*Running head: pest consumption by generalist predators*

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

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**Abstract**

Applying biocontrol agents is critical to pest management in sustainable agriculture. Arthropod generalist predators may hold a great potential as biocontrol agents because they are ubiquitous and consume pests in agro-ecosystems. However, their diet composition over crop season has rarely been quantified, hindering our ability to assess their biocontrol potential in real field conditions that foster temporal dynamics of pest and alternative prey populations. To fill the knowledge gap and clarify the role of arthropod generalist predators as biocontrol agents, this study quantified these predators’ diet composition over crop season in different types of farms. Specifically, we surveyed arthropod communities over crop stages in organic and conventional rice farms (n = 7 for each farm type), and then applied stable isotope analysis (δ13C and δ15N) to quantify the diet composition of arthropod generalist 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 predators in both organic and conventional farms shifted trophic niches over the crop season. Furthermore, these predators in both farms consumed a higher percentage of rice herbivores in their diet at late than at early crop stages (e.g., 90-93% at ripening vs. 34-55% at tillering stage), suggesting an increasing biocontrol value of generalist predators over time regardless of farm type. Surprisingly, predators consumed higher proportions of rice herbivores in conventional than organic farms at tillering and flowering stages, highlighting their underappreciated role as biocontrol agents in conventional farms. In conclusion, this study demonstrates that although arthropod generalist predators consume non-pest alternative preys, they have a high biocontrol potential (per capita pest consumption) in both organic and conventional rice farms. Therefore, we encourage modern agriculture to develop techniques to facilitate these predators’ populations and their associated ecosystem services.

*Keywords: biocontrol, rice herbivores, detritivores, diet composition, arthropod community, predator-prey interactions, trophic interactions, generalist predators, rice paddy, organic and conventional farms, crop stage, stable isotope analysis*

**Introduction**

The use of arthropod natural enemies to control pests is an essential component of biocontrol programs and sustainable agriculture (add Kromp 1999, Hand 2016, Wezel et al. 2014, Wojtkowski 2019 (Obrycki and Kring 1998, Symondson et al. 2002, Ali et al. 2019, Snyder 2019). Natural enemies include specialists and generalists — while specialists (e.g., parasitoids) often receive public attentions for their high specificity in regulating pest populations (Hǻgvar 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) (add Michalko et al. 2019 GEB), and their removal has been shown to cause a 13-fold surge in pest populations in rice farms (Kenmore et al. 1984). Since generalist predators are ubiquitous in nature and capable of producing consistent top-down control on various pests (Schmitz et al. 2000, Halaj and Wise 2001, Porcel et al. 2018), they may hold a 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 in field conditions. This necessity arises from a concern that generalist predators feed on not only targeted species (e.g., herbivorous pests) but also alternative prey (e.g., detritivores) in the field (Symondson et al. 2002, Michalko et al. 2019). Therefore, the biocontrol potential of generalist predators may be affected by the presence of alternative prey, either positively or negatively. For example, on one hand, alternative prey could support higher densities of predators when pest populations are low early in the crop season, facilitating pest control by predators when pests become abundant later in the season (Settle et al. 1996, Muñoz-Cárdenas et al. 2017). On the other hand, alternative prey may disrupt biocontrol if these predators exhibit a stronger preference for alternative prey (Musser and Shelton 2003, Koss and Snyder 2005, Birkhofer et al. 2008b).

The aforementioned context dependency suggests that the biocontrol by generalist predators depends on the temporal dynamics of pest and alternative prey populations. Although a small number of studies have examined generalist predators’ diet composition in agro-ecosystems (Cite Birkhofer et al. 2011, Jacobsen et al. 2019 EAA), it remains unclear how these predators’ diet composition may vary temporally in response to prey population dynamics during 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 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 predators’ diet composition over the course of crop season should provide important insights for biocontrol applications.

Besides temporal variations in prey populations, farm type (e.g., organic vs. conventional) could affect the biocontrol by generalist predators. In efforts to reduce 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 effect on biocontrol efficacy of predators remains unclear, 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) and 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 preys, leading to biased biocontrol results. Therefore, investigating pest consumption by predators under natural conditions, as we do using stable isotope analysis, should help clarify the potential of generalist predators as biocontrol agents in organic and conventional farms.

To understand the biocontrol potential of arthropod generalist predators (e.g., per capita pest consumption) in agro-ecosystems, this study examined these predators’ diet composition in organic and conventional rice farms over the crop season. Specifically, we 1) examined the resource partitioning (trophic niches) in arthropod generalist predators, 2) quantified predators’ diet composition from potential prey sources (rice herbivores, tourist herbivores, and detritivores), and 3) investigated the effects of farm type and crop stage on pests (rice herbivore) consumption by predators. We sampled arthropod prey and generalist predators from seven sub-tropical organic vs. seven conventional rice farms at the seedling, tillering, flowering, and ripening stages in Miaoli County, Taiwan in 2018. Stable isotope analysis (δ13C and δ15N), a common method used to determine diet composition of focal species, was applied to infer trophic interactions in the field. This approach provides time-integrated dietary information in 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 vs. seven conventional rice farms within the same landscape context in Miaoli County, Taiwan (Fig. 1). These farms were typical rice farms in Taiwan (mean area (±SD) = 0.19±0.1 hectares) and irrigated with similar quality of surface water (unpublished data). Synthesized fertilizers and pesticides were used in conventional but not 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 first growing season from April to July of 2018. Samples were bagged, iced, and stored without chemical preservatives (e.g., ethanol) at −20ºC in the laboratory. Arthropods were then identified to the finest taxonomic resolution possible under a dissecting scope.

***Preparation for stable isotope analysis*** Whole-body arthropods were oven dried at 50ºC for a 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 UC Davis Stable Isotope Facility for analysis of 13C and 15N using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Resulting isotope ratios (δ13C and δ15N) were expressed in per mil (‰) relative to the international standards of Vienna PeeDee Beleminte and atmospheric N2 for carbon and nitrogen, respectively.

***Determination of trophic guilds*** 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). Since they represent distinct functional groups in communities by condensing arthropod taxonomic information (Dominik et al. 2018), using trophic guilds instead of individual species would be appropriate for studying community-level trophic dynamics in rice agro-ecosystems. We first assigned spiders and ladybugs into the “Predator” guild, which represents the primary arthropod generalist predators inhabiting rice farms. To determine prey sources, we performed k-means clustering (k = 3) with Euclidean distance on stable isotope ratios (δ13C and δ15N) 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 morphospecies were assigned into ecological meaningful clusters. Rice herbivores consisted of major rice pests; tourist herbivores (Moran and Southwood 1982) consisted of herbivorous species with no direct trophic association with rice plants; 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 (Appendix S1: Fig. S2). Because this study focused on generalist predators and their potential prey resources, we did not consider other trophic guilds (e.g., parasitoids). Detailed information of guild assignment of arthropod families is provided in Table S1.

***Predators’ trophic niches*** 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 (Fig. S1), stable isotope mixing models served 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 mixing model to estimate the proportional contribution of each source to predators’ diet. For the predator data, individual farm and crop stage were treated as fixed effects in the mixing model. Since predator samples at seedling stage were not enough 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) (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. The 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 of farmers, we further examined how farm type and crop stage affect rice herbivore consumption by predators. We fit a beta regression model with farm type, crop stage, and their interaction as fixed effects with 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 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 (α = 0.05), we conducted Tukey's post hoc tests for all pair-wise comparisons of rice herbivore consumption using the “cld” function in the emmeans package (Lenth et al. 2017). Lastly, 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 in R (R Core Team 2018).

**Results**

***Predators’ trophic niches*** Trophic niches (consisting of niche position and niche breadth) of arthropod generalist predators varied with farm type (PERMANOVA *F*1,97 = 5.83, *P* = 0.008) and crop stage (PERMANOVA *F*2,97 = 15.06, *P* < 0.001) (Fig. 2). Regarding trophic niche position, the centroids of predators’ isotope signatures in the δ-space shifted progressively from upper-right corner at tillering stage (higher δ13C and δ15N) to lower-left corner at ripening stage (lower δ13C and δ15N) regardless of farm type (Fig. 2). 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 (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 ± 1.38‰ and 2.13 ± 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, *t95* = 2.10, *P* = 0.04; Fig. 2).

***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. 3). Specifically, from tillering to ripening stage, rice herbivores in predators’ diet 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 (Table S3).

***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 predators’ consumption on rice herbivores — a primary concern of farmers. Two-way ANOVA indicated that farm type (χ21 = 24.68, *P* < 0.001) and crop stage (χ22 = 112.95, *P* < 0.001), but not their interaction (χ22 = 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 on rice herbivores increased over crop stages regardless of farm type (Fig. 4).

**Discussion**

To understand the biocontrol potential of arthropod generalist predators in agro-ecosystems (e.g., per capita pest consumption), we conducted field surveys and stable isotope analysis to examine these predators’ diet composition in organic and conventional rice farms over the course of the crop season. Our results showed that generalist predators exhibited a switch in trophic niches (Fig. 2) and consumed increasing proportions of rice herbivores over crop stages compared to other prey items (Fig. 3), resulting in a predominance of rice herbivores in their diet (ca. 90%) at later crop stages in both organic and conventional farms. This underlines the great potential of arthropod generalist predators as biocontrol agents in rice agro-ecosystems regardless of farm type. Our results also 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 tillering and flowering stages. This surprising finding reveals the important yet overlooked role of arthropod generalist predators as biocontrol agents in conventional farms. Based on the results, we discuss a) the biocontrol value of arthropod generalist predators in rice agro-ecosystems, b) the effect of alternative prey on biocontrol, c) the effect of farm type on biocontrol, and d) the caveats of this study. We finish by considering the implications of this study for agricultural management.

***Biocontrol value of predators in rice agro-ecosystems***

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

Contrasting to previous studies based on snap-shot observations or experimental manipulations of certain predator taxon (Birkhofer et al. 2008a), our stable isotope approach over crop stage reveals temporal variation in predators’ biocontrol roles under natural conditions. Namely, generalist predators consumed higher proportions of pest species at later crop stages (Fig. 3 and 4). This may be due to the feeding nature of generalist predators, whose diet composition could depend 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, compared with that of tourist herbivores and detritivores (Appendix S1: Fig. S2). Accordingly, the predators consumed more rice herbivores when herbivore abundance was high (Appendix S1: Fig. S3). This finding suggests that generalist predators are capable of tracking pest populations and increasing their consumption on pests accordingly. Therefore, farming practices promoting generalist predators in early crop season will likely benefit pest control in later season when pest populations build up

***Effect of alternative prey on biocontrol***

While arthropod generalist predators are ubiquitous in agro-ecosystems, their potential as biocontrol agents has been questioned because they can feed on non-target pests. Our study eases this concern because although these predators did feed on alternative prey, still exerted strong per capita effect on pests — rice herbivores accounted for 90-93% of predators’ diet at ripening stage, which is a critical period for crop production (Fig. 3; Appendix S1: Table S3). As the demand for biocontrol has increased in agriculture, we suggest that farming practitioners consider the use of generalist predators as biocontrol agents in complement with specialist predators. Furthermore, we suggest that agroecological studies may systematically examine the potential benefit of non-pest alternative preys (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 service in the field over time because they can maintain their populations by feeding on alternative prey when targeted pest density is low, and increase in pest consumption rapidly when pest density rises (Murdoch et al. 1985, Symondson et al. 2002). Although our study was not designed to test this proposal, , we did find high abundance of detritivores (alternative prey) in early season (Appendix S1: Fig. S2), which may have supported predator populations before the establishment of rice herbivores. The sustained predator populations could then suppress pests that emerge in later season (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 predators’ role as biocontrol agents remains to be clarified (Birkhofer et al. 2008a, Crowder et al. 2010, Porcel et al. 2018). Our analysis showed that rice herbivores accounted for 90% and 93% of predators’ diet at the ripening stage in organic and conventional farms, respectively (Fig. 4; Appendix S1: Table S3) — the high per capita consumption of pests suggests a great potential of predators as biocontrol agents regardless of farm type. Surprisingly, we found that the pest consumption by predators was even higher in conventional farms at the tillering and flowering stages (Fig. 4; Appendix S1: Table S3), highlighting their underappreciated role in pest management in conventional farms.

Why did predators consume higher proportions of rice herbivores in conventional farms? We propose two possible non-mutually exclusive explanations. First, conventional farming may lead to higher densities of pest species (Porcel et al. 2018), thereby increasing predators’ consumption on these pests due to higher encounter rates. Second, organic farming may promote arthropod diversity (Bengtsson et al. 2005, Hole et al. 2005), providing diverse prey items and therefore lowering predators’ consumption on targeted pests. This is supported by the wider trophic niches of predators in organic farms observed in this study (Fig. 2). We encourage further studies in various agricultural systems to verify if predators generally consume more crop herbivores (pests) in their diet in conventional than in organic farms.

***Potential caveats***

To our understanding, this study is among the first to apply stable isotope analysis to quantify the diet composition of arthropod generalist predators over crop season in both organic and conventional farms. It provides insightful information for agricultural management, but there exist some limitations. First, we did not investigate how the predators’ diet composition is influenced by landscape. Instead, we selected farms such that organic and conventional farms 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 in predator-prey interactions in agro-ecosystems. Second, it is possible that we did not capture all prey sources of predators for our analysis. However, these potentially missing prey items, if any, are most likely rare in the field and do not constitute a significant part of predators’ diet. In fact, the three prey guilds in this study are the most common and abundant arthropods in our study farms. Due to the feeding nature of generalist predators (opportunistic foraging with low prey preference), our stable isotope analysis should reflect the general picture of predators’ diet. Finally, a strong per capita effect of predators on pests (i.e., consumption effect) revealed by this study may not necessarily translate into an effective suppression of pest populations in the field, since the suppression will depend on not only the per capita effect of predators, but also the density and diversity of predators in the field (Duelli and Obrist 2003, Letourneau et al. 2009). To clarify the link between per capita pest consumption by predators and pest population dynamics, future work could complementing stable isotope analysis with field experiments and molecular gut-content analysis

***Conclusions***

While arthropod generalist predators are ubiquitous in agro-ecosystems, their potential to control pests over crop season has been a subject of debate. To clarify the role of arthropod generalist 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) Arthropodgeneralistpredators in both organic and conventional farms consumed increasing proportions of rice herbivores in their diet over the crop season (from 34-55% at tillering to 90-93% at ripening stage), suggesting an increasing biocontrol value of generalist predators over time regardless of farm type. 2) The per capita pest consumption by the predators was surprisingly higher in conventional farms than organic farms at the tillering and flowering stages, highlighting the important yet underappreciated role of predators as biocontrol agents in conventional farms. 3) Contrary to the common view that arthropod generalist predators feed on non-target pests and may not be efficient biocontrol agents, this study demonstrated strong per capita pest consumption by the predators even at the presence of alternative preys. Taken together, we conclude that agricultural management schemes promoting populations of arthropod generalist predators will likely benefit pest control and should be integrated into modern agriculture.

**Authors’ contributions**

G.-C. Hsu, J.-A. Ou, and C.-K. Ho designed and conducted the experiments and wrote the manuscript. G.-C. Hsu and J.-A. Ou performed statistical analyses.

**Data Accessibility**

We will archive our data in Dryad Digital Repository should the manuscript be accepted.

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**Figure legends**

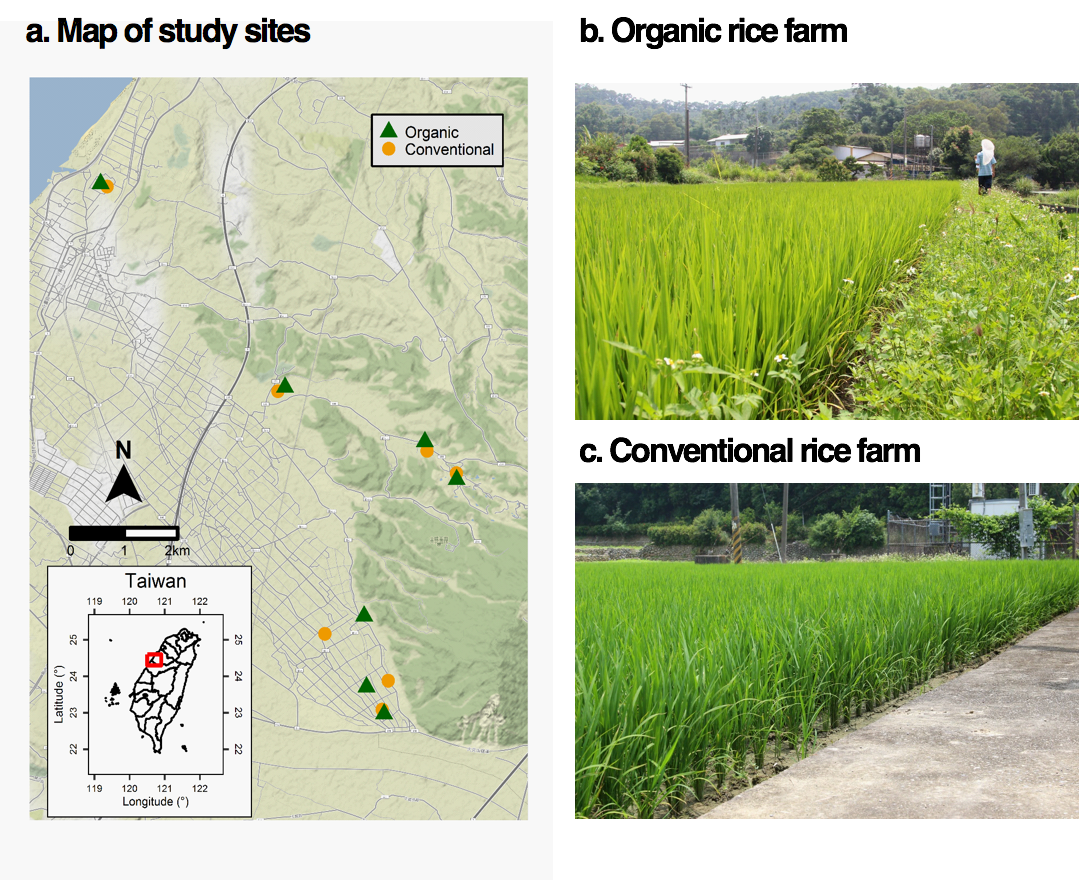
**Figure 1.** (a) Map of study sites and examples of (b) organic and (c) conventional rice farms.

**Figure 2.** Predators’ trophic niches (δ13C and δ15N) in organic and conventional farms over crop stages. Note that predators at seedling stage were omitted due to insufficient sample sizes. Each point represents a capsule sample containing one or more predator individuals. The ovals show the 50% standard ellipse area (SEA). Statistical analyses indicate that 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).

**Figure 3.** Predators’ diet composition in organic and conventional farms over crop stages. Due to insufficient sample sizes, there was no diet estimation at seedling stage. Means and SEs were computed from the mean of Bayesian posterior draws of replicate farms.

**Figure 4.** Rice herbivore consumption by predators in organic and conventional farms over crop stages. Error bars represent Tukey-adjusted 95% confidence intervals. Different letters denote statistical significance (*P* < 0.05).

**Figure 1**



**Figure 2**

Isospace.tiff

**Figure 3.**

**Proportion_Or.Cv.tiff**

**Figure 4.**

**Confint.Farm_Stage.tiff**