage

|  |  |  |  |
| --- | --- | --- | --- |
| Family/Genus | Year 2017 | Year 2018 | Year 2019 |
| Cicadellidae/*Nephotettix* | 69.4% | 74.9% | 83.5% |
| Delphacidae/*Nilaparvata* | 28.9% | 13.4% | 6.2% |
| Lygaeidae/*Pachybrachius* | *NA* | 0.2% | 4.1% |
| Pentatomidae/*Scotinophara* | 1.7% | 10.4% | 4.5% |
| Others | *NA* | 1.1% | 1.7% |
| *Total* | 100% | 100% | 100% |

Diet_proportion_2017.tiff Diet_proportion_2018.tiffDiet_proportion_2019.tiff

**Figure S1**. The proportions (mean ± SE) of prey sources (rice herbivores, tourist herbivores, detritivores) consumed in the diet of predators in organic and conventional rice farms over crop stages in each study year: (a), (d), (g) all predators as a whole feeding guild; (b), (e), (h) spiders; (c), (f), (i) ladybeetles. The proportions are the posterior mean estimates from the Bayesian stable isotope mixing models averaged over the replicate farms.

**weather.tiff**

**Figure S2.** Daily mean temperature and precipitation of the study sites during the first rice growth season (April to July) in the three study years. Observation data from the closest local weather station (Yuanli station) to the study farms were retrieved from Central Weather Bureau Observation Data Inquire System (https://e-service.cwb.gov.tw/HistoryDataQuery/index.jsp).