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Organic farming and associated management practices benefit multiple wildlife taxa: A large-scale field study in rice paddy landscapes

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Abstract

1. Organic farming has potential for the conservation of global biodiversity and associated ecosystem services. Despite this, knowledge of the effects of organic farming systems on farmland biodiversity is limited in Asia, the worldwide leader in rice production.

2. We conducted the first national-scale study to investigate the effects of three different rice farming systems (conventional, low-input and organic) and specific management practices (e.g. herbicide and insecticide applications, crop rotation and levee-vegetation management) on species richness and abundance of multiple taxonomic groups (plants, invertebrates, *Pelophylax* and *Hyla japonica* frogs, cobitid loaches and birds) in Japan during 2013–2015.

3. Organic fields supported the highest richness and abundance of several taxonomic groups (native/Red List plants, *Tetragnatha* spiders, *Sympetrum* dragonflies and *Pelophylax* frogs), followed by low-input and conventional fields. We also found taxon-specific responses to specific management practices. For instance, plant richness and *Tetragnatha* and *Sympetrum* abundance increased with reduced herbicide and/or insecticide applications. *Sympetrum* and cobitid loach abundance increased in the absence of crop rotation, whereas *H. japonica* abundance increased with crop rotation. *Pelophylax* abundance increased with an increased height of levee vegetation.

4. At spatial scales larger than single fields, waterbird richness and abundance were positively correlated with the proportion of organic rice fields, presumably due to increased prey abundance. Meanwhile, landbird richness and abundance were positively associated with annual precipitation and annual mean temperature, suggesting that such climate increases food availability.

5. *Synthesis and applications.* We highlight the positive effects of organic and low-input farming for biodiversity relative to conventional farming in rice paddies. We also provide the scientific basis of the current agri-environmental schemes in Japan, subsidising organic and low-input farming for biodiversity. The

taxon-specific associations with management practices indicate that avoiding crop rotation, maintaining levee vegetation and organic farming at large spatial scales can also be wildlife friendly. These practices may thus be incorporated into agri-environment schemes for effective biodiversity conservation.

KEYWORDS

agricultural intensification, agri-environmental scheme, farmland biodiversity, low-input farming, organic farming, pesticide application, rice field, wildlife-friendly farming

1 | INTRODUCTION

Agriculture is among the most serious threats to biodiversity across the globe (Newbold et al., 2015). The world's growing population is expected to exceed nine billion people by 2050, which poses a critical challenge to the conservation of global biodiversity while maintaining food security (Godfray et al., 2010). One promising approach to this goal is organic agriculture, which avoids the use of agrochemicals to reduce the negative impacts of agriculture on the environment. Studies have shown that organic farming supports higher richness and abundance of organisms than conventional farming does (e.g. Bengtsson, Ahnstrom, & Weibull, 2005; Lichtenberg et al., 2017; Tuck et al., 2014). Such wildlife-friendly farming practices are also expected to play a crucial role in food production because some organisms on the farm support essential ecosystem services, such as pollination and pest control (Tscharntke et al., 2012). Enhanced-ecosystem services associated with farmland biodiversity may thus enable wildlife-friendly farming to be more sustainable compared with conventional agriculture.

The paucity of data on wildlife benefits of organic farming in regions other than Europe and North America poses a major knowledge gap (Seufert & Ramankutty, 2017). Organic farming now takes place on 1.1% of global agricultural lands, comprising many parts of the world: Oceania (45% of global organic agricultural land), Europe (25%), Latin America (13%), North America (6%), Asia (6%) and Africa (3%; table 2 in Willer & Lernoud, 2017). However, studies on the wildlife benefits of organic farming have been heavily biased towards Europe and North America, comprising more than 90% of the earlier studies (Tuck et al., 2014). Thus, for many other regions and the agricultural systems therein, there is currently limited information regarding the reported positive effects of organic farming on biodiversity (e.g. Bengtsson et al., 2005; Tuck et al., 2014). Filling this knowledge gap would enable a more balanced and global assessment of the effects of organic farming on the biodiversity and associated ecosystem services.

Asia is an important region in terms of high-biodiversity value, where one-third of the 35 global hotspots of biodiversity are included (Mittermeier, Turner, Larsen, Brooks, & Gascon, 2011). Asia is also the world's leading producer of rice, contributing 87.9% of total rice production (FAO, 2016). Rice has been the primary staple food of more than half of the world's population, providing over 20% of the daily calories for more than 3.5 billion people (Dawe, Pandey, & Nelson, 2010). Rice fields, which are usually flood-irrigated or rain-fed during at least the growing season of rice plants (Maclean et al., 2013), provide habitats for a variety of wildlife species, including aquatic plants, invertebrates, frogs, fish and birds, in many parts of the world (Elphick, Baicich, Parsons, Fasola, & Mugica, 2010; Lawler, 2001). Since the late 20th century, however, agricultural intensification has threatened these rice paddy organisms (Bambaradeniya & Amerasinghe, 2004). Considering future increases in population and the associated economic growth in Asia (Laurance, Sayer, & Cassman, 2014), there is an urgent need to find alternatives to conventional farming to halt the loss of biodiversity in Asian rice paddies.

Growing evidence suggests positive effects of organic farming and less strict low-input farming (i.e. reduced use of agrochemicals) for biodiversity relative to conventional farming in rice paddies (e.g. Baba, Kusumoto, & Tanaka, 2018; Ibáñez, Curcó, Riera, Ripoll, & Sánchez, 2010; Wilson, Watts, & Stevens, 2008). Low-input systems are expected to provide lower wildlife benefits and higher yield on a per-area basis than organic ones do, which can be important for improving biodiversity over large areas (Elphick et al., 2010). Other studies have focused on specific management practices such as agrochemical use, water management and vegetation in the levee (e.g. Amano et al., 2011; Elphick, 2004; Settle et al., 1996). However, the relative importance of overall farming systems and specific practices, especially for multiple taxonomic groups, has rarely been quantified. Quantifying taxon-specific responses to farming systems and practices would enable understanding the strengths and limitations of specific farming systems or practices for biodiversity. This is also relevant to policy-making because some organic and low-input farming systems, often combined with specific practices (e.g. winter flooding), are subsidized through agri-environment schemes for biodiversity conservation (Ibáñez et al., 2010; Katayama, Baba, Kusumoto, & Tanaka, 2015), and an efficient allocation of subsidies to farming systems or practices that might provide wildlife benefits is critical.

Here, we present the first multi-taxon study exploring the effects of organic and low-input rice farming systems and associated management practices at the national scale by surveying more than 1,000 rice fields during 2013–2015 across Japan. Low-input farming was defined as rice cultivation using 50% or less of the chemical pesticide/fertilizer inputs of conventional farming in each prefecture (Usio, Saito, Akanuma, & Watanabe, 2014). This study focused on five taxonomic groups (plants, invertebrates, frogs, fish and birds), all of which have attracted much attention for their conservation values and for the ecosystem services

they provide, such as pest control and nutrient cycling (Katayama, Baba, et al., 2015). We specifically addressed two questions. First, how do farming practices (e.g. agrochemical inputs, crop rotation, first flood-irrigation date) differ among the three rice farming systems (conventional, low-input and organic)? Second, what farming systems or practices better explain the richness or abundance of each taxon?

2 | MATERIALS AND METHODS

We provide an overview of methods here; further details on study fields, variable selection and sampling schemes are described in Appendix S1 and Figure S1.

2.1 | Field surveys

This study was carried out in Japan on 28 paired sites of conventional and conservation blocks from 2013 to 2015 (Figure 1, left panel). Each pair of sites was more than 10 km apart, except for one pair (5 km). Conservation blocks contained variable amounts of organic/low-input rice farming, certified by local and national governments [on average, 24.5% (range: 3.2%–41.1%)]. Conventional blocks contained <1.0% of organic/low-input rice farming, except for one site (13.3% in the conventional block vs. 23.3% in the conservation block). Each site was surveyed for 1–3 years during 2013–2015; in every year, 1–10 fields were chosen as surveyed fields in each block (Figure 1, right). In total, 1,074 rice fields (541 conventional, 238 low-input, and 295 organic fields) were surveyed during the 3 years. The proportional forest cover surrounding each field and field size differed little among the three farming systems (Table S1).

Seven representative taxonomic groups in rice fields were surveyed by field experts in each site during the rice-growing season (May–August; Table 1). All taxa were surveyed at the field level (within the field for plants, invertebrates and fish, and in levees for frogs), except birds, which were recorded at the block level (as point counts covered multiple fields). For plants, we used observed richness due to the same number of samples (three quadrats) in each field. For arthropods, *Tetragnatha* spiders, *Sympetrum* dragonflies and Coleoptera were chosen as key indicator animals for evaluating wildlife benefits of organic/low-input farming; their abundance, not species richness, was calculated because species identification was insufficient in several sites. For frogs and fish, because the number of species observed in each field was generally very low (fewer than three species), the abundance of the dominant species groups was calculated. Rarefied bird richness was calculated to control for survey effort differences among blocks. Each taxonomic group was mostly sampled within a week in the paired conventional and organic/low-input fields. We explicitly considered the effects of the differences in survey effort and number of surveyed fields among farming systems, taxonomic groups, and sites on our results (Appendix S2).

2.2 | Environmental data

Information on farming practices and rice yields in each field was collected through farmer interviews. We selected 'biologically reasonable' variables at the field and block scales (Tables 2 and 3) for each taxon (Table 1) according to the findings of previous studies (Appendix S1). At the field scale, the farming system category was considered to represent the effects of overall management
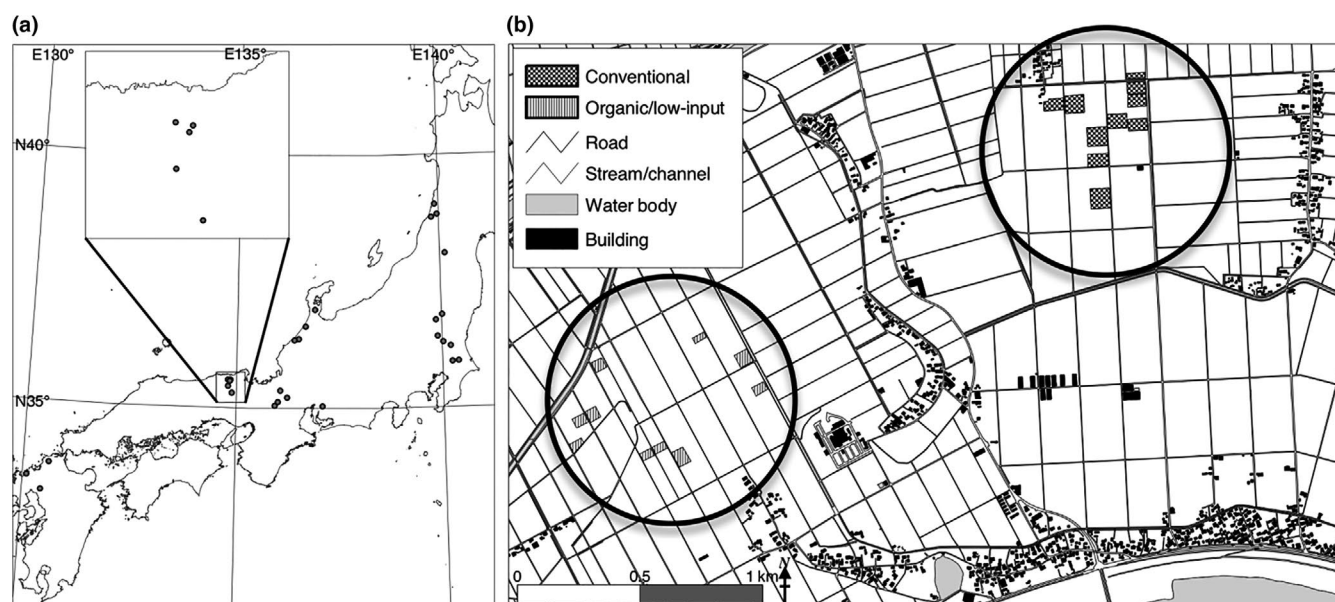

FIGURE 1 (a) Paired sites (28) of conventional and conservation blocks in Japan (grey circles). (b) Example of the two blocks within a site (open circles with 0.5 km radius). Each 'block', which was a virtually defined spatial extent to guide the selection of survey fields in each site, contains 1–10 rice fields surveyed in each year during 2013–2015. Land use with white colour depicts mostly rice fields. Background map sources were as follows: boundary data of Global Map Japan version 2.1 (a) and topographic data of Fundamental Geospatial Data (b), both developed by the Geospatial Information Authority of Japan

TABLE 1 Summary description of sampling methods for conventional, low-input and organic rice fields in Japan, mean survey efforts per field (range), number of fields, and number of fields (sites) in each farming system and year for each response variable of taxonomic groups. Survey effort was calculated as the number of sampling units per field (or per block for birds) × number of survey times per season

Response variable	Sampling method	Mean survey effort	N_{sites}	N_{total}	N_{fields} (N_{sites}) in each system and year								
					2013			2014			2015		
					Con.	Low.	Org.	Con.	Low.	Org.	Con.	Low.	Org.
Richness of (1) native plants and (2) Red List plants	Quadrat sampling	3.0 (3) m²	22	445	63 (10)	23 (4)	48 (7)	80 (14)	35 (6)	67 (12)	65 (9)	24 (4)	40 (6)
Abundance of *Tetragnatha* spiders	Sweep net	74.51 (20–120) swings	26	335	46 (15)	30 (9)	18 (8)	58 (16)	33 (9)	34 (12)	60 (16)	29 (7)	27 (9)
Abundance of nymphal exuviae of *Sympetrum* dragonflies	Line transect	95.35 (40–160) m	26	353	44 (15)	25 (8)	18 (8)	58 (16)	32 (8)	34 (12)	71 (16)	44 (7)	27 (9)
Abundance of Coleoptera larvae	D-frame fishing net	11.55 (5–20) times	26	376	53 (15)	34 (8)	18 (8)	53 (15)	43 (8)	35 (12)	69 (15)	43 (7)	28 (9)
Abundance of (1) *Pelophylax* frogs and (2) *Hyla japonica* frogs	Line transect count	111.69 (40–160) m	25	171	15 (7)	8 (3)	9 (4)	29 (11)	12 (5)	30 (12)	34 (12)	10 (2)	24 (9)
Abundance of Cobitidae loaches	Minnow trap	8.61 (2–10) traps	25	257	22 (10)	10 (4)	13 (6)	40 (16)	16 (8)	32 (12)	60 (14)	39 (5)	25 (9)
Richness and abundance of (1) water-birds and (2) landbirds	Point count	6.54 (2–18) times	15	50	–	–	–	–	–	–	–	–	–

practices associated with each system, including their additive and synergistic effects. Flood-irrigation dates indicate the timing when temporal aquatic habitats (i.e. flooded rice fields) were created. Young rice plants are transplanted in flooded fields, which are kept flooded until mid-summer drainage. Winter flooding is usually combined with straw incorporation. At the block scale, five variables (ORG, ORLO, FORE, TEMP and PREC) were calculated as their average values at the corresponding scale of all surveyed points for bird counts in each block. Vegetation height was not included owing to missing data in several sites. All the continuous variables were standardized (zero mean, unit standard deviation) before analyses.

2.3 | Data analysis

2.3.1 | Differences in farming practices among the three farming systems

Differences in farming practices (variables 2–8 in Table 2) and rice yields among farming systems were tested using linear mixed models

TABLE 2 List of environmental variables at the field scale. A check mark (✓) indicates that the corresponding variable was used to explain richness or abundance of each taxonomic group in rice fields. For categorical variables other than farming system and survey year, each field was assigned 0 (not used) or 1 (used)

Abbreviation	Variable	Type	Range	Plants	Invertebrates and fish	Frogs
					Taxonomic group	
FARM	1. Farming system type (0 = Conventional, 1 = Low-input, 2 = Organic)	Categorical	0, 1, 2	✓	✓	✓
HRBF	2. No. herbicide active ingredients applied (fields)	Continuous	0–8	✓	✓	
HRBL	3. No. herbicide active ingredients applied (levees)	Continuous	0–6			✓
INSE	4. Neonicotinoid or phenylpyrazole insecticide use (nursery boxes)	Categorical	0, 1		✓	✓
ROTA	5. Crop rotation every other year (or winter-spring) with upland crops	Categorical	0, 1	✓	✓	✓
IRRI	6. Date of first flood irrigation into rice fields (1st April = 0)	Continuous	0–79	✓	✓	✓
FLOD	7. Winter flooding	Categorical	0, 1	✓	✓	✓
VEG	8. Vegetation height of levees (m)	Continuous	0–0.75			✓
VEG2	9. Quadratic term of VEG	Continuous	0–0.56			✓
YEAR	10. Survey year (0 = 2013, 1 = 2014, 2 = 2015)	Categorical	0, 1, 2	✓	✓	✓

Abbreviation	Variable	Range
HRBF.B	1. Mean no. herbicide active ingredients applied (fields)	0–7
INSE.B	2. Proportion of fields with neonicotinoid or phenylpyrazole insecticide use (nursery boxes)	0–1
ROTA.B	3. Proportion of fields with crop rotation	0–1
IRRI.B	4. Average date of first flood irrigation	4–76
FLOD.B	5. Proportion of fields with winter flooding	0–0.64
ORG	6. Proportional area of organic rice fields at 200 m scale	0–0.41
ORLO	7. Proportional area of organic and low-input rice fields at 200 m scale	0–0.41
FORE	8. Proportional forest area at 1.0 km scale	0–0.59
TEMP	9. Annual mean temperature at 2.5 km scale (°C)	11.8–16.1
PREC	10. Annual precipitation at 2.5 km scale (mm/year)	1,192–2,418
YEAR	11. Survey year (1 = 2014, 2 = 2015)	1, 2

TABLE 3 List of environmental variables used to explain the richness and abundance of birds at the block scale. All the environmental variables other than the survey year were continuous variables

(LMMs) for continuous variables and generalized LMMs (GLMMs) with a binomial error structure and logit link for categorical variables. Continuous variables were log-transformed to normalize their distributions; effects of normality assumptions on model estimates were also tested (Appendix S3). The explanatory variables were FARM and YEAR (see Table 2). The random variable was site ID (assigned to each of 28 sites); field ID (assigned to each of the 709 different fields because several fields were surveyed for multiple years) was not included owing to the problem of model convergence. For each response variable, the differences between each pair of the three farming systems were tested using *post hoc* Tukey HSD tests.

2.3.2 | Relationships among biodiversity and environmental factors

GLMMs and an information theoretic approach to model selection and multi-model inference were used to examine the relationships among species richness or abundance of each taxon (Table 1) and environmental factors (Tables 2 and 3; see Tables S2 and S3 for the correlation coefficients). Log-transformed survey effort was used as the offset term for abundance to model their densities. The random variables were site ID and field ID at the field scale, and site ID at the block scale. We used four families of distributions (Poisson, negative binomial, zero-inflated Poisson and zero-inflated negative binomial), and for each distribution, we fitted the full model and all submodels containing different combinations of predictors. We ranked all submodels across the four distributions according to their corrected Akaike's information criterion (AICc; Burnham & Anderson, 2002). To address multicollinearity, we excluded submodels with variance

inflation factor >3 (Appendix S4). We then calculated Akaike weights (w_i) in each model, the sum of Akaike weights (SW), model-averaged coefficients and associated unconditional standard errors for each predictor (Appendix S4). An additional analysis was conducted to compare richness and abundance between each farming-system pair (Appendix S5). Spatial correlograms of model residuals showed no strong spatial autocorrelation (Appendix S6). A list of R packages is shown in Appendix S7.

3 | RESULTS

3.1 | Taxonomic diversity in rice paddies

Field surveys in the flood-irrigation periods (from spring to summer) identified 69 native species, including 27 Red List species of plants in 767 rice fields; 5,302 *Tetragnatha* spiders, including seven species in 437 fields; 6,352 *Sympetrum* dragonfly nymphs of five species in 456 fields; 3,054 Coleoptera larvae of 35 species in 497 fields; 2,900 *Pelophylax* frogs of three species in 433 fields; 5,613 *Hyla japonica* frogs in 433 fields; 1,135 Cobitidae loaches in 343 fields; 20 waterbird species, including 968 individuals; and 21 landbird species, including 1,790 individuals. The numbers of non-native species were eight for plants, one for frogs, two for fish and one for birds. Species lists are shown in Tables S4–S6.

3.2 | Farming practices and their effects

LMMs/GLMMs and post hoc Tukey tests showed significant differences in all the farming practices among farming systems (Figure 2,
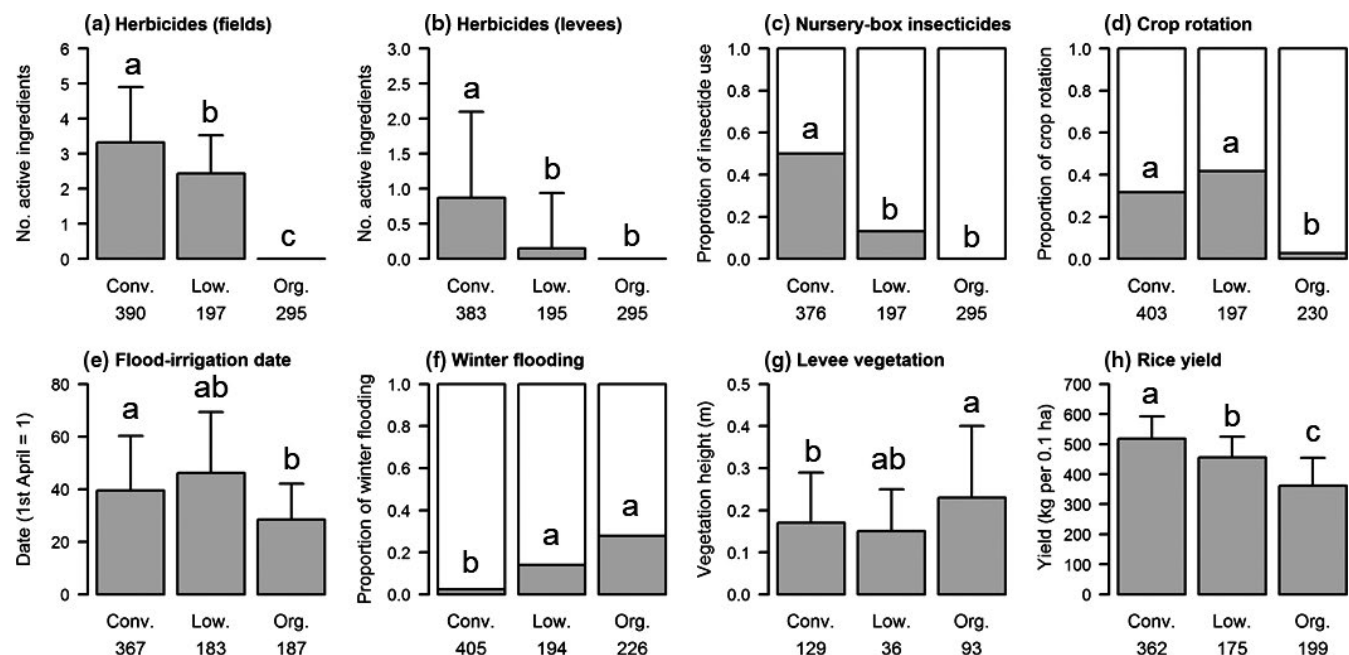

FIGURE 2 Average (+*SD*) values in farming practices and yield weight of threshed rice (a–h) in the three farming systems (conventional, low-input and organic rice fields in Japan). Numbers below the bars are sample sizes (i.e. number of fields). Same letters (a, b, c) above columns indicate no significant differences (*p* > 0.05) in the mean values between the farming systems. See Tables S7 and S8 for model coefficients

Tables S7 and S8). Compared to low-input and organic farming, conventional farming was characterized by higher frequency of herbicide/insecticide applications and higher rice yield (+14%, +43%). Organic farming was denoted by no use of chemical pesticides, 29% lower crop rotation frequency, 26% higher winter flooding frequency, 11 days earlier flood irrigation dates and 6 cm higher vegetation height on levees, although robust LMMs showed no significant difference in flood-irrigation dates (Table S7). Low-input farming was intermediate but showed the latest flood-irrigation date.

3.3 | Farming practices and wildlife diversity

Model selection showed that no single model of richness or abundance was clearly superior to others for any taxonomic group (Table S9). For native and Red List plant richness, farming system had large SW (>0.99, Figure 3a,b), with richness decreasing in the order of organic, low-input and conventional fields (Tables

S10 and S11). Herbicide applications also had large SW (>0.99, Figure 3a,b), with negative coefficients and small standard errors (Figure 4a,b).

For *Tetragnatha* abundance, farming system had large SW (>0.99, Figure 3c), with higher abundance in organic and low-input fields than in conventional ones (Tables S10 and S11). Herbicide and insecticide applications also had large SW (0.99 and 0.71, Figure 3c) and were negatively associated with spider abundance (Figure 4c). For *Sympetrum* abundance, the order of SW decreased in the order of crop rotation > insecticide applications > year > farming system (0.99, 0.98, 0.93 and 0.82, Figure 3d), with strong negative correlations of crop rotation and insecticide applications (Figure 4d). Organic fields supported their higher abundance than conventional and low-input ones did (Tables S10 and S11). For Coleoptera abundance, no predictor (except for year) had large SW (<0.57, Figure 3e), and standard errors of all the coefficients were large (Figure 4e).
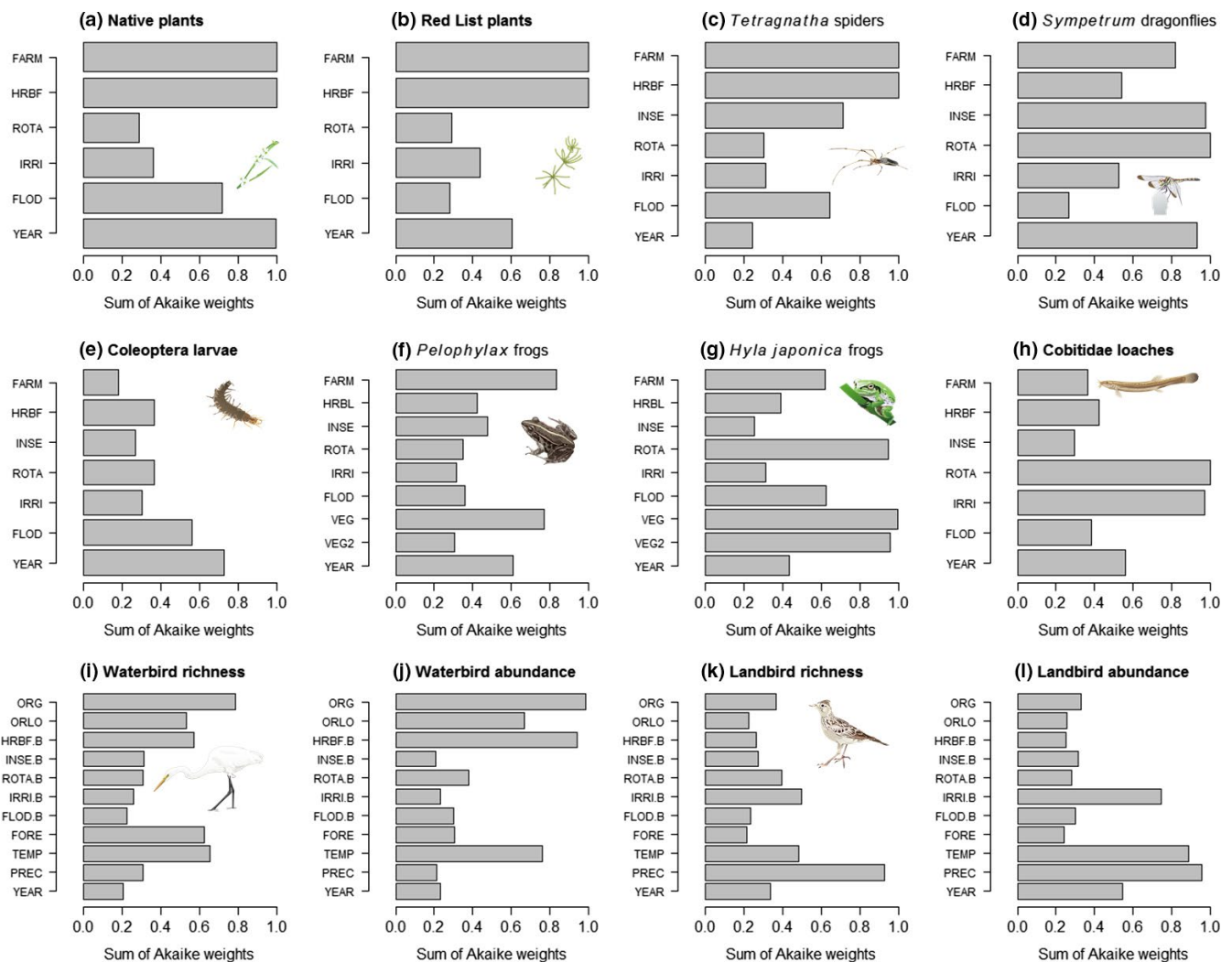

FIGURE 3 Sum of Akaike weights of predictor groups for each of the response variables: (a) native plant richness, (b) Red List plant richness, (c) *Tetragnatha* abundance, (d) *Sympetrum* abundance, (e) Coleoptera abundance, (f) *Pelophylax* abundance, (g) *Hyla japonica* abundance, (h) Cobitidae loaches, (i) waterbird richness, (j) waterbird abundance, (k) landbird richness and (l) landbird abundance. Variable abbreviations are shown in Tables 2 and 3
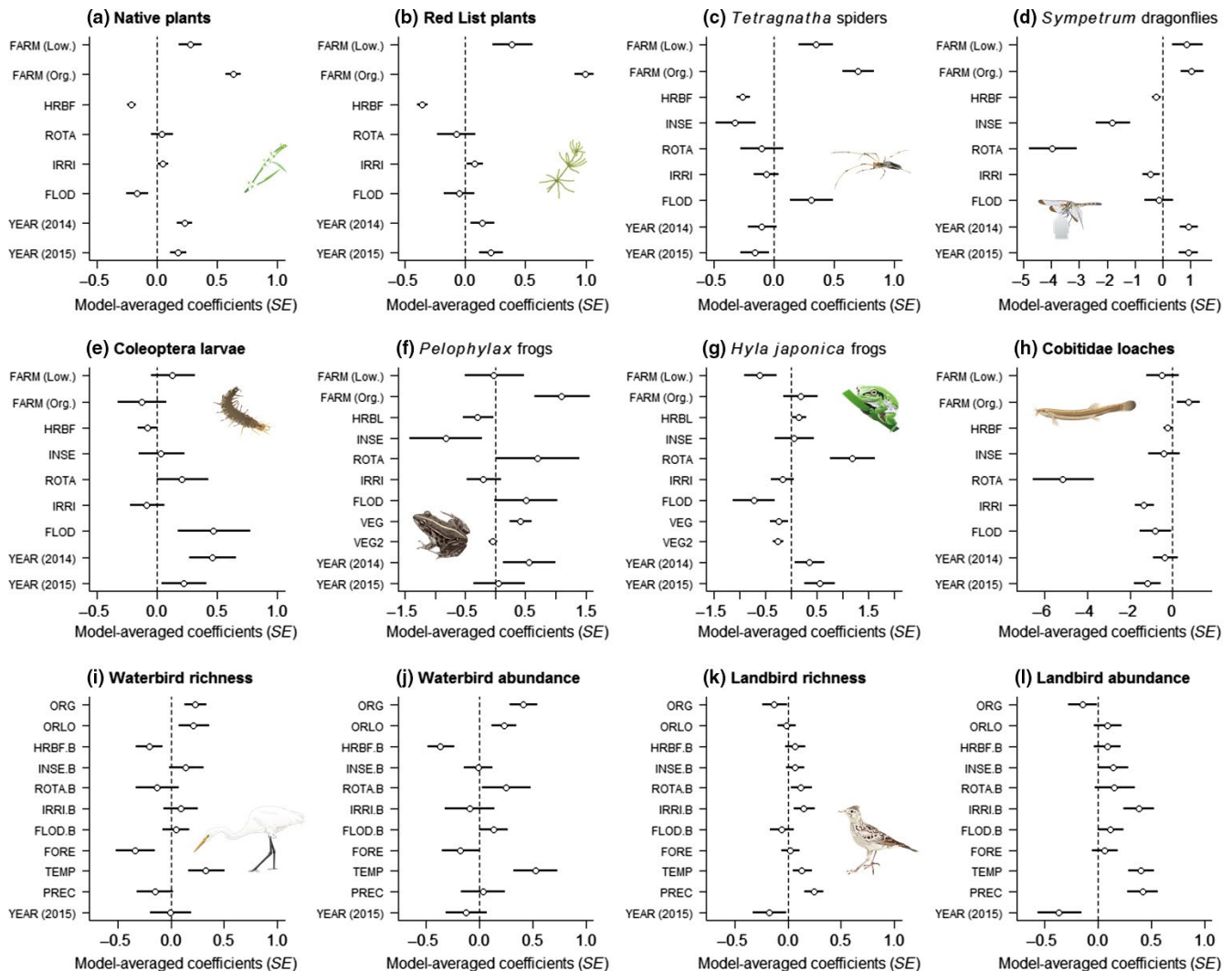
FIGURE 4 Model averaged coefficients (unconditional *SE*) of predictor groups for each of the response variables: (a) native plant richness, (b) Red List plant richness, (c) *Tetragnatha* abundance, (d) *Sympetrum* abundance, (e) Coleoptera abundance, (f) *Pelophylax* abundance, (g) *Hyla japonica* abundance, (h) Cobitidae loaches, (i) waterbird richness, (j) waterbird abundance, (k) landbird richness and (l) landbird abundance. All the continuous variables were standardized. Variable abbreviations are shown in Tables 2 and 3

For *Pelophylax* abundance, farming system had the largest SW (0.83, Figure 3f), with higher abundance in organic fields than in conventional ones (Tables S10 and S11). Vegetation height also had large SW (0.77, Figure 3f) and was positively associated with frog abundance (Figure 4f, see also Figure S2a). For *H. japonica* abundance, SW was large for vegetation height, its quadratic term, and crop rotation (>0.95, Figure 3g); model averaging showed a positive association with crop rotation and nonlinear association with vegetation height (Figure 4g), with its peak at 10–20 cm (Figure S2b). For Cobitidae abundance, crop rotation and flood-irrigation date had large SW (>0.97, Figure 3h), with strong negative correlations (Figure 4h).

For waterbird richness and abundance, the proportion of organic farming had the largest SW (0.79 and 0.98, Figure 3i,j), with positive associations (Figure 4i,j) up to 40% (Figure 5). In addition, the absolute values of standardized coefficients were greater for temperature (and forest cover for richness; Figure 4i,j). For landbird richness and abundance, precipitation had the largest SW (>0.93, Figure 3k,

l) and the largest positive associations (Figure 4k,l), followed by temperature and flood-irrigation date for abundance.

4 | DISCUSSION

The three farming systems differed in both management practices (i.e. pesticide applications, crop rotation, winter flooding and vegetation height in levees) and biodiversity. Among the three farming systems, organic farming supported the highest richness and abundance in many taxonomic groups at multiple spatial scales (native/ Red List plants, *Tetragnatha*, *Sympetrum*, *Pelophylax* and waterbirds), followed by low-input and conventional ones. To our knowledge, this is the first study quantifying taxon-specific associations with farming systems and practices, showing that no single system or practice could satisfactorily explain the richness and abundance of entire taxonomic groups.
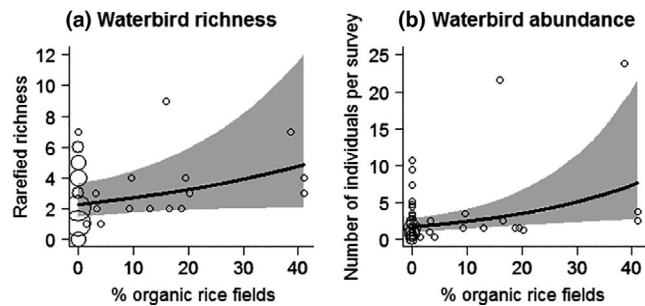
FIGURE 5 The relationships between the proportion of organic rice fields and (a) richness and (b) abundance of waterbirds at the block scale. Point size is proportional to sample size. Solid lines and grey polygons show average regression lines and their 95% confidence intervals, respectively, drawn from model-averaged coefficients

4.1 | Relationships among biodiversity and environmental factors

The high native/Red List plant richness in organic fields, followed by low-input and conventional fields, was best explained by herbicide application differences. In this regard, laboratory experiments have shown the adverse effects of herbicides on the growth of threatened aquatic ferns (e.g. Aida, Ikeda, Itoh, & Usui, 2006), and, consistently, the findings of the present study indicate that herbicide use is the most detrimental factor affecting plant diversity in agricultural fields. Moreover, although not quantified in the present study, chemical fertilizer use in conventional fields may also be detrimental, especially for rare plant species preferring wet and oligotrophic habitats (Uematsu & Ushimaru, 2013).

The high *Tetragnatha* abundance in organic and low-input fields seemed to be mainly due to both reduced herbicide and insecticide applications to nursery boxes. Herbicide applications may have affected these spiders directly or indirectly through changes in prey abundance (Amano et al., 2011). However, because the spiders were not directly exposed to the insecticides applied in nursery boxes, the negative insecticide effect likely arose from reduced prey availability, such as flying insects emerging from paddy water (Baba et al., 2018; Tsutsui, Tanaka, Baba, & Miyashita, 2016), although bioaccumulation was also possible for insecticides like fipronil (Chaton, Ravanel, Tissut, & Meyran, 2002). In contrast to the observations reported by Takada, Takagi, Iwabuchi, Mineta, and Washitani (2014), we identified no clear benefit of winter flooding, which may be dependent on actual prey abundance and surrounding landscapes.

Sympetrum abundance was better explained by the negative associations with crop rotation and insecticide applications than by the positive association with organic farming. In *Sympetrum* dragonfly life cycles, eggs deposited on wet mud in rice fields before/after harvest in autumn overwinter on the soil surface and hatch immediately when water is poured into the paddies in spring (Jinguji, Tashiro, Sato, Tsuyuzaki, & Kondo, 2006). Aridification and intensive tillage, as for crop rotation with upland crops, therefore seem to be detrimental for their survival. Moreover, neonicotinoid

or phenylpyrazole insecticides are known to be highly toxic to Odonata nymphs, reducing their abundance (Jinguji, Thuyet, Uéda, & Watanabe, 2013).

Neither farming system nor practice explained the coleopteran larval abundance, which may be explained by their high tolerance to water pollution relative to other aquatic invertebrates (Chang, Lawrence, Rios-Touma, & Resh, 2014). Earlier studies found a higher diversity or abundance of invertebrates in organic fields than in conventional fields (Hesler, Grigarick, Oraze, & Palrang, 1993; Wilson et al., 2008) and detrimental effects of pesticide use on arthropod diversity (Settle et al., 1996), suggesting higher benefits to other aquatic invertebrate species for reduced pesticide applications. In contrast to the findings of previous studies (e.g. Lawler & Dritz, 2005), we found that winter flooding also has no clear benefit, which seems to be due to high variations in the water cover among fields in Japan (Usio et al., 2014).

Pelophylax abundance was best explained by organic farming, suggesting the importance of overall effects of management practices associated with the system, including less-intensive vegetation management in levees. Since *Pelophylax* frogs inhabit waterbodies such as rice fields and adjacent ditches throughout the year (Naito, Sakai, Natuhara, Morimoto, & Shibata, 2013), the species is likely to benefits from habitat improvement within and adjacent fields through increased prey abundance by disuse of pesticides and predator avoidance by tall vegetation in levees connecting fields and ditches.

In contrast, *H. japonica* abundance was not influenced by organic farming and rather high in fields with crop rotation. Unlike *Pelophylax*, these frogs have adapted to temporally flooded habitats to avoid aquatic predators (Iwata & Fujioka, 2006), and use drier habitats such as grasslands and trees during the non-breeding seasons (Naito et al., 2013), implying that crop rotation sites provide suitable habitat heterogeneity for these frogs. Their high abundance with short vegetation (~20 cm: Figure S2) was also reported for juveniles (Naito et al., 2013). However, there is no clear evidence showing why the intermediate vegetation height supports their high abundance.

Cobitidae abundance was high in fields without crop rotation and with earlier flood-irrigation. The negative association with crop rotation indicates the importance of overwintering conditions. Loach individuals overwinter under the ground of rice fields or in adjacent ditches (Tawa, Nakanishi, Murakami, Nishida, & Sawada, 2013) and thus their survival were likely to compromised by aridification and intensive tillage. The negative flood-irrigation date association suggests that earlier flooding dates allow more loach individuals to enter and spawn in the fields over the flooding period (Katayama, Saitoh, Amano, & Miyashita, 2011).

Higher waterbird richness and abundance in blocks with a higher proportion of organic fields indicate the importance of food availability at spatial scales larger than single fields, as reported earlier (e.g. Ibáñez et al., 2010; Lane & Fujioka, 1998). Our direct observations also found that Great egrets achieved higher food intake rates in organic fields than in conventional ones (Katayama, Murayama, & Mashiko, 2015). Considering that egrets and herons during their

breeding seasons are known to fly long distances for foraging (often >10 km: Custer & Galli, 2002), the benefits of organic farming on waterbirds may be even greater at larger spatial scales than that at the block scale.

As many landbirds utilize levees and dry farmlands rather than flooded rice fields in agricultural landscapes (Amano et al., 2008), the positive associations of these birds with annual precipitation and temperature in the present study indicate that such climate provides higher terrestrial food abundance, such as invertebrates (e.g. Amano et al., 2011). Higher landbird abundance in blocks with later flood-irrigation dates can be explained by the increase in their suitable habitats, that is, unflooded rice fields, in the landscape (Elphick, 2004).

4.2 | Conservation implications and future directions

Our findings indicate the positive effects of organic farming on biodiversity in Japanese rice paddies relative to conventional farming, similar to rice paddies in Oceania, North and Central America, Western and Southern Europe, and Eastern and South-Eastern Asia (e.g. Cochard, Maneepitak, & Kumar, 2014; Hesler et al., 1993; Ibáñez et al., 2010; Kumar, Kumar, McCoy Colton, Springer, & Trama, 2013; Wilson et al., 2008), as well as in dry farmlands such as for wheat, vegetable and fruit cultivation (e.g. Katayama, Bouam, Koshida, & Baba, 2019; Tuck et al., 2014). Given the large areas of land currently under agricultural production, our findings suggest the potential role of organic farming in reducing the continued loss of biodiversity in both terrestrial and aquatic agricultural ecosystems. Nevertheless, the overall benefits of organic farming for biodiversity need to be carefully considered; rice fields may be unsuitable for some wetland species, and reduced yield from organic farming may trigger conversion of natural wetlands into rice production (Elphick et al., 2010). To date, however, there have been no studies that have demonstrated a direct link between organic rice production and the expansion of conventional high-input rice production. Therefore, effective conservation policies for aquatic diversity should be implemented through holistic measures, including organic and wildlife-friendly farming, fallow flooding, resuming abandoned paddies and protecting natural wetlands (Koshida & Katayama, 2018; Maltchik, Stenert, & Batzer, 2017). Further research is needed on trade-offs between farm scale biodiversity and yield and yield stability. Such wildlife-friendly systems may vary considerably with region according to the differences in landscape, climate and trophic interactions, which are also known to shape biological communities in rice agroecosystems (e.g. Amano et al., 2011; Dominik, Seppelt, Horgan, Settele, & Václavík, 2018).

Our results also provide three implications for current agri-environmental schemes in Japan. First, we provided scientific evidence of the effectiveness of subsidies to organic and low-input rice farming for biodiversity by local and national governments in Japan, although it should be assumed that low-input farming is beneficial only to taxonomic groups sensitive to agrochemical use (e.g. plants, spiders and dragonflies). Ongoing support to farmers practicing organic/low-input farming, combined with the conservation of remaining natural wetlands, would be crucial for regional biodiversity. Second, we identified farming practices other than agrochemical reduction, which could improve biodiversity, such as avoiding crop rotation and maintaining levee vegetation. These practices should thus be the subject of agri-environment schemes in paddy fields. Finally, spatially aggregating organic farming can improve conservation benefits for waterbird populations. Therefore, collective actions of neighbouring farmers for practicing wildlife-friendly farming should be encouraged by financial incentives to farmers' groups.

AUTHORS' CONTRIBUTIONS

N.K., Y.O., Y.G.B., K.T, and S.O. wrote the paper; N.K. and Y.O. performed the analyses; H.I. and K.T. devised the project; H.I., K.T. and Y.N. were involved in study design. All the authors but Y.O. collected the data. All the authors reviewed and contributed critically to the draft and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.6d66b49 (Katayama et al., 2019).

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