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Submitted on: 2023, 23th December; revised on: 2026, 29th April; accepted on: 2026, 23th July.

Editor: Maria Torres Sánchez

Short running title: Spatial scale in frog abundance estimation

Abstract. Agricultural landscape changes have negatively affected frog species that rely on paddy fields as their habitat. Estimating frog abundance in relation to landscape structure is essential for effective conservation and land use planning. However, understanding the appropriate spatial scale for such estimation is insufficient. We evaluated the critical spatial scales for estimating the relative abundance of the forest green tree frog (*Zhangixalus arboreus*) and the black-spotted pond frog (*Pelophylax nigromaculatus*) in rural landscapes in northeastern Japan. Visiting each of the 42 sites established in the Shonai region five times between May and June 2023, we recorded the presence or absence of advertisement calls from the target species. We constructed Royle-Nichols models to explain the repeated presence or absence data by the proportion of surrounding paddy fields, along with other landscape factors and weather conditions. The proportion of surrounding paddy fields was prepared for radii ranging from 100 to 1,500 m. The optimal spatial scale for both species was the narrowest buffer size with a radius of 100 m. The trend for the forest green tree frog remained consistent across scales, whereas the effect of surrounding landscape on the black-spotted pond frog varied with spatial scale, indicating spatial scale dependence. These findings highlight the importance of evaluating landscapes on a fine scale for estimating frog abundance. They also provide a basis for species-specific conservation and land use planning in agricultural landscapes.

Keywords. Black-spotted pond frogs, forest green tree frogs, *Pelophylax nigromaculatus*, Royle-Nichols model, scale dependency, *Zhangixalus arboreus*

INTRODUCTION

Paddy fields serve as alternative wetlands, providing a habitat for numerous organisms (Natuhara, 2013; Miyashita et al., 2014). Historically, paddy fields have played an important role in rural landscapes, alongside dry fields and forests (Natuhara, 2013), supporting a diverse habitat for various organisms, including plants (Fukamachi et al., 2005; Matsumura et al., 2014), mammals (Aikawa and Saito 2023), birds (Amano et al., 2008; Katayama et al., 2015b), amphibians (Fujioka and Lane, 1997; Naito et al., 2012), and fish (Katano et al., 2003; Katayama et al., 2011). However, paddy fields and their surrounding landscapes have undergone substantial transformations in recent decades due to land consolidation and abandonment of cultivation, particularly in Japan (Katayama et al., 2015a; Koshida and Katayama, 2018; Zheng and Natuhara, 2020). These changes in agricultural activities may reduce landscape heterogeneity, negatively impacting organisms that depend on multiple habitat types (Katoh et al., 2009; Katayama et al., 2015a). Therefore, assessing the impact of landscape structures, including paddy fields, on organisms is important.

Frogs represent one of the most significant taxa utilizing paddy fields (Miyashita et al., 2014). Among the native frogs in Honshu, Shikoku, and Kyushu, Japan, 12 of the 17 species and 2 subspecies breed in paddy fields (Matsui and Maeda, 2018; Herpetological Society of Japan, 2023). Frogs occupy a middle-ranked position in paddy field ecosystems and play an important role in trophic dynamics (Hasegawa, 2003; Christoffel and Lepczyk, 2012). However, agricultural activities and their associated landscape changes can negatively affect frog species that rely on paddy fields as their habitat (Matsushima et al., 2022; Fukushima and Naito, 2024; Naito et al., 2024). Given that amphibian habitat use is influenced by the surrounding landscape context (Sawatzky et al. 2019; Aikawa and Saito, 2024, 2025; Matsushima and Hasegawa, 2025), accurately estimating frog abundance in relation to landscape structure is essential for effective frog conservation and land use planning. However, such an estimation requires careful consideration of the spatial scale at which landscape factors are evaluated because the relationship between organism abundance and landscape composition often varies with scale.

Landscape factors that affect the abundance of organisms often exhibit spatial scale dependence. This means that the strength or direction of the relationship between abundance and landscape composition varies depending on the spatial scale considered (Mochizuki and Murakami, 2013; Mochizuki, 2021). Because habitat selection by organisms is hierarchically structured across spatial scales (Johnson, 1980; Kie et al., 2002), evaluating landscape effects at multiple scales is necessary to fully understand the factors driving abundance. In practice, however, wildlife management and land use planning must operate at a defined spatial scale. Therefore, identifying the optimal spatial scale at which landscape factors most accurately explain organism abundance is important (Mochizuki, 2021). If the relationship between abundance and landscape factors in landscapes with many paddy fields remains consistent across spatial scales, managing at the scale with the highest explanatory power is considered most effective (Mochizuki, 2021). Despite the importance of these considerations, spatial scale dependence and the identification of the optimal spatial scale have not been thoroughly examined in the context of frog abundance estimation using advertisement calls.

The objective of this study was to evaluate the critical spatial scales for estimating the relative abundance of frogs utilizing paddy fields for breeding in rural landscapes of northeastern Japan. We assessed whether spatial scale dependence exists in the relationship between frog abundance and surrounding landscape structure. We selected two target species with contrasting ecological characteristics: the forest green tree frog (*Zhangixalus arboreus*: Rhacophoridae) and the black-spotted pond frog (*Pelophylax nigromaculatus*: Ranidae) (Fig. 1). The forest green tree frog utilizes wetlands temporarily for breeding and resides in forests outside of the breeding season (Hasegawa, 2003). In contrast, the black-spotted pond frog rarely leaves the water throughout its life history (Kikuchi, 1958), relying heavily on paddy fields in the rural landscape (Goto et al., 2011). The contrasting dependencies on landscape elements make these two species well suited for comparing how spatial influences abundance estimation across species with different habitat requirements.

MATERIAL AND METHODS

Study area

This study was conducted in the Shonai region of Yamagata Prefecture, northeastern Japan (139°49'E, 38°43'N; Fig. 2). The region falls within the cool-temperate zone, characterized by an average annual temperature of 12.9 °C and an annual precipitation of 2191.4 mm (Japan Meteorological Agency, 2023). The plains, including the urban area, are surrounded by an extensive area of paddy fields. The southeastern part of the Shonai region is covered by forest areas, and the mosaic landscape comprises paddy fields, dry fields, orchards, and settlements scattered along the forest area. The forests primarily consist of deciduous broadleaf forests featuring the Japanese beech (*Fagus crenata*) and Japanese oak (*Quercus crispula*), along with planted forests of the Japanese cedar (*Cryptomeria japonica*). Most of the paddy fields in the Shonai region are flooded in early May, initiating the breeding season for numerous frog species (pers. obs.).

Field survey

Advertisement calls were used as the primary survey method because they allow efficient and non-invasive detection of breeding activity across a large number of sites in a short amount of time. This is particularly important given the short breeding season of frogs. Field surveys were conducted between May 29 and June 29, 2023, during the presumed active breeding period of the target species (Matsui and Maeda, 2018). We prepared two primary survey areas, the Atsumi and Asahi areas (Fig. 2). A total of 21 survey sites were established in each area, encompassing a range of landscapes from rural to forest, resulting in 42 sites overall. Each survey site constituted a 100 m road section with low traffic. The observation of the target species was carried out by a single observer (E. Aikawa) who walked slowly through each 100 m survey section on foot, recording the presence or absence of advertisement calls by ear. Species identification was based solely on the acoustic characteristics of the calls, not to visual confirmation. Prior to the surveys, the observer underwent training to familiarize himself with the advertisement calls of the target species using reference audio recordings. No recording devices were used, and all detections were based on direct auditory observation. Additionally, we also measured air temperature (°C) and humidity (%) in the center of each survey site using a thermo-hygrometer (PC-5110, Sato Keiryoki Mfg. Co., Ltd., Japan). Since frog breeding behavior typically occurs at night (Farina and James, 2016; Guerra et al., 2020), surveys commenced one hour after sunset, ensuring sufficient darkness, and finished as much as possible one hour before sunrise. All sites within either of the two study areas were visited during a single day of survey, with each site revisited a total of five times throughout the survey period.

Environmental factors

To prepare landscape factors, we extracted paddy field and forest polygons from the 1/25,000 vegetation map (Biodiversity Center of Japan, 2021). Following the methodology outlined by Ogawa et al. (2020), we identified the target land use polygons based on the legend of the vegetation map. Subsequently, the polygons were converted into raster data with 10 m cell resolution for further work.

To elucidate important spatial scales, we adopted the approach of arbitrarily generating multiple buffers and constructing models based on the proportions of landscape elements within these buffers (e.g., Kato et al., 2010; Saito and Koike, 2013; Saito and Sonoda, 2017). Generally, the size of arbitrary buffer is often determined based on the home range and movement ability of the studied animals. While information on the home range size of frogs is limited, a study on the movement of forest green tree frogs from breeding ponds to non-breeding habitats indicated a maximum distance traveled of approximately 125 m (Kusano, 1998). Previous studies have emphasized that optimal spatial scale is not always solely explained by home range and body size (Saito and Koike, 2013; Mochizuki, 2021). Although each survey site consisted of a 100-m road section, the center point of each section was used as the focal point for landscape analysis. This approach reflects the assumption that the advertisement calls detected along the transect represent the abundance of individuals in the surrounding landscape rather than within the transect itself. We created buffer sizes with radii of 100, 500, 1,000, and 1,500 m, calculating the proportions of surrounding paddy fields and forest areas within each buffer size at each site. However, due to a high negative correlation between these proportions ($r < -0.9$), we opted to use only the proportions of surrounding paddy fields in our analysis. We also calculated the proportion of surrounding forest edges within the buffer based on cells containing forest edges. Furthermore, we calculated the distance from the nearest forest to each site (km), as forest green tree frogs move from the forest to the paddy fields for breeding. These calculations were performed using ArcGIS ver 10.7 (ESRI, USA).

Statistical analysis

To estimate the abundance of the given species, we employed the Royle-Nichols model (RN model; Royle and Nichols, 2003). This model allows for heterogeneity in the detection probability of the event of interest from repeated presence or absence data and estimates relative abundance using a Poisson distribution. The RN model can be applied to the detected and non-detected frog call data for estimating their relative abundance (Eskew et al., 2012; Barata et al., 2022; Matsushima et al., 2022).

In this study, the presence or absence of advertisement calls of the target species in each survey was used as the objective variable. To estimate relative abundance, explanatory variables included the proportion of surrounding paddy fields, the squared term of the proportion of surrounding paddy fields, the proportion of surrounding forest edges, and the distance from the nearest forest. The squared term accounts for upward or downward convex nonlinear relationships for that variable (e.g., Saito and Koike, 2013). To estimate the detection probability in the RN model, temperature and humidity were used as explanatory variables. For each species, RN models were constructed for each buffer size, and model fits were compared based on the Akaike's Information Criterion (AIC) and the percentage of deviance explained (%DE). The RN model was implemented using the package "unmarked" (Fiske and Chandler, 2011) in R ver 4.2.2 (R Core Team, 2022). The raw data used in this study are publicly available on Zenodo (DOI: 10.5281/zenodo.19875179).

RESULTS

For both the black-spotted pond frog and the forest green tree frog, we detected advertisement calls at 29 and 23 sites, respectively, obtaining 111 and 41 presence data (Table 1). The results of the RN model showed that the AIC was minimized and the %DE was maximized at a spatial scale of 100 m radius for both species (Table 2). Both species exhibited an upward convex nonlinear relationship with the proportion of surrounding paddy fields, reaching peaks of relative abundance at approximately 0.7 and 0.8, respectively (Fig. 3a, b). At spatial scales with a radius greater than 500 m, the peak shifted toward lower proportions of surrounding paddy fields for the forest green tree frog (Fig 3a). For the black-spotted pond frog, the significance of the squared term of surrounding paddy fields diminished at a spatial scale of 1,000 m radius, and the model at a spatial scale of 1,500 m radius was no longer significantly influenced by the surrounding paddy fields (Table 2; Fig. 3b). The effect of distance from the nearest forest was positive at spatial scales with a radius greater than 1,000 m for the black-spotted pond frog and positive at spatial scales with a radius of 1,500 m for the forest green tree frog (Table 2).

In the detection probability model, both species were negatively affected by temperature, with no significant effect of humidity (Table 2).

DISCUSSION

Important spatial scale

The optimal spatial scale for elucidating the relative abundance of the two frog species utilizing paddy fields for breeding was the narrowest buffer size with a radius of 100 m, indicating that a finer spatial scale offers greater explanatory power. Despite the differing ecological characteristics of the two species targeted in this study, they shared the same optimal spatial scale. Throughout the survey period, both species utilized paddy fields for breeding, explaining the high concentration of individuals in these areas. Consequently, predictions were most accurate on a finer scale.

A previous study in Japan, which predicted abundance from frog calls at various spatial scales, estimated the optimal spatial scale for each species to be a buffer radius of 500 m to 1,000 m, encompassing a broader scale than the present study (Matsushima et al., 2022). For the Tokyo Daruma pond frog (*Pelophylax porosus porosus*), a closely related species to the black-spotted pond frog targeted in this study, the optimal spatial scale is also a buffer with a radius of 500 m (Matsushima et al., 2022). However, this discrepancy in results does not necessarily imply that all species will exhibit higher prediction accuracy at finer spatial scales. The variation in model accuracy might stem from the fact that Matsushima et al. (2022) conducted their study over a large alluvial plain, where changes in landscape factors influencing frog abundance are more likely to shown over a relatively broader scale.

According to a previous study that investigated the forest green tree frog abundance and identified the optimal spatial scale through egg mass surveys (Kato et al., 2010), the most critical scale was a 1,000 m radius. This finding contrasts with the optimal spatial scale estimated in our study. Considering the reported movement distance (125 m) by Kusano (1998), the optimal spatial scale identified in our study appears reasonable, while the one identified by Kato et al. (2010) deviates from the observed movement distance. Kato et al. (2010) discussed this discrepancy in terms of meta-populations, suggesting that the 1,000 m radius spatial scale may reflect occasional long-distance movements. The significance of the finer scale identified in our study might imply that the study area possesses a landscape structure that impedes formation of meta-populations. Alternatively, it is possible that forest green tree frogs in the Shonai region exhibit ecological characteristics making long-distance movement challenging. A more comprehensive study on forest green tree frog movement and an assessment of optimal spatial scale in other regions would enhance our understanding regarding habitat use or meta-populations.

Even within the optimal spatial scale model, some estimates appeared inconsistent with the ecological characteristics of the species in the black-spotted pond frog. Despite these frogs typically inhabiting wetlands such as paddy fields (Kikuchi, 1958; Goto et al., 2011), the relative abundance was estimated to be low in this study when the proportion of surrounding paddy fields was too high. While forests are not mandatory for the black-spotted pond frog, they play a crucial role in providing food resources, such as insects and spiders (Miyashita et al., 2012, 2014), and may have been indirectly affected. Simultaneously examining food resources can provide more detailed information on factors beyond landscape influences.

Scale dependency

At spatial scales other than the optimal spatial scale, the responses of both species differed

(Fig. 3). The trend for the forest green tree frog remained consistent across the investigated scales, with higher relative abundance estimated in environments featuring a moderate amount of surrounding paddy fields. Conversely, the effect of the surrounding landscape on the black-spotted pond frog varied with spatial scale, revealing a spatial scale dependency. The presence or absence of spatial scale dependency may be attributed to differences in sensitivity to the surrounding landscape between these species. Given that the forest green tree frog requires both water bodies and forests (Matsui and Maeda 2018), the relative abundance may have been higher in landscapes with a moderate combination of paddy fields and forests, regardless of spatial scale. The estimated peak of relative abundance shifted toward lower proportion of paddy fields from fine to broad scales, likely reflecting the strong dependence of the forest green tree frog on forests. For the black-spotted pond frog, previous studies have suggested a greater sensitivity to local factors, such as concrete channels, than landscape factors (Fujioka and Lane, 1997; Watabe et al., 2009, 2011). At a broad spatial scale, the landscape factors incorporated in this model may not fully explain the abundance. Simultaneously considering landscape and local factors may unveil factors that more accurately characterize the abundance of the black-spotted pond frog.

As spatial scale increased, a positive relationship was observed between distance from the nearest forest and relative abundance for both species. This finding is unexpected, especially for a species that faces challenges in leaving the forest, such as the forest green tree frog. In this study, a gradient ranging from rural landscapes to forest landscapes was used for the study sites. The relative abundance was estimated to be higher in landscape structures relatively distant from forests within that gradient, specifically in areas where paddy fields and forests are mixed. To obtain a more comprehensive understanding of landscape structures, it would be beneficial to collect data on landscapes that include paddy fields located away from forests, as well as in intensive agricultural landscapes.

Limitations

There are several limitations to this study that should be acknowledged. First, the number of survey sites (42 sites) was relatively small compared to those in similar studies (e.g., Matsushima et al., 2022), which may limit the generalizability of our results. Second, a single observer conducted all surveys using direct auditory detection without recording devices, which precludes post hoc verification of species identification. Third, the optimal spatial scale identified in this study (100-m radius) is comparable to the length of the survey transect (also 100 m). This overlap may limit the interpretation of the 100-m buffer results as a measure of the surrounding landscape. However, since this scale was determined by comparing models across multiple buffer sizes rather than being set a priori, we consider the result to reflect the fine-scale habitat association of the two species during the breeding season. Future studies with larger sample sizes, standardized recording methods, and broader spatial coverage would help to further validate the findings presented here.

CONCLUSION

We identified important spatial scales in the relative abundance estimation of two frog species utilizing paddy fields for breeding. The optimal spatial scale determined in this study holds significance for various conservation and land use planning purposes. The distinctions from previous studies highlighted in this study underscore the importance of concentrating on multiple spatial scales, particularly finer scales, in frog abundance estimation. However, the varying sensitivity to changes in spatial scale varied between different species, suggesting that a single land use plan may not suit all taxa. Consequently, future investigations should explore the optimal spatial scale and spatial scale dependency not only a species-specific basis but also within the context of broader ecological community.

Acknowledgements

We thank the associates of Yamagata University for supporting our field survey.

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Table 1. Summary of the detection of advertisement calls in forest green tree frogs and black-spotted pond frogs.

Species	Scientific name	Number of sites detected advertisement calls at least once survey			Whole number of detections of advertisement calls		
		Atsumi area	Asahi area	Total	Atsumi area	Asahi area	Total
Forest green tree frog	*Zhangixalus arboreus*	14	15	29	55	56	111
Black-spotted pond frog	*Pelophylax nigromaculatus*	12	11	23	24	17	41

Table 2. The results of estimation of the Royle-Nichols models for each buffer size in forest green tree frogs and black-spotted pond frogs. %DE represents the percentage of deviance explained.

Variable	Forest green tree frog					Black-spotted pond frog				
	Coefficients			AIC	%DE	Coefficients			AIC	%DE
	Estimate	Standard error	p-value			Estimate	Standard error	p-value		
Buffer = 100 m										
Abundance model				156.0	31.0				167.4	24.6
Intercept	-1.51	0.64	0.019			-2.35	1.25	0.059		
Surrounding paddy fields	12.01	2.90	<0.001			10.84	3.95	0.006		
Surrounding paddy fields^2	-8.60	2.77	0.002			-7.15	3.29	0.030		
Distance from the nearest forest	-2.42	2.27	0.286			-0.28	2.51	0.910		
Surrounding forest edge	-8.97	4.59	0.051			-1.80	4.73	0.704		
Detection model										
Intercept	-1.94	2.46	0.432			5.51	2.91	0.058		
Air temperature	-0.11	0.05	0.014			-0.25	0.06	<0.001		
Humidity	0.04	0.02	0.076			-0.04	0.03	0.109		
Buffer = 500 m										
Abundance model				167.9	25.1				172.6	22.0
Intercept	-0.87	0.57	0.124			-1.75	0.92	0.058		
Surrounding paddy fields	15.70	3.02	<0.001			10.98	3.27	<0.001		
Surrounding paddy fields^2	-19.01	4.36	<0.001			-9.82	4.30	0.022		
Distance from the nearest forest	5.42	3.64	0.137			2.10	3.11	0.501		

Surrounding forest edge	-12.35	8.46	0.145			5.75	9.23	0.533		
Detection model										
Intercept	-2.12	2.58	0.413			6.04	3.09	0.051		
Air temperature	-0.12	0.05	0.011			-0.27	0.06	<0.001		
Humidity	0.05	0.03	0.048			-0.04	0.03	0.145		
Buffer = 1,000 m										
Abundance model				172.6	22.8				181.1	17.8
Intercept	-0.86	0.55	0.116			-1.53	0.80	0.056		
Surrounding paddy fields	24.20	5.07	<0.001			11.53	5.22	0.027		
Surrounding paddy fields^2	-47.33	8.72	<0.001			-18.71	9.74	0.055		
Distance from the nearest forest	10.75	2.28	<0.001			4.90	3.20	0.125		
Surrounding forest edge	-18.91	12.60	0.133			9.46	13.81	0.494		
Detection model										
Intercept	-1.88	2.64	0.476			6.63	3.08	0.032		
Air temperature	-0.12	0.05	0.012			-0.26	0.06	<0.001		
Humidity	0.05	0.03	0.055			-0.05	0.03	0.114		
Buffer = 1,500 m										
Abundance model				182.3	18.0				183.4	16.6
Intercept	-0.94	0.52	0.072			-1.45	0.75	0.054		
Surrounding paddy fields	20.34	7.08	0.004			9.36	7.62	0.220		
Surrounding paddy fields^2	-52.61	13.50	<0.001			-23.21	14.83	0.118		
Distance from the nearest forest	11.39	2.48	<0.001			6.75	2.85	0.018		
Surrounding forest edge	-5.44	15.30	0.722			18.14	18.55	0.328		
Detection model										
Intercept	-1.83	2.65	0.490			6.78	3.08	0.028		

Air temperature	-0.12	0.05	0.016	-0.26	0.06	<0.001
Humidity	0.05	0.03	0.056	-0.05	0.03	0.101

Fig. 1. Photographs of target species, the forest green tree frog (*Zhangixalus arboreus*: Rhacophoridae) (a) and the black-spotted pond frog (*Pelophylax nigromaculatus*: Ranidae) (b).

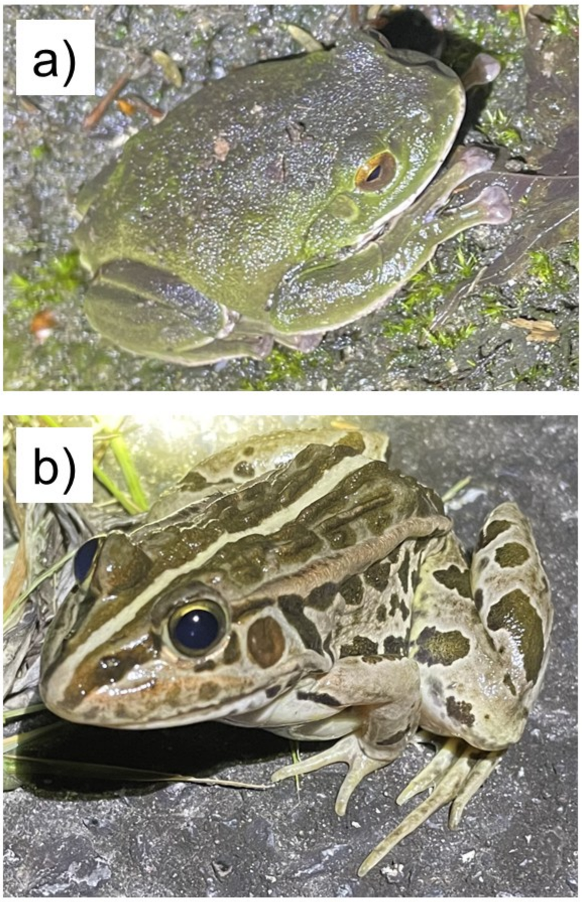

Fig. 2. Location of the study area.

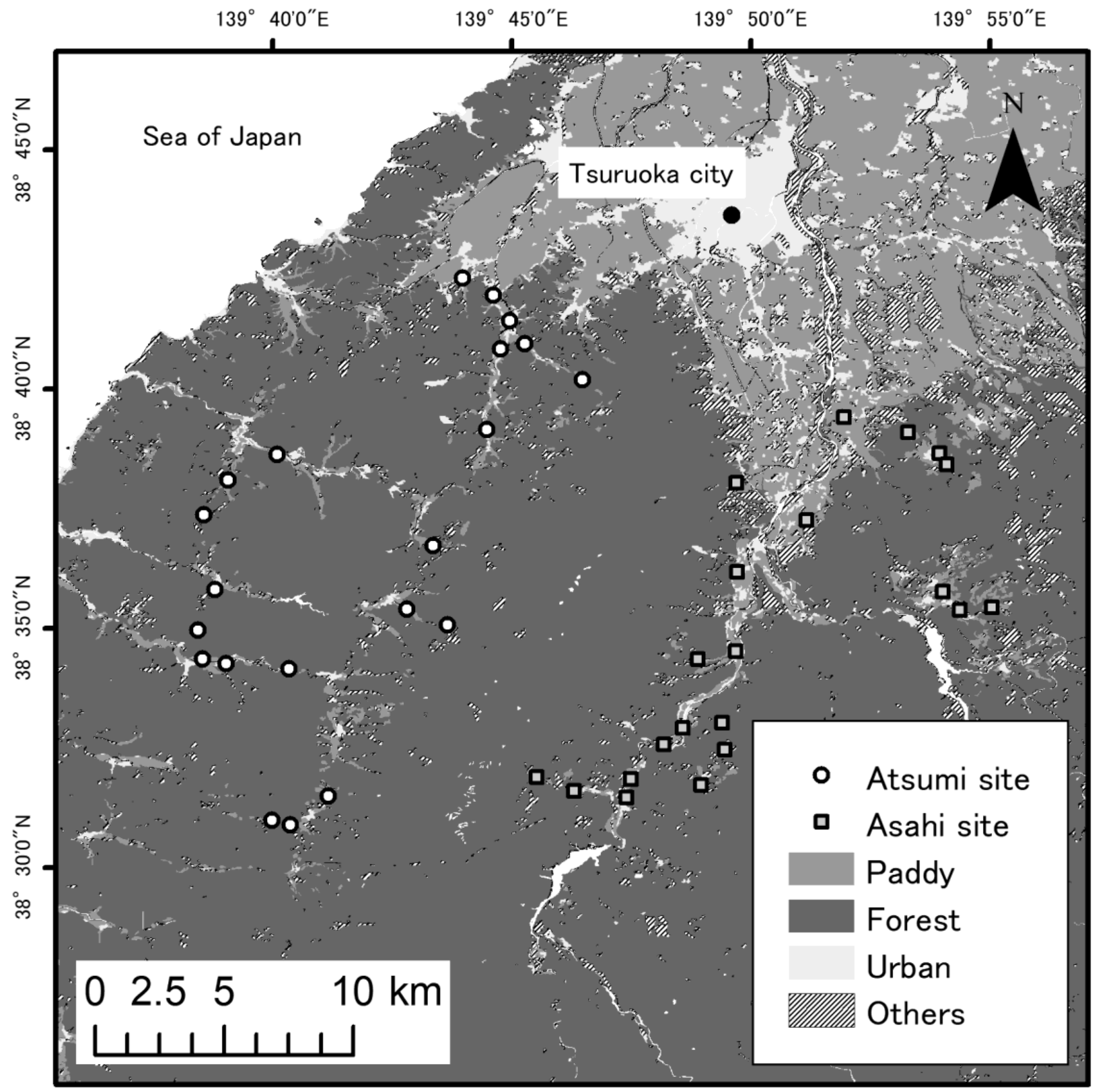

Fig. 3. Response curves depicting the predicted relative abundance in forest green tree frogs (a) and black-spotted pond frogs (b) in relation to the proportion of surrounding paddy fields. These curves were generated using estimates from the Royle-Nichols models (see Table 2). Solid lines indicate estimated values and dotted lines indicate 95% confidence intervals.