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Pest consumption by generalist arthropod predators increases with crop stage in both organic and conventional farms

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Abstract. Biocontrol agents are critical for pest management in sustainable agriculture. Generalist arthropod predators may hold a great potential as biocontrol agents because they are ubiquitous and consume pests in agroecosystems. However, their diet composition over the entire crop season has rarely been quantified, which hinders our ability to assess their biocontrol potential in real field conditions that foster temporal dynamics of pest and alternative prey populations. To fill this knowledge gap, we surveyed arthropod communities over crop stages in organic and conventional rice farms (n = 7 each) and used stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) to quantify the diet composition of generalist arthropod predators over time. We aimed to (1) examine the resource partitioning (trophic niches) in these predators, (2) quantify these predators' diet composition from potential prey sources (rice herbivores, tourist herbivores, and detritivores), and (3) investigate the effects of farm type (organic/conventional) and crop stage (tillering/flowering/ripening stage) on pest (rice herbivore) consumption by the predators. The results show that generalist predators in both organic and conventional farms shifted trophic niches over the crop season and consumed a higher percentage of rice herbivores at late than at early crop stages (e.g., 90–93% at ripening vs. 34–55% at tillering), suggesting an increasing biocontrol value over time regardless of farm type. Surprisingly, generalist predators consumed higher proportions of rice herbivores in conventional than organic farms at tillering and flowering stages, highlighting their underappreciated potential as biocontrol agents in conventional farms. These results demonstrate that although generalist arthropod predators do consume non-pest alternative prey, they have a high biocontrol potential (per capita pest consumption) in both organic and conventional rice farms. We encourage modern agriculture to develop techniques to support robust populations of these predators and the ecosystem services that they provide.

Key words: arthropod community; biocontrol; crop stage; detritivores; diet composition; generalist predators; organic and conventional farms; predator–prey interactions; rice herbivores; rice paddy; stable isotope analysis; trophic interactions.

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Introduction

The use of natural arthropod enemies to control pests is an essential component of biocontrol programs and sustainable agriculture (Obrycki and Kring 1998, Kromp 1999, Symondson et al. 2002, Wezel et al. 2014, Hand 2016, Ali et al. 2019, Snyder 2019, Wojtkowski 2019). Natural enemies include specialists and generalists. While specialists (e.g., parasitoids) often receive attention because of their high specificity in regulating pest populations (Hågvar and Hofsvang 1991, Hoy and Nguyen 2001, Flores and Ciomperlik 2017), generalists (e.g., arthropod predators) may also have the capacity to control various pests. For example, generalist predators have reportedly reduced the populations of diverse pest species in agricultural fields (Riechert and Lockley 1984, Obrycki and Kring 1998, Sunderland 1999, Stiling and Cornelissen 2005, Michalko et al. 2019*a*, Mabin et al. 2020), and their removal has been shown to cause a 13-fold surge in the pest populations of rice farms (Kenmore et al. 1984). Generalist predators are ubiquitous in nature and capable of producing consistent top-down control on various prey species (Schmitz et al. 2000, Halaj and Wise 2001, Porcel et al. 2018), and therefore, they may possess great potential as biocontrol agents, by either acting alone or complementing specialists (Murdoch et al. 1985, Sunderland 1999, Symondson et al. 2002, Stiling and Cornelissen 2005).

To realize the full potential of generalist predators as biocontrol agents in agricultural systems, it is necessary to first quantify their diet composition under field conditions. This necessity arises from the concern that generalist predators feed on not only target species (e.g., herbivorous pests) but also alternative prey (e.g., detritivores) in the field (Symondson et al. 2002, Krey et al. 2017, Michalko et al. 2019*b*). Therefore, the biocontrol potential of generalist predators may be affected by the presence of alternative prey, either positively or negatively. For example, on the one hand, alternative prey could support higher densities of predators early in the crop season when pest populations are low, which could facilitate pest control later in the season when pests become abundant (Settle et al. 1996, Muñoz-Cárdenas et al. 2017, Roubinet et al. 2017); on the other hand, alternative prey may disrupt biocontrol if these predators exhibit a stronger preference for the alternative prey (Musser and Shelton 2003, Koss and Snyder 2005, Birkhofer et al. 2008*b*).

The aforementioned context dependency suggests that biocontrol by generalist predators likely depends on the temporal dynamics of pest and alternative prey populations. Although a small number of studies have examined the diet composition of generalist predators in agroecosystems (Birkhofer et al. 2011, Roubinet et al. 2018, Jacobsen et al. 2019), it remains unclear how these diet compositions may vary temporally in response to prey population dynamics during the crop growing season. This knowledge gap hinders our ability to assess the biocontrol potential of generalist predators in agricultural systems, which typically exhibit large temporal variations in species composition (e.g., predators, herbivores, and detritivores) in response to crop growth and disturbance (e.g., management practice). For example, different arthropod trophic guilds tend to peak at different stages of rice growth (Schoenly et al. 1996, Settle et al. 1996). This temporal variation will likely influence pest consumption by predators. Therefore, quantifying the diet composition of predators over the course of the crop season should provide important insights for biocontrol applications.

Besides temporal variations in prey populations, the farm type (e.g., organic vs. conventional) could also affect biocontrol by generalist predators. In an effort to reduce the environmental impacts of agriculture, organic farming has seen tremendous growth in recent years (Reganold and Wachter 2016). While organic farming may promote the abundance and diversity of predators (e.g., Bengtsson et al. 2005, Porcel et al. 2018), its effects on the biocontrol efficacy of predators remain to be addressed, with both positive and non-significant results reported (e.g., Crowder et al. 2010, Birkhofer et al. 2016, Porcel et al. 2018). Although previous studies have examined pest population responses to experimental manipulations of predators in organic and conventional farms, they typically used confined settings (e.g., a fixed number of predators in cage experiments; Crowder et al. 2010, Porcel et al. 2018), which may not reflect the seasonal variations in predator–pest populations and interactions in the field. Moreover, confined settings may increase the encounter rates of predators and prey, leading to biased biocontrol results (Sih et al. 1985). Therefore, investigating pest consumption by predators under natural conditions, which was achieved through using stable isotope analysis in this study, should help clarify the potential of generalist predators as biocontrol agents in organic and conventional farms.

To understand the biocontrol potential of generalist arthropod predators (e.g., per capita pest consumption) in agroecosystems, this study examined the diet composition of these predators in organic and conventional rice farms during the crop season. Specifically, we (1) examined resource partitioning (trophic niches) in generalist arthropod predators, (2) quantified the diet composition of predators concerning potential prey sources (rice herbivores, tourist herbivores, and detritivores), and (3) investigated the effects of farm type and crop stage on pest (rice herbivore) consumption by predators. We sampled arthropod prey and generalist predators from seven sub-tropical organic and seven conventional rice farms at the seedling, tillering, flowering, and ripening stages in Miaoli County, Taiwan, in 2018. Stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$), a common method used to determine the diet composition of focal species (Post 2002, Birkhofer et al. 2011, Boecklen et al. 2011, Layman et al. 2012), was applied to infer trophic interactions and estimate pest consumption by predators (i.e., proportional contribution of rice herbivores to predators' diet) in the field. This approach provides time-integrated dietary information concerning predator–prey trophic interactions, which may not be revealed by conventional snapshot techniques (e.g., field observations and gut–content analysis; Post 2002, Boecklen et al. 2011, Newton 2016).

Materials and Methods

Arthropod sampling

We selected seven organic and seven conventional rice farms within the same landscape context in Miaoli County, Taiwan (Fig. 1). These farms were typical rice farms in Taiwan, had a mean area of 0.2 ± 0.1 hectares (mean ± standard deviation), and were irrigated with similar quality of surface water (Y.-P. Lin et al. *unpublished data*). Synthetic nitrogen fertilizers (2–3 applications/crop season) and organophosphate pesticides (1 application/crop season) were used in conventional farms. Organic fertilizers (e.g., manure; 2–3 applications/crop season) and natural pesticides (e.g., tea saponins; one application/crop season) were used in organic farms. For each of the 14 farms, we sweep-netted terrestrial arthropods 60 times along the ridges of the farm at each of the four major crop stages (seedling, tillering, flowering, and ripening) during the growing season from April to July of 2018. Samples were bagged, iced, and stored without chemical preservatives (e.g., ethanol) at −20°C in the laboratory. Arthropods were then identified to the finest taxonomic resolution possible under a dissecting scope. Major arthropod families and genera are provided in Appendix S1: Table S1.

Preparation for stable isotope analysis

Whole-body arthropods were oven-dried at 50°C for one week, pulverized, and weighed into tin capsules (5 × 9 mm). When necessary, several individuals were pooled into a single capsule to meet the minimum weight requirement (0.5 mg) for reliable results. Capsules were sent to the UC Davis Stable Isotope Facility for analysis of ^{13}C and ^{15}N using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (SerCon, Cheshire, UK). The resulting isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) were expressed in per mil (‰) relative to the international standards of Vienna PeeDee Belemnite and atmospheric N_2 for carbon and nitrogen, respectively. The sample size for stable isotope analysis was summarized in Appendix S1: Table S4.

Determination of trophic guilds

This study adopted the concept of trophic guilds to understand community-level trophic dynamics in rice agroecosystems. Trophic guilds are aggregations of species that utilize similar dietary sources (i.e., occupy similar trophic niches) and constitute the basic components of food webs (Root 1967, Hawkins and Macmahon 1989), and they can represent distinct functional groups in communities by condensing arthropod taxonomic information (Dominik et al. 2018). We first assigned spiders (Araneidae, Clubionidae, Oxyopidae, Tetragnathidae, Thomisidae) and ladybugs (Coccinellidae) into the predator guild, which represents the primary generalist arthropod predators inhabiting rice farms. To determine prey sources, we performed *k*-means clustering ($k = 3$) with Euclidean distance on stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) to classify the prey samples into one of the following three guilds: rice herbivore, tourist herbivore, and detritivore, according to a previous study that has identified these prey guilds in rice farms (Dominik et al. 2018). The resulting clusters were then examined to ensure that prey samples were assigned to ecologically meaningful clusters. Rice herbivores consisted of major rice pests; tourist

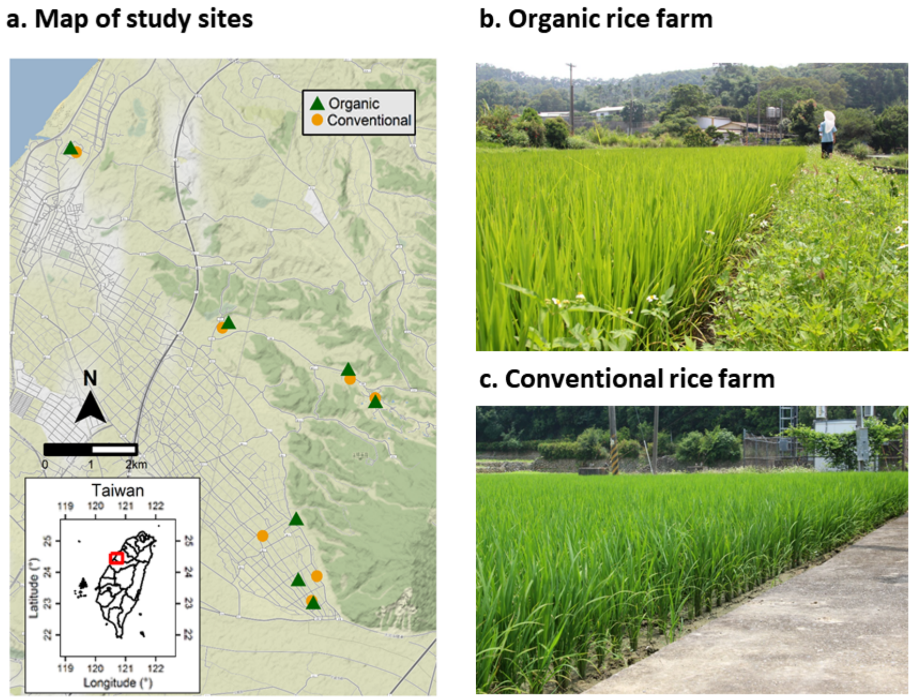

Fig. 1. (a) Map of study sites and examples of (b) organic and (c) conventional rice farms.

herbivores (Moran and Southwood 1982) consisted of herbivorous species with no direct trophic association with rice plants; and detritivores consisted of arthropods that feed on decaying organic material or plankton (Settle et al. 1996). The relative abundances of each prey guild in the sweep net samples were also determined (Fig. 3b). Because this study focused on generalist predators and their potential prey resources, we did not consider other trophic guilds (e.g., parasitoids). Detailed information on guild assignment of arthropod families is provided in Appendix S1: Table S1.

Predators' trophic niche

Trophic niche in this study is defined as the distribution of isotope signatures in δ-space occupied by a given group of organisms (Newsome et al. 2007). This definition consists of two niche aspects: (1) niche position, which is measured as the centroid of isotope signature distribution and represents the average resource use by a group of organisms, and (2) niche breadth, which is measured as the multivariate dispersion of isotope signature distribution and represents within-group variation in resource use. To examine whether predators' trophic niches (position and breadth) differed between farm types and among crop stages, we performed PERMANOVA (Anderson 2001) with farm type, crop stage, and their interaction as fixed effects. This statistical technique provides a flexible and robust way to test for multivariate differences in community structure (Anderson and Walsh 2013). A significant PERMANOVA result indicates that either the centroids (niche position) and/or dispersions (niche breadth) are different among groups. Therefore, in this case, PERMDISP (Anderson 2004) was performed to specifically test for the differences in multivariate dispersions (niche breadth). PERMANOVA and PERMDISP were conducted using the adonis and betadisper functions, respectively, in the vegan package (Oksanen et al. 2013).

Predators' diet composition

We constructed a Bayesian stable isotope mixing model using the MixSIAR package (Stock and Semmens 2016) to quantify predators' diet composition from potential prey sources (i.e., the three prey guilds including rice herbivores, tourist herbivores, and detritivores). Given that our prey sources had distinct isotope signatures (Appendix S1: Fig. S1), stable isotope mixing models serve as a robust tool for estimating the relative contribution of each source to predators' diet (Layman et al. 2012). In addition, after correcting for trophic discrimination factors (TDFs), the mean isotope signature of predators in δ-space fell within the polygon defined by the three prey sources, justifying the use of a mixing model to estimate the proportional contribution of each source to the predator's diet. For the predator data, individual farm and crop stage were treated as fixed effects in the mixing model (interaction term not included due to the limitation of MixSIAR). Since predator samples at the seedling stage were not sufficient for diet estimation, the model included predator data only from tillering, flowering, and ripening stages. For the prey data, samples across farms and stages were pooled to generate fixed source values. We incorporated concentration dependencies for both carbon and nitrogen, as well as residual error and process error to improve model estimates (Phillips and Koch 2002, Stock and Semmens 2016). TDFs were estimated from the diet-dependent discrimination equation proposed by Caut et al. (2009; Appendix S1: Table S2). We ran three Markov chain Monte Carlo (MCMC) chains, each with 50,000 iterations and a burn-in number of 25,000 (short option in MixSIAR) using a non-informative Dirichlet prior. Model diagnostics (Gelman-Rubin test and Geweke test) were performed to ensure chain convergence. Bayesian posterior mean estimates of each individual farm-crop stage combination were extracted for further analysis.

Effects of farm type and crop stage on rice herbivore consumption

Since rice herbivores are a primary concern for farmers, we further examined how farm type and crop stage affect rice herbivore consumption by predators. The taxonomy and abundance of our predators and major rice herbivores are provided in Appendix S1: Table S3. We fit a beta regression model with farm type, crop stage, and their interaction as fixed effects and rice herbivore consumption (i.e., proportional contribution of rice herbivores to predators' diet) as the response variable using the betareg package (Zeileis et al. 2018). Model parameters were estimated by maximum likelihood. A scatterplot of standardized residuals against standardized predicted values was used to confirm the homogeneity of variance. Because the interaction between farm type and crop stage was non-significant, we then analyzed the model with type II ANOVA using the Anova function in the car package (Fox and Weisberg 2018). For significant effects ($\alpha = 0.05$), we conducted Tukey's post hoc tests for all pairwise comparisons of rice herbivore consumption using the cld function in the emmeans package (Lenth et al. 2017). Finally, we examined whether rice herbivore consumption is associated with background rice herbivore density by fitting another beta regression model, including rice herbivore consumption as a response variable and the relative abundance of rice herbivores as an explanatory variable. All analyses were performed using R (R Core Team 2018).

Results

Predators' trophic niche

Trophic niches (consisting of niche position and niche breadth) of generalist arthropod predators varied with farm type (PERMANOVA $F_{1,97} = 5.83$, $P = 0.008$; Fig. 2a) and crop stage (PERMANOVA $F_{2,97} = 15.06$, $P < 0.001$; Fig. 2b). Regarding trophic niche position, the centroids of the predators' isotope signatures in the δ-space shifted progressively from the upper-right corner at the tillering stage (higher $\delta^{13}C$ and $\delta^{15}N$) to the lower-left corner at the ripening stage (lower $\delta^{13}C$ and $\delta^{15}N$) regardless of farm type (Fig. 2b). This temporal change in predators' trophic niche position indicated a progressive switch in prey items, such as from detritivores and tourist herbivores to rice herbivores (Appendix S1: Fig. S1). Regarding trophic niche breadth, PERMDISP revealed a difference in multivariate dispersions between farm types (PERMDISP $F_{1,101} = 4.37$, $P = 0.04$) but not among crop stages (PERMDISP $F_{2,100} = 0.01$, $P = 0.994$). Mean distance-to-centroids were $2.64 \pm 1.38‰$ and $2.13 \pm 1.05‰$ (mean ± standard deviation) for organic and conventional farms, respectively, suggesting broader trophic niches of predators in organic farms compared with those in conventional farms (Welch two-sample t test, $t_{95} = 2.10$, $P = 0.04$; Fig. 2a).

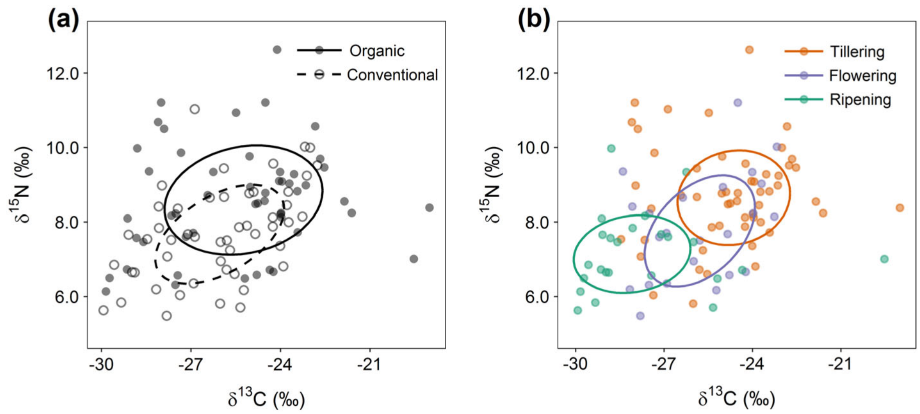

Fig. 2. Predators' trophic niches ($\delta^{13}C$ and $\delta^{15}N$) in (a) organic and conventional farms (crop stages pooled) and at (b) different crop stages (farm types pooled). Note that predators at the seedling stage were omitted due to insufficient sample sizes. Each point represents a capsule sample containing one to five predator individuals, depending on predator body mass. The ovals show a 50% standard ellipse area (SEA). Statistical analyses indicated that the predator's trophic niche position (centroid) varied with farm type and crop stage, while trophic niche breadth (dispersion) varied with farm type only (details in *Results*).

Predators' diet composition

A further analysis using Bayesian stable isotope mixing model revealed dietary shifts of predators over crop stages. Overall, predators in both organic and conventional farms consumed proportionally more rice herbivores but fewer tourist herbivores and detritivores over the course of the crop season, resulting in a predominance of rice herbivores in predators' diet at later crop stages (Fig. 3a). Specifically, from tillering to ripening stage, rice herbivores in predators' diets increased from 34% to 90% in organic farms and from 55% to 93% in conventional farms; tourist herbivores decreased from 27% to 5% in organic farms and from 18% to 5% in conventional farms; detritivores decreased from 39% to 5% in organic farms and from 26% to 2% in conventional farms (Fig. 3a; Appendix S1: Table S4).

Effects of farm type and crop stage on rice herbivore consumption

We fitted a beta regression model to examine the effects of farm type and crop stage on predator consumption on rice herbivores, a primary concern of farmers. Two-way ANOVA indicated that farm type ($\chi^2_1 = 24.68$, $P < 0.001$) and crop stage ($\chi^2_2 = 112.95$, $P < 0.001$), but not their interaction ($\chi^2_2 = 1.85$, $P = 0.40$), affected rice herbivore consumption. Specifically, predators consumed higher proportions of rice herbivores in conventional than organic farms, especially at tillering and flowering stages (Fig. 4). In addition, predators' consumption of rice herbivores increased over crop stages regardless of farm type (Fig. 4).

Discussion

To understand the biocontrol potential of generalist arthropod predators in agroecosystems, we conducted field surveys and stable isotope analysis to examine the diet composition of these predators in organic and conventional rice farms over the course of the crop season. Our results showed that, as the crop season progressed, generalist predators exhibited a switch in trophic niches (Fig. 2b), consuming increasing proportions of rice herbivores compared to other prey items (Fig. 3a). This resulted in a predominance of rice herbivores in the diet of generalist predators (~90%) at later crop stages in both organic and conventional farms. This highlights the potential of generalist arthropod predators as biocontrol agents in rice agroecosystems, regardless of farm type. In addition, our results showed that predators in conventional farms were able to consume higher proportions of rice herbivores in their diet compared with those in organic farms, especially at the tillering and flowering stages.

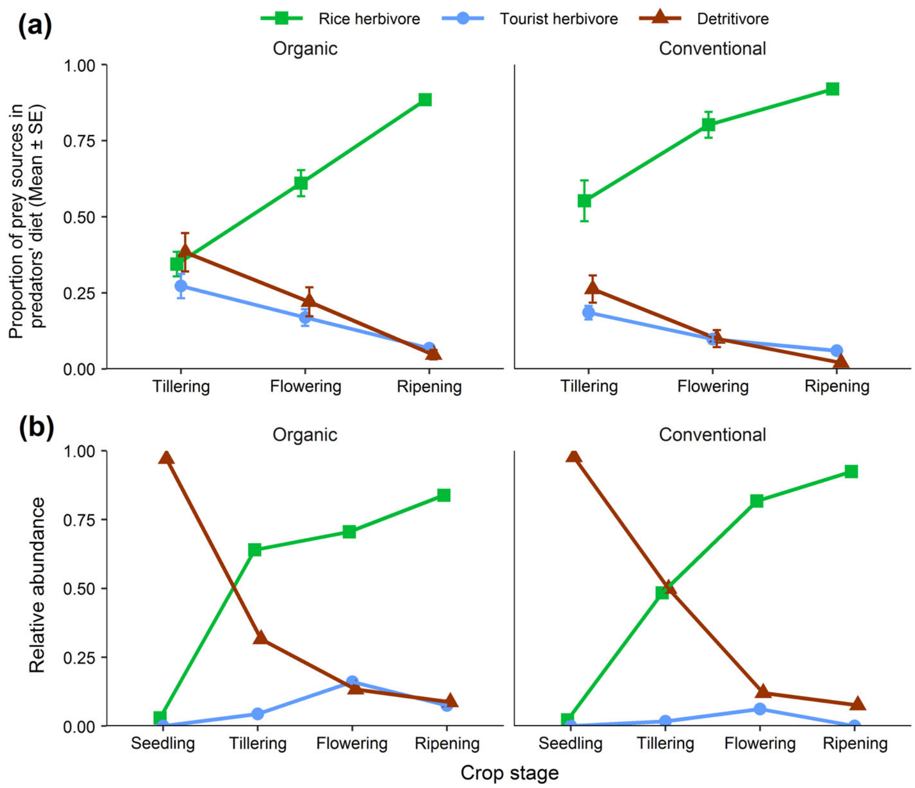

Fig. 3. (a) Predators' diet composition in organic and conventional farms over crop stages. The proportions of different prey sources in predators' diet were estimated using a Bayesian stable isotope mixing model, and the means and SEs were computed from the Bayesian posterior means of replicate farms. Due to insufficient sample sizes, there was no diet estimation at the seedling stage. (b) Relative abundances of prey sources in organic and conventional farms over crop stages based on our sweep net samples. Samples within each farm type (organic vs. conventional) were pooled and relative abundances were calculated as the proportion of each prey source to the total abundance of all prey sources.

This surprising finding reveals the underappreciated potential of generalist arthropod predators as biocontrol agents in conventional farms. Based on these results, we discuss (1) the biocontrol value of generalist arthropod predators in rice agroecosystems, (2) the effect of alternative prey on biocontrol, (3) the effect of farm type on biocontrol, and (4) the caveats of this study. We conclude by considering the implications of this study for agricultural management.

Biocontrol value of predators in rice agroecosystems

Despite large temporal variations in the species composition of agricultural systems (Schoenly et al. 1996, Settle et al. 1996), quantitative studies concerning the diet composition of generalist predators (e.g., pest vs. alternative prey) over the course of the crop season have been lacking, which has hindered our understanding of these predators as biocontrol agents. Based on stable isotope analysis, this study shows that generalist arthropod predators in both organic and conventional farms consumed high average proportions of rice herbivores (Fig. 3a). This result provides evidence for a strong per capita effect of predators on pests (i.e., high pest consumption by predators) regardless of farm type, highlighting the valuable potential of generalist predators as biocontrol agents in rice agroecosystems. Moreover, pest consumption by predators increased as the crop stages progressed (Fig. 3a), suggesting an increasing per capita effect of predators on pests over the crop season.

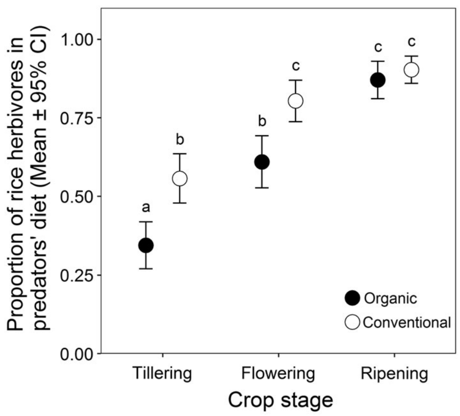

Fig. 4. Rice herbivore consumption by predators in organic and conventional farms over crop stages. The means were computed from the Bayesian posterior means of replicate farms; error bars represent Tukey's adjusted 95% confidence intervals. Different letters indicate statistical significance ($P < 0.05$).

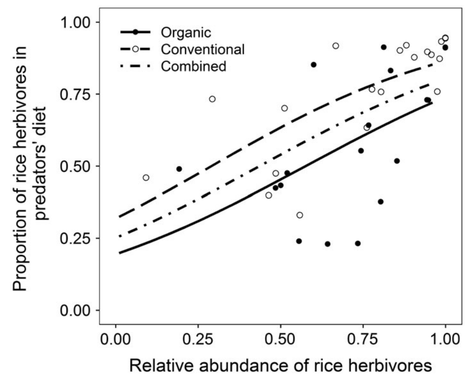

Fig. 5. Scatterplot showing the relationship between rice herbivore consumption by predators and relative abundance of rice herbivores. Points represent predators' consumption for each individual farm-crop stage combination. The lines were fitted with beta regression models individually for organic (solid line, $Z = 2.52$, $P = 0.01$), conventional (dashed line, $Z = 4.60$, $P < 0.001$), and both farms combined (dot-dashed line, $Z = 4.41$, $P < 0.001$).

In contrast to previous studies based on snapshot observations or experimental manipulations of certain predator taxa (Birkhofer et al. 2008*a*), our stable isotope approach over the crop season reveals temporal variation in predators' biocontrol roles under natural conditions. Namely, generalist predators consumed higher proportions of pest species at later crop stages (Figs. 3a, 4). This may be due to the feeding behavior of generalist predators, whose diet composition depends on the availability of prey items (Kiritani et al. 1972, Nyffeler 1999). In our study sites, the relative abundance of rice herbivores increased as the crop developed, whereas that of tourist herbivores and detritivores decreased (Fig. 3b). Accordingly, the predators consumed higher proportions of rice herbivores when the herbivore abundance was high (Fig. 5). This finding suggests that generalist predators are capable of tracking pest populations and increasing their consumption of pests accordingly. Therefore, farming practices that promote generalist predators early in the crop season will likely benefit pest control later in the season, when pest populations reach the economic threshold.

Effect of alternative prey on biocontrol

While generalist arthropod predators are ubiquitous in agroecosystems, their potential as biocontrol agents has been questioned because they can feed on non-target pests. Our study eases this concern, because although generalist arthropod predators did feed on alternative prey, they still exerted a strong per capita effect on pests—rice herbivores accounted for 90–93% of the diet of predators during the ripening stage, a critical period for crop production (Fig. 3a; Appendix S1: Table S4). As the demand for biocontrol has increased in agriculture, we suggest that farming practitioners consider the use of generalist predators as biocontrol agents to complement the action of specialist predators. Furthermore, we suggest that future agroecological studies should systematically examine the potential benefits of non-pest alternative prey (e.g., detritivores) in pest management programs that include generalist predators as biocontrol agents. In fact, a small number of studies have proposed that generalist predators, compared to specialist predators (e.g., parasitoids), could provide more effective biocontrol services in the field over time (Symondson et al. 2002, Stiling and Cornelissen 2005). This is because they can maintain their populations by feeding on alternative prey when the target pest density is low, and then, pest consumption rapidly increases as pest density rises

(Murdoch et al. 1985, Symondson et al. 2002). Although our study was not designed to test this proposal, we did find a high abundance of detritivores (alternative prey) in the early season (Fig. 3b), which may have supported predator populations before the establishment of rice herbivores (target pest). The sustained predator populations could then suppress pests that emerge in later seasons (Chiverton 1987, Settle et al. 1996, Symondson et al. 2002).

Effect of farm type on biocontrol

Compared with conventional farming, organic farming has been suggested to promote predator diversity and abundance (Bengtsson et al. 2005), yet its effect on the role of predators as biocontrol agents remains to be clarified (Birkhofer et al. 2008*a*, Crowder et al. 2010, Porcel et al. 2018). Our analysis showed that rice herbivores accounted for 90% and 93% of predators' diets at the ripening stage in organic and conventional farms, respectively (Fig. 4; Appendix S1: Table S4). The high per capita consumption of pests suggests the great potential of predators as biocontrol agents, regardless of farm type. Surprisingly, we found that pest consumption by predators was higher in conventional farms at the tillering and flowering stages (Fig. 4; Appendix S1: Table S4), highlighting their underappreciated potential in the pest management of conventional farms.

Two possible non-mutually exclusive explanations may explain why predators consumed higher proportions of rice herbivores in conventional farms. First, conventional farming may lead to higher densities of pest species (Porcel et al. 2018), thereby increasing predators' consumption of these pests due to higher encounter rates. This explanation, however, is not supported by the density of the most abundant rice herbivores (pests) from our sweep net samples (Appendix S1: Table S3). Second, organic farming may promote arthropod diversity (Bengtsson et al. 2005, Hole et al. 2005), providing diverse prey items and therefore lowering predators' consumption of target pests. This is supported by the wider trophic niches of predators in organic farms observed in this study (Fig. 2a). We encourage further studies in various agricultural systems to verify if predators generally consume more crop herbivores (pests) in their diet in conventional farms than organic farms.

Potential caveats

To our knowledge, this study is among the first to apply stable isotope analysis to quantify the diet composition of generalist arthropod predators over the crop season in both organic and conventional farms. This has provided insightful information for agricultural management, but there are some limitations. First, we did not investigate how the diet composition of predators is influenced by the landscape. Instead, we selected organic and conventional farms that were embedded within the same landscape context. Given that landscape alone and its interaction with farming practices can affect arthropod population dynamics (Marino and Landis 1996, Bianchi et al. 2006, Winqvist et al. 2011, Marja et al. 2019), future studies incorporating landscape effects will help advance our knowledge of predator–prey interactions in agroecosystems. Second, the strong per capita effect of predators on pests (i.e., high pest consumption by predators in this study) may not necessarily translate into an effective suppression of pest populations in the field, since the suppression will depend on the per capita effect of predators, as well as the density and diversity of predators in the field (Duelli and Obrist 2003, Letourneau et al. 2009). To clarify the link between the per capita pest consumption by predators and pest population dynamics, future work should complement stable isotope analysis with field experiments and molecular gut–content analysis. Third, the current stable isotope mixing model is not capable of accurately estimating cannibalism or intraguild predation. For example, if predators were included as their own food resource, they would account for 100% of their diet. Although estimating intraguild predation remains a challenge, it may not be a major concern in this study for two reasons. The first reason is that most ladybugs collected in our rice farms were adults, which rarely cannibalized each other. While intraguild predation among spiders has been widely reported (Michalko et al. 2019*b*), the structural complexity of vegetation can significantly reduce such predation pressure (Finke and Denno 2006). This reduction would likely occur in our study period, during which rice plants grew rapidly and formed dense vegetation. We did not observe intraguild predation between adult ladybugs and spiders, although it might exist. The second reason is that if intraguild predation had been common in our rice farms, it would have increased the $\delta^{15}N$ value in predators, leading to markedly high consumption of detritivores (with higher $\delta^{15}N$ than other prey items; Appendix S1: Fig. S1) in our mixing model results. Since this was not the case (high consumption of herbivores instead of detritivores; Fig. 3a), it is reasonable to assume that intraguild predation was not pervasive in our rice farms.

Conclusions

While generalist arthropod predators are ubiquitous in agroecosystems, their potential to control pests over the crop season has been a subject of debate. To clarify the role of generalist arthropod predators as biocontrol agents, this study surveyed arthropod communities and applied stable isotope analysis to quantify the diet composition of the predators at different crop stages in organic and conventional rice farms. The findings indicate three main points: (1) Generalist arthropod predators in both organic and conventional farms consumed increasing proportions of rice herbivores in their diet as the crop season progressed (from 34% to 55% at tillering to 90% to 93% at ripening), suggesting an increasing biocontrol value of generalist predators over time regardless of farm type. (2) Surprisingly, the proportion of rice pests in predators' diet was higher in conventional farms than organic farms at the tillering and flowering stages, highlighting the underappreciated potential of predators as biocontrol agents in conventional farms. (3) Contrary to the common view that generalist arthropod predators feed on non-target pests and may not be efficient biocontrol agents, this study demonstrated the strong per capita pest consumption by generalist predators, even in the presence of alternative prey. Taken together, we conclude that agricultural management schemes promoting populations of generalist arthropod predators will likely benefit pest control and should be integrated into modern agriculture.

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Data Availability

Data are available in Figshare: https://doi.org/10.6084/m9.figshare.14413808.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3625/full