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Effects of Landscape Heterogeneity at Multiple Spatial Scales on Paddy field-breeding Frogs in a Large Alluvial Plain in Japan

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Abstract

Enhancing the environmental heterogeneity of habitats is essential to decelerate the degradation of biodiversity in rice paddy ecosystems caused by the recent rapid changes in agricultural landscapes. However, paddy field environments hierarchically belong to agricultural landscapes and river basins. Therefore, the spatial scale of environmental heterogeneity affecting the distribution patterns and abundance of the organisms inhabiting paddy fields, such as frog species, varies. Thus, in the Kanto Plain, the largest alluvial plain in Japan, we conducted an extensive frog survey to ascertain multiple spatial scale heterogeneities of frog abundance in relation to topography, climate, land use pattern, and features of paddy fields. Across 200 field sites, five frog species were detected during calling surveys. The statistical, niche and abundance models revealed differences in distribution patterns, spatial heterogeneity of abundance, and environmental preference of these frogs at the spatial levels of river basins, landscapes, and paddy fields. While the distribution pattern and abundance of *Zhangixalus schlegelii* were affected by the percentage of forest area, those of *Pelophylax porosus porosus* were sensitive to features relating to water availability of the paddy fields. Despite the small diversity of species detected, the presence of two species with unique habitat preferences revealed significant benefits of habitat heterogeneity in the agricultural landscape, allowing us to suggest management strategies for improving frog diversity in agricultural landscapes dominated by paddy fields.

Keywords Abundance model · Anuran call surveys · Species distribution model · MaxEnt · Rice paddy ecosystems

Introduction

Pristine wetland habitats that have developed in the alluvial plains have historically been replaced by rice paddy fields since BC 1,000 year in south, southeast and east Asia, including Japan (Fuller et al. 2010). However, flooded rice paddy fields maintain various functions similar to natural wetlands (Elphick 2000; Yoon 2009). Consequently, paddy fields, including the surrounding banks and irrigation channels, have become valuable habitats for diverse wetland and flood plain plants and animals in Japan (Matsuno et al. 2006; Washitani 2007; Katoh et al. 2009; Natuhara 2013). However, recent drastic changes in agricultural landscapes, including modernization of farming practices, urbanization and abandonment of cultivation, have caused an overall loss of habitat availability and resultant biodiversity (Katayama et al. 2015; Koshida and Katayama 2018). Efforts to decelerate the deterioration and improve biodiversity in paddy fields are crucial to the conservation of wetland species in agricultural landscapes (Katoh et al. 2009; Natuhara 2013; Koshida and Katayama 2018).

Species richness and abundance in agricultural landscapes increases with increasing environmental heterogeneity (Benton et al. 2003; Tscharntke et al. 2005; Miyashita et al. 2012). However, the spatial size of the landscape and the grain size of the spatial heterogeneity to adequately assess the spatial variation in the distribution, composition, and abundance of species depends on the species and region (Tscharntke et al. 2005; Miyashita et al. 2012; Katayama et al. 2014; Collins and Fahrig 2017). While environmental factors of large scales such as climate and topology impact

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species distributions and agricultural landscapes, abundance of species within a given region would be influenced by fine-scale land-use. In addition, although paddy fields are treated as homogeneous farmlands in the agricultural landscape and land-use classifications because of monoculture, they have a spatial-temporal heterogeneous environment. For example, there are differences among fields and regions in the vegetation on paddy field banks, types of ditches constructed for field improvement, water management using irrigation practices, and agricultural practices, which affect species composition and abundance (Kato et al. 2010; Fujita et al. 2015; Moreira and Maltchik 2014). Therefore, it is difficult to understand environmental heterogeneity effects on the distribution patterns of organisms. For conservation purposes, however, areas which have the potential to increase biodiversity can be determined by revealing the relationship between environmental factors at multiple scales and the distribution patterns of species.

This study aimed to reveal the effects of multi-scale heterogeneity in an agricultural landscape over the extensive alluvial plain by using frogs as an indicator species and estimating the distribution patterns of frogs by statistical modeling. Paddy field-breeding frogs are representative animals amenable to agricultural landscape. Although they are similar in their use of paddy fields as breeding sites, depending on the species' ecological traits, they are affected differently by the environments around and within the paddy fields. Therefore, the distribution of each species would be affected by environmental heterogeneity at multi-spatial scales. Depending on the region, several previous studies have indicated that environmental factors at different spatial levels (i.e., topography and climate, the composition of land use in the agricultural landscape, and the feature of each paddy field) influence the species composition and abundance of frogs (Fujioka and Lane 1997; Guerry and Hunter 2002; Van Buskirk 2005; Kato et al. 2010; Tsuji et al. 2011; Moreira and Maltchik 2014; Fujita et al. 2015; Collins and Fahrig 2017; Zheng and Natuhara 2020). Although environmental factors at the field level such as the timing of paddy flooded and types of ditches, are often assessed, it is not easy to obtain an environmental layer that provides coverage of an extensive area. In this study, we used satellite and public data to grasp the features of paddy fields. In particular, we focused on the hydroperiod of paddy fields (da Silva et al. 2011; Naito et al. 2012; Kidera et al. 2018), controlled by the farmers for the purpose of rice cultivation, while water levels of floodplains and wetlands would fluctuate naturally due to rain and flooding. Modern paddy field improvement is one of the causes of population decline of some frogs because it results in the construction of deep concrete ditches that disrupt migration, causes loss of water from the paddy fields in the agricultural off-season, and reduces the area of levees due to enlarged fields (Fujioka and Lane 1997; Azuma and Takeuchi 1999; Fujita et al. 2015; Katayama et al. 2015; Kidera et al. 2018).

To survey a large area in a short period during the frog breeding season, we conducted field surveys by recording advertisement calls of frogs. A simple method of recording calls by traveling between many preset survey sites is very effective (e.g., Shimada et al. 2015). In the Kanto Plain and surrounding areas, while some native frog species are declining (Fujioka and Lane 1997; Kidera et al. 2018), a non-native frog species from Western Japan (*Fejervarya kawamurai*) has rapidly expanded (Hasegawa and Ogano 1998; Ushioda et al. 2016). Therefore, this study, conducted over a short period, would provide an overview of the declining paddy field-breeding frog distributions and changing rice paddy ecosystems in the alluvial plain of Kanto district, Japan.

Materials and Methods

Study Area and Frog Species

In the Kanto plain, the largest alluvial plain in Japan (approximately 17,000 km^2), we selected 200 sites adjacent to paddy fields between an elevation of 0 m and 180 m. This area included four river basins: Tone, Arakawa, Naka, and Kuriyama rivers (Fig. 1, Supplement 1). The distance between the sites was set to at least 3 km.

Out of 11 species, including invasive species inhabiting the study area (Matsui and Maeda 2018), we attempted to detect frogs that use lowland paddy fields with breeding seasons in April and June (Hasegawa 1998). Of these species, there are only a few records of *Glandirana rugosa* in the lowlands in the study area (The Committee of the Red Data Book Chiba 2011). However, *Fejervarya kawamurai*, native to Western Japan, was observed in the Kanto district in the late 1990s and its distribution has rapidly expanded its distribution in this area so far (Hasegawa and Ogano 1998; Ushioda et al. 2016).

Field Survey, Species Identification, and Abundance of Frogs

To collect abundance data from a large area within a short period, we simplified the field survey method by only recording advertisement calls at night-time. The advertisement call is species-specific. Therefore, the chorus of frogs represents presence, breeding activity, and relative abundance of each species (Shirose et al. 1997; Corn et al. 2011). No visual searches were conducted. We performed two

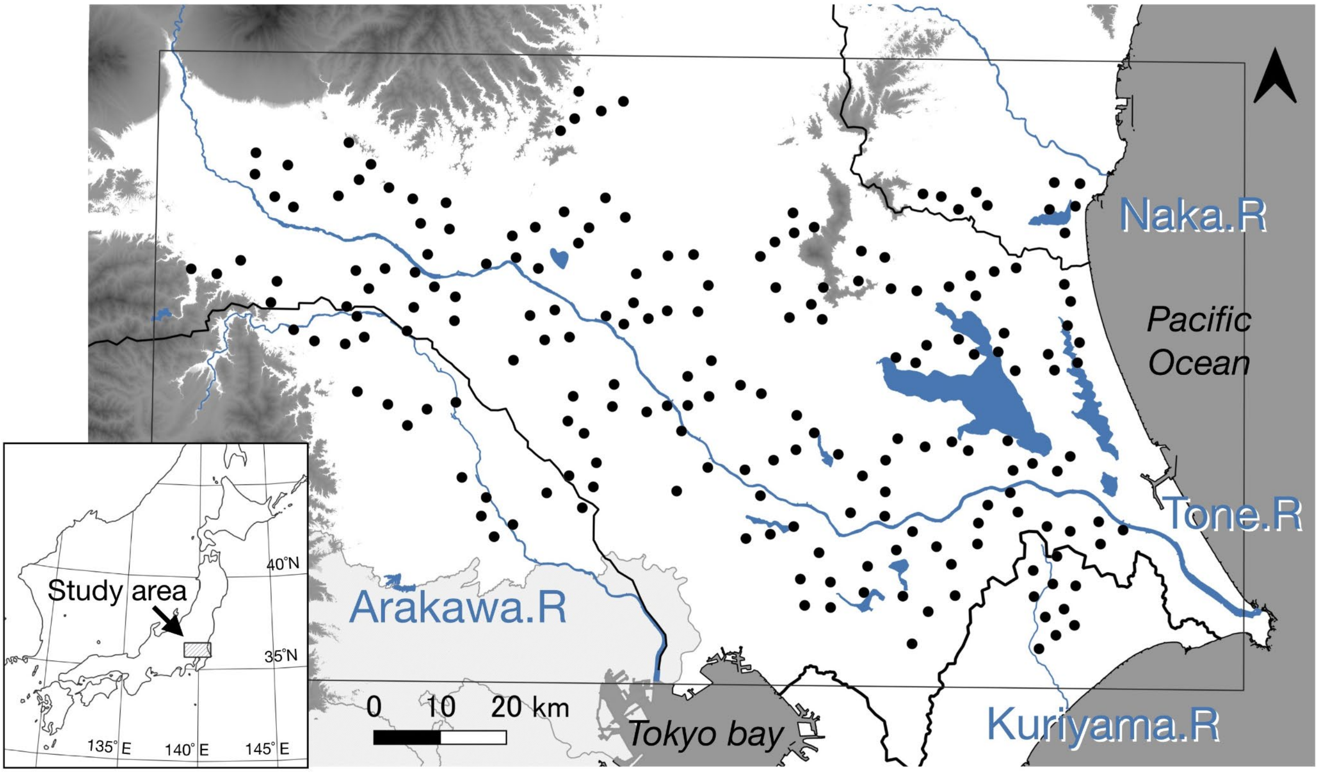


Fig. 1 Maps of Japan and the study area. Circles indicate survey sites. Blue zones show lakes and rivers, and the lines indicate the boundaries of the river basin

surveys at each survey site (May survey, 5/2–31/2018; June survey, 6/14 – 7/1/2018).

Twelve people, including the authors, experts, and beginners, conducted field surveys. Since they conducted surveys according to their convenience, the surveyors randomly selected the order of site visits over two survey periods. The surveyors recorded the condition of the paddy field (occurrence of rice planting and flooding) during the day before the May survey. Semi-automated audio recording systems were used to collect frog-calling data (e.g., Lotz and Allen 2007). The surveyors drove to each site, directed microphones toward the paddy fields from the roadside, and recorded frog calls for three minutes using a digital voice recorder (Olympus, Voice-Trek DM-720) attached to a microphone (Olympus, Stereo microphone, ME51SW). All recordings were conducted between 19:00 or sunset and 23:00. To protect the recording devices from rain and avoid rain sounds disturbances in the recordings, the survey was not performed in the rain. Upon arrival at the site, the lights and vibrations from the car could disturb frog behavior; therefore, only the last two minutes of the recording was used for analysis. All the recordings were played back by the author, Matsushima, and confirmed by Hasegawa.

Frog calls are often used as a substitute for abundance by classifying them into several levels (e.g., calling index: a step-wise measure of the number of individuals calling, Shirose et al. 1997; Nelson and Graves 2004; Steelman et al. 2010; Corn et al. 2011; Shearin et al. 2012). However, it is difficult for the surveyors with no training to identify frog species and calling levels (Lotz and Allen 2007). Therefore, a proxy for abundance was calculated using the recorded data. The 2-minute recording data were divided into ten segments, and the presence or absence of the call for each species was recorded in one segment (12 s). The number of segments with calls was defined as the "number of call segments" of each species at each site and was used for abundance analysis.

In the field survey, the surveyors recorded the calling levels of each species (0 = no calling, 1 = one or two individuals calling, 2 = individuals can be counted, 3 = chorus). We assessed the relationship between the number of call segments and call levels (1, 2, 3) and considered this approach appropriate (Supplement 2). A significant positive correlation between calling levels and the number of call segments was observed, except for *Z. schlegelii*, when the sample size was small.

Environmental Variables

To construct distribution and abundance models of each species, we selected 11 environmental variables, except for one of each pair of variables with Pearson's correlation coefficients greater than 0.75 (Supplement 3). These variables could be categorized as topography (distance from rivers and lakes), climate (annual minimum temperature, and precipitation of June (average over 30 years), land-use (the ratios of paddy fields, cropland except paddy fields, forest, urban area, and the aggregation index of forest (AI forest) and urban area (AI urban)), and four features of paddy fields. The aggregation index measures the degree of aggregation of a given land-use patch in the landscape and indicates the spatial pattern of land-use (He et al. 2000). We calculated aggregation index of each land-use using R package "landscapemetrics" (Hesselbarth et al. 2019). There were high positive correlations between ratios and aggregate indices for rice paddies and fields, and were therefore excluded from the variables. The available database and maps relating to microhabitats of paddy fields are unknown because most of the features of paddy fields frequently depend on the decisions of each farmer, local area, or year. Therefore, we created four features of paddy field datasets: the length of the boundary between the paddy field and the forest (BPF), timing of paddy fields being inundated (TPI), the ratios of paddy fields performed with field improvement (PFI), and low elevation area in paddy fields (LEA)). TPI, PFI, and LEA were related to water availability in frog habitats (Supplements 3 and 4). We used the boundary between the paddy field and the forest to describe the accessibility of frogs between forests and paddy fields. The timing of water availability within the paddy fields affects the presence and density of frogs (Naito et al. 2012; Kidera et al. 2018). The low-elevation area was assumed to be indicative of the accumulation of water. The ratio of each land-use within each of the circular buffers of different radii (250, 500, 750, 1000, 1250 m) was calculated. To create the background layers and project the models to the study area, the environmental variables were calculated for each buffer size per 1 km in the study area.

Principal component analysis (PCA) was performed to compare the environmental preferences of each species. The PC scores were calculated from each of the categories for land-use and features of paddy fields in the 750 m buffers. For the pairwise comparisons of PC scores among frogs, Mann-Whitney U tests were performed with p-values corrected by the Bonferroni method. All statistical analyses were performed using the R software (v. 3.5.3; R Core Team 2019) and Quantum GIS 3.4 software (QGIS Development Team 2018) was used to prepare the datasets and visualize the resulting distribution maps.

Distribution Models

To investigate the distribution pattern of each species and the factors determining those patterns, we constructed distribution models and abundance models from field survey data and projected them to the Kanto Plain. We intended to assess the adequacy of the models and used two approaches for distribution models: (1) generalized linear models (GLMs), a common distribution model that uses presence-absence models, and (2) maximum entropy modeling (MaxEnt), which is a machine-learning method that is widely used as presence-only models (Phillips et al. 2006; Elith et al. 2011).

We defined a site in which calls were detected as an occurrence site. Subsequently, GLMs with a binomial distribution and a log-link function were applied. To determine the best land scale for analysis, we built models with all variables of each buffer and selected the model with the lowest Akaike information criterion (AIC) value. Next, models within two units of ΔAIC (the difference between the model AIC and the lowest AIC) were selected from candidate models built with all combinations of the explanatory variables, and model averaging was performed based on AIC (Burnham and Anderson 2002) using the R package "MuMin" (Barton 2020). A squared term was included because the land-use effects could be nonlinear. We also calculated the relative importance (RI) of the variables to quantify the importance of the variables.

We used MaxEnt software (version 3.4.1.) (Phillips et al. 2017) for modeling species niches and distributions. For each species, the MaxEnt model was built using 80% of the occurrence sites randomly selected for training and all environmental variables. It was run with 2 for the regulation multiplier and 5000 iterations, and the other values were kept at their default, and repeated 30 times for each buffer size. The model performance was evaluated based on the area under the receiver operating characteristic curve (AUC). Means of MaxEnt outputs were calculated, and average models were constructed for each species. Background points for *F. kawamurai* were sampled from the Tone and Arakawa basins. To compare suitable areas among species, the potential distributions were divided into suitable and unsuitable cells using threshold values that maximized the sum of sensitivity and specificity (Liu et al. 2013).

Abundance Model

Among the frog species found, for *Pelophylax porosus porosus*, *Zhangixalus schlegelii* (*Rhacophorus schlegelii*), and *Dryophytes japonicus* (*Hyla japonica*), we estimated abundance by using the hierarchical model by Royle and Nichols (2003) and "the number of call segments" as an index of relative abundance. We used this model to estimate abundance from repeatable binomial observation data (i.e., detection/non-detection (0 or 1)) by exploiting the relationship between abundance and detection probability (Royle

Table 1 Distribution of frog species at various sites, and per river basin and survey. Numbers in parentheses indicate the number of survey sites in each river basin

		Survey season		River basin			
Species	Total	May	June	Tone (163)	Arakawa (17)	Kuriyama (10)	Naka (10)
Dryophytes japonicus	197	181	183	162	16	10	9
Pelophylax porosus porosus	131	97	110	110	4	10	7
Zhangixalus schlegelii	75	75	2	50	6	9	10
Fejervarya kawamurai	87	35	76	76	11	0	0
Lithobates catesbeianus	22	12	15	18	0	0	4

and Nicols 2003; Nakashima 2020). Response variables, that is, the number of call segments, were the number of counts per 20 segments (10 segments in May and 10 segments in June) constructed in a unit of 12 s calling or none. With the increase in frog numbers at a site, the more continuous the chorus would be; we expected that in abundance models (Royle and Nichols 2003), more call segments would get a value of 1 at a site, assuming that the presence-absence of species at each segment is sampled with the number of times of "call segments". It is assumed that abundance at a site remains constant during two surveys, and segments are independent. However, this latter assumption might be violated when a frog calls continuously (i.e., pseudoreplication), and then the abundance might be overestimated. However, there are positive correlations between the number of individuals and the duration of the continuous calling (Llusia et al. 2013), and the frogs we surveyed chorus frequently during the breeding season (Yamamoto 2012). Therefore, we considered that the number of call segments is a viable method to indicate relative abundance. In addition, we examined the relationships between the estimated number of call segments and the probability of presence to support the utility as the index of relative abundance (Weber et al. 2017).

Frog activity is influenced by weather conditions, such as temperature, wind, and rain (Weir et al. 2005; Steelman et al. 2010; Shearin et al. 2012). Therefore, we built models of detection probability with all combinations of air temperature (°C) and wind speed (m/s) at 19:00 on the observation day, observation date (1 d = May 1st), whether or not rice planting was completed (categories), and the total number of call segments while using a null model for abundance. Air temperature and wind speed data for the survey sites were obtained from the nearest meteorological observation stations of the Japan Meteorological Agency (Supplement 1). Next, we selected the detection model for each species with the lowest AIC value. We selected a suitable buffer size and then a combination of environmental variables explaining the abundances of each frog and performed model averaging (Burnham and Anderson 2002) using the same procedure as that used for building GLM models. We used the R package "unmarked" v. 0.13-2 (Fiske and Chandler 2011) for these analyses.

Results

Field Survey

Five species were recorded in the four river basins; *D. japonicus*, *P. p. porosus*, *Z. schlegelii*, *F. kawamurai* (native species from Western Japan), and *Lithobates catesbeianus* (invasive species, native to the eastern United States) (Supplement 1), and the number of sites with observed calls of each species varied among river basins (Table 1). *Dryophytes japonicus* was observed most frequently (90–100% of the sites in each river basin); *P. p. porosus* was observed less frequently in Arakawa basin (23.5%) than other basins (67.5–100%); and *Z. schlegelii* was observed less frequently in Tone and Arakawa basins (30.7–35.3%) and more in Naka and Kuriyama basins (90–100%). *Fejervarya kawamurai* was found frequently in the Tone and Arakawa basins (46.6–64.7%) but not found in the Naka and Kuriyama basins, suggesting that it has not yet expanded into all basins. *Lithobates catesbeianus* were excluded from the other analyses because it was found only at a few sites (11% of all sites) and because their main breeding site is ponds rather than paddy fields (Matsui and Maeda 2018) (Supplement 5).

We expected to find *G. rugosa* inhabiting the study area (The Committee of the Red Data Book Chiba 2011; Matsui and Maeda 2018), but it was not detected at any of the sites. However, this call could be detected outside the survey sites (at the lower part of a mountain on the northeast side of the plain, altitude 45 m, a cooperator of field survey).

Distribution Patterns

Species detected at larger number of sites also had a higher number of suitable cells estimated by the distribution models both in the study area and within the Tone and Arakawa basins (the ratio of suitable area to the study area, *D. japonicus* 39.0%, *P. p. porosus* 31.4%, *Z. shlegelii* 21.7%; the Tone and Arakawa basins, *D. japonicus* 37.9%, *P. p.*

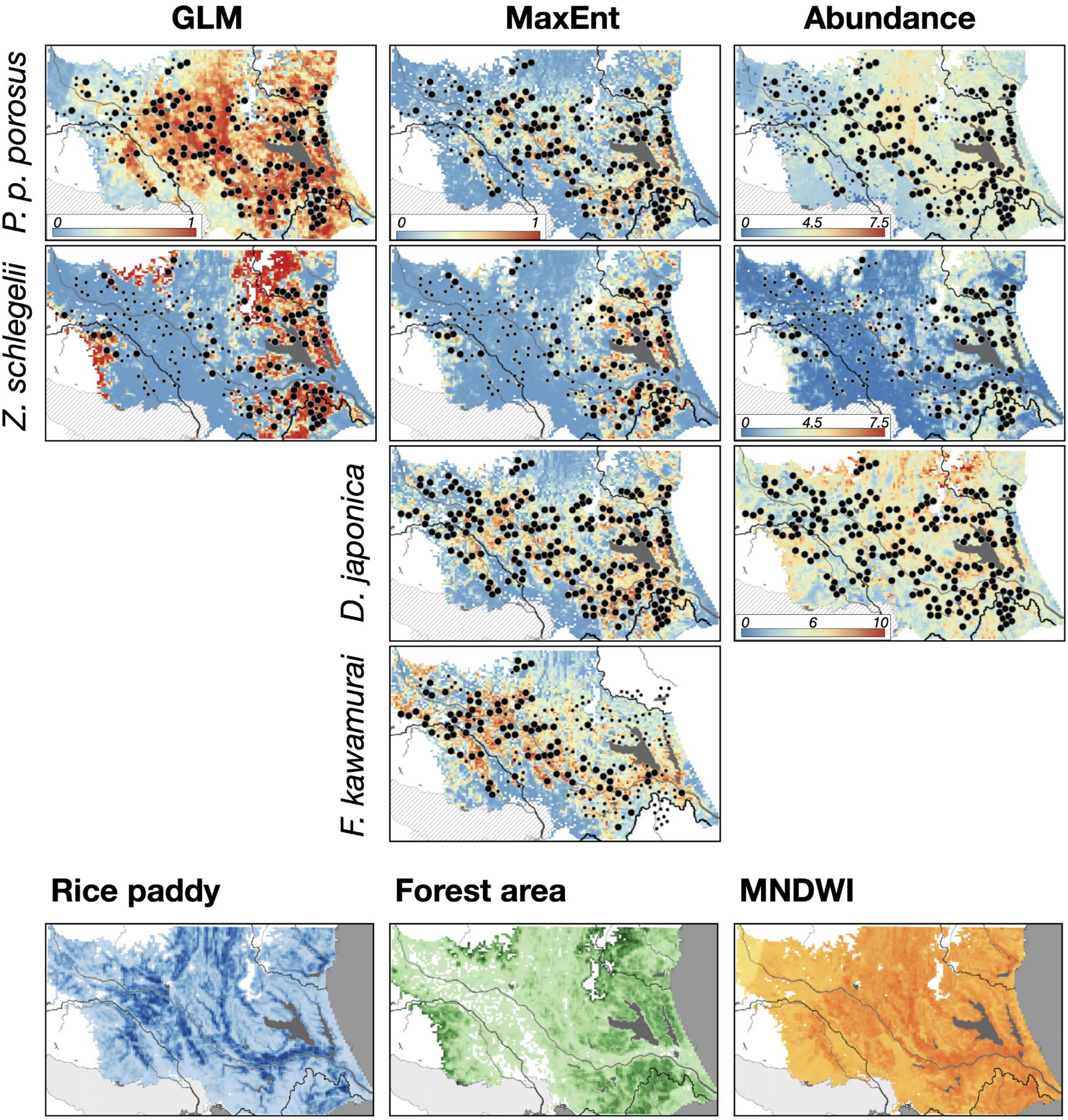


Fig. 2 Distribution maps of the presence and abundance distributions of *Pelophylax porosus porosus*, *Zhangixalus schlegelii*, and *Dryophytes japonicus* in the Kanto Plain, and presence distributions of *Fejervarya kawamurai* estimated by MaxEnt (Upper panel), and land use (rice paddy and forest area) and MNDWI (Modification of normalized difference water index, see Supplement 4) (lower panel). Large and small circles represent occurrence and absence points, respectively

porosus 29.9%, *F. kawamurai* 27.5%, *Z. shlegelii* 18.2%; Supplement 6). The distribution patterns of *P. p. porosus*, *D. japonicus*, and *F. kawamurai* from the distribution models were similar (Fig. 2). However, compared with the other two species, the cells with high probabilities of *P. p. porosus* presence had diminished towards the west. In contrast to these species, *Z. shlegelii* appeared on the margins of the plains surrounded by hilly areas with high ratios of forest area (Fig. 2). In *P. p. porosus* and *Z. shlegelii*, the results of GLM and MaxEnt were similar, but there were partial discrepancies in the northern and eastern marginal areas for *P. p. porosus*. Presence and abundance distributions tended

Table 2 Number of sites with combinations of frog species.

(1) All area.

Ppor	Zsch	Both	None
81	25	50	44

X-squared = 0.036, df = 3, p-value = 0.998

(2) Tone and Arakawa basins.

Ppor	Zsch	Fkaw	Ppor & Zsch	Ppor & Fkaw	Zsch & Fkaw	3 species	None
37	13	26	25	43	9	9	18

X-squared = 5.395, df = 7, p-value = 0.612

Ppor: *Pelophylax porosus porosus*, Zsch: *Zhangixalus schlegelii*, Fkaw: *Fejervarya kawamurai*

to be roughly similar to *Z. shlegelii*, but the distribution of *P. p. porosus* was spread across the entire Kanto Plain, with a high abundance in the central part of the plain (Fig. 2). Thus, *D. japonicus* data were not analyzed by GLM because it was present in most sites. Similarly, *F. kawamurai* data were not analyzed by the GLM and abundance models because it is possible that at some sites environmental factors result in a false negative due to its ongoing distribution expansion.

There was no significant difference between the observed and expected frequencies of species combinations (Table 2). This suggests that the interactions between species may not be exclusive and may not influence the distribution of each frog.

Differences in the Environmental Preferences Among frog Species

In GLM, the buffer sizes with the lowest AIC were 1000 m and 750 m for *P. p. porosus* and *Z. schlegelii*, respectively. In MaxEnt, the buffer sizes at the highest AUC were 500, 750, 500, and 500 m for *P. p. porosus*, *Z. schlegelii*, *D. japonicus*, and *F. kawamurai*, respectively (Supplement 7). The accuracies of the models constructed using MaxEnt had high AUC scores for all species, and these models showed good fit (mean AUC scores of MaxEnt: *P. p. porosus*: 0.830 ± 0.029 SD, *Z. schlegelii*: 0.881 ± 0.036 SD, *D. japonicus*: 0.776 ± 0.037 SD, *F. kawamurai*: 0.772 ± 0.048 SD). For *P. p. porosus* and *Z. Schlegelii*, there were only a few environmental variables with high RI (> 0.9) in GLM and high contributions ($> 10\%$) in MaxEnt (Table 3 and Supplement 8). With respect to *Z. Schlegelii* distribution, variables with high RI in GLM and high contributions in MaxEnt were land-use variables (paddy fields, crop land, and urban area), and the ratios of forest were high for both. In *P. p. porosus*, TPI and LEA, variables of the features of paddy fields, had high RI in GLM and high contributions in MaxEnt. The environmental variables with high contributions in Maxent were almost consistent between *D. japonicus* and *F. kawamurai*. In these species, the variables of the features of paddy fields had low contributions in MaxEnt. AI forest, AI urban, and PFI had low RI in GLMs and low contributions in MaxEnt for all species, while AI urban was high RI in GLM for *P. p. porosus.*

For the calculations of the PC scores, a 750 m buffer size was used as the intermediate values of optimal buffer sizes of distribution models for each species. The first PCs of the categories for land-use and features of paddy fields explained 40.8% and 39.9% of the variance of the data, respectively. In both categories, the PC1 scores of *Z. schlegelii* were significantly different from those of any other frogs (Fig. 3). There were no significant differences in the PC1 scores among *P. p. porosus, D. japonicus* and *F. kawamurai*, although there were some differences in the variables with high contributions in the distribution model.

Abundance Model

The best buffer sizes of the abundance model were 500, 750, and 1000 m for *P. p. porosus*, *Z. shlegelii*, and *D. japonicus*, respectively (Supplement 7). In these species, variables with high RI in the abundance model were not much similar to those with high RI in the GLM or high contributions in MaxEnt (Table 4). Although the variables related to land use had high RI for all species, TPI for *P. p. porosus* and the variables related to the forest (the ratios of forest, AI forest, and BPF) for *Z. shlegelii* had high RI. Significant positive correlations were found between the prediction of abundance and probabilities of the presence of each species, except for *D. japonicus* (Fig. 4; correlation test, *P. p. porosus*: GLM, $r = 0.690$, $P < 0.001$, MaxEnt, $r = 0.549$, $P < 0.001$; *Z. shlegelii*: GLM, $r = 0.822$, $P < 0.001$, MaxEnt, $r = 0.763$, $P < 0.001$; *D. japonicus*: $r = 0.124$, $P = 0.008$).

Discussion

By investigating the distribution patterns of frogs, this study revealed that paddy field environments in the Kanto Plain have heterogeneities at various scales, including agricultural landscapes, paddy fields, and river basins. The landscape sizes and environmental factors in the land-use category and within paddy fields by which the presence of frogs was affected differed among species. Indeed, *P. p. porosus*

Table 3 Results of model averaging for the habitat models. The coefficient in italics indicates the variable included in the best model. Asterisks indicate a statistically significant coefficient ($P < 0.05$, derived from Wald statistic)

Species	*P. p. porosus*			*Z. schlegelii*			*D. japonicus*	*F. kawamurai*
	GLM		MaxEnt	GLM		MaxEnt	MaxEnt	MaxEnt
Variable	Estimate (SE)	Relative importance	Contribution (%)	Estimate (SE)	Relative importance	Contribution (%)	Contribution (%)	Contribution (%)
Annual minimum temperature	0.005(0.074)	0.063	8.28	-0.003(0.070)	0.023	7.54	12.46	10.61
Precipitation of June	*-0.043(0.030)*	0.909	2.90	-0.002(0.011)	0.053	0.12	2.96	0.73
water distance	2.945(14.242)	0.134	2.02	-0.318(6.931)	0.023	1.76	2.65	1.09
% Paddy field	-0.104(0.453)	0.142	11.59	*12.847(7.514)*	1.000	1.10	21.80	35.02
% Forest	0.028(0.328)	0.064	5.64	*20.543(7.417)**	1.000	38.51	6.26	0.90
% Crop land	0.045(0.363)	0.069	3.57	*12.47(7.52)*	1.000	0.38	3.42	1.02
% Urban area	0.048(0.503)	0.065	18.97	1.304(6.265)	0.115	19.53	26.12	30.46
AI forest	0.001(0.004)	0.079	2.83	*0.021(0.025)*	0.576	1.32	2.54	0.73
AI urban	*0.043(0.017)**	1.000	6.64	*0.011(0.014)*	0.654	0.86	5.40	7.54
BPF	*26.589(7.827)**	1.000	7.58	5.840(8.097)	0.507	23.59	5.20	0.84
TPI	*7.086(1.800)**	1.000	11.04	-0.858(1.809)	0.300	0.48	1.41	2.65
PFI	-0.162(0.390)	0.248	4.70	0.382(0.643)	0.404	2.74	4.47	1.16
LEA	*1.922(0.947)**	1.000	14.24	-0.246(0.737)	0.202	2.07	5.31	7.25
Intercept	2.622(4.527)			-17.019(8.030)*				

AI: aggregation index, BPF: the boundary between the paddy field and the forest, TPI: timing of paddy fields being inundated, PFI: the ratios of paddy fields where field improvement was performed, LEA: low elevation area in paddy fields

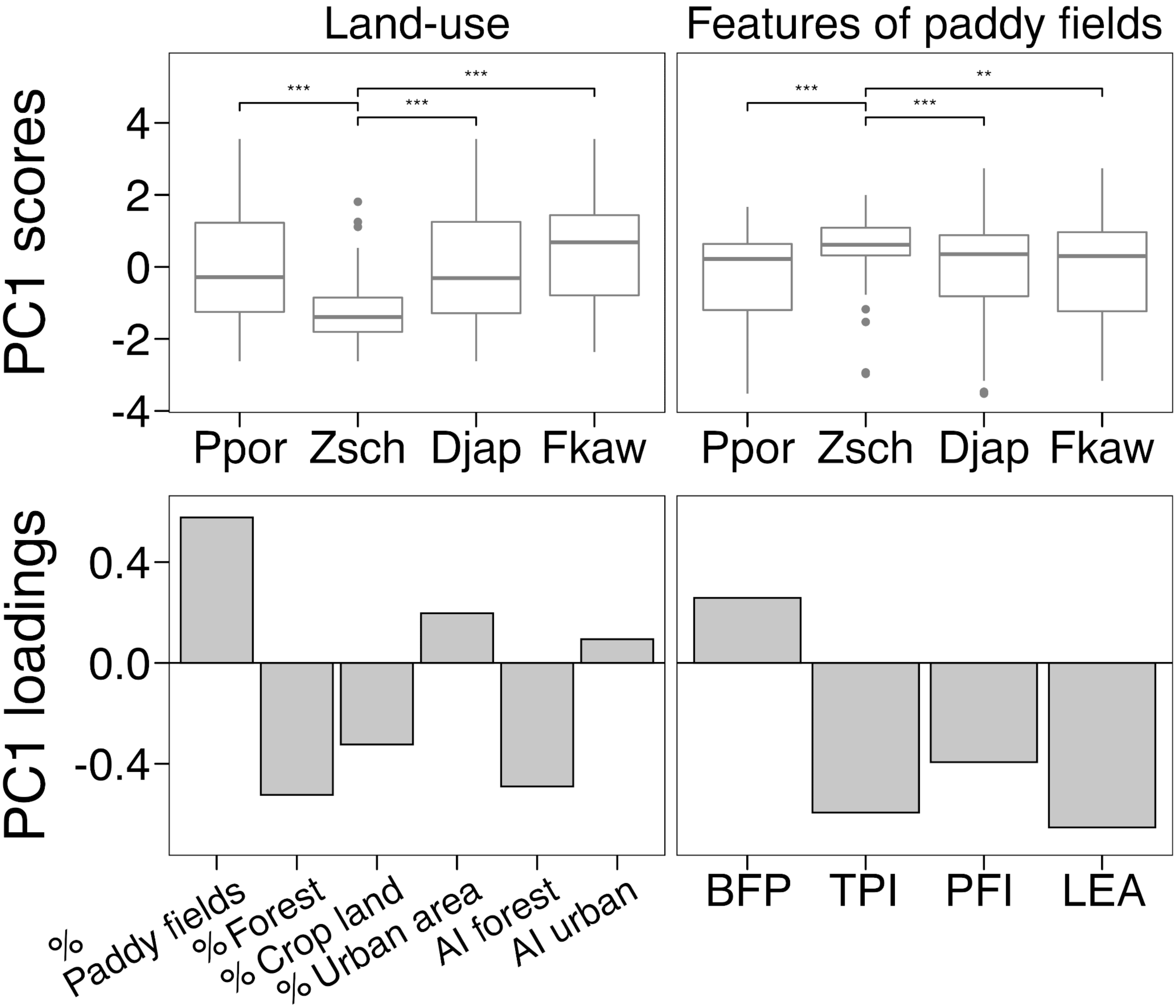


Fig. 3 Principal component analysis scores for land-use and features of paddy fields of each species. Asterisks indicate significant differences. Ppor: *Pelophylax porosus porosus*, Zsch: *Zhangixalus schlegelii*, Djap: *Dryophytes japonicus*, Fkaw: *Fejervarya kawamurai*, BPF: the boundary between the paddy field and the forest, TPI: timing of paddy fields being inundated, PFI: the ratios of paddy fields where field improvement was performed, LEA: low elevation area in paddy fields

was influenced by environmental factors within the paddy field and landscape, while factors at the landscape level strongly influenced other frogs. This study also showed the abundance distribution of each species. Large-scale or long-term monitoring where non-experts may be involved would need simplified field survey methods that require no specialized knowledge and technique and an approach for determining frog abundance mechanically using only recording data. Our target species have long breeding seasons (about two months), resident in the paddy fields during the breeding season, and call continuously; therefore, this approach would be effective. However, it would be necessary to modify the number of visits to a site, survey seasons, and recording time depending on the species and the region. Furthermore, the relationship between this index and population density would need to be assessed for each species, and improvement of the abundance model would also be required in future studies.

In addition, from the perspective of an extensive plain, it appears that the distribution of each species across the Kanto Plain was influenced by topography and past river basins. In the Nakagawa and Kuriyama basins, and the area adjacent to the uplands on the east side of the Tone Basin, there were many survey sites where *Z. shlegelii* and *P. p. porosus* were observed. However, the eastern side of the Tone Basin was not included in the Tone Basin before

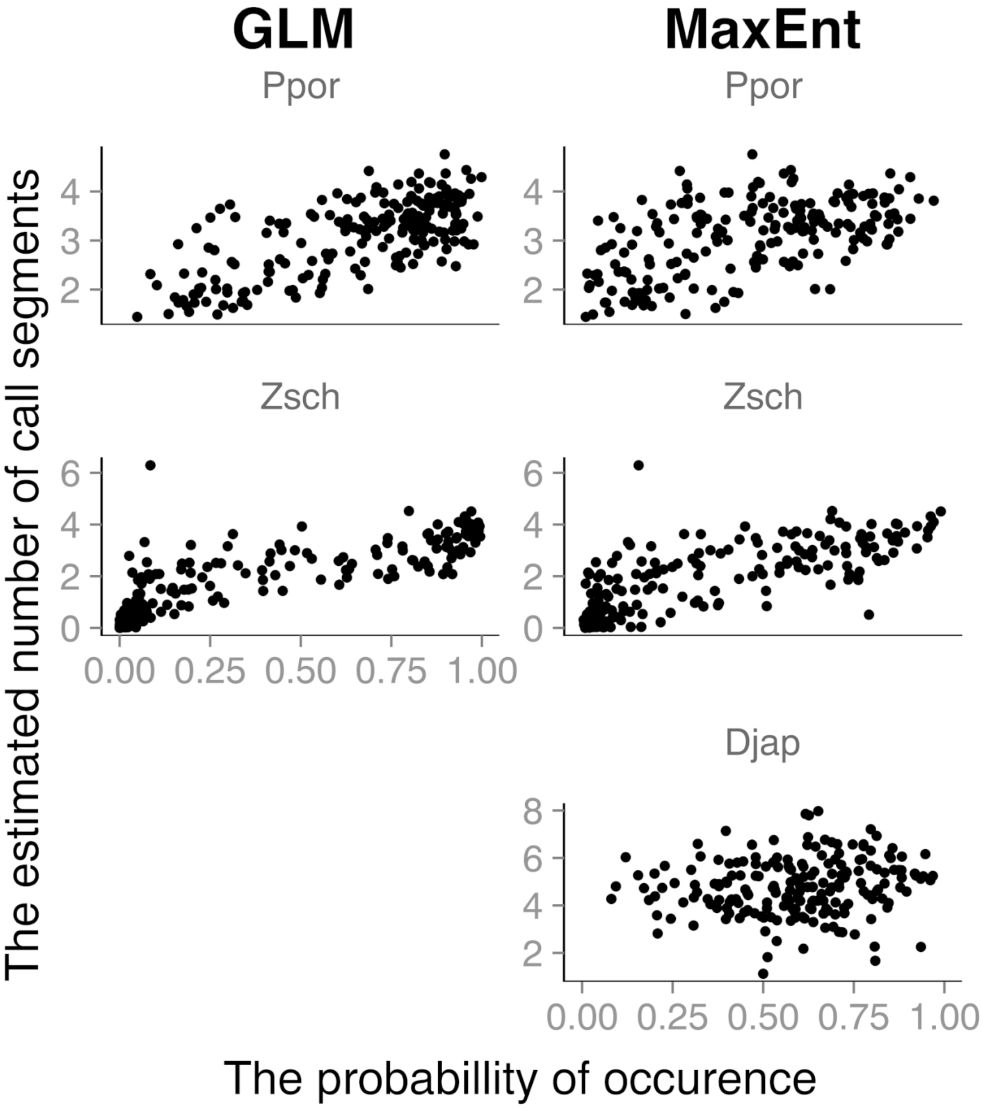
Table 4 Results of model averaging for the abundance models. The coefficient in italics indicates the variable included in the best model. Asterisks indicate a statistically significant coefficient (P < 0.05, derived from Wald statistic)

Species	*P. p. porosus*		*Z. schlegelii*		*D. japonicus*	
Variable	Estimate (SE)	Relative importance	Estimate (SE)	Relative importance	Estimate (SE)	Relative importance
Detection probability						
Temperature	0.193(0.066)*		-1.567			
Temperature^2	-0.003(0.002)		0.043		-0.001(0.001)	
Wind speed	-0.568(0.060)*				-0.480(0.045)*	
Observation date	0.004(0.003)		-0.198(0.012)*		-0.048(0.006)*	
Presence of rice	1.106(0.230)*		-1.821(0.425)*		3.621(0.189)*	
Call	0.481(0.023)*		0.715(0.058)*		0.510 (0.050)*	
Intercept	-7.910(0.613)*		14.200		-4.413 (0.531)*	
Abundance model						
Annual minimum temperature	*-0.068(0.104)*	0.413	0.053(0.134)	0.236	-0.042(0.081)	0.307
Precipitation of June			0.000(0.005)	0.097		
water distance	-0.166(3.946)	0.122	-0.587(7.457)	0.118	*-27.225(10.660)**	1.000
% Paddy field	*-0.533(0.417)*	0.810	*4.136 (5.037)*	0.752	*-0.125(0.267)*	0.260
% Forest	*-0.197(0.361)*	0.585	*5.529(5.137)*	0.904	0.268(0.373)	0.458
% Crop land			*6.379(5.101)*	1.000	0.018(0.142)	0.083
% Urban area	*-0.358(0.705)*	0.360	0.966(4.210)	0.117	0.013(0.174)	0.059
AI forest			*0.039(0.022)*	1.000	*0.010(0.004)*	1.000
AI urban	0.002(0.002)	0.883	-0.000(0.002)	0.116	0.007(0.005)	0.942
BFP	0.133(0.619)	0.067	*7.859(5.079)*	0.901		
TPI	*1.951(0.658)**	1.000	-0.265(0.740)	0.181	*0.577(0.578)*	0.674
PFI	0.032(0.094)	0.190	-0.008(0.089)	0.099	*0.302(0.154)*	1.000
LEA			*1.505(0.852)*	1.000	*-0.043(0.146)*	0.186
Intercept	1.110(0.474)*		-8.171(5.089)		0.175(0.535)	

the Tone River course was changed by river improvement works conducted approximately 400 years ago (the estuary of the Tone River was located in Tokyo Bay) (Inazaki et al. 2014, Fig. 1). Three native species inhabit all basins, but their distribution is shaped not only by landscape and local level environmental factors, but also by basin-level differences. Although there were positive correlations between the prediction of abundance and probabilities of presence, the distribution pattern of abundance and presence of *P. p. porosus* was not similar. Thus, from the viewpoint of the large map, the abundance and number of native species were lower in the west of the Kanto Plain, although there was a difference in the distribution of species between the margin and the lowland of the plain.

The previously known ecological traits of each species could explain the responses to environmental factors at each level. *Z. schlegelii* is arboreal, uses paddy fields for breeding, and migrates to forests during the non-breeding season and hibernation (Ihara 1999; Osawa and Katsuno 2000; Matsui and Maeda 2018); therefore, it was a natural consequence that factors relating to the forest affected their distribution. The valleys at the edge of the uplands in the Kanto Plain, where suitable habitats of *Z. schlegelii* are distributed, are essential for wetland species because of the water springs (Kim et al. 2020). In addition, as the breeding season of *Z. schlegelii* starts earlier than the rice planting season (Hasegawa 1998), its presence implies that wetlands other than flooded paddy fields may be available as spawning sites. As *P. p. porosus* is terrestrial and inhabits paddy fields throughout the year (Togane et al. 2010), it is reasonable that it is sensitive to environmental factors within the paddy fields. Of these, TPI (timing of paddy fields being inundated) is possibly associated with its phenology. The smaller the TPI value, the later the date of rice planting, and the delay in the rice planting season are expected to have caused the failure to provide breeding pools in paddies. Therefore, the timing of local water availability, which is not coincident with the phenology of *P. p. porosus*, would affect their local decline. Although the outcome of field improvement does not necessarily exclude *P. p. porosus* (Fujioka and Lane 1997; Azuma and Takeuchi 1999), our results showed that PFI (the ratios of paddy fields performed with field improvement) had a weak or no effect. However, in this study, as we could not identify the details and extent of the field improvements in each field, it is unclear whether current paddy fields recover as frog habitats after these improvements; therefore, the effect of field improvement on frogs might be underestimated. Aggregation indices showed higher RI in the abundance models than in the distribution models. In the future, it would be necessary to determine

Fig. 4 The relationship between the probability of occurrence estimated by GLM and MaxEnt and the number of call segments estimated by the abundance model. Abbreviations are the same as those in Fig. 3



how patch size rather than the total area of given land-use affects the abundance of these species.

In contrast, *D. japonicus*, the most common arboreal frog in paddy fields, has adapted to the current paddy environment. In *D. japonicus* and *F. kawamurai* (a terrestrial frog), variables of the features of paddy fields had low contributions, and the ratio of paddy fields and the urban area had high contributions in MaxEnt. It may indicate that they are more tolerant to changes in the paddy environment than other species.

In the Arakawa basin and to west of the Tone basin, *F. kawamurai* has a high probability of occurrence, but the two native species have a low abundance. Since *P. p. porosus* was previously threatened in this area due to the loss and modernization of rice paddies (Saitama Prefectural Government 2018), it is unlikely that the decline is directly related to interspecific interactions with *F. kawamurai*, although their impact on native species is unknown. Although this study did not account for the biological factors such as competitors, prey, and predators (Katayama et al. 2012; Noha and Shimada 2017), the frequencies of species combinations obtained from the field survey suggested that interactions between species did not influence the presence of each species. Therefore, it could be helpful to provide maps of frog habitats, both to start monitoring changes in biodiversity in the extensive agricultural area and to determine conservation priorities. In addition, the coexistence of frogs with unique environmental preferences, such as *P. p. porosus* and *Z. schlegelii*, may be a helpful indicator of paddy fields with high environmental heterogeneity. It would be easier to select and preserve areas where the two species coexist as landscapes with high environmental heterogeneity rather than increasing the environmental heterogeneity of each paddy field. The effect of changes in species composition and the abundance of each species in the paddy field ecosystems in the Kanto district will be a subject for future research.

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Author Contributions All authors contributed to the study conception and design. Data collection was performed by Noe Matsushima, and Jun Nishihiro. All the recordings were played back by Noe Matsushima, and confirmed by Masami Hasegawa. Noe Matsushima performed data analysis and wrote the first draft of the manuscript, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data Availability The datasets generated during the current study are available from the corresponding author on reasonable request.

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

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