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RESEARCH ARTICLE

# Generalist predators function as pest specialists: Examining diet composition of spiders and ladybeetles across rice crop stages

Gen-Chang Hsu <sup>1</sup>	Jia-Ang Ou <sup>2,3</sup>	Min-Hsuan Ni <sup>2</sup>	Zheng-Hong Lin <sup>2</sup>
Chuan-Kai Ho <sup>1,2</sup> 💿			

<sup>1</sup>Department of Life Science, National Taiwan University, Taipei, Taiwan

<sup>2</sup>Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei, Taiwan

<sup>3</sup>Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada

Correspondence Chuan-Kai Ho Email: ckho@ntu.edu.tw

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## Abstract

- Biocontrol, the use of natural enemies to manage pests, has a long history in agriculture. It has gained renewed interest because of its importance in sustainable agriculture. To solve a long-standing puzzle in biocontrol—how well the ubiquitous generalist arthropod predators (GAPs) function as biocontrol agents—this study aimed to (1) quantify the diet composition of GAPs (spiders and ladybeetles) at different crop stages using stable isotope analysis, (2) examine the consistency of GAPs in pest consumption over years and (3) investigate how abiotic and biotic factors (farm type, crop stage, surrounding vegetation and relative prey abundance) affect pest consumption by GAPs.
- 2. Specifically, we sampled arthropod prey and GAPs in seven pairs of sub-tropical organic and conventional rice farms over crop stages (seedling, tillering, flowering and ripening) in three consecutive years. Among our sweep-net samples, 352 arthropod predator and 828 prey isotope samples were analysed to infer predator-prey interactions.
- 3. Our results show the following: (a) The proportion of rice pests in GAPs' diets in both organic and conventional rice farms increased over the crop season, from 21% to 47% at the tillering stage to 80%–97% at the ripening stage, across the three study years. The high percentage in pest consumption at late crop stages (flowering and ripening) suggests that GAPs can function as specialists in pest management during the critical period of crop production. Regarding individual predator groups, spiders and ladybeetles exhibited distinct dietary patterns over crop stages. (b) The high pest consumption by GAPs at late crop stages was similar across years despite variable climatic conditions and prey availability, suggesting a consistency in GAP feeding habits and biocontrol value. (c) The proportion of rice pests in GAPs' diets varied with farm type and crop stage (e.g. higher in conventional farms and during flowering/ripening stages).

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- 4. *Synthesis and applications*. By quantifying the diet composition of GAPs over crop stages, farm types and years, this study reveals that generalist predators have potential to produce a stable, predictable top-down effect on pests in rice agro-ecosystems. Therefore, promoting the field densities of ubiquitous generalist predators will likely enhance pest management and support sustainable agriculture.

#### KEYWORDS

biocontrol, organic and conventional farms, rice paddy, stable isotope analysis, trophic interactions

## 1 | INTRODUCTION

Using natural arthropod enemies for pest control has a long history in agriculture. The earliest record of biocontrol was documented in the book Plants of the Southern Regions (ca. 304 A.D.): people sold ants and their nests in the markets to control citrus insect pests (Huang & Yang, 1987). While synthetic pesticides have become the main method for controlling pests in the past century, this comes at a cost, such as posing risks to people, reducing biodiversity and hampering ecosystem functions (Geiger et al., 2010; Kehoe et al., 2017). As agriculture has become the largest land use type worldwide and a major driver for the global biodiversity crisis in the Anthropocene (Campbell et al., 2017), a shift from synthetic pesticides to environmentally friendly practices (e.g. biocontrol) is urgently needed to make agriculture more sustainable (Gomiero et al., 2011). For example, the European Commission has announced its plan to reduce the use of chemical pesticides in European Union agricultural systems by 50% by 2030 (European Commission, 2020). To achieve this ambitious sustainability goal, biocontrol by natural enemies has been considered a key approach and has regained importance in modern agriculture (Baker et al., 2020; Power, 2010).

Natural enemies used for pest control can be classified into two major groups based on their prey range: specialist and generalist predators. While specialist predators (e.g. parasitoid wasps) have been widely advocated in agriculture because they target specific pest species and produce less undesirable non-target effects (Stiling & Cornelissen, 2005), generalist predators (e.g. spiders) have been increasingly appreciated for their conspicuous existence and consistent biocontrol effect on pests (Gajski et al., 2023; Hsu et al., 2021; Michalko et al., 2019; Stiling & Cornelissen, 2005; Symondson et al., 2002). For example, generalist predators were commonly reported in various agro-ecosystems (Cuff et al., 2022; Mezőfi et al., 2020; Morente & Ruano, 2022) and significantly reduced pest abundance in approximately 75% of cases in 181 field manipulative studies (Symondson et al., 2002). Moreover, a meta-analysis suggests that generalist predators may exert stronger biocontrol effects on pest populations over time compared to specialists (Stiling & Cornelissen, 2005).

While the value of generalist predators has been increasingly appreciated, a few fundamental knowledge gaps need to be filled to better understand their biocontrol potential and the underlying mechanisms in agro-ecosystems. For example, while studies have

qualitatively analysed the diets of generalist predators (e.g. using molecular gut content analysis to identify prey species; Albertini et al., 2018; Eitzinger & Traugott, 2011; Ingrao et al., 2017), very few have quantified their diet composition over a growth season in the field (knowledge gap 1; Hsu et al., 2021; Otieno et al., 2023). Quantifying diet composition (e.g. the proportions of different prey items in the predators' diet) will help address concerns that generalist predators may switch their diet from pests to alternative prey or interfere with each other (e.g. intraguild predation), thereby reducing their pest control effectiveness (Cuff et al., 2022; Hambäck et al., 2021; Michalko et al., 2019). For instance, if generalist predators still consume a high proportion of pests in their diet with the presence of alternative prey in the field, this result would help end a long debate on whether generalist predators serve well as biocontrol agents (Krey et al., 2017; Michalko et al., 2019; Symondson et al., 2002). Moreover, fluctuations in abiotic factors and habitat conditions reportedly contribute to seasonal and yearly variations in prey density and species composition in agro-ecosystems (Dominik et al., 2018; Settle et al., 1996; Wardle et al., 1999), potentially influencing predator foraging behaviour. Therefore, examining the consistency of pest consumption by generalist predators in the field over years is crucial to evaluate the stability of these predators as biocontrol agents in agriculture, although this information is lacking (knowledge gap 2).

To understand the mechanisms underlying the biocontrol effect of generalist predators, we also need to examine how their diet composition in agro-ecosystems is affected by various abiotic and biotic factors (e.g. crop stage, farm type, relative prey abundance and surrounding vegetation) (knowledge gap 3). First, the foraging behaviour of generalist predators is strongly influenced by prey availability and species interactions (e.g. predator-prey interactions). Because arthropod community composition (e.g. pest vs. alternative prey density) may vary with crop stages and affect predator-prey trophic interactions (Roubinet et al., 2017), it is important to examine how crop stage affects pest consumption by generalist predators within a growth season. Second, we should examine whether farming practices (e.g. organic and conventional) influence the diet composition of predators (e.g. pest consumption; Birkhofer et al., 2011). This will demonstrate whether generalist predators provide varying biocontrol values in specific farm types. Third, we should investigate the relationship between the relative prey abundance and the diet composition of their predators. This will clarify whether pest

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abundance or predator preference mainly explains pest consumption by predators (Eitzinger et al., 2019; Kuusk & Ekbom, 2012; Roubinet et al., 2017; Wise et al., 2006). Lastly, we should examine how surrounding vegetation (e.g. forest cover) affects the diet composition of generalist predators. While surrounding vegetation reportedly affected arthropod diversity and predator-prey interactions in agroecosystems (Altieri, 1999; Altieri & Letourneau, 1982; Barbosa & Castellanos, 2005; Diehl et al., 2013; Lichtenberg et al., 2017), its effect on predators' diet composition is unclear. Understanding this will provide insights for managing the agricultural landscape and promoting biocontrol services by generalist predators.

To address these three knowledge gaps, this study aimed to (1) quantify the diet composition of generalist predators, (2) examine the consistency of predators in pest consumption over years and (3) investigate how abiotic and biotic factors may affect the diet composition of these predators. Filling these gaps will provide insights for applying generalist predators in biocontrol programs. Specifically, this study sampled arthropod prey and generalist arthropod predators (GAPs) in sub-tropical organic and conventional rice farms over the rice growth season (seedling, tillering, flowering and ripening stages) in central

Taiwan from 2017 to 2019 and quantified the diet composition of GAPs (ladybeetles and spiders) at each rice stage using stable isotope analysis ( $\delta^{13}$ C and  $\delta^{15}$ N) (Figure 1). Stable isotope analysis has been widely applied in ecology to infer predator-prey trophic interactions and estimate the proportional contribution of different prey sources to predators' diets across various ecological levels, from individuals to trophic groups (Boecklen et al., 2011; Layman et al., 2012; Post, 2002). Compared to "snap-shot" techniques (e.g. field observations and molecular gut content analysis), which primarily provide qualitative information about the presence or absence of prey items in predators' diets, stable isotope analysis (e.g. Bayesian stable isotope mixing models) quantifies the biomass proportion of different prey items in predators' diets over an extended time period (Newton, 2016; Stock et al., 2018). Although GAPs may consume various prey items, we expected them to consistently consume a high proportion of pests in their diet at late crop stages regardless of the year, due to the high pest densities in this period. We also expected that the diet composition of GAPs would be affected by local abiotic and biotic factors, such as farm type (farming practice), crop stage, surrounding vegetation (per cent forest cover) and the relative abundance of pests in the field.



FIGURE 1 Sampling design and analyses of the study: (a) Map of the paired organic and conventional rice farms across the three study years (three farm pairs in 2017 and seven farm pairs each in 2018 and 2019). The red rectangle in the inset map indicates the region in central Taiwan where the farms were located. (b) Arthropods were sampled in each rice farm at four major crop stages (seedling, tillering, flowering and ripening) using the sweep-net method. (c) Field arthropod samples were categorized into three prey guilds (rice herbivores, tourist herbivores and detritivores) and one predator guild. Stable isotope analysis was used to quantify the proportions of these prey sources in predators' diets. (d) The proportion of rice herbivores (pests) consumed by predators, derived from (c), was analysed to examine how pest consumption by predators varied with farm type, crop stage, per cent forest cover, and the relative abundance of rice herbivores in the field over the three study years.

## 2 | MATERIALS AND METHODS

## 2.1 | Study system and sample collection

We collected terrestrial arthropods in paired organic and conventional rice farms in sub-tropical Taiwan (120.656-120.721°E; 24.364-24.489°N) from 2017 to 2019 (three farm pairs in 2017 and seven farm pairs each in 2018 and 2019; Figure 1a). While farms in the same pair were relatively close to each other (e.g. within a few hundred meters in distance), different farm pairs were at least 1 km apart from each other to reduce confounding effects. The study farms were 0.2 hectares on average and irrigated with surface water. The organic farms were managed with organic fertilizers (manure; 2-3 applications/crop season) and natural pesticides (tea saponins; 1 application/crop season during the seedling or tillering stage). The conventional farms were managed with synthetic nitrogen fertilizers (2-3 applications/ crop season) and organophosphate pesticides (1 application/crop season during the tillering or flowering stage). At each major rice crop stage (seedling, tillering, flowering and ripening stages) during the growing season (April-July) in each study year, we collected arthropod samples by sweep-netting (36 cm in diameter with a mesh size of  $0.2 \times 0.2$  mm) the crop canopy 30 times in each of two transects inside a rice field. Each transect (ca 30 m long) was parallel to but 1.5 m away from a randomly selected farm ridge. Samples were sealed in bags without chemical preservatives, iced and transferred to a refrigerator (-20°C) in the laboratory. The arthropod samples from the two transects in each farm were pooled to represent the farm. We identified and counted arthropods under a dissecting scope to the lowest possible taxonomic level (usually species, genus, or family). Main orders, families and genera have been documented in a previous study by Hsu et al. (2021). Note that the samples collected in 2018 for this study are the same as those in Hsu et al. (2021), but different statistical models were applied.

## 2.2 | Stable isotope analysis of arthropod samples

After identification, arthropod samples were prepared for stable isotope analysis. First, samples were oven dried ( $50^{\circ}$ C) for 1 week, ground and weighed into individual tin capsules ( $5 \times 9$  mm). If necessary, several conspecifics would be pooled into a capsule to meet the minimum weight required for stable isotope analysis (i.e. 2 mg in this study). The number of isotope capsules for each species generally mirrored the arthropod community composition in the field. Stable isotope analysis (352 arthropod predator and 828 prey isotope samples) was conducted at the UC Davis Stable Isotope Facility using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). The standards for carbon and nitrogen stable isotope ratios were Vienna PeeDee Belemnite and atmospheric N<sub>2</sub>, respectively. The results of our HSU ET AL.

samples were expressed in per mil (‰) relative to the international standards ( $\delta^{13}$ C and  $\delta^{15}$ N).

## 2.3 | Arthropod trophic guild assignment

A trophic guild represents a group of species using similar resources and forms a basic component of food webs. The concept has been proved to be practical in current ecology because it condenses broad taxonomic information into distinct functional groups in communities (Blondel, 2003). In this study, we classified arthropod samples into four trophic guilds (one predator and three prey guilds): (1) "Predators" consisted of spiders and ladybeetles, which are the primary GAPs in rice farms. (2) "Rice herbivores" consisted of major rice pests, including planthoppers, leafhoppers and stink bugs. (3) "Tourist herbivores" consisted of herbivorous species without direct trophic association with rice plants, including some grasshoppers and leaf beetles. (4) "Detritivores" consisted of arthropods that feed on decaying organic material or plankton, including various midge and fly species. The classification of prey guilds was based on a combination of literature surveys and k-means clustering of stable isotope signatures of arthropod samples (see Appendix A: Figure S1 for a stable isotope biplot for the three prey sources). The arthropod families/ genera in each trophic guild are detailed in Appendix A: Table S1. This study focused on the trophic interactions between generalist predators and their prey sources and therefore did not consider less abundant trophic guilds (e.g. parasitoids) in subsequent analyses.

## 2.4 | Data analyses

To quantify the diet composition of predators, we constructed Bayesian stable isotope mixing models using the R MixSIAR package (Stock et al., 2018) to estimate the proportions of different prey sources (i.e. the three prey guilds including rice herbivores, tourist herbivores and detritivores) in predators' diet. The Bayesian framework allows for the incorporation of prior information on the diets of predators as well as various sources of uncertainty in the diet estimation (Moore & Semmens, 2008; Parnell et al., 2013). In the mixing models, individual farm-year combination and crop stage were included as fixed effects for predator isotope data; isotope data for the three prey guilds were pooled respectively to generate fixed source values because of their high mobility across farms (Mazzi & Dorn, 2012; Sun et al., 2015). Isotope data at the seedling stage for the three study years were omitted from the mixing model analysis due to insufficient sample sizes for reliable model estimation of predators' diet composition. To improve our model estimates, we incorporated carbon and nitrogen concentration dependencies (C and N contents of the isotope samples) as well as the residual/process errors (Phillips & Koch, 2002; Stock & Semmens, 2016). Trophic discrimination factors (TDFs) were estimated from the diet-dependent discrimination equation proposed by Caut et al. (2009). We ran three Markov Chain Monte Carlo (MCMC) chains, each with 50,000 iterations and a burn-in number of 25,000,

along with a non-informative Dirichlet prior (Stock et al., 2018). Chain convergence was assessed via Gelman-Rubin and Geweke diagnostics (Gelman & Rubin, 1992). Bayesian posterior median estimates of diet composition (for each year-farm-stage combination) were extracted for further analyses. Bayesian posterior means, SDs, medians and 95% credible intervals are provided in Appendix B.

To examine how local abiotic and biotic factors may affect the pest consumption by GAPs over the years of our study, we fit weighted generalized linear mixed models (GLMMs) with a beta distribution and a logit link function using the R glmmTMB package, with year, farm type, crop stage, per cent forest cover and the relative abundance of rice herbivores as fixed effects, farm ID nested within pair ID as a random effect, and the proportion of rice herbivores consumed in predators' diet as the response (i.e. posterior medians from the Bayesian stable isotope mixing models). Weights were computed based on the number of diet estimates in each year. Model parameters were estimated using maximum likelihood, and their significance was analysed via Wald chi-square test using the "Anova" function in the R car package (Fox & Weisberg, 2018). Tukey's post-hoc tests  $(\alpha = 0.05)$  were performed for the significant factors using the "cld" function in the R emmeans package. The per cent forest cover around each study farm was estimated from Google Earth images by manually delimiting the forested areas within a 1-km radius circular buffer surrounding the farm and computing the fraction of these areas in the buffer zone (Appendix A: Table S4). The 1-km radius was based on previous studies (Karp et al., 2018; Rusch et al., 2016). Because spiders and ladybeetles may have different feeding behaviour and preferences, we also performed all the aforementioned analyses separately for each of the two predator groups. All analyses were conducted in R version 4.0.3 (R Core Team, 2021). This study was not specifically designed to survey predator and pest (rice herbivore) abundance, as this would require greater sampling efforts to include diverse and less common species. However, a preliminary analysis of predator and pest abundance is provided in Appendix A: Table S5.

## 2.5 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Predator and prey stable isotope analysis & mixing model analysis for predators' diet composition	Predator, rice herbivore, tourist herbivore and detritivore individuals collected at each rice stage in organic and conventional farms over three study years	352 predator stable isotope samples (capsules) 828 prey stable isotope samples (capsules)
Patterns of pest consumption by predators in rice agro-ecosystems	Proportion of rice herbivores (pests) in predators' diet at each rice stage in organic and conventional farms over three study years	Year 1: 3 crop stages × 6 farms Year 2: 3 crop stages × 14 farms Year 3: 3 crop stages × 14 farms

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## 2.6 | Ethics and permit statement

Ethical approval and permits were not required for this study.

# 3 | RESULTS

## 3.1 | Diet composition of predators in rice farms

Across organic and conventional rice farms during 2017–2019, the proportion of rice herbivores in predators' diet increased over the course of the crop season from 21% to 47% at the tillering stage to 80%–97% at the ripening stage; the proportion of detritivores in predators' diet decreased from 35% to 61% at the tillering stage to <1% at the ripening stage; the proportion of tourist herbivores in predators' diet also decreased from 13% to 20% at the tillering stage to 3%–18% at the ripening stage (Figure 2a; Appendix A: Table S2, Figure S2).

Regarding individual predator groups, spiders and ladybeetles showed a marked difference in their diet composition over crop stages during 2017–2019. Across organic and conventional farms, spiders consumed a higher proportion of detritivores (31%–55%) in their diet at the beginning of the crop season (tillering stage) and substantially increased the consumption of rice herbivores to 78%–95% in the late crop season (ripening stage) (Figure 2b; Appendix A: Table S2, Figure S2). In contrast, ladybeetles in both organic and conventional farms consumed a low proportion of detritivores (≤8%) and a steadily high proportion of rice herbivores (≥80%) in their diet throughout the crop season (Figure 2c; Appendix A: Table S2, Figure S2). Tourist herbivores generally did not constitute an important prey source and contributed less than 33% to the diet of spiders and ladybeetles (Figure 2b,c; Appendix A: Table S2, Figure S2).

# 3.2 | Patterns of rice herbivore consumption by predators

We further analysed rice herbivore consumption by GAPs since these herbivores are the primary pests of concern. The patterns of rice herbivore consumption by both predators in organic and conventional rice farms were generally similar across the three study years: Consumption increased and reached a high proportion during the late crop stages, indicating consistency in the feeding habits of GAPs (Figure 3). Interestingly, spiders and ladybeetles exhibited distinct within-season patterns of rice herbivore consumption. For spiders in organic and conventional farms, the proportion of rice herbivores in their diet increased toward later crop season, ranging from 17% to 48% (tillering) to 78%-95% (ripening) (Figure 3b; Appendix A: Table S2, Figure S2), whereas for ladybeetles in organic and conventional farms, the proportion of rice herbivores in their diet remained relatively stable throughout the season, ranging from 80% to 93% (tillering) to 97%-98% (ripening) (Figure 3c; Appendix A: Table S2, Figure S2).



FIGURE 2 The proportions  $(\text{mean} \pm \text{SE})$ of prey sources (rice herbivores, tourist herbivores and detritivores) consumed in the diet of (a) both predators, (b) spiders and (c) ladybeetles in organic and conventional rice farms over crop stages. The proportions were computed from the Bayesian posterior medians of diet estimates in replicate farms over the three study years.

## 3.3 | Factors associated with rice herbivore consumption by predators

The proportion of rice herbivores in GAPs' diet differed between organic and conventional farms for both predators ( $\chi^2 = 7.92$ , p = 0.01) and spiders ( $\chi^2 = 4.93$ , p = 0.03), but not ladybeetles ( $\chi^2 = 0.47$ , p = 0.49; Table 1). Specifically, both predators consumed a higher proportion of rice herbivores in their diet in conventional vs. organic farms (Table 2). The proportion of rice herbivores in GAPs' diet also differed among crop stages (both predators:  $\chi^2 = 249.84$ , p < 0.001; spiders:  $\chi^2 = 119.01$ , p < 0.001; ladybeetles:  $\chi^2 = 184.32$ , p < 0.001; Table 1). Specifically, GAPs consumed higher proportions of rice herbivores in their diet at the flowering and/or ripening stage vs. the tillering stage (Table 3).

The proportion of rice herbivores consumed in GAPs' diet was not associated with the per cent forest cover within a 1-km radius buffer surrounding the study farms (both predators:  $\chi^2 = 0.06$ , p=0.80; spiders:  $\chi^2 = 0.12$ , p=0.73; ladybeetles:  $\chi^2 = 0.34$ , p=0.56; Table 1). Furthermore, the proportion of rice herbivores consumed was not associated with the relative abundance of rice herbivores in the field (both predators:  $\chi^2 = 0.38$ , p=0.46; spiders:  $\chi^2 = 0.38$ , p=0.45; ladybeetles:  $\chi^2 = 0.38$ , p=0.54; Figure 4; Table 1).

## 4 | DISCUSSION

In response to the growing global demand for environmentally friendly agricultural practices that support both biodiversity and

food production (Rader et al., 2024), we investigated the potential of GAPs (ubiquitous in nature) as biocontrol agents in rice agroecosystems. Specifically, we used stable isotopes to quantify the diet composition of GAPs in organic and conventional rice farms during the crop season in three consecutive years. Our main results include the following: (1) Across the three study years, the rice herbivore consumption by GAPs increased in both organic and conventional farms over the crop season, from 20% to 47% at the tillering stage to 80%-97% at the ripening stage. The high percentage at the ripening stage indicates that GAPs could function as pest specialists during critical growth (late crop) stages. Notably, rice herbivore consumption by spiders increased gradually toward the later crop season, whereas the consumption by ladybeetles remained stable throughout the season. (2) Our results revealed similar among-year patterns in rice herbivore consumption by GAPs in organic and conventional rice farms, suggesting a consistency in GAPs' feeding habits and biocontrol value. (3) The proportion of rice herbivores in GAPs' diets varied with farm type and crop stage (e.g. higher in conventional farms and during flowering/ripening stages). However, contrary to results from previous studies, pest consumption by GAPs was not associated with per cent forest cover or the relative abundance of rice herbivores in the field. We discuss the following: (1) GAPs function as pest specialists at late crop stages, (2) GAPs exhibit consistent pest consumption patterns over years, (3) factors associated with pest consumption by GAPs and (4) the potential caveats of this study (e.g. pest suppression and intraguild predation). We finish by highlighting the implications of our results for agricultural management.

FIGURE 3 The proportion  $(\text{mean} \pm \text{SE})$ of rice herbivores consumed in the diet of (a) both predators, (b) spiders and (c) ladybeetles in organic and conventional rice farms over crop stages in the three study years. The proportions were computed from the Bayesian posterior medians of diet estimates in replicate farms.



TABLE 1Statistical results from GLMMbeta regression models for examining theeffects of abiotic and biotic factors onpest consumption by spiders, ladybeetlesand both predators over the years of ourstudy.

Model	Factor	df	$\chi^2$	р
Both predators	Year	2	8.00	0.02
	Farm type	1	7.29	0.01
	Crop stage	2	249.84	< 0.001
	Per cent forest cover	1	0.06	0.80
	Relative abundance of rice herbivores	1	0.56	0.46
Spiders	Year	2	9.30	0.01
	Farm type	1	4.93	0.03
	Crop stage	2	119.01	< 0.001
	Per cent forest cover	1	0.12	0.73
	Relative abundance of rice herbivores	1	0.58	0.45
Ladybeetles	Year	2	17.29	< 0.001
	Farm type	1	0.47	0.49
	Crop stage	2	184.32	< 0.001
	Per cent forest cover	1	0.34	0.56
	Relative abundance of rice herbivores	1	0.38	0.54

# 4.1 | Generalist predators function as pest specialists at late crop stages

biocontrol agents remains a concern because GAPs may switch diets between pests and alternative prey (Albajes & Alomar, 1999; Prasad & Snyder, 2006; Roubinet et al., 2018). This study addressed this concern and revealed a consistency in high pest consumption by GAPs at late crop stages over years. The results provide not only

While biocontrol, a farming practice with a long history, offers a promising solution for sustainable agriculture, the use of GAPs as

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Model	Farm type	EMMs ( <u>+</u> SE)	Lower 2.5%	Upper 2.5%
Both predators	Organic	0.61 <sup>a</sup> (±0.08)	0.45	0.76
	Conventional	0.81 <sup>b</sup> (±0.05)	0.69	0.90
Spiders	Organic	0.55 <sup>a</sup> (±0.10)	0.35	0.73
	Conventional	0.79 <sup>b</sup> (±0.07)	0.63	0.90
Ladybeetles	Organic	0.95 <sup>a</sup> (±0.01)	0.93	0.96
	Conventional	0.95 <sup>a</sup> (±0.01)	0.94	0.96

*Note*: Different superscript letters indicate significant differences in the estimated marginal means (EMMs) of the posterior medians from Bayesian stable isotope mixing models ( $\alpha$ =0.05).

Model	Crop stage	EMMs ( <u>+</u> SE)	Lower 2.5%	Upper 2.5%
Both predators	Tillering	0.24 <sup>a</sup> (±0.06)	0.14	0.36
	Flowering	0.85 <sup>b</sup> (±0.04)	0.76	0.91
	Ripening	0.91 <sup>c</sup> (±0.03)	0.85	0.95
Spiders	Tillering	0.27 <sup>a</sup> (±0.07)	0.16	0.43
	Flowering	0.81 <sup>b</sup> (±0.05)	0.69	0.89
	Ripening	0.86 <sup>b</sup> (±0.04)	0.75	0.93
Ladybeetles	Tillering	0.92 <sup>a</sup> (±0.01)	0.89	0.93
	Flowering	0.92 <sup>a</sup> (±0.01)	0.90	0.93
	Ripening	0.98 <sup>b</sup> (±0.01)	0.98	0.99

TABLE 3 Tukey's post-hoc tests

comparing the proportion of rice herbivores consumed in the diet of predators at three crop stages (tillering, flowering and ripening stages).

TABLE 2 Tukey's post-hoc tests comparing the proportion of rice herbivores consumed in the diet of predators in organic and conventional rice

farms.

*Note*: Different superscript letters indicate significant differences in the estimated marginal means (EMMs) of the posterior medians from Bayesian stable isotope mixing models ( $\alpha$ =0.05).

strong support for using GAPs in sustainable pest management, but also a novel aspect in biocontrol—generalist predators may function as guild-level specialist predators of pests during the late crop season. Specifically, across the three study years, GAPs in both organic and conventional farms consumed an increasing proportion of rice herbivores over the crop season, reaching 80%–97% in predators' diets at the ripening stage, whereas the proportions of alternative prey (detritivores and tourist herbivores) in their diets gradually decreased below 18% at the ripening stage (Figure 2; Appendix A: Table S2, Figure S2). The increase in rice herbivore consumption over time suggests that the biocontrol potential of predators increases toward late crop stages and peaks at the critical stage of crop production. This could be because of a higher herbivore (pest) density at late crop stages, suggested by a correlation between rice herbivore consumption and crop stage (see Section 4.3).

While GAPs consumed a high proportion of pests at late crop stages, the two major predator groups in our study system, spiders and ladybeetles (Table S1), exhibited distinct dietary patterns over the crop season. Specifically, pest consumption by spiders increased substantially, but pest consumption by ladybeetles remained stable over the season (Figure 3b vs. Figure 3c). This may be because different foraging modes—sit-and-wait (spiders) or actively hunting (ladybeetles)—can lead to different prey capture and thus diet composition (Klecka & Boukal, 2013; Nyffeler, 1999). For example, long-jawed orb-weavers (*Tetragnatha*), the most abundant genus in our spider samples, are sit-and-wait predators. The diet composition of these predators generally reflects prey availability (Nyffeler, 1999).

In contrast, ladybeetles are actively hunting predators and may preferentially feed on rice herbivores, resulting in stable pest consumption over time. Because predator foraging modes shape predator-prey-plant interactions (Schmitz, 2008), we encourage future studies to examine different assemblages of sit-and-wait vs. actively hunting predators in field conditions to reveal the most efficient biocontrol practice over the entire crop season.

# 4.2 | Generalists exhibit consistent pest consumption patterns over years

Ideal biocontrol agents provide a consistent, predictable effect on pests under various environmental conditions. Accordingly, GAPs in this study showed consistent pest consumption across years, despite various abiotic and biotic environmental conditions. Specifically, regarding the abiotic factors, the daily mean temperature, particularly from April to June, varied substantially among years (Appendix A: Figure S3). The daily precipitation also fluctuated over the three study years, with multiple high precipitation events in 2017, overall low precipitation in 2018, and relatively uniform precipitation in 2019 (Appendix A: Figure S3). Regarding the biotic factors, the composition of rice herbivores at the flowering and ripening stages differed substantially among the 3 years, in particular the two most dominant groups: leafhoppers (Cicadellidae/Nephotettix) and planthoppers (Delphacidae/Nilaparvata) (Appendix A: Table S3). Although both **FIGURE 4** The relative abundance of prey sources in organic and conventional rice farms over crop stages during the three study years: (a) 2017, (b) 2018 and (c) 2019. The relative abundance was determined from the sweep-net samples pooled across replicate farms.



abiotic and biotic factors varied substantially over the years of our study, pest consumption by GAPs generally remained stable, suggesting that GAPs can be a predictable, valuable tool for pest control in rice fields (but see Eitzinger et al., 2021).

# 4.3 | Factors associated with pest consumption by predators

The proportion of rice pests in GAPs' diets differed between farm types and among crop stages but was not associated with the per cent forest cover surrounding the farms or the relative abundance of rice herbivores in the field. Overall, GAPs in conventional farms consumed a higher proportion of rice pests in their diet compared to those in organic farms. There are two explanations for this: (1) Organic farming may promote arthropod diversity and therefore distract predators from feeding on target pests (Bengtsson et al., 2005; Birkhofer et al., 2008; Lichtenberg et al., 2017). (2) Pest densities may be higher in conventional farms (Porcel et al., 2018), leading to higher predator-prey encounter rates and thus pest consumption by GAPs. Regardless of the potential mechanisms, our results highlight the important but overlooked biocontrol value of GAPs in conventional farming systems. On the other hand, GAPs remain crucial for pest management in organic farms, particularly in the absence of pesticides. We encourage future studies to investigate their biocontrol effectiveness and interactions with other natural enemies in organic systems.

Besides farming practices, crop stages also affected pest consumption. Overall, pest consumption by GAPs increased from early (tillering) to late (ripening) stages, consistent with previous studies where predators consumed more pests in the late crop season (Hsu et al., 2021; Roubinet et al., 2017). This may be because pest populations increased with rice development and eventually predominated, leading to high pest consumption by GAPs at the flowering and ripening stages. These findings indicate a higher biocontrol value of predators when the crop production is most vulnerable to pest damage. Therefore, farming practitioners may want to avoid practices that harm predators (e.g. chemical applications) during this period to maintain healthy predator populations, preserve predator biodiversity and sustain the ecosystem services they provide.

Complex habitat structure (e.g. surrounding vegetation) has been suggested to promote predator abundance and diversity (Diehl et al., 2013; Langellotto & Denno, 2004), but such higher complexity did not affect predators' diet composition in our study. This might be because the prey species in our study system were mostly associated with rice plants but not the surrounding vegetation, consistent with a meta-analysis where habitat complexity had no effect on crop herbivore densities (Langellotto & Denno, 2004). Note that surrounding vegetation (e.g. cropping system mosaic) may still influence pest control efficacy by affecting the population dynamics and persistence of predators and prey (Vasseur et al., 2013). Furthermore, although the diet composition of generalist predators may correlate with prey availability in the field (Hsu et al., 2021; Wise et al., 2006), our beta regression models suggest no such correlation between rice BRITISH Journal of Applied Ecology

herbivores and GAPs. An explanation is that the relative abundance of rice herbivores was highly correlated with crop stage, a significant factor likely associated with various covariates (e.g. rice plant height) and explaining most variations in pest consumption by GAPs. We encourage further experiments, both observational and manipulative, to clarify the link between prey availability and generalist predators' diet composition in the field.

## 4.4 | Potential caveats of this study

Our study demonstrates high pest consumption by GAPs in rice fields over 3 years and examines the factors influencing GAPs' diet composition. While our study provides evidence for GAPs' biocontrol potential, some caveats may exist. First, high pest consumption in GAPs' diets does not necessarily imply a strong suppression of pest populations in the field, since pest population dynamics depend not only on the per capita effect of predators but also predator density and diversity (Letourneau et al., 2009; Rusch et al., 2016). To unveil the connection between per capita pest consumption and overall pest dynamics, future work may require complementing stable isotope analysis with field experiments (e.g. manipulating predator density), along with assessments of crop damage and production, to better understand the overall effect of GAPs on pest control and crop performance.

Second, while intraguild predation potentially influences pest control by GAPs (Michalko et al., 2019; Straub et al., 2008), it was not quantified in our diet composition analysis. Intraguild predation can compromise pest control by predators. For example, hunting spiders in apple orchards exhibit high levels of intraguild predation, thereby reducing pest control (Hambäck et al., 2021; Mezőfi et al., 2020). We did not quantify intraguild predation in our diet composition analysis because we were unable to accurately distinguish predator individuals engaging in intraguild predation from those that did not in the stable isotope mixing models. However, this may not be a major concern in our study for the following reasons: (1) Rice plants grow in dense clumps, especially at late crop stages (Figure 1b), forming a complex structure that likely reduces intraguild predation pressure (Finke & Denno, 2006; Janssen et al., 2007); (2) The primary spider families in our study were web-building sit-and-wait predators, which are less prone to intraguild predation (Denno et al., 2004); (3) The  $\delta^{15}$ N values of predators were close to those of rice herbivores (Figure S1), suggesting that if intraguild predation occurred, it was likely minor; otherwise, predators'  $\delta^{15}N$  values would be higher. Nevertheless, we caution that our diet estimates of predators (without predator-predator interference) might not apply to systems where intraguild predation prevails.

Third, the trophic discrimination factors (TDFs) used to calculate diet composition in this study were derived from general equations by Caut et al. (2009) rather than from feeding experiments, which were not feasible given our field study's diverse prey and generalist predator system. Nonetheless, we validated our results using other published TDFs relevant to our study taxa and found consistent outcomes, revealing the robustness of our findings to variations in TDF values (Appendix C).

## 5 | CONCLUSIONS

While biocontrol has been recognized as a valuable tool for sustainable agriculture, whether generalist predators can serve as effective biocontrol agents in pest management remains unclear. Our study helps solve this long-standing puzzle by using stable isotope analysis to quantify the diet composition of GAPs (spiders and ladybeetles) over the rice growth season and identifying the underlying mechanisms for enemy-pest interactions in rice farms over three consecutive years. The results show a high proportion of rice pests in GAPs' diets in both organic and conventional rice farms (e.g. 80%-97% at the ripening stage), suggesting that these generalist predators function as "pest specialists" at late crop stages (when rice plants are fruiting and pests are abundant). The high pest consumption remained consistent across years regardless of abiotic and biotic conditions, demonstrating the potential that generalist predators may produce a stable, predictable top-down effect on pests. Overall, our study lends support to applying generalist predators as biocontrol agents in both organic and conventional rice farms. As sustainable agriculture has become more important than ever in human history, incorporating the ubiquitous generalist predators into pest management, such as maintaining healthy populations of these predators, will likely open a promising avenue towards this goal.

#### AUTHOR CONTRIBUTIONS

Gen-Chang Hsu, Jia-Ang Ou, Min-Hsuan Ni, Zheng-Hong Lin, and Chuan-Kai Ho conducted the experiments; Gen-Chang Hsu and Chuan-Kai Ho designed and wrote the manuscript; Gen-Chang Hsu and Jia-Ang Ou performed the statistical analyses.

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### CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository Dataset https://doi. org/10.5061/dryad.r7sqv9spj (Hsu et al., 2025).

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## ORCID

Chuan-Kai Ho 🕩 https://orcid.org/0000-0002-6437-0073

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# sources in this study. (c), (f), and (i) indicate ladybeetles. of study.

Figure S1. Stable isotope biplot showing the predator and three prey

Figure S2. The proportions (mean  $\pm$  SE) of prey sources (rice herbivores, tourist herbivores, detritivores) consumed in the diet of predators in organic and conventional rice farms over crop stages in each study year: (a), (d), and (g) indicate both predators (spiders and ladybeetles) as a whole feeding guild; (b), (e), and (h) indicate spiders;

Figure S3. Daily mean temperature and precipitation of the study sites during the rice growth season (April-July) of the three years

Appendix B. Posterior means, SDs, medians, and 95% credible intervals for the proportion of prey sources in predators' diet based on Bayesian stable isotope mixing models.

Appendix C. Comparison of models using published trophic discrimination factors (TDFs) and TDFs derived from Caut et al. (2009).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix A. Table S1. Taxonomic composition of trophic guilds and the number of stable isotope capsules prepared for each of the three study years.

Table S2. The proportions (mean  $\pm$  SE) of prey sources (rice herbivores, tourist herbivores, and detritivores) consumed in predators' diet in organic and conventional rice farms over crop stages in each study year.

Table S3. The relative abundance of the major families/genera in rice herbivore guild at the flowering and ripening stages in organic and conventional farms in the three study years.

 
 Table S4. Percent forest cover within a 1-km radius circular buffer
surrounding the study farms.

Table S5. Statistical results from GLMM models for examining the effects of year, farm type, crop stage, and percent forest cover (fixed effects) on predator abundance and rice herbivore abundance, with farm ID nested within farm pair ID as a random effect.

**Table S6.** Number of individuals (mean  $\pm$  SE) from three prev guilds collected using the sweep-net method during the flowering and ripening stages in organic and conventional farms over three study years.

Table S7. The trophic discrimination factors (TDFs) (mean  $\pm$  SD) for the three prey sources in the stable isotope mixing models.