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ORIGINAL RESEARCH PAPER

Title

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

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Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Availability of data, material, and code

The datasets and code generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Abstract (249 / 250 words)

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

Keywords

Abundance, grassland, Hokkaido, land-use, species richness, temperature

1. Introduction

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

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

Previous work has suggested that the habitat suitability of abandoned farmland, relative to active farmland, may vary based on geographic region (Queiroz et al. 2014). However, habitat suitability of abandoned farmlands may also differ greatly among species groups within communities (e.g., functional groups). Since disturbances cease after farmland abandonment, suitability of abandoned farmland may vary among species in responses to established vegetation. Most studies have failed to detect such group-specific differences because they have assessed community-level abundance and species richness in active and abandoned farmlands (Plieninger et al. 2014; but see Sirami et al. 2008). Therefore, examining functional group-level responses may provide greater insight into the conservation value of abandoned farmland and provide inferences beyond specific study regions. To address the gap, birds would be useful since they can respond to environmental changes well and exhibit diverse range of ecological functions (Gregory et al. 2005; Sekercioglu 2006).

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

We would expect to detect marked differences between the responses of these two groups to farmland abandonment, and hence explain the contrasting results observed in previous studies. For example, because bare ground or short grassland conditions are maintained in active farmland, their abandonment would negatively impact bare-ground species (e.g., Schmitt and Rákosy 2007; Brambilla et al. 2010; Uchida and Ushimaru 2014). In contrast, perennial vegetation that establish in abandoned farmland due to succession

(Benjamin et al. 2005; Dahlström et al. 2010) can serve as valuable habitat for grassland species (e.g., Yamanaka et al. 2017; Hanioka et al. 2018a).

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

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

2. Methods

2.1. Study area

This study was carried out across Hokkaido, northern Japan (41° 21′–45° 33′ N, 139° 20′–148° 53′ E; 400 × 500 km; Fig. 1). Hokkaido is located in a transitional zone between the temperate and boreal zones. Therefore, climatic conditions in Hokkaido vary among areas; average temperatures range from 4.4 to 16.5°C (Fig. A.1) and average precipitation ranges from 50 to 220 mm (Fig. A.2) during the bird breeding season (May–July). Several studies revealed that the climatic conditions affect bird abundance and distribution on Hokkaido (Fujimaki 2007; Kawamura et al. 2016). Within the last century, 60% of the natural wetland area in Hokkaido was converted into farmland (GSI 2000). Farmland expansion slowed during the 1990s and there is currently at least 3,050 ha of abandoned farmland on Hokkaido (MAFF 2019). Abandoned farmland is found in mountainous and floodplain areas on Hokkaido (Kobayashi and Nakamura 2018), where wetland vegetation may now be re-established in floodplain areas.

2.2. Land-use types

We focused on five land-use types: natural wetland (hereafter wetland) (Fig. A.1), abandoned farmland (Fig. A.2), and active pasture, cropland, and rice paddy (collectively termed active farmland hereafter) (Fig. A.3). We mapped these land-use types on Hokkaido using a vegetation map (scale: 1:50 000–1:25 000) provided by the Natural Conservation Bureau of the Ministry of Environment (http://www.biodic.go.jp/trialSystem/top.html). The dominant species in surveyed wetlands were common reed (*Phragmites australis*), bluejoint reedgrass (*Calamagrostis canadensis* subsp. *langsdorffii*), and sedges (*Carex* spp.). We ensured that all surveyed abandoned farmlands had been active in the 1970s and were no longer actively farmed by examining aerial imagery, interviewing land managers, and using field observations. In most instances we could not obtain an abandonment age (i.e., the time since cultivation ceased) due to the absence of previous land managers (Fig. A.2). Surveyed abandoned farmlands were characterized by common reed, sedges, Japanese iris (*Iris ensata*), Amur silver grass (*Miscanthus sacchariflorus*), and Japanese silver grass (*Miscanthus* *sinensis*). Tree growth (e.g., willowleaf meadowsweet [*Spiraea salicifolia*] and alders [*Alnus* spp.]) was patchy in some abandoned farmland (Fig. A.2).

2.3. Sampling plot selection

To assess the influence of spatial climatic differences, specifically in average temperature and precipitation during the breeding season, we established 13 study areas across Hokkaido accounting for correlations between temperature and precipitation obtained from Mesh Climate Value 2010 (MLIT 2012; Fig. A.4, A.5). We then established one to four sampling plots within each land-use type in each area, for a total of 113 sampling plots (22 in wetlands and abandoned farmland, respectively, 26 in pasture, 27 in cropland, and 16 in rice paddy; Fig. 1; Table A.1). Sampling plots were located in agriculture-dominated floodplains (i.e., alluvial fans or deltas). We could not establish cropland plots in four areas and rice paddy plots in eight areas due to a lack of suitable sites (cultivation in these areas is limited by temperature). We were also unable to locate suitable abandoned farmland plots in two areas due to a lack of suitable sites.

All sampling plots were 300 m in length and 100 m in width (3 ha), and we ran a survey line through the center of each plot. Plots were randomly placed within pre-defined compartments of a single land-use type to avoid recording birds that breed in different land-use types adjacent to sampling plots. We then checked that each plot met the following criteria by using the vegetation map (http://www.biodic.go.jp/trialSystem/top.html) and site visits: (1) each plot was separated by at least 1 km to prevent double-counting (Ralph et al. 1993); (2) a bare-ground and grassland ratio of plots (i.e., the ratio of wetland and active and abandoned farmland) was more than 50%. This was done by generating 300 m buffers around each plot and determining the proportion of bare ground and grassland within each buffer, as this is known to affect the densities of grassland and forest birds on Hokkaido (Hanioka et al.

2018a, 2018b). We thus did not consider landscape structure as explanatory variables in our models.

2.4. Bird surveys

We performed three bird community surveys in each sampling plot throughout the breeding season (May–July) of 2017. The first, second, and third surveys were conducted from May 15 to June 7, from June 9 to July 5, and from July 8 to July 29, respectively. We avoided surveying on rainy, foggy, or windy (windspeeds > 4 m/s) days. Surveys were conducted from dawn to 10:00 h, when bird activity and singing is greatest (Bibby et al. 2000). To reduce time of day bias, we divided surveys into two time zones, from dawn to 07:00 h and from 07:00 h to 10:00 h, and ensured at least one survey per plot represented each zone.

A single surveyor (M.K.) slowly walked the survey lines (2 km/h) using a global positioning system device and recorded the species, sex, location, and behavior (e.g., singing, territorial conflict) of individuals within plots (territory mapping; Bibby et al. 2000). Then, we recorded the putative territories of individual species on a map based on observations from all three visits (Bibby et al. 2000) and estimated territory size (e.g., Hanioka et al. 2018a; Table A.2). We used the summed number of territories for each species within a given plot as our abundance metric. We considered that we detected any inhabited territory in at least one survey. This is because bare-ground and grassland birds have relatively high detectability (~0.6; Yamaura et al. 2016a), and hence three times surveys are considered to be enough to detect almost all territories. Furthermore, detectability of birds' songs within 50 m from the observer is high and stable among different habitats (Schieck 1997).

2.5. Statistical analyses

We estimated the effects of land-use and climate variables on the abundance of each detected bird species and functional group using abundance-based hierarchical community models (HCMs; Yamaura et al. 2016b). We also estimated interactive effects between abandoned farmland and climate variables to test if the relative habitat suitability of abandoned farmland was consistent to those of other land-use types across Hokkaido. We first assumed that the abundance of species *i* in plot *j* (Z_{ij}) followed a Poisson distribution (Z_{ij} ~ Poisson[λ_{ij}]). We then assumed that the expected abundance of species *i* in plot *j* (λ_{ij}) was a function of five land-use categories (i.e., wetland, abandoned farmland, pasture, cropland, and rice paddy), two climate variables (i.e., the 30-year average monthly temperature and precipitation estimates extracted from Mesh Climate Value 2010; see details in Fig. A.1, A.2), and interaction terms between the binary abandoned farmland category (i.e., 0: active farmland and wetland; 1: abandoned farmland) and climate variables. Climate variables were standardized prior to analyses. The intercept of the linear predictor was omitted (i.e., we employed the cell means method; Kéry 2010) to allow for easy comparison of expected abundance values among habitats using parameter estimates, derived using the equation:

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

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

We also conducted alternative analysis which assumed that expected abundance was a function of land-use categories, two climate variables, and interaction terms between climate variables and another binary land-use category (i.e., 0: active farmland; 1: wetland and abandoned farmland). This was done to consider the effects of the presence of management. The results (Fig. A.6) were similar to those of the binary abandoned farmland category, which we hereafter showed. Furthermore, the 30-year average climate values could underestimate the effects of climatic events which uniquely occurred in the surveyed year in a specific area. However, we adopted the average values since our focus is to examine the large-scale effects of land-use types and its spatial variations. We thus used 30-year average values, which is assumed to better represent the spatial characteristics of each area.

We categorized observed bird species as (i) bare-ground species, (ii) grassland species, and (iii) forest species according to published references (Takagawa et al. 2011; Hanioka et al. 2018a; Table A.2). We defined grassland species as any species inhabiting areas dominated by high perennial grass; hence, we included wetland species in this category. We then assumed that the species-level parameter β_i followed a functional group-level normal distribution with hyperparameters. This parameterization allowed us to model rare species using information from common species (Yamaura et al. 2012). Hyperparameters describe the mean values of the functional group and among-species heterogeneity as:

$$\beta_{i1} \sim \text{Normal}\left[\mu_{\beta 1}, \sigma_{\beta 1}^2\right], \qquad \beta_{i2} \sim \text{Normal}\left[\mu_{\beta 2}, \sigma_{\beta 2}^2\right], \ldots \qquad (2)$$

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

We obtained parameter estimates from field survey data using a Markov Chain Monte Carlo method with three chains, a burn-in of 50,000, a thinning interval of five, and 100,000 post-iterations. We conducted these analyses using R ver. 3.2.0 (R Core Team 2015), JAGS ver. 4.2.0 (Plummer 2016), and the R package jagsUI ver. 1.4.2 (Kellner 2016). To determine HCMs were appropriate for our dataset, we constructed generalized linear models assuming a Poisson distribution and generalized linear mixed models with surveyed area as a random effect to account for spatial autocorrelation. The parameter estimates of these models were qualitatively similar to those obtained from HCMs (Table A.3).

Community and functional group-level total abundance were estimated by summing species-level expected abundance, λ_{ij} (hereafter abundance), for each. Similarly, we defined expected species richness (hereafter species richness) as the expected value of the number of species with at least one individual (i.e., $Z_{ij} \geq 1$). The probability of at least one individual occurring ($Pr[z_{ij} \geq 1]$) was expressed using Eq. (3), and we summed this value for each functional group and community (Yamaura et al. 2016b).

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

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

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

3. Results

We recorded a total of 1,466 individuals of 56 bird species across all surveys (Table A.2). We excluded passage visitors, introduced species, and species whose territory sizes were larger than the sampling plots. Therefore, we focused on 1,389 individuals of 33 species (bare-ground species: 206 individuals of four species; grassland species: 1,144 individuals of 23 species; forest species: 39 individuals of six species) in subsequent analyses. The five most commonly observed species were black-browed reed warbler (*Acrocephalus bistrigiceps*, 300 individuals), Middendorff's grasshopper-warbler (*Locustella ochotensis*, 164 individuals), Eurasian skylark (*Alauda arvensis*, 162 individuals), Stejneger's stonechat (*Saxicola stejnegeri*, 135 individuals), and reed bunting (*Emberiza schoeniclus*, 124 individuals). We observed fewer than 100 individuals of all remaining species.

3.1. Functional group differences in habitat suitability

The abundance of two of the four bare-ground species (Eurasian skylark and Eurasian tree sparrow [*Passer montanus*]) was significantly greater in pasture, cropland, or rice paddy than in abandoned farmland (Fig. A.7). The hyperparameters of bare-ground species did not differ significantly among land-use types (Fig. 2a). However, total abundance (i.e., the sum of the expected abundance for all bare-ground species) was significantly higher in cropland and pasture relative to wetland, abandoned farmland, and rice paddy (Fig. 2b). The species richness was higher in pasture and cropland than in abandoned farmland and wetland (Fig. 2c).

The abundance of 14 of the 23 observed grassland species was significantly greater in abandoned farmland than in pasture, cropland, or rice paddy. The abundance of 21 species in abandoned farmland was comparable to or higher than in wetland (Fig. A.7). Reflecting species-level patterns, the hyperparameter in abandoned farmland was greater than in cropland and rice paddy, and comparable to that in wetland (Fig. 2d). Total abundance and species richness exhibited similar patterns to those of hyperparameters (Fig. 2e, f).

For forest species, the abundance of Japanese bush warbler (*Horornis diphone*) was significantly higher in abandoned farmland than in pasture, cropland, and rice paddy. The abundance of the remaining five forest species and the hyperparameters did not differ among the five land-use types (Fig. A.7, Fig. 2g). Total abundance and species richness were higher in abandoned farmland than in cropland and pasture, but differences between other pairs of land-use types were not significant (Fig. 2h, i). The results of community-level total abundance and species richness were very similar to those found for grassland species (Fig. 2j, k), which was the dominant group in the survey sites.

3.2. Spatial differences in habitat suitability

For 30 of the 33 observed species and each functional group, interaction terms between abandoned farmland (represented as a binary variable) and climate variables (i.e., average temperature and precipitation) were not significantly related to abundance (Fig. 3; Fig. A.7). For bare-ground species, the partial regression coefficient for average temperature was positive but non-significant (Fig. 3a), and total abundance and species richness were significantly higher in areas with higher average temperature, excluding in abandoned farmlands (Fig. 4a, b). For grassland species, average temperature and precipitation had significant positive effects on five and four species, respectively (Fig. A.7). Group-level partial regression coefficients of both average temperature and precipitation were positive and significant (Fig. 3b, A.8). Total abundance and species richness were also significantly higher in areas with higher average temperature and precipitation, excluding in rice paddies (Fig. 4e–h, A.9). For forest species, neither climate variable had a significant effect on species-level or group-level partial regression coefficients, total abundance, or species richness (Fig. 3c; Fig. 4i–l; Fig. A.7). The results of community-level hyperparameters were similar to those observed in grassland species (Fig. A.10).

4. Discussion

4.1. Functional groups

The habitat suitability of abandoned farmland differed markedly depending on functional group, but was consistent throughout Hokkaido for each group. We showed a clear difference in the habitat suitability of abandoned farmland for bare-ground and grassland species. The abundance and richness of bare-ground species was higher in active farmlands than in abandoned farmland, consistent with previous studies in Europe and southern Japan (Sirami et al. 2008; Katayama et al. 2015). For example, skylark, a bare-ground species, was found to avoid the tall dense perennial plant cover that had established in abandoned farmlands in Poland (Orłowski 2005). Our results suggest that abandoned farmland is unsuitable habitat for bare-ground species, meaning that continued farmland abandonment will result in loss of suitable habitat for these species.

By contrast, the abundance and richness of grassland species in abandoned farmland was higher than in active farmland, and comparable to natural wetlands. This is likely due to vegetation succession and the establishment of perennial grasses in abandoned farmland, which provides foraging and breeding habitat for these species (Kennerley and Pearson 2010). The importance of abandoned farmland as habitat for grassland species was also identified in some studies in Europe (e.g., Orłowski 2005; Berg and Gustafson 2007; Radovic et al. 2013; Kamp et al. 2018). Abandoned farmland likely becomes suitable habitat for grassland species once perennial grasses establish; farmland abandonment can provide valuable alternative habitat for species whose habitats have been lost to agricultural expansion. This could especially be the case in floodplain or valley plain landscapes where perennial grasses continue to dominate 20–50 years after farmland abandonment (e.g., Rosenthal 2010; Saito et al. 2018), possibly due to a rise in groundwater level (Morimoto et al. 2017). However, there is a possibility of tree species colonization in the future (Sirami et al. 2007; Zakkak et al.

2018). We also note that, due to high stem length, some types of grassland might not be included in openland, though we divided openland into bare ground and grassland.

Although the abundance and species richness of forest species in abandoned farmland was higher than in cropland, the estimated abundance in abandoned farmland (0.22 individuals/ha) was substantially lower than an estimate obtained for forest habitat on Hokkaido (9.3 individuals/ha; Hanioka et al. 2018a). It is likely that these species do not occupy abandoned farmland due to the relatively lower level of shrub or tree cover in the sampling plots than those in forests (Fig. A.2). Previous studies have reported that tree and shrub cover are likely to establish in abandoned farmland in tropical and mountainous regions (e.g., Benjamin et al. 2005; Sirami et al. 2007; Rozendaal et al. 2019) and provide suitable habitat for forest species (Navarro and Pereira 2015; Acevedo-Charry and Aide 2019).

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

4.2. Spatial differences in habitat suitability

It has been suggested that impact of farmland abandonment on biodiversity varies between geographic regions (Queiroz et al. 2014). However, we observed weak and non-significant interactive effects between climate variables and abandoned farmland for 30 of the 33 species used in our analyses and group hyperparameters. Instead, abandoned farmland was found to be more suitable for grassland species than active farmland, and was even comparable to natural wetlands, but abandoned farmland was less suitable for bare-ground species, and these trends were consistent across all of Hokkaido. It is possible that regional differences in habitat suitability could be detected at a larger spatial scale than that used here, for example at the continental scale, at which landscape composition and vegetation types change remarkably (Brown et al. 1995; Randin et al. 2006).

Average temperature and precipitation positively affected the abundance and richness of grassland species. This is likely a result of higher vegetation productivity. Temperature exerts a strong influence on shoot growth in reeds (Engloner 2009) and thus stem length of reed is likely to be higher in areas with higher average temperatures (Fig. A.1). Areas with rich vegetation and high precipitation provide abundant nesting sites (Fujimaki and Takami 1986) and terrestrial food sources (Gorzo et al. 2016) for grassland species. Bird communities could also be affected by vegetation composition and plant species richness, which differ across Hokkaido (Ishikawa 1983). Although the relative importance of abandoned farmlands as habitat was consistent across Hokkaido, we note that climate factors influenced how many species or individuals abandoned farmland can harbor.

5. Conclusion and conservation implications

Farmland abandonment has negative impacts on bare-ground species and positive impacts on grassland and forest species. Therefore, distinct conservation strategies are required for these functional groups. Wetland cover has been reduced on Hokkaido, particularly in the warmer areas (e.g., Ishikari and Tomakomai; GSI 2000), and abandoned farmland in those warmer areas can harbor double the abundance of grassland species as that in cool areas. Therefore, abandoned farmland represents a potential mitigation to the dramatic negative effects of wetland loss, especially in the warmer areas of Hokkaido. Maintaining active farmlands is also important in the warmer areas in Hokkaido since the abundance of bare-ground species was also high in those areas.

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

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Figure captions

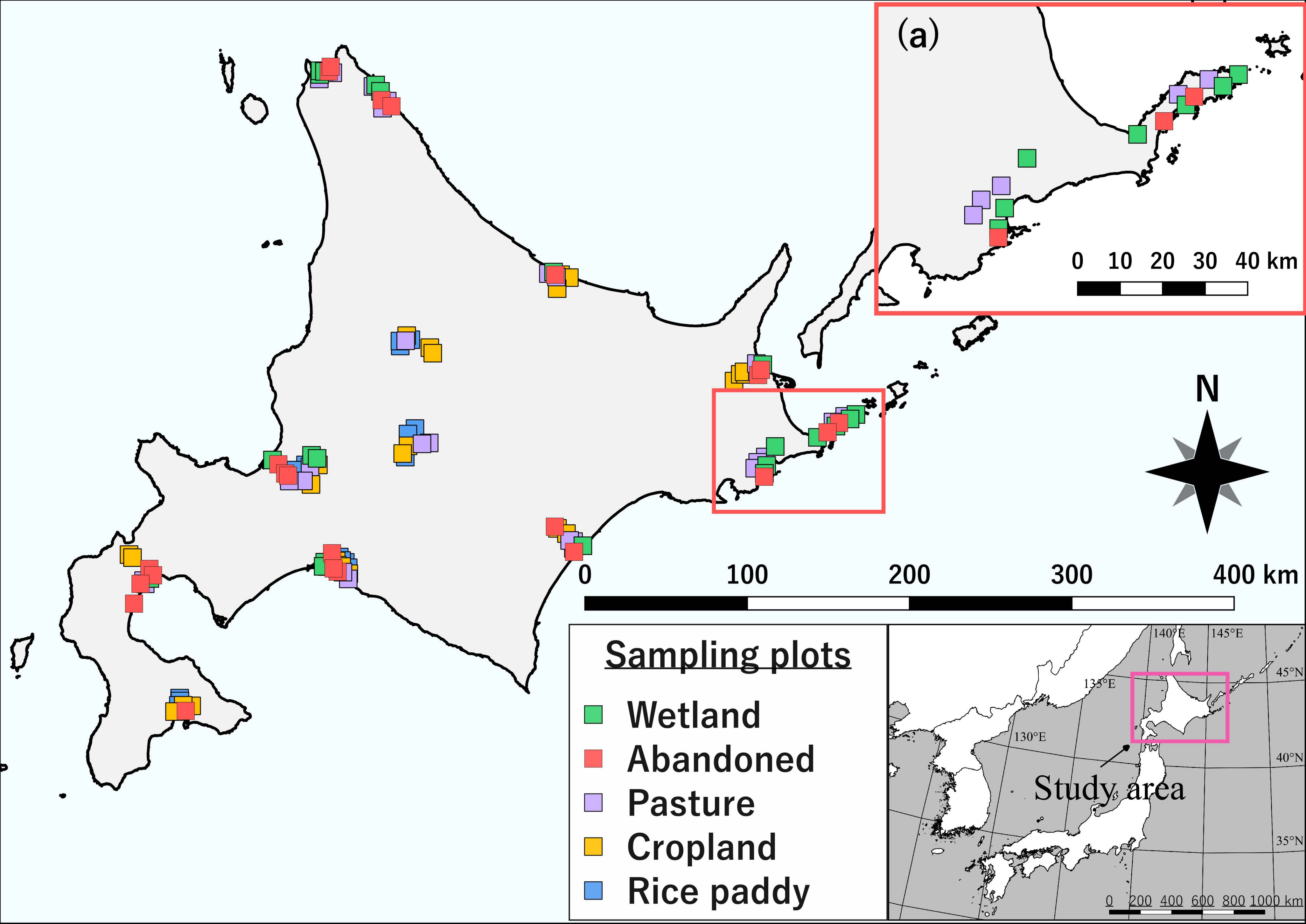
Fig. 1. Study area and the locations of the sampling plots. (a) Enlarged map of the study area, indicated by the red square, displaying the Hamanaka and Nemuro areas. The 113 sampling plots are represented by squares and land-use types are indicated by color. Source: DIVA-GIS Free spatial data.

Fig. 2. Estimates of hyperparameters, total abundance, and species richness for each land-use type (per 3 ha). Results are shown for each functional group in panels a–i. Community-level results are shown in panels j and k. Total abundance was calculated by summing the expected abundance of each species within a functional group. Climate variables were held to their means. Dots indicate median values and bars indicate 95% credible intervals. W = wetland, A = abandoned farmland, P = pasture, C = cropland, and R = rice paddy.

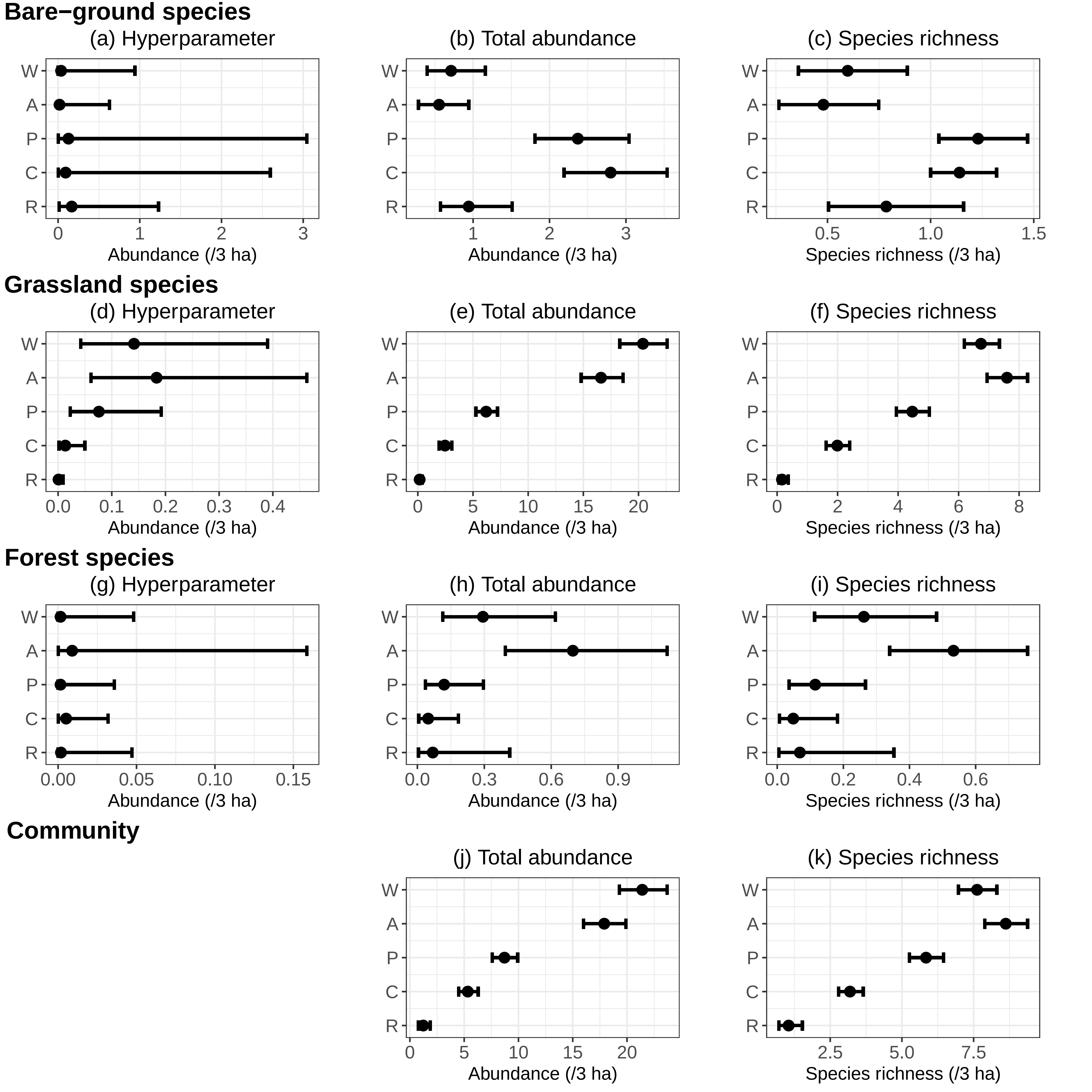
Fig. 3. Hyperparameters for climate variables and interaction terms for each functional group. Black dots indicate median values and bars indicate 95% credible intervals. T:Ab and P:Ab represent interaction terms between average temperature and abandoned farmland, and between average precipitation and abandoned farmland, respectively. Temp = temperature, Prec = precipitation.

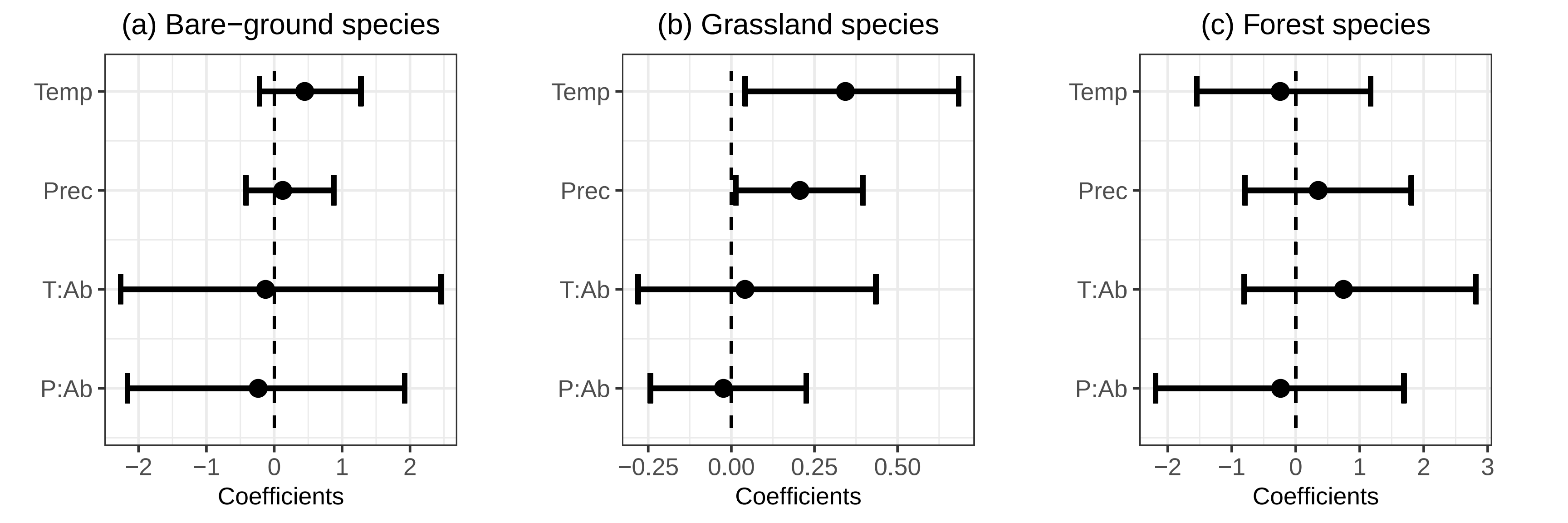
Fig. 4. The relationships between total abundance or species richness and climate variables for three functional groups. In each panel, the other climate variable is held to its mean value (i.e., 0). Solid lines represent median values and shading indicates 95% credible intervals. Land-use types are represented by colors. Because cropland and rice paddy only occurred in areas with higher average temperature, we also analyzed these data by excluding these two land-use types; the results were qualitatively similar, see Fig. A.8 and A.9. Green = wetland,

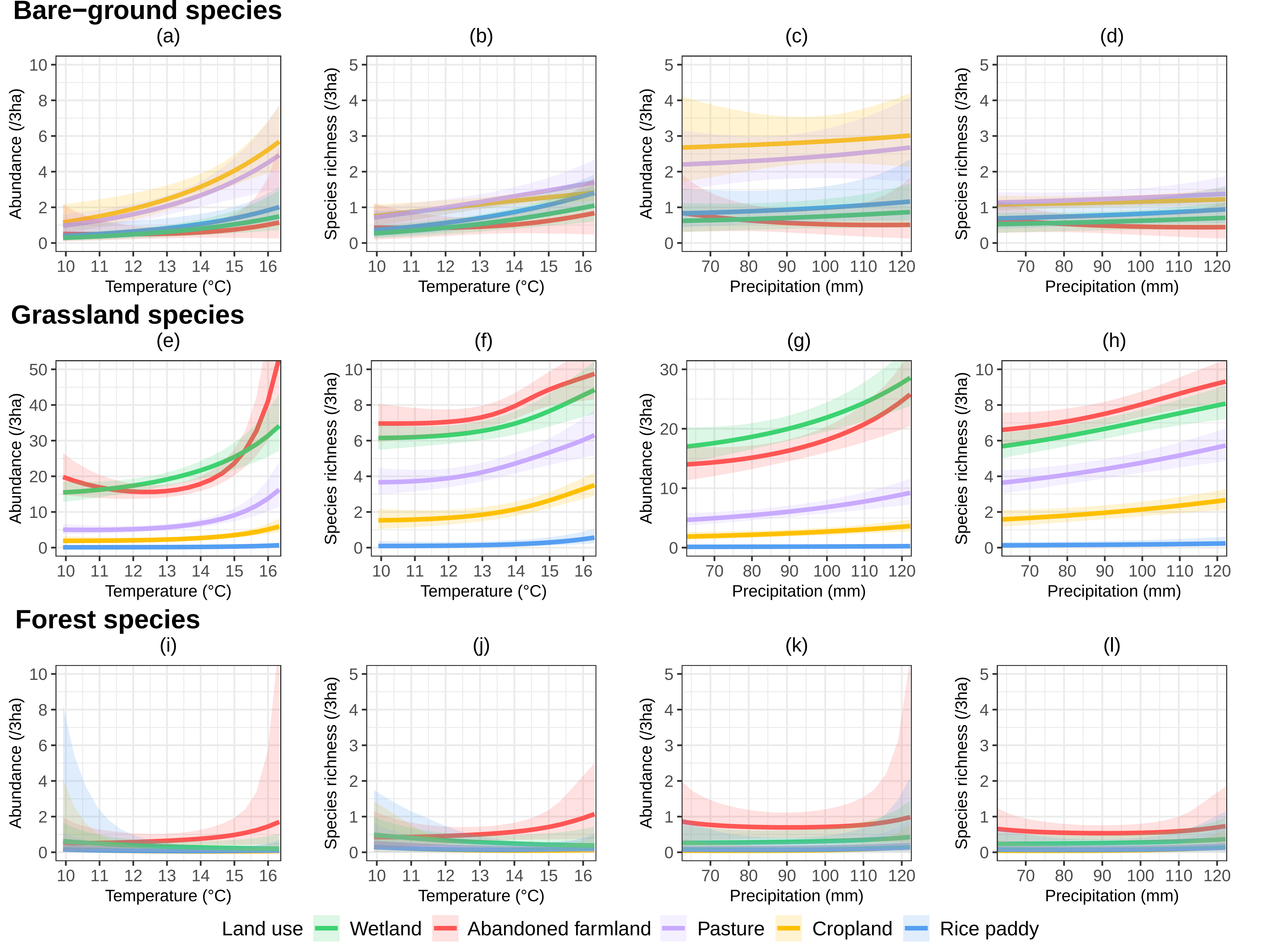
Red = abandoned farmland, Purple = pasture, Yellow = cropland, and Blue = rice paddy.



(a)
0 10 20 30 40 km
N
0 100 200 300 400 km
Sampling plots
Wetland
Abandoned
Pasture
Cropland
Rice paddy
140°E 145°E
135°E
45°N
130°E
40°N
Study area
35°N
0 200 400 600 800 1000 km


Bare−ground species
(a) Hyperparameter
(b) Total abundance
(c) Species richness
W
A
P
C
R
0
1
2
3
0.5
1.0
1.5
Abundance (/3 ha)
Species richness (/3 ha)
Grassland species
(d) Hyperparameter
(e) Total abundance
(f) Species richness
0.0
0.1
0.2
0.3
0.4
0
5
10
15
20
0
2
4
6
8
Forest species
(g) Hyperparameter
(h) Total abundance
(i) Species richness
0.00
0.05
0.10
0.15
0.0
0.3
0.6
0.9
0.0
0.2
0.4
0.6
Community
(j) Total abundance
(k) Species richness
0
5
10
15
20
2.5
5.0
7.5


(a) Bare−ground species
(b) Grassland species
(c) Forest species
Temp
Prec
T:Ab
P:Ab
−2
−1
0
1
2
3
−0.25
0.00
0.25
0.50
Coefficients



Bare−ground species
(a)
(b)
(c)
(d)
Abundance (/3ha)
Species richness (/3ha)
Temperature (°C)
Precipitation (mm)
Grassland species
(e)
(f)
(g)
(h)
Forest species
(i)
(j)
(k)
(l)
Land use
Wetland
Abandoned farmland
Pasture
Cropland
Rice paddy