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Title

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

Authors

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Abstract (299 words)

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

abandonment of farmland surrounded by open land would significantly improve the conservation of wetland/grassland birds in the agricultural landscape. Given the decline in the area of grassland, wetland, and low-intensity farmland, farmland abandonment provides an opportunity to conserve and restore the declining populations of wetland and grassland birds.

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

1. Introduction

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

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

72 abandoned farmland and the remnants of natural habitats) for organisms in agricultural
73 landscapes remain unknown.
74 The abundance and species richness of organisms in agricultural landscapes are
75 expected to vary depending on the surrounding environment (e.g., the quality of the matrix
76 or the amount of surrounding habitat) (Dauber *et al.*, 2003; Quesnelle *et al.*, 2015; Ernst *et*
77 *al.*, 2017) via various ecological processes, such as the provision of additional feeding
78 habitats (Dunning *et al.*, 1992; Taylor *et al.*, 1993). It would also be important to examine
79 how the abundance and species richness of organisms for each land use type varies
80 depending on the surrounding environment. Indeed, our previous study revealed that
81 abandoned farmland with large amounts of surrounding wetland/grassland had a high
82 abundance and species richness of wetland/grassland birds (Hanioka *et al.*, in press).
83 The objectives of the present study were to compare the abundance and species
84 richness of birds among the major land use types in agricultural landscapes (i.e., wetland,
85 grassland, forest, farmland, and abandoned farmland) and to assess their dependency on the
86 surrounding landscape structure. We used recently developed hierarchical community
87 models (HCMs), which allowed us to model rare and common species simultaneously
88 (Iknayan *et al.*, 2014; Warton *et al.*, 2015; Ovaskainen *et al.*, 2017), and therefore even
89 functional groups and entire communities could be assessed (Dorazio *et al.*, 2006; Yamaura
90 *et al.*, 2012b; Kéry and Royle, 2016). We specifically adopted abundance-based HCMs to
91 evaluate the value of farmland abandonment not only to total bird abundance, but also bird

92 species richness (Yamaura *et al.*, 2016a; 2016b; Yamaura and Royle, 2017).

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

102 It is known that farmland abandonment can negatively affect open land bird species
103 in Europe (e.g., Sirami *et al.*, 2008), and agricultural intensification also has negative effects
104 (Donald *et al.*, 2001; Flohre *et al.*, 2011). Because farmlands are usually abandoned in
105 marginal unproductive areas where traditional low-intensity farming is common (Queiroz *et*
106 *al.*, 2014), we hypothesized unimodal responses of wetland and grassland bird abundance to
107 the post-management habitat trajectory for xeric (dry) sites (Fig. 1). According to this
108 conceptual model, low-intensity (or extensively managed) farmland would provide optimal
109 habitats for many wetland/grassland species, and management practices that change the
110 farmland from this status will result in the decline of wetland/grassland species. The model
111 is based on the premise that farmland abandonment in Europe shifts low-intensity (dry)

farmland to forest land (Sirami *et al.*, 2008). However, farmlands in our lowland landscape are situated in both mesic and xeric sites, and have been cultivated by intensive management (with machinery and chemical fertilizer: Appendix 1). Thus, we hypothesized that abandoned farmlands in our study region would succeed to semi-natural wetland/grassland, which may increase the abundance of wetland and grassland birds (Fig. 1).

2. Materials and methods

2.1.Study area

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

remaining wetlands in the study area, which are primarily located in its southern portion (Fig. 2a).

2.2.Definition of land use

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

2.3.Establishment of sampling plots

Based on a vegetation map (scale 1:25,000 and resolution: 25 m) provided by the Natural Conservation Bureau of the Ministry of Environment (http://www.biodic.go.jp), we

created a land use map composed of the aforementioned six land uses and other unsuitable land uses (e.g., urban areas and open water) for the birds of interest. Then, we established 48 sampling plots of 2 ha each (width 100 m × length 200 m) to range the ratio of each land use from 0 to 1. We considered the center of the long side of each sampling plot to be the transect line (200 m), and recorded the birds observed in a 50-m band on each side of a 200-m long straight line. To ensure that the sampling plots were independent from each other (to avoid double counting of the same individuals), the plots were spaced 500 m apart (Ralph *et al.*, 1993: radius of territory sizes for common species were basically <100 m). This spatial separation was considered since spatial autocorrelation can greatly affect the analysis when spatial autocorrelation occurs both in response (birds in this study) and environmental variables (Legendre *et al.*, 2002). We calculated the ratio of focal land uses (0–1) within each sampling plot. We generated 400-m buffers from the edge of each sampling plot (width 900 m × length 1000 m; the area of each buffer was 88 ha). We then measured the surrounding wetland/grassland ratio (0–1; hereafter termed ‘landscape openness’), which included wetland, grassland, wet abandoned farmland, dry abandoned farmland, and farmland (except for paddy fields) in each buffer. We excluded paddy fields because their low vegetation and open water surfaces were unlikely to provide a suitable habitat for land birds. Landscape openness was negatively correlated with the proportional area of forest in the surrounding area ($r < -0.7$, $p < 0.001$). Therefore, we used this ratio as a single landscape variable in all analyses. We established sampling plots (i.e., determined their locations) by confirming low correlations

among the previously mentioned environmental covariates (the ratio of each land use type and landscape openness ($|r| < 0.52$); see Appendix 2 for the mean ± standard deviation (SD) of each environmental variable in the sampling plots). The directions of the census lines were determined to represent the environmental conditions, vegetation structure, and composition. We performed these procedures using QGIS ver. 2.16.0 (QGIS Development Team, 2016).

2.4.Bird survey

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

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

192 Otherwise, we assigned a value of 0.5 (Bibby *et al.*, 2000). For species in which it was
193 difficult to distinguish between males and females, or which birds were always in a flock
194 consisting of multiple individuals, we assigned one territory if the species was present in the
195 plot, and 0 territories if it was absent. We summed and rounded these quantities to obtain the
196 number of territories (as an integer) within the sampling plots, which was used as the
197 abundance. Because it has been reported that open land songbirds have a relatively high
198 detection probability in Hokkaido (~ 0.6: Yamaura *et al.*, 2016a), we considered that each
199 inhabited territory within the sampling plots was detected in at least one of the survey visits.
200 Although forest species can have a lower detection probability, we did not consider imperfect
201 detection and assumed that each territory was also detected during the field survey. Because
202 open land with a high detection probability had smaller abundance estimates of forest species
203 (see Results) and detection probabilities were high within a 50-m range, even in forests
204 (Schieck, 1997; Alldredge *et al.*, 2007; Yamaura and Royle, 2017), we concluded that an
205 undesirable confounding of abundance and detectability was avoided using the territory
206 mapping methods with a 50-m census range. Eight species, including the grey heron (*Ardea*
207 *cinereal*) and eastern marsh harrier (*Circus spilonotus*), were excluded from the analyses
208 because their territory sizes were larger than our census and buffer areas (90 ha).
209
210 2.5.Statistical analysis
211 We estimated the effects of land use and surrounding habitats on the abundance of

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

$$\log(\lambda_{ij}) = \beta_{i1} \times x_{1j} + \beta_{i2} \times x_{2j} + \beta_{i3} \times x_{3j} + \beta_{i4} \times x_{4j} + \beta_{i5} \times x_{5j} + \beta_{i6} \times x_{6j} + \beta_{i7} \times x_{7j}$$

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

We categorized the observed bird species as: (i) wetland species (ii) grassland species, (iii) farmland species, or (iv) forest species (see Appendix 3) according to published

232 references (e.g., Takagawa *et al.*, 2011). We divided open land species into three groups
233 because wetland and grassland species are specialists of their respective habitats, while
234 farmland species are generalists of open land habitats (e.g., Japanese pied wagtail *Motacilla*
235 *alba*, Eurasian skylark *Alauda arvensis*) that can also be observed in farmlands. We then
236 assumed that the species-level parameter β_i followed a functional group-level normal
237 distribution with hyperparameters. This parameterization allowed us to model rare species
238 using the information from common species (Kéry and Royle, 2016):
239 $$\beta_{i1} \sim \text{Normal}[\mu_{\beta_1}, \sigma^2_{\beta_1}], \quad \beta_{i2} \sim \text{Normal}[\mu_{\beta_2}, \sigma^2_{\beta_2}].$$
240 where μ_{β_1} and σ_{β_1} are the mean and standard deviation of β_{i1}, respectively, which indicates
241 that different functional groups can have different means and variations for each coefficient,
242 because we expected that the effects of land use and the landscape openness would differ
243 between the species groups. We obtained the parameter estimates from bird survey data using
244 a Markov Chain Monte Carlo (MCMC) method with three chains, 100,000 burn-in, a thinning
245 interval of 10, and 900,000 post-iterations. We conducted these analyses using R ver. 3.2.0 (R
246 Core Team, 2015), JAGS ver. 4.2.0 (Plummer, 2016), and jagsUI ver. 1.4.2 R package
247 (Kellner, 2016). We determined each covariate to be significant at the 5% significance level.
248 To determine whether we could appropriately use HCMs (assuming a Poisson distribution
249 while not considering over-dispersion), we constructed generalized linear models (GLMs
250 assuming a Poisson distribution), generalized linear mixed models (GLMMs with random site
251 effects to account for over-dispersion) with random site effects, and spatial GLMMs

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

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

2.6.Predicting the effects of farmland abandonment

Based on the constructed HCMs, we examined how the abundance and species richness of four bird groups and the overall bird community varied with farmland abandonment and landscape openness. We assumed that a given ratio of farmland (0–1) in a given plot (2 ha) was completely converted into abandoned farmland (hereafter referred to as

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

2.7.Mapping the predicted bird abundance

We divided the land use map of the study area into 2-ha grids (width 100 m × length 200 m) and stored the values of each explanatory variable in each grid. Then, we calculated

292 the expected abundance of each bird species in each grid (grid λ_{ij}) and obtained the abundance
293 of each bird group and the total bird community for each grid. We excluded grids with no
294 focal land uses from the mapping analysis. When the focal land uses were less than 1 (i.e.
295 only partially covering the grid), grid-level abundance was overestimated because non-focal
296 land-uses were unsuitable habitats for the birds considered in this study. Given our model
297 formulation of $\log(\lambda_{ij})$, the expected abundance of these unsuitable habitats (likely 0) was
298 modeled to be 1 per plot (i.e., when unsuitable habitats completely covered the grids, grid λ_{ij}
299 = exp[0] = 1, assuming a mean value of landscape openness). In other words, this was
300 because we modeled the plot-level abundance by summing the abundance of individual
301 habitats, which were assumed to completely cover the plots as a whole ($\sum_{i=1}^{6} x_{ij} = 1$). To
302 avoid overestimation of the abundance, we calculated the abundance of each species (λ_{ij}) by
303 assuming the ratio of the total area of the focal land uses in the grid was 1 and multiplied λ_{ij}
304 by the total ratio of the focal land uses in the 2-ha grid (S_j) (i.e., grid $\lambda_{ij} = \lambda_{ij} \times S_j$).
305
306
307 **3. Results**
308 We recorded a total of 743 individuals of 56 bird species during the survey (see
309 Appendix 3 for details). After excluding eight species whose territory sizes were larger than
310 the census and buffer areas, we focused on 48 species (9 wetland, 10 grassland, 6 farmland,
311 and 23 forest species) in the following analyses.

312

313 3.1.Effects of land use and surrounding habitats on birds

314 The group-level mean of the expected abundance (hereafter ‘abundance’) for the
315 wetland and grassland bird species tended to be highest in wetland and/or grassland areas and
316 lowest in farmlands and forests (Fig. 3a,b). Thus, the abundance values of wetland and
317 grassland species for both types of abandoned farmland were generally between the
318 abundance values of wetland/grassland and farmland/forest (Fig. 3a,b). In terms of
319 species-specific responses, the abundances of three wetland birds (Middendoff’s grasshopper
320 warbler [*Loucustella ochotensis*: code W6], great reed warbler [*Acrocephalus orientalis*: W7],
321 and common reed bunting [*Emberiza schoeniclus*: W9]) were significantly higher in wet
322 abandoned farmland than in farmland and forest (Appendixes 5–6). The abundance of the
323 black-browed reed warbler (*Acrocephalus bistrigiceps*: W8) was also significantly higher in
324 wet abandoned farmland than in dry abandoned farmland, farmland, and forest (Appendixes
325 5–6). In contrast, the abundance of the lanceolated grasshopper warbler (*Locustella*
326 *lanceolata*: W5) was significantly lower in both types of abandoned farmland than in
327 wetlands (Appendixes 5–6). Landscape openness tended to have positive effects on the
328 abundance of wetland and grassland groups, and the effects on the abundances of four of the
329 19 wetland/grassland species were significant (e.g., black-browed reed warbler and
330 Middendoff’s grasshopper warbler) (Appendixes 5–6). In contrast, farmland species
331 consistently had a high abundance in the farmland among the five open land uses, and

332 landscape openness tended to have a positive effect (Fig. 3c, Appendixes 5–6).

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

340

341 3.2.Predicting the effects of farmland abandonment

342 For the wetland and grassland bird groups, abundance and species richness were
343 predicted to increase with increases in farmland abandonment and landscape openness (Fig.
344 4a,b,f,g). For wetland species, whereas abundance was primarily mediated by landscape
345 openness (Fig. 4a), species richness was primarily mediated by the farmland abandonment
346 ratio (Fig. 4f). Farmland abandonment had negative effects on farmland species (Fig. 4c,h).
347 Although the abundance and species richness of forest birds decreased with increases in
348 farmland abandonment and landscape openness, the rates of decrease were small (Fig.
349 4c,d,h,i). The combination of these results revealed that the abundance of the total bird
350 community increased with an increase in the farmland abandonment ratio, and its rate of
351 increase tended to be acute under conditions with a higher landscape openness (Fig. 4e). In

contrast, species richness for the total bird community increased moderately with an increase in the farmland abandonment ratio (Fig. 4j). Community-level responses were therefore mainly determined by the responses of wetland/grassland species, because forest species were insensitive to the proportional area of farmland and abandoned farmland and farmland species were negatively influenced by farmland abandonment.

3.3.Mapping the predicted bird abundance

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

4. Discussion

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

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

We also found that differences in the dominant vegetation of abandoned farmland (i.e., wet abandoned farmland or dry abandoned farmland) did not affect the abundance of the wetland and grassland bird groups. This outcome was expected because both types of

abandoned farmland in our study area were dominated by the tall grasses that these species prefer (wet abandoned farmland: common reed, *Calamagrostis canadensis* subsp. *langsdorffi*, dry abandoned farmland: amur silver grass, Japanese silver grass: Appendix 1) rather than by trees, which these species avoid (Kennerley and Pearson, 2010; Copete and Christie, 2017).

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

Previous studies of dry abandoned farmland have found that the abundance or species richness of forest birds increases with tree encroachment following land abandonment (Sirami *et al.*, 2008; Zakkak *et al.*, 2014; Ernst *et al.*, 2017). However, we found that the abundance of the forest bird group in abandoned farmland was comparable to that in active farmland (Fig. 3d). This inconsistency can again be explained by the dominant vegetation of the dry abandoned farmland in our study area (i.e., tall grasses: personal observation by M. Hanioka). Some researchers have suggested that in dry abandoned farmland, the recovery of

412 woody vegetation equivalent to forests can take several decades (Shoo *et al.*, 2016). Most of
413 the dry abandoned farmland in our study sites has been abandoned within the past 20 years
414 (personal observation by M. Hanioka), and woody vegetation had not yet colonized the sites.
415 Future studies should examine whether the abundance or species richness of each bird group
416 (i.e., wetland/grassland birds and forest birds) varies not only with the number of years from
417 initial abandonment but also with the succession of related vegetation (Fig. 1).
418
419 4.2.Landscape effects on the habitat value for birds
420 Our results suggest that the effect of the landscape variable also differs between the
421 habitat groups. As in previous studies (Quesnelle *et al.*, 2015; Ernst *et al.*, 2017), the
422 abundance of the wetland and grassland bird groups (and farmland species also) increased
423 with landscape openness (Fig. 3a,b). This was likely because the surrounding habitats can
424 supplement the food resources and resting places needed by wetland/grassland birds
425 (Quesnelle *et al.*, 2015). In contrast, the effect of landscape openness on the forest bird group
426 was not significant (i.e., the abundance of the forest bird group did not increase with a
427 decrease in landscape openness [an increase in the proportion of forest in the surrounding
428 area]). This result was inconsistent with those of previous studies (Villard *et al.*, 1999; Smith
429 *et al.*, 2011). There are likely to be variations in the effects of landscape structure on the
430 abundance of forest birds among regions.
431

4.3.Predicted bird responses to land abandonment

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

4.4.Future land use management for conserving bird communities

The mapping results revealed that the abundance of the wetland/grassland birds were higher in the southern lowland of the study area, where there were remnants of wetlands and abandoned farmland (Fig. 5). A previous study predicted that abandoned farmland would likely increase in the area between the mountains and lowlands, where crop productivity may

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

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References

Alldredge, M.W., Simons, T.R., Pollock, K.H., 2007. Factors affecting aural detections of songbirds. Ecol. Appl. 17, 948-955.

Askins, R.A., 2001. Sustaining biological diversity in early successional communities: the challenge of managing unpopular habitats. Wildl. Soc. Bull. 29, 407-412.

Bibby, C.J., Burgess, N.D., Hill, D.A., Mustoe, S.H., 2000. Bird census techniques. Academic Press, San Diego.

Bini, L.M., Diniz‐Filho, J.A.F., Rangel, T.F.L.V.B., Akre, T.S.B., Albaladejo, R.G., Albuquerque, F.S., Aparicio, A., Araújo, M.B., Baselga, A., Beck, J., Bellocq, M.I., Böhning‐Gaese, K., Borges, P.A.V., Castro‐Parga, I., Chey, V.K., Chown, S.L., de Marco, J.P., Dobkin, D.S., Ferrer‐Castán, D., Field, R., Filloy, J., Fleishman, E., Gómez, J.F., Hortal, J., Iverson, J.B., Kerr, J.T., Kissling, W.D., Kitching, I.J., León‐Cortés, J.L., Lobo, J.M., Montoya, D., Morales‐Castilla, I., Moreno, J.C., Oberdorff, T., Olalla‐Tárraga, M.Á., Pausas, J.G., Qian, H., Rahbek, C., Rodríguez, M.Á., Rueda, M., Ruggiero, A., Sackmann, P., Sanders, N.J., Terribile, L.C., Vetaas, O.R.,

492 Hawkins, B.A., 2009. Coefficient shifts in geographical ecology: an empirical
493 evaluation of spatial and non‐spatial regression. Ecography 32, 193-204.
494 Boakes, E.H., Mace, G.M., McGowan, P.J.K., Fuller, R.A., 2010. Extreme contagion in
495 global habitat clearance. Proc. R. Soc. Lond., Ser. B. 277, 1081-1085.
496 Copete, J.L., Christie, D.A., 2017. Reed Bunting (*Emberiza schoeniclus*). In: del Hoyo, J.,
497 Elliott, A., Sargatal, J., Christie, D.A., de Juana, E. (Eds.), Handbook of the Birds of
498 the World Alive. Lynx Edicions, Barcelona. http://www.hbw.com/node/61900.
499 Cramer, V.A., Hobbs, R.J., Standish, R.J., 2008. What's new about old fields? Land
500 abandonment and ecosystem assembly. Trends Ecol. Evol. 23, 104-112.
501 Cramp, S., 1977-1994. Handbook of the birds of Europe, the Middle East and North Africa:
502 the birds of the Western Palearctic. Oxford University Press, New York.
503 Dauber, J., Hirsch, M., Simmering, D., Waldhardt, R., Otte, A., Wolters, V., 2003. Landscape
504 structure as an indicator of biodiversity: matrix effects on species richness. Agric.
505 Ecosyst. Environ. 98, 321-329.
506 Davidson, N.C., 2014. How much wetland has the world lost? Long-term and recent trends in
507 global wetland area. Marine Freshw. Res. 65, 934-941.
508 Donald, P.F., Green, R.E., Heath, M.F., 2001. Agricultural intensification and the collapse of
509 Europe's farmland bird populations. Proc. R. Soc. Lond., Ser. B. 268, 25-29.
510 Dorazio, R.M., Royle, J.A., Söderström, B., Glimskär, A., 2006. Estimating species richness
511 and accumulation by modeling species occurrence and detectability. Ecology 87,

842-854.

Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schroder, B., Schurr, F.M., Wilson, R., 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30, 609-628.

Dunning, J.B., Danielson, B.J., Pulliam, H.R., 1992. Ecological processes that affect populations in complex landscapes. Oikos 65, 169-175.

Ellis, E.C., 2011. Anthropogenic transformation of the terrestrial biosphere. Phil. Trans. R. Soc. Lond., Ser. A. 369, 1010-1035.

Ernst, L.M., Tscharntke, T., Batáry, P., 2017. Grassland management in agricultural vs. forested landscapes drives butterfly and bird diversity. Biol. Conserv. 216, 51-59.

Flohre, A., Fischer, C., Aavik, T., Bengtsson, J., Berendse, F., Bommarco, R., Ceryngier, P., Clement, L.W., Dennis, C., Eggers, S., Emmerson, M., Geiger, F., Guerrero, I., Hawro, V., Inchausti, P., Liira, J., Morales, M.B., Oñate, J.J., Pärt, T., Weisser, W.W., Winqvist, C., Thies, C., Tscharntke, T., 2011. Agricultural intensification and biodiversity partitioning in European landscapes comparing plants, carabids, and birds. Ecol. Appl. 21, 1772-1781.

Fujimaki, Y., Takamata, M., Sato, F., 1994. Breeding biology of the stonechat in southeastern Hokkaido, Japan. Res. Bull. Obihiro Univ. 19, 37-46.

532 Goldewijk, K.K., 2001. Estimating global land use change over the past 300 years: The
533 HYDE Database. Global Biogeochem. Cy. 15, 417-433.
534 GSI, 2000. National survey of lakes and wetlands. Geospatial Information Authority of Japan
535 (GSI), http://www.gsi.go.jp/kankyochiri/gsilake.html (in Japanese).
536 Hanioka, M., Yamaura, Y., Yamanaka, S., Senzaki, M., Kawamura, K., Terui, A., Nakamura,
537 F., in press. How much abandoned farmland is required to harbor comparable species
538 richness and abundance of bird communities in wetland? Hierarchical community
539 model suggests the importance of habitat structure and landscape context. Biodivers.
540 Conserv.
541 Hokkaido Regional Development Bureau, 2013. Improvement project of Ishikari River (flood
542 retension ponds of Chitose
543 River). http://www.hkd.mlit.go.jp/topics/singi/h25_5/h251128_2_3_1.pdf (in
544 Japanese).
545 Iknayan, K.J., Tingley, M.W., Furnas, B.J., Beissinger, S.R., 2014. Detecting diversity:
546 emerging methods to estimate species diversity. Trends Ecol. Evol. 29, 97-106.
547 Kéry, M., 2010. Introduction to WinBUGS for ecologists: a Bayesian approach to regression,
548 ANOVA, mixed models and related analysis. Academic Press, San Diego.
549 Kéry, M., Royle, J.A., 2016. Applied hierarchical modeling in ecology: analysis of
550 distribution, abundance and species richness using R and BUGS. Volume 1. Prelude
551 and static models. Academic Press, San Diego.

552 Katayama, N., Osawa, T., Amano, T., Kusumoto, Y., 2015. Are both agricultural
553 intensification and farmland abandonment threats to biodiversity? A test with bird
554 communities in paddy-dominated landscapes. Agric. Ecosyst. Environ. 214, 21-30.
555 Kawaji, N., Kawaji, K., Hirokawa, J., 1996. Breeding ecology of the Short-tailed Bush
556 Warbler *Cettia squameiceps* in western Hokkaido. Jpn. J. Ornithol. 45, 1-15.
557 Kellner, K., 2016. jagsUI: a wrapper around rjags to streamline JAGS
558 analyses. https://cran.r-project.org/web/packages/jagsUI/.
559 Kennerley, P., Pearson, D., 2010. Reed and bush warblers. Christopher Helm, London.
560 Legendre, P., Dale, M.R.T., Fortin, M.-J., Gurevitch, J., Hohn, M., Myers, D., 2002. The
561 consequences of spatial structure for the design and analysis of ecological field
562 surveys. Ecography 25, 601-615.
563 MAFF, 2011. On the current status of abandoned farmland. Ministry of Agriculture, Forestry
564 and Fisheries (MAFF),
565 Tokyo. http://www.maff.go.jp/j/nousin/tikei/houkiti/pdf/genjou1103.pdf (in Japanese).
566 McCollin, D., 1998. Forest edges and habitat selection in birds: a functional approach.
567 Ecography 21, 247-260.
568 ME, 2005. Ecosystems and human well-being: synthesis. Millennium Ecosystem Assessment
569 (ME), Island Press, Washington D. C.
570 Meli, P., Rey Benayas, J.M., Balvanera, P., Martínez Ramos, M., 2014. Restoration enhances
571 wetland biodiversity and ecosystem service supply, but results are context-dependent:

572 a meta-analysis. PLoS ONE 9, e93507.
573 Morimoto, J., Shibata, M., Shida, Y., Nakamura, F., 2017. Wetland restoration by natural
574 succession in abandoned pastures with a degraded soil seed bank. Restor. Ecol. 25,
575 1005-1014.
576 Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Borger, L.,
577 Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Diaz, S.,
578 Echeverria-Londono, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K.,
579 Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer,
580 M., Correia, D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P.,
581 Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers,
582 R.M., Mace, G.M., Scharlemann, J.P.W., Purvis, A., 2015. Global effects of land use
583 on local terrestrial biodiversity. Nature 520, 45-50.
584 Ovaskainen, O., Tikhonov, G., Norberg, A., Blanchet, F.G., Duan, L., Dunson, D., Roslin, T.,
585 Abrego, N., 2017. How to make more out of community data? A conceptual
586 framework and its implementation as models and software. Ecol. Lett. 20, 561-576.
587 Pereira, H.M., Navarro, L.M., 2015. Rewilding European landscapes. Springer, Cham.
588 Plummer, M., 2016. JAGS: Just Another Gibbs Sampler. http://mcmc-jags.sourceforge.net/.
589 QGIS Development Team, 2016. QGIS Geographic Information System. Open
590 SourceGeospatial Foundation Project. http://www.qgis.org/.
591 Queiroz, C., Beilin, R., Folke, C., Lindborg, R., 2014. Farmland abandonment: threat or

592 opportunity for biodiversity conservation? A global review. Front. Ecol. Environ. 12,
593 288-296.
594 Quesnelle, P.E., Lindsay, K.E., Fahrig, L., 2015. Relative effects of landscape-scale wetland
595 amount and landscape matrix quality on wetland vertebrates: a meta-analysis. Ecol.
596 Appl. 25, 812-825.
597 R Core Team, 2015. R: a language and environment for statistical computing. R Foundation
598 for Statistical Computing. Vienna, Austria.
599 Ralph, C.J., Geupel, G.R., Pyle, P., Martin, T.E., DeSante, D.F., 1993. Handbook of field
600 methods for monitoring landbirds. USDA For. Serv. Gen. Tech. Rep. PSW-GTR-144.
601 Ramankutty, N., Foley, J.A., 1999. Estimating historical changes in global land cover:
602 croplands from 1700 to 1992. Global Biogeochem. Cy. 13, 997-1027.
603 Renwick, A., Jansson, T., Verburg, P.H., Revoredo-Giha, C., Britz, W., Gocht, A.,
604 McCracken, D., 2013. Policy reform and agricultural land abandonment in the EU.
605 Land Use Policy 30, 446-457.
606 Schieck, J., 1997. Biased detection of bird vocalizations affects comparisons of bird
607 abundance among forested habitats. Condor 99, 179-190.
608 Shoo, L.P., Freebody, K., Kanowski, J., Catterall, C.P., 2016. Slow recovery of tropical
609 old-field rainforest regrowth and the value and limitations of active restoration.
610 Conserv. Biol. 30, 121-132.
611 Sirami, C., Brotons, L., Burfield, I., Fonderflick, J., Martin, J.-L., 2008. Is land abandonment

612 having an impact on biodiversity? A meta-analytical approach to bird distribution
613 changes in the north-western Mediterranean. Biol. Conserv. 141, 450-459.
614 Smith, A.C., Fahrig, L., Francis, C.M., 2011. Landscape size affects the relative importance
615 of habitat amount, habitat fragmentation, and matrix quality on forest birds.
616 Ecography 34, 103-113.
617 Takagawa, S., Ueta, M., Amano, T., Okahisa, Y., Kamioki, M., Amamo, T., Takahashi, M.,
618 Hayama, S., Hirano, T., Hayama, S., Mikami, O.K., Mori, S., Morimoto, G., Yamaura,
619 Y., 2011. JAVIAN Database: a species-level database of life history, ecology and
620 morphology of bird species in Japan. Bird Res. 7, R9-R12 (in Japanese).
621 Tanentzap, A.J., Lamb, A., Walker, S., Farmer, A., 2015. Resolving conflicts between
622 agriculture and the natural environment. PLoS Biol. 13, e1002242.
623 Taylor, P.D., Fahrig, L., Henein, K., Merriam, G., 1993. Connectivity is a vital element of
624 landscape structure. Oikos 68, 571-573.
625 Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D.,
626 Schlesinger, W.H., Simberloff, D., Swackhamer, D., 2001. Forecasting agriculturally
627 driven global environmental change. Science 292, 281-284.
628 Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape
629 perspectives on agricultural intensification and biodiversity – ecosystem service
630 management. Ecol. Lett. 8, 857-874.
631 Uchida, K., Ushimaru, A., 2014. Biodiversity declines due to abandonment and intensification

of agricultural lands: patterns and mechanisms. Ecol. Monogr. 84, 637-658.

Villard, M.-A., Trzcinski, M.K., Merriam, G., 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. Conserv. Biol. 13, 774-783.

Warton, D.I., Blanchet, F.G., O'Hara, R.B., Ovaskainen, O., Taskinen, S., Walker, S.C., Hui, F.K.C., 2015. So many variables: joint modeling in community ecology. Trends Ecol. Evol. 30, 766-779.

Yamanaka, S., Akasaka, T., Yabuhara, Y., Nakamura, F., 2017. Influence of farmland abandonment on the species composition of wetland ground beetles in Kushiro, Japan. Agric. Ecosyst. Environ. 249, 31-37.

Yamaura, Y., Amano, T., Koizumi, T., Mitsuda, Y., Taki, H., Okabe, K., 2009. Does land-use change affect biodiversity dynamics at a macroecological scale? A case study of birds over the past 20 years in Japan. Anim. Conserv. 12, 110-119.

Yamaura, Y., Connor, E.F., Royle, J.A., Itoh, K., Sato, K., Taki, H., Mishima, Y., 2016a. Estimating species – area relationships by modeling abundance and frequency subject to incomplete sampling. Ecol. Evol. 6, 4836-4848.

Yamaura, Y., Kéry, M., Royle, J.A., 2016b. Study of biological communities subject to imperfect detection: bias and precision of community *N*-mixture abundance models in small-sample situations. Ecol. Res. 31, 289-305.

Yamaura, Y., Oka, H., Taki, H., Ozaki, K., Tanaka, H., 2012a. Sustainable management of

planted landscapes: lessons from Japan. Biodivers. Conserv. 21, 3107-3129.

Yamaura, Y., Royle, J.A., 2017. Community distance sampling models allowing for imperfect detection and temporary emigration. Ecosphere 8, e02028.

Yamaura, Y., Royle, J.A., Shimada, N., Asanuma, S., Sato, T., Taki, H., Makino, S., 2012b. Biodiversity of man-made open habitats in an underused country: a class of multispecies abundance models for count data. Biodivers. Conserv. 21, 1365-1380.

Zakkak, S., Kakalis, E., Radović, A., Halley, J.M., Kati, V., 2014. The impact of forest encroachment after agricultural land abandonment on passerine bird communities: the case of Greece. J. Nat. Conserv. 22, 157-165.

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

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

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

684 WETLND (wetland), GRSS (grassland), WETAB (wet abandoned farmland), DRYAB (dry
685 abandoned farmland); FARM (farmland); FOR (forest); LAND (landscape openness).
686
687 Fig. 4. Changes in total abundance (a–e) and species richness (f–j) as functions of the
688 farmland abandonment ratio and landscape openness. The results are shown for wetland
689 species (a,f), grassland species (b,g), farmland species (c,h), forest species (d,i), and all
690 species (e,j). Solid lines indicate changes in (a–e) total abundance (i.e., 10 indicates an
691 increase in 10 individuals), and (f–j) species richness (i.e., -0.5 indicates a decrease in 0.5
692 species).
693
694 Fig. 5. Maps predicting the total abundance of (a) wetland species, (b) grassland species, (c)
695 farmland species, (d) forest species, and (e) all species. Total abundance was calculated in
696 each 100 × 200 m grid. (a,b,e) An enlarged map of the area indicated by the square at the
697 bottom of the whole map is shown in the upper right of the figure.
698
699