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EFFECTS OF FIELD MARGINS AND OTHER UNCULTIVATED FIELDS ON ORTHOPTERA ASSEMBLAGES IN THE MOUNTAINOUS PADDY FIELD AREA OF NORTHEAST JAPAN

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Abstract. To understand how farmlands help maintain biodiversity, we investigated the relationship between habitat heterogeneity and Orthoptera community composition on multiple spatial scales. First, we determined the impact of 12 environmental variables on the Orthoptera community diversity by sampling 37 quadrats in uncultivated fields over a broad spatial scale. Canonical correspondence analysis (CCA) demonstrated that environmental parameters influenced species composition. The first two canonical axes were associated with forest cover, grass (including harvested dried grass in some cases), bare or paddy fields, and plants with tall stems. Secondly, we conducted a local-scale survey of Orthoptera assemblages in an operational farm unit consisting of paddy fields, fallow fields, marginal grass fields, and secondary forests. Eleven Orthoptera species (46%) were found exclusively on specific vegetation types. Thirdly, we carried out a habitat-scale survey to elucidate the correspondence between consecutive spatial changes in vegetation and Orthoptera community composition in a paddy field and surrounding marginal fields. Even within narrower ranges, the compositional habitat heterogeneity induced changes in the dominant Orthoptera species composition. These results indicate that a high degree of habitat segregation occurs among Orthoptera species in field margins and in uncultivated fields, and that farmland management significantly affects spatial distribution of Orthoptera.

INTRODUCTION

Agricultural land use must conserve natural resources in a sustainable manner. However, drastic changes in farmland use and farming intensification are causing biodiversity loss (Cunningham et al. 2013; Gabriel et al. 2013). To understand how farmlands influence biodiversity maintenance, it is necessary to evaluate how land management practices impact on various wildlife taxa (Marini et al. 2008; Gabriel et al. 2010; Gonthier et al. 2014; Dudley and Alexander 2017).

Agricultural land use is strongly influenced by climate, terrain, geological features, and spatial configuration. In Japan, rice paddy fields are distributed over large areas of lowlands and plains. In hilly and mountainous regions, paddy fields that are often adjacent to other crop fields, secondary forests, and uncultivated fields are terraced in small-scale farmlands. This cultivation method involves mixing various land uses so that multiple types of the vegetation cover provide spatial and seasonal heterogeneity, which in turn affects animal species composition and diversity.

Several studies have shown that various taxonomic groups differ in terms of their habitat requirements and their responses to landscape composition (Gabriel et al. 2013; Lengyel, Déri, and Magura 2016; Melliger, Rusterholz, and Baur 2017). Orthoptera are the main consumers in agricultural land and inhabit a broad range of environments, including grasslands and forests. They show high sensitivity and specific responsiveness to environmental changes. Therefore, their distribution and community composition might be determined by the extent and type of local vegetation cover (Joern 2005; Schouten et al. 2007; Fartmann, Behrens, and Loritz 2008). However, only a few studies have focused on the effects of agricultural land use on Orthoptera communities, particularly along field margins and in uncultivated fields (e.g. Giuliano and Bogliani 2018).

To understand how field margins and uncultivated space affect the richness and abundance of Orthoptera species, we investigated habitat heterogeneity influences on community composition of Orthoptera at multiple spatial scales. Firstly, we examined associations among environmental variables, land use type, and/or vegetation cover with the Orthoptera community over a broad spatial scale. The impact of 12 environmental variables on Orthoptera community diversity was evaluated by sampling 37 quadrats in uncultivated fields on a broad spatial scale. Secondly, we investigated Orthoptera habitat segregation on a local spatial scale among various farm patches and their surrounding marginal fields. A local-scale survey of Orthoptera assemblages was conducted in an operational farm unit consisting of paddy fields, fallow fields, marginal grass fields, and secondary forests. Thirdly, we evaluated the small-scale distribution of the Orthoptera community on habitat scale with respect to crop cover and vegetation type. This fine-scale survey was conducted to elucidate how consecutive spatial changes in vegetation correspond with the Orthoptera community composition in the paddy field and surrounding marginal fields. Our results are expected to provide insights as to how farmland management practices help sustain Orthopteran biodiversity.

MATERIALS AND METHODS

Study area

The study was conducted in the southern part of the Samegawa-mura village (the approximate central point of the village is 36°59'26"N 140°31'08"E), Fukushima Prefecture, north-eastern Honshu, Japan (Figure 1). This region is hilly and mountainous (elevation range: 400–740 m). The climate of the region is temperate with the annual temperature of 10.5°C ranging from -0.5°C to 22.6°C, and the annual rainfall of 1500 mm ranging from 39 mm to 212 mm per month (Climate-data.org). The area is covered with a typical mosaic of farmlands, including paddy fields, crop fields, forests, and human habitation.

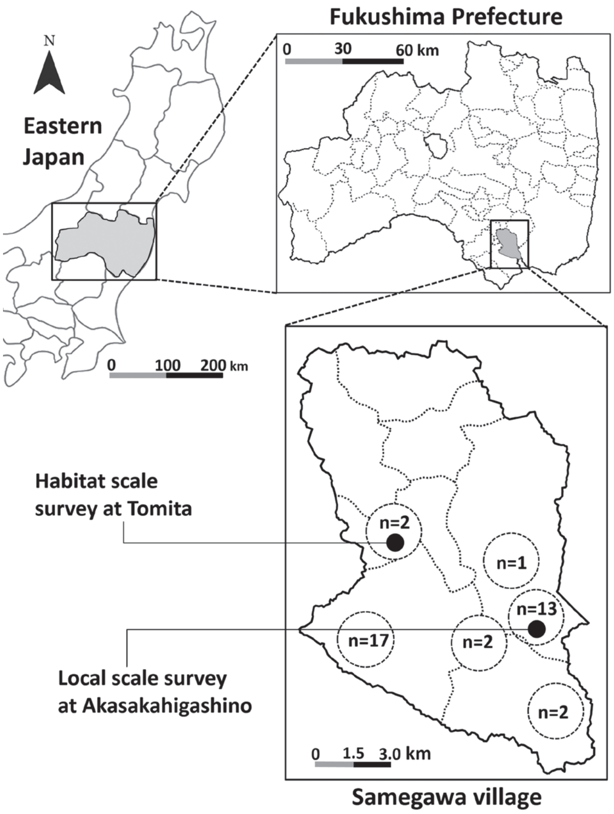

Figure 1. Study area locations and sampling sites used in the three surveys of this study in Samegawa-mura Village. Circles with dashed lines and numbers indicate sampling areas for the broad spatial scale survey and the total number of sampling points, respectively.

To provide an overview of the average ambient temperatures, temperature sensors (RS-14; ESPEC MIC Corp., Aichi, Japan) were installed in the Tomita (37°00'31"N 140°29'32"E) survey area between May 2017 and September 2017. Four typical vegetation fields, including paddy fields, a slope situated between arable fields, a thicketed long-term fallow paddy field, and a cedar plantation forest, were targeted. The average monthly temperatures were 17.9°C in the cedar plantation forest, 18.0°C in the thicketed abandoned field, 19.0°C in the paddy field, 19.2°C on the slope situated between farm fields, and 19.2°C in the fallow paddy field. Temperatures were higher in open environments than in forested areas, including the cedar planting forest and the thicket ($p < 0.05$ by repeated-measures ANOVA, followed Tukey's multiple comparisons).

Orthoptera community composition in various types of vegetation on a broad spatial scale

The study was conducted between September 2011 and October 2011. Thirty-seven sampling points were selected in six areas in the southern part of the village (Figure 1). The vegetation cover was classified into eleven types. These included three grass fields: (1) meadows (n = 2), (2) Japanese pampas grass fields (n = 3), and (3) lawns (n = 2); four herbaceous plant communities: (4) fallow crop fields (n = 8), (5) slope vegetation (n = 2), (6) managed short-stalk grass communities (n = 3), and (7) Kudzu *Pueraria lobata* communities (n = 2); and three forest fields: (8) oak secondary forests (n = 3), (9) cedar planting forests (n = 4), (10) forest edges (n = 4), and (11) dry bare fields (n = 4).

A quadrat sampling method using a square-shaped framed area was adopted to measure environmental variables and collect Orthoptera specimens. If quadrats are arranged appropriately, this method can represent the habitat for several species; therefore, it is one of the most efficient sampling methods used to assess the abundance and richness of species in ecological studies. A quadrat (10 m × 10 m) was established to determine the impact of environmental variables on the Orthoptera community diversity. Twelve local-scale environmental variables were used to measure habitat structural complexity at each site. These included nine structural complexity levels of field coverage % with canopy, herbaceous plants, Poaceae, Cyperaceae, shrubs, dried grass, fallen leaves, gravel and rock, and bare ground. Average grass height, soil moisture (seven levels), and degree of shading by vegetation (three levels) were recorded.

To ensure consistent sampling performance at all sites, 20 min was spent at each site and sampling time was staggered between 09:00 and 16:00. Individuals were captured in nets, stored in containers, and counted at all sampling points, including those hidden under leaf litter and live vegetation. Most specimens were identified and counted in the field and then were released. *Loxoblemmus* spp. individuals were collected and identified later. Tetrigidae (*Formosatettix* and *Tetrix*) and part of Trigonidiidae (mainly *Svistella bifasciata* larvae) that could not be identified in the field were treated as Tetriginae spp. and Trigonidiinae spp., respectively.

Orthoptera community composition on local and habitat spatial scales in mixed agricultural fields

In August 2010, the relationship between environmental heterogeneity and the Orthoptera community was investigated in a local agricultural region within the Akasakahigashino District in eastern Samegawa-mura Village (Figure 1). A survey was conducted in seven different habitat types within an operational farm unit consisting of paddy fields (PF), levees between the paddy fields (LR), Japanese pampas grass fields (MG), an abandoned wet grass field (WG), a farm road (FR), the *Pinus densiflora* forest (PD), and forest edge vegetation (FE). These fields were in close proximity to one another within a 6 ha area and at ~700 m elevation. A smaller quadrat (2 m × 20 m) was established to capture and count Orthoptera species. To ensure that as many species were detected as possible, 20 min-sampling was replicated twice per habitat type both day and night. A bait trap was also used to collect Rhaphidophoridae. Pupal powder was placed in nine traps, which were then randomly distributed on the site and left for two nights. Individuals that could not be identified in the field (*Loxoblemmus*, Tetrigidae and Rhaphidophoridae) were collected and identified later.

In August 2017, spatial changes in the dominant Orthoptera species within a farm field were surveyed on the habitat spatial scale. This analysis was conducted in the Tomita district (elevation 480 m) in the western part of the Samegawa-mura Village (Figure 1). The Orthoptera composition was investigated at a farming site where noticeable spatial changes in vegetation structure occurred due to the implemented farming practices. The paddy units that were evaluated included paddy fields and their incidental margins (sleeves, slopes, and fallow fields). Traditional paddy fields are often associated with characteristic marginal and uncultivated fields. Nevertheless, we focused on the relationship between consecutive environmental changes and spatial dynamics of Orthoptera assemblages within a narrow range of paddy land.

We established two transects (A and B) that were 100 m apart for this survey. Transect A was 35 m long. It consisted of six contiguous vegetation spaces, including a paddy field (14 m), the edge of the paddy field without paddy rice planting (2 m), two levees (1 m each), a fallow paddy field (12 m), two slopes (1 m and 3 m, respectively), and an abandoned grass field adjacent to a long-term fallow paddy field (1 m). Transect B was 14 m long. It consisted of three different vegetation spaces, including a fallow paddy field (9 m), a gentle slope (2 m), and a farm road (3 m). The transects were selected to facilitate precise sampling, accounting for habitat heterogeneity and providing an area that could be effectively surveyed by one researcher.

Orthoptera abundance was determined by the quadrat sampling method. Along transect A, visual and sample capture censuses were performed in 35 contiguous quadrats (1 m × 1 m). The quadrats were arranged in a zigzag configuration to minimize the escape of insects during sample collection. The abundance of Orthoptera along transect B was found to be low. Therefore, 14 large (5 m × 1 m) contiguous quadrats were established. There were three replicates per transect. *Formosatettix* and *Tetrix* that could not be identified in the field were treated as Tetriginae spp.

To measure the environmental variables, box quadrats (1 m × 1 m) were randomly placed over each vegetation type. Six replicates were used. Environmental parameters included the herbaceous plant cover, the bare ground cover, the dried grass cover, and the number of plant species, maximum and average herbaceous plant heights, and the relative soil water content. Soil water content was measured with a DM-18 soil moisture meter (Takemura Electric Works Ltd., Toshima-ku, Tokyo, Japan).

Data analysis

Broad spatial scale

For this survey, the association between the Orthoptera composition and the farmland environment was determined by the canonical correspondence analysis (CCA). CCA is a direct gradient analysis. It is a multivariate method that is used to relate species communities to known variation in the environment. An ordination diagram displays the pattern of community variation that can be best explained by the known environmental variable. When using this direct gradient technique, important environmental variables are selected *a priori*. Our dataset included 12 explanatory environmental variables. These variables were tested for interdependency by calculating Spearman's correlation coefficients. If predictor variables were highly correlated ($rs > 0.6$), they were combined using the first axis of principal components analysis (PCA) into a new independent variable. PCA is a statistical procedure that reduces the number of hypothetical variables accounting for variance in the multivariate data as much as possible. These new variables are transformed by combinations of the original variables, and are shown as new dimensions called principal components PCs. Herbaceous plants, Poaceae, and shading were combined into the new factor “PCA-Grass.” Canopies, shrubs, and fallen leaves were combined into the new factor “PCA-Tree.” Gravel/rock and bare ground were combined into the new factor “PCA-Bare.” These three combined factors and percentage cover of dried grass, Cyperaceae, and average grass height were introduced as predictors in the CCA. The 37 sampling points were classified as uncultivated fields (n = 24), forests (n = 7), forest edges (n = 4), and meadows (n = 2), each being represented by a unique symbol on the ordination diagram. Species recorded on <3 plots and/or represented by <3 specimens were excluded from the ordination to de-emphasize rare species. Individual abundance and proportion data were logarithm- and arcsine transformed, respectively. These analyses were made with the statistical software package Paleontological Statistics (PAST by Hammer, Harper, and Ryan 2001).

For the broad spatial scale survey, a generalized linear mixed model (GLMM) was used to assess the impacts of six independent variables, which were the same as those used in the CCA, on species richness. GLMM is based on generalized linear models, which are nonlinear regression models. This model provides a more flexible generalization of an ordinary linear regression for a variety of non-normal data, when random effects are present. In our data, a Poisson error structure was used, and six sampling areas were treated as a random factor. The models explaining variation in species richness were selected using the Akaike information criterion (AIC) in the SAS University Edition (SAS Institute, Cary, NC, USA). All models for which the AIC differed by <2.0 from that of the best model were selected (Burnham and Anderson 2002). AIC is an estimated measure of the quality of various statistical models, describing how well each model fits the observed data.

Local and habitat spatial scales

For the local spatial scale survey of a farm unit, species composition was compared among seven different habitat types. A seriation analysis using an absence-presence matrix was conducted in PAST (Hammer, Harper, and Ryan 2001). This ordination method builds an association matrix consisting of the Orthoptera species in the rows and the seven habitats in the columns. The species represented by only one individual were excluded from the ordination. The number of observed specimens per species is also shown.

For the spatial scale survey of the habitats, a set of contiguous quadrats was used. Associations between spatial variations in the vegetation environment and Orthoptera composition structure were depicted. We showed three indices in relation to Orthoptera composition, including species richness, individual abundance, and species diversity by Shannon’s diversity index. Species represented by fewer than three specimens were excluded from the analysis. To test if the seven environmental parameters differed among the vegetation spaces, one-way ANOVA was conducted, and the Kruskal-Wallis test was applied for no variance data (six samplings of a covering degree was all “0”).

RESULTS

Community composition on the broad spatial scale

A total of 38 species and 1,384 individuals were recorded in this survey. The abundance of individuals of each species ranged from 1 to 616 (Appendix 1). The CCA of 23 Orthoptera species and six environmental variables, including three PCA axes, is shown in Figure 2. The

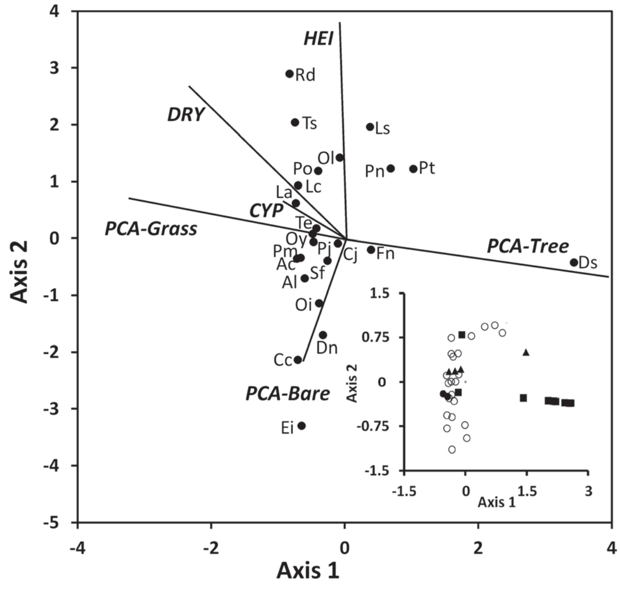

Figure 2. Canonical correspondence analysis (CCA) showing correlations between Orthoptera species found on >3 land use types and six environmental variables, including three on the first PCA axis. Al (*Atractomorpha lata*), Cc (*Conocephalus chinensis*), Cj (*Conocephalus japonicus*), Dn (*Dianemobius nigrofasciatus*), Ds (*Diestrammena* spp.), Ei (*Euparatettix insularis*), Fn (Tetriginae spp.), La (*Loxoblemmus aomoriensis*), Lc (*Loxoblemmus campestris*), Ac (*Acrida cinerea*), Ls (*Loxoblemmus sylvestris*), Sf (*Stenobothrus fumatus*), Oi (*Oedaleus infernalis*), Ol (*Oecanthus longicauda*), Oy (*Oxya yezoensis*), Pj (*Patanga japonica*), Pm (*Polionemobius mikado*), Pn (*Phaneroptera nigroantennata*), Po (*Pteronemobius ohmachii*), Pt (*Parapodisma takeii*), Rd (*Ruspolia dubia*), Te (*Teleogryllus emma*), and Ts (Trigonidiinae spp.) HEI: average grass height; DRY: dried grass coverage; CYP: Cyperaceae coverage. Small scatter diagram shows 37 sampling plots; ○: uncultivated fields; ■: forests; ▲: forest edges; ●: meadows.

eigenvalue and percentage (%) that explained variance were 0.496 and 50.06% on axis 1 and 0.163 and 16.51% on axis 2, respectively.

Each of the canonical axes was correlated with two specific environmental variables in both positive and negative directions. Consequently, the ecological status of each species could be identified. Along the first canonical axis, each species was assigned to two distinct groups characterized by PCA-Tree extending in the positive direction and PCA-Grass extending in the negative direction. *Diestrammena* spp. was strongly correlated with PCA-Tree. Its range was limited to forest environments. In contrast, several species positioned along and near the PCA-Grass were found in various types of uncultivated grass fields. *Loxoblemmus campestris* and *Loxoblemmus aomoriensis* occurred mainly in herbaceous fields with harvested grass.

The second axis reflected gradients in average grass height (HEI), and PCA-Bare, which combines the gravel/rock and bare ground cover. *Ruspolia dubia*, Trigonidiinae spp., *Loxoblemmus sylvestris*, and *Oecanthus longicauda* were associated with tall plant stems. *Euparatettix insularis*, *Conocephalus chinensis*, *Dianemobius nigrofasciatus*, and *Oedaleus infernalis* were correlated with PCA-Bare and were often found in paddy fields and/or bare fields where grass was scarce.

To identify the best models, we used GLMMs to fit the data for six environmental variables, including three PCA axes. Model selection based on the Akaike information criterion (AIC) shows that the four models explained nearly the same level of species richness (Table 1). Except for PCA-Grass in Model 2, grass height in Model 3 and dried grass in Model 4, all other selected variables in the four models had significant negative impacts on species richness. Cyperaceae, PCA-Tree, and PCA-Bare contributed to the explanatory power of these good models in terms of the species richness index. This trend corresponded to the fact that many species were not defined in the PCA-Bare and PCA-Tree axial directions in the CCA diagram (Figure 2).

Community composition on the local and habitat spatial scales

In the seven different types of fields, we recorded 490 individuals from 28 Orthoptera species, of which, only one representative specimen was identified for *Acrida cinerea* and *Conocephalus exemptus* in the paddy levee, for *Hexacentrus hareyamai* in the Japanese pampas grass field, and for *Prosopogryllacris japonica* in the forest edge with shrubs and mantle vegetation.

Seriation of an absence-presence matrix with the concomitant number of the individuals encountered is given in Table 2. The highest species richness was recorded in the Japanese pampas grass community (11 species) and the two marginal fields (levee and forest edge; nine species each). Only three species were detected in the *Pinus densiflor* forest. The highest abundance was found in the levee between the rice fields (176 specimens, including two dominant species *Oxya yezoensis* and *Polionemobius mikado*. The association matrix containing Orthoptera species in the rows and the seven habitat environments in the columns indicated habitat preferences of each of the 11 species (46%) found in limited habitats. These specimens were relatively more abundant in the *Pinus densiflor* forest and on the forest edge. *Diestrammena japanica* and *Diestrammena elegantissima* (Rhaphidophoridae) inhabited the forest floor. *Nippancistroger testaceus* (Gryllacrididae) and two *Tettigonia* (Tettigoniidae) were arboreal species living along the forest edges. Another 13 species occurred in multiple habitats types. The range of *Oxya yezoensis*, which was detected in all habitats except the *Pinus densiflor* forest, was the widest among all of the species ranges.

For the habitat spatial scale survey of consecutive farm fields, we recorded 17 species and 1,146 individuals. We identified 16 species and 828 individuals along transect A and 12 species and 318 individuals along transect B. Seven environmental variables, including tree coverage %, tree plant identities, and % soil water content, are summarized in Table 3. All environmental parameters differed among the vegetation spaces along transect A. Nevertheless, the unmanaged grass field had high plant

Table 1. GLMMs correlating Orthoptera species richness with environmental parameters.

	AIC	Intercept	Cyperaceae	PCA-Tree	PCA-Bare	PCA Grass	Grass height	Dried grass
Model 1	145.65	**2.026**	**-0.807**	**-0.756**	**-0.396**			
		(0.039)	(0.069)	(0.125)	(0.079)			
Model 2	147.43	**2.177**	**-0.753**	**-0.804**	**-0.440**	-0.056		
		(0.175)	(0.114)	(0.158)	(0.062)	(0.067)		
Model 3	147.64	**2.033**	**-0.806**	**-0.7558**	**-0.397**		-0.004	
		(0.127)	(0.080)	(0.125)	(0.077)		(0.079)	
Model 4	147.64	**2.018**	**-0.802**	**-0.752**	**-0.392**			0.010
		(0.078)	(0.079)	(0.129)	(0.082)			(0.073)

Estimates (SE in parentheses). Parameter estimates for the predictors with significant effect are shown in bold font.

coverage and dried grass area, and plants with tall stalks. Plant species richness was low in the managed paddy field. Bare ground cover also differed among vegetation spaces. The managed paddy field had relatively greater bare ground cover than the other vegetation spaces. High soil moisture content was measured at the site associated with the paddy fields. The % dried grass cover and plant species richness statistically differed among the

Table 2. Seriation of 24 Orthoptera species observed in a farming unit at a local scale.

Species	PD	PF	WG	MG	LR	FR	FE	Sum of specimens	No.occupied sites
Diestrammena japanica	2							2	1
Diestrammena elegantissima	3							3	1
Formosatettix spp.	5							5	1
Loxoblemmus aomoriensis		2						2	1
Atractomorpha lata		8	10		34			52	3
Conocephalus chinensis		20	2	2		2		26	4
Eobiana engelhardti			20	11	2			33	3
Mecostethus parapleurus				3				3	1
Ruspolia dubia				3				3	1
Mongolotettix japonicus			4	6		5		15	3
Stenobothrus fumatus			3	2	6	12		23	4
Oxya yezoensis		20	30	9	42	14	8	123	6
Teleogryllus emma				3	13			16	2
Stethophyma magister			5				3	8	2
Dianemobius nigrofasciatus					5			5	1
Polionemobius mikado				7	43	10		60	3
Oecanthus longicauda				12			6	18	2
Pteronemobius ohmachii					4	2		6	2
Loxoblemmus campestris				12			2	14	2
Tetrix spp.					27	3	4	34	3
Nippancistroger testaceus							2	2	1
Tettigonia orientalis							7	7	1
Parapodisma takeii							2	2	1
Tettigonia sp.							12	12	1
Sum of specimens observed	10	50	74	70	176	48	46	474	
No. of species occurred	3	4	7	11	9	7	9		

PD: *Pinus densiflor* forest, PF: paddy field, WG: abandoned wet-grass field, MG: Japanese pampas grass field, LR: levees between rice fields, FR: farm road; and FE: forest edge.

Table 3. Environmental parameters for contiguous vegetation spaces at two farm transects.

	% cover			Plant identity			% soil water content
	herbaceous plant	dried grass	bare ground	species richness	average height (cm)	maximum height (cm)	
Transect A							
paddy field	66.7	0.0	73.3	1.8	85.8	97.7	49.7
edge of paddy field	36.7	0.0	63.3	3.0	32.3	51.3	50.5
slope 1	58.3	40.0	10.8	5.8	18.2	30.2	43.1
levee 1	58.3	45.0	3.3	6.2	12.5	28.2	47.7
fallow paddy field	40.0	8.3	53.3	4.3	24.5	40.7	48.9
levee 2	66.7	35.0	7.5	8.8	16.8	35.0	45.7
slope 2	28.3	68.3	4.2	5.2	21.2	37.3	45.6
grass field	100.0	78.3	0.0	6.2	76.7	147.3	43.4
	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$
Transect B							
fallow paddy field	13.3	85.0	3.3	4.7	17.7	35.7	48.2
gentle slope	38.3	65.0	3.3	5.2	20.7	34.3	46.6
farm road	78.3	19.2	1.7	5.5	19.2	33.8	47.8
	$p = 0.575$	$p < 0.001$	$p = 0.791$	$p < 0.001$	$p = 0.562$	$p = 0.882$	$p = 0.697$

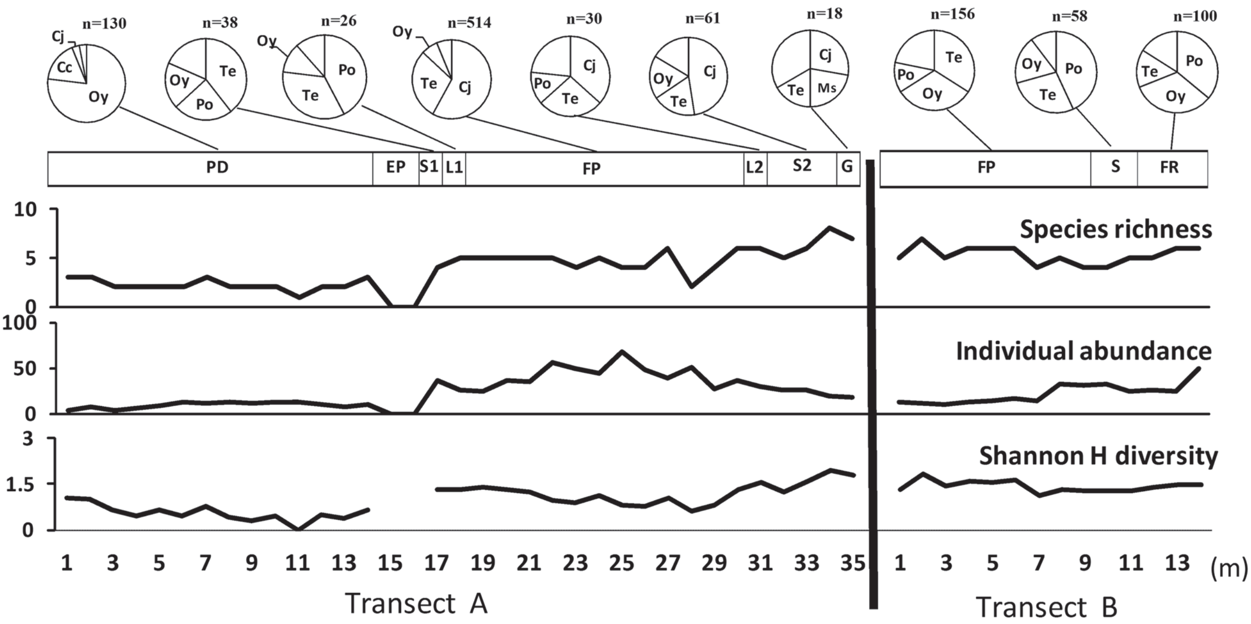

Figure 3. Changes to Orthoptera species richness, abundance, and diversity index in contiguous farming areas comprised of different vegetation structures. Vegetation spaces included PD: paddy field; EP: edge of paddy field without paddy rice planting; S: slope; L: levee; FP: fallow paddy field; G: grass field; and FR: farm road. The top three dominant Orthoptera species are shown in the pie chart. Oy: (*Oxya yezoensis*); Cc: (*Conosephalus chinensis*); Cj: (*Criotettix japonicus*); Te: (*Teleogryllus emma*); Po: (*Pteronemobius ohmachii*); and Ms: (*Modicogryllus siamensis*).

vegetation spaces along transect B. The % herbaceous plant cover decreased in the following order: farm road > gentle slope > fallow paddy. The % dried grass cover was comparatively higher on the slopes and in the fallow paddy field because of mowing.

For the habitat spatial scale survey, the associations between spatial variation in the vegetation environment and the composition of Orthoptera assemblages on contiguous quadrats are shown in Figure 3. Sixteen and eight species were analysed along transects A and B, respectively. Species richness, individual abundance, and the diversity index for the Orthoptera community structure, and the composition of the top three dominant species, considerably differed among vegetation spaces. Along transect A, species richness increased with the distance of the vegetation spaces located between 17 m and 35 m from the slopes and grass fields. Paddy fields had low species richness relative to the other vegetation spaces. Although species richness was comparatively low in the paddy field, the range of *Conocephalus chinensis* was limited to paddy rice stalks. No insects were found on the unplanted edge of the paddy (EP) along transect A. Individual abundance was the highest in a fallow paddy field (FP) because it supported great abundance of *Criotettix japonicus*. Diversity indices were comparatively high on the slopes and in the grasslands because there were many species but few individuals. However, along transect B, where environmental differences among vegetation spaces were small, variation in species richness and diversity was minor. Depending on spatial vegetation changes, all dominant species were *Oxya yezoensis*, *Teleogryllus emma*, or *Pteronemobius ohmachii*. We concluded that even within a narrow range, Orthoptera communities significantly change with the vegetation environment.

DISCUSSION

In the Samegawa-mura Village, small-scale farming consists of rice cultivation on typical mosaic-like farmlands traditionally operated by private farmers. This farm management style is directly linked to land use and has resulted in the arrangement of various types of vegetation on a multispatial scale.

Previous studies revealed that species richness of various taxonomic communities is significantly influenced by vegetation in the habitat, both on the local and landscape scales (Gonthier et al. 2014; Sutcliffe et al. 2015; Löffler and Fartmann 2017). Here, by integrating both previous and current findings, we evaluated how the spatial heterogeneity of farmlands affects the regional diversity of the Orthoptera community on multiple spatial scales. Orthoptera habitat segregation was confirmed by previous studies (e.g. García-García et al. 2008; Kuppler et al. 2015). The effectiveness of multi-environmental land use has been determined on the landscape scale for such taxa as Orthoptera, with distinct habitat segregation tendencies (Weking et al. 2016). For instance, Löffler and Fartmann (2017) reported that the number of grassland Orthoptera species increased with habitat heterogeneity and was correlated with patch size at the landscape level. Yoshio, Kato, and Miyashita (2009) revealed that landscape factors significantly affected four of the five selected Orthoptera species (*Teleogryllus emma*, *Oxya yezoensis*, *Ruspolia lineosa, Conocephalus maculatus*).

Although many Orthopterans prefer grassland ecosystems, to a limited extent, certain specialist species favour forest environments. Marini et al. (2009) stated that the proportion of woody vegetation and well-developed forest edges strongly and positively influenced species richness. In addition, Zografou et al. (2017) showed that canopy cover is one of determining factors for Orthoptera. In the local-scale survey on a farm field at Akasakahigashino, habitat preferences of the 11 species (46%) found in limited habitats primarily included the *Pinus densiflor* forest and the forest edge. Therefore, the areas that are set aside from forests and structurally complex forest edges (including shrubs and mantle vegetation) within an arable field and surroundings might benefit forest-related species by providing additional habitats. Thus, Orthopteran diversity might be enhanced by increasing the proportion of these types of habitats in the agricultural landscape.

On the local and habitat scale, Orthoptera also exhibit species-specific habitat preferences (Bieringer and Zulka 2003; García-García et al. 2008; Jain and Balakrishnan 2011; Badenhausser et al. 2015; Eckert, Möller, and Buchholz 2017). Vegetation cover and structural complexity are the most important factors for establishing the local Orthoptera community (Kuppler et al. 2015; Gardiner 2018). In the broad-scale survey of the present study, CCA demonstrated that significant environmental parameters (forest and herbaceous plant coverage) were correlated with the first axis, whereas bare field cover and plant stalk height were correlated with the second axis. Our local scale survey of the paddy field and the surrounding uncultivated fields showed that changes in the field management type (vegetation structure) induced compositional variation of Orthoptera species. Although species richness was comparatively low in the paddy field, the range of *Conocephalus chinensis* was limited to paddy rice stalks.

Several previous studies demonstrated that the Orthoptera community varies on small spatial scales. Influential factors are vegetation structure and such abiotic environmental variables as irradiance, soil temperature, and soil moisture (Bieringer and Zulka 2003; Löffler and Fartmann2017). The habitat spatial scale survey evaluated associations between the spatial variation in the vegetation environment and the composition of Orthoptera assemblages in contiguous quadrats. It was found that Orthoptera are highly sensitive and strongly respond to small-scale environmental changes when substituting dominant species within a narrow range. Different types of vegetation increase spatial heterogeneity, which, in turn, widen insect niche space. Jain and Balakrishnan (2011) investigated cricket microhabitat selection in forests and found that 10 out of 13 species preferred very specific environments. The authors proposed that all habitats in the forest should be maintained for the interest of Orthopteran biodiversity conservation.

Thus, Orthoptera community structure is established for managed agricultural environments with different vegetation structures. Marginal vegetation fields consisting of levees, slopes, short-term fallows, and abandoned fields associated with paddy rice cultivation create multifunctional mosaic-like habitats. A combination of many different types of fields in farmland may increase species richness (Kuppler et al. 2015). Conventional mowing of various marginal vegetation fields could help maintain plant communities as functional habitats for such herbivorous insects as the Orthoptera. However, intentional field restoration and the introduction of suitable management practices might further enhance Orthoptera species richness and population persistence.

Orthoptera diversity on rice paddy-based farmland could be augmented in several ways. Firstly, management practices for marginal grass vegetation should be improved. New farm field management techniques are associated with fertilization type, grazing intensity and mowing frequency. Thus, environmentally friendly-practices should be implemented on the habitat scale (Vickery et al. 2001; Marini et al. 2008; Uchida and Ushimaru 2015; Kirmer, Rydgren, and Tischew 2018). In terms of habitat heterogeneity, vegetation structure, including plant height, strongly influences Orthoptera community composition (Zografou et al. 2017). Therefore, seasonal timing and the number of mowing events must be considered in habitat management planning. Yoshio, Kato, and Miyashita (2009) suggested that the maintenance of fallow areas and reduced mowing frequency in and around lowland paddy fields also increase the abundance and diversity of insects. Secondly, complementary and/or supplementary arrangements of vegetation fields can create biotopes. In the present study, comparatively higher levels of species richness were detected in abandoned grass fields and Japanese pampas grass fields. Vegetation fields that are associated with paddy rice cultivation could be modified to consist of mixed herbaceous plants, including tall-stalk grass and moisture-specific fallow vegetation spaces. In particular, disturbance intensity is one of the determinants of Orthoptera assemblages. For instance, very intense perturbations shorten grass stems and eliminate insect hiding places, whereas moderate disturbances increase species diversity (Fartmann, Behrens, and Loritz 2008; Uchida and Ushimaru 2015).

Some studies have reported that Orthoptera species richness could be increased by regenerating grasslands using appropriate vegetation management practices (e.g. Borchard, Schulte, and Fartmann 2013; Marini et al. 2008). The most effective grassland management depends on comprehensive understanding of the habitat environments required by each of the species in the target community. Complex, diverse vegetation could provide food for many taxa by creating species-specific habitats. Furthermore, highly varied vegetation composition provides refuges for insects during mowing and other agricultural management practices. Therefore, effective field management practices within fields and surrounding green spaces could help increase local species richness (Gardiner 2018).

Enlargement of the Orthopteran species diversity should contribute to the biological conservation of agricultural land. However, Orthoptera is one of the major plant-consuming taxa, and many of the species identified in our survey are considered pests (twenty-nine species; The Japanese Society of Applied Entomology and Zoology, 2006). Thus, some conflicts might arise between increasing diversity of orthopteran insects and ensuring sustained agricultural productivity. Unfortunately, we do not know the degree of the threat posed by individual species as agricultural pests; however, among all the Orthoptera encountered, only two species (*Oxya yezoensis* and *Conocephalus chinensis*) were recorded in large numbers in the paddy fields.

Ultimately, the restoration of habitats with spatial mosaic-like arrangements is expected to conserve biodiversity and strengthen such ecosystem services important for agriculture as pest control. In a pioneering study, Inagaki et al. (2014) showed that the introduction of specific covering plants into paddy rice field edges and farm roads enhanced cricket abundance. Crickets contribute to pest management, by eating the seeds of grass weeds that often contain host plants of pest insect species such as bugs. Furthermore, several field studies showed that Friendly-Farming could provide environments that support natural enemies arthropods (Miyashita, Yamanaka, and Tsutsui 2014; Usio 2014; Baba and Tanaka 2016; Baba, Kusumoto, and Tanaka2018; Brévault and Clouvel 2019). Ideally, sustainable management of both agricultural production and biodiversity conservation without conflicts should be practiced. Therefore, it is important to identify the types of marginal fields that are beneficial for pest management in paddy field farmland and decide how best to maintain these habitats.

CONCLUSIONS

Our study demonstrated that marginal vegetation fields consisting of levees, slopes, short-term fallows, and abandoned fields associated with paddy rice cultivation provide fine-scale multifunctional mosaic-like habitats for Orthoptera. These heterogeneous agricultural matrices strongly contribute to the overall Orthoptera diversity through the increased availability of species-specific preferred habitats. In other words, the Orthoptera community structure appears to depend on agricultural management and practices generating different vegetation structures. Thus, conventional farmland management for rice cultivation and marginal vegetation fields could help maintain various type of plant communities as functional habitats for Orthoptera. Additionally, manipulative field management could further contribute towards Orthoptera diversity enhancement. Open habitats covered by high-stem grasses, which are preferred by this insect group, might be provided by maintaining fallow areas, such as slopes, that are situated between arable fields, and by reducing mowing frequency. If fallow fields are left to stand for a long time, they transition to dense vegetation, consisting of thickets, bushes, and mantle vegetation, providing habitats for those species dependent on forest and forest edge environments. However, strong focus is needed on how to manage the marginal and fallow fields for both biodiversity conservation and pest control without conflict, because Orthoptera is a major plant-consumer. Although, the restoration of habitat with spatial mosaic-like arrangements is expected to conserve biodiversity and strengthen such ecosystem services important for agriculture as pest control, there is a knowledge gap in our ability to understand the value of field margins and other uncultivated fields for biodiversity. Thus, more information is needed about the functioning of various vegetation types in organically managed habitats. Ultimately, the practice of sustainable management of both agricultural production and biodiversity conservation without conflicts, and experimental manipulation of grassland structure and surrounding vegetation on the habitat scale should be implemented systematically.

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DECLARATION OF INTEREST

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Appendix 1. Orthoptera community composition on the broad spatial scale.

Taxa	Field margins and uncultivated fields																																				
	ME		JP			LA		FC								SV		MC			KC		OF			CF				FE				BF			
Gryllidae																																					
Teleogryllus emma	5	3				1	6	15			1					10			18	7										4	2				8		
Modicogryllus siamensis	1											2							15																		
Loxoblemmus sylvestris	4									2			10		1						9	1									6	6	7				
Loxoblemmus campestris		3	2	4	1	3		1	10								29	5	5	2																	
Loxoblemmus aomoriensis																22																					
Eneopteridae																																					
Oecanthus longicauda		2	2		2			4	10								1				8										1		2				
Trigonidiidae																																					
Trigonidiinae spp.			3	1					7	2							3	1		1											2						
Pteronemobius ohmachii				1				3											5																2		
Dianemobius nigrofasciatus	1			3		4		5										1		1										1				9	1	4	
Polionemobius mikado	2	2		1	7	2	5		5							4	4	3	1	11															13		6
Polionemobius flavoantennalis									1																						1						
Rhaphidophoridae																																					
Diestrammena spp.																					1	8	2	4	25	12	15	15	18			2	1				
Gryllacrididae																																					
Nippancistroger testaceus																															1	1					
Tettigoniidae																																					
Eobiana engelhardti																		3																			
Chizuella bonneti																			3																		
Ruspolia lineosa																		4																			
Ruspolia dubia									1							1		1																			
Conocephalus chinensis		3									2	7		3						2															2		
Conosephalus japonicus											2	1						7												4							
Conocephalus melaenus																															1						

Taxa	Field margins and uncultivated fields																																				
	ME		JP			LA		FC								SV		MC			KC		OF			CF				FE				BF			
Hexacentrus hareyamai																																1					
Phaneropteridae																																					
Phaneroptera nigroantennata									3												2	2										3	2	1			
Ducetia japonica																					1																
Kuwayamaea sapporensis																						1										2					
Holochlora japonica																						1															
Tetrigidae																																					
Criotettix japonicus												9			3																						
Euparatettix insularis		1									19	2																									1
Tetriginae spp.	15	11	10	7	5	11		11	4	5	10	3	5	2	5	3	18	2	18	15	2	1	8	2	10	2	2	3	12	5	4	3	6	8	10	4	23
Pyrgomorphidae																																					
Atractomorpha lata	4		3	1		2	3		6	2	1	6		23		1		3	19	40	2													1	10		18
Acrididae																																					
Parapodisma takeii	1																				1	3										3	2				
Ognevia longipennis	1																																				
Patanga japonica								1			2							3																	1		
Oxya yezoensis	24	20	9	12	2	1	1	3	2	6	3	19	4	30	32	6	2		30	49		1								7	3	1			45		4
Acrida cinerea																1		4		2																	2
Stenobothrus fumatus				2													1													1	1						6
Stethophyma magister				2																																	
Locusta migratoria																																			4		
Oedaleus infernalis								3								2																		1			10
	58	45	29	34	17	24	15	46	49	17	40	49	19	58	41	50	58	37	114	130	26	18	10	6	35	14	17	18	30	22	22	22	20	20	96	8	70

ME: meadows (n = 2), JP: Japanese pampas grass fields (n = 3), LA: lawns (n = 2), FC: fallow crop fields (n = 8), SV: slope vegetation (n = 2), MC: managed short-stalk grass communities (n = 3), KC: Kudzu *Pueraria lobata* communities (n = 2), OF: oak secondary forests (n = 3), CF: cedar planting forests (n = 4), FE: forest edges (n = 4), and BF: dry bare fields (n = 4).