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Original Research Article

Landscape associations of farmland bird diversity in Germany and Japan

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A B S T R A C T

Spatial heterogeneity of landscapes is a key factor for the diversity of biota. There are a rich variety of agricultural landscapes around the globe that differ with respect to composition and spatial configuration of land-use types, reflecting different levels of human impacts. To test whether landscape structure influences biodiversity in similar ways in different geographical regions, our study explored the relationship between landscape characteristics and farmland bird diversity in Germany and Japan. The two countries represent regions with similar Palearctic avifauna, but with contrasting climatic, biogeographical, and socio-economic conditions. We used distribution data for 31 (Germany) and 29 (Japan) species of farmland birds and applied multiple regression analysis to examine the effect of landscape structure on species richness of total farmland birds and of several ecological groups. In both regions, farmland cover was the key variable determining species numbers. Species numbers also increased with increasing proportion of semi-natural habitats up to a maximum and then decreased if semi-natural habitat became more abundant. Optimum landscape structure for each ecological group differed according to their respective habitat needs, but the direction of shifts toward their preferred habitats was similar in both regions, suggesting common ecological mechanisms underlying the patterns of farmland bird diversity. Significant interactions of structural characteristics with the region variable indicated that associations between species richness and landscape structure varied regionally. In Germany, where landscapes are covered by a large extent of farmland, woodland edge density had a pronounced effect on species numbers. By contrast, associations with woodland edges were weak in Japan, where forest is the dominant form of land-use. The differences in landscape associations imply that different conservation strategies should be taken according to the landscape context. In farmland-dominated landscapes, edge habitats provided by forest patches are an important feature for maintaining farmland bird diversity, whereas maintaining open habitats is crucial in forest-dominated landscapes. The importance of maintaining grassland, paddy fields, and semi-natural habitats as part of agricultural landscapes was also underlined by the results of our study. Measures for conserving farmland bird diversity should focus on maintaining heterogeneity of agricultural landscapes.

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1. Introduction

Agricultural landscapes, consisting of various land-use types with different levels of human impact, occupy the largest part of Earth's terrestrial surface (Foley et al., 2011). The composition and spatial configuration of land-use types differ greatly among such landscapes. The effects of these differences on biological diversity at different spatial scales have been the focus of many studies, not least because of the need for effective management strategies to address the dramatic decline of farmland biodiversity that has been observed worldwide (Tscharntke et al., 2005, 2012; Batáry et al., 2011). In most cases, local to landscape scales have been considered. However, only a few studies have tested the generality of landscape structure – biodiversity relationships in agricultural regions of different continents (Václavík et al., 2016), or have taken a comparative approach to differentiate between region-specific responses and those that are universally applicable across biogeographical regions (Queiroz et al., 2014; Zeller et al., 2017). We tested the effects of landscape structure on the diversity of farmland birds using information from agricultural landscapes in Germany and Japan.

The two regions provide an opportunity to test the generality of landscape structure – diversity associations beyond regional scales because they have different climatic, biogeographical, and socio-economic conditions. Germany is located in the temperate deciduous forest biome, whereas Japan stretches across several biomes ranging from subboreal coniferous forest in the north to subtropical evergreen broad-leaved forest in the south (see supplementary material 1; SM1). Climatic conditions as well as geological and topographical settings determine land-use options available to farmers, and agricultural land-use at a given point in time is likely to reflect the efforts of land managers to optimize household income within the given environmental and socio-economic constraints. Such interactions between farming practices and natural ecosystems over long time periods have shaped the landscapes in both regions (Berglund, 1991; Takeuchi et al., 2003). Germany is characterized by open landscapes with 52% farmland and 30% forest, and non-irrigated land such as cropland and grassland represent 71% and 28% of farmland, respectively (Destatis, 2015). In contrast, Japan has higher forest cover, comprising 67% of the land, and farmland takes up only 12% (Statistics Bureau, 2015). Irrigated land, i.e. paddy fields, is the major land-cover accounting for 54% of farmland, while cropland and grassland contribute 26% and 14%, respectively (MAFF, 2016). In both regions, agriculture started during the Neolithic (Crawford, 2011; Bollongino et al., 2013), and broad distribution patterns of agricultural areas that persist today were established by the medieval period (with the notable exception of Hokkaido where large-scale forest clearance and wetland reclamation for agriculture started in the second half of the 19th century). The resulting cultural landscapes, especially those maintained by traditional agricultural management, are considered to be of importance for biodiversity conservation (Queiroz et al., 2014), as they harbor unique floral and faunal communities through long-term interactions between human and nature (Katoh et al., 2009; Bignal and McCracken, 2000).

Biogeographically, Germany and Japan belong to the Palearctic realm; 155 bird species occur in both regions (BirdLife International, 2016), and their ecological niches are broadly similar (Fig. 1). In a large-scale analysis regarding landscape structure – biodiversity relationships, Stein et al. (2014) found a general trend across biomes that environmental

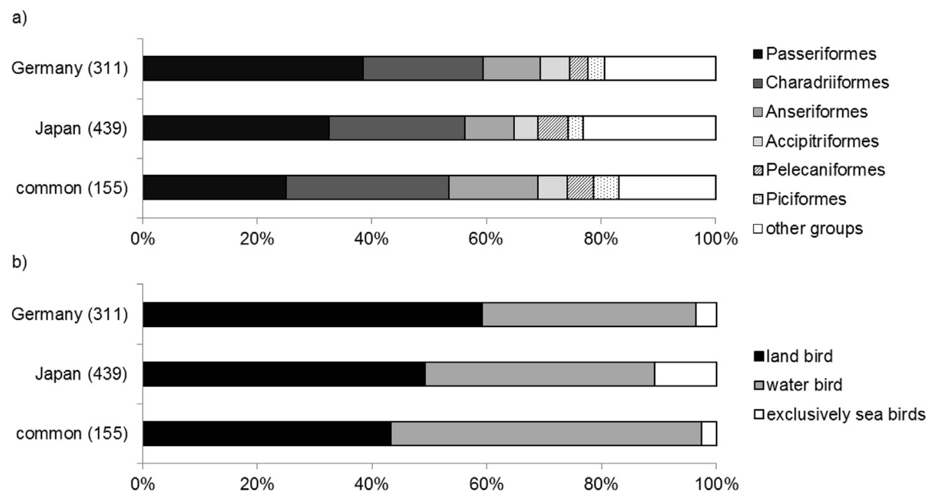

Fig. 1. Proportion of a) taxonomic groups and b) broad ecological groups of birds occurring in Germany, in Japan, or in both regions. Numbers in brackets indicate the number of species. Data extracted from BirdLife International (2016).

heterogeneity has positive effects on biodiversity. According to Benton et al. (2003), this also applies to farmland biodiversity. Metrics describing farmland-woodland mosaics have often been used to express landscape heterogeneity (Berg, 2002; Herzon and O'Hara, 2007; Desrochers et al., 2011). Moreover, semi-natural elements along field margins, water courses, and reservoirs are generally thought to enhance farmland biodiversity in agricultural landscapes (Maeda, 2001; Amano, 2009; Doxa et al., 2010; Zhou et al., 2018), though there are some cases where the strength of statistical relationships was weaker than expected (e.g. Aue et al., 2014) or such relationship did not hold (Tscharntke et al., 2016).

Farmland birds have experienced population declines and range contractions over the last decades in both regions (Amano and Yamaura, 2007; DDA, 2014) mainly due to loss of habitat heterogeneity in time and space arising from agricultural intensification and land abandonment (Benton et al., 2003; Amano, 2009; Koshida and Katayama, 2018). Similar ecological characteristics of birds and the parallels in their historical development of cultural landscapes set the rationale for the comparison between Germany and Japan. The application of common landscape measurements allows us to derive information on the effects of landscape structure on the diversity of farmland birds in regions with parallel socio-economic trends but with contrasting environmental conditions. Our comparative approach contributes to addressing common applicability of landscape drivers underlying the enhancement of species richness in a quantitative manner and thus broadens our understanding of biodiversity patterns shared among agroecosystems of different regions.

Using bird distribution data and common landscape measurements, our study compared how species richness was associated with structural characteristics of German and Japanese agricultural landscapes, and identified ecological mechanisms underlying the patterns of farmland bird diversity. We provide suggestions for maintaining the key characteristics of landscape structure that support the diversity of farmland birds beyond regional scales.

2. Methods

2.1. Bird data

We used breeding bird data compiled by the Federation of German Avifaunists (Dachverband Deutscher Avifaunisten e.V., DDA) and the Ministry of Environment Japan. Data for the German breeding bird atlas project (ADEBAR) were collected between 2005 and 2009 mostly by volunteers. The atlas accumulates data on the distribution and population sizes of breeding birds in Germany at a resolution of approximately 11 km × 11 km, corresponding to the size of a quadrant of the standard 1:25,000 topographical map (Gedeon et al., 2014). Birds meeting the possible, probable, and confirmed breeding criteria of the European Bird Census Council (EBCC, 2015) were recorded, and different survey methods were used according to the frequency levels of species occurrence: frequent (45 species), semi-frequent (156), and rare (75) (Gedeon et al., 2014). The distributions of frequent species were derived from modeling outputs of observations gathered under the German Common Breeding Bird Survey scheme, in which 903 sampling plots of 1 km^2 established across Germany were surveyed along transects of approximately 3–4 km. Semi-frequent species were surveyed in all habitat types present in 11 km × 11 km grid cells, and rare species were recorded through specifically designed projects. The Japanese data were collected under the 6th National Survey of the Natural Environment organized between 1997 and 2002, where distribution data of breeding birds were compiled at a 10 km × 10 km resolution based on field studies and questionnaire surveys among bird experts (MOE, 2004). We only used data derived from field observations of individual birds whose breeding status was A (confirmed breeding), B (probable breeding), or C50 (species observed in breeding season in possible nesting habitat) to be consistent with the EBCC breeding criteria (see SM2 for further details about the categories). Half of the grid cells were evenly chosen across the land, and each contained a 3-km transect. The sampling intensity is thus lower, and the distribution data are more heterogeneous than Germany. Nevertheless, the spatial resolution of the data sets for Germany and Japan is roughly similar, and it is the best distribution data available in Japan, which have been successfully used to answer important ecological questions (e.g. Amano and Yamaura, 2007; Yamaura et al., 2009; Kadoya and Washitani, 2011).

For the selection of farmland species, we used lists published by NABU (2004) and Amano and Yamaura (2007) for Germany and Japan, respectively. Both references defined farmland species as birds that utilize agricultural landscapes for nesting or foraging during the breeding period, and listed 47 species for Germany and 58 for Japan. We assumed that agricultural areas had been surveyed if grid cells contained at least one of the farmland species above. This corresponded to 2966 grid cells in Germany and 2280 in Japan. Next, we excluded species that were infrequently encountered and those whose geographic ranges are known to cover only a small part of the study regions (MOE, 2004; Gedeon et al., 2014). As a result, 31 species occurring in at least 500 out of 2966 grid cells across Germany and 27 species occurring in at least 100 out of 1728 grid cells on the islands of Honshu, Shikoku, and Kyushu were retained (SM3). Grid cells on the northernmost island Hokkaido, the Ryukyu Islands south of Kyushu as well as the Japanese Pacific islands were excluded ($n = 552$) because their avifauna differs considerably from the three main islands. Common buzzard *Buteo buteo* and Gray lapwing *Vanellus cinereus* were added to the list of Japan because the former is also included in the list of Germany and the latter has a similar ecological niche to Lapwing *Vanellus vanellus* in Germany. Thus, the final list from Japan included a total of 29 species. The lists for Germany and Japan had six species in common (SM3).

Habitat use such as foraging or nesting was extracted from the literature, namely Cramp (1977–1994) for species in Germany and Nakamura and Nakamura (1995a; 1995b) for species in Japan. The following broadly defined habitat types were noted based on the density of tree cover and hydrological conditions: dry grassland i.e. farmland including dry grassland and non-irrigated arable land, wet grassland i.e. farmland including wet grassland and irrigated arable land, and woodland.

Species were then assigned to one of the following ecological groups of each category according to the habitat types defined above (SM3): (1) edge-habitat species (those that use both dry/wet grassland and woodland), open-habitat species (mainly dry/wet grassland), or woodland species (mainly woodland) and (2) agricultural land species (those that prefer dry grassland, including species that mainly use woodland) or agricultural wetland species (wet grassland). The former category considered multi-habitat uses with regard to forested and open land, while the latter took into account the preferred level of soil moisture of farmland.

The number of species per grid cell was calculated using ArcView GIS 9.3 (ESRI Inc., Redlands, CA, USA; Table 1).

2.2. Landscape data

2.2.1. Land-cover data

The European CORINE Land Cover inventory 2006 version 17 (EEA, 2014a) and the actual vegetation map (Environment Agency and Asia Air Survey Co. Ltd., 1999) were used as base land-cover maps for Germany and Japan, respectively. CORINE land-cover data consist of 44 land-cover types. The raster format has a standard resolution of 100 m and a minimum mapping unit of 25 ha. To distinguish between farmland and woodland in the CORINE classes “Complex cultivation patterns” and “Land principally occupied by agriculture, with significant areas of natural vegetation” at higher spatial resolution, the Forest Type Map 2006 provided by the Joint Research Centre of the European Union (EC, 2015) was overlaid on the CORINE land-cover map, which was converted to 25 m resolution beforehand. We also integrated maps of water bodies from ESRI (2004) and Degree of Soil Sealing (EEA, 2014b), which accumulates information on the percentage of sealed area, e.g. built-up and non-built-up impervious areas such as pavement, per 20 m raster cell. The Japanese land-cover map was compiled at the scale of 1:50,000 with a minimum mapping unit of 1 ha, and consists of 774 types of vegetation communities. Both land-cover maps were converted to raster data with a spatial resolution of 50 m.

The Land Cover Classification System developed by the Food and Agriculture Organization (Gregorio and Jansen, 2000) was used to reclassify the 44 and 774 land-cover types in Germany and Japan, respectively. The categories are cropland, grassland, paddy fields, bamboo, natural shrub, natural herbaceous, sparse vegetation, lichen/moss, water body, wetland, salt marsh, bare area, snow/ice, broad-leaved forest, mixed forest, coniferous forest, mangrove, trees in open landscapes, tree crop, shrub crop, vegetated urban, urban, and unknown. The resulting maps for Germany and Japan consisted of 18 and 22 land-cover types, respectively.

2.2.2. Landscape variables

Nine farmland-based variables related to landscape structure that were considered relevant for farmland birds were derived from the land-cover maps (Table 2). The first four variables relate to the proportion of farmland to the total land area and were calculated per grid cell. ‘Farmland cover’ accounts for the extent of open farmland (3 types: cropland, grassland, and paddy fields; hereafter addressed as farmland). The other three variables were separate proportions for cropland (‘cropland cover’), grassland (‘grassland cover’), and paddy fields (‘paddy field cover’) to the total land area. Note that paddy field cover did not apply to Germany and that grassland cover was not computed for Japan, as this land cover type was scarce in the Japanese study area. ‘Number of habitat types’ is the combined number of land-cover types per grid cell including ten land-cover types belonging to semi-natural habitats (bamboo, natural shrub, natural herbaceous, sparse vegetation, lichen/moss, water body, wetland, salt marsh, bare area, and snow/ice) and five land-cover types belonging to woodland (broad-leaved forest, mixed forest, coniferous forest, mangrove, and trees in open landscapes).

To examine the effects of land-cover types neighboring farmland, we generated agricultural landscape sections by buffering 250 m around farmland edges. Within these sections, we calculated the proportions of semi-natural habitats (‘semi-natural habitat cover’) and woodland (‘woodland cover’) to the area of agricultural landscape sections for each grid cell. In Germany, semi-natural habitats in agricultural land sections were composed of 69% water body, 19% wetland, and 7% natural herbaceous cover, while those in Japan were 41% natural herbaceous cover, 33% water body, and 10% wetland. To assess effects of edges between farmland and non-farmland on bird distributions, edge densities of semi-natural habitats and woodland adjacent to farmland were extracted by dividing the edge length of semi-natural habitats (‘semi-natural habitat edge density’) and woodland (‘woodland edge density’) by total farmland area.

Table 1
Summary of descriptive statistics of species richness per grid cell in Germany and Japan.

	Germany				Japan			
	Minimum	Maximum	Mean	SD	Minimum	Maximum	Mean	SD
Total farmland birds	2	31	24.0	4.8	1	23	9.7	4.3
Edge-habitat species	0	9	7.5	1.4	0	11	4.5	2.3
Open-habitat species	0	19	14.2	3.6	0	12	3.8	2.3
Agricultural land species	2	22	18.6	3.0	0	15	7.8	3.1
Agricultural wetland species	0	9	5.4	2.4	0	10	1.9	1.8

Table 2
List of landscape variables used. Values refer to mean ± 1 standard deviation.

Variables	Description	Unit	Germany	Japan
Farmland cover	Proportion of farmland to total land area	%	54.5 ± 22.1	18.9 ± 17.1
Cropland cover	Proportion of cropland to total land area	%	43.0 ± 23.0	5.4 ± 7.4
Grassland cover	Proportion of grassland to total land area	%	11.6 ± 13.7	N.A.
Paddy field cover	Proportion of paddy fields to total land area	%	N.A.	13.4 ± 14.1
Number of habitat types	Number of semi-natural habitat and woodland types per grid cell	n	4.9 ± 1.3	5.9 ± 1.2
Semi-natural habitat cover	Proportion of semi-natural habitats to agricultural landscape section	%	2.0 ± 4.3	5.9 ± 6.0
Woodland cover	Proportion of woodland to agricultural landscape section	%	23.2 ± 15.2	49.6 ± 24.0
Semi-natural habitat edge density	Edge density of semi-natural habitats adjacent to farmland per hectare of farmland	m ha^{-1}	1.2 ± 1.4	2.5 ± 2.7
Woodland edge density	Edge density of woodland adjacent to farmland per hectare of farmland	m ha^{-1}	10.5 ± 5.8	12.4 ± 10.7
Elevation	Mean elevation	m	252.4 ± 247.2	367.1 ± 368.9

Total land area: area of each grid cell covered by the study area.
Agricultural landscape section: area within 250 m from farmland edges.
Farmland: cropland, grassland, and paddy fields.
Woodland: broad-leaved forest, mixed forest, coniferous forest, mangrove, and trees in open landscapes.
Semi-natural habitat: bamboo, shrub, natural herbaceous, sparse vegetation, lichen/moss, water body, wetland, salt marsh, bare area, and snow/ice.
Tree crop, shrub crop, vegetated urban, urban, and unknown land-cover type were not considered.
N.A.: data not available.

All variables were calculated based on 50 m pixels except for edge density, which was derived using vector data converted and smoothed from the raster data. Permanent crops were different from other land-cover categories in terms of management intensity and woody structure over an extended period of time. However, the cover of permanent crops was too small to establish its own category and to be included in landscape analysis (0.68% of the land surface in Germany and 1.89% in Japan), so tree crop and shrub crop were considered non-informative for the study. Vegetated urban, urban, and unknown land-cover type were not considered.

2.2.3. Elevation data

We selected elevation as a variable accounting for large-scale bird distributions since it showed strong correlations with average precipitation in Germany (Spearman's rank correlation = 0.84) and average temperature in Japan (Spearman's rank correlation = 0.66) during the surveyed breeding period. German data were acquired from the Digital Terrain Model with a grid width of 200 m (Federal Agency for Cartography and Geodesy, 2013), and the Japanese data were obtained from the Elevation, Degree of Slope Tertiary Mesh Data (MLIT, 2011). Mean values were calculated per grid cell ('elevation').

The German and Japanese datasets were combined, and the landscape variables were standardized together based on the mean and standard deviation.

2.3. Statistical analysis

Grid cells that contained missing data for calculating the landscape variables were excluded, resulting in a total of 2957 grid cells in Germany and 1728 in Japan. Relationships among the landscape variables were then examined using Spearman's rank correlations in each region. Variables that showed correlations higher than the absolute value of 0.5 (i.e. number of habitat types, woodland cover, and semi-natural habitat edge density; SM4; Booth et al., 1994) were not used in the subsequent regression analysis, even if correlations existed only in one of the regions, to keep consistency in the datasets.

Using the first set of landscape variables as multiple explanatory variables (farmland cover, semi-natural habitat cover, woodland edge density, and elevation), we modeled the species richness, i.e. the number of species, in generalized linear models with a log link function for the following ecological groups: total farmland birds, edge-habitat species, open-habitat species, agricultural land species, and agricultural wetland species. The woodland group was excluded from analysis as it contained only three species in both regions that are not specifically dependent on open agricultural fields (SM3). The assumption of a Poisson distribution was verified by visual inspection of the frequency distribution of species numbers and the regression residuals. Linear and quadratic terms of each landscape variable were included to account for non-linear relationships, and interaction terms encoding the regions as a two-level factor parameter were added to address whether landscape associations vary regionally. Correlograms of Moran's I (Legendre and Legendre, 1998) were then constructed to assess the degree of spatial autocorrelation in the regression residuals using the 'ncf' package in R (Bjornstad and Cai, 2019). Intersample distance classes were formed using a lag of 50 km up to the maximum distance. Since significant autocorrelation was not detected, no further methods were applied. A full model approach was taken to compare the effects of different explanatory variables on the distributions of farmland bird diversity (Whittingham et al., 2006).

Based on the parameter estimates of linear and quadratic terms, shapes of landscape structure − farmland bird diversity relationships were visualized, and values at which the maxima of species richness were reached (hereafter addressed as optimum values) were calculated for each landscape variable and each ecological group. In order to determine the relative importance of subclasses of agricultural land for farmland bird diversity, a second set of models was similarly constructed using cropland, grassland, paddy field cover as individual variables instead of including farmland cover. The explanatory variables here were centered on zero mean so that the changes in species richness could be compared based on the original unit of measurement (i.e. cropland, grassland, paddy field, and semi-natural habitat cover in percent, woodland edge density in meters per hectare, and elevation in meters).

Statistical analyses were conducted using R-3.2.4 (R Development Core Team, http://www.r-project.org/).

3. Results

In general, heterogeneity in the bird data among grid cells was smaller in Germany compared to Japan due to the differences in sampling intensity (see 2.1. Bird data; Table 1). Of the 31 and 29 farmland species used in Germany and Japan, the former consisted of 9 edge-habitat species, 19 open-habitat species, 22 agricultural land species, and 9 agricultural wetland species, while the latter included 12, 14, 17, and 12 species, respectively.

Multiple regression analysis revealed that species richness of total farmland birds and the ecological groups was negatively correlated with elevation in both regions (Table 3), indicating a decline in species richness with increasing altitude (Fig. 2).

Among the variables related to landscape structure, farmland cover was the key variable determining species numbers in Germany and Japan (Table 3). The coefficients for the linear term were positive for total farmland birds and all ecological groups considered, and they were larger than those for semi-natural habitat cover and woodland edge density. Significant interactions between farmland cover and region indicated that the effects of farmland cover on species richness differed in Germany and Japan. The difference in slopes revealed that the associations between species richness and farmland cover were stronger in Japan (Table 3). Moreover, the unimodal relationship between farmland cover and species richness suggested that there is an optimal proportion of farmland for the diversity of farmland birds (Fig. 2). In Germany, the optimum values of farmland cover where the maxima of species numbers were reached were located around the mean or slightly larger (mean farmland cover 54.5%, range of optimum values 48.5–69.6%). In Japan, the maxima were found more or less in the same range (44.7–62.8%), but landscapes with such farmland extent were rare as these values lay beyond 89th percentile of its distribution (mean 18.9%).

Models including the cover of particular subclasses of agricultural land (i.e. cropland, grassland, and paddy fields) showed that the proportion of grassland and paddy fields had larger positive effect size on species richness than cropland cover (except for agricultural land species in Germany; SM5). Furthermore, there was only a small difference in R^2 between the first (considering farmland cover) and second (considering the cover of subclasses of agricultural land) sets of models (Table 3; SM5).

Species richness showed a unimodal relationship with semi-natural habitat cover (Fig. 2), and the effects of the linear term were significantly stronger in Japan (Table 3). Species numbers increased with increasing proportion of semi-natural habitats up to a maximum and then decreased if semi-natural habitat became more abundant. In both regions, the optimum values were larger than the mean for most of the ecological groups considered (mean Germany 2.0%, Japan 5.9%; Fig. 2). Edge-habitat species and agricultural land species in Germany deviated from this pattern. They were negatively related to semi-natural habitat cover (Table 3), and their maxima were estimated at zero (Fig. 2). Low species richness in grid cells with high semi-natural habitat cover was associated with a small number of data points which had special land cover patterns. At these points, small farmland areas were surrounded by larger areas of semi-natural habitats such as sparse vegetation and salt marshes in Germany and herbaceous cover and water body in Japan (range of farmland cover with the top ten highest proportion of semi-natural habitats: Germany 0.9–18.4%, Japan 0.2–9.9%). Such land cover patterns were apparently not conducive to the diversity of farmland birds and led to a drop in species numbers.

The most pronounced differences between Germany and Japan were observed in the effect of woodland edge density on farmland bird diversity (Table 3; Fig. 2). In Germany, species richness showed a unimodal relationship with woodland edge density, with maximum richness close to the mean value of woodland edge density (mean 10.5 m ha^{-1}, range of optimum values 7.5–11.7 m ha^{-1}). In Japan, on the other hand, the relationship was an almost horizontal line, suggesting that species richness was only marginally influenced by woodland edge density. The effects of the quadratic term were significantly stronger in Germany compared to those in Japan where the coefficients were all close to zero. The shape of relationship confirmed such differences in the landscape associations (Fig. 2).

Different ecological groups responded differently to landscape structure according to their respective habitat needs. However, the direction of change how the numeric values of optima shifted among the ecological groups was similar between Germany and Japan (Fig. 2). For example, it was common to both regions that edge-habitat species showed preference for higher woodland edge density (optimum values Germany 11.7 m ha^{-1}, Japan 30.2 m ha^{-1}) but required less farmland cover compared to other groups (Germany 48.5%, Japan 44.7%). By contrast, open-habitat species required higher farmland cover (Germany 66.9%, Japan 61.2%) and higher semi-natural habitat cover instead (Germany 19.3%, Japan 22.4%). Agricultural land species showed intermediate responses compared to edge-habitat species and open-habitat species. The positive effect of farmland cover was most pronounced for agricultural wetland species (Table 3). Models including the cover of subclasses of agricultural land indicated that this was driven mostly by grassland and paddy field cover in Germany and Japan, respectively (SM5). The proportion of semi-natural habitats was also most relevant for these species. Maxima in species richness in this group were found at 31.4% in Germany and at 24.6% in Japan (Fig. 2).

Table 3
Results of generalized linear models explaining the species number of total farmland birds, edge-habitat species, open-habitat species, agricultural land species, and agricultural wetland species as a function of farmland cover, semi-natural habitat cover, woodland edge density, and elevation. Note that landscape variables were standardized based on the mean and standard deviation before model construction. The number of species used in Germany and Japan is shown in brackets. Linear and quadratic terms of each landscape variable were included in the analysis. Regression coefficients are expressed as means ± standard errors.

	Total farmland birds						
	Germany (31)			Japan (29)			P^2
	Coefficient±SE	Z	P^1	Coefficient±SE	Z	P^1	
Intercept	3.203 ± 0.007	462.94	<0.001	2.501 ± 0.019	131.90	<0.001	<0.001
Farmland cover	0.061 ± 0.007	8.85	<0.001	0.107 ± 0.019	5.73	<0.001	<0.05
(Farmland cover)^2	−0.044 ± 0.006	−6.79	<0.001	−0.147 ± 0.019	−7.82	<0.001	<0.001
Semi-natural habitat cover	0.007 ± 0.008	0.87	0.38	0.049 ± 0.012	3.89	<0.001	<0.01
(Semi-natural habitat cover)^2	−0.005 ± 0.001	−3.56	<0.001	−0.009 ± 0.002	−3.51	<0.001	0.15
Woodland edge density	−0.026 ± 0.007	−3.55	<0.001	0.011 ± 0.010	1.07	0.29	<0.01
(Woodland edge density)^2	−0.050 ± 0.006	−8.71	<0.001	−0.003 ± 0.003	−1.06	0.29	<0.001
Elevation	−0.131 ± 0.007	−19.22	<0.001	−0.086 ± 0.014	−6.19	<0.001	<0.01
(Elevation)^2	−0.021 ± 0.005	−4.49	<0.001	0.008 ± 0.004	1.74	0.08	<0.001
	Edge-habitat species						
	Germany (9)			Japan (12)			P^2
	Coefficient±SE	Z	P^1	Coefficient±SE	Z	P^1	
Intercept	2.078 ± 0.012	170.10	<0.001	1.681 ± 0.028	59.22	<0.001	<0.001
Farmland cover	0.018 ± 0.012	1.52	0.13	0.040 ± 0.028	1.42	0.16	0.48
(Farmland cover)^2	−0.034 ± 0.012	−2.95	<0.01	−0.161 ± 0.028	−5.72	<0.001	<0.001
Semi-natural habitat cover	−0.010 ± 0.016	−0.66	0.51	0.042 ± 0.019	2.26	<0.05	<0.05
(Semi-natural habitat cover)^2	−0.007 ± 0.003	−2.49	<0.05	−0.009 ± 0.004	−2.38	<0.05	0.65
Woodland edge density	0.009 ± 0.013	0.67	0.50	0.030 ± 0.015	2.00	<0.05	0.30
(Woodland edge density)^2	−0.071 ± 0.010	−6.80	<0.001	−0.006 ± 0.004	−1.57	0.12	<0.001
Elevation	−0.036 ± 0.012	−2.98	<0.01	−0.174 ± 0.021	−8.32	<0.001	<0.001
(Elevation)^2	−0.019 ± 0.007	−2.60	<0.01	0.016 ± 0.007	2.28	<0.05	<0.001
	Open-habitat species						
	Germany (19)			Japan (14)			
	Coefficient±SE	Z	P^1	Coefficient±SE	Z	P^1	P^2
Intercept	2.655 ± 0.009	289.37	<0.001	1.638 ± 0.029	55.60	<0.001	<0.001
Farmland cover	0.103 ± 0.009	11.28	<0.001	0.237 ± 0.028	8.48	<0.001	<0.001
(Farmland cover)^2	−0.054 ± 0.008	−6.41	<0.001	−0.160 ± 0.029	−5.55	<0.001	<0.001
Semi-natural habitat cover	0.026 ± 0.011	2.40	<0.05	0.072 ± 0.020	3.61	<0.001	<0.05
(Semi-natural habitat cover)^2	−0.004 ± 0.002	−2.80	<0.01	−0.010 ± 0.004	−2.63	<0.01	0.16
Woodland edge density	−0.039 ± 0.009	−4.19	<0.001	−0.033 ± 0.016	−2.06	<0.05	0.74
(Woodland edge density)^2	−0.043 ± 0.007	−5.85	<0.001	0.004 ± 0.004	1.01	0.31	<0.001
Elevation	−0.189 ± 0.009	−21.01	<0.001	−0.051 ± 0.022	−2.30	<0.05	<0.001
(Elevation)^2	−0.028 ± 0.007	−4.12	<0.001	0.017 ± 0.006	2.66	<0.01	<0.001
	Agricultural land species						
	Germany (22)			Japan (17)			P^2
	Coefficient±SE	Z	P^1	Coefficient±SE	Z	P^1	
Intercept	2.965 ± 0.008	377.61	<0.001	2.267 ± 0.021	106.44	<0.001	<0.001
Farmland cover	0.030 ± 0.008	3.96	<0.001	0.056 ± 0.022	2.60	<0.01	0.26
(Farmland cover)^2	−0.036 ± 0.007	−4.85	<0.001	−0.149 ± 0.022	−6.90	<0.001	<0.001
Semi-natural habitat cover	−0.022 ± 0.010	−2.29	<0.05	0.038 ± 0.014	2.77	<0.01	<0.001
(Semi-natural habitat cover)^2	−0.003 ± 0.002	−1.95	0.05	−0.008 ± 0.003	−2.87	<0.01	0.12
Woodland edge density	−0.015 ± 0.008	−1.88	0.06	0.036 ± 0.012	3.07	<0.01	<0.001
(Woodland edge density)^2	−0.038 ± 0.006	−5.96	<0.001	−0.008 ± 0.003	−2.65	<0.01	<0.001
Elevation	−0.071 ± 0.008	−9.19	<0.001	−0.052 ± 0.015	−3.36	<0.001	0.27
(Elevation)^2	−0.036 ± 0.005	−7.09	<0.001	0.000 ± 0.005	−0.03	0.98	<0.001
	Agricultural wetland species						
	Germany (9)			Japan (12)			P^2
	Coefficient±SE	Z	P^1	Coefficient±SE	Z	P^1	
Intercept	1.626 ± 0.015	107.95	<0.001	0.894 ± 0.042	21.10	<0.001	<0.001
Farmland cover	0.175 ± 0.016	11.25	<0.001	0.262 ± 0.037	7.13	<0.001	<0.05
(Farmland cover)^2	−0.083 ± 0.014	−6.01	<0.001	−0.163 ± 0.039	−4.18	<0.001	0.05
Semi-natural habitat cover	0.091 ± 0.017	5.53	<0.001	0.090 ± 0.028	3.17	<0.01	0.98
(Semi-natural habitat cover)^2	−0.009 ± 0.002	−3.64	<0.001	−0.011 ± 0.005	−2.08	<0.05	0.65
Woodland edge density	−0.068 ± 0.015	−4.45	<0.001	−0.078 ± 0.022	−3.63	<0.001	0.71

(*continued on next page*)

Table 3 (*continued*)

	Agricultural wetland species						
	Germany (9)			Japan (12)			P^2
	Coefficient±SE	Z	P^1	Coefficient±SE	Z	P^1	
(Woodland edge density)^2	−0.102 ± 0.013	−7.91	<0.001	0.016 ± 0.005	2.98	<0.01	<0.001
Elevation	−0.358 ± 0.015	−23.83	<0.001	−0.240 ± 0.033	−7.30	<0.001	<0.01
(Elevation)^2	0.029 ± 0.011	2.60	<0.01	0.043 ± 0.010	4.26	<0.001	0.33

P^1 *p*-values for the explanatory variables in each region.
P^2 *p*-values for interaction terms of the variables between the regions.

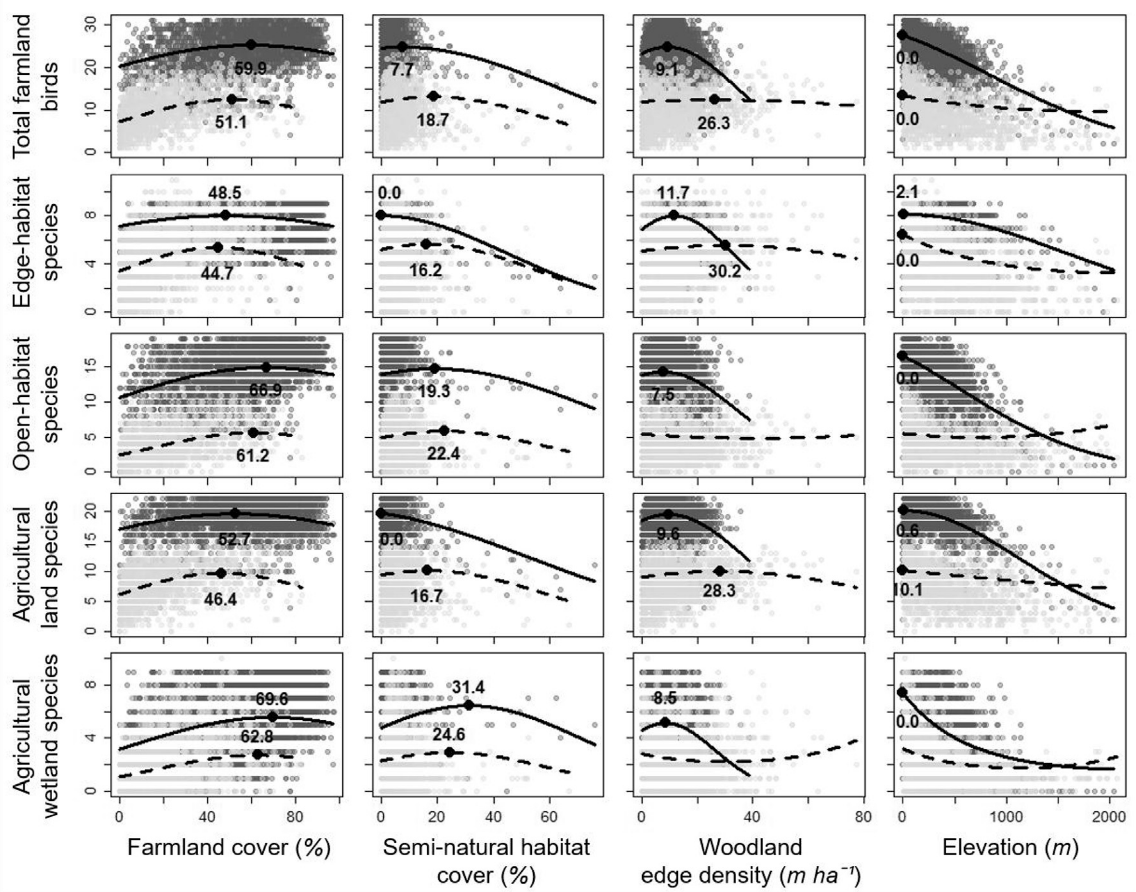

Fig. 2. Changes in the species number of total farmland birds, edge-habitat species, open-habitat species, agricultural land species, and agricultural wetland species as a function of farmland cover, semi-natural habitat cover, woodland edge density, and elevation in Germany (dark gray circles) and Japan (light gray circles). The regression lines for changes in species richness (Germany solid lines, Japan dashed lines) are shown using the estimated mean coefficients, with values of all other significant variables being zero. The optimum values at which the maxima of species richness are reached are also represented (closed circles, values shown below or above).

4. Discussion

Our study tested the generality of relationships between species richness of farmland birds and landscape structure using two distant geographical regions with similar Palearctic avifauna. Germany and Japan represent regions of contrasting land-use patterns with respect to farmland extent and farming systems, i.e. irrigated and non-irrigated agriculture. Nevertheless, given the differences, our results suggest that farmland cover plays a central role in enhancing species numbers of farmland bird communities of both study regions, with maxima found within similar ranges. Species numbers also increased with increasing proportion of semi-natural habitats up to maxima reached above the mean (except for edge-habitat species and agricultural land species). In addition, the direction of shifts of the ecological groups toward their respective preferred landscape structure was similar in both regions, suggesting common ecological mechanisms underlying the patterns of farmland bird diversity. One should note, however, that the landscape associations observed here concerned only common species; those of rare or threatened species were not examined. As demonstrated by Katayama et al. (2014), wide- and narrow-ranging species show different responses to landscape structure, with the former being more associated with heterogeneous landscapes and the latter with homogeneous landscapes. The inclusion of narrow-ranging species, which are often open-landscape specialists of high conservation priority, may thus increase the relevance of farmland extent than it was observed in our study.

Our analysis revealed several significant regional interactions, indicating that the way species richness responds to landscape structure varies between the regions. Such regional differences in landscape associations could be related to structural characteristics in agricultural landscapes as well as to different responses of farmland species included in the bird data sets. Furthermore, differences in the methodologies of the land-use surveys in Germany and Japan could have played a role. For example, different minimum mapping units might have influenced the strength and direction of relationships, as different levels of information loss may have occurred, especially with regard to small habitat features. In Germany, adopting a coarser minimum mapping unit (25 ha) compared to Japan (1 ha) may have resulted in a remarkably low proportion of semi-natural habitats across the grid cells (mean 2.0%). With the frequency distribution of semi-natural habitat cover in Germany being strongly skewed to the right, much of the variability of species numbers occurred in a narrow range of this variable. In such a situation, statistical relationships are weak. Aggregation of presence data into species numbers should have reduced possible effects arising from the use of different bird lists. There was also no apparent influence of species composition on the response to landscape composition, as the number of species included in each ecological group did not differ greatly between the regions. Our results suggest regional differences in the response to farmland cover and woodland edge density. Because Germany and Japan are characterized by contrasting farmland-woodland mosaics, i.e. the former by larger farmland extent and the latter by larger forest extent, we consider structural differences in agricultural landscapes to be the main reasons for the observed associational differences between the regions.

In Germany, agricultural landscapes structured by average amounts of farmland cover and woodland edge density supported the highest species numbers, suggesting that forest patches and edge habitats are beneficial to the diversity of farmland bird communities in farmland-dominated landscapes. Such landscapes structured by mosaics of farmland and woodland are known to support high farmland bird diversity (Berg, 2002; Herzon and O'Hara, 2007). For instance, Herzon and O'Hara (2007), who studied farmland bird communities along a gradient of farmland-woodland mosaics in the Baltic States, found that the abundance of farmland birds was frequently associated with semi-open landscapes. Berg (2002) also observed higher abundance and richness of farmland birds in mosaic farmland landscapes, and emphasized the importance of woodland edges as they provide nesting habitats, especially if they are rich in shrubs and deciduous trees. The presence of forest patches might also be important for providing food resources for insectivorous farmland birds since farmland landscapes surrounded by a high proportion of non-crop habitats are known to harbor a high amount of prey animals such as spiders, beetles, and butterflies (Weibull et al., 2000; Schmidt and Tscharntke, 2005; Bianchi et al., 2006; Chaplin-Kramer et al., 2011). Increasing woodland edges can, however, also increase the risk of nest predation on ground-nesting farmland birds (Krüger et al., 2018). Further fragmentation of remaining forest patches should thus be avoided.

Farmland birds in Japan showed significantly stronger associations with farmland cover compared to Germany, with maxima reached at high farmland extent, but were hardly related to woodland edge density. The importance of open land in forest-dominated landscapes is in line with previous studies in mountain areas (Pino et al., 2000; Ichinose, 2007; Zakkak et al., 2014, 2015). Desrochers et al. (2011) showed that loss of natural land cover up to 44% led to an overall increase in avian richness through a gain of 20 open-habitat species with a loss of two forest species. They explained that conversion of small amounts of natural areas to human-dominated land covers contributed to habitat heterogeneity and benefited especially open-habitat species as only a few natural open habitats remain nowadays. In Japan, open land has been made available by converting natural areas into agricultural land as well. Over the past century, agricultural fields have been lost substantially due to abandonment and development of rural areas (Statistics Bureau, 2018), especially grasslands that were historically more widespread than it is in today's landscape (<1% of total area; MOE, 2011). There, a number of breeding bird species have declined significantly in recent decades (Fujioka and Yoshida, 2001), and the loss, fragmentation, and degradation of open land have been identified as possible causes for their range contractions and narrow ranges (Amano and Yamaura, 2007; Katayama et al., 2014). Remaining open-habitats might have become more critical for the survival of farmland bird species, thus resulting in strong associations between the two variables. The effects of woodland edge density could have been mediated by the functional link between farmland cover and woodland edge density, i.e. woodland edges become available where agricultural land is extended ($r = 0.57$).

The difference in the relative importance of habitat types between the regions (i.e. higher relevance of forest patches in farmland-dominated landscapes vs. higher relevance of open-habitat patches in forest-dominated landscapes) may imply that the strength of associations for farmland bird diversity differs according to the studied landscape context. Similar landscape-moderated effects of habitat patches were also reported in landscape and regional level studies, where effects of hedges and agri-environment schemes were found to be more pronounced in simple than in complex landscapes (Batáry et al., 2010, 2011), residual habitats in open landscapes (Herzon and O'Hara, 2007), and arable fields in grassland landscapes (Robinson et al., 2001). These previous studies argued that food resources and nesting sites were probably the limiting factors in landscapes where relevant habitats were scarce, so increasing these habitats in such landscapes had contributed to increasing richness up to a threshold of the local or regional species pool. Our study supports these findings based on observations in two distant regions. This is an important difference because it points out the need for different management strategies according to landscape context, as suggested by Batáry et al. (2011) and Aue et al. (2014).

Similar responses of edge-habitat species and open-habitat species to landscape structure between the regions imply common ecological mechanisms underlying how farmland bird diversity is distributed in space. The edge-habitat species studied here are known to show preferences for forest edges (Cramp, 1977−1994; Nakamura and Nakamura, 1995a, 1995b) because they provide both necessary foraging areas and nesting sites. Among the edge-habitat species in Germany, *Buteo*, *Corvus corax*, *Milvus milvus*, and *Turdus pilaris* in particular require such combinations of habitats as they prefer to nest in woodland nearby farmland in structurally-rich landscapes (Cramp, 1977−1994; Gedeon et al., 2014). In Japan, Ardeidae and *Butastur indicus* are the species that particularly depend on the simultaneous presence of paddy fields and surrounding forest (Fujioka and Yoshida, 2001; Katoh et al., 2009). The pronounced responses of edge-habitat species to landscapes with farmland-woodland mosaics were also observed elsewhere (e.g. Pino et al., 2000; Sanderson et al., 2009) as such landscapes provide high accessibility to a variety of resources necessary for species that make use of multiple habitats.

Open-habitat species in contrast showed a stronger association with open land that has been created by farming practices. In open landscapes, farmland birds are known to have strong associations with local management practices and habitat heterogeneity. This includes management intensity of fields and the presence of non-cropped habitats between fields (Maeda, 2001; Berg, 2002; Benton et al., 2003; Doxa et al., 2010; Zhou et al., 2018). Low-intensity farming and mosaics of semi-natural habitats (e.g. hedges, field margins, and ditches), which are classified as farming areas of high nature value in the European Union's Rural Development Program (Andersen et al., 2003), are acknowledged to offer an array of habitats for plant and animal species (Doxa et al., 2010; Aue et al., 2014). In irrigated farming systems, simultaneous management of irrigation channels, irrigation ponds, paddy levee, and grassland patches creates spatial and temporal habitat heterogeneity, allowing organisms to move among different habitats (e.g. fish, amphibians and Odonata; Fujioka and Lane, 1997; Lane and Fujioka, 1998; Kadoya et al., 2009), which then results in enhanced farmland biodiversity (Amano, 2009; Katoh et al., 2009). In our study, although small habitat features may have been underrepresented due to the coarse mapping unit of the land-cover maps, we still observed an increase in species richness with increasing proportion of semi-natural habitats on agricultural land, especially in the case of open-habitat species and agricultural wetland species. Exceptions found in edge-habitat species and agricultural land species in Germany were probably due to a lack of relevant habitat types included in the land-cover map (breakdown of the composition in Germany: water body 69%, wetland 19%, and herbaceous cover 7%).

Grassland and paddy field cover were the most influential cover crop types for avian species richness in agricultural landscapes of Germany and Japan, respectively (except for agricultural land species in Germany). Many of the bird species studied here are known to show some level of association with pastoral landscapes or rice paddy landscapes because grassland and paddies under traditional management practices host a diverse and rich amount of food resources (Vickery et al., 1999; Fujioka et al., 2010). Grassland, which covers only 12.9% of the total land (Destatis, 2015), supports half of the native plant species in Germany (BMELV, 2013), and a high proportion of grassland invertebrates and a rich soil fauna are found above- and below-ground, respectively (Curry, 1994). The availability of small birds and mammals also make it suitable as a foraging site for birds of prey (Vickery et al., 1999). In Japan, paddy fields serve as foraging sites for many species. The wetland habitat created by rice farming provides aquatic prey animals (i.e. earthworms, fish, and frogs) for carnivorous birds (Fujioka et al., 2010), and associated paddy levees facilitate foraging activity of water and land birds (Maeda, 2001). Moreover, grassland and paddy fields function as alternative habitats for many avian species, especially for agricultural wetland species, because much of their original habitats such as natural marsh and floodplains have been lost (Fujioka and Yoshida, 2001; BMELV, 2013).

Grasslands and paddy fields are both under pressure due to socioeconomic trends. Factors such as conversion to cropland and land abandonment have led to substantial losses over the past decades (MAFF, 2012; BfN, 2014). Land abandonment, which occurs as a result of agricultural intensification and market globalization (Cramer and Hobbs, 2007), is known to have both positive and negative influences on biodiversity (Queiroz et al., 2014; Pereira and Navarro, 2015; MacDonald et al., 2000). Abandoned farmland is seen as an opportunity for rewilding in some parts of Europe, as it can facilitate plant succession and provide habitats for organisms that suffered from the past expansion and intensification of agriculture (Pereira and Navarro, 2015). However, since abandonment is likely to occur in less favored areas where high nature value farming systems remain (Keenleyside and Tucker, 2010), withdrawal of agricultural management can lead to a significant loss of semi-natural habitats and associated species of conservation importance as well (Pointereau et al., 2008). The contribution of abandoned farmland to ecological restoration has also been tested in Japan. Although some studies reported its high conservation values for open-habitat bird communities (Kitazawa et al., 2019; Hanioka et al., 2018), a meta-analysis specifically done for rice-farming systems depicted a pronounced decline in biodiversity, indicating that abandonment is not likely to contribute to or even have negative impacts on ecological restoration (Koshida and Katayama, 2018). A continuation of livestock and rice farming systems is thus crucial for conservation of farmland biodiversity. In addition to the decrease in the area of these habitats, agricultural intensification like mechanization, increased use of agrochemicals, improvement of irrigation and drainage to maximize productivity, and loss of field margins due to enlargement of fields have simplified the diversity and structural complexity of vegetation. The habitat suitability of grassland and paddy fields has thus been reduced (for further details, see Vickery et al. (2001) and Amano (2009) for livestock and rice farming systems, respectively), and policies that reverse these trends are needed.

5. Conservation implications

Based on the finding that the relative importance of a habitat type changes according to the landscape context, we conclude that conservation of farmland bird diversity should follow different strategies in Germany and Japan. In Germany where the extent of farmland is large in most areas, policies should aim at maintaining the cover of woodland in farmland-woodland mosaics. By contrast, the focus should be on maintaining open habitats in Japan where forest dominates in most areas. This is a particular challenge in Japan because socio-economic trends are putting pressure on the farming sector, leading to a decline in the farming population and to farmland abandonment. Policies that promote farming as an attractive profession are thus needed as part of a conservation strategy. In addition, our study revealed the importance of grassland and paddy fields for farmland bird diversity. Given the increasing trends in agricultural intensification and abandonment of livestock and rice farming systems, conservation focus in open landscapes should be targeted toward maintaining or expanding these land-cover types through environmentally friendly farming practices.

Declaration of competing interest

None.

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Appendix A. Supplementary data

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