*sl*

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

Gen-Chang Hsu1, Jia-Ang Ou2, and Chuan-Kai Ho1,2\*

1Department of Life Science, National Taiwan University, Taipei, Taiwan

2Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei, Taiwan

\* Correspondence author. ORCiD ID: http://orcid.org/0000-0002-6437-0073 Email: [ckho@ntu.edu.tw](mailto:ckho@ntu.edu.tw)

**Abstract**

1. Although generalist predators are ubiquitous in agro-ecosystems, their functional role in pest consumption has been debated because the diet choice of generalist predators may vary with prey composition, crop stage, and farm type. Quantitative studies on the trophic dynamics of generalist predators are needed to assess their potential as biocontrol agents.
2. To examine the trophic dynamics of arthropod generalist predators under field conditions, we surveyed arthropod communities and applied stable isotope analysis to determine the diet composition of these predators at different crop stages in paired organic and conventional rice farms. Specifically, we 1) examined the resource partitioning (trophic niches) of these predators, 2) quantified atheir diet composition from potential prey sources (rice herbivores, tourist herbivores, and detritivores), and 3) investigated the effects of farm type (organic vs.conventional) and crop stage (tillering/flowering/ripening stage) on rice herbivore (pest) consumption by the predators.
3. Our results show that predators in both organic and conventional farms shifted trophic niches and consumed increasing proportions of rice herbivores in their diet over crop stage (from 34-55% at tillering to 90-93% at ripening stage), suggesting an increasing per capita suppression on pests by these predators over time e 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 functional role as potential biocontrol agents in conventional farms.
4. *Synthesis and applications*. We demonstrate high per capita pest consumption by arthropod generalist predators in both organic and conventional rice farms. Therefore, agricultural management schemes should aim at maintaining an abundance of these predators in the field to preserve their ecological role and 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 (Ali et al. 2019; Obrycki & Kring 1998; Symondson, Sunderland & Greenstone 2002). While natural enemies include specialists and generalists, specialists (e.g., parasitoids) often receive more attentions for their high specificity in regulating pest populations (Flores & Ciomperlik 2017; Hǻgvar & Hofsvang 1991; Hoy & Nguyen 2001). On the other hand, although less emphasized, generalist predators may also have the capacity to control various pests. For example, arthropod generalist predators have reportedly reduced the populations of diverse pest species in agricultural fields (Obrycki & Kring 1998; Riechert & Lockley 1984; Stiling & Cornelissen 2005; Sunderland 1999), 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 agro-ecosystems and capable of producing consistent top-down control on various pests (Halaj & Wise 2001; Porcel et al. 2018; Schmitz, Hamback & Beckerman 2000), they may hold a great potential as biocontrol agents by either acting alone or complementing specialists (Murdoch, Chesson & Chesson 1985; Stiling & Cornelissen 2005; Sunderland 1999; Symondson, Sunderland & Greenstone 2002).

To realize the biocontrol potential of generalist predators, it is necessary to first quantify their diet composition, an important but less studied subject. 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 (Michalko, Pekar & Entling 2019; Symondson, Sunderland & Greenstone 2002). 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 may maintain higher densities of predators that suppress pest populations emerging later in the crop season (Muñoz-Cárdenas et al. 2017; Settle et al. 1996). On the other hand, alternative prey may disrupt biocontrol if these predators exhibit a stronger preference for alternative prey (Birkhofer, Wise & Scheu 2008; Koss & Snyder 2005; Musser & Shelton 2003).

The aforementioned context dependency suggests that the biocontrol by generalist predators depends on the temporal dynamics of pest and alternative prey populations. Although there have been several quantitative studies examining the trophic interactions of generalist predators in agro-ecosystems, it remains unclear how these interactions are affected by the natural temporal variations of prey sources, hindering our ability to assess the biocontrol potential of these predators.”ge This is particular relevant for agricultural systems which 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) and this temporal variation will likely influence pest consumption by predators; therefore, quantifying predators’ diet composition over the course of crop season should provide useful insights for biocontrol applications.

Besides temporal variations in prey populations, farm type (e.g., organic vs. conventional) could affect the trophic dynamics of generalist predators. In efforts to reduce environmental impacts of agriculture, organic farming has seen tremendous growth in recent years (Reganold & Wachter 2016). While organic farming may promote the abundance and diversity of generalist predators (e.g., Bengtsson, Ahnstrom & Weibull 2005; Porcel et al. 2018), its effect on biocontrol remains unclear, with both positive and non-significant results reported (e.g., Birkhofer et al. 2016; Crowder et al. 2010; Porcel et al. 2018). Previous studies have examined pest population responses to experimental manipulations of predators (e.g., cage experiments) in organic and conventional farms. However, the densities of predators in these experiments are typically fixed, which may not reflect the seasonal variations in predator-pest interactions in the field. Moreover, confining predators and prey in experimental settings may alter their movements and artifically increase encounter rates, leading to biased estimations of predation rates. As a result, investigating pest consumption by predators under natural conditions, as we do using stable isotopes, should complement previous studies and help clarify the potential of generalist predators as biocontrol agents in organic and conventional farms.

ssyIn this study, we investigated the trophic dynamics of arthropod generalist predatorsf in organic and conventional rice farms over crop stage. Specifically, we 1) examined the resource partitioning (trophic niches) among 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 pest (i.e., rice herbivores) consumption by predators. We sampled arthropod prey and generalist predators from seven paired sub-tropical organic vs. 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) (Boecklen et al. 2011; Newton 2016; Post 2002).

**Materials and Methods**

***Arthropod sampling*** We selected seven pairs of organic vs. conventional rice farms in Miaoli County, Taiwan (Fig. 1). 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 (Hawkins & Macmahon 1989; Root 1967). 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 three following guilds: “Rice herbivore”, “Tourist herbivore”, and “Detritivore”, according to a previous study that has identified these gprey guilds in rice farms (Dominik et al. 2018).The resulting clusters were then examined to ensure morphospecies were assigned into ecologically meaningful clusters. Rice herbivores consisted of major rice pests; tourist herbivores (Moran & 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 sources, 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, measured as the centroid of isotope signature distribution and represents the average resource use of the organismal group, and 2) niche breadth, measured as the multivariate dispersion of isotope signature distribution and represents the 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 & 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 & 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 & Koch 2002; Stock & 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 & 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, Love & Hervé 2017). Lastly, we examined whether rice herbivore consumption is associated with background rice herbivore density by fitting another beta regression model with rice herbivore consumption as a response and relative abundance of rice herbivore as a 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). 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 switch in diet from relatively more detritivores/tourist herbivores to progressively more rice herbivores. (Fig. S1). Regarding trophic niche breadth, PERMDISP further 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 (± SD) were 2.64 ± 1.38‰ and 2.13 ± 1.05‰ 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). s fmrr e 35rrδ 5f schy.

***Predators’ diet composition*** A further analysis using Bayesian stable isotope mixing model revealed dietary shifts of predators over crop stage. 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 stage regardless of farm type (Fig. 4).

**Discussion**

To examine the trophic dynamics of arthropod generalist predators in agro-ecosystems, we coupled field surveys and stable isotope analysis to quantify predator-prey trophic interactions 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 stage (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 to exert top-down control on pests in rice agro-ecosystems regardless of farm type. Our results also showed that predators in conventional farms consumed overall 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 functional role of arthropod generalist predators in conventional farms. Based on the above results, we discuss a) the functional role of arthropod generalist predators in rice agro-ecosystems, b) the effect of alternative prey on predators’ consumption of pest, c) the effect of farm type on trophic dynamics of generalist predators, and d) the caveats of this study. We finish by considering the implications of this study for agricultural management.

***Functional role of predators in rice agro-ecosystems***

Quantifying the trophic dynamics of generalist predators is critical for understanding their functional roles in agricultural systems, yet this information remains scarce (see Introduction). Based on stable isotope analysis, we show that arthropodgeneralistpredators in both organic and conventional farms consumed high proportions of rice herbivores in their diet on average (Fig. 3), providing direct evidence for a strong per capita effect of predators on pests regardless of farm type. Moreover, pest consumption by predators increased over crop stage (Fig. 3), highlighting the important functional role of generalist predators in rice agro-ecosystems over time. yContrasting to previous studies based on snap-shot observations or experimental manipulations of certain predator taxon (Birkhofer et al. 2008), our stable isotope approach over crop stage reveals temporal variations in trophic dynamics of generalist predators under natural settings. 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 pest consumption***

While arthropod generalist predators are ubiquitous in agricultural lands, their potential as biocontrol agents has been questioned because they can feed on non-target species. In our study, although the predators did feed on alternative prey, they still exerted strong per capita effect on pests — rice herbivores accounted for 90-93% of predators’ diet at ripening stage, which is the critical period for crop production (Fig. 3; Appendix S1: Table S3). This finding echoes the underappreciated notion that generalist predators, compared to specialist predators (e.g., parasitoids), can provide more effective biocontrol service 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, Chesson & Chesson 1985; Symondson, Sunderland & Greenstone 2002). 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.

Our study demonstrates the importance of temporal dynamics of prey populations on the outcome of predator-pest interactions . Despite large temporal variations in species composition in agricultural systems (Schoenly et al. 1996; Settle et al. 1996), studies on the diet composition of generalist predators over the course of crop season have been lacking, hampering our understanding of these predators as potential biocontrol agents. In this study, our quantitative results not only show an increasing pest consumption by generalist predators over crop stage (Fig. 3 and 4), but also imply the importance of alternative prey in sustaining predator populations. For example, we found 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 emerging in later season (Chiverton 1987; Settle et al. 1996; Symondson, Sunderland & Greenstone 2002). Therefore, we propose that pest management schemes should not consider just the time when pests occur, but rather the whole crop season altogether.

***Effect of farm type on trophic dynamics***

Compared with conventional farming, organic farming has been suggested to promote predator diversity and abundance (Bengtsson, Ahnstrom & Weibull 2005), yet its effect on predator-prey trophic interactions remains to be clarified (Birkhofer et al. 2008; 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),suggesting the potential of generalist predators to exert strong per capita effect on pests regardless of farm type. Furthermore, we found that the pest consumption in predators’ diet was even higher in conventional farms at the tillering and flowering stages (Fig. 4; Appendix S1: Table S3), highlighting their underappreciated functional role 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, Ahnstrom & Weibull 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 in relation to arthropod diversity and abundance in the field

***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 whether the trophic dynamics of predators is landscape dependent. Instead, we paired organic and conventional farms to minimize the confounding effects of surrounding landscape. Given that landscape alone and its interaction with farming practices can affect arthropod population dynamics (Bianchi, Booij & Tscharntke 2006; Marino & Landis 1996; Marja et al. 2019; Winqvist et al. 2011), 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 to capture all prey sources of predators in our analysis. However, these potentially missing prey items, if any, are most likely to be rare in the field, and therefore they may 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 & Obrist 2003; Letourneau et al. 2009). As a result, future work would require incorporating these two aspects to investigate the overall ecological effects of predators on pests, and complementing stable isotope analysis with field observations and other experimental approaches such as molecular gut-content analysis should help clarify the link between per capita pest consumption by predators and pest population dynamics.

***Conclusions***

While arthropod generalist predators are ubiquitous in agro-ecosystems, their trophic interactions with pests and alternative prey under field conditions remains unclear. To examine the trophic dynamics of arthropod generalist predators, this study surveyed arthropod communities and applied stable isotope analysis to quantify the diet composition of 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 over crop stage (from 34-55% at tillering to 90-93% at ripening stage), suggesting an increasing per capita suppression on pests by these predators over time. 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 their important yet underappreciated functional role as potential biocontrol agents in conventional farms. 3) Contrary to the common view that biocontrol by arthropod generalist predators may be attenuated by the presence of non-pest species, this study demonstrated increasing per capita pest consumption by the predators with increasing pest abundance in the field. 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.

**Acknowledgements**

We thank anonymous reviewers, Yu-Pin Lin, Chih-Wei Tsai, Chi-Lun Huang, Su-Chen Chang, and Hung-Ju Chen. We also thank Miaoli District Agricultural Research and Extension Station for logistic supports, and Council of Agriculture, Executive Yuan, Taiwan (106AS-4.2.5-ST-a1, 107AS-4.2.3-ST-a1, 108AS-4.2.2-ST-a1) and Ministry of Science and Technology (108-2621-B-002-003-MY3) for funding support.

**Literature Cited**

Ali, M.P., Bari, M.N., Haque, S.S., Kabir, M.M.M., Afrin, S., Nowrin, F., . . . Landis, D.A. (2019) Establishing next-generation pest control services in rice fields: eco-agriculture. *Scientific Reports,* 9, 10180.

Anderson, M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology,* 26, 32-46.

Anderson, M.J. (2004) PERMDISP: a FORTRAN computer program for permutational analysis of multivariate dispersions (for any two-factor ANOVA design) using permutation tests. *Department of Statistics, University of Auckland, New Zealand,* 24.

Anderson, M.J. & Walsh, D.C.I. (2013) PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? *Ecological Monographs,* 83, 557-574.

Bengtsson, J., Ahnstrom, J. & Weibull, A.C. (2005) The effects of organic agriculture on biodiversity and abundance: a meta-analysis. *Journal of Applied Ecology,* 42, 261-269.

Bianchi, F.J.J.A., Booij, C.J.H. & Tscharntke, T. (2006) Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society B-Biological Sciences,* 273, 1715-1727.

Birkhofer, K., Arvidsson, F., Ehlers, D., Mader, V.L., Bengtsson, J. & Smith, H.G. (2016) Organic farming affects the biological control of hemipteran pests and yields in spring barley independent of landscape complexity. *Landscape Ecology,* 31, 567-579.

Birkhofer, K., Fliessbach, A., Wise, D.H. & Scheu, S. (2008) Generalist predators in organically and conventionally managed grass-clover fields: implications for conservation biological control. *Annals of Applied Biology,* 153, 271-280.

Birkhofer, K., Wise, D.H. & Scheu, S. (2008) Subsidy from the detrital food web, but not microhabitat complexity, affects the role of generalist predators in an aboveground herbivore food web. *Oikos,* 117, 494-500.

Boecklen, W.J., Yarnes, C.T., Cook, B.A. & James, A.C. (2011) On the use of stable isotopes in trophic ecology. *Annual Review of Ecology, Evolution, and Systematics,* 42, 411-440.

Caut, S., Angulo, E. & Courchamp, F. (2009) Variation in discrimination factors (Delta N-15 and Delta C-13): the effect of diet isotopic values and applications for diet reconstruction. *Journal of Applied Ecology,* 46, 443-453.

Chiverton, P.A. (1987) Predation of *Rhopalosiphum padi* (Homoptera, Aphididae) by polyphagous predatory arthropods during the aphids' prepeak period in spring barley. *Annals of Applied Biology,* 111, 257-269.

Crowder, D.W., Northfield, T.D., Strand, M.R. & Snyder, W.E. (2010) Organic agriculture promotes evenness and natural pest control. *Nature,* 466, 109-U123.

Dominik, C., Seppelt, R., Horgan, F.G., Settele, J. & Vaclavik, T. (2018) Landscape composition, configuration, and trophic interactions shape arthropod communities in rice agroecosystems. *Journal of Applied Ecology,* 55, 2461-2472.

Duelli, P. & Obrist, M.K. (2003) Biodiversity indicators: the choice of values and measures. *Agriculture Ecosystems & Environment,* 98, 87-98.

Flores, D. & Ciomperlik, M. (2017) Biological control using the ectoparasitoid, *Tamarixia radiata*, against the Asian citrus psyllid, *Diaphorina citri*, in the Lower Rio Grande Valley of Texas. *Southwestern Entomologist,* 42, 49-59.

Fox, J. & Weisberg, S. (2018) *An R companion to applied regression*. Sage Publications.

Hǻgvar, E.B. & Hofsvang, T. (1991) Aphid parasitoids (Hymenoptera, Aphidiidae): biology, host selection and use in biological control. *Biocontrol news and Information,* 12, 13-42.

Halaj, J. & Wise, D.H. (2001) Terrestrial trophic cascades: How much do they trickle? *American Naturalist,* 157, 262-281.

Hawkins, C.P. & Macmahon, J.A. (1989) Guilds - the multiple meanings of a concept. *Annual Review of Entomology,* 34, 423-451.

Hole, D.G., Perkins, A.J., Wilson, J.D., Alexander, I.H., Grice, P.V. & Evans, A.D. (2005) Does organic farming benefit biodiversity? *Biological Conservation,* 122, 113-130.

Hoy, M.A. & Nguyen, R. (2001) Classical biological control of Asian citrus psylla. *Citrus Industry,* 81, 48-50.

Kenmore, P.E., Perez, C.A., Dyck, V.A. & Gutierrez, A.P. (1984) Population regulation of the rice brown planthopper (*Nilaparvata lugens* Stǻl) within rice fields in the Philippines. *Journal of Plant Protection in the Tropics,* 1, 19-37.

Kiritani, K., Kawahara, S., Sasaba, T. & Nakasuji, F. (1972) Quantitative evaluation of predation by spiders on the green rice leafhopper, *Nephotettix cincticeps* Uhler, by a sight-count method. *Researches on Population Ecology,* 13, 187-200.

Koss, A.M. & Snyder, W.E. (2005) Alternative prey disrupt biocontrol by a guild of generalist predators. *Biological Control,* 32, 243-251.

Layman, C.A., Araujo, M.S., Boucek, R., Hammerschlag-Peyer, C.M., Harrison, E., Jud, Z.R., . . . Bearhop, S. (2012) Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biological Reviews,* 87, 545-562.

Lenth, R., Love, J. & Hervé, M. (2017) Package ‘emmeans’. *Underst Stat,* 34, 216-221.

Letourneau, D.K., Jedlicka, J.A., Bothwell, S.G. & Moreno, C.R. (2009) Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. *Annual Review of Ecology Evolution and Systematics,* 40, 573-592.

Marino, P.C. & Landis, D.A. (1996) Effect of landscape structure on parasitoid diversity and parasitism in agroecosystems. *Ecological Applications,* 6, 276-284.

Marja, R., Kleijn, D., Tscharntke, T., Klein, A.M., Frank, T. & Batáry, P. (2019) Effectiveness of agri‐environmental management on pollinators is moderated more by ecological contrast than by landscape structure or land‐use intensity. *Ecology Letters,* doi: 10.1111/ele.13339.

Michalko, R., Pekar, S. & Entling, M.H. (2019) An updated perspective on spiders as generalist predators in biological control. *Oecologia,* 189, 21-36.

Moran, V.C. & Southwood, T.R.E. (1982) The guild composition of arthropod communities in trees. *Journal of Animal Ecology,* 51, 289-306.

Muñoz-Cárdenas, K., Ersin, F., Pijnakker, J., van Houten, Y., Hoogerbrugge, H., Leman, A., . . . Janssen, A. (2017) Supplying high-quality alternative prey in the litter increases control of an above-ground plant pest by a generalist predator. *Biological Control,* 105, 19-26.

Murdoch, W.W., Chesson, J. & Chesson, P.L. (1985) Biological control in theory and practice. *American Naturalist,* 125, 344-366.

Musser, F.R. & Shelton, A.M. (2003) Predation of *Ostrinia nubilalis* (Lepidoptera : Crambidae) eggs in sweet corn by generalist predators and the impact of alternative foods. *Environmental Entomology,* 32, 1131-1138.

Newsome, S.D., del Rio, C.M., Bearhop, S. & Phillips, D.L. (2007) A niche for isotopic ecology. *Frontiers in Ecology and the Environment,* 5, 429-436.

Newton, J. (2016) Stable isotopes as tools in ecological research. *Encyclopedia of Life Sciences*.John Wiley & Sons, Ltd.

Nyffeler, M. (1999) Prey selection of spiders in the field. *Journal of Arachnology,* 27, 317-324.

Obrycki, J.J. & Kring, T.J. (1998) Predaceous Coccinellidae in biological control. *Annual Review of Entomology,* 43, 295-321.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O’hara, R.B., . . . Oksanen, M.J. (2013) Package ‘vegan’. *Community ecology package, version 2.9*, 1-295.

Phillips, D.L. & Koch, P.L. (2002) Incorporating concentration dependence in stable isotope mixing models. *Oecologia,* 130, 114-125.

Porcel, M., Andersson, G.K.S., Palsson, J. & Tasin, M. (2018) Organic management in apple orchards: Higher impacts on biological control than on pollination. *Journal of Applied Ecology,* 55, 2779-2789.

Post, D.M. (2002) Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology,* 83, 703-718.

Reganold, J.P. & Wachter, J.M. (2016) Organic agriculture in the twenty-first century. *Nature Plants,* 2, 15221.

Riechert, S.E. & Lockley, T. (1984) Spiders as biological control agents. *Annual Review of Entomology,* 29, 299-320.

Root, R.B. (1967) The niche exploitation pattern of the blue‐gray gnatcatcher. *Ecological Monographs,* 37, 317-350.

Schmitz, O.J., Hamback, P.A. & Beckerman, A.P. (2000) Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *American Naturalist,* 155, 141-153.

Schoenly, K., Cohen, J.E., Heong, K.L., Litsinger, J.A., Aquino, G.B., Barrion, A.T. & Arida, G. (1996) Food web dynamics of irrigated rice fields at five elevations in Luzon, Philippines. *Bulletin of Entomological Research,* 86, 451-466.

Settle, W.H., Ariawan, H., Astuti, E.T., Cahyana, W., Hakim, A.L., Hindayana, D., . . . Sartanto (1996) Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. *Ecology,* 77, 1975-1988.

Stiling, P. & Cornelissen, T. (2005) What makes a successful biocontrol agent? A meta-analysis of biological control agent performance. *Biological Control,* 34, 236-246.

Stock, B.C. & Semmens, B.X. (2016) Unifying error structures in commonly used biotracer mixing models. *Ecology,* 97, 2562-2569.

Sunderland, K. (1999) Mechanisms underlying the effects of spiders on pest populations. *Journal of Arachnology,* 27, 308-316.

Symondson, W.O.C., Sunderland, K.D. & Greenstone, M.H. (2002) Can generalist predators be effective biocontrol agents? *Annual Review of Entomology,* 47, 561-594.

Winqvist, C., Bengtsson, J., Aavik, T., Berendse, F., Clement, L.W., Eggers, S., . . . Bommarco, R. (2011) Mixed effects of organic farming and landscape complexity on farmland biodiversity and biological control potential across Europe. *Journal of Applied Ecology,* 48, 570-579.

Zeileis, A., Cribari-Neto, F., Gruen, B., Kosmidis, I., Simas, A.B., Rocha, A.V. & Zeileis, M.A. (2018) Package ‘betareg’.

**Figure legends**

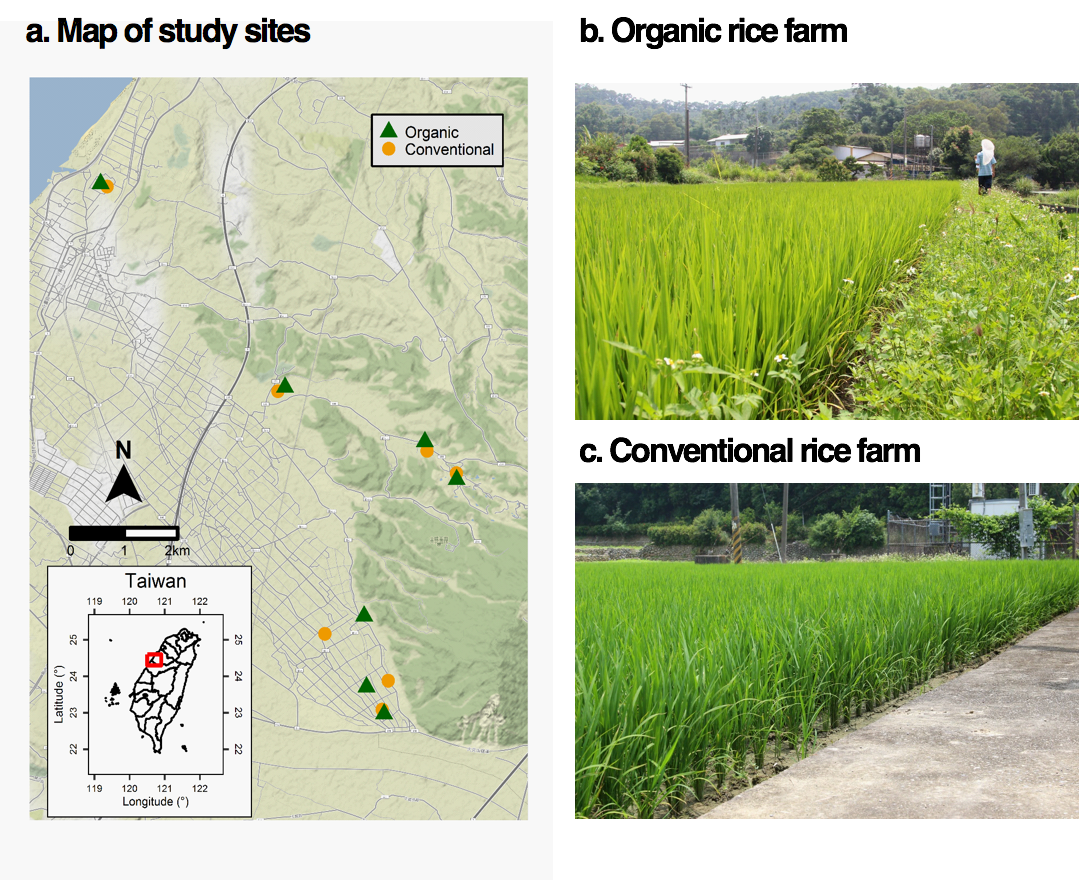
**Figure 1.** (a) Map of study sites and examples of (b) organic and (c) conventional rice farms.

**Figure 2.** Predators’ trophic niches (δ13C and δ15N) in organic and conventional farms over crop stage. 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 stage. Due to insufficient sample sizes, there was no diet estimation at seedling stage. Means and SEs were computed from the Bayesian posterior mean estimates of individual replicate farms.

**Figure 4.** Rice herbivore consumption by predators in organic and conventional farms over crop stage. 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**