



Title	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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1 How much abandoned farmland is required to harbor comparable species richness and
2 abundance of bird communities in wetland? Hierarchical community model suggests the
3 importance of habitat structure and landscape context

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27 While wetlands have been converted into farmlands, large amounts of farmlands are now
28 being abandoned, and this novel habitat is expected to be inhabited by species which depend
29 on wetlands. Here we examined the effects of habitat and landscape variables on the densities
30 of wetland bird species in abandoned farmlands. We surveyed birds in abandoned farmlands
31 with varied patch area, habitat, and landscape variables in Kushiro district, eastern Hokkaido,
32 northern Japan. We also surveyed birds in 15 ha of the remaining wetlands as a reference
33 habitat. We used abundance-based hierarchical community model (HCM) to estimate
34 patch-level estimates of abundance of each species based on sampling plots data that only
35 partially covered the studied patches. We observed 14 wetland species and analyzed them
36 with HCM. Abandoned farmland patch areas had significant positive effects on the densities
37 of two species. Tree densities and shrub coverage exerted positive and negative effects on
38 some species. Amounts of surrounding wetland/grassland had positive effects on many
39 species. Ensemble of species-level models suggested that 24.7 ha and 10.6 ha of abandoned
40 farmlands would be needed to harbor a comparable total abundance and species richness in
41 15-ha wetlands, respectively. These required amounts can be increased/decreased depending
42 on the covariates. The use of HCM allows us to predict species- and community-level
43 responses under varied conditions based on incomplete sampling data. A quantity of 1.6 times
44 larger areas of abandoned farmlands may be required to restore wetland bird communities in
45 eastern Hokkaido.

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47 Keywords: hierarchical community model; incomplete spatial coverage; multispecies

48 abundance model; pasture; patch area; wetland

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1. Introduction

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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 km²) are now reduced to less than half (821 km²), 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).

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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

70 wetland species.

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

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

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

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2. Material and methods

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2.1. Study area

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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).

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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

110 or forest remnants; we treated fens dominated by above-grass species and *Calamagrostis*
111 *canadensis* without land-use histories as wetlands (reference habitat).

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113 2.2. Bird survey

114 We identified abandoned farmlands through aerial photographs and preliminary field
115 survey. Then, we created a land use map composed of forest, abandoned farmland, wetland,
116 grassland, urban, open water, dwarf bamboo and other land uses, based on the vegetation map
117 (scale: 1:25,000 and resolution: 25 m) provided by the Natural Conservation Bureau, Ministry
118 of Environment (<http://www.biodic.go.jp>). We generated 300-m buffers from the edges of
119 abandoned farmland patches, and measured the wetlands (including abandoned farmland) and
120 grasslands proportions. We used this wetland/grassland proportion as a single landscape
121 variable (landscape context) in this study (see below). Preliminary analysis showed that this
122 landscape variable was the most strongly associated with bird abundance than variables with
123 other habitat classifications and spatial scales. We then used 23 survey patches (mean \pm SD:
124 42.4 ± 57.8 ha, range: 1.2–210.2 ha) controlling for the correlations among the patch area and
125 the above mentioned landscape variable (Fig. 1). We also selected three reference sites in the
126 Kushiro wetland. We conducted these procedures using ArcMap version 10.0 (ESRI Inc.,
127 Redlands, CA).

128 We surveyed birds in 23 abandoned farmland patches and three reference wetland
129 sites during the morning period (4:00–10:00 a.m.) throughout June, 2014. All migratory

130 wetland/grassland species arrived at the study area before the initiation of the survey. Every
131 site was surveyed three times, and the bias of survey time was avoided by visiting each site in
132 three different times: (i) 4:00–6:00, (ii) 6:00–8:00, and (iii) 8:00–10:00. We established the
133 transect lines in the patches (100 m width) and recorded the observed individuals in the maps
134 (territory mapping: Bibby et al. 2000). Locations of transect lines were determined to
135 represent the vegetation types of the entire patches (Fig. 2). Sampling plots (transect length \times
136 100 m width) covered the total area of patches < 2 ha; plot area was 2 ha for 2–20-ha patches,
137 and 10% of 20–50-ha patches. We established 5-ha plots for patches >50 ha. The edge-to-edge
138 distances of the plots were 500 m to make sampling plots independent from each other (Ralph
139 et al. 1993).

140 The single surveyor (M.H.) and an attendant, who slowly walked through transects,
141 recorded the species, sex, and location of individuals in the plots. Our focal species were
142 considered as wetland species because: (i) their original habitats were previously lost because
143 of the farmlands expansion, (ii) and current farmland abandonment can be an opportunity for
144 their restoration. We classified wetland species according to published references (e.g.,
145 Takagawa et al. 2011), and drew the territories of individual species in map based on their
146 known territory sizes (Nakamura et al. 1968; Higuchi et al. 1997) and field records (e.g.,
147 locations, aggressive behavior, and sex) via three visits (Bibby et al. 2000). The territories
148 which had >0.5 areas in the plots were treated as one territories (see Appendix A for the
149 detailed procedure); otherwise we assigned 0.5 (Bibby et al. 2000). We summed and rounded

150 these quantities and obtained the number of territories (integer) within the sampling plots.
151 Although bird individuals are only imperfectly detected by the single survey, open-land
152 songbirds have relatively high detection probability (~ 0.6: Yamaura et al. 2016a). We
153 considered that each individual inhabiting the sampling plots was detected in at least one of
154 the survey visits.

155

156 2.3.Plant survey

157 We established the sampling points at every 10 m along the transect lines. We placed
158 the measuring pole (2 m height) at each point and measured the maximum height at which the
159 grass touched the pole as the vegetation height by 10 cm increments (cf. Rotenberry and
160 Wiens 1980). But we did not use this data concerning the plant height in the analysis since our
161 preliminary analysis suggested its weak association with bird abundance. We also counted the
162 number of trees (>3 m height) and visually estimated the shrubs coverage (*Salicifolia* sp.) by
163 5% increments in the bird sampling plots.

164

165 2.4.Statistical analysis

166 We conducted the analyses according to what Yamaura et al. (2016b) developed for
167 abundance-based HCMs. In this model, communities are treated as ensembles of models of
168 individual species comprising communities. Patch-level species abundance and
169 community-level properties (total abundance/species richness) are inferred by accounting for

170 the incomplete spatial coverage of patches by the sampling plots. Specifically, we estimated
171 the abundance of individual species in the entire patches as function of environmental
172 covariates (including patch area) using the number of detected individuals and the proportion
173 of spatial coverage by the sampling plots (see below for the formulations). We then inferred
174 the relationships between community-level properties and patch area by considering the
175 effects of covariates.

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

$$180 \quad \log(\lambda_{ij}) = \beta_{0i} + \beta_{1i} \times \log(A_j) + \beta_{2i} \times x_{2j} + \beta_{3i} \times x_{3j} + \beta_{4i} \times x_{4j} \quad \text{eqn 1}$$

181 where β_{0i} is the logarithmically transformed expected abundance when area is 1 ($\lambda_{ij} =$
182 $\exp[\beta_{0i}]$). This model means that the expected abundance is a power function of the area with
183 the exponent of β_{1i} : $\lambda_{ij} = \exp(\beta_{0i}) \times (A_j)^{\beta_{1i}}$ (Connor et al. 1997), and density is
184 $\lambda_{ij}/A_j = \exp(\beta_{0i}) \times (A_j)^{(\beta_{1i}-1)}$. When β_{1i} is equal to 1, density is constant in relation to the
185 patch area; $\beta_{1i} > 1$, indicates that population density increases with the area (density decreases
186 when $\beta_{1i} < 1$). The other three coefficients (β_{2i} , β_{3i} , and β_{4i}) are the effects of covariates. Our
187 preliminary analysis showed that these three covariates were the most important ones.

188 Our bird survey only partially covered the total area of most patches; we then
189 assumed that detected individuals during the survey (y_{ij} : obtained from the territory mapping

190 through three visits) depended on the plots coverage over the patches (ϕ_j):

$$191 \quad y_{ij} \sim \text{Binomial}(z_{ij}, \phi_j). \quad \text{eqn 2}$$

192 where ϕ_j was obtained by dividing the plot area by the patch area. This means that only 10%
193 of individuals would be detected when 10% of the patch was covered by the plot.

194 Species-level parameters β_i follow the community-level normal distribution with
195 hyper-parameters, e.g., $\beta_{i0} \sim \text{Normal}(\mu_{\beta_0}, \sigma_{\beta_0}^2)$. This parameterization can allow us to model
196 rare species by borrowing the information from common species (Kéry and Royle 2016).

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

$$203 \quad E[\text{species richness}_j] = \sum_{i=1}^R [1 - \exp(-\lambda_{ij})] \quad \text{eqn 3}$$

204 where R is the species pool size (number of species possibly occurring in the studied patches).

205 We believe that all possible species were detected in the field survey (Hanioka and Senzaki,
206 pers. observ.), and R was the number of detected wetland species (= 14). We derived the
207 predicted responses of total abundance and species richness to patch area and covariates by
208 changing the values of covariates in the species-level models (eqn 1). We standardized
209 environmental covariates other than patch area before the analysis. We conducted the analysis

210 using R version 3.1.2 (R Core Team 2015), JAGS version 3.4.0 (Plummer 2013), and R2jags
211 version 0.5-7 (Su and Yajima 2013). We obtained the parameter estimates using Markov
212 Chain Monte Carlo (MCMC) with three chains, 50,000 burn-in, no-thinning, and 100,000
213 post iterations. We decided that chain convergence was achieved when the Gelman-Rubin
214 statistic of species- and community-level parameters was < 1.1 ; otherwise, we ran additional
215 100,000 iterations until we achieved chain convergence using the ‘autojags’ function.

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

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3. Results

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3.1. Bird survey

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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*)

230 and Middendorff's grasshopper warbler (*Locustella ochotensis*) were the dominant species
231 (Appendix C).

232

233 3.2. Species responses to environmental covariates

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

245

246 3.3. Community responses to environmental covariates

247 Based on the species-level estimates, we obtained the predicted responses of total
248 abundance and species richness to patch area and three environmental covariates. Effects of
249 tree density and shrub coverage on total abundance was concave (Fig. 4a, b), meaning that

250 total abundance was minimized at the intermediate values of tree density and shrub coverage.
251 There were species that showed both positive and negative responses to these two covariates,
252 and such species increased the dominance and total abundance at the marginal values of the
253 covariates. On the other hand, no species showed negative responses to the wetland/grassland
254 proportion, and total abundance monotonically increased with wetland/grassland proportion
255 increase (Fig. 4c).

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

263

264 3.4. Comparison to wetland communities

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

270 abandoned farmlands.

271

272

273 4. Discussion

274 4.1. Species responses to environmental covariates

275 Only two dominant species (black-browed reed warbler and Middendorff's
276 grasshopper warbler) showed significant deviation of constant densities in relation to patch
277 area. This indicates that the dominance of these species increased with the increase of
278 abandoned farmland patch areas. These positive effects of patch area on population densities
279 were also reported in other grassland and forest habitats (e.g., Davis 2004; Yamaura et al.
280 2008b). It is suggested that large abandoned farmland patches would have higher conservation
281 values per area and highly contribute to regional abundance and population persistence for at
282 least these wetland species compared with small abandoned farmland patches (sensu Connor
283 et al. 2000).

284 Effects of tree densities and shrub coverage varied among species. There were
285 species showing positive and negative responses, while densities of other species were
286 insensitive to these covariates. Species with positive responses (particularly black-faced
287 bunting and Siberian rubythroat) inhabit not only wetlands but also forest edges and/or
288 shrub-lands (Toyoshima et al. 2013; Yamaura et al. 2016a). They use trees and shrubs in
289 abandoned farmlands as song posts (Hanioka and Senzaki, pers. observ.). On the other hand,

290 species showing negative responses to tree density and shrub cover are wetland or grassland
291 specialists (e.g., black-browed reed warbler and Middendorff's grasshopper warbler), which is
292 also consistent with previous evidence that tree or shrub development decrease the densities
293 of grassland species (Grant et al. 2004; Sirami et al. 2009). Succession of abandoned
294 farmlands would lead to the succession of the bird communities, specifically, decreased
295 abundance in these wetland/grassland specialist species.

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

306

307 4.2. Community responses to environmental covariates

308 Since our model treats communities as ensembles of species-level models, it can
309 provide the mechanistic understanding how communities are organized by the species-level

310 underlying processes. Effects of tree densities and shrub coverage on the community-level
311 total abundance were concave. Responses to these covariates were species-specific; different
312 species dominated the community and increased the total abundance depending on the values
313 of covariates. At the intermediate values of covariates, communities had the lowest total
314 abundance, but the total abundance was equally distributed among the species (i.e., high
315 evenness). In other words, even if the total abundance was similar, communities with high and
316 low values of these covariates had quite different community structures.

317 In contrast to the total abundance, species richness greatly depends on the abundance
318 of rare species rather than common species. This is because species richness was treated as
319 the summation of occupancy probabilities (probability that at least one individual occurs)
320 across the species (eqn 3). Occupancy probabilities of common species quickly reached nearly
321 1 within the small range of the patch area, and what is important is those of rare species (see
322 also Yamaura et al. 2016a). Therefore, it can be said that changes in species richness along
323 with the covariates, including patch area, depend on the effects of covariates on rare species
324 abundance. HCMs can deal with rare species by borrowing the strength of common species,
325 and this is the advantage of our approach to model species richness. Our simultaneous
326 modeling of species richness and total abundance also showed that they differently responded
327 to tree density and shrub cover (Fig. 4).

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

330 1999; Yamaura et al. 2008a; Ruffell and Didham 2016). Studies surveyed organisms within
331 the sampling plots with equal areas, and examined the effects of environmental covariates on
332 the plot-level (per area) abundance or species richness. On the other hand, although habitat
333 (patch) area is long known to play a crucial role in determining abundance and species
334 richness (Connor and McCoy 1979; Triantis et al. 2012), the role of patch area on patch-level
335 species richness/total abundance has not been actively compared with those of other habitat
336 and landscape variables. Williams et al. (2009) analyzed the number of plant species in the
337 British islands, and showed the importance of considering covariates (e.g., latitude, elevation)
338 as well as area to model species richness. Combined analysis of the habitat/patch area,
339 habitat- and landscape variables can provide an important basis of conservation
340 recommendations (Huth and Possingham 2011). Our modeling framework provides one
341 approach to this issue by modeling abundance of individual species comprising communities.
342 However, our approach entails model complexity and detailed data, i.e., we need the
343 information about how sampling plots cover the area of interest, and abundance of individual
344 species in the plots (Taki et al. in press).

345

346 4.3. Comparison with wetland communities

347 Our results suggested that habitat and landscape variable have important roles in the
348 conservation problems. For example, to harbor comparable total abundance of wetland
349 species in 15-ha wetlands, increasing habitat quality would lower the required amounts of

350 abandoned farmlands from 25 ha to 20 ha. Although < 10 ha of abandoned farmlands are
351 likely to harbor comparable species richness in 15-ha wetlands; this would be because the
352 existence of trees and shrubs increases densities of species that prefer these habitat structures.
353 However, wetland specialists (e.g., black-browed reed warbler and Middendorff's grasshopper
354 warbler) had lower densities in the abandoned farmlands (Appendix C), suggesting that
355 wetlands have irreplaceable conservation values for them, and cannot be completely
356 substituted by the abandoned farmlands.

357

358 4.4.Conclusion

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

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369

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377

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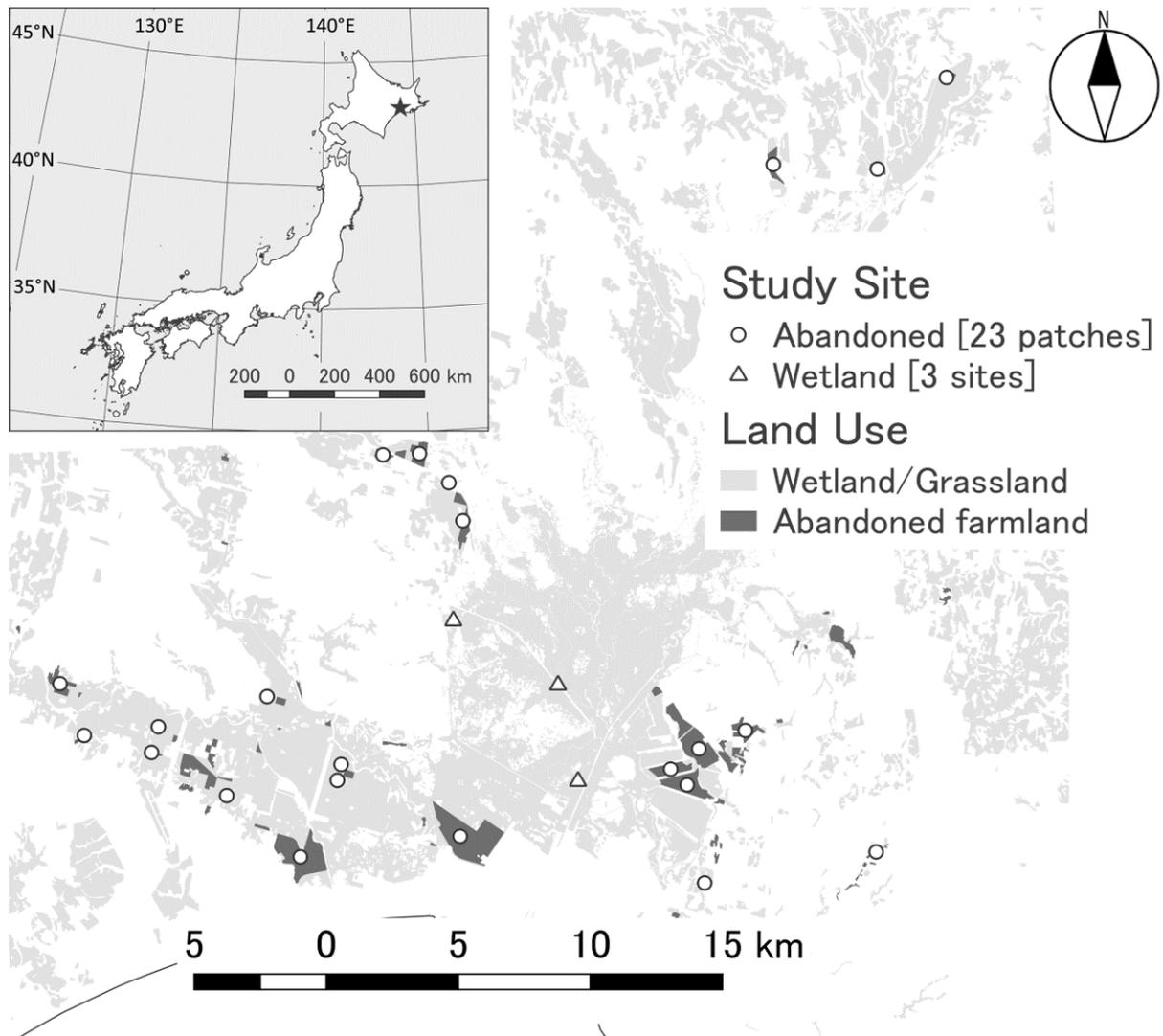
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490 Fig. 1. Study area.

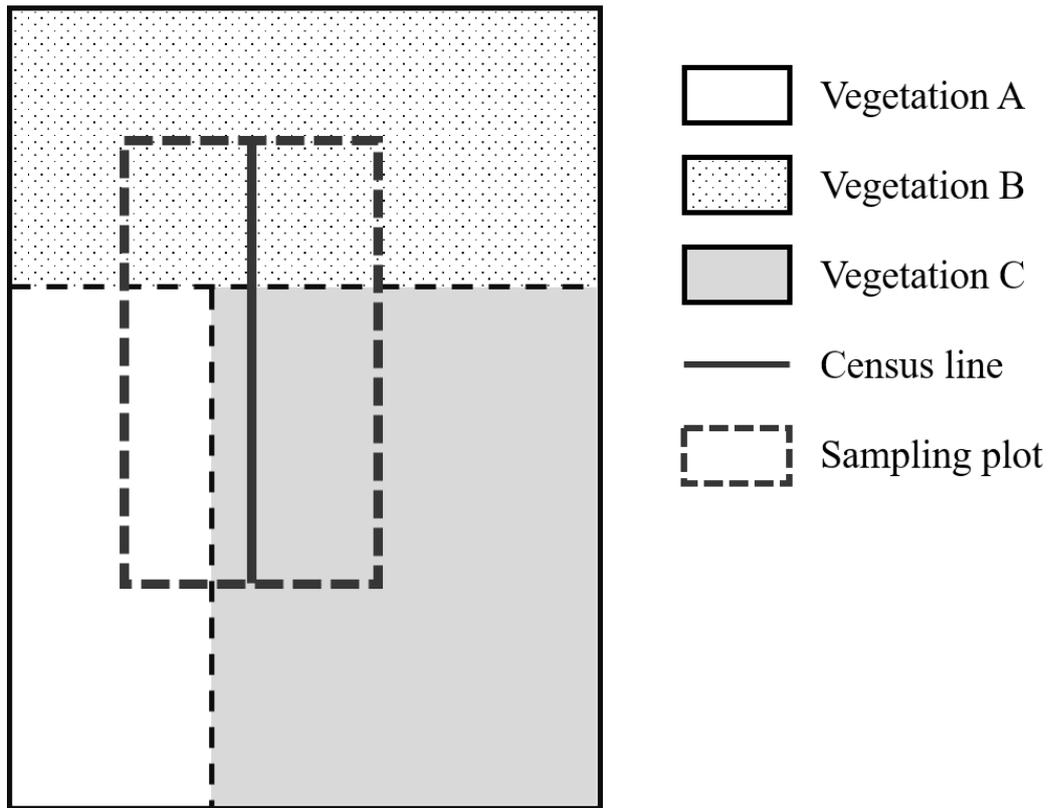
491 We established sampling plots in 23 abandoned farmland patches and three wetland sites.

492 White area indicates land-uses other than wetland/grassland and abandoned farmland, e.g.,

493 forests, urban, and open waters.

494

Abandoned farmland patch



495

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

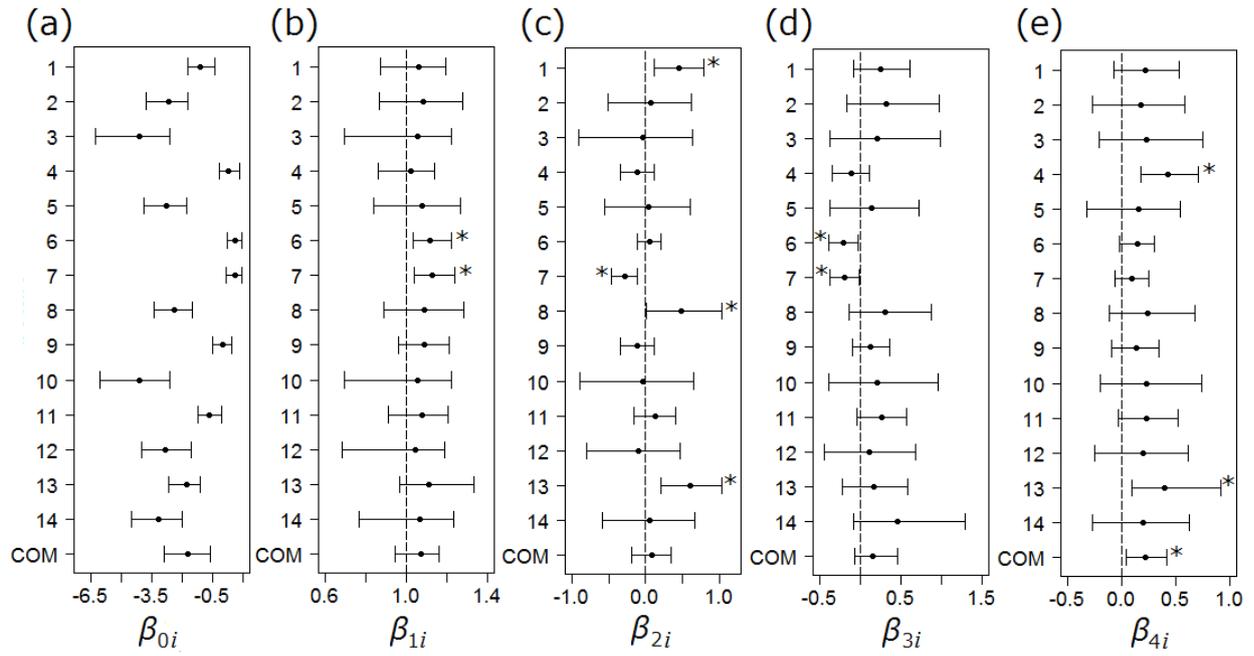
497 We first examined the distributions of dominant vegetation types in the studied patches, and

498 established the rectangular plots (100-m width \times length) to represent the vegetation types.

499 Plant survey was conducted along the center lines of the bird sampling plots (i.e., transect

500 lines: see main text).

501



502

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

504 Median estimates and 95% credible intervals are shown. Dots indicate median values, and

505 bars indicate intervals between 95% lower and upper limits. Species ID are shown in

506 Appendix B, and COM indicates community-level hyper parameters (community-means). For

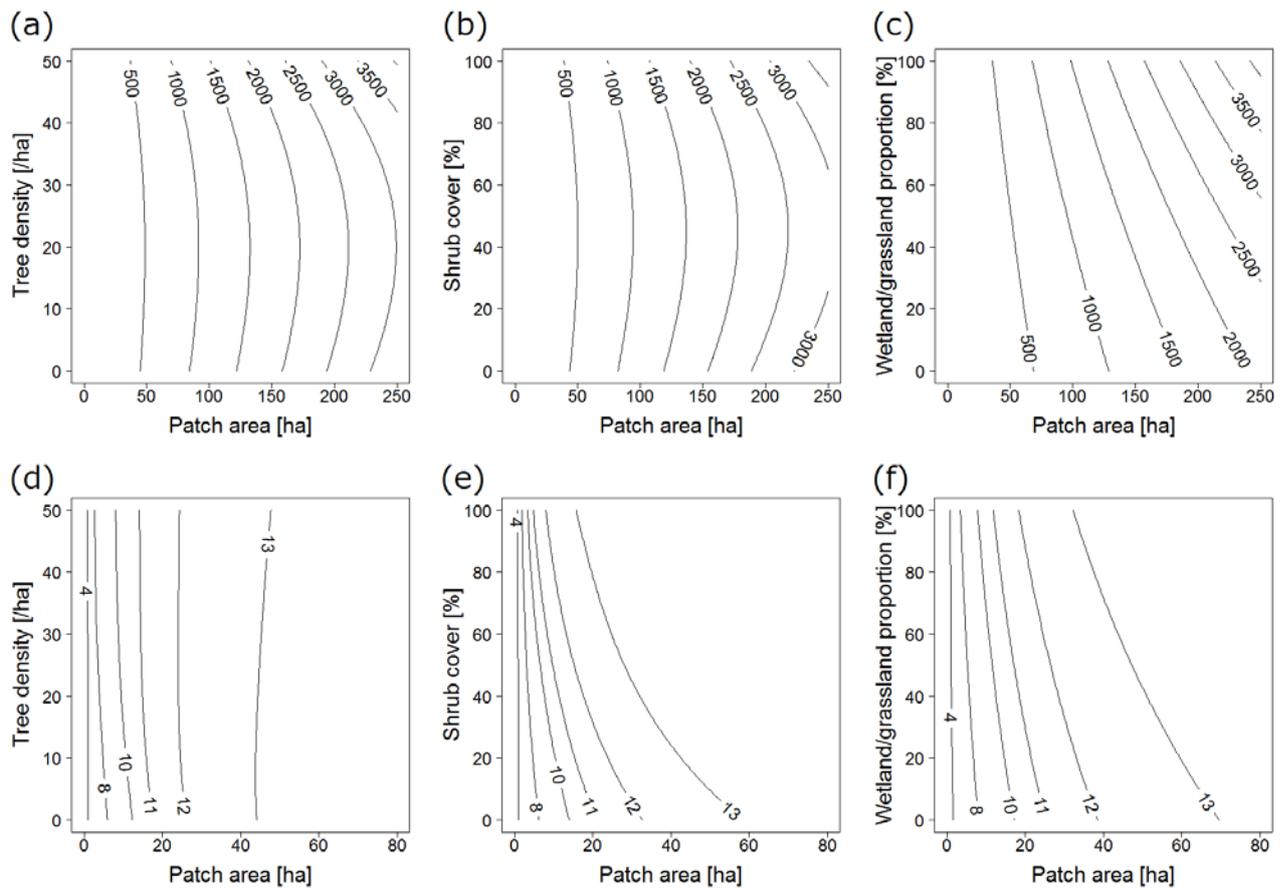
507 β_{1-4} , statistical significance at 5% level is indicated by *. (a) β_{0i} was logarithmically

508 transformed when expected abundance when area was 1 ha. (b) Effect of patch area. (c–e) β_{2i} ,

509 β_{3i} , and β_{4i} are the effects of tree density [1/ha], shrub cover [%], and wetland/grassland

510 proportion in the surroundings [%], respectively.

511



512

513 Fig. 4. Total abundance and species richness as function of patch areas and covariates.

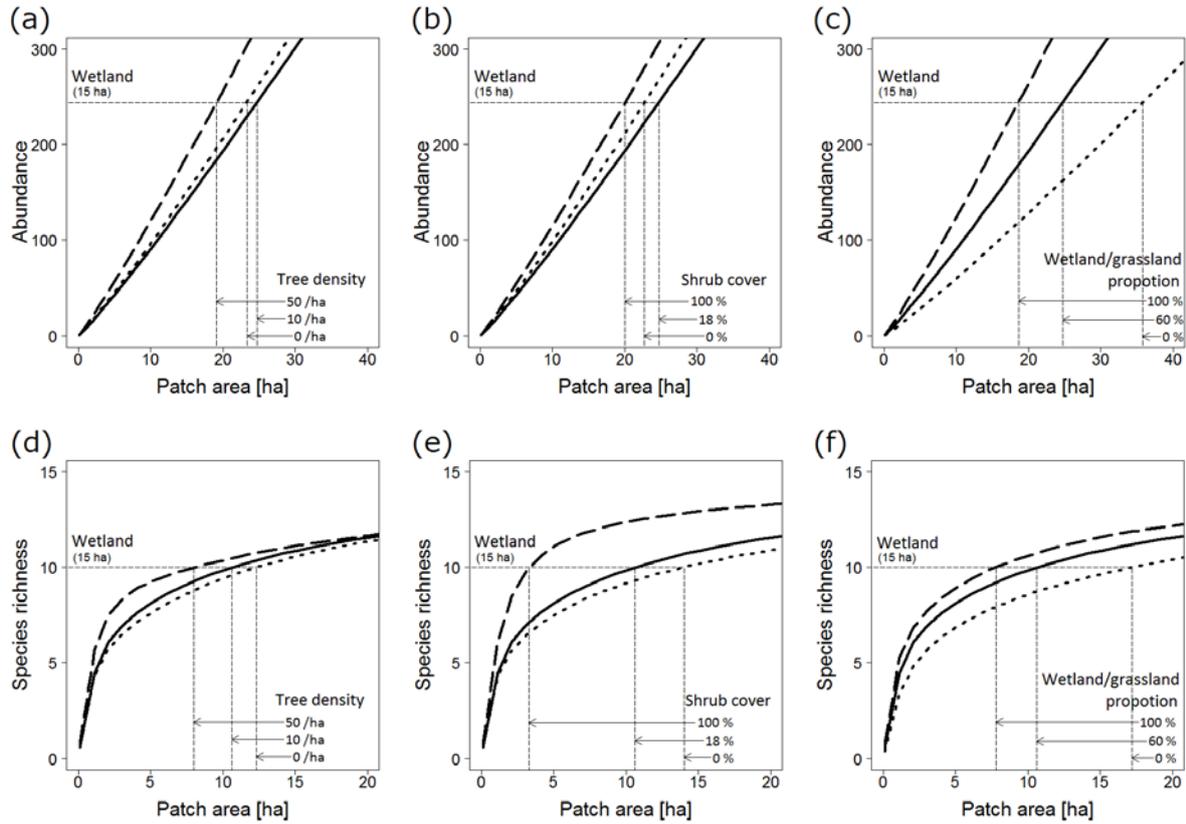
514 Vertical axes indicate (a, d) tree density [/ha], (b, e) shrub cover [%], and (c, f)

515 wetland/grassland proportion in the surroundings [%]. Solid lines indicate estimates of (a–c)

516 abundance and (d–f) species richness. In each figure, the other covariates are fixed to mean

517 values.

518



519

520 Fig. 5. Abundance-area and species-area relationships in relation to wetland communities in
 521 15-ha wetlands.

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

523 (a–c) Abundance-area relationships. (d–f) Species-area relationships. In each figure, three

524 curves indicate the cases in the covariates for minimum (dotted), mean (solid), and maximum

525 (broken) values of (a, d) tree densities, (b, e) shrub cover, and (c, f) wetland/grassland

526 proportions in the surroundings. In each figure, the other covariates are fixed to mean values.

527