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Broad-scale and long-term assessment of bird diversity in agricultural landscapes: Focusing on farmland intensification and abandonment

（農地景観における鳥類多様性の広域・長期評価：耕作放棄と農業集約化に着目して）

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Summary

Context

Farmland occupies one third of the Earth's land surface, and hence expansion of farmland is assumed to drastically impact global terrestrial biodiversity. Furthermore, farmland intensification and abandonment are spreading worldwide and presumed to be major drivers of biodiversity changes in agricultural landscapes. However, it has been reported that their impacts vary depending on surveyed regions and species assessed, resulting in the lack of understanding of their detailed impacts and the spatial and temporal variations.

Objectives

This thesis aims to evaluate the impacts of agricultural expansion, farmland intensification, and abandonment on bird diversity and assess the spatiotemporal variations of the impacts of those drivers on bird community and functional groups, simultaneously.

Methods

First, I evaluated the effects of broad-scale land-cover conversion for agriculture in the Ishikari Lowland in Hokkaido, northern Japan. The Ishikari Lowland offers an excellent opportunity to assess the impact, as hunter–gatherer lifestyles dominated this region until the mid-nineteenth century. The estimation was done by applying digitization of historical land-use maps with a hierarchical community model dealing with the relationships between breeding bird abundance and land-cover types. Second, I conducted field surveys to assess the conservation values of abandoned farmland for breeding bird communities by comparison with active farmland (pasture, cropland, and rice paddy) and natural wetland across Hokkaido. Third, I evaluated the spatiotemporal variations of bird habitat suitability of high- and low-intensity, and abandoned farmland by nationwide field surveys covering both breeding and wintering seasons.

Results

My hindcasting approach revealed that broad-scale land cover change over a 166-year period was associated with a more than 70% decline in local total abundance of avian communities in the Ishikari Lowland. My survey across Hokkaido suggested that conservation values of abandoned farmland differed among functional groups, and abandoned farmland plays an important role as a habitat for grassland and forest species at large scales. My nationwide surveys revealed that the response of the dominant functional group within communities would explain spatially complicated biological consequences of farmland abandonment and intensification. In a region/season with high forest, wetland, and grassland species diversity, community-level abundance and species richness in abandoned farmland were higher than in active farmland. In a region/season with high bare-ground and aquatic species diversity, community-level abundance and species richness in low-intensity farmland were higher than in abandoned and high-intensity farmland.

Conclusions

My study suggested that large parts of the Northern Hemisphere have already experienced drastic reductions in forest and wetland species. Protecting remnant habitats thus ought to be given the highest priority to conserve forest and wetland species. Furthermore, farmland abandonment would provide a valuable alternative habitat for species whose primary habitats have been lost by agricultural expansion. My functional group approach explicitly quantified the negative impacts of land-use change for agriculture, while it successfully identified the condition under which negative impacts of agricultural abandonment and intensification can be mitigated. My proposed framework would help identifying the most effective conservation measure for

each region, and ultimately contribute to developing management policy in a rapidly changing world.

1. Chapter 1. Introduction

1.1. Biodiversity loss and its driving factors

Biodiversity is declining across every ecosystem on the earth (Barnosky *et al.* 2011). In the last century, over 100 species of avian, mammal, and amphibian species went extinct (Pereira *et al.* 2012). The driving factors of biodiversity loss include the expansion of alien species, climate change, and environmental pollution, but the impact of the conversion of natural ecosystems to agricultural land is considered to be particularly significant (DeFries *et al.* 2004; Foley *et al.* 2005; Maxwell *et al.* 2016). Farmland occupies one third of the Earth's land surface (Ramankutty & Foley 1999; DeFries *et al.* 2004), and approximately 90% of past global land-use changes were related to agricultural activity (Hurtt *et al.* 2006). Furthermore, 62% of the threatened terrestrial species on the IUCN Red List were negatively affected by agriculture (Maxwell *et al.* 2016). It is therefore critical to understand and mitigate the negative impacts of agriculture on biodiversity to conserve terrestrial biodiversity.

1.2. The impact of land-use change for agriculture on biodiversity

The dominant land-cover type within a landscape generally follows a series of transitions from wildlands such as undisturbed wetlands or forests to traditional and subsistence farmland, to intensive farmland (Foley *et al.* 2005; Fig. 1.1). Though large parts of the Northern Hemisphere have already been converted to farmland (Ramankutty *et al.* 2008), the impacts of land-cover conversion from wildland to farmland have rarely been quantified in the Northern Hemisphere (but see Newbold *et al.* 2015; Hallman *et al.* 2021). This is because these changes have occurred until 1400-1700s (Beckmann *et al.* 2019), and hence time-series biodiversity data prior to broad-scale land-cover conversion for agriculture are rarely available, which undermines our ability to quantify the consequences of the land-cover conversion (Butchart *et al.* 2010; Dornelas *et al.* 2014). Therefore, especially in the Northern Hemisphere, it has been underappreciated when,

how much, and which species have been decreased by the land-cover conversion from wildland to farmland. Filling these gaps is key to assessing long-term population trends of concerned species (Grace *et al.* 2019; Rodrigues *et al.* 2019) or informing quantitative targets of varied conservation actions at species to ecosystem levels (Swetnam *et al.* 1999).

Farmland now occupies one third of the Earth's land surface (Ramankutty & Foley 1999; DeFries *et al.* 2004). To further increase food production to meet growing food demands, agricultural lands have been intensified by increasing field size and chemical inputs, introducing machinery, or shifting monoculture and thus result in simple landscapes. Those agricultural intensification have mainly occurred in the Northern Hemisphere (Mueller *et al.* 2012), and its negative impacts on biodiversity have received substantial attention throughout the Northern Hemisphere (Donald *et al.* 2001; Reif & Vermouzek 2019a). For example, cereal yield in EU countries has tripled from the 1960s to 1990s, while farmland bird population estimated to be declined 50% between the 1970s and 1990s (Donald *et al.* 2001, 2006). Farmland intensification is thus considered to be the major driver of current and future biodiversity loss since further intensification is predicted to occur (Tilman *et al.* 2011; Mueller *et al.* 2012).

In parallel with agricultural intensification, farmland has been abandoned especially in remote and rural areas and the area of abandoned farmland around the world has been exponentially increasing since the 1950s (Rey Benayas *et al.* 2007; Cramer *et al.* 2008). The reasons for those abandonment were suggested to be socio-economic factors such as declines in human population or rural-urban migration (Rey Benayas *et al.* 2007; Kobayashi *et al.* 2020). Since it has been suggested that farmland abandonment causes soil erosion and degradation, and reduction in water stock, farmland abandonment is sometimes assumed to be another major driver of biodiversity loss (Young *et al.* 2005; Batáry *et al.* 2015).

1.3. Spatiotemporal variations in the effects of farmland abandonment and intensification

Though farmland abandonment were considered as major drivers of biodiversity loss, meta-analyses and review papers suggest that the effects of abandonment are complex (Queiroz *et al.* 2014; Koshida & Katayama 2018a). Indeed, some empirical studies in western Europe and southern Japan have shown that species richness and abundance are lower in abandoned farmlands than in active farmlands (Verhulst *et al.* 2004; Öckinger *et al.* 2006; Normile 2016), indicating that farmland abandonment is a threat for biodiversity for those regions. Others in central Asia and northern Japan have shown the opposite pattern (Kamp *et al.* 2011; Kitazawa *et al.* 2019), suggesting farmland abandonment as an opportunities for biodiversity conservation and restoration for the regions (Pereira & Navarro 2015). While the consequences of agricultural intensification on biodiversity is consistently negative, the extent of their impacts varies among regions (Uchida *et al.* 2018; Beckmann *et al.* 2019).

Since agricultural intensification and abandonment are spreading worldwide, assessing the detailed impacts of those two drivers and predicting their ecological impacts would be essential to conserve terrestrial biodiversity. However, studies on the impacts of those drivers have been heavily biased towards Europe and North America (Queiroz *et al.* 2014; Beckmann *et al.* 2019). Thus, there is currently limited information regarding their impacts in other regions, where further agricultural intensification and abandonment are predicted. Therefore, understanding the conservation values of abandoned farmland and high- and low-intensity farmland and its spatial variations is important to help developing conservation strategies at large spatial scales.

Assessing functional group-level responses would be key to understand and predict the impacts of land-use changes. Functional group is defined as the group sharing similar roles or process (Blondel 2003). Disturbance regimes, water availability, or nesting and food resources strongly dictate habitat selection, and thus composition of biological communities respond strongly to changes in resource availabilities and the frequency of disturbance, which vary

among land-cover types (Newton 1998; Uchida & Ushimaru 2014; Newbold *et al.* 2020). I thus focused on habitat-based functional group, which is one of biological traits (Violle *et al.* 2007). Evaluating functional-group level abundance and species richness allowed us to infer the variations in responses to land-use change and factors driving changes in community composition. Furthermore, focusing on the responses of habitat-based functional group would enable us to predict the spatial variations of the impacts of farmland abandonment and intensification on biodiversity. This is because the dominant functional group within communities could drive the spatial variations of the impact of farmland abandonment and intensification.

Birds would be useful for the aims since they can respond to environmental changes well and exhibit diverse range of ecological functions (Gregory *et al.* 2005; Sekercioglu 2006). Birds use varied ranges of land-use types from aquatic (e.g., lakes, rivers, or shallows), to terrestrial habitats (bare-ground, wetland, grassland, or forest) depending on preferences of each species. Clear differences in community composition among land-use types would enable us to easily detect the impacts of land-use changes such as farmland abandonment and intensification. Furthermore, bird community composition can shift among seasons due to migration. For example, migratory bird species dominate the local bird communities in the Palearctic and Nearctic regions in breeding season (Somveille *et al.* 2013).

1.4. Historical changes in land-use and biodiversity in Japan

Japan offers an excellent opportunity to evaluate the impacts of land-cover changes on biodiversity because the history of land-cover changes was spatially varied within the country. Rice cultivation was introduced in the late Jomon period in southern part of Japan, and it expanded to northern Honshu by the early Yayoi period (Toyama & Nakayama 1992). On the contrary, in Hokkaido, northern Japan, hunter–gatherer lifestyles dominated until the mid-19th

century, and thus majority of the land base was not converted to farmland until 1860s (Ōnishi 2014). In 1869, the Japanese government began systematic forest clearing and wetland drainage to produce large tracts of arable land in Hokkaido (Himiyama *et al.* 1995; Seki *et al.* 2006).

Agricultural intensification has rapidly progressed across Japan, including Hokkaido, after 1950s (Katayama *et al.* 2015a). Sixty percent of the rice fields have consolidated to enlarge field size and earthen ditches were replaced to deep concrete-lined ditches or culvert pipes. However, farmland area in Japan has decreased since 1970s, and abandoned farmland now represents approximately 10% of the total farmland area (i.e., 396,000 ha). Further population decline and urban migration are predicted to be continued, which will result in additional abandonment of farmland, secondary forest, and residential areas (Ministry of the Agriculture Forestry and Fisheries 2019).

1.5. Aims of this thesis

The aim of this study is threefold. First is to quantify the impact of broad-scale land cover changes for agriculture on biodiversity. In Chapter 2, I estimated avian community- and functional group-level impact of the broad-scale land-cover change in the Ishikari Lowland by combining digitization of historical land-use maps with modeling the relationships between bird abundance and land-cover types. Second is to evaluate conservation value of abandoned farmland. In Chapter 3, I compared habitat suitability of abandoned farmland at the species-, community-, and functional group-level for birds by comparison with active farmland (pasture, cropland, and rice paddy) and natural wetland across Hokkaido in breeding season. Third is to identify the underlying ecological drivers of the spatial and temporal variations of the impact of farmland abandonment and intensification. In Chapter 4, I presented a hypothetical framework that explains the spatial/temporal variations and assessed them by evaluating community- and functional group-level bird abundance and species richness in six major land cover types in

agricultural landscapes (i.e., wetland, abandoned farmland, traditional rice paddy, consolidated rice paddy, cropland, and forest) throughout Japan in breeding and wintering seasons. I predicted that abandoned farmland in southern Japan would provide important habitat especially in winter, since many migratory bird species overwinter in the region. Finally, I discussed the effective conservation measures under a declining population society.

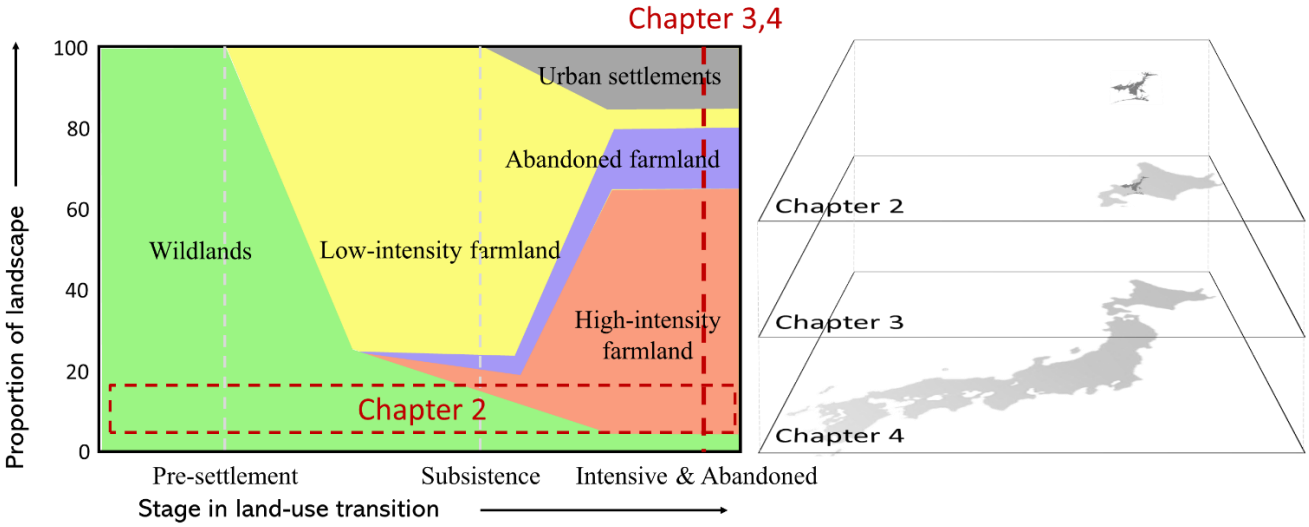


Fig. 1.1. Land-use transition in agricultural landscapes and the focus of my studies.

2. Chapter 2. Quantifying the impacts of 166 years of land cover change on lowland bird communities

Abstract

Land cover change for agriculture is thought to be a major threat to global biodiversity. However, its ecological impact has rarely been quantified in the Northern Hemisphere, as broad-scale conversion to farmland mainly occurred until the 1400 s–1700 s in the region, limiting the availability of sufficient data. The Ishikari Lowland in Hokkaido, Japan, offers an excellent opportunity to address this issue, as hunter–gatherer lifestyles dominated this region until the mid-nineteenth century and land cover maps are available for the period of land cover changes, i.e. 1850–2016. Using these maps and a hierarchical community model of relationships between breeding bird abundance and land cover types, I estimated that broad-scale land cover change over a 166-year period was associated with more than 70% decline in both potential abundance of avian communities. I estimated that the abundance of wetland and forest bird species declined by greater than 88%, whereas that of bare-ground bird species increased by greater than 50%. The results suggested that broad-scale land cover change for agriculture has led to drastic reductions in wetland and forest bird species and promoted changes in avian community composition in large parts of the Northern Hemisphere. This study provides potential baseline information that could inform future conservation policies.

2.1 Introduction

Biodiversity loss is accelerating across every ecosystem on Earth (Barnosky *et al.* 2011). Land cover changes, particularly the conversion of wildland to farmland, are assumed to be the major drivers of these losses (DeFries *et al.* 2004; Foley *et al.* 2005). Farmland occupies one third of the Earth's land surface, and approximately 90% of past global land cover changes were related to agricultural activity (Foley *et al.* 2005; Hurtt *et al.* 2006). It is therefore critical to understand the environmental consequences of broad-scale land cover changes for agriculture for informing terrestrial biodiversity conservation actions (Hallman *et al.* 2021).

Broad-scale land cover changes for agriculture are currently ongoing in tropical regions and are suggested to be the major threat to biodiversity in the regions (Brooks *et al.* 2002; Edwards *et al.* 2013). On the contrary, those changes occurred until 1400-1700s in large parts of the Northern Hemisphere (Ramankutty & Foley 1999; Beckmann *et al.* 2019), and environmental consequences of ongoing agricultural intensification are of concern (Cousins 2001; Donald *et al.* 2001; Beckmann *et al.* 2019; Reif & Vermouzek 2019b). Few studies have examined the degree to which past broad-scale land cover change impacted biodiversity in temperate Northern Hemisphere before the agricultural intensification (Newbold *et al.* 2015; Hallman *et al.* 2021).

Past land cover change may have had a comparable, or even greater, impact on species richness and abundance of biological communities than the agricultural intensification currently occurring in the Northern Hemisphere (Collen *et al.* 2009). Furthermore, I would expect high variation in the timing and rate of reduction among ecological functional groups, given that responses to land cover change vary among these groups (Edwards *et al.* 2013; Smith *et al.* 2015). These knowledge gaps could mask the detailed impacts of land cover change on biodiversity and lead to underestimate its impact on vulnerable species or groups. Filling these gaps is key to informing current and future conservation actions (Levy 2017), assessing the long-term population trends of species of conservation concern, and providing quantitative

conservation targets from species (e.g., IUCN Red and Green Lists) (Grace *et al.* 2019; Rodrigues *et al.* 2019) to ecosystem levels (White & Walker 1997; Swetnam *et al.* 1999).

Long-term biodiversity monitoring data are suitable for quantifying the impacts of human disturbance, including land cover change (Butchart *et al.* 2010; Dornelas *et al.* 2014; Rosenberg *et al.* 2019). However, time-series biodiversity data are rarely available for the pre-clearance period (i.e., the period prior to land cover conversion to farmland), which undermines our ability to quantify the consequences of broad-scale land cover change for agriculture (Ceballos & Ehrlich 2002; Butchart *et al.* 2010; Newbold *et al.* 2015; Daskalova *et al.* 2020). In fact, available time-series datasets that span more than 40 years are very rare worldwide (Dornelas *et al.* 2014). Furthermore, time-series data are usually collected in already modified landscapes or protected areas (Cardinale 2014). Therefore, an alternative approach is required to estimate the spatial distribution of species richness and abundance during the pre-clearance period (Newbold *et al.* 2015).

Combining digitization of historical land cover maps with species distribution modeling provides an alternative approach to quantifying the potential impacts of land cover change on biodiversity (Bonebrake *et al.* 2010). For example, potential species richness and abundance in the pre-clearance period can be estimated by modeling current abundance in various land cover types and projecting the results across historical land cover maps (Swetnam *et al.* 1999; Newbold *et al.* 2015). Though it is unfeasible in many regions (e.g., Europe, East and South Asia including southern Japan) to obtain land cover maps covering periods of more than 100 years, fine-scale land cover maps from the 1850s are available throughout Japan. In particular, one of the largest alluvial plains in northern Japan, the Ishikari Lowland (140 × 60 km) in central Hokkaido, was not converted to farmland until the 1860s (Matsuura 1863). This is because hunter–gatherer lifestyles dominated from the Paleolithic to the mid-19th century in Hokkaido (Abe *et al.* 2016).

Based on this socio-economic history and the land cover maps, I aimed to quantify the impacts of broad-scale land cover change for agriculture on breeding bird communities in the Ishikari Lowland over the past 166 years. Assessing habitat-based functional group-level (e.g., forest species) responses is key to understand and derive community-level responses to broad-scale land cover change since each land cover type has different types of key resources such as food and nest sites for birds (Newton 1998; Newbold *et al.* 2020), and hence the abundance of each species or species group is associated with a certain type of land cover (Kitazawa *et al.* 2021). I thus examined the timing and extent of functional group- (forest, wetland, grassland, and bare-ground species) and community-level bird species richness and abundance changes.

I used a hierarchical community model (HCM) (Yamaura *et al.* 2016) to estimate habitat–abundance relationships for breeding birds. Birds were suitable for my objective as they can respond well to environmental change and exhibit a diverse array of ecological functions (Gregory *et al.* 2005; Sekercioglu 2006). I georeferenced historical land cover maps from five periods (the pre-clearance period, 1900, 1950, 1985, and 2016). I then projected bird abundance estimates across those land cover maps to quantify the degree to which land cover change has reduced bird abundance and species richness at the community and functional-group levels.

2.2 Materials and Methods

2.2.1 Study area

Hokkaido, northern Japan, spans a transitional area between temperate and boreal zones. The mean annual temperature and precipitation in Sapporo, located in the center of the Ishikari Plain, are 9.2 °C and 1,146 mm, respectively (Japan Meteorological Agency, http://www.jma.go.jp). The Ishikari Lowland (comprising the Ishikari and Yufutsu Plains; 42° 32'–43° 50' N, 141° 08'–142° 10' E; Fig 2.1) is now dominated by rice paddy and cropland, but the majority of the land base was not converted into farmland until the 1860s (Matsuura 1863; Seki *et al.* 2006). This is because the Ainu, the Indigenous people of northern Japan, relied mainly on salmon fishing, deer and bear hunting, and gathering edible plants (Matsuura 1863; Seki *et al.* 2006) until the Japanese government established a colonial government in Sapporo in 1869. An explorer from southern Japan investigated the Ishikari Lowland in the 1850s and reported that the landscape was dominated by dense forests (e.g., dominated by alders [*Alnus* spp.] or japanese elm [*Ulmus japonica*]) and large wetlands (dominated by common reed [*Phragmites australis*] or sedges [*Carex* spp.]) (Matsuura 1863; Hokkaido 1891). In 1869, the Japanese government began systematic forest clearing and wetland drainage to produce large tracts of arable land and expanded economic control of the region.

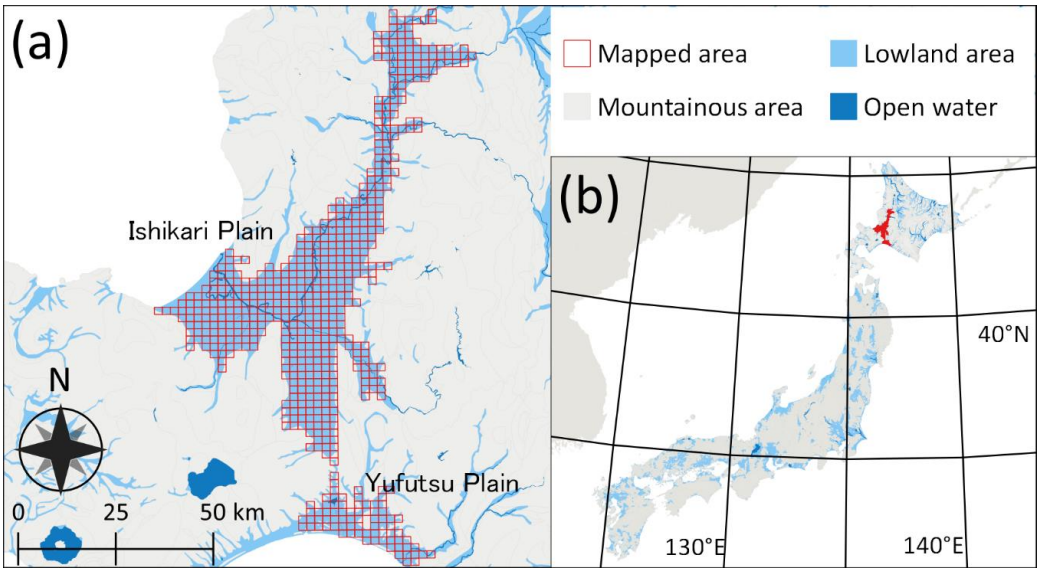


Fig. 2.1 Extent of mapped areas (red grids = 2 × 2 km resolution).

2.2.2 Field sampling and bird functional group

I used bird data from published studies from our research group (Hanioka *et al.* 2018a; Kitazawa *et al.* 2021), and details of the bird surveys are shown in the Chapter 3 of this paper. Bird surveys were conducted throughout the breeding season (May–July) in 2015 and 2017 in 79 sample plots (2 ha, 100 × 200 m) located throughout the Ishikari Lowland. I visited each plot three times and plotted the putative territories of individual species in each plot on a map based on field observations and estimates of territory size (Hanioka *et al.* 2018a). I used the summed number of territories for each species within each plot as a metric of abundance.

I focused on habitat-based functional groups and classified all observed species into one of four functional groups based on habitat preferences and nesting habitats listed in the JAVIAN database (Takagawa *et al.* 2011): forest species, wetland species, grassland species, and bare-ground species. I defined bare-ground species as those that prefer frequently disturbed habitats, including agricultural habitats, such as cropland or rice paddy and short grassland (Kitazawa *et al.* 2021). Although some of bare-ground species nest on trees or shrubs, I focused on foraging habitat because the availability of foraging habitat could be more important for those species

than that of nesting habitat in Japan.

2.2.3 Explanatory variables and land cover maps

I ranged the proportion of seven land cover types [wetland, grassland, wet abandoned farmland, dry abandoned farmland, cropland, rice paddy, and forest] (representing the major land cover types currently present in the lowland) within sample plots, and calculated the proportion of each land cover type within each sample plot (0–1) using a vegetation map provided by the Nature Conservation Bureau of the Ministry of Environment. I then generated 400-m-wide buffers around each plot and measured the proportion of surrounding open land (0–1; hereafter referred to as "landscape openness"; open land is defined as summed area of wetland, grassland, wet abandoned farmland, dry abandoned farmland, and cropland) in the buffer area (Hanioka *et al.* 2018a). I used this variable because previous studies showed that this landscape variable was the most strongly associated with bird abundance in Hokkaido (Hanioka *et al.* 2018b, a). I tested for collinearity between variables using variance inflation factors (VIF), and the values were ≤2.

I analyzed land cover maps from five different periods between 1850 (prior to the land cover change) and 2016 (present). The maps from 1900, 1950, and 1985 were based on 1:50,000 topographical maps and were provided by (Himiyama *et al.* 1995). The 1850 map was produced by Himiyama et al. (1995) and was partly based on a literature review; therefore, I assumed that this map included a higher level of uncertainty than the other maps, which were based on survey data. In particular, this map might underestimate the extent of wetlands, as explorers noted that "there are no trees in sight, only reeds, sedges, and silver grass, and rarely a few alder trees" in some parts of the Ishikari Lowland (Hokkaido 1891).

I thus also used a map produced in 1880, created by Hokkaido (1891) to aid in the selection of suitable colonial sites. This map is the oldest surveyed map of the Ishikari Lowland. Although the land cover changes for agriculture began in the 1860s, the 1880 map may still represent

ecosystems in their natural state as clearance had not yet occurred in the majority of the lowland as of the 1880s. I used both the reviewed and surveyed maps to estimate bird population prior to the land cover changes to farmland. Paper maps were digitized and georeferenced by Haruka Ohashi, Michio Oguro, and Tetsuya Matsui from Forestry and Forest Products Research Institute, and I used these data for analysis. I also used a categorical land cover map issued in 2016 by the Geospatial Information Authority of Japan (Geospatial Information Authority of Japan 2016). I confined the mapped area to lowlands (i.e., alluvial fans and deltas) to quantify the impact of land cover changes for agriculture on bird communities, because agricultural land is concentrated in lowlands (Hoshino 2001), and because lowlands and mountainous areas differ with respect to bird community composition (Rahbek 1997; Kawabe 2005).

2.2.4 Estimating current abundance and species richness

I used an abundance-based HCM to estimate the effects of land cover types and surrounding habitat on the abundance of each bird species and functional group (Yamaura *et al.* 2016). I did not consider the detection process in the model because openland songbirds have relatively high detectability in Hokkaido (~ 0.66) (Yamaura *et al.* 2016), and I conducted surveys three times for each plot. I first assumed that the abundance of species *i* in plot *j* (Z_{ij}) followed a Poisson distribution ($Z_{ij} \sim \text{Poisson}[\lambda_{ij}]$). I then assumed that the expected abundance of species *i* in plot *j* (λ_{ij}) was a function of the proportion of the seven land cover types within the plot, as well as landscape openness. Only landscape openness was standardized prior to analysis. I treated the proportion of the seven land cover types and landscape openness as continuous explanatory variables (0–1), and omitted the intercept of the linear predictor (i.e., I employed the cell means method (Kéry 2010)) using the parameter estimates:

$$\text{Log}(\lambda_{ij}) = \beta_{i1} \times x_{j1} + \beta_{i2} \times x_{j2} + \beta_{i3} \times x_{j3} + \beta_{i4} \times x_{j4} + \beta_{i5} \times x_{j5} + \beta_{i6} \times x_{j6} + \beta_{i7} \times x_{j7} + \beta_{i8} \times x_{j8} \quad (1)$$

where $x_{j1\text{-}7}$ indicates the proportion of each land cover type (0–1) in plot j and x_{j8} indicates landscape openness (0–1) surrounding plot j. β_{i1-8} indicates the partial regression coefficients of species i for each explanatory variable.

I assumed that species-level parameters followed a functional group-level normal distribution with hyperparameters. This implies that different functional groups can have different means and standard deviations for each coefficient, reflecting my assumption that the effects of land cover type and landscape openness differ among functional groups. I obtained median parameter estimates from the field survey data using a Monte Carlo Markov Chain with three chains, a burn-in of 50,000, a thinning interval of 5, and 100,000 post-iterations. I used uninformative normal distributions (0, 100^2) for the mean value of β_{i1-8} and half-Cauchy distributions (0, 5) for any variance of coefficients as weakly informative prior distributions (Gelman 2006). I performed 10-fold cross-validation to test and evaluate the ability of the HCM to predict bird abundance, and the root mean square error and mean absolute error values were 8.11 and 6.28, respectively. I conducted these analyses using R ver. 3.2.0 (R core team 2015), JAGS ver. 4.2.0 (Plummer 2016), and the R package jagsUI ver. 1.4.2 (Kellner 2016).

2.2.5 Predictive mapping

I calculated potential bird abundance and species richness in the Ishikari Plain in past periods, assuming habitat–abundance relationships for the breeding avian communities stay constant over 1850–2016 (table 2.1). I first standardized the spatial resolution of land cover maps. The maps from Himiyama et al. (1995) are available at a resolution of 2 km, and I converted the remaining maps to the same resolution. I then generated 2 × 2 km grid cells and overlaid these grids onto the maps. I extracted the dominant land cover type within each grid cell, assuming that grid cells were fully occupied by a single land cover type (Fig. 2a). To estimate bird abundance in the lowland, I converted the 2-km categorical land cover maps to 2-ha grid maps. I first divided all

maps into 2-ha grids (100 × 200 m) so that they corresponded to the same resolution as my sample plots. The proportion of each of the five land cover types (wetland, grassland, cropland, rice paddy, and forest) was stored in the grid.

I assumed open water and urban areas as unsuitable habitats for birds and assigned them an abundance of zero individuals because terrestrial bird abundance is low in these land cover types (Fujimaki & Toda 1981; Yamanaka *et al.* 2020). For each grid cell in each land cover map, I calculated the expected abundance (hereafter "abundance") of each species, as well as the expected species richness, based on the median parameter estimates from the HCM (Yamaura *et al.* 2016). I defined expected species richness in a plot (hereafter "species richness") as the expected number of species represented by at least one individual. I then obtained community- and functional group-level abundance and species richness within each grid by summing the expected abundances of the constituent species and mapped these values across the Ishikari Lowland.

I calculated total bird abundance for each period by summing the abundance values of all grids over the Ishikari Plain. This was done only in the Ishikari Plain because Hokkaido (1891) did not include the Yufutsu Plain in the 1880 map. I also calculated median values of species richness (i.e., α-diversity) for all grids in the Ishikari Plain, as well as the total area of each land cover type during each period. I quantified the changes in community composition by dividing functional group-level total abundance by community-level total abundance (hereafter "functional group proportion"). Finally, I compared these values among periods. I estimated 90% credible intervals for total bird abundance, species richness (α-diversity), and functional group proportions by projecting abundance and species richness 500 times from randomly resampled parameters from posterior distributions. I note that the calculated abundance and species richness were the estimates of potential values since suitable habitats are not always saturated to their full capacity, and I could not consider all breeding bird species in the Ishikari Lowland.

Table 2.1 I assumed that the bird abundance (per 2 ha) is constant regardless of the time periods, though past abundance would be higher than that assumed in my analyses (see discussion). To quantify the changes in bird abundance (per 2 ha) among time periods, I reviewed the previous studies estimating past bird densities in the Ishikari Lowland. I searched for literature using a standardized search of two databases: Google Scholar for publications in English and J-STAGE for publications in Japanese. We used the search string 'Ishikari' AND 'Bird' for Google Scholar and translated the same search string to Japanese for J-STAGE searches.

I showed the abundance values estimated in existing studies in table 2.1. The years when the surveys were conducted, surveyed land-cover types, and estimated abundance (which are scaled to abundance per 2 ha) in existing studies are shown. I compared those values with expected abundance in our study. * indicates estimated abundance in existing studies are included in the 95% confidential interval estimated in my study. The expected abundance in my study is the abundance assuming that the plot is completely covered by the corresponding land-cover type where landscape openness is set to the average value and ignored.

	Values in existing studies				Expected abundance in our study (per 2 ha)				
	Surveyed years	Land-cover types	Abundance (per 2 ha)	Reference	Land cover types	Lower 95% CI	Median values	Upper 95% CI	Included
Oriental turtle-dove	1979	Forest	0.84	(The Hokkaido Nature Conservation 1980)	Forest	0.11	0.38	1.12	*
Oriental turtle-dove	1979	Wetland	0.34	(The Hokkaido Nature Conservation 1980)	Wetland	0.068	0.23	0.52	*
Pygmy woodpecker	1976-2014	Mixed forest	0.04	(Fujimaki 2015a)	Forest	0.048	0.25	0.95	
Pygmy woodpecker	1976-2014	Broad leaved forest	0.06	(Fujimaki 2015a)	Forest	0.048	0.25	0.95	*

Pygmy woodpecker	1976-2014	Cropland	0.001	(Fujimaki 2015a)	Cropland	0.0012	0.028	0.090	
Great spotted woodpecker	1979	Forest	0.12	(The Hokkaido Nature Conservation 1980)	Forest	0.16	0.54	1.56	
Coal tit	1979	Forest	0.04	(The Hokkaido Nature Conservation 1980)	Forest	0.030	0.19	0.77	*
Japanese tit	1976-2009	Mixed forest	0.1	(Fujimaki 2010)	Forest	0.15	0.51	1.43	
Japanese tit	1976-2009	Broad leaved forest	0.1	(Fujimaki 2010)	Forest	0.15	0.51	1.43	
Japanese tit	1976-2009	Cropland	0.03	(Fujimaki 2010)	Cropland	0.014	0.075	0.22	*
Japanese tit	1979	Forest	0.76	(The Hokkaido Nature Conservation 1980)	Forest	0.15	0.51	1.43	*
Japanese tit	1979	Wetland	0.12	(The Hokkaido Nature Conservation 1980)	Wetland	0.0051	0.079	0.28	*
Brown-eared bulbul	1979	Forest	0.24	(The Hokkaido Nature Conservation 1980)	Forest	0.16	0.54	1.59	*
Japanese bush warbler	1976-2011	Mixed forest	0.15	(Fujimaki 2012)	Forest	0.16	0.49	1.25	
Japanese bush warbler	1976-2011	Broad leaved forest	0.18	(Fujimaki 2012)	Forest	0.16	0.49	1.25	*
Japanese bush warbler	1976-2011	Cropland	0.01	(Fujimaki 2012)	Cropland	0.0064	0.047	0.14	*
Asian stubtail	1976-2011	Mixed forest	0.22	(Fujimaki 2012)	Forest	0.12	0.45	1.37	*
Asian stubtail	1976-2011	Broad leaved forest	0.23	(Fujimaki 2012)	Forest	0.12	0.45	1.37	*
Asian stubtail	1976-2011	Cropland	0.004	(Fujimaki 2012)	Cropland	0.0032	0.037	0.12	*
Chestnut-cheeked starling	1976-1997	Cropland	0.03	(Fujimaki 1998)	Cropland	0.0039	0.033	0.12	*

Chestnut-cheeked starling	1979	Forest	0.16	(The Hokkaido Nature Conservation 1980)	Forest	0.016	0.11	0.51	*
Brown-headed thrush	1979	Forest	0.12	(The Hokkaido Nature Conservation 1980)	Forest	0.017	0.13	0.62	*
Narcissus flycatcher	1976-2006	Mixed forest	0.16	(Fujimaki 2007)	Forest	0.34	1.03	2.47	
Narcissus flycatcher	1976-2006	Broad leaved forest	0.16	(Fujimaki 2007)	Forest	0.34	1.03	2.47	
Narcissus flycatcher	1976-2006	Cropland	0.01	(Fujimaki 2007)	Cropland	0.012	0.052	0.20	
Common cuckoo	1968	Wetland	0.2	(Nakamura *et al.* 1968)	Wetland	0.00017	0.046	0.23	*
Middendorff's grasshopper-warbler	1979	Forest	0.1	(The Hokkaido Nature Conservation 1980)	Forest	0.00029	0.011	0.12	*
Black-browed reed warbler	1968	Wetland	5.11	(Nakamura *et al.* 1968)	Wetland	5.89	7.72	9.85	
Black-browed reed warbler	1979	Forest	1.84	(The Hokkaido Nature Conservation 1980)	Forest	0.017	0.11	0.47	
Black-browed reed warbler	1979	Wetland	2.46	(The Hokkaido Nature Conservation 1980)	Wetland	5.89	7.72	9.85	
Yellow-breasted bunting	1968	Wetland	0.35	(Nakamura *et al.* 1968)	NA	NA	NA	NA	
Reed bunting	1968	Wetland	1.8	(Nakamura *et al.* 1968)	Wetland	1.58	2.60	3.89	*
Bull-headed shrike	1968	Wetland	0.06	(Nakamura *et al.* 1968)	Wetland	0.058	0.27	0.67	*
Bull-headed shrike	1979	Forest	0.34	(The Hokkaido Nature Conservation 1980)	Forest	0.00061	0.028	0.30	

Bull-headed shrike	1979	Wetland	0.04	(The Hokkaido Nature Conservation 1980)	Wetland	0.058	0.27	0.67	
Sakhalin grasshopper-warbler	1968	Wetland	0.2	(Nakamura *et al.* 1968)	Wetland	0.17	0.48	0.97	*
Sakhalin grasshopper-warbler	1979	Forest	0.58	(The Hokkaido Nature Conservation 1980)	Forest	0.21	0.74	2.10	*
Siberian rubythroat	1968	Wetland	1.04	(Nakamura *et al.* 1968)	Wetland	0.28	0.70	1.35	*
Siberian rubythroat	1976-1998	Broad leaved forest	0.004	(Fujimaki 1999)	Forest	0.0048	0.078	0.55	
Siberian rubythroat	1976-1998	Mixed forest	0.01	(Fujimaki 1999)	Forest	0.0048	0.078	0.55	*
Siberian rubythroat	1976-1998	Cropland	0.03	(Fujimaki 1999)	Cropland	0.011	0.072	0.26	*
Stejneger's stonechat	1968	Wetland	0.6	(Nakamura *et al.* 1968)	Wetland	0.54	1.12	1.94	*
Long-tailed rosefinch	1976-1996	Grassland	0.14	(Fujimaki 1997)	Grassland	0.064	0.38	1.33	*
Long-tailed rosefinch	1976-1996	Cropland	0.05	(Fujimaki 1997)	Cropland	0.024	0.11	0.34	*
Long-tailed rosefinch	1976-1996	Broad leaved forest	0.03	(Fujimaki 1997)	Forest	0.0046	0.069	0.48	*
Long-tailed rosefinch	1976-1996	Mixed forest	0.005	(Fujimaki 1997)	Forest	0.0046	0.069	0.48	*
Long-tailed rosefinch	1979	Forest	0.52	(The Hokkaido Nature Conservation 1980)	Forest	0.0046	0.069	0.48	
Chestnut-eared bunting	1968	Wetland	0.48	(Nakamura *et al.* 1968)	Wetland	0.16	0.48	1.02	*
Carrion crow	1979	Forest	0.28	(The Hokkaido Nature Conservation 1980)	Forest	0.012	0.21	1.48	*

Carrion crow	1979	Wetland	0.66	(The Hokkaido Nature Conservation 1980)	Wetland	0.000021	0.0070	0.12	
White-cheeked starling	1976-1997	Broad leaved forest	0.01	(Fujimaki 1998)	Forest	0.000024	0.017	0.50	*
White-cheeked starling	1976-1997	Cropland	0.1	(Fujimaki 1998)	Cropland	0.011	0.073	0.26	*
White wagtail	1976-2014	Mixed forest	0.01	(Fujimaki 2015b)	Forest	0.000019	0.016	0.48	*
White wagtail	1976-2014	Broad leaved forest	0.01	(Fujimaki 2015b)	Forest	0.000019	0.016	0.48	*
White wagtail	1976-2014	Cropland	0.15	(Fujimaki 2015b)	Cropland	0.0075	0.062	0.24	*
Oriental greenfinch	1979	Forest	1.52	(The Hokkaido Nature Conservation 1980)	Forest	0.26	1.04	3.14	*
Oriental greenfinch	1979	Wetland	0.76	(The Hokkaido Nature Conservation 1980)	Wetland	0.18	0.41	0.67	
Black-faced bunting	1976-2010	Mixed forest	0.53	(Fujimaki 2011)	Forest	1.65	3.38	6.41	
Black-faced bunting	1976-2010	Broad leaved forest	0.63	(Fujimaki 2011)	Forest	1.65	3.38	6.41	
Black-faced bunting	1976-2010	Cropland	0.48	(Fujimaki 2011)	Cropland	0.28	0.56	1.00	*
Black-faced bunting	1968	Wetland	0.3	(Nakamura *et al.* 1968)	Wetland	0.71	1.31	2.11	
Black-faced bunting	1979	Forest	1.18	(The Hokkaido Nature Conservation 1980)	Forest	1.65	3.38	6.41	

433

434

2.3 Results

2.3.1 Land cover changes in the Ishikari Plain in 1850-2016

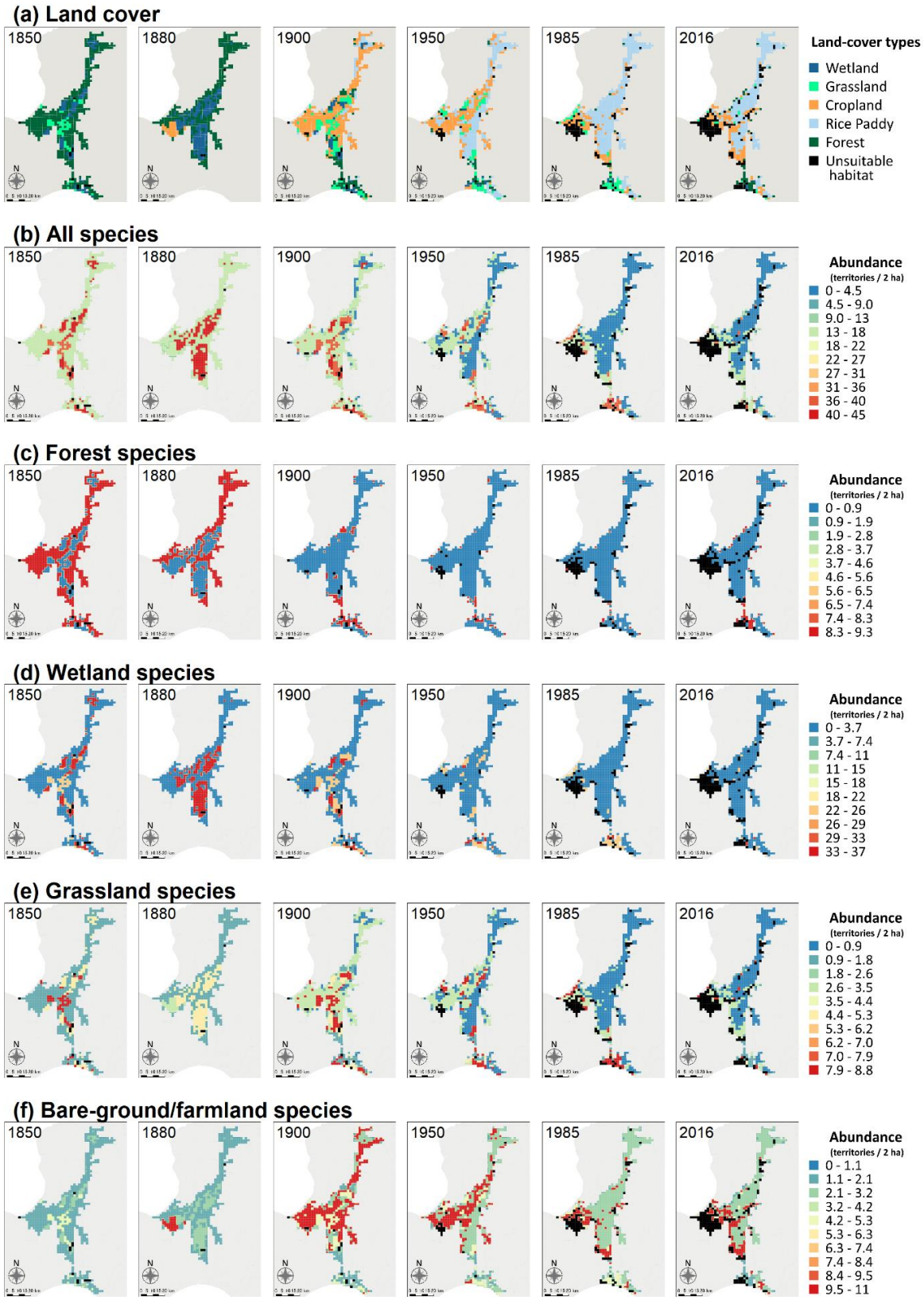
Forest was the dominant land cover type during the pre-clearance period, occupying 60% (1880) to 75% (1850) of the Ishikari Plain. However, forest area declined by 88% between 1850 and 1900, and by 95% by 2016 (Fig. 2.2a; 2.3a). Wetland was the second most dominant land cover type and occupied 32% (1880) of the plain during the pre-clearance period, but was nearly eliminated by 1985 (Fig. 2.2a; 2.3a). Grassland cover expanded slightly until 1900 but has since decreased, exhibiting a net decline of 68% since the pre-clearance period (Fig. 2.2a; 2.3a). Cropland has increased substantially, occupying 57% of the plain in 1900, after which time it gradually declined (Fig. 2.2a; 2.3a). Rice paddies, in turn, became the dominant land cover type by 1950 and occupied 52% of the plain in 2016 (Fig. 2.2a; 2.3a). In 2016, urban areas occupied 23% of the plain, and their expansion has mainly occurred during the last 66 years (Fig. 2.2a; 2.3a).

2.3.2 Impacts of land cover changes on bird communities

The results of the HCM indicated that community-level abundance and species richness were higher in wetlands, grasslands, and forests than in croplands and rice paddies and higher in croplands than in rice paddies. Forest species were more abundant in forests than in the other land cover types, and the abundances of wetland and grassland species were higher in wetlands and grasslands than in croplands or rice paddies. The abundance of bare-ground species was higher in croplands than in rice paddies.

Total bird abundance was predicted to decline by 72.0% (90% CI: 38.2%-81.7%, 1850) or 75.5% (90% CI: 44.8%-84.4%, 1880) since the pre-clearance period, i.e., from approximately 2,100,000 (1850) or 2,400,000 (1880) territories in the pre-clearance period to 590,000 in 2016 (Fig. 2.2b; 2.3b). Similarly, community-level species richness (per 2 ha) was predicted to decline

460 by 76.3% (90% CI: 62.1%-81.1%), from 9.3 in 1850 to 2.2 in 2016 (Fig. 2.4). Responses to
461 broad-scale land cover changes varied markedly among the four functional groups. Forest
462 species were estimated to be the second most abundant group during the pre-clearance period but
463 exhibited declines of 86% by 1900 and 94% by 2016 (Fig. 2.2c; 2.3b-c) compared to 1850.
464 Wetland species were estimated to be dominant during the pre-clearance period and comprised
465 >34% of the bird community, but have since declined by >88% (Fig. 2.2d; 2.3b-c). The sharpest
466 decline (about 60%) in wetland species was estimated to have occurred between 1900 and 1950.
467 The abundance of grassland species was predicted to increase to >147% by 1900 but has since
468 declined. The abundance of grassland species was estimated to decline by 65% since the pre-
469 clearance period (Fig. 2.2e; 2.3b). The abundance of bare-ground species was estimated to have
470 increased by >229% between the pre-clearance period and 1900 (Fig. 2.2f; 2.3b) and this group
471 has become dominant, comprising 59% of the community (Fig. 2.3c). The abundance of bare-
472 ground species was estimated to have decreased since 1900 but has exhibited an overall increase
473 of >58% since the pre-clearance period.
474

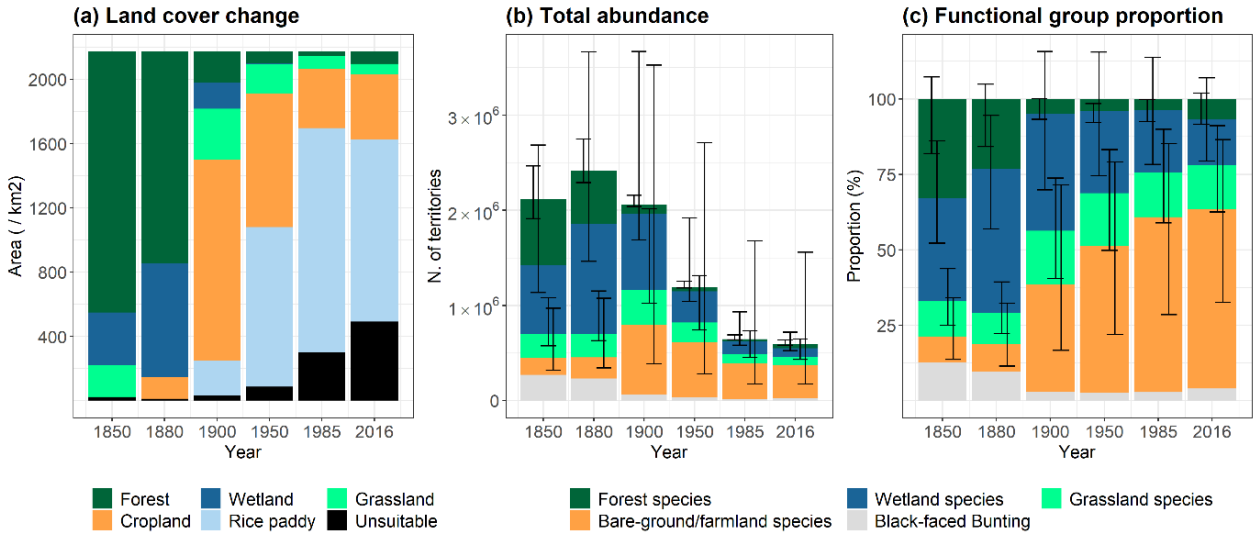


475

476 Fig. 2.2 (a) Land cover maps (2 × 2 km resolution) from each period (1850, 1880, 1900, 1950,

477 1985, and 2016), and maps predicting the abundance of (b) all species, (c) forest species, (d)

478 wetland species, (e) grassland species, and (f) bare-ground species (100 m × 200 m resolution).
479 The maps “1850” and “1880” are based on the reviewed (Himiyama *et al.* 1995) and surveyed
480 (Hokkaido 1891) maps, respectively. The black area indicates unsuitable habitats assumed to
481 support no bird individuals.
482



483

484 Fig. 2.3 Estimated historical changes in (a) the area of each land cover type, (b) bird abundance,
485 and (c) functional group proportion. Land cover types are represented by colors in (a), and
486 functional groups are represented by colors in (b) and (c). I categorized black-faced bunting as
487 grassland species when conducted HCM. However, I excluded the species from grassland
488 species when calculating group-level abundance and species richness. This is because the species
489 was fairly abundant in every land cover type in the Ishikari Lowland. The maps “1850” and
490 “1880” are based on the reviewed and surveyed maps, respectively. Bars indicate 90% CI: forest
491 species, wetland species, grassland species, and bare-ground species (from left to right for each
492 period).

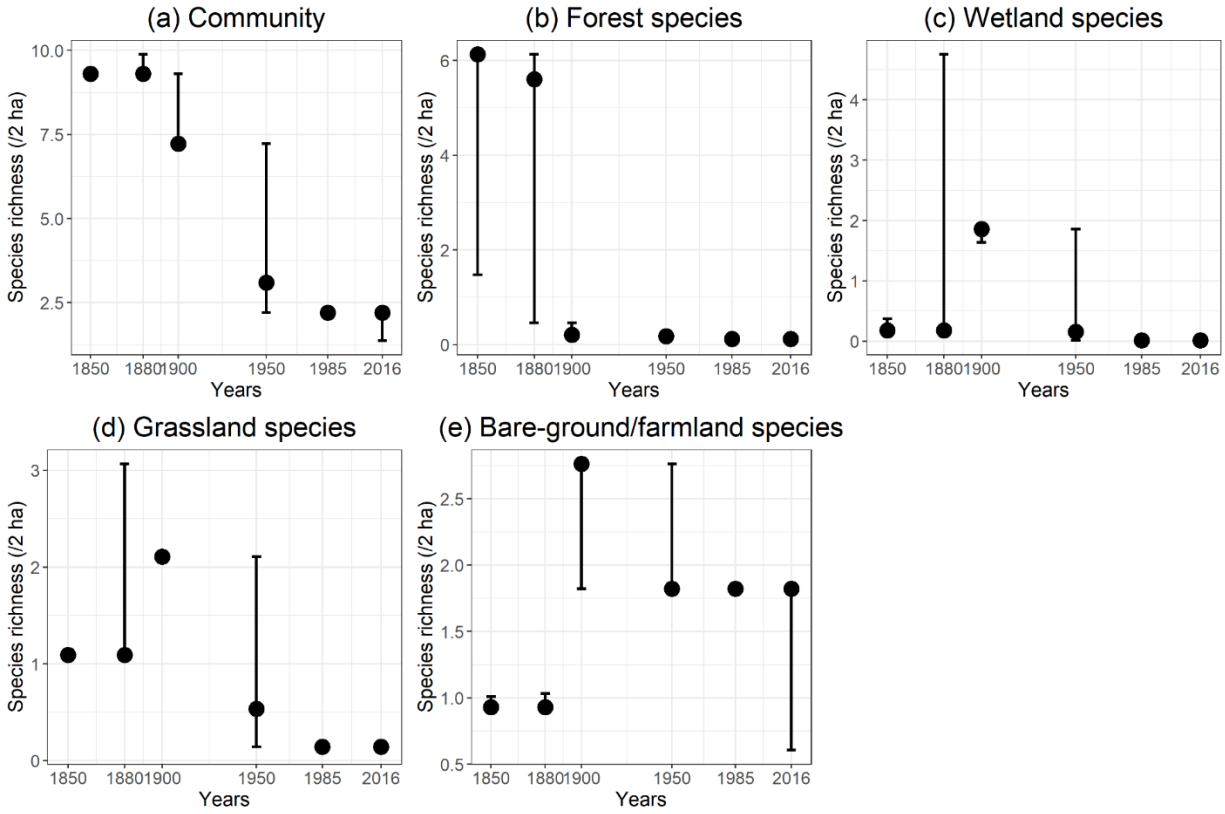


Fig. 2.4 The median values of species richness (i.e., α-diversity) for each functional group (b) – (e) for each time period. Community-level results are shown in panel (a). Dots and bars indicate median and 75% quantile ranges of species richness for all grids over the Ishikari Plain, for each. Some quantile values agreed with median values.

2.4 Discussion

Focusing on a large, unique landscape where land cover maps were available for the pre-clearance period, I estimated avian richness and abundance prior to land cover change and found that broad-scale land cover change over the Ishikari Lowland resulted in a >70% reduction in total abundance (approximately 1,500,000 territories) and species richness over the past 166 years. I also estimated that the abundances of wetland and forest species declined by >88% (630,000 and 650,000 territories, respectively), whereas the abundance of bare-ground species increased by >50% (170,000 territories). These results suggested that land cover change throughout the Ishikari Lowland resulted in community-level species loss because the dominant

functional group in the lowland has shifted from the species-rich forest and wetland groups (23 and 10 species, respectively) to the species-poor bare-ground group (six species).

Given the long history of land cover change in the Northern Hemisphere (Ramankutty & Foley 1999; Beckmann *et al.* 2019), my results suggest that turnover in community composition and drastic reductions in forest and wetland species had already occurred in large parts of the Northern Hemisphere prior to agricultural intensification. This is supported by archeological studies suggesting drastic changes in bird community composition in Europe during the Bronze Age, when broad-scale land cover change was predicted to have occurred (Yalden & Albarella 2009). North America shares a similar history with Hokkaido and a study suggested that broad-scale land cover change might have resulted in drastic reductions in woodland and prairie specialist bird species (Hallman *et al.* 2021). These findings suggest that broad-scale land cover change caused by lifestyle changes from hunter-gatherer to agriculture can be one of the major anthropogenic drivers of biodiversity loss. Historical dynamics of biodiversity suggested by my results would provide baseline information to implement current conservation actions.

Protecting remnant habitats ought to be given the highest priority to conserve forest and wetland species that have drastically declined. Valuing abandoned farmland would also be effective, as the habitat suitability of abandoned farmland can be comparable to that of undisturbed habitats (Pereira & Navarro 2015; Kitazawa *et al.* 2021), and these habitats have become increasingly prevalent worldwide since the 1950s (Ramankutty & Foley 1999; Hurtt *et al.* 2006; Ohashi *et al.* 2019). Such measures may be valuable in the Ishikari Lowland. However, conservation actions should also focus on immediate problems resulting from current pressures, such as agricultural intensification. Conserving grassland and bare-ground species would be equally, or more, important in regions where both groups are severely threatened (Donald *et al.* 2001; Reif & Vermouzek 2019b).

My results suggested that assessing changes in the area occupied by various land cover types over multiple periods is key to understanding when, how, and to what extent communities and functional groups have changed. I found that each functional group responded to changes in the area of particular land cover types. For example, conversion from forest to cropland prior to 1900 might have led to drastic declines in forest species, but increases in bare-ground species. The expansion of grassland prior to 1900 may have mitigated the negative effects of wetland loss on wetland and grassland species; however, the subsequent expansion of croplands and rice paddies might have triggered declines in these groups. Photographs taken in Hokkaido between 1900 and the 1910s (Hokkaido University Library 1992) indicated that there were few trees or wetland patches in cropland and rice paddy areas, supporting my assumption that these land cover types do not support forest, wetland, or grassland species. Each functional group experienced a different trajectory of abundance changes in the Ishikari Lowland, resulting in turnover in the dominant functional group and ultimately community-level biodiversity losses.

I did not include the detection process in my statistical model and assumed that the detection probability was constant across land-cover types. Since detection probability in forest might be low, I might underestimate bird abundance in forest. However, abundance of forest species was generally higher in forest than other land cover types and bird detectability within 50 m can be constant across land-cover types (Schieck 1997; Yamaura & Royle 2017). I also reiterate that my calculated values represent somewhat crude estimates. Notably, I did not quantify species richness or abundance in urban areas or open water due to data limitations. These should be considered in future studies. Nevertheless, my literature review (table 2.1) revealed that, in most cases, estimates of past abundance (per 2 ha) from other field studies were within the 95% credible intervals of my analyses. Furthermore, it is worth noting that my estimates of reductions in bird abundance and species richness might be conservative. This is because I was unable to include some locally extinct or large-bodied species that are especially

vulnerable to habitat loss (Bregman *et al.* 2014). For example, the yellow-breasted bunting, *Emberiza aureola*, was historically quite common throughout the Ishikari Lowland, but its population had collapsed by the 1990s (Kamp *et al.* 2015). In addition, the Blakiston's fish-owl, *Ketupa blakistoni*, has not been confirmed in the Ishikari lowland since the 1950s.

5. Conclusion

Combining reconstruction of historical land cover maps with modeling the relationships between bird abundance and land cover types allowed us to infer the role of long-term and broad-scale land cover change in the transformation of terrestrial biodiversity. The estimated reductions in bird communities are not expected to be confined to the Ishikari Plain, as other plains in Hokkaido have experienced similar land cover change over the same timeframe (Himiyama *et al.* 1995). My results suggested that the transition from hunter-gatherer to the farming lifestyles triggered serious biodiversity losses, and these changes likely would have occurred in any landscape where farmland is now dominant.

Furthermore, 72% of the breeding bird species in the Ishikari Lowland are migratory and their main wintering grounds are located between southern Japan and southeastern Asia. Therefore, the broad-scale land cover change that occurred in Hokkaido 66–166 years ago might have triggered massive bird declines and losses in ecosystem function in bird migration flyways. Migratory species breeding in the Northern Hemisphere are suggested to be negatively affected by contemporary wintering habitat loss and degradation of their habitats in tropical regions (Bradshaw *et al.* 2009; Yamaura *et al.* 2009); however, my results indicated that historical broad-scale land cover change in the Northern Hemisphere might have already triggered declines in migratory species until 1400-1900s, suggesting the current threatening drivers are in tropical regions. The conservation of wetlands and forests remains a key challenge to the conservation of global biodiversity, as massive agricultural and bioenergy expansion is predicted to occur in boreal regions, where the richness of migratory species including many wetland and forest species, is at its highest (Somveille *et al.* 2013; Hannah *et al.* 2020).

3. Chapter 3 Conservation values of abandoned farmland for birds: a functional group approach

Abstract

Abandoned farmland area has been expanding globally for decades. Studies showed that conservation value of abandoned farmland differed among studies and regions, and thus is difficult to predict. However, predicting the effects of farmland abandonment on biodiversity remains vital to the development of appropriate conservation strategies. Here, I compared the species-, community-, and functional group-level habitat suitability of abandoned farmland for birds by comparison with active farmland (pasture, cropland, and rice paddy) and natural wetland on Hokkaido, Japan, over a study area of 400 km×500 km. Results differed markedly between functional groups. The abundance and species richness of grassland species in abandoned farmland were higher than that in active farmland, and comparable to that in wetland. In contrast, abundance and richness of bare-ground species was highest in active farmland. For most species, interactive effects between climate variables and abandoned farmland were not significant, suggesting a consistent habitat suitability of abandoned farmland irrespective of varied climatic conditions. My results suggest that abandoned farmland plays an important role as habitat for grassland and forest species at large scales; farmland abandonment provides a valuable alternative habitat for species whose primary habitats have been lost to agricultural expansion. Especially, abandoned farmland in warmer areas in Hokkaido would represent a potential mitigation to the negative effects of wetland loss. A functional group approach synthesizes varied species-level responses and allows for a comprehensive understanding of the habitat suitability of abandoned farmland. Adopting this approach will contribute to establishing appropriate conservation strategies.

3.1 Introduction

The conversion of land for agriculture has dramatically altered natural ecosystems worldwide (Foley *et al.* 2005; Newbold *et al.* 2015). Mainly due to the conversion to farmlands, approximately 80% and 20% of the world's wetlands and forests, respectively, have been lost since the 1700s (Ramankutty & Foley 1999; Davidson 2014). Thus, farmland now accounts for more than one third of Earth's ice-free land surface (Ramankutty & Foley 1999). Agricultural expansion and intensification are expected to continue and thus pose an ongoing threat to biodiversity (Tilman *et al.* 2001; Foley *et al.* 2011). On the other hand, farmland abandonment has been caused by rural depopulation or an aging farming population (Rey Benayas *et al.* 2007; Kobayashi *et al.* 2020), and its area has increased exponentially since the 1950s (Ramankutty & Foley 1999; Cramer *et al.* 2008).

Meta-analyses and review papers suggest that the effects of farmland abandonment on biodiversity are more complex (Queiroz *et al.* 2014; Normile 2016; Koshida & Katayama 2018a) than the consistent negative effects that result from agricultural expansion and intensification (Newbold *et al.* 2015; Beckmann *et al.* 2019). Indeed, some empirical studies have shown that species richness and abundance are lower in abandoned farmlands than in active farmlands (Verhulst *et al.* 2004; Öckinger *et al.* 2006), yet others have shown the opposite pattern (Kamp *et al.* 2011; Kitazawa *et al.* 2019). Understanding these discrepancies and developing subsequent conservation strategies are of increasing importance, since farmland abandonment is predicted to be a key driver of global biodiversity change (Pereira *et al.* 2012; Ockendon *et al.* 2018).

Previous work has suggested that the habitat suitability of abandoned farmland, relative to active farmland, may vary based on geographic region (Queiroz *et al.* 2014). However, habitat suitability of abandoned farmlands may also differ greatly among species groups within communities (e.g., functional groups). Since disturbances cease after farmland abandonment, suitability of abandoned farmland may vary among species in responses to established

vegetation. Most studies have failed to detect such group-specific differences because they have assessed community-level abundance and species richness in active and abandoned farmlands (Sirami *et al.* 2008; Plieninger *et al.* 2014). Therefore, examining functional group-level responses may provide greater insight into the conservation value of abandoned farmland and provide inferences beyond specific study regions. To address the gap, birds would be useful since they can respond to environmental changes well and exhibit diverse range of ecological functions (Gregory *et al.* 2005; Sekercioglu 2006).

The few studies that focused on bird functional group-level abundance or species richness in abandoned farmlands mainly dealt with two groups: forest and open-land species (Sirami *et al.* 2008; Katayama *et al.* 2015b; Zakkak *et al.* 2015). It is widely acknowledged that abandoned areas may be preferable for forest species (Dyulgerova *et al.* 2015; Regos *et al.* 2016) if tree regeneration follows farmland abandonment. However, the responses of open-land species may be more accurately understood if divided into two groups: bare-ground species and grassland species. I here defined bare-ground species as species that prefer bare-ground and short grassland. I also defined grassland species as species that prefer perennial or tall grassland (e.g., reed bed). Though bare-ground species and grassland species have not been separated, there would be large differences in habitat preferences between the groups (see Chapter 2).

I would expect to detect marked differences between the responses of these two groups to farmland abandonment, and hence explain the contrasting results observed in previous studies. For example, because bare ground or short grassland conditions are maintained in active farmland, their abandonment would negatively impact bare-ground species (Schmitt & Rákosy 2007; Brambilla *et al.* 2010; Uchida & Ushimaru 2014). In contrast, perennial vegetation that establish in abandoned farmland due to succession (Benjamin *et al.* 2005; Dahlström *et al.* 2010) can serve as valuable habitat for grassland species (Yamanaka *et al.* 2017; Hanioka *et al.* 2018b).

Focusing on grassland species to evaluate abandoned farmland as alternative habitat for this group is also important (Hanioka *et al.* 2018a; Kitazawa *et al.* 2019), since these species have experienced drastic declines worldwide due to habitat loss (WWF 2008; Newbold *et al.* 2016). Existing evaluations of abandoned farmland have been heavily biased toward Europe, where the diversity of bare-ground species is high (Covas & Blondel 1998), and conservation actions are often focused on this group (Queiroz *et al.* 2014; Batáry *et al.* 2015). Therefore, the habitat suitability and conservation value of abandoned farmlands for grassland species has not yet been fully examined.

I examined whether the habitat suitability of abandoned farmland was consistent among three bird functional groups (bare-ground, grassland, and forest species) using a larger scale survey (400 × 500 km) than that used in previous studies (< 100 × 100 km) (Plieninger *et al.* 2014). Surveying a broad area may provide greater insight because climatic factors are determinants of species' habitat selection (Martin 2001); therefore, preferences for abandoned farmland may spatially vary with different climates, even for the same species. I compared the abundance and species richness of these three functional groups in five land cover types in floodplains (abandoned farmland, active farmland [pasture, cropland, and rice paddy], and natural wetland; see Method for detail definitions) and investigated spatial variations in climate and interactions between climate and land cover type.

3.2 Methods

3.2.1 Study area

This study was carried out across Hokkaido, northern Japan (41° 21′–45° 33′ N, 139° 20′–148° 53′ E; 400 × 500 km; Fig. 3.1). Hokkaido is located in a transitional zone between the temperate and boreal zones. Therefore, climatic conditions in Hokkaido vary among areas; average temperatures range from 4.4 to 16.5°C and average precipitation ranges from 50 to 220 mm during the bird breeding season (May–July). Several studies revealed that the climatic conditions affect bird abundance and distribution on Hokkaido (Fujimaki 2007; Kawamura *et al.* 2016). Within the last century, 60% of the natural wetland area in Hokkaido was converted into farmland (GSI 2001). Farmland expansion slowed during the 1990s, and there is currently at least 3,050 ha of abandoned farmland on Hokkaido. Abandoned farmland is found in mountainous and floodplain areas on Hokkaido, where wetland vegetation may now be re-established in floodplain areas.

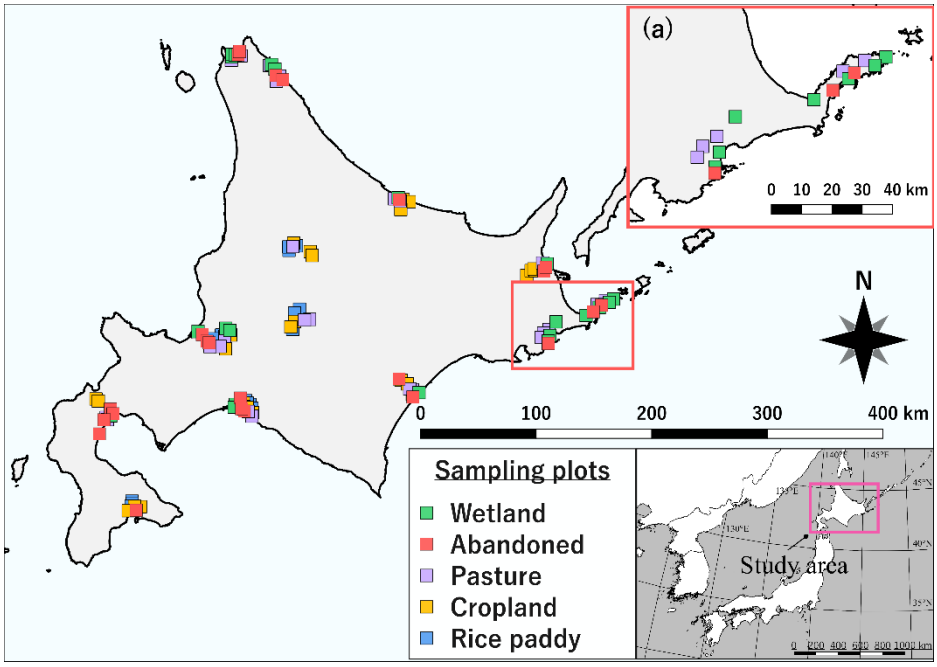


Fig. 3.1 Study area and the locations of the sampling plots. (a) Enlarged map of the study area, indicated by the red square, displaying the Hamanaka and Nemuro areas. The 113 sampling plots

are represented by squares and land cover types are indicated by color. Source: DIVA-GIS Free spatial data.

3.2.2 Land cover types

I focused on five land cover types: natural wetland (hereafter wetland), abandoned farmland, and active pasture, cropland, and rice paddy (collectively termed active farmland hereafter). I mapped these land cover types on Hokkaido using a vegetation map (scale: 1:50 000–1:25 000) provided by the Nature Conservation Bureau of the Ministry of Environment (http://www.biodic.go.jp/trialSystem/top.html). The dominant species in surveyed wetlands were common reed (*Phragmites australis*), bluejoint reedgrass (*Calamagrostis canadensis* subsp. *langsdorffii*), and sedges (*Carex* spp.). I ensured that all surveyed abandoned farmlands had been active in the 1970s and were no longer actively farmed by examining aerial imagery, interviewing land managers, and using field observations. In most instances I could not obtain an abandonment age (i.e., the time since cultivation ceased) due to the absence of previous land managers. Surveyed abandoned farmlands were characterized by common reed, sedges, Japanese iris (*Iris ensata*), Amur silver grass (*Miscanthus sacchariflorus*), and Japanese silver grass (*Miscanthus sinensis*). Tree growth (e.g., willowleaf meadowsweet [*Spiraea salicifolia*] and alders [*Alnus* spp.]) was patchy in some abandoned farmland.

3.2.3 Sample plot selection

To assess the influence of spatial climatic differences, specifically in average temperature and precipitation during the breeding season, I established 13 study areas across Hokkaido accounting for correlations between temperature and precipitation obtained from Mesh Climate Value 2010 (MLIT 2012). I then established one to four sample plots within each land cover type in each area, for a total of 113 sample plots (22 in wetlands and abandoned farmland,

718 respectively, 26 in pasture, 27 in cropland, and 16 in rice paddy; Fig. 3.1). Sample plots were
719 located in agriculture-dominated floodplains (i.e., alluvial fans or deltas). I could not establish
720 cropland plots in four areas and rice paddy plots in eight areas due to a lack of suitable sites
721 (cultivation in these areas is limited by temperature). I was also unable to locate suitable
722 abandoned farmland plots in two areas due to a lack of suitable sites.
723 All sample plots were 300 m in length and 100 m in width (3 ha), and I ran a survey line
724 through the center of each plot. Plots were randomly placed within pre-defined compartments of
725 a single land cover type to avoid recording birds that breed in different land cover types adjacent
726 to sampling plots. I then checked that each plot met the following criteria by using the vegetation
727 map (http://www.biodic.go.jp/trialSystem/top.html) and site visits: (1) each plot was separated
728 by at least 1 km to prevent double-counting (Ralph *et al.* 1993); (2) a bare-ground and grassland
729 proportions of plots (i.e., the proportion of wetland and active and abandoned farmland) was
730 more than 50%. This was done by generating 300 m buffers around each plot and determining
731 the proportion of bare ground and grassland within each buffer, as this is known to affect the
732 densities of grassland and forest birds on Hokkaido (Hanioka *et al.* 2018b, a). I thus did not
733 consider landscape structure as explanatory variables in my models.
734
735 **3.2.4 Bird surveys**
736 I performed three bird community surveys in each sample plot throughout the breeding season
737 (May–July) of 2017. The first, second, and third surveys were conducted from May 15 to June 7,
738 from June 9 to July 5, and from July 8 to July 29, respectively. I avoided surveying on rainy,
739 foggy, or windy (windspeeds > 4 m/s) days. Surveys were conducted from dawn to 10:00 h,
740 when bird activity and singing is greatest (Bibby *et al.* 2000). To reduce time of day bias, I
741 divided surveys into two time zones, from dawn to 07:00 h and from 07:00 h to 10:00 h, and
742 ensured at least one survey per plot represented each zone.

743 I slowly walked the survey lines (2 km/h) using a global positioning system device and
744 recorded the species, sex, location, and behavior (e.g., singing, territorial conflict) of individuals
745 within plots (Bibby *et al.* 2000). Then, I recorded the putative territories of individual species on
746 a map based on observations from all three visits (Bibby *et al.* 2000) and estimated territory size
747 (Hanioka *et al.* 2018a). I used the summed number of territories for each species within a given
748 plot as my abundance metric. I considered that I detected any inhabited territory in at least one
749 survey. This is because bare-ground and grassland birds have relatively high detectability (~0.6)
750 (Yamaura *et al.* 2016), and hence three times surveys are considered to be enough to detect
751 almost all territories. Furthermore, detectability of birds' songs within 50 m from the observer is
752 high and stable among different habitats (Schieck 1997).
753
754 **3.2.5 Statistical analyses**
755 I estimated the effects of land cover and climate variables on the abundance of each detected bird
756 species and functional group using abundance-based hierarchical community models (HCMs)
757 (Yamaura *et al.* 2016). I also estimated interactive effects between abandoned farmland and
758 climate variables to test if the relative habitat suitability of abandoned farmland was consistent to
759 those of other land cover types across Hokkaido. I first assumed that the abundance of species *i*
760 in plot *j* (Z_{ij}) followed a Poisson distribution ($Z_{ij} \sim \text{Poisson}[\lambda_{ij}]$). I then assumed that the expected
761 abundance of species *i* in plot *j* (λ_{ij}) was a function of five land cover categories (i.e., wetland,
762 abandoned farmland, pasture, cropland, and rice paddy), two climate variables (i.e., the 30-year
763 average monthly temperature and precipitation estimates extracted from Mesh Climate Value
764 2010), and interaction terms between the binary abandoned farmland category (i.e., 0: active
765 farmland and wetland; 1: abandoned farmland) and climate variables. Climate variables were
766 standardized prior to analyses. The intercept of the linear predictor was omitted (i.e., I employed

767 the cell means method) (Kéry 2010) to allow for easy comparison of expected abundance values
768 among habitats using parameter estimates, derived using the equation:

769 $$\mathrm{Log}(\lambda_{ij}) = hab_i \times x_{j1} + \beta_{i1} \times x_{j2} + \beta_{i2} \times x_{j3} + \beta_{i3} \times x_{j4} + \beta_{i4} \times x_{j5} \quad (1)$$

770 where x_{j1} indicates the land cover category of plot j, x_{j2} and x_{j3} indicate the average temperature
771 and precipitation of plot j, respectively, and x_{j4} and x_{j5} indicate interaction terms between
772 abandoned farmland and average temperature and precipitation. hab_i and β_{i1-4} represent the
773 partial regression coefficients of species i for each explanatory variable.

774 The 30-year average climate values could underestimate the effects of climatic events
775 which uniquely occurred in the surveyed year in a specific area. However, I adopted the average
776 values since my focus is to examine the large-scale effects of land cover types and its spatial
777 variations. I thus used 30-year average values, which is assumed to better represent the spatial
778 characteristics of each area.

779 I categorized observed bird species as (i) bare-ground species, (ii) grassland species, and
780 (iii) forest species according to published references (Takagawa *et al.* 2011; Hanioka *et al.*
781 2018a). I defined grassland species as any species inhabiting areas dominated by high perennial
782 grass; hence, I included wetland species in this category. I then assumed that the species-level
783 parameter β_i followed a functional group-level normal distribution with hyperparameters. This
784 parameterization allowed us to model rare species using information from common species
785 (Yamaura *et al.* 2012). Hyperparameters describe the mean values of the functional group and
786 among-species heterogeneity as:

787 $$\beta_{i1} \sim \mathrm{Normal}[\mu_{\beta 1}, \sigma^2_{\beta 1}], \qquad \beta_{i2} \sim \mathrm{Normal}[\mu_{\beta 2}, \sigma^2_{\beta 2}], \ldots \quad (2)$$

788 where $\mu_{\beta 1}$ and $\sigma_{\beta 1}$ are the mean and standard deviation of β_{i1}, respectively. These terms assume
789 that different functional groups can have different means and variation for each coefficient; I
790 expected that the effects of land cover and climate would differ among functional groups.

I obtained parameter estimates from field survey data using a Markov Chain Monte Carlo method with three chains, a burn-in of 50,000, a thinning interval of five, and 100,000 post-iterations. I conducted these analyses using R ver. 3.2.0 (R core team 2015), JAGS ver. 4.2.0 (Plummer 2016), and the R package jagsUI ver. 1.4.2 (Kellner 2016). Community and functional group-level total abundance were estimated by summing species-level expected abundance, λ_{ij} (hereafter abundance), for each. Similarly, I defined expected species richness (hereafter species richness) as the expected value of the number of species with at least one individual (i.e., $Z_{ij} \geq 1$). The probability of at least one individual occurring ($Pr[z_{ij} \geq 1]$) was expressed using Eq. (3), and I summed this value for each functional group and community (Yamaura *et al.* 2016).

$$Pr\left[z_{ij} \geq 1\right] = 1 - \exp\left(-\lambda_{ij}\right) \quad (3)$$

I calculated the community- and functional group-level median values and 95% credible intervals of total abundance and species richness on the basis of the posterior distributions obtained for each species. When the 95% credible intervals did not overlap between two land cover categories, I interpreted the difference as significant. For climate variables and interaction terms, I determined each covariate to be significant at the 5% significance level. To examine the response of each functional group to climate variables, I generated curves representing the effects of climate variables on the total abundance and species richness of each functional group in each land cover type using the estimated posterior distributions of each group. Curves were drawn for each climate variable, while the other climate variable was held to its mean. When the 95% credible intervals of total abundance or species richness did not overlap between the lowest and highest average temperature or precipitation value, I interpreted this as a significant effect of climate on total abundance or species richness.

3.3 Results

I recorded a total of 1,466 individuals of 56 bird species across all surveys. I excluded passage visitors, introduced species, and species whose territory sizes were larger than the sample plots. Therefore, I focused on 1,389 individuals of 33 species (bare-ground species: 206 individuals of four species; grassland species: 1,144 individuals of 23 species; forest species: 39 individuals of six species) in subsequent analyses. The five most commonly observed species were black-browed reed warbler (*Acrocephalus bistrigiceps*, 300 individuals), Middendorff's grasshopper-warbler (*Locustella ochotensis*, 164 individuals), Eurasian skylark (*Alauda arvensis*, 162 individuals), Stejneger's stonechat (*Saxicola stejnegeri*, 135 individuals), and reed bunting (*Emberiza schoeniclus*, 124 individuals). I observed fewer than 100 individuals of all remaining species.

3.3.1 Functional group differences in habitat suitability

The abundance of two of the four bare-ground species (Eurasian skylark and Eurasian tree sparrow [*Passer montanus*]) was significantly greater in pasture, cropland, or rice paddy than in abandoned farmland. The hyperparameters of bare-ground species did not differ significantly among land cover types (Fig. 3.2a). However, total abundance (i.e., the sum of the expected abundance for all bare-ground species) was significantly higher in cropland and pasture than in wetland, abandoned farmland, and rice paddy (Fig. 3.2b). The species richness was higher in pasture and cropland than in abandoned farmland and wetland (Fig. 3.2c).

The abundance of 14 of the 23 observed grassland species was significantly greater in abandoned farmland than in pasture, cropland, or rice paddy. The abundance of 21 species in abandoned farmland was comparable to or higher than in wetland. Reflecting species-level patterns, the hyperparameter in abandoned farmland was greater than in cropland and rice paddy,

and comparable to that in wetland (Fig. 3.2d). Total abundance and species richness exhibited similar patterns to those of hyperparameters (Fig. 3.2e, f).

For forest species, the abundance of Japanese bush warbler (*Horornis diphone*) was significantly higher in abandoned farmland than in pasture, cropland, and rice paddy. The abundance of the remaining five forest species and the hyperparameters did not differ among the five land cover types (Fig. 3.2g). Total abundance and species richness were higher in abandoned farmland than in cropland and pasture, but differences between other pairs of land cover types were not significant (Fig. 3.2h, i). The results of community-level total abundance and species richness were very similar to those found for grassland species (Fig. 3.2j, k), which was the dominant group in the survey sites.

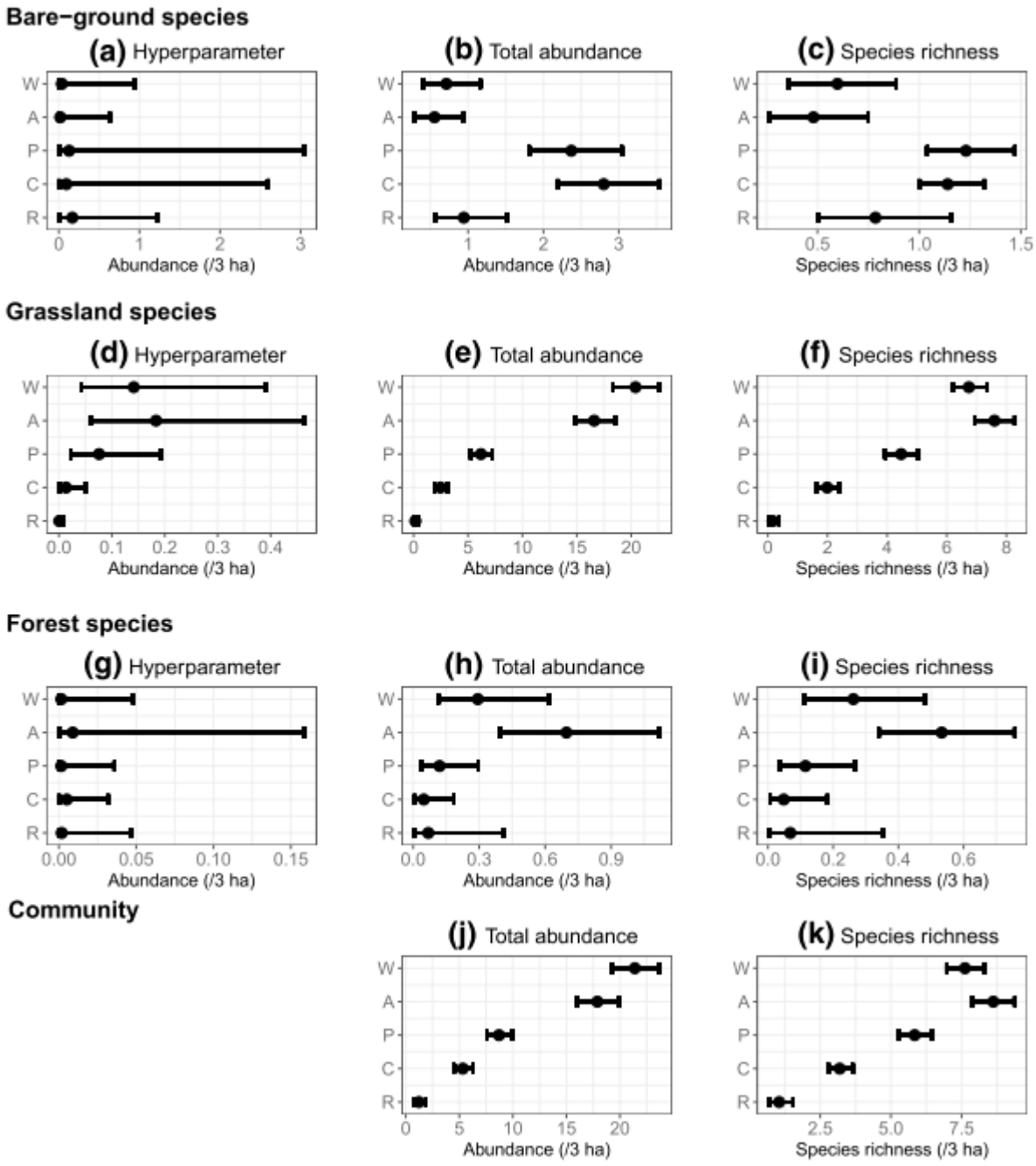
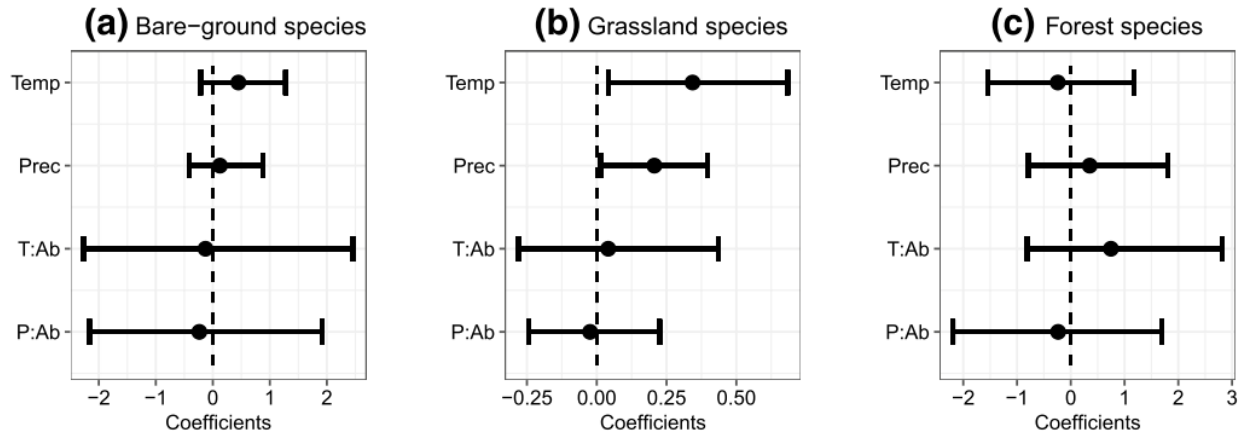


Fig. 3.2 Estimates of hyperparameters, total abundance, and species richness for each land cover type (per 3 ha). Results are shown for each functional group in panels a–i. Community-level results are shown in panels j and k. Total abundance was calculated by summing the expected abundance of each species within a functional group. Climate variables were held to their means. Dots indicate median values and bars indicate 95% credible intervals. W = wetland, A = abandoned farmland, P = pasture, C = cropland, and R = rice paddy.

3.3.2 Spatial differences in habitat suitability

For 30 of the 33 observed species and each functional group, interaction terms between abandoned farmland (represented as a binary variable) and climate variables (i.e., average temperature and precipitation) were not significantly related to abundance (Fig. 3.3). For bare-ground species, the partial regression coefficient for average temperature was positive but non-significant (Fig. 3.3a), and total abundance and species richness were significantly higher in areas with higher average temperature, excluding in abandoned farmlands (Fig. 3.4a, b). For grassland species, average temperature and precipitation had significant positive effects on five and four species, respectively. Group-level partial regression coefficients of both average temperature and precipitation were positive and significant (Fig. 3.3b). Total abundance and species richness were also significantly higher in areas with higher average temperature and precipitation, excluding in rice paddies (Fig. 3.4e–h). For forest species, neither climate variable had a significant effect on species-level or group-level partial regression coefficients, total abundance, or species richness (Fig. 3.3c; Fig. 3.4i–l). The results of community-level hyperparameters were similar to those observed in grassland species.



869

870 Fig. 3.3 Hyperparameters for climate variables and interaction terms for each functional group.
871 Black dots indicate median values and bars indicate 95% credible intervals. T:Ab and P:Ab
872 represent interaction terms between average temperature and abandoned farmland, and between
873 average precipitation and abandoned farmland, respectively. Temp = temperature, Prec =
874 precipitation.

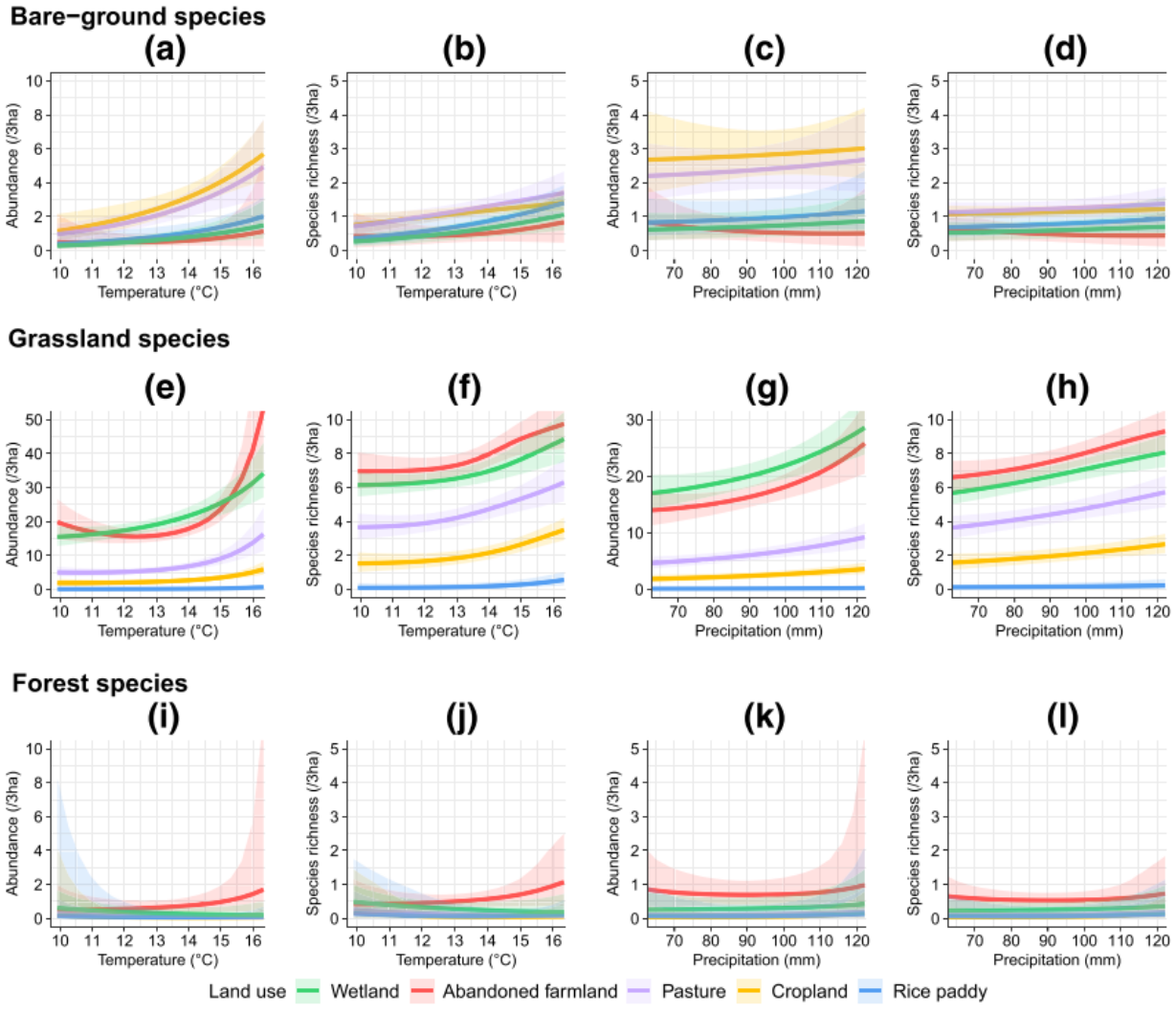


Fig. 3.4. The relationships between total abundance or species richness and climate variables for three functional groups. In each panel, the other climate variable is held to its mean value (i.e., 0). Solid lines represent median values and shading indicates 95% credible intervals. Land cover types are represented by colors. Green = wetland, Red = abandoned farmland, Purple = pasture, Yellow = cropland, and Blue = rice paddy.

3.4 Discussion

3.4.1 Functional groups

The habitat suitability of abandoned farmland differed markedly depending on functional group, but was consistent throughout Hokkaido for each group. I showed a clear difference in the

habitat suitability of abandoned farmland for bare-ground and grassland species. The abundance and richness of bare-ground species was higher in active farmlands than in abandoned farmland, consistent with previous studies in Europe and southern Japan (Sirami *et al.* 2008; Katayama *et al.* 2015b). For example, skylark, a bare-ground species, was found to avoid the tall dense perennial plant cover that had established in abandoned farmlands in Poland (Orłowski 2005). My results suggest that abandoned farmland is unsuitable habitat for bare-ground species, meaning that continued farmland abandonment will result in loss of suitable habitat for these species.

By contrast, the abundance and richness of grassland species in abandoned farmland was higher than in active farmland, and comparable to natural wetlands. This is likely due to vegetation succession and the establishment of perennial grasses in abandoned farmland, which provides foraging and breeding habitat for grassland species (Kennerley and Pearson 2010). The importance of abandoned farmland as habitat for grassland species was also identified in some studies in Europe (Orłowski 2005; Berg & Gustafson 2007; Radović *et al.* 2013; Kamp *et al.* 2018). Abandoned farmland likely becomes suitable habitat for grassland species once perennial grasses established; farmland abandonment can provide valuable alternative habitat for species whose habitats have been lost to agricultural expansion. This could especially be the case in floodplain or valley plain landscapes where perennial grasses continue to dominate 20–50 years after farmland abandonment (Rosenthal 2010), possibly due to a rise in groundwater level (Morimoto *et al.* 2017). However, there is a possibility of tree species colonization in the future (Sirami *et al.* 2007; Zakkak *et al.* 2018). I also note that, due to high stem length, some types of grassland might not be included in openland, though I divided openland into bare ground and grassland.

Although the abundance and species richness of forest species in abandoned farmland was higher than in cropland, the estimated abundance in abandoned farmland (0.22 individuals/ha)

was substantially lower than an estimate obtained for forest habitat on Hokkaido (9.3 individuals/ha), (Hanioka *et al.* 2018a). It is likely that forest species do not occupy abandoned farmland due to the relatively lower level of shrub or tree cover in the sample plots than those in forests. Previous studies have reported that tree and shrub cover are likely to establish in abandoned farmland in tropical and mountainous regions (Benjamin *et al.* 2005; Sirami *et al.* 2007; Rozendaal *et al.* 2019) and provide suitable habitat for forest species (Pereira & Navarro 2015; Acevedo-Charry & Aide 2019).

I note that I have evaluated only six forest and four bare-ground species. Future works should evaluate habitat suitability of abandoned farmland in other regions to test generality of my findings for those groups. Furthermore, habitat preferences of a species could differ among regions (Báldi & Batáry 2011), suggesting that a species might belong to other functional groups in other regions. For example, Eurasian tree sparrow prefers foraging in wetlands in the UK (Field & Anderson 2004), but in bare grounds such as levee, harvested, or plowed land in southern Japan (Maeda 2001). Thus, care is needed when extrapolating my species-level results to other regions. Future studies should also focus on breeding success in abandoned farmland since breeding success is sometimes lower in abandoned farmland than in undisturbed habitat (Lameris *et al.* 2016; but see Kitazawa *et al.* 2019).

3.4.2 Spatial differences in habitat suitability

It has been suggested that impact of farmland abandonment on biodiversity varies between geographic regions (Queiroz *et al.* 2014). However, I observed weak and non-significant interactive effects between climate variables and abandoned farmland for 30 of the 33 species used in my analyses and group hyperparameters. Instead, abandoned farmland was found to be more suitable for grassland species than active farmland, and was even comparable to natural wetlands. In addition, abandoned farmland was less suitable for bare-ground species, and these

936 trends were consistent across all of Hokkaido. It is possible that regional differences in habitat
937 suitability could be detected at a larger spatial scale than that used here, for example at the
938 continental scale, at which landscape composition and vegetation types change remarkably
939 (Brown *et al.* 1995; Randin *et al.* 2006).

940 Average temperature and precipitation in bird breeding season positively affected the
941 abundance and richness of grassland species. This is likely a result of higher vegetation
942 productivity. Temperature exerts a strong influence on shoot growth in reeds (Engloner 2009)
943 and thus stem length of reed is likely to be higher in areas with higher average temperatures.
944 Areas with rich vegetation and high precipitation provide abundant nesting sites (Fujimaki &
945 Takami 1986) and terrestrial food sources (Gorzo *et al.* 2016) for grassland species. Bird
946 communities could also be affected by vegetation composition and plant species richness, which
947 differ across Hokkaido. Although the relative importance of abandoned farmlands as habitat of
948 birds was consistent across Hokkaido, I note that climate factors influenced how many species or
949 individuals abandoned farmland can harbor.

3.5 Conclusion and conservation implications

Farmland abandonment has negative impacts on bare-ground species and positive impacts on grassland and forest species. Therefore, distinct conservation strategies are required for these functional groups. Wetland cover has been reduced on Hokkaido, particularly in the warmer areas (e.g., Ishikari and Tomakomai), (GSI 2001), and abandoned farmland in those warmer areas can harbor double the abundance of grassland species as that in cool areas. Therefore, abandoned farmland represents a potential mitigation to the dramatic negative effects of wetland loss, especially in the warmer areas of Hokkaido. Maintaining active farmlands is also important in the warmer areas in Hokkaido, since the abundance of bare-ground species was also high in those areas.

A functional group approach can provide a synthesis of varied species-level responses to agricultural abandonment and thus enable a comprehensive understanding of the habitat suitability of abandoned farmland. As demonstrated, the suitability of abandoned farmland was consistent across broad scales for all functional groups. However, the conservation priority of the functional groups may spatially vary depending on historical and biogeographical backgrounds (Betts *et al.* 2019). Therefore, adopting a functional group approach can contribute to developing regionally appropriate conservation strategies and targets in the era of agricultural abandonment.

4. Chapter 4 Disentangling the spatial/temporal variations of the effects of farmland abandonment and intensification on bird communities and functional group

Abstract

Farmland abandonment and intensification have suggested to be two major drivers of terrestrial biodiversity loss. However, their impacts on biodiversity vary spatially from positive to negative, and ignoring the variations could result in inefficient implementations of conservation actions and overlook the unique conservation opportunities. Therefore, identifying the underlying drivers of the variation is essential to reverse terrestrial biodiversity deterioration. I conducted nationwide surveys to assess the responses of bird communities to agricultural intensification and abandonment in breeding and wintering seasons across Japan. My results suggest that functional group-level responses to agricultural intensification and abandonment were consistent across regions and seasons, but community-level responses were spatially and temporally varied depending on the climate-driven variations of functional-group abundance. In cool regions in breeding season, forest, wetland, or grassland species dominated communities, and community-level abundance and species richness were higher in abandoned farmland than those in low-intensity farmland. In warm regions in breeding season, bare-ground and aquatic species dominated communities, and community-level abundance and species richness in low-intensity farmland were higher than high-intensity and abandoned farmland. Assessing functional group-level responses would be a powerful approach to gain a holistic understanding of the ecological consequences of agriculture and enable the effective implementations of conservation measures under land use and climate changes.

4.1 Introduction

Biodiversity is rapidly declining across every ecosystem on earth (Barnosky *et al.* 2011). One of the major drivers of biodiversity loss is agriculture. Farmland has extended to one thirds of the terrestrial land surfaces (Ramankutty & Foley 1999; DeFries *et al.* 2004), and 62% of the threatened terrestrial species on the IUCN Red List were negatively affected by habitat degradation owing to land use changes for agriculture and changes in agricultural activities (Maxwell *et al.* 2016). Though massive conservation efforts have been made to overcome the biodiversity crisis (Kleijn *et al.* 2006; Batáry *et al.* 2015), existing conservation measures are unable to reverse the general trend of farmland biodiversity deterioration (Butchart *et al.* 2010; Gamero *et al.* 2017; Gregory *et al.* 2019).

One of a key reasons for the difficulty in reversing the trend is spatial variations in the effectiveness of conservation measures and conservation values of each land use type (Kleijn & Sutherland 2003; Whittingham 2007; Báldi & Batáry 2011; Kleijn *et al.* 2011). Implementing an effective measure in a region does not necessary result in the same success in other regions (Tscharntke *et al.* 2005, 2012; Gonthier *et al.* 2014), or even worsen rather than improve conservation status (Tryjanowski *et al.* 2011; Sutcliffe *et al.* 2015). Identifying the underlying ecological drivers of the spatial variations is, therefore, critical to develop effective biodiversity conservation strategies (Catford *et al.* 2022).

Farmland abandonment and agricultural intensification are two major drivers of biodiversity changes in agricultural landscapes (Young *et al.* 2005; Batáry *et al.* 2015), and there are regional- to continental-level spatial variations in their consequences on biodiversity (Queiroz *et al.* 2014; Beckmann *et al.* 2019). For example, studies in the Mediterranean region and southern Japan showed that farmland abandonment negatively affected biodiversity (Plieninger *et al.* 2014; Koshida & Katayama 2018a), yet studies in Western Siberia and northern Japan showed the opposite pattern (Kamp *et al.* 2011; Kitazawa *et al.* 2019). While the consequences of

agricultural intensification on biodiversity is consistently negative, the extent of their impacts varies among regions (Uchida *et al.* 2018; Beckmann *et al.* 2019). Since further spread and advances of intensification and abandonment is predicted worldwide (Tilman *et al.* 2011; Ceauşu *et al.* 2015), revealing underlying drivers of the spatial variations in their effects would be a key to implement effective conservation actions and predict effective conservation measures for each region (Amano *et al.* 2011).

The spatial variations would be better understood and predicted if examining the responses of functional group (Concepción *et al.* 2020), especially functional groups based on biological or response traits (Violle *et al.* 2007). Existing studies showed that habitat suitability of agricultural land use types, including abandoned farmland, was consistent across a region for each habitat-based functional group (Kitazawa *et al.* 2021). For example, abundance and species richness of grassland bird species (i.e., species preferring perennial grassland) were higher in abandoned farmland than active (i.e., low- to high-intensity) farmlands, but those of bare-ground bird species (i.e., species preferring frequently disturbed habitat like farmland) were lower in abandoned farmland than active farmlands, and these trends were consistent across Hokkaido (400 km × 500 km) (Kitazawa *et al.* 2021).

Therefore, I here proposed a novel hypothetical framework that the community-level conservation values of abandoned, low-intensity, and high-intensity farmland in a region was determined by the response of the dominant functional group in the region (Fig.4.1). I predicted that abandoned, low-intensity, and high-intensity farmland have consistent conservation values for each functional group across regions and seasons. That is, in any region or season, species richness and abundance of forest, grassland, and wetland species would be higher in abandoned farmland than in active (i.e., low- to high-intensity) farmland (Fig.4.1). Also, species richness and abundance of bare-ground/aquatic species would be higher in low-intensity farmland than in abandoned and high-intensity farmland (Katayama *et al.* 2015b) (Fig.4.1). However, the

dominant functional group in species pool would spatially and temporally varies, resulting in spatial and temporal variation of community-level conservation values of each land use type (Fig. 4.1).

The dominant functional group in a species pool can differ among regions due to differences in climate and historical backgrounds (Katayama *et al.* 2014; Betts *et al.* 2019). Specifically, in temperate and boreal zones, diversity of wetland and grassland species would be higher in cool regions since grassland and wetland has long been maintained (Suga *et al.* 2012), suggesting community-level conservation values of abandoned farmland are high in those regions. Diversity of bare-ground and aquatic species would be higher in warm regions since frequent disturbances such as seasonal rainfall and tropical cyclone events in those regions could have maintained suitable habitats for those species (Betts *et al.* 2019). Low-intensity farmland are frequently disturbed by agricultural activities, suggesting the land-use type provides suitable habitats for bare-ground and aquatic species and hence community-level conservation values of low-intensity farmland are high in those regions. Furthermore, even in the same region, the dominant functional group can shift with seasons due to migration (Kawamura *et al.* 2019). For example, migratory bird species dominate the local bird communities in the Palearctic and Nearctic regions in breeding season (Somveille *et al.* 2013). These could result in the temporal variations in relative conservation values of each agricultural habitat.

To assess the hypothetical framework, I evaluated community- and functional group-level bird abundance and species richness patterns to temperature gradient in six major land use types in agricultural landscapes (i.e., wetland, abandoned farmland, low-intensity rice paddy, high-intensity rice paddy, cropland, and forest) throughout Japan in both breeding and wintering seasons. Japan covers varied climate area, ranging from the subarctic to subtropical, and hence breeding migratory birds in northern area move to southern area in winter, making great spatiotemporal variations in bird community compositions (Kawamura *et al.* 2019).

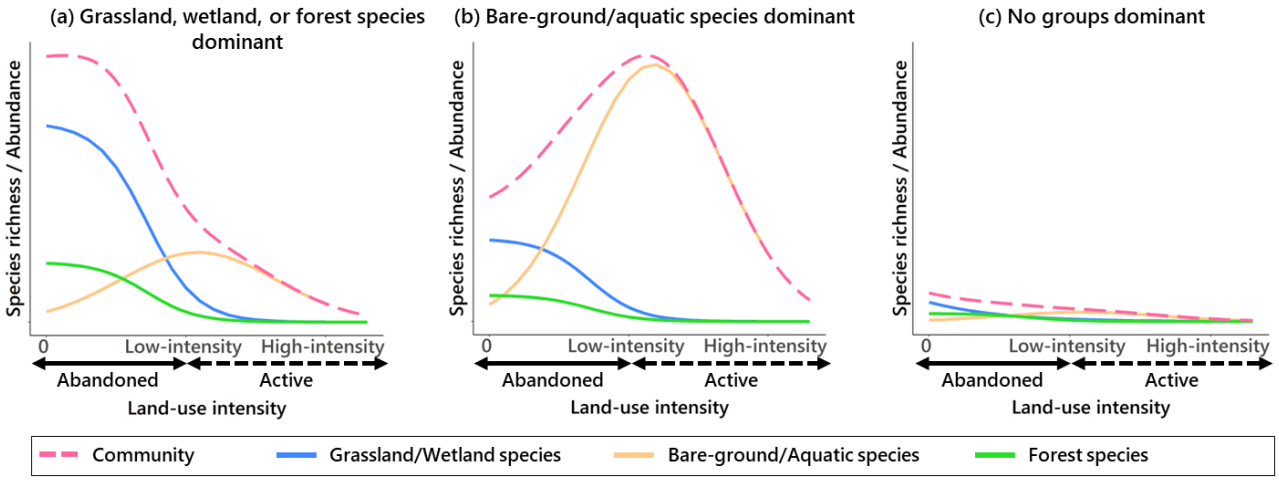


Fig. 4.1. Hypothetical framework. In this model, the x-axis represents the intensity of farmland management from no anthropogenic disturbances (e.g., abandoned for decades: denoted "0") to low- and high-intensity farmland. The solid line (hereafter, intensity-functional group curve) shows the response of the species richness or abundance for each functional group to the intensity of management. The dotted line shows the response of the community-level species richness and abundance (sum of all functional groups). The shape of the intensity-functional group curve (i.e., suitability of each land-use type) is expected to be consistent across regions and seasons. In a region/season in which grassland/wetland species dominate communities (a), community-level abundance and species richness in abandoned farmland (0 to low-intensity in x-axis) will be higher than in active farmland (low to high-intensity in x-axis). The similar patterns with (a) would be detected in a region/season in which forest species dominate communities. Also, in a region/season in which bare-ground/aquatic species dominate communities (b), community-level abundance and species richness will be higher in low-intensity farmland than in abandoned farmland. Furthermore, in those cases, community-level abundance and species richness in low-intensity farmland would be significantly higher than those in high-intensity farmland. On the other hand, in a region/season in which the abundance and species richness for all functional groups are low (c), differences of abundance and species richness among land use types will not be significant.

4.2 Materials and Methods

4.2.1 Study area

This study was carried out across Japan, where climatic conditions vary among areas; average temperatures range from 4.1 to 24.2 °C and from -16.7 to 11.0 °C during the bird breeding season (May–July) and wintering season (Dec–Feb), respectively. Cultivated lands account for 13% of the land in Japan, and 48.4% of the total cultivated area is rice paddy (Katayama *et al.* 2015a). Rice paddy has been consolidated since the 1960s, and >60% area of rice paddy has been consolidated in Japan. Since the 1980s, agricultural abandonment has rapidly increased due to aging farmers and depopulation in rural areas, and abandoned farmland now constitute >10% of the total farmland area (Katayama *et al.* 2015a).

4.2.2 Land use types

I focused on six land use types: natural wetland (hereafter wetland), abandoned farmland, traditional rice paddy, consolidated rice paddy, cropland, and forest. Wetland includes undisturbed wetland, reed or sedge vegetation established after reclamation, and riverbed wetland vegetation. I ensured that all surveyed abandoned farmlands had been active in the 1960s or 1970s and were no longer actively farmed by examining aerial imagery and using field observations. The elapsed years after abandonment were varied from 5 to 50 years, and farmland types before abandonment were also varied from managed grassland to cropland and rice paddy.

I divided abandoned farmland into lowland and hillslope abandoned farmland, since reestablished vegetation in abandoned farmland can differ depending on topographical conditions (Benjamin *et al.* 2005). Water availability, which would be higher in lowlands, would be one of the most influential determinants of established vegetation, because high groundwater level facilitates colonization of wetland grass species (Morimoto *et al.* 2017) but impedes establishment of tree species (Staaland *et al.* 1998). In hillslope areas, wood vegetation would

establish after the abandonment (Bonet & Pausas 2004; Zakkak *et al.* 2018). Therefore, I presumed that lowland abandoned farmland follows mesic succession and hillslope abandoned farmland follows xeric succession.

I conducted surveys in three types of active farmland (i.e., currently managed by farmers: cropland and two-types of rice paddies) (Fig. 4.2). I considered land-use intensity of farmland categorically by surveying two-types of active rice paddies which have different intensity levels (i.e., traditional and consolidated rice paddy) (Fig. 4.2). The typical traditional rice paddy is irrigated and drained via shallow earthen ditches, and size of a single field is very small (< 0.3 ha) and they are irregularly spaced (MAFF 2014). Therefore, traditional rice paddy can be regarded as low-intensity farmland and I surveyed traditional rice paddy whose single field size are <0.2 ha or irrigated/drained by earthen ditches. The traditional rice paddy have been consolidated to enlarge field size, to be more regularly spaced, and to be more efficiently drained (Katayama *et al.* 2015a). These consolidations helped farmers to efficiently use agricultural machinery and improve agricultural productivity, that resulted in habitat degradation of birds and fragmentation for aquatic and bare-ground species (Amano 2009; Katayama *et al.* 2015b). Therefore, consolidated rice paddy can be regarded as high-intensity farmland, and I surveyed consolidated rice paddy whose single field size are >0.5 ha and drained by deep concrete-sided ditches or underground pipes.

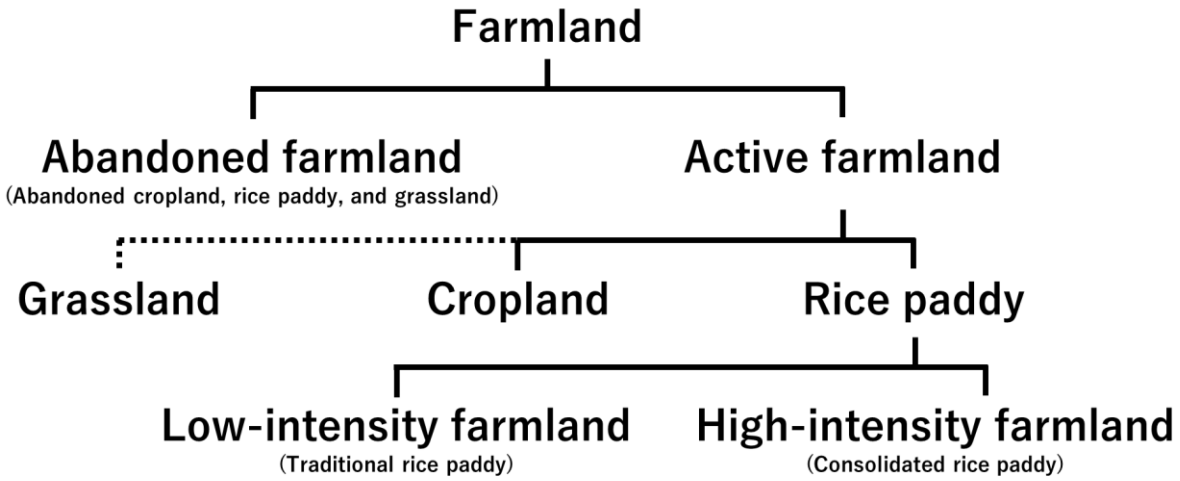


Fig. 4.2. Description of farmland types in my study. I conducted surveys in abandoned and active farmland. Active farmland includes cropland and two types of rice paddies. I focused on two types of rice paddies, which have different intensity levels (i.e., low- and high-intensity rice paddy). I surveyed traditional and consolidated rice paddy as low-intensity and high-intensity farmland, respectively. I have not surveyed grassland and have not considered land-use intensity of cropland.

4.2.3 Sample plot selection

I selected 10 study areas and established one to six sample plots for each land use type in each area, for a total of 199 sample plots (30, 29, 21, 49, 33, 18, and 19 plots for wetland, lowland abandoned farmland, hillslope abandoned farmland, traditional rice paddy, consolidated rice paddy, cropland, and forest, respectively; Fig. 4.3) based on aerial photos and field observation. All sample plots were 200 m in length and 100 m in width (2 ha), and I ran a survey line through the center of each plot. Plots were randomly placed within pre-defined compartments of a single land use type to avoid recording birds that inhabit in different land use types adjacent to sample plots. Each plot was separated by at least 1 km to prevent double-counting (Ralph *et al.* 1993). I could not survey 14 sample plots during wintering season due to deep snow.

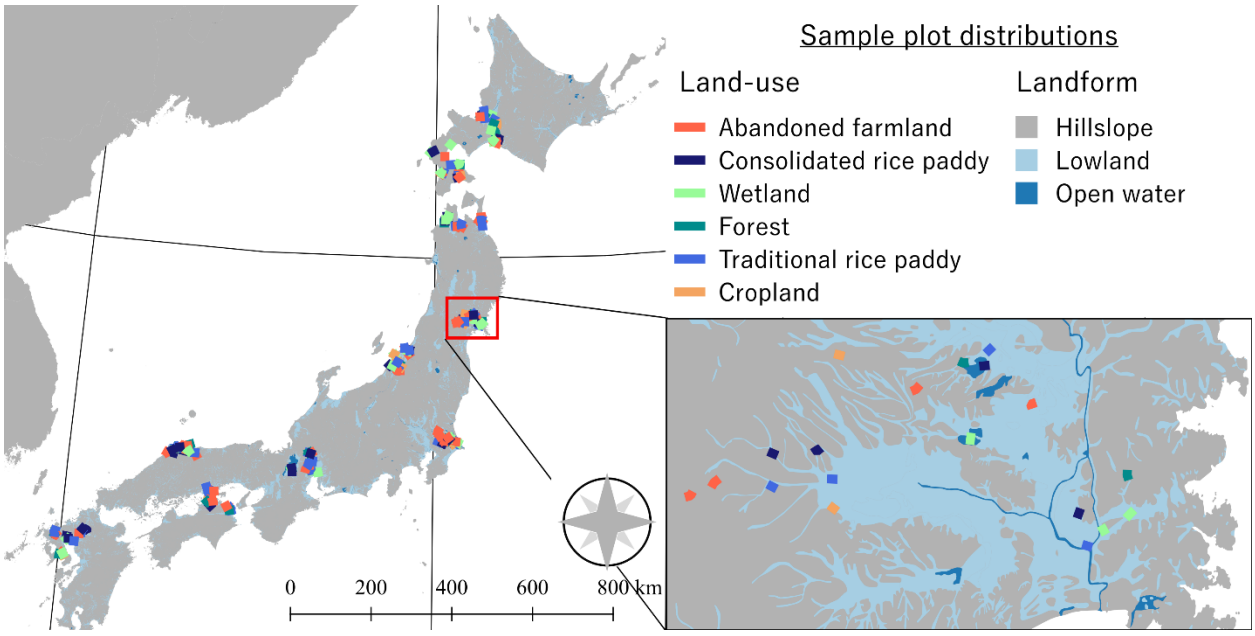


Fig. 4.3. Study area and the locations of the sample plots. The 199 sample plots are represented by squares and land use types are indicated by color. Sample plots are located in both hillslopes and lowlands.

4.2.4 Bird surveys and functional group

I performed bird community surveys in each sample plot throughout the breeding season (May–July) and wintering season (Dec–Feb) of 2019-2021. Each plot was surveyed three times in each season. I avoided surveying on rainy, foggy, or windy (windspeeds >4 m/s) days. Surveys were conducted from dawn to 12:00 h, when bird activity and singing is greatest (Bibby *et al.* 2000). To reduce time of day bias, I divided surveys into two time zones, from dawn to 07:00 h and from 07:00 h to 10:00 h in breeding season and from dawn to 09:00 h and from 09:00 h to 12:00 h in wintering season and ensured at least one survey per plot represented each zone for each season.

I slowly walked the survey lines (2 km/h) using a global positioning system device and recorded the species, sex, location, and behavior (e.g., singing, territorial conflict) of all individuals within plots (territory mapping; Bibby *et al.* 2000). I used the maximum number of

observed individuals for each species across the three surveys for each season as my abundance metric.

Each land use type provides different types of key resources such as food and nest sites (Newton 1998; Newbold *et al.* 2020), and hence the abundance of each species or species groups is associated with certain type of land use (Kitazawa *et al.* 2021). I thus focused on habitat-based functional group (forest, grassland, wetland, bare-ground, and aquatic species; main groups inhabiting agricultural landscapes in Japan), which is one of the biological traits (Violle *et al.* 2007), to assess the differences of species composition for each land use type. I classified all observed species into one of five functional groups based on the JAVIAN database (Takagawa *et al.* 2011). I considered that clear differences in habitat suitability of each land use type will be detected by this classification. I defined bare-ground species as those that prefer bare ground or short vegetation and aquatic species as those that prefer shallow water area.

4.2.5 Environmental variables

I used average temperature for each season (May–July and Dec–Feb, respectively) since it could represent changes in community composition from northern to southern part of Japan (Kawamura *et al.* 2019). I derived mean temperature for each sample plot from Mesh Climate Value 2010, which is a contiguous nationwide grid consisting of 1-km^2 squares with 30-year (1981-2010) mean monthly temperature (MLIT 2012). I did not consider precipitation due to high correlation with temperature. I generated 300-m buffers from the edges of sample plots and measured the forest proportions. Preliminary analysis showed that this landscape variable was the most strongly associated with bird abundance than variables with other spatial scales (100 m and 1,000 m).

4.2.6 Statistical analysis

1189 I estimated the effects of land use, mean temperature, and the landscape variable on the
1190 abundance of each detected bird species and functional group using abundance-based
1191 hierarchical community models (HCMs; Yamaura *et al.* 2012). The detection process was not
1192 considered in the model because openland songbirds have relatively high detectability (~ 0.66)
1193 (Yamaura *et al.* 2016), and detectability of birds' calls within 50 m from the observer is high and
1194 stable among different habitats (Schieck 1997). I first assumed that the abundance of species i in
1195 plot *j* (Z_{ij}) followed a Poisson distribution (Z_{ij} ~ Poisson[λ_{ij}]). I then assumed that the expected
1196 abundance of species *i* in plot *j* (λ_{ij}) was a function of seven land use categories (i.e., wetland,
1197 lowland abandoned farmland, hillslope abandoned farmland, traditional rice paddy, consolidated
1198 rice paddy, cropland, and forest), mean temperature, squared values of mean temperature, and
1199 forest proportions around sample plots. All continuous explanatory variables were standardized
1200 prior to the analysis. The intercept of the linear predictor was omitted (i.e., I employed the cell
1201 means method; Kéry 2010) to allow for easy comparison of expected abundance values among
1202 habitats using parameter estimates, derived using the equation:

1203 $$\mathrm{Log}(\lambda_{ij}) = hab_i \times x_{j1} + \beta_{i1} \times x_{j2} + \beta_{i2} \times (x_{j2})^2 + \beta_{i3} \times x_{j3} \quad (1)$$

1204 where x_{j1} indicates the land use category of plot *j*, x_{j2} indicate the mean temperature of plot *j*, and
1205 x_{j3} indicate the forest proportions around sample plot, respectively. hab_i and β_{i1-3} represent the
1206 partial regression coefficients of species *i* for each explanatory variable.

1207 I assumed that species-level parameters followed a functional group-level normal
1208 distribution with hyperparameters. This implies that different functional groups can have
1209 different means and standard deviations for each coefficient, reflecting my assumption that the
1210 effects of land use type and landscape openness differ among functional groups. I obtained
1211 median parameter estimates from the field survey data using a Monte Carlo Markov Chain with
1212 three chains, a burn-in of 50,000, a thinning interval of 5, and 100,000 post-iterations. I used
1213 uninformative normal distributions (0, 100^2) for the mean value of hab_i and β_{i1-3} and half-

Cauchy distributions (0, 5) for any variance of coefficients as weakly informative prior distributions (Gelman 2006). I conducted these analyses using R ver. 3.2.0 (R core team 2015), JAGS ver. 4.2.0 (Plummer 2016), and the R package jagsUI ver. 1.4.2 (Kellner 2016).

To determine HCMs to be appropriate for my dataset, I constructed generalized linear models assuming a Poisson distribution and generalized linear mixed models with surveyed area as a random effect to account for spatial autocorrelation. The parameter estimates of these models were qualitatively similar to those obtained from HCMs. Community and functional group-level total abundance were estimated by summing species-level expected abundance, λ_{ij} (hereafter abundance), for each. Similarly, I defined expected species richness (hereafter species richness) as the expected value of the number of species with at least one individual (i.e., $Z_{ij} \geq 1$). The probability of at least one individual occurring ($Pr[z_{ij} \geq 1]$) was expressed using Eq. (2), and I summed this value for each functional group and community (Yamaura *et al.* 2012).

$$Pr[z_{ij} \geq 1] = 1 - \exp(-\lambda_{ij}) \quad (2)$$

I calculated the community- and functional group-level median values and 95% credible intervals of total abundance and species richness on the basis of the posterior distributions obtained for each species. When the 95% credible intervals did not overlap between two land use categories, I interpreted the difference as significant.

4.3 Results

I recorded and calculated a total of 3,096 individuals of 95 bird species (40, 14, 14, 11, and 16 species for forest, grassland, wetland, bare-ground, and aquatic species, respectively) in breeding season and 7,956 individuals of 72 species (34, 12, 6, 20, and 19 species for forest, grassland, wetland, bare-ground, and aquatic species, respectively) in wintering season.

4.3.1 Functional group-level response

Responses to land-use types varied among the five functional groups, but suitability of land-use types for each group were consistent across seasons and regions (i.e., cool to warm regions) (Fig. 4.4 and 4.5). For example, the abundance and species richness of wetland and grassland species in lowland abandoned farmland were comparable to those in wetland (Fig.4.4/4.5b, c, g, h), and those of forest species in hillslope abandoned farmland were comparable to or lower than those in forest (Fig.4.4/4.5a, f) in any regions/seasons. Abundance and species richness of those three groups were higher in abandoned farmland than those in active farmland (i.e., cropland, and traditional and consolidated rice paddy). The abundance and species richness of bare-ground and aquatic species in abandoned farmlands were lower than those in cropland and rice paddies, and the abundance and species richness of those species tended to be higher in traditional rice paddy than in consolidated rice paddy and abandoned farmland in any regions/seasons (Fig.4.4/4.5d, e, i, j).

Though responses to average temperature markedly varied among the functional group in breeding season, their responses were consistent across the groups in wintering season (Fig. 4.4 and 4.5). In breeding season, functional group-level partial regression coefficients of mean temperature were positive for bare-ground and aquatic species but negative for forest, grassland, and wetland species. In wintering season, functional group-level partial regression coefficients of mean temperature were positive for all groups.

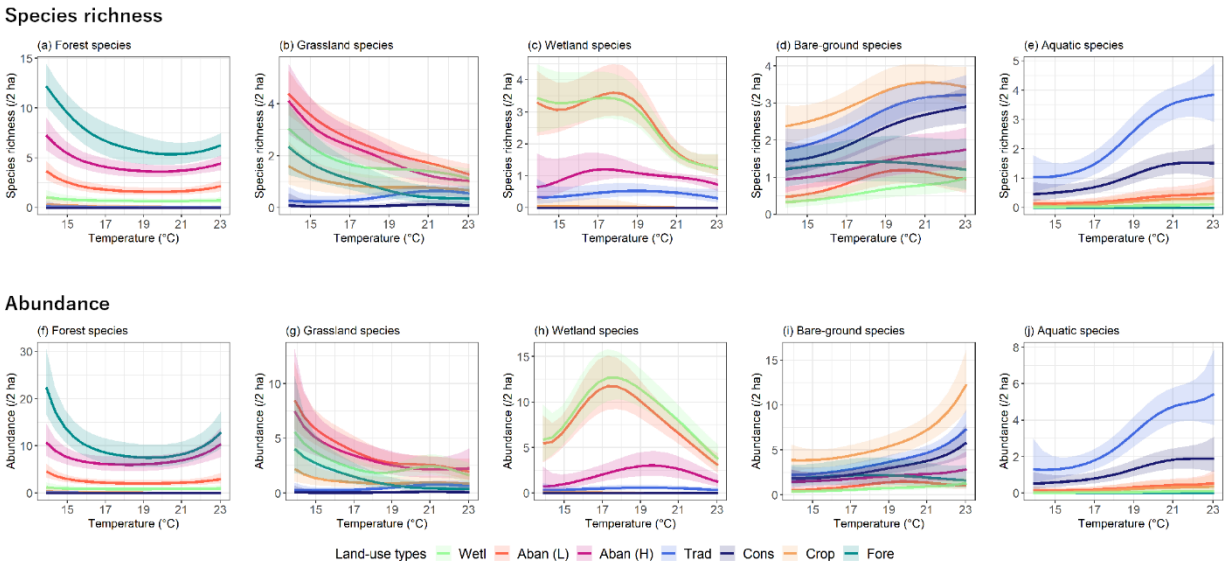


Fig. 4.4. The relationships between functional group-level species richness or abundance and average temperature during breeding season. The landscape variable is held to its mean value (i.e., 0). Solid lines represent median values and shading indicates 95% credible intervals. Land use types are represented by colors. Wetl = wetland, Aban(L) = lowland abandoned farmland, Aban(H) = hillslope abandoned farmland, Trad = Traditional rice paddy, Cons = Consolidated rice paddy, Crop = Cropland, and Fore = forest.

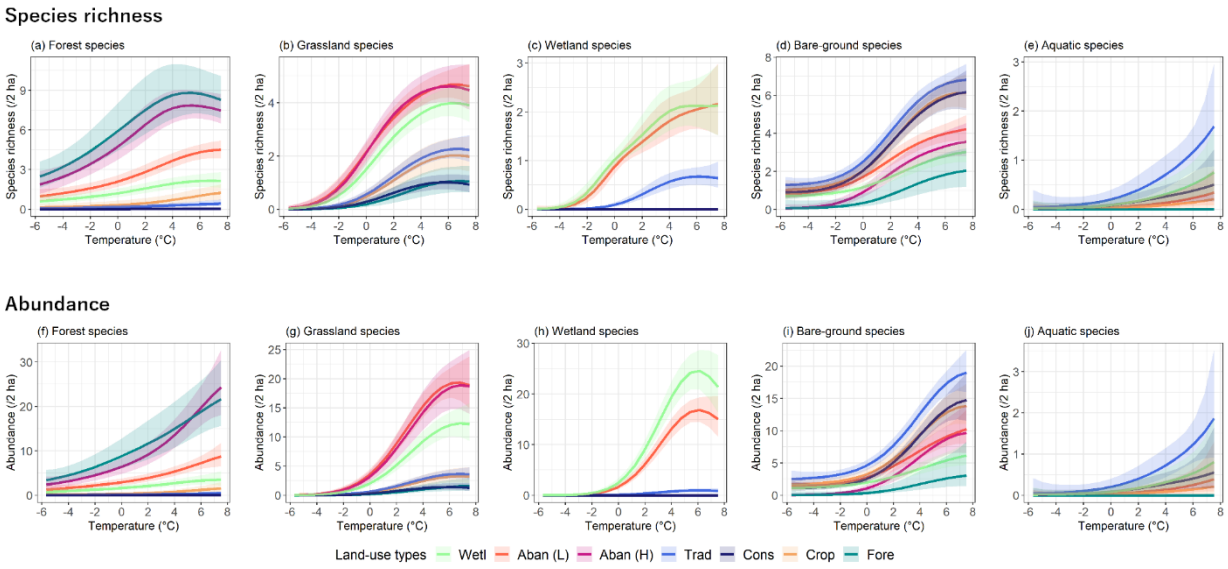


Fig. 4.5. The relationships between functional group-level species richness or abundance and average temperature during wintering season. The landscape variable is held to its mean value

(i.e., 0). Solid lines represent median values and shading indicates 95% credible intervals. Land use types are represented by colors. Wetl = wetland, Aban(L) = lowland abandoned farmland, Aban(H) = hillslope abandoned farmland, Trad = Traditional rice paddy, Cons = Consolidated rice paddy, Crop = Cropland, and Fore = forest.

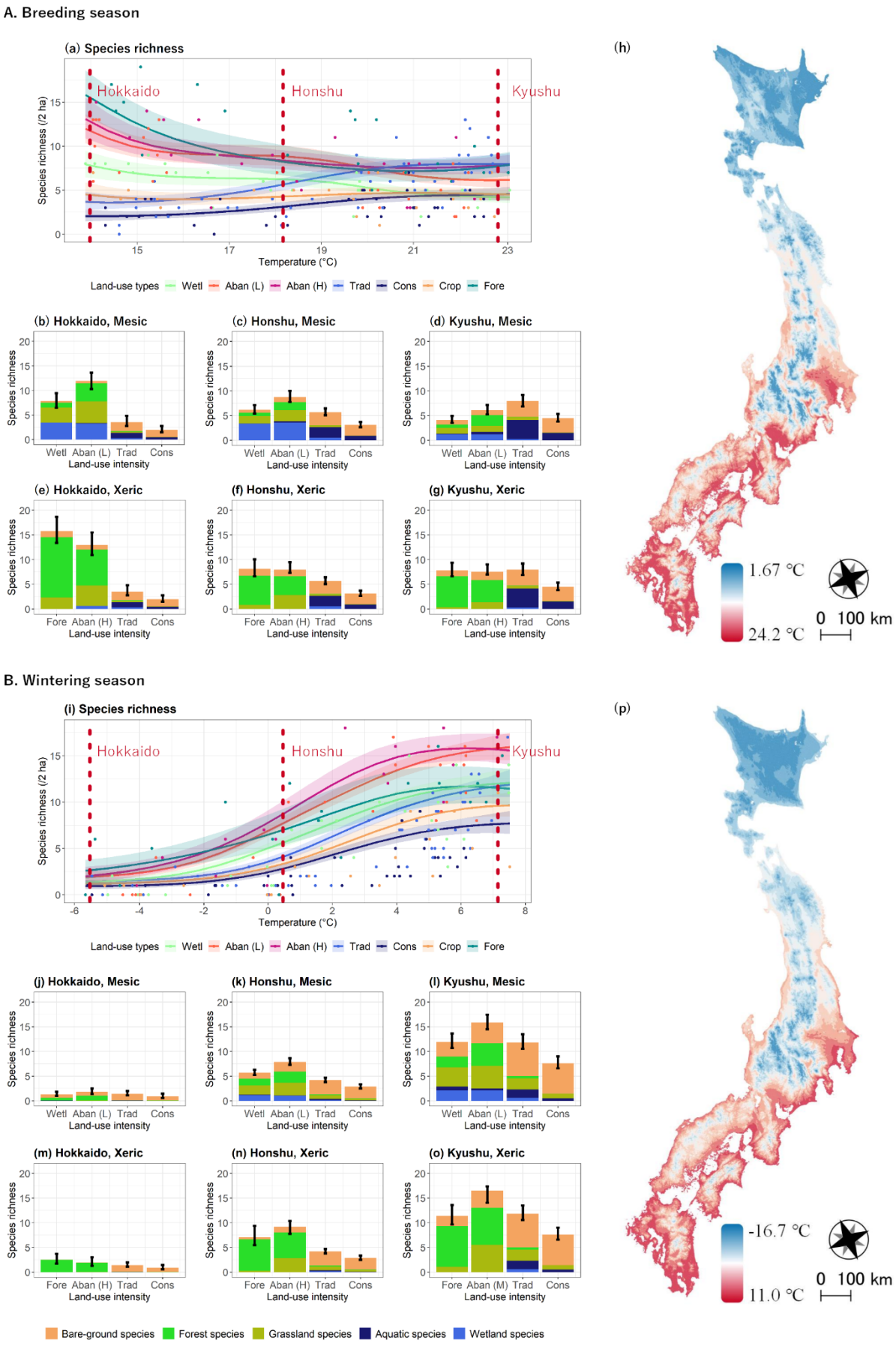
4.3.2 Community-level response

Across regions and seasons, community-level abundance and species richness in abandoned farmland were consistently comparable to forest and wetland, and those in traditional rice paddy were also tended to be higher than those in consolidated rice paddy (Fig. 4.6). However, as predicted in my hypothetical framework (Fig. 4.1), there were spatial and temporal variations in bird species richness/abundance between abandoned and active farmland (i.e., cropland and rice paddies) depending on the dominant functional group in the region/season (Fig. 4.6).

In breeding season, abundance and species richness of forest, wetland, and grassland species were higher in cool regions, and these species dominated communities (Fig. 4.4, Fig. 4.6b, e). Reflecting the responses of the dominant functional groups, community-level species richness and abundance were significantly higher in wetland, abandoned farmlands, and forest than those in traditional and consolidated rice paddy and cropland in cool regions (Fig.4.6a, b, e). Species richness and abundance in traditional rice paddy were comparable to those in consolidated rice paddy in cool regions (Fig. 4.6b, e). These results corresponded to “Grassland, wetland, or forest species dominant” community composition in Fig. 4.1. In warm regions, abundance and species richness of bare-ground and aquatic species were high, and these species dominated communities (Fig. 4.4, 4.6d, g). Community-level species richness and abundance in traditional rice paddy thus tended to be higher than those in wetland, abandoned farmlands, and consolidated rice paddy, corresponding to “Bare-ground/aquatic species dominant” community composition in Fig. 4.1.

In wintering season, abundance and species richness of all functional groups were higher in warm regions (Fig. 4.6). Forest, wetland, and grassland species dominated communities in the areas (Fig. 4.6i, l, o). Bare-ground and aquatic species abundance and species richness were also high in warm regions, but not enough to dominate communities. Therefore, community-level abundance and species richness were higher in forest, abandoned farmland, and wetland than

those in cropland and rice paddies, and those in traditional rice paddy were higher than those in consolidated rice paddy in warm regions (Fig. 4.6i, l, o, corresponding to “Grassland, wetland, or forest species dominant” community in Fig. 4.1). In cool regions, almost all species, except for forest species, did not appear in any land use types (Fig.4.6). Community- and functional group-level abundance and species richness were thus not significantly differed among land use types (Fig. 4.6j, m), which corresponded to “No groups dominant” community in Fig. 4.1.


A. Breeding season
(a) Species richness
Hokkaido
Honshu
Kyushu
Species richness (/2 ha)
Temperature (°C)
Land-use types Wetl Aban (L) Aban (H) Trad Cons Crop Fore
(b) Hokkaido, Mesic
(c) Honshu, Mesic
(d) Kyushu, Mesic
(e) Hokkaido, Xeric
(f) Honshu, Xeric
(g) Kyushu, Xeric
Species richness
Land-use intensity
Wetl Aban (L) Trad Cons
Fore Aban (H) Trad Cons
(h)
1.67 °C
24.2 °C
0 100 km
B. Wintering season
(i) Species richness
(j) Hokkaido, Mesic
(k) Honshu, Mesic
(l) Kyushu, Mesic
(m) Hokkaido, Xeric
(n) Honshu, Xeric
(o) Kyushu, Xeric
Fore Aban (M) Trad Cons
(p)
-16.7 °C
11.0 °C
Bare-ground species
Forest species
Grassland species
Aquatic species
Wetland species

1302

Fig. 4.6. The relationships between community-level species richness and avereage temperature during breeding season (a) and wintering season (i). Species richness in some land-use types (wetland, forest, lowland and hillslope abandoned farmland, and traditional and consolidated rice paddy) for each region (Hokkaido: cool region; Honshu: middle region; Kyushu: warm region) were also shown (b-g and j-o).

4.4 Discussion

Since farmland expansion, agricultural intensification, and abandonment have been dramatically spreading worldwide, effective implementation of conservation actions in agricultural landscapes is essential to conserve terrestrial biodiversity. Spatially complicated biological consequences of farmland abandonment and intensification (Queiroz *et al.* 2014; Beckmann *et al.* 2019) have hindered effective implementations of conservation measures, and their underlying drivers were yet to be revealed. Furthermore, farmland abandonment has been viewed as the major driver of biodiversity loss, and hence the unique opportunities provided by abandonment have sometimes been overlooked.

My work provided novel framework for understanding spatial/temporal variations in conservation values of agricultural habitats, that would be baselines to develop effective conservation strategies. My nationwide study highlights the role of the dominant functional group in driving the variation of the community-level impacts of farmland abandonment and intensification, and identified the situations in which farmland abandonment can contributes to biodiversity conservation. In a region/season in which forest and wetland species dominate species pool (i.e., northern Japan in breeding season and southern Japan in wintering season), community-level species richness and abundance in abandoned farmland were higher than those in traditional rice paddy. In contrast, in a region/season in which bare-ground and aquatic species dominate (i.e., southern Japan in breeding season), community-level species richness and abundance in traditional rice paddy were higher than those in abandoned farmland and consolidated rice paddy.

The spatial variations can be stem from climatic and palaeogeographical factors such as long-term distribution changes of habitats and connection to the continent. Grassland and wetland has been maintained in northern Japan due to the cool climate (Suga *et al.* 2012), and Hokkaido was connected by the continent via Sakhalin as a grassland corridor during the last

glacial period. Those historical background might facilitate colonization of wetland and grassland species in northern Japan from the continent (Yamaura *et al.* 2017). Southern Japan is frequently disturbed by seasonal heavy rainfall and tropical cyclone events (Kataoka 2007) and characterized by a long history of agriculture because rice cultivation was introduced approximately 2,000 years ago (Toyama & Nakayama 1992). Therefore, disturbed habitat such as bare ground or shallow water, which are suitable habitat for bare-ground and aquatic species, would have been steady provided in the region.

The present study further indicates that habitat suitability of abandoned farmland for each group varies with geomorphic conditions, suggesting that abandoned farmland have different conservation opportunities depending on moisture gradient driven by geomorphology. Abandoned farmlands in lowlands might follow mesic succession and provided suitable habitat for wetland species. In contrast, those in hillslopes, where they were presumed to follow xeric succession, provided habitats for forest species. The vegetation established after abandonment would determine the patterns of bird community composition. Wetland perennial grass vegetation (e.g., reedbed), the key nesting habitat for wetland and grassland bird species (Kennerley and Pearson 2010), establish soon after abandonment due to high ground water level (Morimoto *et al.* 2017). Therefore, wetland and grassland bird abundance and species richness in lowland abandoned farmland were comparable to those in undisturbed wetland. Relatively xeric environments on hillslopes could provide opportunity for tree regeneration (Staaland *et al.* 1998). However, since it takes decades for trees to grow up to adult stage, forest bird abundance and species richness in hillslope abandoned farmland tended to be lower than those in forest.

This study indicated that traditional rice paddy is key to conserve bare-ground and aquatic species. The abundance and species richness of these groups in traditional rice paddy were higher than those in abandoned farmland. This would be due to the loss of foraging site (e.g., bare ground and open water area) led by the cessation of disturbance after abandonment. The

abundance and species richness of those species were generally higher in traditional rice paddy, compared to consolidated rice paddy. Traditional rice paddies have been consolidated in Japan, and the field size have been enlarged and earthen ditches were converted to deep-concrete ditches or underground pipe. This would lead to the low abundance of prey species and loss of suitable bird habitat within consolidated rice paddy (Katayama *et al.* 2011, 2015b). However, in wintering season, swans and geese benefit from consolidated rice paddy possibly due to low predatory threats and abundant food resources (Zhao *et al.* 2018).

Understanding functional group-level responses enables more spatially optimized and effective implementation of conservation strategies to address farmland abandonment and intensification. For example, expanding protected and/or conservation-oriented areas to include abandoned farmland that located near protected area would be one of the promising conservation measures (Ceaușu *et al.* 2015; Yamaura *et al.* 2022), especially in northern Japan, where the diversity of breeding forest, wetland, and grassland species were high. The measure would be important to maintain some wetland and grassland bird species, since they might use abandoned farmland and wetland in northern Japan as breeding grounds and then move to abandoned farmland in southern Japan for overwintering. Maintaining traditional agricultural practices (Kleijn *et al.* 2011; Sutcliffe *et al.* 2015) and implementing organic farming (Bengtsson *et al.* 2005; Katayama *et al.* 2019) would especially be effective in southern Japan, where the diversity of breeding bare-ground and aquatic species were high.

Existing meta-analysis suggested that consequences of farmland abandonment vary depending on biological taxa (Koshida & Katayama 2018b). However, my results suggest that it depends on resource use types, implying my proposed framework can also be applied for other taxa. Aquatic species in my study showed lower abundance and richness in abandoned farmland than in active rice paddy. This would be consistent with other studies suggesting the relatively strong negative impacts of farmland abandonment on fishes, aquatic insects, and amphibians,

which are highly dependent on open water habitat (Koshida & Katayama 2018a). An existing study suggested that both farmland intensification and absence of anthropogenic disturbance negatively affect annual grass species, which prefer intermediate level of disturbance (Uchida & Ushimaru 2014). Therefore, species preferring open water or intermediate-level disturbance (i.e., aquatic and bare-ground species) would be fairly sensitive to farmland abandonment and intensification, and community-level negative impacts of the abandonment and intensification would be detected in regions where diversity of aquatic and bare-ground species is high.

4.5 Conclusion

Contrasting conservation strategies (e.g., single large or some small, land sharing or sparing) has been proposed over the last several decades, and assessing effectiveness of the conservation measures has been central to conservation ecology (Fazey *et al.* 2005; Cannon *et al.* 2019; Kok *et al.* 2020). Though conservation scientists have explored the single best solution, we still lack a basic understanding of the variations in the effectiveness of each conservation strategy and its drivers (Catford *et al.* 2022). In this paper, I proposed a novel hypothetical framework to resolve this situation – ecological significance of farmland abandonment and intensification – based on nationwide bird surveys. Dominant functional group in the targeted area determine the ecological consequences of land use change and implementations of conservation actions, and hence enables predictions of the ecological impacts of land-use changes. For example, future expansion of abandoned farmland in South America (Ceaușu *et al.* 2015) would provide new suitable habitats and conservation opportunity to regions with high forest, wetland, and grassland species diversity. My hypothetical framework also imply that future climate change could alter conservation values of each land-use type due to shifts in species distributions (Davey *et al.* 2013), raising a question of whether current conservation strategies would work in the future. My proposed framework would provide the baselines of understanding spatial variations in the effectiveness of conservation measures and hence help identifying the most effective measure for each region, and ultimately contribute to developing management policy in a rapidly changing world.

5. Chapter 5. General discussion and conclusion

Farmland occupies one thirds of the Earth's land surface, and hence addressing the negative impacts of agricultural activities are crucial for terrestrial biodiversity conservation. Nevertheless, the impacts of land-cover conversion from wildland to farmland have rarely been quantified in the Northern Hemisphere. The impacts of farmland abandonment and intensification and their variations have also been understudied, though the two drivers are now spreading worldwide and thus considered as major drivers for terrestrial biodiversity changes.

In Chapter 2, I estimated that broad-scale land-cover change over a 166-year period was associated with more than 70% decline in both potential species-richness and abundance of avian communities. Responses to broad-scale land-cover changes varied markedly among the four functional groups. The abundance of wetland and forest species declined by >88%, whereas that of bare-ground species increased by >50%, compared to 1850. In Chapter 3, I revealed that the abundance and species richness of grassland species in abandoned farmland were higher than those in active farmland (pasture, cropland, and rice paddy), and comparable to those in wetland, suggesting farmland abandonment provides a valuable alternative habitat for species whose primary habitats have been lost to agricultural expansion.

In Chapter 4, I proposed and tested a hypothetical framework and revealed that the community-level responses to farmland abandonment and intensification in a region was determined by the response of the dominant functional group in species pool in the region. Since functional group-level responses to farmland abandonment and intensification were consistent across regions, conservation values of abandoned farmland and high-/low-intensity farmland depends on conservation focus, which can spatially and temporally vary. Therefore, if we could assess the functional group-level responses to environments and climate gradients, the conceptual framework presented in this thesis would enable us to predict the ecological consequences of land use and management changes. In this chapter, I first proposed effective

conservation strategies in changing landscapes based on my studies. I then discuss the limitation of the studies and future challenges to address current biodiversity crisis.

5.1. Establishing conservation strategies based on regional species pool and land cover history

Broad-scale land-cover changes for agriculture are currently ongoing in tropical regions. Land-cover conversion for agriculture thus assumed to be urgent to be addressed to conserve terrestrial biodiversity in those regions (Brooks *et al.* 2002; Edwards *et al.* 2013). However, my results suggested that turnover in community composition and drastic reductions in forest and wetland species have already occurred in large parts of the Northern Hemisphere until 1400s-1700s. Therefore, protecting remnant habitats and restoring forest and wetland ecosystem ought to be given the highest priority to conserve forest and wetland species, even in the Northern Hemisphere.

My nationwide survey revealed that lowland abandoned farmland plays an important role as habitat for wetland and grassland species. Lowland abandoned farmland in northern Japan, where wetland and grassland bird species dominated the community, harbored a lot of wetland and grassland bird species in breeding season. Furthermore, in southern Japan, the area of natural grassland and wetland has decreased over hundreds to thousands of years since the time human started cultivation (Ramankutty & Foley 1999; Pereira *et al.* 2012; Davidson 2014), and community-level bird abundance and species richness in lowland abandoned farmland were higher than those in other land-cover types in wintering season. Therefore, valuing abandoned farmland as habitat for those species would be one of the promising conservation options.

In fact, I confirmed 11 endangered wetland and grassland bird species in lowland abandoned farmlands. For example, I observed breeding of Japanese reed bunting (Fig.5.1) and Marsh grassbird (Fig.5.2), whose population size in Japan is estimated to be around 650

(Takahashi *et al.* 2017) and 2,500 (Ueda 2003), respectively, at several surveyed abandoned farmlands. I have also confirmed two individuals of Eurasian bittern, whose recent breeding status in Japan is unavailable, in an abandoned farmland in breeding season. This abandoned farmland can possibly harbor the largest breeding population of the species in Japan because I also confirmed several other individuals around the sample plot. In an abandoned rice paddy in Inashiki city, Ibaraki prefecture, central Japan, I confirmed a lot of breeding individuals of Japanese reed bunting and Marsh grassbird. I have established a project to conserve those species in cooperation with the Ibaraki Branch of the Wild Bird Society of Japan in the abandoned farmland.

I here proposed four management measures considering abandoned farmland as conservation opportunities. First, expanding protected areas to include abandoned farmland that located near protected areas would contribute to conserving those species (Ceauşu *et al.* 2015; Yamaura *et al.* 2022). Using the OECM framework currently under discussion would be one promising option to protect species-rich abandoned farmland (Ministry of the Environment 2021), since most of the abandoned land is privately owned. Second, applying a global conservation framework may also contribute to conserving wetland ecosystems established on abandoned farmland. For example, Hotokenuma, Aomori prefecture, was abandoned after being reclaimed for rice cultivation, but now it designated as a Ramsar site (Osari *et al.* 2017). Third, keeping property taxes for biodiverse abandoned farmland at the same level as for active farmland would also be a possible conservation strategy. Abandoned farmland is now subject to higher property taxes than active farmland (Ministry of Agriculture, Forestry and Fisheries 2020). Fourth, afforestation of abandoned farmland and abandoned residential areas could also be effective restoration measures to conserve lowland forest ecosystems (Motosugi *et al.* 2021).

Conservation actions should also focus on immediate problems resulting from current pressures, such as agricultural intensification. In Europe, where the history of agriculture is long,

the diversity of bare-ground species and aquatic species is high (Covas & Blondel 1998). The diversity of those species should also be high in southern Japan (Suga *et al.* 2012), since southern Japan also has the long history of agriculture (Toyama & Nakayama 1992). In those regions, conserving bare-ground and aquatic species would be equally, or more, important as wetland and grassland species. In southern Japan in breeding season, the abundance and species richness of those species tended to be high in low-intensity rice paddy than those of other land-cover types. The results suggest that preventing abandonment and intensification of those low-intensity fields are important to conserve those species. This can be achieved by introducing a financial system that can secure a certain level of agricultural income (e.g., agri-environmental scheme in the UK and food labeling) in traditional fields and establishing novel farmland consolidation techniques considering biodiversity would be worth considering for conserving biodiversity within fields. These measures would especially be effective in lowland rice paddy landscapes in southern Japan (e.g., the Chikushi, Nobi, or Kanto Plain), where species richness of bare-ground and aquatic species is high.

Fig. 5.1 Japanese reed bunting in abandoned farmland in Aomori Prefecture.

Fig. 5.2 Marsh grassbird in the Hotokenuma reclaimed Land.

Fig.5.3 Abandoned farmland in Inashiki city, Ibaraki Prefecture

5.2. Challenges for biodiversity conservation under human population decline

My results indicated that abandoned farmland can provide substitutional habitat for wetland and forest species, whose population sizes were estimated to be decline due to broad-scale land cover change. However, my results failed to predict which abandoned farmland is important for biodiversity conservation in a spatially explicit manner. Abandoned farmland is now assumed to be potential site for installing renewable energy power plant, suggesting future habitat conversion (Kim *et al.* 2021). Furthermore, due to vegetation succession (Benjamin *et al.* 2005; Sirami *et al.* 2007), it does not necessary ensure that the current vegetation in abandoned farmland will continue to be remained. Future studies should reveal factors affecting established vegetation after abandonment by focusing on topographical wetness index, land cover history prior to farmland abandonment, landscape variables, and elapsed years after abandonment.

Predicting and mapping the conservation values of abandoned farmland would enable us to identify abandoned farmland with high conservation priority.

5.3. Conclusions

Since farmland expansion, intensification, and abandonment have been dramatically spreading worldwide, understanding the spatial variations of the effect of those threats is key to implementing effective conservation actions in agricultural landscapes (Amano *et al.* 2011; Kleijn *et al.* 2011). A past study (Amano *et al.* 2010) has suggested two different conservation strategies to conserve terrestrial biodiversity under human population decline: maintaining traditional farmland and secondary forest by spending labor effort and cost or accepting passive wetland and forest ecosystem restoration in abandoned farmland. However, it has not been examined which conservation strategies are more effective in which regions. I here revealed the driving factors of spatial variations of the effect of land cover changes on biodiversity and explicitly identified the ecological condition that defined the effectiveness of conservation strategies. Applying the hypothetical framework (in Chapter 4), that is, assessing functional group-level responses, would allow us to predict the ecological consequences of future landscape and management changes and help us to identify effective conservation strategies.

This study revealed how the two major drivers of biodiversity changes impacted community-level avian diversity. However, there are many other agricultural managements and conservation activities that were not addressed in this study. All of these would have modified and impacted agricultural biodiversity in various ways. Examining each of these factors individually and assessing regional differences would be extremely time-consuming and therefore still been understudied. Furthermore, those current methods will no longer be able to meet society's demands for more rapid implementation of conservation measures and evaluation of their impacts, since recently developed TNFD (Taskforce on Nature-related Financial

Disclosures) framework requires companies to disclose nature-related financial information and integrate nature into decision making.

This study suggest two effective solutions to this situation. The first is a meta-analysis focusing on functional groups. Based on the results of this study, responses of each functional group to land-use change should be consistent across the globe, and assessing the relationships between functional groups and managements would boost identifying conservation measures, that work consistently across regions. Mapping functional groups and combining these with the results of meta-analysis will enable us to predict the community-level consequences of the impacts of agricultural management and conservation measures.

The second is identifying key microhabitats that is important for each functional group. The bird distribution within agricultural landscapes was closely related to the distribution of microhabitats, that is important for each functional group. For example, wetland species occurred wetland grass patches within agricultural landscapes, while aquatic species occurred when water was irrigated in rice paddy. By identifying the microhabitats that define the distribution of each functional group, it will be possible to consider which microhabitats should be maintained or created within agricultural landscape. Combining remote sensing techniques such as LiDAR with bird distribution modeling would help identifying important microhabitat in agricultural landscapes.

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