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How much abandoned farmland is required to harbor comparable species richness and abundance of bird communities in wetland? Hierarchical community model suggests the importance of habitat structure and landscape context

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Abstract (242 words)

While wetlands have been converted into farmlands, large amounts of farmlands are now being abandoned, and this novel habitat is expected to be inhabited by species which depend on wetlands. Here we examined the effects of habitat and landscape variables on the densities of wetland bird species in abandoned farmlands. We surveyed birds in abandoned farmlands with varied patch area, habitat, and landscape variables in Kushiro district, eastern Hokkaido, northern Japan. We also surveyed birds in 15 ha of the remaining wetlands as a reference habitat. We used abundance-based hierarchical community model (HCM) to estimate patch-level estimates of abundance of each species based on sampling plots data that only partially covered the studied patches. We observed 14 wetland species and analyzed them with HCM. Abandoned farmland patch areas had significant positive effects on the densities of two species. Tree densities and shrub coverage exerted positive and negative effects on some species. Amounts of surrounding wetland/grassland had positive effects on many species. Ensemble of species-level models suggested that 24.7 ha and 10.6 ha of abandoned farmlands would be needed to harbor a comparable total abundance and species richness in 15-ha wetlands, respectively. These required amounts can be increased/decreased depending on the covariates. The use of HCM allows us to predict species- and community-level responses under varied conditions based on incomplete sampling data. A quantity of 1.6 times larger areas of abandoned farmlands may be required to restore wetland bird communities in eastern Hokkaido.

Keywords: hierarchical community model; incomplete spatial coverage; multispecies abundance model; pasture; patch area; wetland

1. Introduction

Wetlands are one of the endangered ecosystems that have been converted into agricultural and industrial areas (Finlayson and Spiers 1999). By reviewing 189 reports of the changes in wetland area, Davidson (2014) suggested that 87% of the world's wetlands may have been lost since 1700s, and that wetland conversion rate during the past 100 years can be 3.7 times faster than before. Japan has also been experiencing a great decrease of wetland areas. Large amounts of these areas which existed at the early 20th century (approximately 2,110 km^2) are now reduced to less than half (821 km^2), indicating that more than 60% of wetlands have been lost during the past 100 years in Japan (GSI 2000). This reduction caused the immense decrease of wetland species (ME 2005).

On the other hand, since 1800s, especially 1900s, farmlands have been abandoned over the world (Ramankutty and Foley 1999; Ellis et al. 2010). Farmland abandonment has ramifying effects on biodiversity. For example, in eastern North America, forest development at the abandoned farmlands caused the substantial decrease in early-successional species (Litvaitis 1993; Askins 2001). In Japan, abandoned farmland increased from 130,000 ha in the late 1980s to 400,000 ha in 2011 (MAFF 2011). They are likely to increase because of the decrease and aging of farmers in Japan. Although abandoned farmland can provide habitats for varied organisms, their values differ among regions (Queiroz et al. 2014), and are likely to depend on the prior farmland management (Cramer et al. 2008). We therefore expected that abandoned farmlands originally converted from wetlands may also serve as habitat for wetland species.

Studies in wetlands and grasslands show that bird species densities can change according to various factors, including vegetation composition, structure, patch area, and landscape structure (Wiens and Rotenberry 1981; Fairbairn and Dinsmore 2001; Davis 2004). It can be noted that species richness and abundance are known to show contrasted responses to the patch/habitat area: abundance may linearly increase with the area while species richness nonlinearly increases with the area (Connor and McCoy 1979; James and Wamer 1982; Connor et al. 2000; Yamaura et al. 2016a). These suggest that possible conservation values of abandoned farmlands would depend on the local habitat structure, surrounding landscape structure, farmland area, and conservation targets (in this study, species richness and abundance).

Here we examined the effects of environmental covariates (local habitat structure, habitat area, and landscape context) on densities of individual bird species using abundance-based hierarchical community models (HCMs: Yamaura et al. 2016a; 2016b). Using HCMs, we inferred the relationships between community-level properties (total abundance and species richness) and patch area based on incomplete sampling data (i.e., focal patches were only partially covered by the field survey). This is important since we cannot usually cover studied patches entirely by the field survey, and many species and individuals are expected to remain undetected during the survey (Cam et al. 2002). Nevertheless, individual patches are usually the management units in the habitat and landscape management

(Urban and Keitt 2001), and we therefore need to estimate patch-level and community-level properties based on the incomplete sampling data, which can be done by the recently developed HCMs (Yamaura et al. 2016a). We then considered the effects of habitat structure and landscape context on patch-level and community-level properties by including these environmental covariates into species-level models. We finally obtained required amounts of abandoned farmlands to harbor comparable bird species richness and abundance in the 15-ha wetlands under the varied environmental conditions.

2. Material and methods

2.1.Study area

Our study area was located in the Kushiro District, eastern Hokkaido, northern Japan (43°01-17’N, 144°08-34’E). The area is covered by forests, farmlands, and Kushiro wetland (the largest wetland in Japan). We defined abandoned farmland as former wetlands transformed into uncultivated farmlands. We treated abandoned farmland patches, with an edge-to-edge distance of 50 m, as a single patch, because 50-m gaps restrict bird movements (Matthysen et al. 1995; Desrochers and Hannon 1997).

Major plant species dominating the abandoned farmlands included common reed (*Phragmites australis*), reed canary grass (*Phalaris arundinacea*), *Carex* spp., and a dwarf tree species (*Spiraea salicifolia*). Abandoned farmlands can be surrounded by shelter-woods or forest remnants; we treated fens dominated by above-grass species and *Calamagrostis canadensis* without land-use histories as wetlands (reference habitat).

2.2.Bird survey

We identified abandoned farmlands through aerial photographs and preliminary field survey. Then, we created a land use map composed of forest, abandoned farmland, wetland, grassland, urban, open water, dwarf bamboo and other land uses, based on the vegetation map (scale: 1:25,000 and resolution: 25 m) provided by the Natural Conservation Bureau, Ministry of Environment (http://www.biodic.go.jp). We generated 300-m buffers from the edges of abandoned farmland patches, and measured the wetlands (including abandoned farmland) and grasslands proportions. We used this wetland/grassland proportion as a single landscape variable (landscape context) in this study (see below). Preliminary analysis showed that this landscape variable was the most strongly associated with bird abundance than variables with other habitat classifications and spatial scales. We then used 23 survey patches (mean ± SD: 42.4 ± 57.8 ha, range: 1.2–210.2 ha) controlling for the correlations among the patch area and the above mentioned landscape variable (Fig. 1). We also selected three reference sites in the Kushiro wetland. We conducted these procedures using ArcMap version 10.0 (ESRI Inc., Redlands, CA).

We surveyed birds in 23 abandoned farmland patches and three reference wetland sites during the morning period (4:00–10:00 a.m.) throughout June, 2014. All migratory wetland/grassland species arrived at the study area before the initiation of the survey. Every site was surveyed three times, and the bias of survey time was avoided by visiting each site in three different times: (i) 4:00–6:00, (ii) 6:00–8:00, and (iii) 8:00–10:00. We established the transect lines in the patches (100 m width) and recorded the observed individuals in the maps (territory mapping: Bibby et al. 2000). Locations of transect lines were determined to represent the vegetation types of the entire patches (Fig. 2). Sampling plots (transect length × 100 m width) covered the total area of patches < 2 ha; plot area was 2 ha for 2–20-ha patches, and 10% of 20–50-ha patches. We established 5-ha plots for patches >50 ha. The edge-to-edge distances of the plots were 500 m to make sampling plots independent from each other (Ralph et al. 1993).

The single surveyor (M.H.) and an attendant, who slowly walked through transects, recorded the species, sex, and location of individuals in the plots. Our focal species were considered as wetland species because: (i) their original habitats were previously lost because of the farmlands expansion, (ii) and current farmland abandonment can be an opportunity for their restoration. We classified wetland species according to published references (e.g., Takagawa et al. 2011), and drew the territories of individual species in map based on their known territory sizes (Nakamura et al. 1968; Higuchi et al. 1997) and field records (e.g., locations, aggressive behavior, and sex) via three visits (Bibby et al. 2000). The territories which had >0.5 areas in the plots were treated as one territories (see Appendix A for the detailed procedure); otherwise we assigned 0.5 (Bibby et al. 2000). We summed and rounded these quantities and obtained the number of territories (integer) within the sampling plots. Although bird individuals are only imperfectly detected by the single survey, open-land songbirds have relatively high detection probability (~ 0.6: Yamaura et al. 2016a). We considered that each individual inhabiting the sampling plots was detected in at least one of the survey visits.

2.3.Plant survey

We established the sampling points at every 10 m along the transect lines. We placed the measuring pole (2 m height) at each point and measured the maximum height at which the grass touched the pole as the vegetation height by 10 cm increments (cf. Rotenberry and Wiens 1980). But we did not use this data concerning the plant height in the analysis since our preliminary analysis suggested its weak association with bird abundance. We also counted the number of trees (>3 m height) and visually estimated the shrubs coverage (*Salicifolia* sp.) by 5% increments in the bird sampling plots.

2.4.Statistical analysis

We conducted the analyses according to what Yamaura et al. (2016b) developed for abundance-based HCMs. In this model, communities are treated as ensembles of models of individual species comprising communities. Patch-level species abundance and community-level properties (total abundance/species richness) are inferred by accounting for the incomplete spatial coverage of patches by the sampling plots. Specifically, we estimated the abundance of individual species in the entire patches as function of environmental covariates (including patch area) using the number of detected individuals and the proportion of spatial coverage by the sampling plots (see below for the formulations). We then inferred the relationships between community-level properties and patch area by considering the effects of covariates.

We first assumed that patch-level abundance of species i in patch j (z_{ij}) follows a Poisson distribution (z_{ij} ~ Poisson[λ_{ij}]). We then assumed that the expected abundance of species i at patch j (λ_{ij}) is a function of patch area (A_j: ha) and three covariates ($x_{2\text{-}4}$: tree density [/ha], shrub cover [%], and wetland/grassland proportion in the surroundings [%]):

$$\log(\lambda_{ij}) = \beta_{0i} + \beta_{1i} \times \log(A_j) + \beta_{2i} \times x_{2j} + \beta_{3i} \times x_{3j} + \beta_{4i} \times x_{4j} \qquad \text{eqn 1}$$

where $\beta_{0\mathrm{i}}$ is the logarithmically transformed expected abundance when area is 1 (λ_{ij} = exp[β_{0i}]). This model means that the expected abundance is a power function of the area with the exponent of β_{1i}: $\lambda_{ij} = \exp(\beta_{0i}) \times \left(A_j\right)^{\beta_{1i}}$ (Connor et al. 1997), and density is $\lambda_{ij}/A_j = \exp(\beta_{0i}) \times \left(A_j\right)^{(\beta_{1i}-1)}$. When β_{1i} is equal to 1, density is constant in relation to the patch area; $\beta_{1i} > 1$, indicates that population density increases with the area (density decreases when $\beta_{1i} < 1$). The other three coefficients (β_{2i}, β_{3i}, and β_{4i}) are the effects of covariates. Our preliminary analysis showed that these three covariates were the most important ones.

Our bird survey only partially covered the total area of most patches; we then assumed that detected individuals during the survey (y_{ij}: obtained from the territory mapping through three visits) depended on the plots coverage over the patches (ϕ_j):

$$y_{ij} \sim \text{Binomail}(z_{ij}, \phi_j). \qquad \text{eqn 2}$$

where ϕ_j was obtained by dividing the plot area by the patch area. This means that only 10% of individuals would be detected when 10% of the patch was covered by the plot. Species-level parameters $\boldsymbol{\beta}_i$ follow the community-level normal distribution with hyper-parameters, e.g., $\beta_{i0} \sim \text{Normal}\left(\mu_{\beta_0}, \sigma^2_{\beta_0}\right)$. This parameterization can allow us to model rare species by borrowing the information from common species (Kéry and Royle 2016).

Based on the median estimates of species-level parameters, we modeled the expected community-level (total) abundance as a function of patch area and covariates (i.e., summation of λ_{ij} across the species). We similarly modeled the expected species richness, which was defined as the number of species with at least one individual (i.e., $z_{ij} \geq 1$). We summed the probability of at least one individual occurs in the area (occupancy probability) across species (Yamaura et al. 2016a):

$$E\left[\text{species richness}_j\right] = \sum_{i=1}^{R}\left[1 - \exp\left(-\lambda_{ij}\right)\right] \qquad \text{eqn 3}$$

where R is the species pool size (number of species possibly occurring in the studied patches). We believe that all possible species were detected in the field survey (Hanioka and Senzaki, pers. observ.), and R was the number of detected wetland species (= 14). We derived the predicted responses of total abundance and species richness to patch area and covariates by changing the values of covariates in the species-level models (eqn 1). We standardized environmental covariates other than patch area before the analysis. We conducted the analysis using R version 3.1.2 (R Core Team 2015), JAGS version 3.4.0 (Plummer 2013), and R2jags version 0.5-7 (Su and Yajima 2013). We obtained the parameter estimates using Marcov Chain Monte Carlo (MCMC) with three chains, 50,000 burn-in, no-thinning, and 100,000 post iterations. We decided that chain convergence was achieved when the Gelman-Rubin statistic of species- and community-level parameters was < 1.1; otherwise, we ran additional 100,000 iterations until we achieved chain convergence using the 'autojags' function.

We finally determined the patch area harboring the comparable total abundance and species richness in 15-ha wetland under the varied values of covariates. We obtained the total abundance and species richness of wetland bird communities per 15 ha from the three 5-ha sampling plots in the wetland. We numerically searched for these values using the 'uniroot' R function.

3. Results

3.1.Bird survey

We observed 29 bird species during the survey; among them, 14 species were classified as wetland species and were therefore analyzed (Appendix B). Red-crowned crane (*Grus japonensis*) and mallard (*Anas platyrhynchos*) were excluded from the analyses because their territory sizes were very large compared with our plot area. For both of the abandoned farmlands and wetlands, black-browed reed warbler (*Acrocephalus bistrigiceps*) and Middendorff's grasshopper warbler (*Locustella ochotensis*) were the dominant species (Appendix C).

3.2.Species responses to environmental covariates

Only two species showed significant deviations from the constant densities in relation to patch area (Fig. 3b, Appendix D-E). Densities of two dominant species (black-browed reed warbler and Middendorff's grasshopper warbler) increased with the patch area increase. For tree density, three species showed positive responses (black-faced bunting *Emberiza spodocephala*, Siberian rubythroat *Luscinia calliope*, and lanceolated grasshopper warbler *Locustella lanceolata*) and one showed negative responses (Middendorff's grasshopper warbler) (Fig. 3c). Shrub cover significantly decreased two species (black-browed reed warbler and Middendorff's grasshopper warbler), while many other species showed marginally positive responses (Fig. 3d). For wetland/grassland proportion, two species (common reed bunting *Emberiza schoeniclus* and lanceolated grasshopper warbler), as well as the community-mean, showed positive responses (Fig. 3e).

3.3.Community responses to environmental covariates

Based on the species-level estimates, we obtained the predicted responses of total abundance and species richness to patch area and three environmental covariates. Effects of tree density and shrub coverage on total abundance was concave (Fig. 4a, b), meaning that total abundance was minimized at the intermediate values of tree density and shrub coverage. There were species that showed both positive and negative responses to these two covariates, and such species increased the dominance and total abundance at the marginal values of the covariates. On the other hand, no species showed negative responses to the wetland/grassland proportion, and total abundance monotonically increased with wetland/grassland proportion increase (Fig. 4c).

Species richness greatly increased in areas below 40 ha (Fig. 4d–f). Occupancy (or incidence) probabilities of rare species (e.g., Latham's snipe) were sensitive to the area, and contributed to the increasing species richness in relation to the area. In contrast to the total abundance, tree density hardly affected species richness, and shrub coverage increased species richness (Fig. 4d, e). This occurred because rare species densities can be insensitive and sensitive to tree density and shrub coverage, respectively. Wetland/grassland proportion increased not only total abundance but also species richness (Fig. 4f).

3.4.Comparison to wetland communities

Under the mean values of covariates, 24.7 ha of abandoned farmlands were required to harbor 244 bird individuals of 15-ha wetlands. For all the three covariates, their specific values can decrease the required amounts to ~ 20 ha (Fig. 5a–c). An area of 10.6 ha of abandoned farmlands with average covariates was required to harbor 10 species of 15-ha wetlands (Fig. 5d-f); it was suggested that covariates would also affect the required amount of abandoned farmlands.

4. Discussion

4.1.Species responses to environmental covariates

Only two dominant species (black-browed reed warbler and Middendorff's grasshopper warbler) showed significant deviation of constant densities in relation to patch area. This indicates that the dominance of these species increased with the increase of abandoned farmland patch areas. These positive effects of patch area on population densities were also reported in other grassland and forest habitats (e.g., Davis 2004; Yamaura et al. 2008b). It is suggested that large abandoned farmland patches would have higher conservation values per area and highly contribute to regional abundance and population persistence for at least these wetland species compared with small abandoned farmland patches (sensu Connor et al. 2000).

Effects of tree densities and shrub coverage varied among species. There were species showing positive and negative responses, while densities of other species were insensitive to these covariates. Species with positive responses (particularly black-faced bunting and Siberian rubythroat) inhabit not only wetlands but also forest edges and/or shrub-lands (Toyoshima et al. 2013; Yamaura et al. 2016a). They use trees and shrubs in abandoned farmlands as song posts (Hanioka and Senzaki, pers. observ.). On the other hand, species showing negative responses to tree density and shrub cover are wetland or grassland specialists (e.g., black-browed reed warbler and Middendorff's grasshopper warbler), which is also consistent with previous evidence that tree or shrub development decrease the densities of grassland species (Grant et al. 2004; Sirami et al. 2009). Succession of abandoned farmlands would lead to the succession of the bird communities, specifically, decreased abundance in these wetland/grassland specialist species.

The existence of wetland/grassland in the surroundings increased the densities of many species, which was also shown by other studies (Fairbairn and Dinsmore 2001). These surrounding habitats would supplement the food resources and allow wetland birds to occupy the abandoned farmlands (cf. Dunning et al. 1992). It was noted that none of the species showed negative responses to this covariate, suggesting the general importance of habitat availability to the wetland bird conservation in abandoned farmlands. As Crouzeilles and Curran (2016) suggested concerning forest restoration, improvement of local habitat quality, such as tree removal (e.g., Thompson et al. 2016), would yield great returns (increases in abundance of wetland species) on the locations with abundant habitats in the surroundings (i.e., not surrounded by forests or urban areas).

4.2.Community responses to environmental covariates

Since our model treats communities as ensembles of species-level models, it can provide the mechanistic understanding how communities are organized by the species-level underlying processes. Effects of tree densities and shrub coverage on the community-level total abundance were concave. Responses to these covariates were species-specific; different species dominated the community and increased the total abundance depending on the values of covariates. At the intermediate values of covariates, communities had the lowest total abundance, but the total abundance was equally distributed among the species (i.e., high evenness). In other words, even if the total abundance was similar, communities with high and low values of these covariates had quite different community structures.

In contrast to the total abundance, species richness greatly depends on the abundance of rare species rather than common species. This is because species richness was treated as the summation of occupancy probabilities (probability that at least one individual occurs) across the species (eqn 3). Occupancy probabilities of common species quickly reached nearly 1 within the small range of the patch area, and what is important is those of rare species (see also Yamaura et al. 2016a). Therefore, it can be said that changes in species richness along with the covariates, including patch area, depend on the effects of covariates on rare species abundance. HCMs can deal with rare species by borrowing the strength of common species, and this is the advantage of our approach to model species richness. Our simultaneous modeling of species richness and total abundance also showed that they differently responded to tree density and shrub cover (Fig. 4).

The roles of habitat and landscape variables for species occupancy, abundance, and species richness have been actively examined during the past 20 years (Mazerolle and Villard

1999; Yamaura et al. 2008a; Ruffell and Didham 2016). Studies surveyed organisms within the sampling plots with equal areas, and examined the effects of environmental covariates on the plot-level (per area) abundance or species richness. On the other hand, although habitat (patch) area is long known to play a crucial role in determining abundance and species richness (Connor and McCoy 1979; Triantis et al. 2012), the role of patch area on patch-level species richness/total abundance has not been actively compared with those of other habitat and landscape variables. Williams et al. (2009) analyzed the number of plant species in the British islands, and showed the importance of considering covariates (e.g., latitude, elevation) as well as area to model species richness. Combined analysis of the habitat/patch area, habitat- and landscape variables can provide an important basis of conservation recommendations (Huth and Possingham 2011). Our modeling framework provides one approach to this issue by modeling abundance of individual species comprising communities. However, our approach entails model complexity and detailed data, i.e., we need the information about how sampling plots cover the area of interest, and abundance of individual species in the plots (Taki et al. in press).

4.3.Comparison with wetland communities

Our results suggested that habitat and landscape variable have important roles in the conservation problems. For example, to harbor comparable total abundance of wetland species in 15-ha wetlands, increasing habitat quality would lower the required amounts of abandoned farmlands from 25 ha to 20 ha. Although < 10 ha of abandoned farmlands are likely to harbor comparable species richness in 15-ha wetlands; this would be because the existence of trees and shrubs increases densities of species that prefer these habitat structures. However, wetland specialists (e.g., black-browed reed warbler and Middendorff's grasshopper warbler) had lower densities in the abandoned farmlands (Appendix C), suggesting that wetlands have irreplaceable conservation values for them, and cannot be completely substituted by the abandoned farmlands.

4.4.Conclusion

Results of our field survey and the analysis showed that abandoned farmland originally converted from wetlands can serve as habitats for wetland bird species. This habitat provision function depends on the local habitat structure, patch area of abandoned farmland, and landscape context. Our model provides the framework to evaluate the relative effects of these relevant factors based on the empirical data accounting for the sampling incompleteness. Of course, abandoned farmland cannot completely substitute the wetland, and larger areas would be required to harbor comparable birds in wetlands. Nevertheless, ongoing farmland abandonment in the world can be an opportunity to restore and conserve declining wetland biodiversity.

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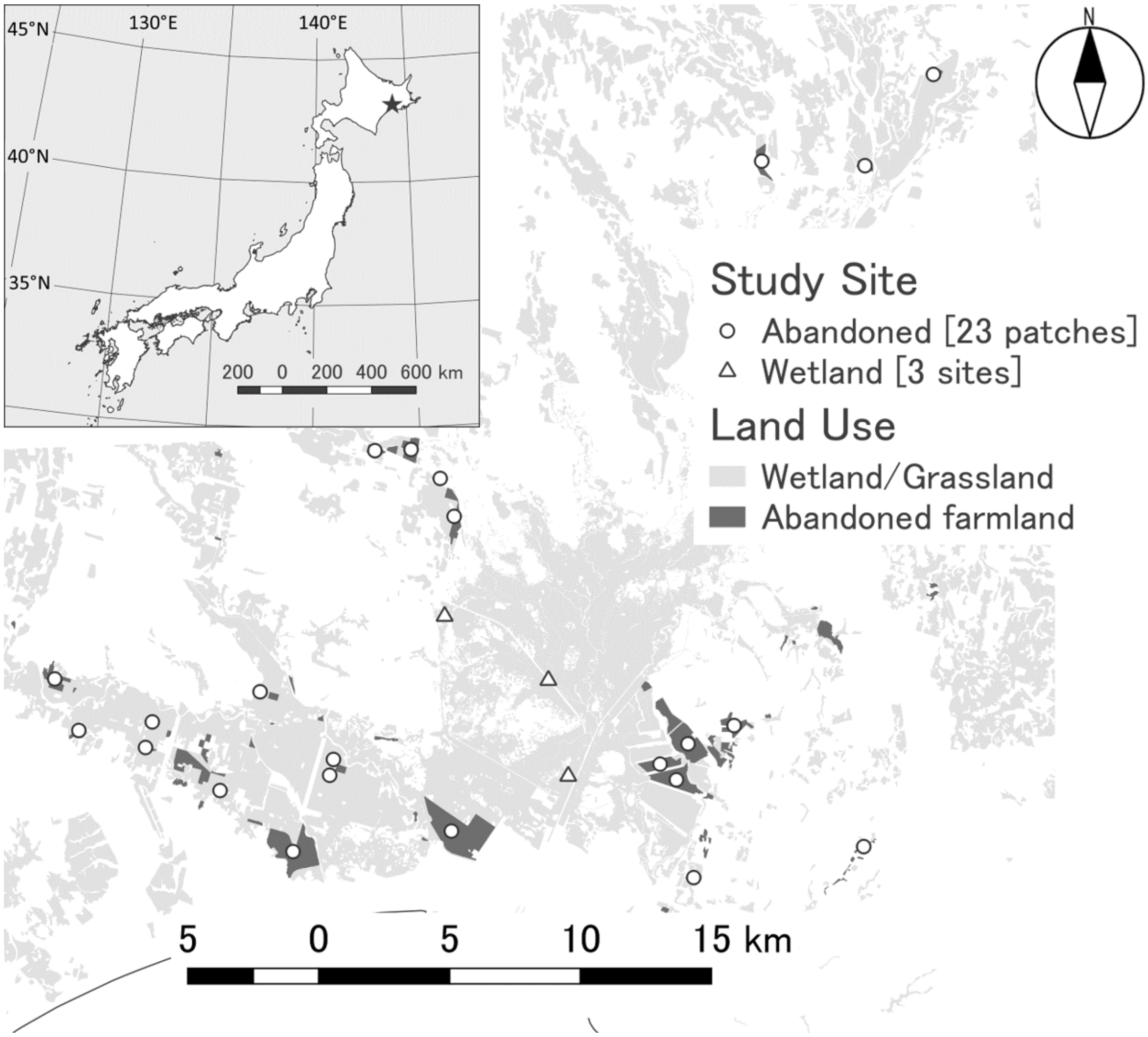

Fig. 1. Study area.

We established sampling plots in 23 abandoned farmland patches and three wetland sites. White area indicates land-uses other than wetland/grassland and abandoned farmland, e.g., forests, urban, and open waters.

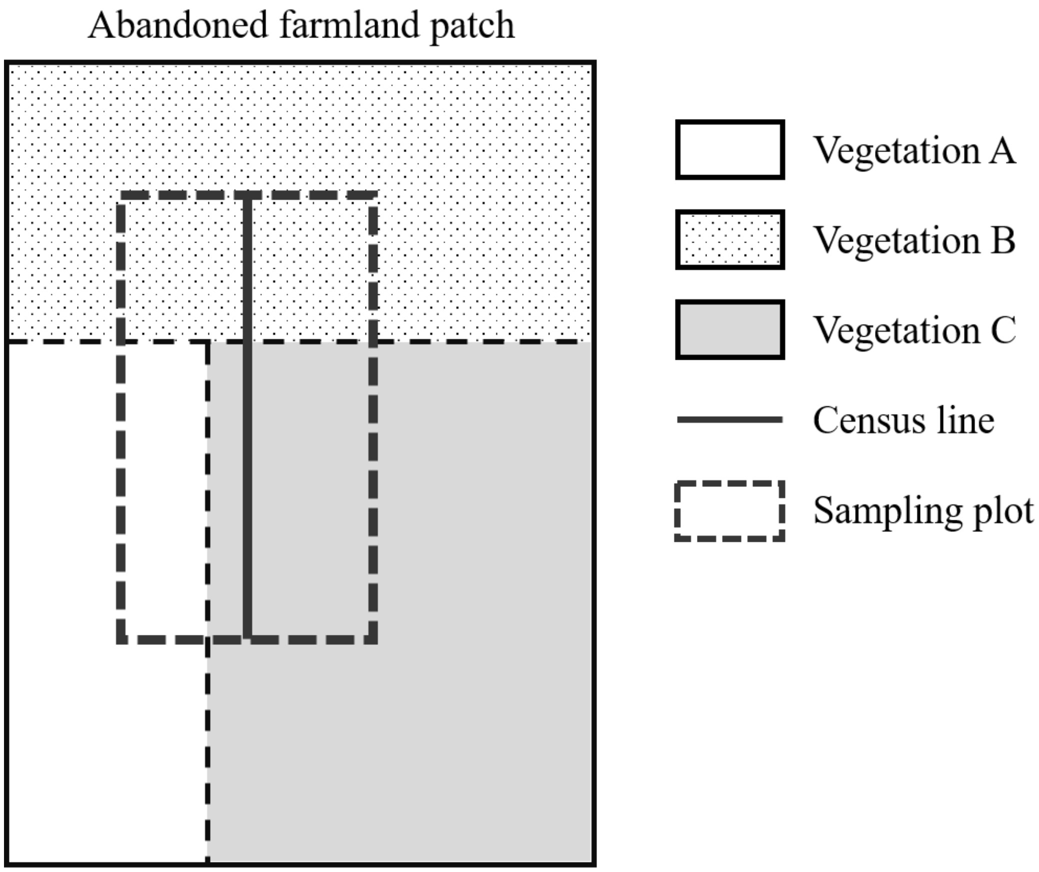

Fig. 2. Schematic illustration of establishment of bird sampling plots.

We first examined the distributions of dominant vegetation types in the studied patches, and established the rectangular plots (100-m width × length) to represent the vegetation types. Plant survey was conducted along the center lines of the bird sampling plots (i.e., transect lines: see main text).

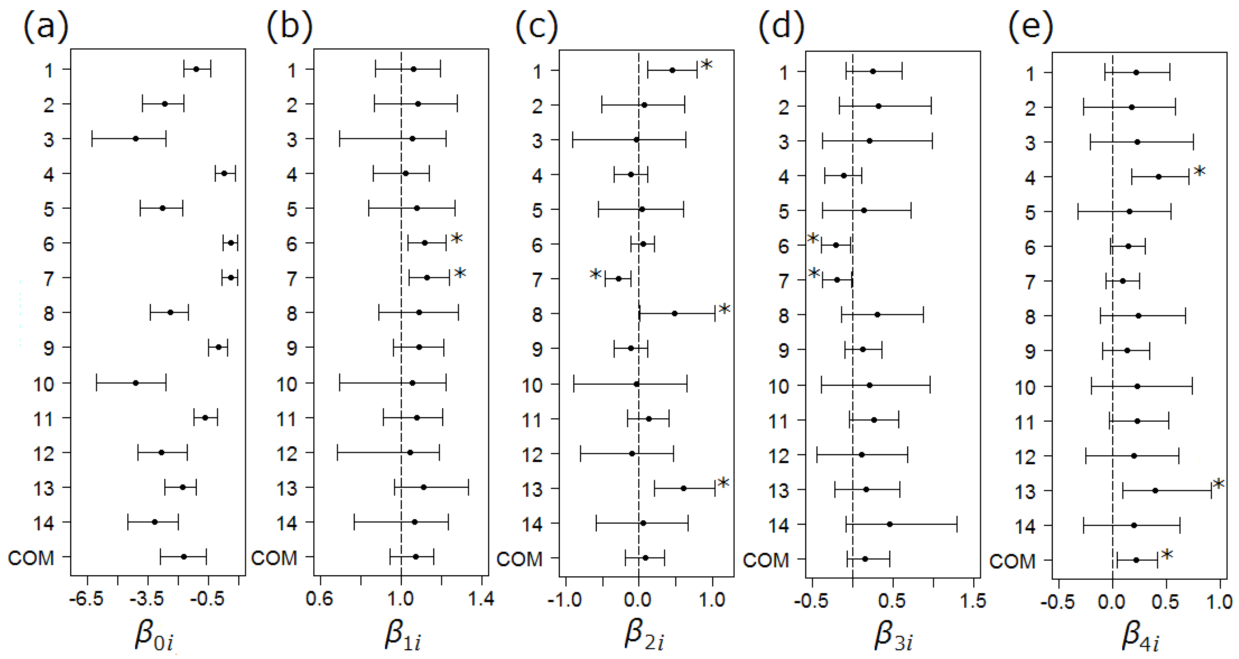

Fig. 3. Parameter estimates of individual species and communities.

Median estimates and 95% credible intervals are shown. Dots indicate median values, and bars indicate intervals between 95% lower and upper limits. Species ID are shown in Appendix B, and COM indicates community-level hyper parameters (community-means). For $\beta_{1\text{-}4}$, statistical significance at 5% level is indicated by *. (a) $\beta_{0\mathrm{i}}$ was logarithmically transformed when expected abundance when area was 1 ha. (b) Effect of patch area. (c–e) β_{2i}, β_{3i}, and β_{4i} are the effects of tree density [/ha], shrub cover [%], and wetland/grassland proportion in the surroundings [%], respectively.

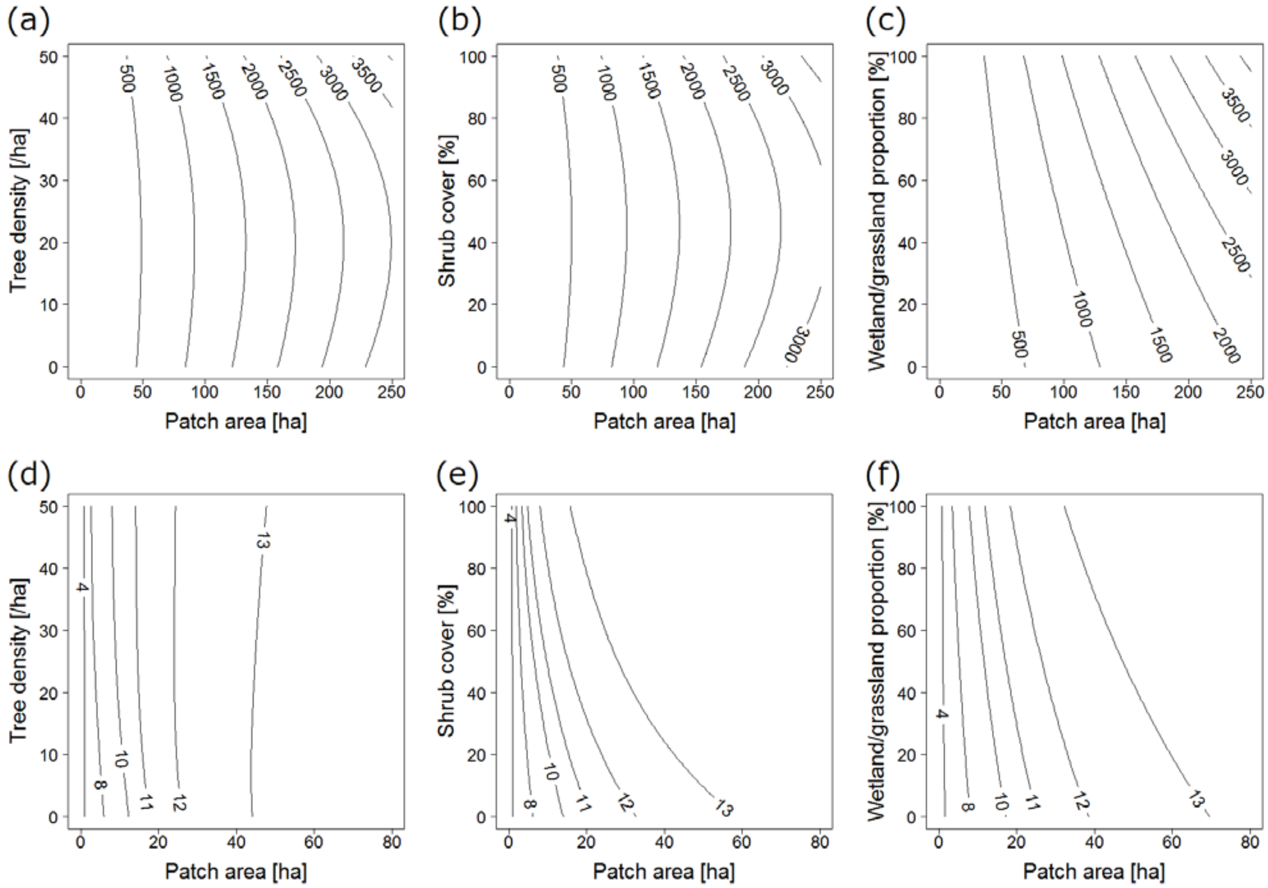

Fig. 4. Total abundance and species richness as function of patch areas and covariates. Vertical axes indicate (a, d) tree density [/ha], (b, e) shrub cover [%], and (c, f) wetland/grassland proportion in the surroundings [%]. Solid lines indicate estimates of (a–c) abundance and (d–f) species richness. In each figure, the other covariates are fixed to mean values.

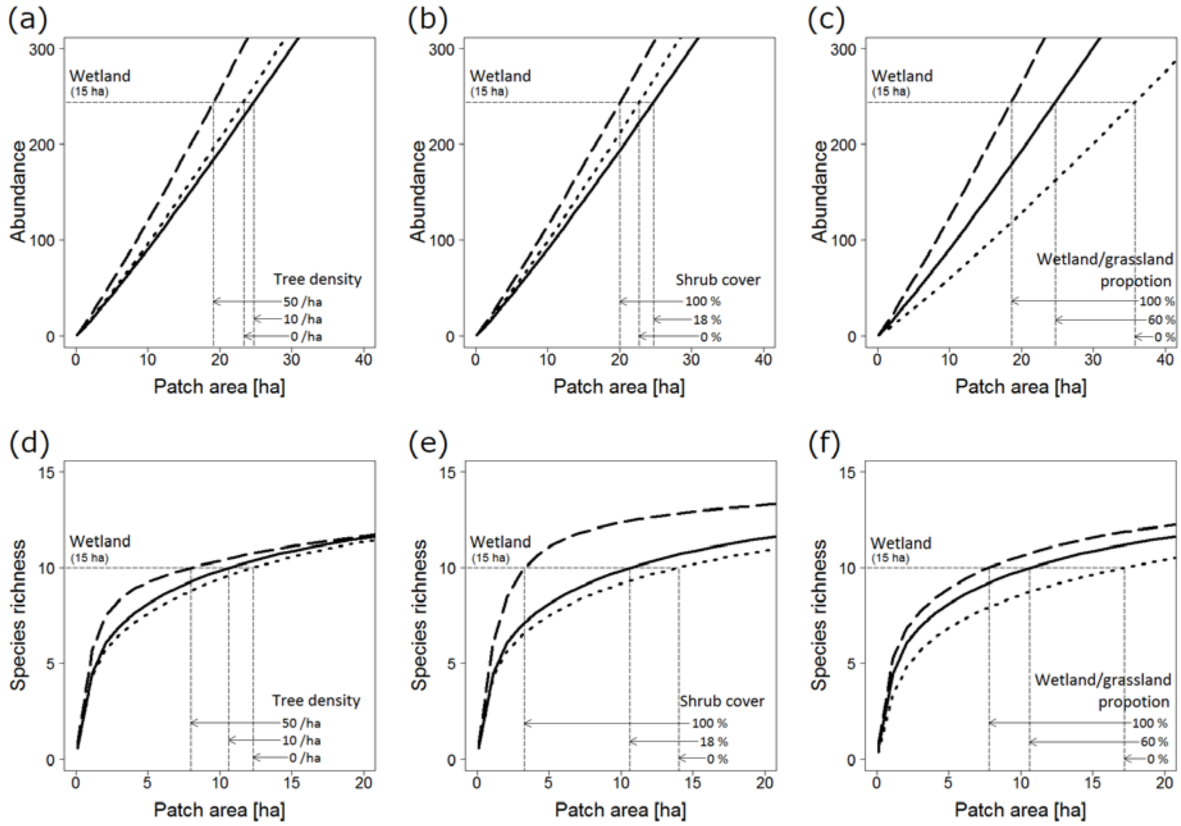

Fig. 5. Abundance-area and species-area relationships in relation to wetland communities in 15-ha wetlands.

Horizontal broken lines indicate total abundance of wetland communities in 15-ha wetlands.

(a–c) Abundance-area relationships. (d–f) Species-area relationships. In each figure, three curves indicate the cases in the covariates for minimum (dotted), mean (solid), and maximum (broken) values of (a, d) tree densities, (b, e) shrub cover, and (c, f) wetland/grassland proportions in the surroundings. In each figure, the other covariates are fixed to mean values.