Highlights

• In Japan, both intensified and abandoned rice fields are found within a small area.

• Effects of intensification and abandonment differed between bird groups and seasons.

• Agricultural wetland species in summer were threatened by both intensification and abandonment.

• Grassland species in both summer and winter benefitted from abandonment.

• High threat status of agricultural wetland species supports the finding of this study.

Are both agricultural intensification and farmland abandonment threats to biodiversity? A test with bird communities in paddy-dominated landscapes

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ABSTRACT

Land-use changes, including agricultural intensification and farmland abandonment, influence biodiversity in agricultural landscapes. However, few studies have focused on how the two major land-use changes affect different types of species at landscape scales. This study examined the relationships between the richness and abundance of five bird groups (agricultural wetland species, agricultural land species, grassland species, edge species, and woodland species) as well as the total species richness and abundance, and intensification or abandonment in 28 square, 100-ha grid cells in paddy-dominated landscapes in the Tone River basin of central Japan. Rice-field intensification and abandonment were not completely segregated spatially: intensification occurred in both plain and hilly areas surrounded by forests, while abandonment tended to occur in hilly areas. The effects of intensification and abandonment differed among species groups and between seasons. The richness or abundance of agricultural wetland species in summer were negatively associated with both intensification and abandonment. While the abundance of agricultural land species in winter and grassland species in both seasons were positively associated with intensification and abandonment, respectively. The total species richness and abundance did not show clear association with intensification and abandonment due to a variety of responses of the five bird groups. Based on prefectural Red Data Books, agricultural wetland species, followed by grassland species, were more threatened than other three groups in both summer and winter. This study found that (1) the diversity of habitats (including consolidated and abandoned farmlands) provides buffer areas for the different bird groups on different times of the year and (2) agricultural wetland species that use flooded rice fields in summer, such as egrets and shorebirds, are particularly threatened by both intensification and abandonment.

Keywords

Agricultural landscapes, Bird diversity, Habitat consolidation, Old fields, Waterbirds

1. Introduction

Recent land use changes by agriculture have rapidly reduced biodiversity globally (Donald et al., 2006; Green et al., 2005; Krebs et al., 1999). To reverse the negative trend, there is an urgent need to understand crucial factors causing the decline in biodiversity and to implement appropriate conservation strategies in agricultural landscapes (Fahrig et al., 2011; Tscharntke et al., 2005).

There are two directions of the recent changes in agricultural land use: agricultural intensification and farmland abandonment (Brambilla et al., 2007; Henle et al., 2008; Sanderson et al., 2013; Uchida and Ushimaru, 2014; Uematsu et al., 2010). Previous studies, particularly those in Western Europe and North America, have shown that outcomes of intensification such as agrochemical use and landscape simplification have severely threatened species diversity of multiple taxa such as birds (Benton et al., 2003; Donald et al., 2006). In contrast, the consequences of farmland abandonment on species diversity are less straightforward: meta-analyses have shown varying effects of abandonment on species richness and abundance, ranging from negative to positive depending on factors such as geographic regions, taxa, and spatio-temporal scales (Plieninger et al., 2014; Queiroz et al., 2014). In fact, abandonment can be either a threat to farmland species in traditional landscapes (Báldi and Batáry, 2011; Katoh et al., 2009; MacDonald et al., 2000) or a chance for the recovery of native non-farmland species (Guilherme and Pereira, 2013; Navarro and Pereira, 2012). Clearly, agricultural intensification and abandonment will have different effects on biological communities, but the differences remain to be fully clarified.

As policy-makers develop future land-use strategies, it is important to consider the impacts of farmland abandonment on species diversity. Despite receiving less attention than agricultural intensification, farmland abandonment is widespread and increasing in several regions of North and South America, Europe, and Asia due to a complex mix of social, economic, and ecological factors that lead to rural depopulation, particularly in isolated and poorer mountain areas (Cramer and Hobbs, 2007; MacDonald et al., 2000; Uematsu et al., 2010). Abandonment may be further accelerated under the implementation of a land-sparing strategy, which is to maximize yields on farmlands suitable for intensification while the remaining farmlands will be abandoned to give opportunity to rewilding and other management options (Navarro and Pereira, 2012). In fact, recent empirical studies have increasingly supported the land-sparing strategy as a way to achieve a better balance between food production and biodiversity conservation (Chandler et al., 2013; Edwards et al., 2010; Gilroy et al., 2014; Hulme et al., 2013; Phalan et al., 2011).

Farmlands in Japan have experienced intensification and abandonment since the 1960s and the 1980s, respectively. Fields of the dominant crop, rice (*Oryza sativa*), have traditionally supported many species of plants, invertebrates, and vertebrates, including waterbirds that originally used natural wetlands (Fujioka et al., 2010; Katoh et al., 2009;

Natuhara, 2013). Over the past five decades, however, modern farming systems have been introduced to reduce labor costs not only in profitable plain areas but also in hilly and mountainous areas, because Japan has a wide topographic gradient and thus many agricultural lands are inevitably located in these marginal areas (Uematsu et al., 2010). Paddy fields have been consolidated to enlarge field size and to be more regularly spaced (see fig. 1 in Katayama et al., 2015). Drainage ditches have also been converted from shallow earthen ditches to deep concrete-sided ones and underground pipes have been installed to promote efficient water drainage. Although these modern farming systems have helped farmers to efficiently use agricultural machinery in rice fields and improve agricultural productivity, they have also caused habitat degradation and fragmentation for many aquatic species in Japan, such as frogs, fish, and waterbirds (for more details, see Amano, 2009; Katayama et al., 2015).

Since the 1980s, however, farmland abandonment has been rapidly expanded throughout the country due to a variety of socio-ecological factors (MAFF, 2012; Osawa et al., 2013): aging farmers and depopulation, decrease in crop price, low productivity in hilly and mountainous areas, and a lack of field consolidation. After abandonment, old fields become dominated by grasses or trees, depending on factors including the number of years since abandonment and soil moisture (Kusumoto et al., 2005; Ohkuro et al., 1996). Although the loss of open aquatic habitats (rice fields) can be a serious threat to waterbirds such as egrets and shorebirds (Fujioka et al., 2001), it may also provide new habitats for grassland or woodland birds. Therefore, paddy-landscapes in Japan provide an ideal system for examining the effects of agricultural intensification and abandonment on the structure of bird communities.

This study focuses on bird communities in paddy-dominated landscapes in the Tone River basin, one of the major rice-growing areas and a typical agricultural landscape in Japan. We test whether and how the effects of intensification and abandonment on species richness and abundance differ between seasons and among bird groups categorized based on their main habitats.

2. Materials and methods

To test the effects of agricultural intensification and abandonment on the species richness and abundance of bird communities, we used previously published data for bird abundance and land cover, including abandoned fields (Amano et al., 2008), and new data on farmland intensification. The bird abundance and land cover data are explained in detail in Amano et al. (2008) and thus are described only briefly here.

2.1. Study area

The Tone River is the second longest river in Japan, running through the entire Kanto Plain in central Japan (Fig. 1a). Our study area, the Tone River basin, is mainly covered by rice paddies but also by arable fields other than rice, semi-natural grasslands, coppice forests, farm villages, and urban areas (Fig. 1b, c). In Japan, forest mostly occurs in hilly and mountain areas. Two examples of land use also show that abandoned and fallow fields were sparsely distributed in both (Fig. 1b) hilly areas and (Fig. 1c) lowland areas. Rice fields in this region are usually flood-irrigated from spring to summer, harvested in autumn, and not flooded in winter.

This area was first divided into 100-ha grid squares, and each square was classified into one of four major land-use types in the region: (1) midstream paddy; (2) downstream lowland paddy; (3) plateau and valley-bottom paddy; and (4) urban fringe. Then, eight grid squares were randomly selected from each land use type as study sites (total number: 32; Fig. 1a). To reduce the effect of spatial autocorrelation among samples, study sites were spaced at least 5 km apart.

2.2. Bird data and response variables

Each 100-ha square was divided into four blocks, each containing one 50-m-radius sampling plot in a major habitat (e.g., rice fields, grassland and forest) near the center of each block, to evaluate the occurrence of species at the landscape level in mosaic landscapes (Bennett et al., 2006). Bird surveys were conducted during the overwintering and breeding seasons from 6 to 20 December 2005 (surveys from sunrise to 10:30) and from 19 May to 24 June 2006 (surveys from sunrise to 08:30), respectively, by a total of six well-trained observers, each with about 10 years of experience in bird surveys. The number and species of birds seen within each plot during a 15-min observation were recorded, except for birds flying over and not using the sampling plots. All four sampling plots in each 100-ha square were surveyed on the same day, once per season. The abundance of a species in each 100-ha square was defined as the sum of individuals in all four plots.

The recorded species were categorized into eight groups based on habitat use and taxonomy according to earlier studies (Table 1). Among them, three groups (open water species, raptors, and urban species) were excluded from the analyses because of their specific habitat requirements or small occurrence numbers. For the other five groups, the number of species (species richness) and total abundance of each group in each 100-ha square were used as the response variables in the analyses. Also the total species richness and abundance, calculated as the sum of richness and abundance in the five bird groups, were used in the analyses.

2.3. Environmental variables

To evaluate the effects of land use on the richness and abundance of each bird group as well as the total species richness and abundance, habitat cover and measure of farmland intensification were recorded for each 100-ha grid square. For habitat-cover variables, the proportional covers of rice fields, abandoned fields (including fallow fields), semi-natural grasslands, and forests were calculated from a digital habitat map created by TNTmips 2006:72 (MicroImages, Inc., 2007) using geographically referenced aerial photographs taken in 2007. Because abandoned and fallow fields could not be distinguished from the photographs, we used the proportional cover of abandoned plus fallow fields as a measure of farmland abandonment (hereafter, field abandonment). The covers of rice fields, grasslands and forests were also used for analyses because they are primary habitats and known to be important for different bird groups in an earlier study (Amano et al., 2008). By using ArcGIS 9.1 (ESRI, Inc., Redland, California , USA, 2004), two landscape variables were also calculated to represent effects of compositional and configurational heterogeneity; the Shannon's diversity index of land cover and the total length of edge between rice fields and forests. But both the two variables were not used in the analyses due to high intercorrelations with the covers of rice fields (r = –0.71) and of forests (r = 0.59), respectively.

To check whether the field abandonment corresponds to abandonment, fallow or both, we used vegetation data collected in the 32 grid cells from July to September 2007. In each grid cell, 1-m^2 quadrats were randomly established in fallow or abandoned fields. The number of quadrates varied from six to 30 depending on the total area of fallow and abandoned fields within the grid cell, but no quadrat was placed in grid cells without any fallow and abandoned fields. In each quadrat, a percent cover of each plant species was recorded and each sampled field was classified into fallow or abandoned based on a dominant plant species, which is known to reflect a management history in this region (Kusumoto et al., 2005); (1) fallow fields: tilled once 1-3 years and dominated by a variety of native annual plant species (<1 m), including *Digitaria ciliaris*, *Echinochloa crus-galli* var. *caudata*, *Monochoria vaginalis* var. *plantaginea* and *Fimbristylis miliacea*, (2) abandoned fields: unmanaged more than 3-6 years and dominated by a few perennial plant species (>1 m), including both native species (*Phragmites australis* and *Miscanthus sacchariflorus*) and exotic species (*Solidago altissima*). Then each grid was assigned to one of three categories (N: no fallow or abandoned field existed in the grid cell, F: fallow fields were more widespread than abandoned fields in the cell, and A: abandoned fields were more widespread than fallow fields in the cell) (hereafter, succession class).

As a measure of agricultural intensification, we chose the proportional area of rice fields consolidated to enlarge field size (>0.3 ha) and to achieve a regular shape (hereafter, field consolidation). This can be a proxy for the entire process of farmland intensification in Japan because the field consolidation is usually accompanied by (1) a reduction in levees, field margins and crop variety (loss of habitat heterogeneity), (2) an introduction of efficient irrigation/drainage systems (degradation of habitat quality) and (3) the efficient use of agricultural machinery (higher disturbance to aquatic plants and animals) (details are shown in Katayama et al., 2015). The proportional area of field consolidation was calculated for each grid square, by using the digital polygon data on the shape of farmland derived from aerial imagery, collected in 2001 by the Ministry of

Agriculture, Forestry, and Fisheries, Japan (MAFF, unpublished). Each polygon was assigned a status according to its current shape: field consolidation was conducted or not. Using ArcGIS, we mapped each polygon to the corresponding grid cell. Where a polygon overlapped two or more cells, we divided it proportionally among the cells.

2.4. Statistical analyses

Of the 32 study sites, four 100-ha grid squares were excluded from the analyses: one was highly urbanized and thus not suitable for the farmland bird survey and the others lacked precise data on field consolidation. As a result, 28 sites were used in the analyses.

Data analyses were conducted in the following three steps. First, the geographical relationships among the field consolidation, succession class and forest cover at the grid level were investigated. Forest cover was used as an index of topography and labor cost (i.e., larger value indicates higher altitude and thus higher costs, as forest mostly occurs in mountains in Japan). The relationship between field consolidation and forest cover was examined by a generalized linear model with a normal distribution and an identity link. The relationships between succession class and field consolidation or forest cover were examined by the Kruskal-Wallis tests because the succession class is the categorical variable with three factors (N, F and A). When the Kruskal-Wallis tests showed significant differences, the pairwise Wilcoxon exact test with Bonferroni corrections was used to identify categorical classes that differed significantly.

Second, the relationships between the species richness and abundance of bird communities and environmental predictors were examined using generalized linear models with a Poisson distribution and a log link function. Response variables were the total species richness and abundance, and the species richness and abundance of five bird groups. Predictor variables were field consolidation, field abandonment and the proportional covers of rice fields, of grasslands and of forests. All data for the predictor variables were centered at their means. The correlation coefficients between the predictors were not high ($|r|<0.45$). An information-theoretical approach (Burnham and Anderson, 2002) was used for model selection and inference. Akaike information criterion adjusted for small sample size (AICc) was used to compare evidence for all possible parameter subsets (Burnham and Anderson, 2002). When the response variable was the abundance of each bird group, the quasi-AICc (QAICc), which incorporates corrections for small sample sizes and overdispersion (Burnham and Anderson, 2002), was used instead because most models had a variance inflation factor ($\hat{c}$) >1; $\hat{c}$ was estimated by dividing the Pearson's χ^2 statistics by its degrees of freedom (Faraway, 2006). Estimated parameters and their 95% confidence intervals in the best model, defined as a model with the lowest value of AICc (QAICc), were used to predict species richness and abundance of each bird group across a range of environmental predictors that were representative of our sample.

Third, conservation statuses among the five bird groups were compared. We referred to a web database (Search System of Japanese Red Data; http://www.jpnrdb.com/), which lists the Red Data Books (RDB) at the national and prefectural levels (47 prefectures in total). Only RDBs in five prefectures (Ibaraki, Tochigi, Gunma, Saitama and Chiba), which cover the whole study area, were used in our study. Each species in each prefecture was defined as 'threatened' when listed as EX (extinct), CR (critically endangered), EN (endangered), VU (vulnerable) or NT (near threatened) in the prefectural RDBs. Then for each species, number of prefectures assigning the species as threated were counted. All analyses were conducted in the statistics program R (R Development Core Team, 2014).

3. Results

3.1. Spatial distribution of intensive and abandoned fields

Vegetation survey showed that the numbers of grid cells assigned to N (no fallow or abandoned field existed in the grid cell), F (fallow fields were more widespread than abandoned fields in the cell) and A (abandoned fields were more widespread than fallow fields in the cell) were 4, 8 and 16, respectively. Thus the field abandonment corresponded to both abandonment and fallow although abandonment was more widespread than fallow in the study area. In fallow fields, a dominant plant was annual species: *D. ciliaris* (3 grid cells), *Persicaria thunbergii* (2), *E. crus-galli* var. *caudata*

(1), *Setaria pumilla* (1) and *F. miliacea* (1). While in abandoned fields, a dominant plant was perennial species: *S. altissima* (7 grid cells), *P. australis* (6), *M. sacchariflorus* (2) and *Pleioblastus chino* (1).

Generalized linear model showed that there was no significant relationship between the field consolidation and forest cover (P = 0.314; Fig. 2a). While the Kruskal-Wallis test showed that there was a significant relationship between the succession class and the forest cover (P =0.035; Fig. 2b) but there was no such relationship between the succession class and the field consolidation (P = 0.182; Fig. 2c). The pairwise Wilcoxon exact tests showed that there was a significant tendency for the late succession class (i.e., abandoned fields) to occur in grid cells where the forest cover was large (i.e., hilly areas) (P = 0.005 <0.0167 with Bonferroni correction; Fig. 2b).

3.2. Responses of bird groups

A total of 38 and 48 bird species were observed in summer (i.e., May–June) and winter (December), respectively (see Appendix A). The values of environmental predictors and species richness and abundance in each group varied considerably among the 28 grid squares (Table 2). Model selection showed that among 24 response variables (richness or abundance of the six groups in the two seasons), three response variables had only one top model, i.e., a model with ⊿AICc or ⊿QAICc <2.0, and other 21 response variables had several top-ranked models (Appendix B). But in ten out of the 21 response variables, the top models were not truly competitive because the best model, i.e., the model with the lowest value of AICc or QAICc, had fewer explanatory variables than other top-ranked models, in which including one additional explanatory variable was not informative to overcome the penalty of 2 AICc (QAICc) units (Arnold, 2010). While in the remaining eight response variables, the top-ranked models were truly competitive and thus the results of best models were carefully discussed. Estimated coefficients in the best model revealed that all of the explanatory variables were useful to explain variations in the richness and abundance of bird species, although the importance varied among bird groups and between seasons (Table 3; Figs. 3, 4).

Rice-field consolidation was found to have negative or positive associations with richness or abundance of three bird groups: agricultural wetland species, agricultural land species, and woodland species (Table 3; Figs. 3, 4). In summer, when rice fields are flood-irrigated, field consolidation showed strong negative relationships with both richness and abundance of agricultural wetland species (Figs. 3, 4). Consolidation also showed a negative relationship with abundance of woodland species, but its effect was very weak (Fig. 4) and was not supported in one of the other competitive models (Appendix B). In winter, when most rice fields are not flooded, field consolidation had a positive association with abundance of land species (Fig. 4) but its effect was not supported in other competitive models (Appendix B).

On the other hand, we found a relationship between the field abandonment and richness or abundance of two bird groups: agricultural wetland species and grassland species (Table 3; Figs. 3, 4). In summer, field abandonment showed a negative association with richness of agricultural wetland species (Fig. 3). In both seasons, abandonment showed a positive association with abundance of grassland species (Fig. 4).

The effects of other habitat variables (i.e., covers of rice fields, of grasslands and of forests) estimated in this study were generally consistent with those reported in an earlier study (Amano et al., 2008). The proportional cover of rice fields was chosen in the best model for the total abundance and richness or abundance of all the bird groups (Table 3; Figs. 3, 4). In both summer and winter, the cover of rice fields had positive associations with agricultural wetland species and grassland species, but had negative associations with the total abundance, agricultural land species, edge species and woodland species (Figs. 3, 4). The cover of grasslands had positive relationships with agricultural wetland species in winter and grassland species in both seasons. The cover of forests had positive relationships with edge species in summer and woodland species in both seasons, while a negative relationship with agricultural land species in summer.

The prefectural RDBs showed that agricultural wetland species, followed by grassland species, were more threatened than other three groups in both summer and winter in the study region (Fig. 5). In agricultural wetland species, several species such as egrets, rails and plovers were nationally or regionally threatened, while in grassland species, several species of warblers and buntings were threatened (Appendix A).

4. Discussion

4.1. Spatial distribution of intensive and abandoned fields

Generally, agricultural intensification and abandonment tend to be segregated in space: intensification occurs in most profitable land whereas abandonment occurs in marginal lands, e.g., mountains, slopes, and isolated areas (MacDonald et al., 2000). But our results in the Tone River basin showed more complex relationships (Fig. 2). In fact, field consolidation occurred in both plain and hilly areas to reduce labor costs in our study region, similarly as other regions in Japan (Uematsu et al., 2010). Since the 2000s, however, the cover of field consolidation has shown signs of leveling off due to socioeconomic changes such as aging farmers and financial difficulties of the national and local governments (Katayama et al., 2015).

Our results also showed that abandonment was more widespread than fallow in the study area. This supports that the variable "field abandonment" largely represents the effects of abandonment, rather than fallow, on bird communities, although we could not rigorously distinguish the effect of fallow fields from that of abandoned fields, as we did not surveyed vegetation in all abandoned and fallow fields in each grid cell. In addition, abandonment tended to occur in hilly areas surrounded by forests (Fig. 2b) while field consolidation occurred in both hilly and plain areas (Fig. 2a). This suggests that the farmland intensification and abandonment were not completely segregated spatially; hilly areas tended to be abandoned since the 1980s even though the field consolidation since the 1960s had been conducted, probably due to low accessibility for aging farmers (MAFF, 2012). Although the proportional cover of abandoned and fallow fields was small in 2007 (Table 2), the cover has increased more than twofold in 2012 (Kusumoto, unpublished). Thus farmland abandonment, rather than intensification, is rapidly increasing in this region.

4.2. Responses of bird groups

The responses of birds to environmental predictors differed considerably among groups and between seasons. As in previous studies, our results illustrate the complex relationship between the structure of bird communities and agricultural land use in spatially and temporally dynamic paddy landscapes (Amano et al., 2008).

Research has shown that flooded rice fields in summer provide substitute habitats for waterbirds in natural wetlands in Japan (Amano et al., 2008; Fujioka et al., 2010) and in other regions such as Europe and North America (e.g., Elphick 2000; Fasola and Ruíz, 1997). The positive relationship between the cover of rice fields and richness and abundance of agricultural wetland species in our study supports the earlier findings. However, we also found that their richness and abundance in summer were negatively associated with the proportional areas of both consolidated and abandoned (plus fallow) fields. Rice-field consolidation has been shown to reduce the abundance of fish and frogs via habitat drainage and fragmentation between agricultural ditches and rivers, thus affecting the foraging-site selection of egrets and herons (Katayama et al., 2011, 2012; Lane and Fujioka, 1998). In addition, farmland abandonment leads to the growth of dense vegetation in rice fields, where not available for many species of egrets, herons, and shorebirds in summer (Fujioka et al., 2001; Maeda, 2005). While in winter when most rice fields are not flooded in the Tone River basin, richness and abundance of agricultural wetland species was positively associated with the area of grasslands. Because many grasslands are distributed near open water (e.g., rivers, ponds and ditches), this result indicates the importance of large areas of open water as overwintering habitats (Amano et al., 2008).

In agricultural land species, richness and abundance in summer were negatively affected by the areas of rice fields and forests, similarly as earlier studies in both Europe (e.g., Hiron et al., 2012) and Japan (Maeda, 2005). In addition, abundance in winter was positively associated with field consolidation, which promotes efficient water drainage from rice fields and decreases soil moisture content during non-flooding periods (Katayama et al., 2011, 2015). This suggests that open dry fields under the modern farming systems may be suitable for some common land birds (e.g., the eurasian skylark *Alauda arvensis*) as overwintering habitats. However, the positive effect was not supported in competitive models other than the best model, and thus the conclusion remains to be determined in our study.

In grassland species, richness or abundance was high in landscapes with large areas of abandoned fields, grasslands and rice fields in both summer and winter. Several common species, including the great reed warbler (*Acrocephalus arundinaceus*) and the zitting cisticolas (*Cisticola juncidis*), are reported to use both grasslands and abandoned fields with grasses 1 m or taller in Japan (Fujioka et al., 2001). The use by some birds of abandoned fields with perennial plants was also reported in Central-Eastern Europe (see Tryjanowski et al., 2011 and references therein). The positive effect of rice fields may also indicate that semi-natural grasslands on levees and field margins around rice fields provide both breeding and overwintering habitats for grassland species (Maeda, 2005).

In accordance with earlier studies (Amano et al., 2008; Katayama et al., 2014), both edge species and woodland species showed positive associations with landscapes with large forest cover and negative associations with landscapes with large areas of rice fields, in terms of richness or abundance. In our study area, the covers of rice fields and forest cover were highly correlated with Shannon diversity index for habitat cover and edge density, respectively (see Methods). Therefore our results may also indicate the importance of compositional and configurational heterogeneity for these species (Fahrig et al., 2011). While the two bird groups (and agricultural land species) did not show any clear response to farmland abandonment in this study. However, further succession in the future may increase the abundance and richness of woodland (and shrubland) species but decrease other bird groups in Japan, as was observed in the northwestern Mediterranean region of Europe (Sirami et al., 2008; Suárez-Seoane et al., 2002). Therefore, long-term studies are needed to examine the dynamic relationships between bird groups and land use in changing agricultural landscapes.

Total species richness in summer and winter did not show any clear response to all of the environmental predictors, while the total abundance in summer showed a negative response to the cover of rice fields. These patterns seem to reflect mixed responses of the five bird groups, particularly dominant groups. Therefore, the evaluation of total species richness or abundance only is not enough to understand the impacts of land use, including farmland intensification and abandonment, on bird communities. In other words, there are both winners and losers (i.e., increasing and decreasing species) and the impacts of changes in land use are also different depending on the season, which is in accordance with earlier studies in Japan and Europe (Doxa et al., 2012; Sirami et al., 2008; Uematsu et al., 2010).

4.3. Conservation implications

Our important finding is that the diversity of habitats (including consolidated fields and abandoned farmland) provides buffer areas for the different bird groups on different times of the year. However, habitat diversity will continue to be reduced by both intensification and abandonment in response to changing socioeconomic conditions in

Europe (Temme and Verburg, 2011; Verburg et al., 2010). This trend seems to be similar in Japan, although agricultural intensification has shown signs of leveling off since the 2000s (see *4.1. Spatial distribution of intensive and abandoned fields*).

The regional RDBs showed that agricultural wetland species, followed by grassland species, have higher conservation priority than other groups in both summer and winter (Fig. 5). This is not surprising given the loss and degradation of wetlands by the rapid population growth in China and Korea, and the intensification of rice fields in Japan (Amano et al., 2010) and the severe loss of semi-natural grasslands by abandonment or development in Japan (Uematsu et al., 2010). These facts suggest that further intensification and abandonment will have especially severe impacts on the most threatened group, agricultural wetland species in summer. To reduce the negative impact of intensification, the implementation of wildlife-friendly farming (e.g., organic farming), which provides more food items than conventional farming for waterbirds, may be useful (Katayama et al., in press; Parsons et al., 2010). While the management of abandoned fields is more complex problem since the old fields also provide new habitats for another threatened group, grassland species. Therefore, the maintenance of landscape heterogeneity, including both rice fields and abandoned fields, is required to conserve the whole biodiversity in both breeding and wintering seasons. Future studies must investigate the value of various habitats, including intensified and abandoned agricultural fields, to assess the effectiveness of land-use strategies ranging from land-sparing to wildlife-friendly farming for biodiversity conservation (Fischer et al., 2008; Miyashita et al., 2014; Navarro and Pereira, 2012).

Acknowledgements

We thank Yoshinori Tokuoka, Susumu Yamada, Eun-Young Kim, and Shori Yamamoto for providing land-use data. We also appreciate two anonymous reviewers for their constructive comments and suggestions. This study was conducted as part of the research project "Developing management techniques for agricultural and aquatic ecosystems in river basins in pursuit of coexistence with nature," funded by the Agriculture, Forestry and Fisheries Research Council of Japan. N.K. and T.O. were also financially supported by JSPS (Japan Society for the Promotion of Science) KAKENHI Grant Numbers 25830154 and 24710038, respectively. T.A. was supported by the European Commission's Marie Curie International Incoming Fellowship Programme (PIIFGA-2011-303221).

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Table 1. Categories and definitions of eight bird groups in this study, following Amano et al. (2008) and references therein.

Bird group	Definition
Agricultural wetland species	Birds mainly foraging on agricultural wetlands, such as rice fields
Agricultural land species	Birds mainly using dry farmland
Grassland species	Birds mainly using dry or wet grassland
Edge species	Birds mainly using forest edges and open forests
Woodland species	Birds mainly using mature forests
Open water species [a]	Birds dependent on water areas
Raptors [a]	Falconiformes and Strigiformes
Urban species [a]	Birds mainly using urban areas

[a] These species were not included in the analyses.

Table 2. Details of environmental predictors and response variables in our analyses for each of the 28 grid squares (1 km × 1 km) in the study area. For environmental predictors, values before centering (i.e., the proportional covers) are shown.

Variable	Minimum	Maximum	Mean	SD
Environmental predictors				
Field consolidation	0.296	1.000	0.837	0.235
Abandoned fields	0.000	0.076	0.020	0.018
Rice fields	0.002	0.881	0.253	0.216
Grasslands	0.005	0.308	0.109	0.083
Forests	0.002	0.670	0.176	0.169
Bird groups				
Agricultural wetland species				
Summer richness	0	5	1.536	1.401
Summer abundance	0	16	2.964	3.796
Winter richness	0	6	1.107	1.663
Winter abundance	0	17	2.179	4.481
Agricultural land species				
Summer richness	1	6	3.643	1.446
Summer abundance	4	39	16.643	9.254
Winter richness	3	7	4.964	1.290
Winter abundance	3	47	17.893	11.279
Grassland species				
Summer richness	0	2	0.786	0.738
Summer abundance	0	14	2.179	3.186

Winter richness	0	5	1.143	0.932
Winter abundance	0	33	6.107	7.073
Edge species				
Summer richness	2	8	4.571	1.794
Summer abundance	4	48	16.250	10.504
Winter richness	2	9	5.893	1.641
Winter abundance	6	77	30.607	17.058
Woodland species				
Summer richness	0	5	1.107	1.100
Summer abundance	0	12	2.321	3.044
Winter richness	0	4	1.821	1.416
Winter abundance	0	11	3.107	3.035

Table 3. Estimated coefficients and their standard errors (in parentheses) on the best generalized linear models for richness and abundance of all birds and each bird group (SR: summer richness, SA: summer abundance, WR: winter richness, WA: winter abundance). See Appendix B for model selection tables.

Bird group	Field consolidation	Field abandonment	Rice fields	Grassland	Forest
Total species					
SR					
SA			–0.61 (0.15)		
WR					
WA					
Agricultural wetland species					
SR	–1.76 (0.63)	–25.43 (12.12)	2.14 (0.64)		
SA	–2.36 (0.43)		2.48 (0.47)		
WR			2.45 (0.84)	9.31 (2.67)	
WA	2.17 (0.71)			11.71 (1.64)	
Agricultural land species					
SR			–1.27 (0.57)		–1.29 (0.73)
SA			–1.43 (0.26)		–2.67 (0.40)
WR					
WA	0.89 (0.23)				
Grassland species					
SR			1.38 (0.85)		
SA		22.40 (6.57)	2.94 (0.56)	6.45 (1.39)	
WR					
WA		17.62 (3.89)	1.62 (0.34)	5.14 (0.83)	
Edge species					
SR			–1.26 (0.49)		
SA			–1.13 (0.31)		1.45 (0.26)
WR			–0.85 (0.41)		
WA			–1.67 (0.22)		
Woodland species					
SR					2.54 (0.86)
SA	–1.57 (0.47)				4.41 (0.63)
WR			–1.54 (0.97)		1.92 (0.75)
WA			–2.69 (0.84)		1.73 (0.57)

Figure legends

Figure 1. (a) Thirty-two grid squares (1 × 1 km) surveyed for bird occurrence and environmental factors in the Tone River basin in the Kanto Plain, central Japan. Each square is labelled according to four major landscape types (MP: midstream paddy, DP: downstream lowland paddy, PVP: plateau and valley-bottom paddy, UF: urban fringe). Blue areas represent rivers, lakes and ponds. Color strength in each square show the percent cover of forests (0–25%, –50%, –75% and –100% from light to dark green). The land use maps of two example grid squares show that abandoned and fallow fields are commonly found in both (b) hilly and (c) lowland areas.

Figure 2. The relationships among the field consolidation, succession class and forest cover in the 28 grids. The succession class in each grid is assigned to one of three categories (N: no fallow or abandoned field existed in the grid cell, F: fallow fields were more widespread than abandoned fields in the cell, and A: abandoned fields were more widespread than fallow fields in the cell). (b) Different letters on the right of the bars indicate significant differences (P <0.0167 with Bonferroni correction) for the three succession classes (Kruskal-Wallis test followed by pairwise Wilcoxon exact tests).

Figure 3. The relationships between environmental predictors and the total species richness and species richness of five bird groups in summer (closed circles) and winter (open circles). For environmental predictors selected in the best model, estimated coefficients and their 95% confidence intervals are also shown.

Figure 4. The relationships between environmental predictors and the total abundance and abundance of five bird groups in summer (closed circles) and winter (open circles). For environmental predictors selected in the best model, estimated coefficients and their 95% confidence intervals are also shown.

Figure 5. Regional conservation status in the five bird groups in the study area. In each bird group, proportional number of prefectures (five prefectures in total) assigning the species as ‘threatened’ is shown (see text for details).

Figure1
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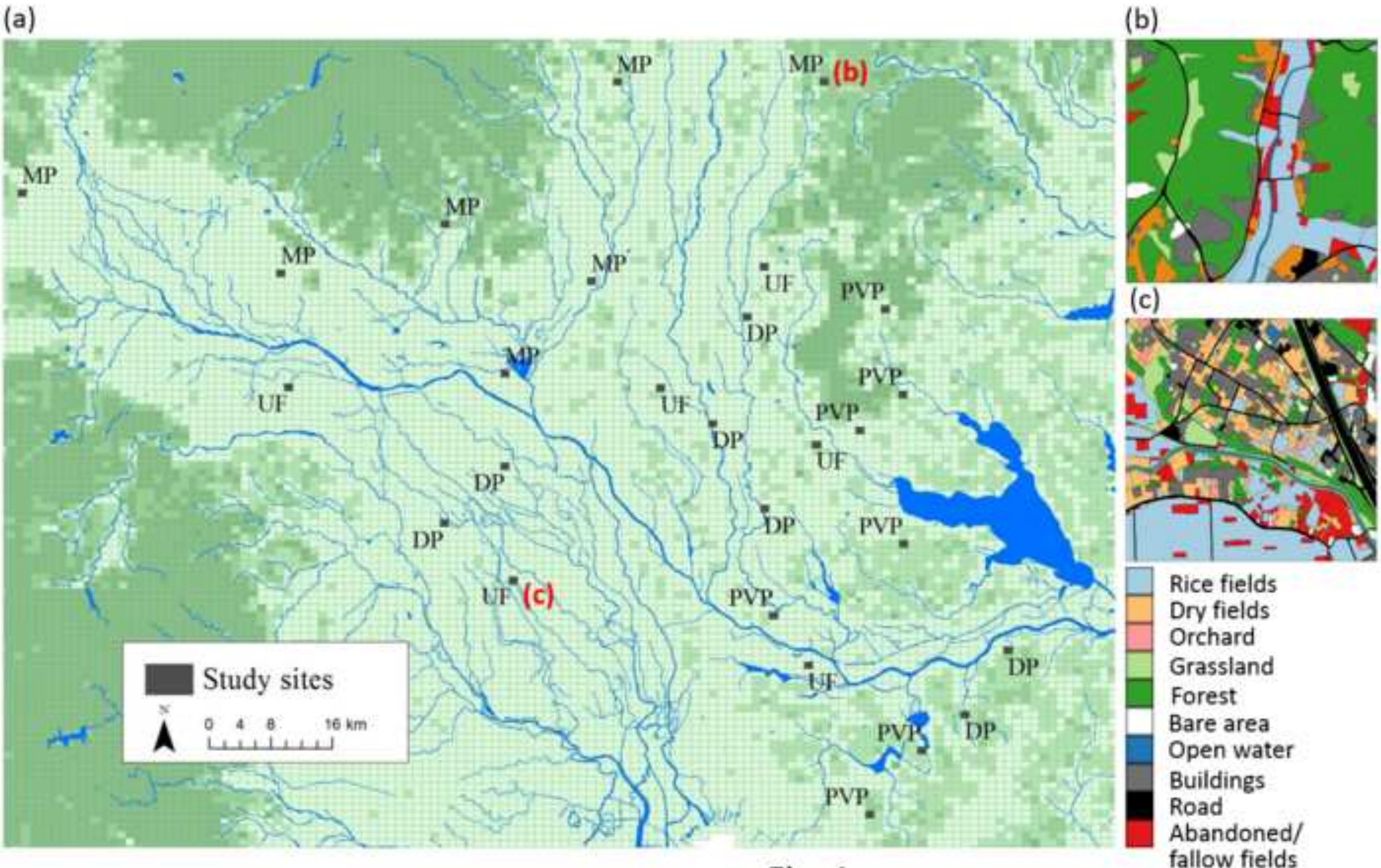

Fig. 1

Figure2
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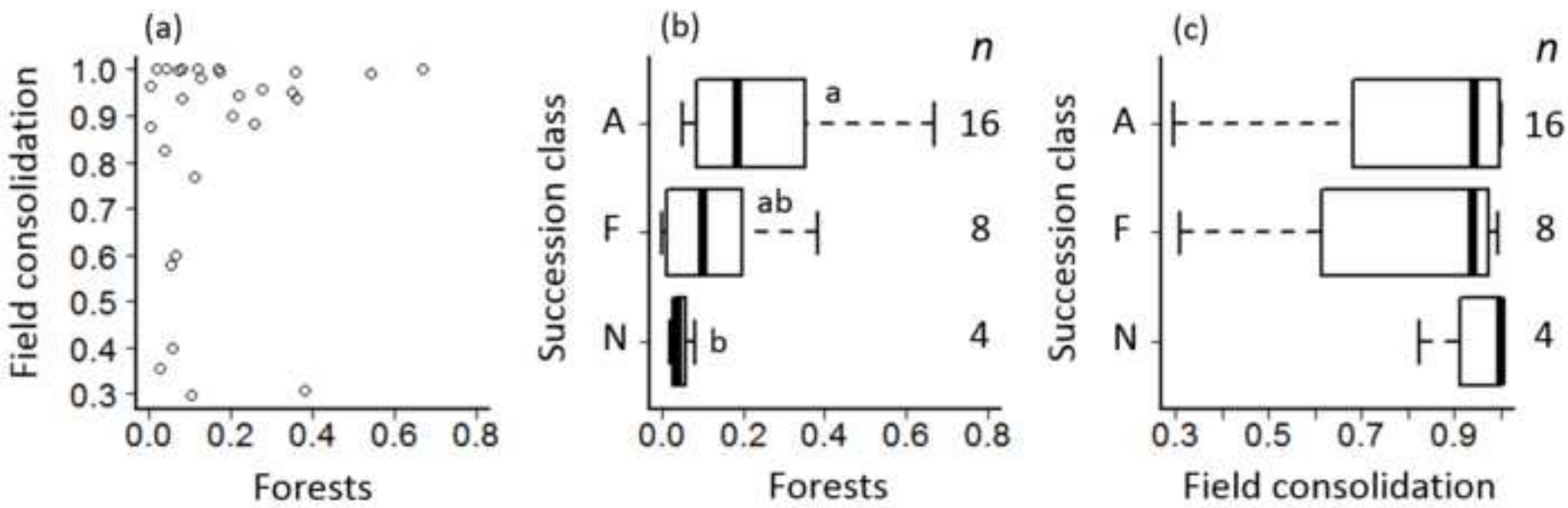

Fig. 2

Figure3

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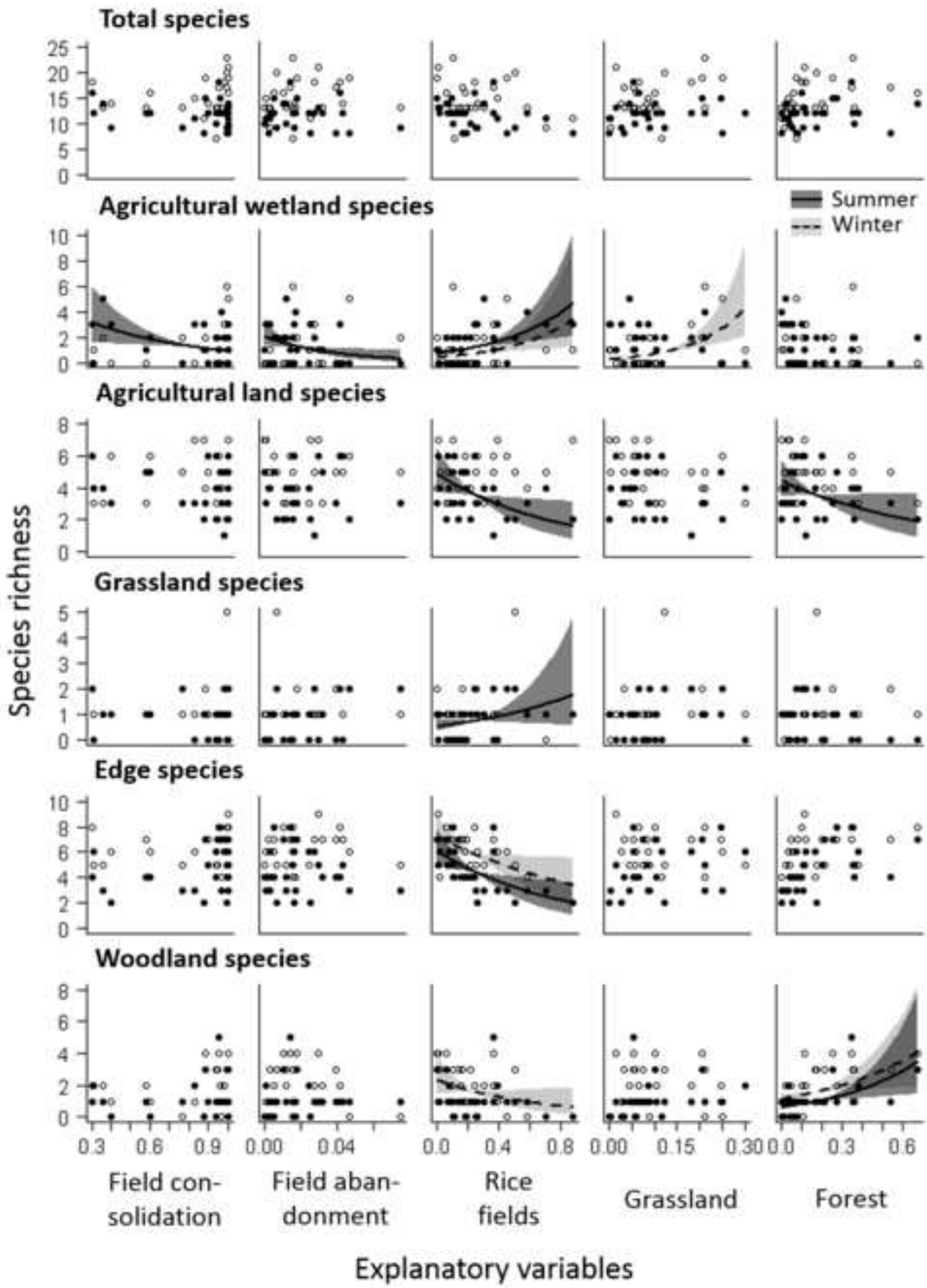

Fig. 3

Figure4

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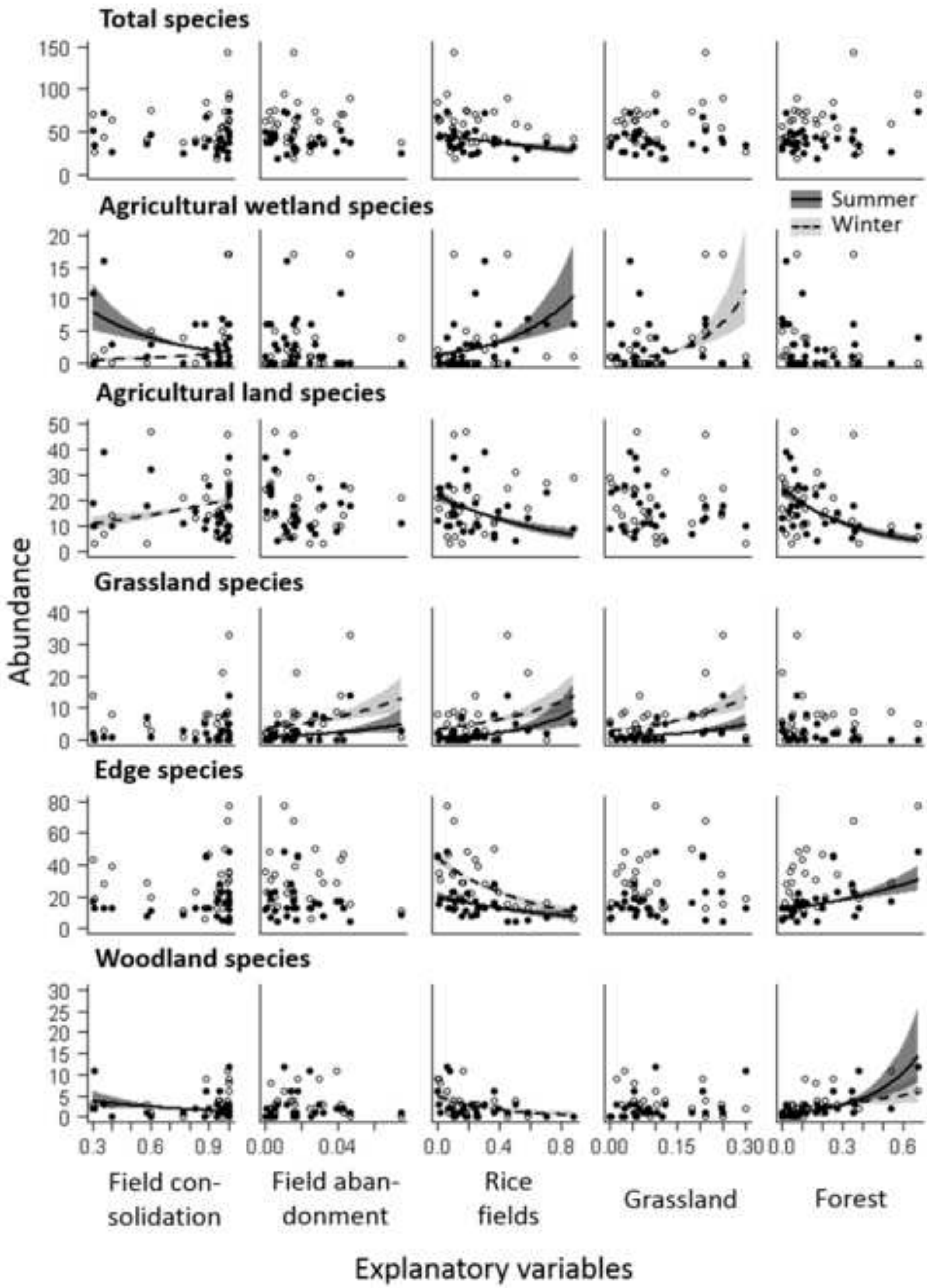

Fig. 4

Figure5
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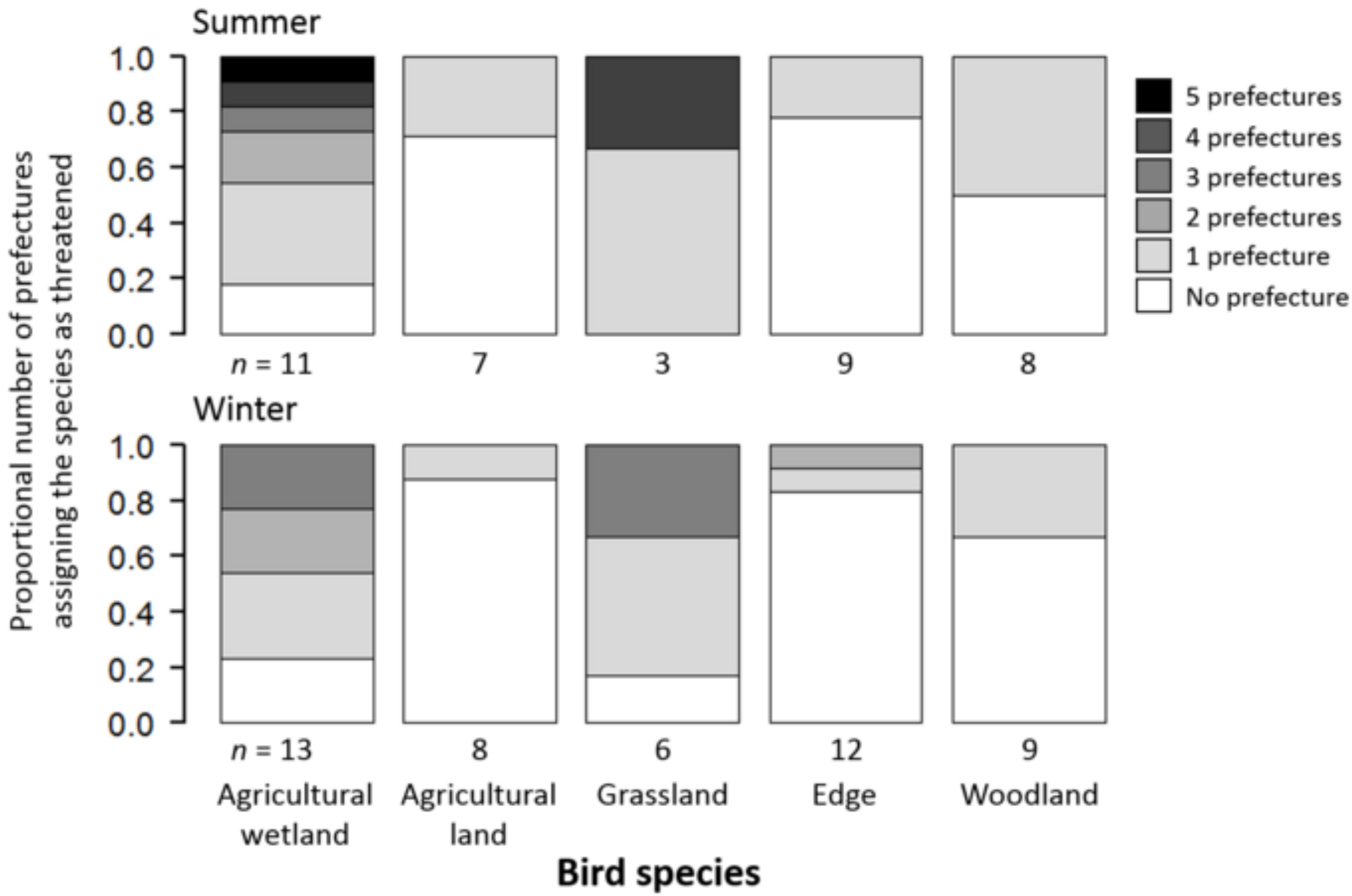

Fig. 5

Appendix A. The 61 bird species observed in our surveys classified into five groups (WET: agricultural wetland species, LND: agricultural land species, GRS: grassland species, EDG: edge species, WOD: woodland species). The range of abundance at each study site and the number of sites observed are shown for the breeding and wintering seasons. The conservation status is the Red List Index at two levels (Search System of Japanese Red Data; http://www.jpnrdb.com/): national (EN: endangered, NT: near threatened) and regional (the number of prefectures of 47 in total in which the species is specified as NT or more threatened status).

Common name	Scientific name	Breeding season			Wintering season			Conservation status	
		Group	Abundance	Site	Group	Abundance	Site	National	Regional
Eurasian bittern	*Botaurus stellaris*	WET	0–1	1	–	–	–	EN	25
Black-crowned night heron	*Nycticorax nycticorax*	WET	0–4	13	WET	0–1	1		0
Cattle egret	*Bubulcus ibis*	WET	0–4	3	–	–	–		4
Grey heron	*Ardea cinerea*	WET	0–2	6	WET	0–3	7		0
Great egret	*Ardea alba*	WET	0–4	4	WET	0–2	4		4
Yellow-billed egret	*Egretta intermedia*	WET	0–5	6	WET	0–1	1	NT	31
Little egret	*Egretta garzetta*	WET	0–2	1	WET	0–1	1		3
Water rail	*Rallus aquaticus*	–	–	–	WET	0–1	1		30
Ruddy crake	*Porzana fusca*	WET	0–1	1	–	–	–	NT	40

Northern lapwing	*Vanellus vanellus*	–	–	–	WET	0–4	3		13
Long-billed plover	*Charadrius placidus*	–	–	–	WET	0–2	2		29
Little ringed plover	*Charadrius dubius*	WET	0–4	6	WET	0–7	2		11
Common snipe	*Gallinago gallinago*	–	–	–	WET	0–4	4		5
Green sandpiper	*Tringa ochropus*	–	–	–	WET	0–1	3		7
Grey-tailed tattler	*Heteroscelus brevipes*	WET	0–3	1	–	–	–		6
Common sandpiper	*Actitis hypoleucos*	WET	0–2	1	WET	0–2	1		11
Dunlin	*Calidris alpine*	–	–	–	WET	0–4	1	NT	11
Common pheasant	*Phasianus colchicus*	LND	0–5	7	LND	0–1	4		1
Bull-headed shrike	*Lanius bucephalus*	LND	0–3	7	LND	0–3	12		0
Eurasian skylark	*Alauda arvensis*	LND	0–25	22	LND	0–14	14		4
Barn swallow	*Hirundo rustica*	LND	0–23	27	–	–	–		1
Dusky thrush	*Turdus eunomus*	–	–	–	LND	0–17	23		0
White wagtail	*Motacilla alba*	LND	0–7	12	LND	0–12	27		0
Japanese wagtail	*Motacilla grandis*	LND	0–3	9	LND	0–5	18		3
Buff-bellied pipit	*Anthus rubescens*	–	–	–	LND	0–16	17		1
Grey-capped greenfinch	*Chloris sinica*	LND	0–14	18	LND	0–32	24		0
Marsh grassbird	*Locustella pryeri*	–	–	–	GRS	0–2	1	EN	9
Great reed warbler	*Acrocephalus orientalis*	GRS	0–7	12	–	–	–		12
Black-browed reed	*Acrocephalus*	GRS	0–1	1	–	–	–		16

warbler	*bistrigiceps*							
Zitting cisticola	*Cisticola juncidis*	GRS	0–8	9	GRS	0–2	1	13
Long-tailed rosefinch	*Uragus sibiricus*	–	–	–	GRS	0–1	4	1
Chestnut-eared bunting	*Emberiza fucata*	–	–	–	GRS	0–0	0	20
Common reed bunting	*Emberiza schoeniclus*	–	–	–	GRS	0–2	2	8
Meadow bunting	*Emberiza cioides*	EDG	0–8	17	GRS	0–31	24	1
Oriental turtle dove	*Streptopelia orientalis*	EDG	0–12	22	EDG	0–14	23	0
Lesser cuckoo	*Cuculus poliocephalus*	EDG	0–4	7	–	–	–	4
Eurasian woodcock	*Scolopax rusticola*	–	–	–	EDG	0–1	1	19
Azure-winged magpie	*Cyanopica cyanus*	EDG	0–2	2	EDG	0–8	3	3
Great tit	*Parus minor*	EDG	0–12	19	EDG	0–10	16	0
Brown-eared bulbul	*Hypsipetes amaurotis*	EDG	0–16	25	EDG	3–30	28	0
Japanese bush warbler	*Cettia diphone*	EDG	0–4	17	EDG	0–7	18	1
Japanese white-eye	*Zosterops japonicus*	EDG	0–8	12	EDG	0–19	18	0
Daurian redstart	*Phoenicurus auroreus*	–	–	–	EDG	0–3	10	0
Hawfinch	*Coccothraustes coccothraustes*	–	–	–	EDG	0–15	10	0
Rustic bunting	*Emberiza rustica*	–	–	–	EDG	0–27	20	1
Black-faced bunting	*Emberiza spodocephala*	–	–	–	EDG	0–14	16	5
Chinese bamboo	*Bambusicola thoracica*	EDG	0–2	7	EDG	0–1	2	0

partridge								
White-bellied green pigeon	*Treron sieboldii*	WOD	0–1	1	–	–	–	9
Japanese pygmy woodpecker	*Dendrocopos kizuki*	WOD	0–3	18	WOD	0–3	14	0
Eurasian jay	*Garrulus glandarius*	–	–	–	WOD	0–2	7	2
Varied tit	*Poecile varius*	WOD	0–3	2	WOD	0–1	2	1
Asian stubtail	*Urosphena squameiceps*	WOD	0–1	1	–	–	–	4
Long-tailed bushtit	*Aegithalos caudatus*	WOD	0–10	4	WOD	0–7	7	1
Japanese leaf warbler	*Phylloscopus borealis*	WOD	0–1	1	–	–	–	10
Eurasian wren	*Troglodytes hiemalis*	–	–	–	WOD	0–1	1	6
White’s thrush	*Zoothera dauma*	–	–	–	WOD	0–1	2	13
Pale thrush	*Turdus pallidus*	–	–	–	WOD	0–3	8	0
Brown-headed thrush	*Turdus chrysolaus*	–	–	–	WOD	0–2	3	3
Red-flanked bluetail	*Tarsiger cyanurus*	–	–	–	WOD	0–2	7	8
Narcissus flycatcher	*Ficedula narcissina*	WOD	0–1	3	–	–	–	12
Japanese grosbeak	*Eophona personata*	WOD	0–3	1	–	–	–	4

7

Appendix B. Top five competing and null (i.e., with only the intercept) generalized linear models for the total species richness and abundance, and species richness and abundance of five bird groups in two seasons. QAICc, instead of AICc, was used to compare the models when the response variable was the total abundance and the abundance of each bird group.

Bird group	Model rank	Explanatory variables						AICc/ QICc	Δi[a]	w_i[b]
		Intercept	Field consolidation	Field abandonment	Rice fields	Grasslands	Forests			
Total species										
Summer richness	1	2.45						137.11	0.00	0.17
	2	2.45			–0.35			137.78	0.67	0.12
	3	2.45					0.29	138.65	1.53	0.08
	4	2.45	–0.18					138.87	1.76	0.07
	5	2.45				0.46		138.98	1.87	0.07
	Null	2.45						137.11	0.00	0.17
Summer abundance	1	3.69			–0.61			68.48	0.00	0.18
	2	3.69		–5.25	–0.61			69.21	0.72	0.13
	3	3.70						70.02	1.54	0.08
	4	3.69		–5.19				70.56	2.08	0.06
	5	3.69	–0.15		–0.61			70.90	2.41	0.05
	Null	3.70						70.02	1.54	0.08
Winter richness	1	2.70						152.44	0.00	0.13
	2	2.70					0.42	152.64	0.19	0.12
	3	2.70				0.73		153.24	0.80	0.09

	4	2.70			–0.23			153.77	1.33	0.07
	5	2.70				0.58	0.36	154.23	1.79	0.05
	Null	2.70						152.44	0.00	0.13
Winter abundance	1	4.09						48.32	0.00	0.13
	2	4.09					0.60	48.96	0.64	0.10
	3	4.09	0.47					48.99	0.67	0.09
	4	4.09			–0.45			49.35	1.03	0.08
	5	4.09				1.10		49.36	1.04	0.08
	Null	4.09						48.32	0.00	0.13
Agricultural wetland species										
Summer richness	1	0.20	–1.76	–25.43	2.14			83.83	0.00	0.41
	2	0.28	–1.43		2.10			86.36	2.53	0.12
	3	0.20	–1.83	–26.21	2.28		0.38	86.73	2.90	0.10
	4	0.20	–1.74	–25.07	2.11	–0.25		86.80	2.97	0.09
	5	0.30		–18.32	1.76			88.33	4.50	0.04
	Null	0.43						94.81	10.99	0.00
Summer abundance	1	0.81	–2.36		2.48			54.99	0.00	0.32
	2	0.74	–2.65	–22.52	2.53			55.17	0.19	0.29
	3	0.81	–2.32		2.33	–0.99		57.81	2.82	0.08
	4	0.81	–2.40		2.55		0.21	57.96	2.97	0.07
	5	0.73	–2.77	–23.82	2.77		0.65	58.29	3.31	0.06
	Null	1.09						65.86	10.87	0.00
Winter richness	1	–0.31			2.45	9.31		75.77	0.00	0.38
	2	–0.30		7.28	2.37	8.96		78.07	2.30	0.12
	3	–0.31	0.46		2.28	9.36		78.24	2.47	0.11
	4	–0.30			2.08	9.44	-0.84	78.29	2.51	0.11

	5	–0.29				10.01	-3.22	78.95	3.18	0.08
	Null	0.10						97.45	21.68	0.00
Winter abundance	1	0.19	2.17			11.70		44.77	0.00	0.14
	2	0.26			2.13	11.12		44.81	0.04	0.13
	3	0.15	2.20	22.36		10.99		45.17	0.40	0.11
	4	0.37				10.17		45.32	0.55	0.10
	5	0.28		21.91		9.96		45.64	0.88	0.09
	Null	0.78						56.99	12.22	0.00
Agricultural land species										
Summer richness	1	1.26			–1.27		–1.29	103.51	0.00	0.17
	2	1.28			–0.85			104.39	0.88	0.11
	3	1.29						104.90	1.40	0.09
	4	1.26	–0.24		–1.24		–1.20	105.92	2.42	0.05
	5	1.26			–1.27	–0.74	–1.18	105.93	2.43	0.05
	Null	1.29						104.90	1.40	0.09
Summer abundance	1	2.74			–1.40		–2.67	78.22	0.00	0.39
	2	2.73		–5.86	–1.38		–2.60	79.61	1.38	0.20
	3	2.74			–1.37	–1.22	–2.43	80.00	1.78	0.16
	4	2.74	–0.03		–1.40		–2.65	81.20	2.98	0.09
	5	2.73		–5.25	–1.36	–1.06	–2.40	81.99	3.77	0.06
	Null	2.81						94.33	16.10	0.00
Winter richness	1	1.60						107.81	0.00	0.18
	2	1.60				–1.15		108.98	1.17	0.10
	3	1.60					–0.57	109.01	1.20	0.10
	4	1.60			0.33			109.42	1.61	0.08
	5	1.60	0.19					109.87	2.06	0.07

	Null	1.60						107.81	0.00	0.18
Winter abundance	1	2.87	0.89					51.33	0.00	0.12
	2	2.85	1.08				–1.24	51.34	0.01	0.12
	3	2.88						51.43	0.10	0.11
	4	2.87					–0.97	52.26	0.93	0.08
	5	2.88			0.56			52.76	1.43	0.06
	Null	2.88						51.43	0.10	0.11
Grassland species										
Summer richness	1	–0.29			1.38			63.64	0.00	0.08
	2	–0.24						63.70	0.05	0.08
	3	–0.30					–2.26	63.79	0.15	0.07
	4	–0.34		16.44	1.45			63.97	0.33	0.07
	5	–0.28		15.75				63.97	0.33	0.07
	Null	–0.24						63.70	0.05	0.08
Summer abundance	1	0.35		22.40	2.94	6.45		60.82	0.00	0.34
	2	0.33		20.38	2.13	6.67	–2.32	62.68	1.86	0.13
	3	0.42			3.01	7.41		62.98	2.16	0.12
	4	0.33		18.87		7.43	–5.08	63.47	2.65	0.09
	5	0.38			2.00	7.75	–2.81	63.75	2.93	0.08
	Null	0.78						80.99	20.17	0.00
Winter richness	1	0.13						72.73	0.00	0.22
	2	0.12				1.86		74.26	1.53	0.10
	3	0.13		5.80				74.71	1.98	0.08
	4	0.13					0.47	74.85	2.12	0.08
	5	0.13			0.33			74.89	2.17	0.08
	Null	0.13						72.73	0.00	0.22

Winter abundance	1	1.60		17.62	1.62	5.13		52.90	0.00	0.26
	2	1.65			1.70	5.71		53.87	0.97	0.16
	3	1.65		18.70		4.77		54.38	1.48	0.12
	4	1.61	0.21	17.87	1.55	5.10		56.10	3.20	0.05
	5	1.60		17.89	1.72	5.10	0.27	56.13	3.23	0.05
	Null	1.81						61.31	8.41	0.00
Edge species										
Summer richness	1	1.49			–1.26			109.13	0.00	0.17
	2	1.48			–0.99		0.72	109.90	0.77	0.11
	3	1.48	0.44		–1.26			110.41	1.29	0.09
	4	1.48			–1.20	1.13		110.52	1.39	0.08
	5	1.50					1.15	111.04	1.92	0.06
	Null	1.52						114.16	5.03	0.01
Summer abundance	1	2.71			–1.13		1.45	70.58	0.00	0.25
	2	2.70		–8.65	–1.11		1.46	71.21	0.63	0.18
	3	2.73					1.89	72.28	1.70	0.11
	4	2.72		–8.83			1.89	72.58	1.99	0.09
	5	2.71	0.26		–1.16		1.37	73.16	2.58	0.07
	Null	2.79						86.48	15.90	0.00
Winter richness	1	1.76			–0.85			113.88	0.00	0.23
	2	1.76		2.79	–0.85			116.01	2.13	0.08
	3	1.76			–0.74		0.29	116.06	2.18	0.08
	4	1.77						116.15	2.27	0.08
	5	1.76			–0.84	0.18		116.36	2.48	0.07
	Null	1.77						116.15	2.27	0.08
Winter abundance	1	3.37			–1.67			53.97	0.00	0.24

	2	3.36			–1.36		0.82	54.29	0.32	0.21
	3	3.36		–4.05	–1.66			56.12	2.16	0.08
	4	3.37	0.23		–1.66			56.36	2.39	0.07
	5	3.36		–4.30	–1.35		0.82	56.64	2.68	0.06
	Null	3.42						63.75	9.78	0.00
Woodland species										
Summer richness	1	0.00					2.54	72.03	0.00	0.30
	2	–0.02				1.92	2.48	73.70	1.67	0.13
	3	–0.01	–0.25				2.61	74.46	2.42	0.09
	4	0.00			0.22		2.64	74.51	2.48	0.09
	5	0.00		1.36			2.55	74.54	2.50	0.09
	Null	0.10						77.36	5.32	0.02
Summer abundance	1	0.50	–1.57				4.41	72.77	0.00	0.32
	2	0.49	–1.17			2.24	4.19	74.21	1.43	0.15
	3	0.50				3.76	3.89	74.45	1.67	0.14
	4	0.49	–1.66	–7.28			4.40	75.32	2.54	0.09
	5	0.49	–1.53		–0.33		4.28	75.69	2.91	0.07
	Null	0.84						102.95	30.18	0.00
Winter richness	1	0.46			–1.53		1.92	88.75	0.00	0.21
	2	0.50					2.45	88.99	0.25	0.19
	3	0.49		–8.02			2.44	90.75	2.01	0.08
	4	0.45		–7.71	–1.50		1.92	90.78	2.04	0.08
	5	0.45			–1.61	–1.12	1.95	91.07	2.33	0.07
	Null	0.60						98.24	9.49	0.00
Winter abundance	1	0.90			–2.69		1.73	66.44	0.00	0.23
	2	0.87			–2.92	–3.26	1.87	66.82	0.38	0.19

3	0.94		–3.40			67.87	1.43	0.11
4	0.92		–3.55	–2.46		69.09	2.66	0.06
5	0.90	0.33	–2.68		1.64	69.21	2.77	0.06
Null	1.13					77.83	11.39	0.00

[a] The difference between each model's AICc or QAICc and the AICc or QAICc of the best model.

[b] Akaike weight