Title

Assessing the landscape-dependent restoration potential of abandoned farmland using a hierarchical model of bird communities

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Abstract (299 words)

Expansion and intensification of agriculture have led to an immense decrease in biodiversity. However, the area of abandoned farmland has been increasing globally in recent years and is expected to provide novel habitats for various organisms. Despite the promising potential for biodiversity conservation in agricultural landscapes, few studies have compared biodiversity among multiple land use types, including abandoned farmland. We examined the effects of major land use types (wetland, grassland, forest, farmland, abandoned farmland) and the surrounding landscape openness (proportion of wetland/grassland in the surrounding area) on the abundance and species richness of bird communities and four functional groups (wetland, grassland, farmland, and forest species) in the agricultural landscape of central Hokkaido in northern Japan. The abundance of wetland/grassland species in abandoned farmland tended to be intermediate between those of their original habitats (wetland and grassland) and other land uses (forest and farmland), and to be positively associated with the landscape openness. The abundance of forest species tended to be higher in forest areas than in areas with other land use types and was not associated with the landscape openness. The abundance and species richness of the bird community were predicted to be high in large abandoned farmland areas surrounded by open land. For wetland species, whereas total abundance was predicted to be primarily mediated by landscape openness, species richness was predicted to be primarily mediated by the farmland abandonment area. The abandoned farmland in our study area would not currently have a high conservation value for forest birds. However, the abandonment of farmland surrounded by open land would significantly improve the conservation of wetland/grassland birds in the agricultural landscape. Given the decline in the area of grassland, wetland, and low-intensity farmland, farmland abandonment provides an opportunity to conserve and restore the declining populations of wetland and grassland birds.

Keywords (6): Abandoned farmland; Abundance; Hierarchical community model; Landscape composition; Species richness; Wetland

1. Introduction

Rapid human population growth over the past few centuries has resulted in the conversion of most of the Earth's land surfaces to human land uses, such as urban areas, transportation networks, and farmland (Ramankutty and Foley, 1999; Ellis, 2011). For example, approximately 80% of the world's wetlands, 40% of grasslands, and 20% of forests have been lost since the 1700s (Goldewijk, 2001; Davidson, 2014), resulting in an immense decrease in biodiversity (e.g., Newbold *et al.*, 2015). Among the various factors associated with this biodiversity loss, the expansion and intensification of agriculture are considered to be the major drivers (Donald *et al.*, 2001; Tilman *et al.*, 2001). For example, Tanentzap *et al.* (2015) found that 53% of the threatened terrestrial species on the International Union for Conservation of Nature (IUCN) Red List were negatively affected by agriculture.

Since the 1900s, farmlands have been abandoned around the world and especially in developed countries due to declines in human population and agriculture (Ramankutty and Foley, 1999). Abandoned farmland can facilitate the recovery and succession of plant communities by providing novel habitats for many animals whose distributions were negatively affected by the past expansion and intensification of agriculture (Cramer *et al.*, 2008; Pereira and Navarro, 2015). Therefore, it is suggested that not only preservation of the remaining natural habitats, but also management of cultivated and abandoned farmlands would be beneficial for organisms in agricultural landscapes (e.g., Tscharntke *et al.*, 2005; Meli *et al.*, 2014). Nevertheless, relative values among various land uses (e.g., active and abandoned farmland and the remnants of natural habitats) for organisms in agricultural landscapes remain unknown.

The abundance and species richness of organisms in agricultural landscapes are expected to vary depending on the surrounding environment (e.g., the quality of the matrix or the amount of surrounding habitat) (Dauber *et al.*, 2003; Quesnelle *et al.*, 2015; Ernst *et al.*, 2017) via various ecological processes, such as the provision of additional feeding habitats (Dunning *et al.*, 1992; Taylor *et al.*, 1993). It would also be important to examine how the abundance and species richness of organisms for each land use type varies depending on the surrounding environment. Indeed, our previous study revealed that abandoned farmland with large amounts of surrounding wetland/grassland had a high abundance and species richness of wetland/grassland birds (Hanioka *et al.*, in press).

The objectives of the present study were to compare the abundance and species richness of birds among the major land use types in agricultural landscapes (i.e., wetland, grassland, forest, farmland, and abandoned farmland) and to assess their dependency on the surrounding landscape structure. We used recently developed hierarchical community models (HCMs), which allowed us to model rare and common species simultaneously (Iknayan *et al.*, 2014; Warton *et al.*, 2015; Ovaskainen *et al.*, 2017), and therefore even functional groups and entire communities could be assessed (Dorazio *et al.*, 2006; Yamaura *et al.*, 2012b; Kéry and Royle, 2016). We specifically adopted abundance-based HCMs to evaluate the value of farmland abandonment not only to total bird abundance, but also bird species richness (Yamaura *et al.*, 2016a; 2016b; Yamaura and Royle, 2017).

In the analysis of field data, we first quantified the effects of local land uses and the surrounding landscape structure (landscape openness) on the abundance of individual bird species and the abundance and species richness of functional groups (wetland, grassland, farmland, and forest species) and whole communities. Then, based on the modeled environmental dependency of every species, we inferred how the potential of farmland abandonment to conserve bird abundance and species richness varied with the landscape structure. Finally, to visualize the significance of the modeling results, we constructed spatial maps of predicted bird abundance and identified areas with great conservation value (i.e., high bird abundance) for groups of individual species in the study area.

It is known that farmland abandonment can negatively affect open land bird species in Europe (e.g., Sirami *et al.*, 2008), and agricultural intensification also has negative effects (Donald *et al.*, 2001; Flohre *et al.*, 2011). Because farmlands are usually abandoned in marginal unproductive areas where traditional low-intensity farming is common (Queiroz *et al.*, 2014), we hypothesized unimodal responses of wetland and grassland bird abundance to the post-management habitat trajectory for xeric (dry) sites (Fig. 1). According to this conceptual model, low-intensity (or extensively managed) farmland would provide optimal habitats for many wetland/grassland species, and management practices that change the farmland from this status will result in the decline of wetland/grassland species. The model is based on the premise that farmland abandonment in Europe shifts low-intensity (dry) farmland to forest land (Sirami *et al.*, 2008). However, farmlands in our lowland landscape are situated in both mesic and xeric sites, and have been cultivated by intensive management (with machinery and chemical fertilizer: Appendix 1). Thus, we hypothesized that abandoned farmlands in our study region would succeed to semi-natural wetland/grassland, which may increase the abundance of wetland and grassland birds (Fig. 1).

2. Materials and methods

2.1.Study area

Our study area was located in the Ishikari and Iburi Districts of central Hokkaido in northern Japan (42°36’–43°06’N, 141°31–54’E, annual average precipitation: 929–1198 mm, average temperature: 6.7–7.6°C; Japan meteorological Agency, Ministry of Land, Infrastructure, Transport, and Tourism http://www.jma.go.jp/jma/indexe.html; Fig. 2). Fewer than half of the wetlands that existed in Japan in the early 20th century (approximately 2110 km^2) now remain (821 km^2) (GSI, 2000). Our study area was dominated by wetlands in the 1900s, but most of these have been converted into farmland or residential areas (GSI: http://www.gsi.go.jp/ENGLISH/index.html; Hokkaido Regional Development Bureau, 2013). Additionally, the amount of abandoned farmland in Japan increased from 130,000 ha in the late 1980s to 400,000 ha in 2011 (MAFF, 2011). Our study area currently contains 2065 ha of abandoned farmland. This area is approximately equivalent to 70% of the area of the remaining wetlands in the study area, which are primarily located in its southern portion (Fig. 2a).

2.2.Definition of land use

We focused on six land uses: wetland, grassland, wet abandoned farmland, dry abandoned farmland, farmland, and forest. We divided abandoned farmland into either wet or dry based on the dominant vegetation, because differences in vegetation may affect the abundance and species richness of birds. Wetland was defined as uncultivated land dominated by wet grass species such as common reed (*Phragmites australis*), sedge (*Carex* spp.), and *Calamagrostis canadensis* subsp. *langsdorffi*. Grassland was uncultivated land dominated by dry grass species such as amur silver grass (*Miscanthus sacchariflorus*) and Japanese silver grass (*Miscanthus sinensis*). Wet abandoned farmland was historically cultivated but is now abandoned land dominated by wet grass species. Dry abandoned farmland was historically cultivated but is now abandoned land dominated by dry grass species. Farmland was arable land used as pasture, cropland, or paddy fields. Forest was uncultivated land dominated by trees.

2.3.Establishment of sampling plots

Based on a vegetation map (scale 1:25,000 and resolution: 25 m) provided by the Natural Conservation Bureau of the Ministry of Environment (http://www.biodic.go.jp), we created a land use map composed of the aforementioned six land uses and other unsuitable land uses (e.g., urban areas and open water) for the birds of interest. Then, we established 48 sampling plots of 2 ha each (width 100 m × length 200 m) to range the ratio of each land use from 0 to 1. We considered the center of the long side of each sampling plot to be the transect line (200 m), and recorded the birds observed in a 50-m band on each side of a 200-m long straight line. To ensure that the sampling plots were independent from each other (to avoid double counting of the same individuals), the plots were spaced 500 m apart (Ralph *et al.*, 1993: radius of territory sizes for common species were basically <100 m). This spatial separation was considered since spatial autocorrelation can greatly affect the analysis when spatial autocorrelation occurs both in response (birds in this study) and environmental variables (Legendre *et al.*, 2002). We calculated the ratio of focal land uses (0–1) within each sampling plot. We generated 400-m buffers from the edge of each sampling plot (width 900 m × length 1000 m; the area of each buffer was 88 ha). We then measured the surrounding wetland/grassland ratio (0–1; hereafter termed 'landscape openness'), which included wetland, grassland, wet abandoned farmland, dry abandoned farmland, and farmland (except for paddy fields) in each buffer. We excluded paddy fields because their low vegetation and open water surfaces were unlikely to provide a suitable habitat for land birds. Landscape openness was negatively correlated with the proportional area of forest in the surrounding area ($r < -0.7$, $p < 0.001$). Therefore, we used this ratio as a single landscape variable in all analyses. We established sampling plots (i.e., determined their locations) by confirming low correlations among the previously mentioned environmental covariates (the ratio of each land use type and landscape openness (|*r*| < 0.52); see Appendix 2 for the mean ± standard deviation (SD) of each environmental variable in the sampling plots). The directions of the census lines were determined to represent the environmental conditions, vegetation structure, and composition. We performed these procedures using QGIS ver. 2.16.0 (QGIS Development Team, 2016).

2.4.Bird survey

We surveyed birds in 48 sampling plots during the morning period (4:00–10:00 a.m.) from the beginning of June to mid-July, 2015. Each plot was surveyed three times, and survey time bias was avoided by visiting each plot at three different times: (i) 4:00–6:00, (ii) 6:00–8:00, and (iii) 8:00–10:00. We also avoided bias resulting from the survey date by visiting each sampling plot on different dates throughout the survey period.

A single surveyor (M. H.) walked through transects slowly (1 km/h) with a geographical position system (GPS), and recorded the species, sex, location, and behavior (e.g., territorial conflicts) of individuals in the plots (territory mapping: Bibby *et al.*, 2000). Then, we recorded the putative territories of individual species on a map based on their known/estimated territory sizes (e.g., Cramp, 1977-1994; Fujimaki *et al.*, 1994; Kawaji *et al.*, 1996) and field records (e.g., locations, aggressive behavior, and sex) from three visits (Bibby *et al.*, 2000). We then calculated the number of territories for each species in each plot. When calculating territories, any territory that had > 0.5 area in the plot were treated as one territory.

Otherwise, we assigned a value of 0.5 (Bibby *et al.*, 2000). For species in which it was difficult to distinguish between males and females, or which birds were always in a flock consisting of multiple individuals, we assigned one territory if the species was present in the plot, and 0 territories if it was absent. We summed and rounded these quantities to obtain the number of territories (as an integer) within the sampling plots, which was used as the abundance. Because it has been reported that open land songbirds have a relatively high detection probability in Hokkaido (~ 0.6: Yamaura *et al.*, 2016a), we considered that each inhabited territory within the sampling plots was detected in at least one of the survey visits. Although forest species can have a lower detection probability, we did not consider imperfect detection and assumed that each territory was also detected during the field survey. Because open land with a high detection probability had smaller abundance estimates of forest species (see Results) and detection probabilities were high within a 50-m range, even in forests (Schieck, 1997; Alldredge *et al.*, 2007; Yamaura and Royle, 2017), we concluded that an undesirable confounding of abundance and detectability was avoided using the territory mapping methods with a 50-m census range. Eight species, including the grey heron (*Ardea cinereal*) and eastern marsh harrier (*Circus spilonotus*), were excluded from the analyses because their territory sizes were larger than our census and buffer areas (90 ha).

2.5.Statistical analysis

We estimated the effects of land use and surrounding habitats on the abundance of each bird species using abundance-based HCMs (Yamaura *et al.*, 2016b). We first assumed that the abundance of species i in plot j (Z_{ij}) followed a Poisson distribution (Z_{ij} ~ Poisson[λ_{ij}]). We then assumed that the expected abundance of species i in plot j (λ_{ij}) was a function of the proportion of the six land uses within the plot (i.e., wetland, grassland, wet abandoned farmland, dry abandoned farmland, farmland, and forest) and the landscape openness (see above for their correlations). We treated the proportion of the six land uses and landscape openness as continuous explanatory variables, and the intercept in the linear predictor was omitted (cell means method: Kéry, 2010) to easily compare the expected abundance among the habitats using the parameter estimates:

$$\log(\lambda_{ij}) = \beta_{i1} \times x_{1j} + \beta_{i2} \times x_{2j} + \beta_{i3} \times x_{3j} + \beta_{i4} \times x_{4j} +$$

$$\beta_{i5} \times x_{5j} + \beta_{i6} \times x_{6j} + \beta_{i7} \times x_{7j}$$

where x_{1j}-$_{6j}$ indicates the proportion of each land use (0–1) in plot j and x_{7j} indicates the landscape openness (0-1) in the surrounding plot j. We centralized the landscape openness before the analysis (subtracted the mean from each value). β_{i1}-$_{i7}$ indicate the partial regression coefficients of species i for each explanatory variable. The roles of the different habitats and landscape openness were treated as additional effects. If a species benefited from multiple habitats, e.g., species that require separate habitats for nesting and foraging (Dunning *et al.*, 1992; McCollin, 1998), more complex formulations (e.g., interaction terms) would be needed.

We categorized the observed bird species as: (i) wetland species (ii) grassland species, (iii) farmland species, or (iv) forest species (see Appendix 3) according to published references (e.g., Takagawa *et al.*, 2011). We divided open land species into three groups because wetland and grassland species are specialists of their respective habitats, while farmland species are generalists of open land habitats (e.g., Japanese pied wagtail *Motacilla alba*, Eurasian skylark *Alauda arvensis*) that can also be observed in farmlands. We then assumed that the species-level parameter β_i followed a functional group-level normal distribution with hyperparameters. This parameterization allowed us to model rare species using the information from common species (Kéry and Royle, 2016):

$$\beta_{i1} \sim \text{Normal}[\mu_{\beta_1}, \sigma^2_{\beta_1}], \quad \beta_{i2} \sim \text{Normal}[\mu_{\beta_2}, \sigma^2_{\beta_2}].$$

where μ_{β_1} and σ_{β_1} are the mean and standard deviation of β_{i1}, respectively, which indicates that different functional groups can have different means and variations for each coefficient, because we expected that the effects of land use and the landscape openness would differ between the species groups. We obtained the parameter estimates from bird survey data using a Markov Chain Monte Carlo (MCMC) method with three chains, 100,000 burn-in, a thinning interval of 10, and 900,000 post-iterations. We conducted these analyses using R ver. 3.2.0 (R Core Team, 2015), JAGS ver. 4.2.0 (Plummer, 2016), and jagsUI ver. 1.4.2 R package (Kellner, 2016). We determined each covariate to be significant at the 5% significance level.

To determine whether we could appropriately use HCMs (assuming a Poisson distribution while not considering over-dispersion), we constructed generalized linear models (GLMs assuming a Poisson distribution), generalized linear mixed models (GLMMs with random site effects to account for over-dispersion) with random site effects, and spatial GLMMs

(Dormann *et al.*, 2007) for nine common species (representing four species groups). We constructed spatial models (spatial GLMMs) since the consideration of spatial autocorrelation can shift the regression coefficients (Bini *et al.*, 2009). The parameter estimates of these models were qualitatively similar to those yielded from HCMs (major effects of the covariates did not change among the models: Appendix 4).

Based on the median estimates of species-level parameters, we modeled the expected functional group- and community-level abundances (i.e., the total abundances of the above four groups and the entire bird community) as a function of the proportion of each land use and landscape openness. Specifically, we summed the expected abundance λ_{ij} within groups for different values of the covariates. Similarly, we modeled the expected species richness, which was expressed as the expected value of the number of species with at least one individual (i.e., $Z_{ij} \geq 1$). We calculated the probability of at least one individual occurring (occupancy probability: $1 - \exp[-\lambda_{ij}]$) across species (Yamaura *et al.*, 2016a). We used these techniques in the following prediction and mapping analyses.

2.6.Predicting the effects of farmland abandonment

Based on the constructed HCMs, we examined how the abundance and species richness of four bird groups and the overall bird community varied with farmland abandonment and landscape openness. We assumed that a given ratio of farmland (0–1) in a given plot (2 ha) was completely converted into abandoned farmland (hereafter referred to as the farmland abandonment ratio). For example, a farmland abandonment ratio of 0.4 indicated that all farmland (0.4) in the plot was converted into abandoned farmland. We assumed that the half of the farmland abandonment ratio was converted into wet abandoned farmland and the other half was converted into dry abandoned farmland based on the minor differences in bird communities between wet and dry abandoned farmland. We used 301 different farmland abandonment ratios (0.0000, 0.0033, …, 0.9967, 1.0000) for the prediction. For a certain farmland abandonment ratio, we also changed the landscape openness to 301 different values (0.0000, 0.0033, …, 0.9967, 1.0000) to simultaneously examine the combined effects of farmland abandonment and landscape openness (a total of 301 × 301 = 90,601 scenarios). In these scenarios, we estimated the changes in the expected values of abundance and occupancy probability of individual species under the different values of farmland abandonment ratio and landscape openness. We assumed that the remaining area in the plot (i.e., 1 – farmland abandonment ratio) was equally covered (and held constant) by the other three land uses (wetland, grassland, and forest). We then summed the changed values within the groups and predicted the abundance and species richness for the bird groups and the total bird community.

2.7. Mapping the predicted bird abundance

We divided the land use map of the study area into 2-ha grids (width 100 m × length 200 m) and stored the values of each explanatory variable in each grid. Then, we calculated the expected abundance of each bird species in each grid (grid λ_{ij}) and obtained the abundance of each bird group and the total bird community for each grid. We excluded grids with no focal land uses from the mapping analysis. When the focal land uses were less than 1 (i.e. only partially covering the grid), grid-level abundance was overestimated because non-focal land-uses were unsuitable habitats for the birds considered in this study. Given our model formulation of log(λ_{ij}), the expected abundance of these unsuitable habitats (likely 0) was modeled to be 1 per plot (i.e., when unsuitable habitats completely covered the grids, grid λ_{ij} = exp[0] = 1, assuming a mean value of landscape openness). In other words, this was because we modeled the plot-level abundance by summing the abundance of individual habitats, which were assumed to completely cover the plots as a whole ($\sum_{i=1}^{6} x_{ij} = 1$). To avoid overestimation of the abundance, we calculated the abundance of each species (λ_{ij}) by assuming the ratio of the total area of the focal land uses in the grid was 1 and multiplied λ_{ij} by the total ratio of the focal land uses in the 2-ha grid (S_j) (i.e., grid λ_{ij} = $\lambda_{ij} \times S_j$).

3. Results

We recorded a total of 743 individuals of 56 bird species during the survey (see Appendix 3 for details). After excluding eight species whose territory sizes were larger than the census and buffer areas, we focused on 48 species (9 wetland, 10 grassland, 6 farmland, and 23 forest species) in the following analyses.

3.1. Effects of land use and surrounding habitats on birds

The group-level mean of the expected abundance (hereafter ‘abundance’) for the wetland and grassland bird species tended to be highest in wetland and/or grassland areas and lowest in farmlands and forests (Fig. 3a,b). Thus, the abundance values of wetland and grassland species for both types of abandoned farmland were generally between the abundance values of wetland/grassland and farmland/forest (Fig. 3a,b). In terms of species-specific responses, the abundances of three wetland birds (Middendoff’s grasshopper warbler [*Loucustella ochotensis*: code W6], great reed warbler [*Acrocephalus orientalis*: W7], and common reed bunting [*Emberiza schoeniclus*: W9]) were significantly higher in wet abandoned farmland than in farmland and forest (Appendixes 5–6). The abundance of the black-browed reed warbler (*Acrocephalus bistrigiceps*: W8) was also significantly higher in wet abandoned farmland than in dry abandoned farmland, farmland, and forest (Appendixes 5–6). In contrast, the abundance of the lanceolated grasshopper warbler (*Locustella lanceolata*: W5) was significantly lower in both types of abandoned farmland than in wetlands (Appendixes 5–6). Landscape openness tended to have positive effects on the abundance of wetland and grassland groups, and the effects on the abundances of four of the 19 wetland/grassland species were significant (e.g., black-browed reed warbler and Middendoff’s grasshopper warbler) (Appendixes 5–6). In contrast, farmland species consistently had a high abundance in the farmland among the five open land uses, and landscape openness tended to have a positive effect (Fig. 3c, Appendixes 5–6).

The abundance of the forest bird group (the average of 23 forest species) tended to be higher in forests than in areas associated with the other five land uses. The differences in abundance between the forest and three land uses (i.e., grassland, wet abandoned farmland, and farmland) were significant (Fig. 3d). Although landscape openness tended to have negative effects at the community level (Fig. 3d), no significantly negative responses to this covariate were observed for individual species, although this was observed in the wetland/grassland species group (see Appendix 5).

3.2.Predicting the effects of farmland abandonment

For the wetland and grassland bird groups, abundance and species richness were predicted to increase with increases in farmland abandonment and landscape openness (Fig. 4a,b,f,g). For wetland species, whereas abundance was primarily mediated by landscape openness (Fig. 4a), species richness was primarily mediated by the farmland abandonment ratio (Fig. 4f). Farmland abandonment had negative effects on farmland species (Fig. 4c,h). Although the abundance and species richness of forest birds decreased with increases in farmland abandonment and landscape openness, the rates of decrease were small (Fig. 4c,d,h,i). The combination of these results revealed that the abundance of the total bird community increased with an increase in the farmland abandonment ratio, and its rate of increase tended to be acute under conditions with a higher landscape openness (Fig. 4e). In contrast, species richness for the total bird community increased moderately with an increase in the farmland abandonment ratio (Fig. 4j). Community-level responses were therefore mainly determined by the responses of wetland/grassland species, because forest species were insensitive to the proportional area of farmland and abandoned farmland and farmland species were negatively influenced by farmland abandonment.

3.3.Mapping the predicted bird abundance

The abundance of the wetland and grassland bird groups was lower in the northern and central lowland parts of the study area, most of which were dominated by farmland. These estimates were higher in the southern lowland area, where wetland and grassland patches were still present (Fig. 5a,b, cf. Fig. 2a). Furthermore, high abundances of these groups were predicted in areas of abandoned farmland surrounded by wetland/grassland rather than by forests (Fig. 5a,b, cf. Fig. 2a). The abundance of farmland species was high in the central part of the study area where farmlands were concentrated (Fig. 5c). The abundance of the forest bird group was lowest in the northern and central lowland area of the study area, although these areas included patches of forest, and highest in the southeastern and southwestern area, where large areas of forest were abundant (Fig. 5d).

4. Discussion

4.1.Habitat value of different land uses for birds in agricultural landscapes

The abundance of the wetland and grassland bird groups was typically lower in abandoned farmland than in wetlands and grasslands, but was higher than in farmland and forests (Fig. 3a,b). This is consistent with the findings of another study conducted in central Japan (Katayama *et al.*, 2015) and our prediction based on the conceptual model stating that the abandonment of intensively managed farmland can increase the abundance of wetland/grassland birds (Fig. 1). While previous studies have produced mixed results regarding the effects of farmland abandonment on biodiversity, farmland intensification has consistently been shown to have negative effects (Flohre *et al.*, 2011; Uchida and Ushimaru, 2014) and nontrivial areas of farmland are already intensively managed (Queiroz *et al.*, 2014). Therefore, the state of farmland before abandonment is key to understanding and predicting the effects of farmland abandonment. Farmland species (i.e., generalist open land species) were the only species group with a higher abundance in active farmlands than in abandoned farmlands. As well-reported in Europe, abandoned farmland in our study region may succeed into forests at xeric sites in the future, while abandoned farmland in mesic sites may become wetland and continue to provide suitable habitats for wetland/grassland birds (e.g., Morimoto *et al.*, 2017; Yamanaka *et al.*, 2017).

We also found that differences in the dominant vegetation of abandoned farmland (i.e., wet abandoned farmland or dry abandoned farmland) did not affect the abundance of the wetland and grassland bird groups. This outcome was expected because both types of abandoned farmland in our study area were dominated by the tall grasses that these species prefer (wet abandoned farmland: common reed, *Calamagrostis canadensis* subsp. *langsdorffi*, dry abandoned farmland: amur silver grass, Japanese silver grass: Appendix 1) rather than by trees, which these species avoid (Kennerley and Pearson, 2010; Copete and Christie, 2017).

However, the abundances of some wetland/grassland bird species, such as the lanceolated grasshopper warbler, tended to be lower in abandoned farmlands than in wetlands or grasslands (Appendixes 5–6). Our previous study also demonstrated that the abundance of wetland/grassland birds in abandoned farmland was approximately equivalent to 60% of the abundance in natural wetlands (Hanioka *et al.*, in press). One possible explanation for these differences is that the vegetation structures in natural wetlands are different from those in abandoned farmland. Some researchers have suggested that the vegetation in abandoned farmland is not natural vegetation due to biotic and abiotic modifications from past agricultural activities (Cramer *et al.*, 2008).

Previous studies of dry abandoned farmland have found that the abundance or species richness of forest birds increases with tree encroachment following land abandonment (Sirami *et al.*, 2008; Zakkak *et al.*, 2014; Ernst *et al.*, 2017). However, we found that the abundance of the forest bird group in abandoned farmland was comparable to that in active farmland (Fig. 3d). This inconsistency can again be explained by the dominant vegetation of the dry abandoned farmland in our study area (i.e., tall grasses: personal observation by M. Hanioka). Some researchers have suggested that in dry abandoned farmland, the recovery of woody vegetation equivalent to forests can take several decades (Shoo *et al.*, 2016). Most of the dry abandoned farmland in our study sites has been abandoned within the past 20 years (personal observation by M. Hanioka), and woody vegetation had not yet colonized the sites. Future studies should examine whether the abundance or species richness of each bird group (i.e., wetland/grassland birds and forest birds) varies not only with the number of years from initial abandonment but also with the succession of related vegetation (Fig. 1).

4.2.Landscape effects on the habitat value for birds

Our results suggest that the effect of the landscape variable also differs between the habitat groups. As in previous studies (Quesnelle *et al.*, 2015; Ernst *et al.*, 2017), the abundance of the wetland and grassland bird groups (and farmland species also) increased with landscape openness (Fig. 3a,b). This was likely because the surrounding habitats can supplement the food resources and resting places needed by wetland/grassland birds (Quesnelle *et al.*, 2015). In contrast, the effect of landscape openness on the forest bird group was not significant (i.e., the abundance of the forest bird group did not increase with a decrease in landscape openness [an increase in the proportion of forest in the surrounding area]). This result was inconsistent with those of previous studies (Villard *et al.*, 1999; Smith *et al.*, 2011). There are likely to be variations in the effects of landscape structure on the abundance of forest birds among regions.

4.3. Predicted bird responses to land abandonment

The abundance and species richness of the wetland and grassland bird groups were predicted to increase with an increase in farmland abandonment and landscape openness (Fig. 4a,b,f,g). Although the abundance and species richness of forest and farmland birds were predicted to decrease with an increase in farmland abandonment/landscape openness, the observed rates of decrease were small (Fig. 4d,i). These results have two implications: i) currently abandoned farmlands in our study area can be more useful for conserving wetland/grassland birds than forest birds; and ii) larger areas of abandoned farmland not surrounded by forests can have particularly significant effects on the conservation of wetland/grassland birds. However, while the abundance of the wetland bird group was mainly determined by landscape openness (Fig. 4a), species richness was mainly determined by the farmland abandonment ratio (Fig. 4f). Therefore, conservation focused on either the area of abandoned farmland or on the landscape structure should depend on abundance (i.e., valuing common species) or species richness (i.e., valuing rare species).

4.4. Future land use management for conserving bird communities

The mapping results revealed that the abundance of the wetland/grassland birds were higher in the southern lowland of the study area, where there were remnants of wetlands and abandoned farmland (Fig. 5). A previous study predicted that abandoned farmland would likely increase in the area between the mountains and lowlands, where crop productivity may be low (Renwick *et al.*, 2013). However, abandoned farmland can occur in lowland areas due to various socioeconomic factors, such as a decline in the number of farmers and agricultural activity (see Fig. 2). Therefore, for effective conservation of wetland/grassland birds in agricultural landscapes, it is important not only to protect the remaining natural wetland/grassland but also to value abandoned farmland, especially in areas surrounded by wetland/grassland areas. Large areas of the world's wetland and grassland have been converted into other land uses during the last 100 years (Boakes *et al.*, 2010; Davidson, 2014), including in Japan (GSI, 2000; Yamaura *et al.*, 2012a), leading to subsequent losses of species dependent on these ecosystems (Askins, 2001; ME, 2005; Yamaura *et al.*, 2009). Given that only tiny amounts of the remnant wetlands, grasslands, and low-intensive farmlands harbor wetland and grassland birds, we suggest that farmland abandonment provides an important opportunity to conserve and restore declining wetland/grassland species.

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Fig. 1. Conceptual model of wetland and grassland bird abundance in relation to management intensity. Farmland abandonment can decrease or increase the abundance of wetland/grassland species depending on the previous management status. We presumed that abandoned farmland that was previously intensively managed will finally return to forest and wetland in dry (xeric) and wet (mesic) sites, respectively. See Appendix 1 for the typical active farmlands in our study area.

Fig. 2. Study area and distribution of sampling plots and each land use. (a) Enlarged map of the area shown in the red square in the center figure. Abbreviations: Wet abandoned, wet abandoned farmland; Dry abandoned, dry abandoned farmland; Unsuitable land uses, unsuitable land uses for the focal birds of this study (e.g., urban areas and open water).

Fig. 3. Estimates of abundance for each land use (/2 ha) and partial regression coefficients for landscape openness. The results are shown for functional group-level hyperparameter (group means) of (a) wetland, (b) grassland, (c) farmland, and (d) forest species. Dots indicate median values, and bars indicate the 95% credible intervals. Statistical significance among the land uses at the 5% level is indicated alphabetically (only detected for forest species). The expected abundance of each land use is the abundance assuming that the plot is completely covered by the corresponding land use, i.e., $\exp(\beta_{i1} \times 1)$ is the abundance in a wetland for species *i* where landscape openness is set to the average value and ignored. Abbreviations:

WETLND (wetland), GRSS (grassland), WETAB (wet abandoned farmland), DRYAB (dry abandoned farmland); FARM (farmland); FOR (forest); LAND (landscape openness).

Fig. 4. Changes in total abundance (a–e) and species richness (f–j) as functions of the farmland abandonment ratio and landscape openness. The results are shown for wetland species (a,f), grassland species (b,g), farmland species (c,h), forest species (d,i), and all species (e,j). Solid lines indicate changes in (a–e) total abundance (i.e., 10 indicates an increase in 10 individuals), and (f–j) species richness (i.e., -0.5 indicates a decrease in 0.5 species).

Fig. 5. Maps predicting the total abundance of (a) wetland species, (b) grassland species, (c) farmland species, (d) forest species, and (e) all species. Total abundance was calculated in each 100 × 200 m grid. (a,b,e) An enlarged map of the area indicated by the square at the bottom of the whole map is shown in the upper right of the figure.