主論文

Multiple stressors on anurans: effects of spatial and local factors in Aichi Prefecture, central Japan

(カエル類への複合的ストレッサー: 愛知県における空間及び局所要因の影響)

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Chapter 1: General Introduction

1.1 Research progress on amphibian ecology

Amphibian population declines are a major severe international issue ongoing throughout the world, and we must act against this crisis based on scientific plan. Since the 1980s, the global decreases of the amphibian population have been recognized as a phenomenon by scientists all over the world (Blaustein and Wake 1990; Wake 1991; Blaustein 1994; Alford and Richards 1999; Blaustein and Kiesecker 2002). By 1993, a previous article reported that more than 500 populations of frogs and salamanders were confirmed to be listed as in declined species (Alford and Richards 1999). Currently, amphibians have become representative of the general loss of populations and species with declining worldwide biodiversity (Houlahan et al. 2000; Alford et al. 2001; Wilson 2002). They also have been listed as of particular conservation concern because of their unique value as indicators of environmental stress (Blaustein 1994; Blaustein and Wake 1995). For example, amphibians could have an important influence on other organisms due to they are the crucial components of many ecosystems (Blaustein et al. 1994b).

Ecologists have studied a systematic examination of amphibian population declines revealed that several interacting factors might be involved in the amphibian population declines (Barinaga 1990; Wake 1991; Alford and Richards 1999; Sodhi et al. 2010; Tsuji et al. 2011). Unfortunately, a large portion of literature studying on the documentation of amphibian declines continues to focus on some single factors (Alford and Richards 1999). I believe that complex interactions among multiple variables should be emphasized to more fully understand the phenomenon of amphibian population decline. Certainly, amphibian population declines are caused by a variety of variables in different areas. Several excellent studies reported that some of the factors that contribute to amphibian population declines, including habitat destruction and alteration (Semlitsch 1998; Alford and Richards 1999; Tanaka 1999; Tsuji et al. 2011; Kidera et al. 2018), global environmental change (Blaustein et al. 2001), diseases (Blaustein et al. 1994a; Johnson et al. 2002; Greenberg and Palen 2019), contaminants (Sparling et al. 2001; Sparling et al. 2010), and introduced species (Kiesecker and Blaustein 1997; Kiesecker et al. 2001; Sarashina and Yoshida 2015; Haramura et al. 2016).

Habitat destruction and alteration are the most common variables leading to the amphibian population declines (Alford and Richards 1999). Urbanization, draining wetlands, agricultural intensification and abandonment, as well as clearcutting forests, may directly cause habitat changes and biodiversity loss of amphibian populations (Petranka et al. 1993; Semlitsch 1998; Sodhi et al. 2010; Kidera et al. 2018). Additionally, a variety of contaminants, including herbicides, pollutants, and pesticides, *etc*, might have adverse effects on amphibian populations (Sparling et al. 2010). However, in Japan, agrochemical contaminations are known to have little effect on amphibians (Yoshida et al. 2006). Introduced species, like

Lithobates catesbeianus, introduced from the United States to Japan may impact on some native amphibians (Kiesecker and Blaustein 1997; 1998). However, this species is not distributed in paddy-field, because it needs water body throughout year.

In Japan, the habitats of amphibians have been deteriorated and fragmented by human activities and rapid urbanization since the 1980s (Katayama et al. 2015). Moreover, since the 1950s, agricultural landscapes have experienced an enormous change by agricultural intensification and abandonment (Krebs et al. 1999; Kidera et al. 2018). This can cause habitat destruction of amphibian populations (Hamer and Parris 2011). Also, over the past 70 years, ~ 70 % of natural wetlands have been converted mainly into paddy fields, and ~ 80% of paddy fields have been converted to the modern-style irrigation system (Fujioka and Lane 1997). Agricultural landscape modifications have tremendous negative effects on amphibian biodiversity, especially in rural areas. Rural landscape consists of a fine-scale mosaic of forests, paddy fields, ponds, wetlands, roads, and residential housings in Japan (Kobori and Primack 2003). In this ecosystem, different spatial scales should be included in the survey. Thus, studying multi-scale limiting variables for the target species will help to predict the achievement of the conservation measures (Kato 1955).

1.2 Study objectives

The main objectives of this study are: (1) clarify the distribution and population status of amphibian in the study regions; (2) examine the linkages between amphibian distribution and environmental stressors and (3) separate the effects of spatial and local factors; (4) clarify how the midsummer drainage and drainage system modernization impact on the tadpoles.

1.3 Summary of the chapters

Chapter 1 provides the framework for this thesis, and Chapter 5 discusses the main result, and summarizes the conclusions. I briefly summarize each chapter (Fig. 1-1), the primary objectives and the hypotheses to be tested.

In chapter 2, I studied the effects of multiple stressors on amphibian oviposition: spatial and local determinants in the study area. I examined the breeding distribution of the three frog species, *Rana japonica*, *Rana ornativentris*, and *Bufo japonicus formosus*, along the ecological gradient from urban to mountain areas. In this chapter, I examined three aspects: (1) whether local habitat quality and spatial environment play essential roles in determining species reproduction distribution at three habitats responses in urban-rural landscapes; (2) which variables contribute to species breeding distribution in amphibians; and (3) how different species respond to an ecological gradient of urban-rural area?

In chapter 3, I investigated the effects of landscape and local factors on two green tree-frogs, *Rhacophorus* (*R. schlegelii* v.s *R. arboreus*), in different habitats in the study area. The purpose of this chapter is to identify landscape and local factors responsible for variations in multiple dimensions of the two tree-frogs, *Rhacophorus* (Amphibia: Rhacophoridae), in different habitats. I hypothesized that *R. arboreus* required larger forest area than *R. schlegelii* at the landscape scale; while I hypothesized that the agricultural landscape fragmentation had more negative effects on the distribution of *R. schlegelii* than *R. arboreus*. Regarding local factors, I hypothesized that the presence of trees adjacent to forests, and the proportion of embankment vegetation in the breeding season are essential for the two tree-frogs.

In chapter 4, I reported on the ecological impacts of the midsummer drainage and drainage system modernization on tadpoles of *Rhacophorus arboreus*, in Japanese paddy fields. I found that the midsummer drainage and intermediate-style drainage system have negatively affected on the tadpole survival. It is necessary to choose a favorable paddy-field with water management and construct suitable ecological engineering, such as catchment ditch and semi-natural habitats for target species. The manuscript is preparing to submit in an international journal.

In chapter 5, I discussed the main result, and summarized the conclusions.

1.4 Study area and species

All field surveys were conducted in different habitats, including wetlands, paddy fields, ponds, abandoned paddy fields, fallow paddy fields, and corn fields, along an ecological gradient on Toyota City, Okazaki City, Shitara Town, and Shinshiro Town, Aichi Prefecture, central Japan (Fig. 1-2). The surveys covered areas from hilly rural zones to urban zones, and the landscapes consist of fine-scale mosaic forests, paddy fields, creeks, wetlands, other farmlands, and human settlements, *etc*.

Based on previous frog surveys in Toyota City (Otake and Shimada 2016), we targeted five species in the study area. The Japanese brown frog, *R. japonica* (Fig.

1-3a), occurs mainly at the edge of forests in hillsides and plains (mainly in the ecotope between grassland and forest) and surrounding breeding sites (Osawa and Katsuno 2001); it is rarely observed in the mountain ranges throughout Honshu, Shikoku, and Kyushu in Japan. This species uses seasonally flooded agricultural land, especially paddy fields with shallow water, swamps, and irrigation ponds, as breeding habitats and soil leaves as foraging, escape, and wintering habitats. Moreover, *R. japonica* breeds explosively within very short periods in the course of its mating season (late January–late March**)** (Osawa and Katsuno 2001). Egg masses hatch in a very short time, and tadpole metamorphosis is complete within 2–3 months (Matsushima and Kawata 2005).

The montane brown frog, *R. ornativentris* (Fig. 1-3b), mainly inhabits forests throughout Honshu, Shikoku, Kyushu, and Sado islands in Japan and China (Sumida and Nishioka 1996). This species uses seasonally flooded agricultural land, water springs, irrigation ponds, wetlands, and abandoned paddy fields as breeding habitats. Unlike *R. japonica* that inhabits the edge of forests, adults of *R. ornativentris* are generally distributed in forests in hilly and mountain regions. Hatching egg masses and tadpoles metamorphosis are the same as those of *R. japonica*. Although both *Rana spp.* species are similar in the configuration of egg masses and tadpoles, the tadpole of *R. japonica* can be readily differentiated from that of *R. ornativentris* (Sumida and Nishioka 1996). The tadpole of *R. japonica* has a pair of dark dorsal markings, whereas *R. ornativentris* lacks these markings (Matsui and Matsui 1990).

The Japanese common toad, *B. japonicus formosus* (Fig. 1-3c), is a large and robust species that is distributed in a variety of habitats ranging from sea level to high mountains, including dry and anthropogenic environments. Water habitats are needed only for short periods for breeding. They occur throughout eastern Japan, from southern Hokkaido to the Kinki districts of Honshu. Many ecologists have referred to this species as an "explosive breeder"; it breeds in early spring (early March-early April) in wetlands, roadside ditches, and small ponds (Maeda and Matsui 1999).

The foam-nesting tree frog, *Rhacophorus schlegelii* (Fig. 1-3d), mainly inhabits forests, and breeds in paddy fields, ponds, and wetlands throughout Honshu, Shikoku, Kyushu and Goto Islands in Japan. The foam nest of *R. schlegelii* is constructed under the soil on the shores of ponds or paddy fields. The breeding season lasts about three months from April to June (Maeda and Matsui 1990).

The forest green tree frog, *Rhacophorus arboreus* (Fig. 1-3e) (adult snout-vent lengths of usually 50-80 mm; egg mass size of usually 88×120 mm), mainly inhabits forest throughout Honshu and Sado Islands, Japan. It breeds from April to July, chiefly in ponds and paddy fields surrounded by forest (Maeda and Matsui 1999; Ramamonjisoa et al. 2019). Unlike other frogs, *R. arboreus* prefer to make foam nests attached to branches or leaves of trees along the shores of still waters (Kusano et al. 2005).

1.5 Figures

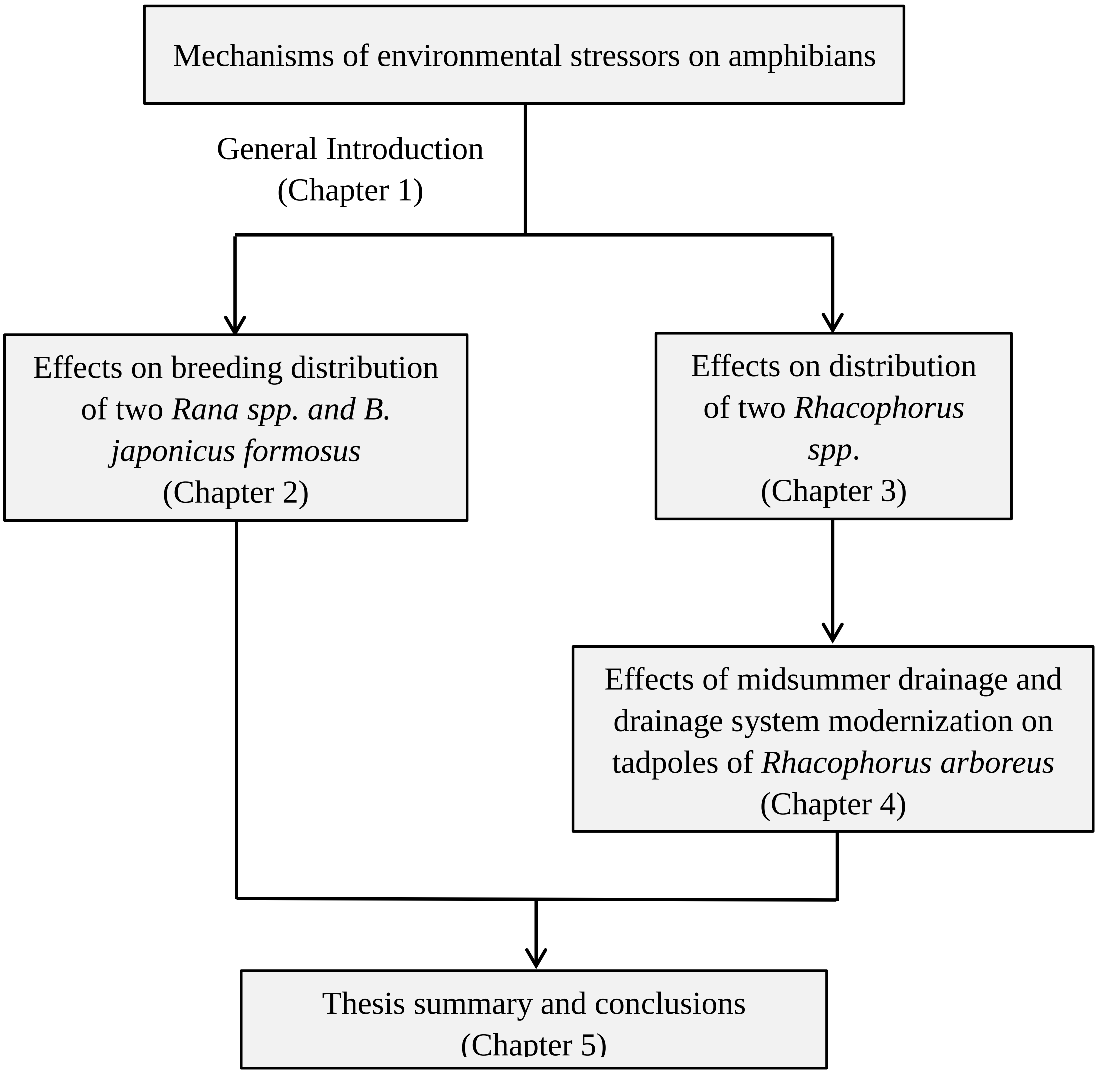


Fig. 1-1 Study steps.

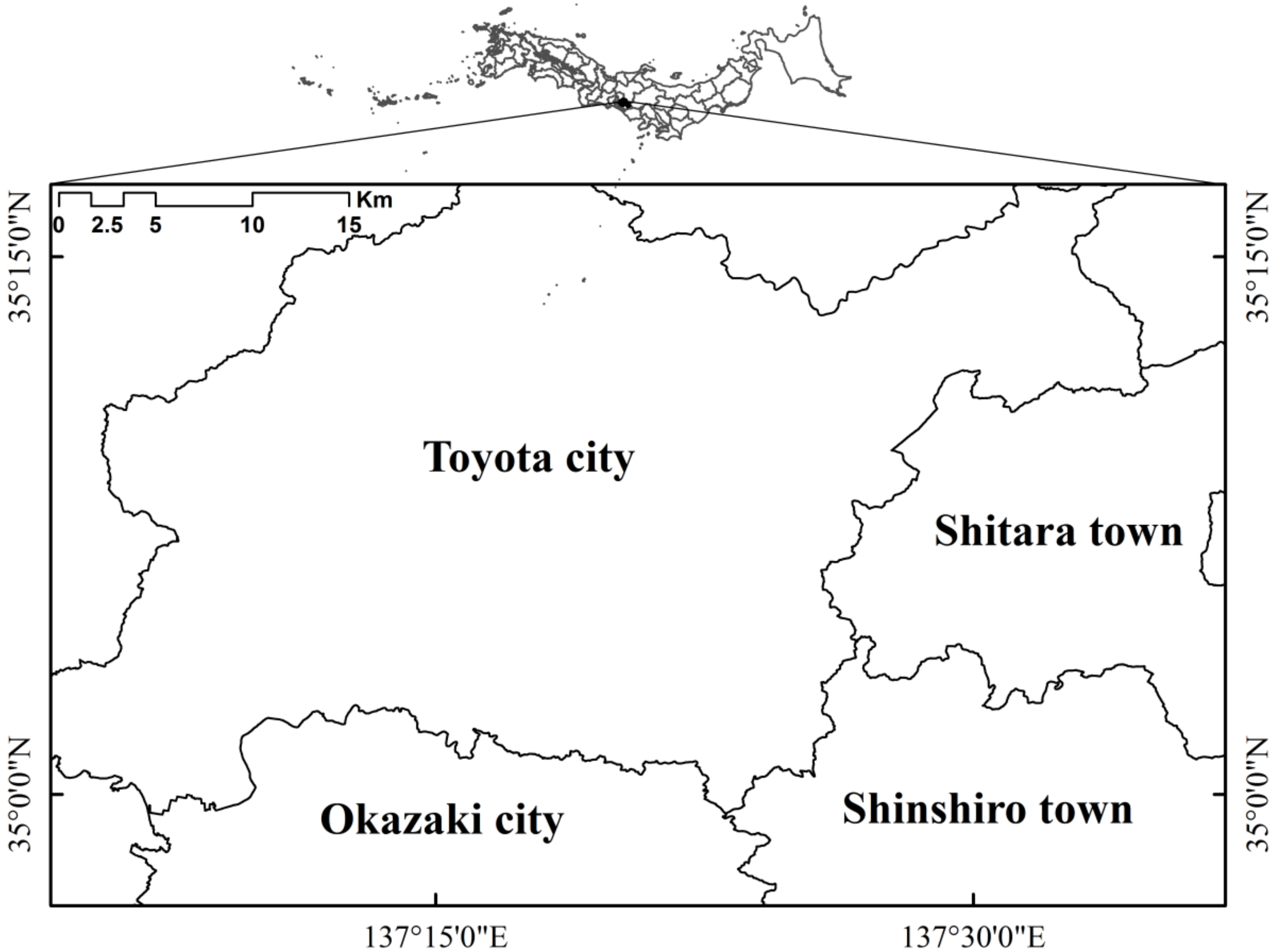


Fig. 1-2 Study areas.

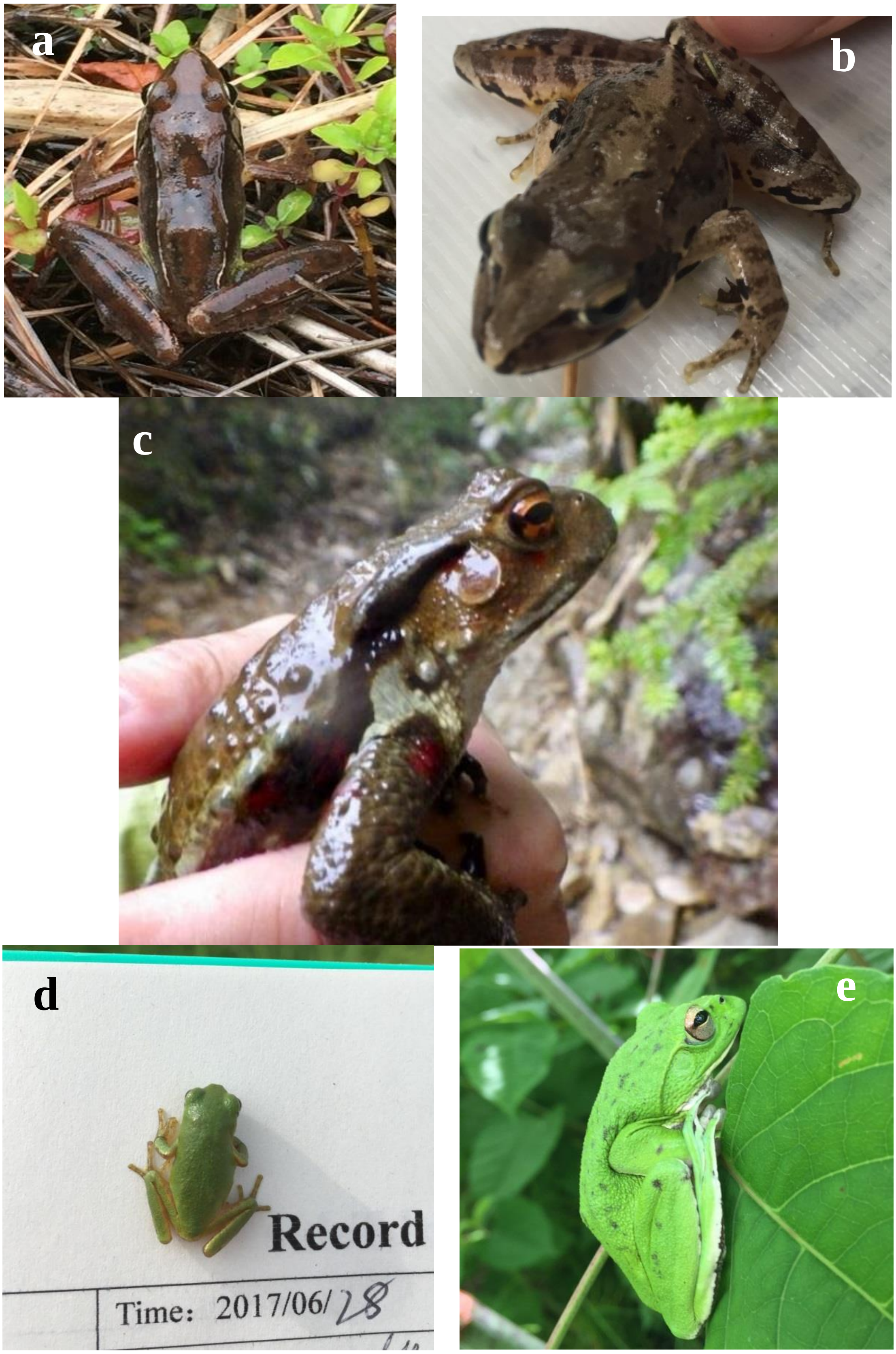


Fig. 1-3 Study species.

Chapter 2: Effects of multiple stressors on amphibian oviposition: spatial and local determinants in central Japan

2.1 Introduction

Since the 1970s, ecologists have suggested that amphibians have suffered a global decline (Alford et al. 2001; Houlahan et al. 2001). Many studies involving the systematic examinations of the amphibian population decreases revealed that human activities (e.g., urbanization, the introduction of nonnative vegetation, and agricultural activities) have a multiplicity of stressors that could influence the amphibian dispersal (Sodhi et al. 2010). Anthropogenic activities can also transform habitats and even create new ones, causing disorders in ecological communities and thus resulting in habitat degradation and loss of amphibian communities (Hamer and McDonnell 2008).

A recent assessment found that ~ 32% of global amphibian species are threatened by the continuous decline in the extent and quality of habitats as a result of human activities (Kiesecker 2011). Amphibians require specific habitats with enough space and resources in both aquatic and terrestrial habitats for reproduction, foraging, sheltering, *etc* (Semlitsch 2002; Hamer and Parris 2011). However, many amphibian populations around the world are damaged because of habitat decline (Parris 2006). Thus, high-quality habitats for breeding and nonbreeding activities are of great significance for amphibians.

Amphibians are often impacted by changes in spatial variables (e.g., roads, development lands, fences, deep concrete revetment, and impaired ecological connectivity). The changes in these variables often have harmful effects on species distribution and ecosystem biodiversity (Flohre et al. 2011; Nowakowski et al. 2017). For example, the conversion to fields equipped with deep ditches for rapid draining has eliminated the connection between the ditches and paddy fields (Natuhara 2013). Intensive farming in paddy fields usually involves the improvement of drainage and irrigation facilities for water management, which promotes machinery use (Natuhara and Kanbara 2001; Katayama et al. 2015; Kidera et al. 2018). Frog species, as essential indicators of change in aquatic habitat, primarily depend on water bodies in the early stages of their life cycles, especially for breeding (Kidera et al. 2018). Previous studies have reported the influences of land-use changes and water management measures on relatively limited taxa (Natuhara and Kanbara 2001; Naito et al. 2012).

Therefore, because of the alarming declines in amphibian populations, it is urgent to understand their functional roles and study how habitat changes might affect amphibian diversity (Drayer and Richter 2016). Many articles revealed that amphibian populations, in urban and rural landscapes, are impacted by variables executed at various landscape scales (Pellet et al. 2004; Rubbo and Kiesecker 2005). Nevertheless, few studies have evaluated how the assemblage of frogs as a whole responds to multiple habitats at both spatial and local scales (but see Van Buskirk 2005; Pillsbury and Miller 2008; Hamer and Parris 2011). A previous study reported that *Rana japonica*, *Rana ornativentris*, and *Bufo formosus japonicus* lay eggs in wet paddy fields (Natuhara 2013). However, during the breeding season of these species, only a few paddy fields are filled with water. Such hydrological conditions in the non-flooded season (i.e., winter to early spring) will also influence the spawning behavior of these three species in abandoned paddies.

Herein, I surveyed to test the following hypotheses: (1) not only the quality of local habitat but spatial environment play essential roles in determining breeding sites of the three species in urban-rural gradient; (2) spatial scale affecting breeding site selection is different among three species; (3) three species respond differently to the urban-rural gradient.

2.2 Materials and methods

2.2.1 Study area and field surveys

Field surveys were conducted at 124 sites in wetlands (10), paddy fields (49), ponds (32), and abandoned paddy fields (33) along an ecological gradient in Toyota City, Okazaki City, and Shitara Town in Aichi Prefecture, Japan (Fig. 2-1; 34°51′38″–35°17′24″N, 137°2′24″–137°40′35″E). I used the field surveys, and Google Earth to verify the accuracy of four habitat types. The surveys covered areas from hilly rural zones to urban zones, and the landscapes consisted mostly of paddy fields, wetlands, cities, and forests, *etc*.

In the study area, the egg-mass number of the three species was recorded from February–early April 2018. All sampling sites consisted of water bodies, and all survey sites were set in branching valleys. I set long distances between each study site to avoid overlaps among large buffer circles. I did not select the water bodies in rivers to survey.

To collect data precisely, I collected newly deposited egg masses of three species several times at each site and recorded the total egg-mass number. Furthermore, the egg-mass number of the three species is related to their sufficient population size because females lay a single egg mass per season (Maeda and Matsui

1989). I also visited the study sites several times to confirm species identification of the egg masses based on the hatched tadpoles between *Rana japonica* and *Rana ornativentris*.

2.2.2 Spatial variables

Using the Spatial Analyst function in ArcGIS Version 10.5 (ESRI, Redlands, CA, USA), a 1/25,000 vegetation map (Ministry of the Environment, Biodiversity Center of Japan, 2008) (Fig. 2-1) and a digital map were downloaded from GIAJ (Geospatial Information Authority of Japan, 2015; https://fgd.gsi.go.jp/download/menu.php). I generated circular buffer zones with three different radii (50 m, 100 m, and 250 m), centered at the sampling sites. Then I analyzed 13 spatial variables (Table 2-1), the total areas (m^2) of forest, grassland, lawn, wetland and riverside, paddy-field, abandoned paddy-field, dry field, residential region with much vegetation, city, open water and total road density (%), elevation (m), and elevation difference (m) within the buffer zones. I used 90 nonoverlapping sites in a 500-m-radius buffer.

2.2.3 Local variables

To explore the effects of environmental changes on the number of egg masses, and in agreement with study site conditions in the study area, I analyzed seven local variables (Table 2-1). The presence or absence of fishes, and the presence of trees on the soil levees of the habitats were recorded. I measured water depth at five different points randomly along the periphery of each site, acquiring an average water depth value, and measured water area using a tape measure (for small water areas) or Google Earth (in March 2018). Concrete revetments of ponds and wetlands are constructed due to modernization of agriculture and urbanization/ safety, *etc*. Thus, for each type of habitat, non-soil levees were included in the percentage of concrete revetment surrounding the habitats. Cover of aquatic vegetation (i.e., emergent + submerged vegetation = total aquatic vegetation) (%), and cover of embankment vegetation (%) were estimated based on visual observations by walking around the habitats. Other variables, such as water agrochemical contamination (because there was no agricultural chemicals application in the season surveyed), pH, and conductivity, are known to have little effect on amphibians' breeding (Yoshida et al. 2006). I established the local models using 64 study sites with an elevation of less than 248 m for *Rana japonica*, and using 124 study sites for other two species.

2.2.4 Statistical analyses

I tested the normality assumption for each independent variable before GLMs analysis and compared the habitat types to egg-mass number distribution of the three species using Steel–Dwass test at $P < 0.05$. I also evaluated the relationships between every combination of explanatory variables to test the collinearity using Spearman's rho (ρ) test. If Spearman correlation coefficients (ρ) were $-0.7 \leq \rho \leq 0.7$, I used both variables in the same model. Then, I used generalized linear models (GLMs) with a negative binomial error distribution and log-link function (Lindén and Mäntyniemi 2011). The logarithm of the survey area was used as an offset term to consider over-dispersion.

I tested models with two different sets of variables: spatial variables and local variables. In the models, the egg-mass number of either species was considered as response variables. Spatial models included 13 spatial explanatory variables in buffers around each study site at four scales: 50 m, 100 m, 250 m, and 500 m. Seven local variables were incorporated as explanatory variables.

I tested all combinations of explanatory variables to detect the most influential buffer scale based on the Akaike Information Criteria (AIC). To distinguish spatial and local variables affecting the dispersion of each frog species, models with ΔAICs < 2.0 were considered to have similar performance (Burnham and Anderson 2003). Additionally, we calculated Akaike weights and performed model averaging (approach with full-model averaging) to make validation of the models (Richards et al. 2011; Symonds and Moussalli 2011).

In the best model, the scale of each spatial explanatory variable was considered the most influential scale. I examined the estimated coefficients in the best model using Wald tests. All statistical analyses were performed using the package ‘MuMIn’ (Bates et al. 2014) in the statistical software R (ver. 3.3.2) (Team RC 2013).

2.3 Results

The information of spearman correlation coefficients (Spearman’s rho, ρ) was shown Table 2-2. I found egg masses of the three species in different habitats (Table 2-3). The habitat type selection of *R. japonica* and *R. ornativentris* were similar among the whole groups (Table 2-4). In contrast, the egg-mass number of *B. japonicus formosus* was significantly higher in the wetlands than paddy fields (P = 0.0087, Steel–Dwass test), paddy fields than ponds (P = 0.0015, Steel–Dwass test), and paddy fields than abandoned paddy fields (*P* < 0.001, Steel–Dwass test) (Table 2-4). The mean number (ranges in parentheses) of egg masses in each of the three species was 18.60 (2–62), 20.45 (2–105), and 6.30 (3–25) for *R. japonica*, *R. ornativentris*, and *B. japonicus formosus*, respectively. The breeding sites of *R. japonica* were widely distributed in low elevations of ~ 45–250 m, whereas *R. ornativentris* and *B. japonicus formosus* bred at high elevations of ~ 150–720 m (Fig. 2-2a). My findings showed that egg masses of the three species are rare at low elevations of 27–45 m and at high elevations of 701–927 m in the study area (Fig. 2-2a).

2.3.1 Effects of spatial variables

The most influential scale was 500 m radius for all three species according to the AIC value (see Table 2-5).

In the best model for *R. japonica*, within the 500-m-radius buffer, wetland and riverside area, forest area, and elevation difference affected positively to the number of egg masses, whereas elevation and grassland area had adverse effects (see Table 2-6).

In the best *R. ornativentris* model, the forest area, open water area, and abandoned paddy-field area were incorporated as explanatory variables (AIC = 412.60, see Table 2-5). Abandoned paddy-field area and forest area were positive values, whereas the open water area was negative (see Table 2-6).

In the best model for *B. japonicus formosus*, the number of egg masses was positively affected by the residential region with much vegetation area, forest area, dry field area, lawn area, and paddy-field area, whereas it was threatened by wetland and riverside area, and elevation difference (see Table 2-6).

Although there were other 18 models, 10 models, and 16 models that showed ▵AIC < 2.0 (see Table 2-5), for *R. japonica*, *R. ornativentris*, and *B. japonicus formosus*, respectively, their coefficients estimated by the model averaging were similar to those of the best model (see Table 2-7).

According to the best model, the forest area had the most substantial effect on the distribution of all three species. At the 500-m-radius buffer, for instance, the abundance of egg masses was ~ 40.7–95.3% of forest cover for the three species (Fig. 2-2b).

2.3.2 Effects of local variables

Table 2-8 showed the detailed results of model selections based on AIC value. No egg masses were found at study sites where fish were present. Therefore, I removed the "presence or absence of fishes" from the GLMs analysis. In the best model for the number of egg masses of *R. japonica* (AIC = 323.50), average water depth and the percentage of concrete revetments could be found to be the most negatively affecting variables (see Table 2-8). In the best model for the number of egg masses of *R. ornativentri*s (AIC = 431.60), the water area was the positively affecting variable and the percentage of concrete revetment was the negatively affecting variable (see Table 2-8). Finally, the best model for the number of egg masses of *B. japonicus formosus* indicates the presence of trees and the percentage of aquatic vegetation positively affect the number of egg masses; in contrast, the percentage of concrete revetment negatively affects it (AIC = 269.47, see Table 2-8).

Although there were other 19 models, 7 models, and 3 models that showed △AIC < 2.0 (see Table 2-8), for *R. japonica*, *R. ornativentris*, and *B. japonicus formosus*, respectively, their coefficients estimated by the model averaging were similar to those of the best model (see Table 2-9).

Regarding this analysis, there was substantial evidence that the presence of trees and water areas had positive effects on the three species (see Table 2-8). A higher abundance of egg masses belonging to *R. japonica* and *B. japonicus formosus* were found at water depths of ~ 3.0–14.0 cm, and *R. ornativentri*s at ~ 3.0–60.0 cm (Fig. 2-2c). The number of egg masses exhibited high values at intermediate to large water areas of approximately 40.0–400.0 m^2 in *R. japonica* and *B. japonicus formosus*, while *R. ornativentri*s preferred to breed at large water areas of ~ 72.0–1322.0 m^2 (Fig. 2-2d).

2.4 Discussion

Breeding assemblage of the three amphibian species was greatly affected by local habitat quality and spatial environment. The average values of water depth, water area, and forest area had strong positive influences on the breeding of the three species (see Tables 2-5 and 2-8; Fig. 2-2). On the other hand, breeding was negatively affected by the percentage of concrete revetment (see Table 2-8). Some variables influenced the breeding behaviors over three frog species differently because of the wide range of ecological gradients in the study area. For example, elevation difference had a positive effect on *R. japonica*, but a negative effect on *B. japonicus formosus* (see Table 2-6). These results test the three hypotheses stated in the end of introduction.

2.4.1 Effects of habitats on frog breeding

In this chapter, the egg mass distributions of *R. japonica* and *R. ornativentris* were roughly segregated in a natural geographical barrier. The elevation and geomorphology in breeding sites distinctly differed between *R. japonica* and *R. ornativentris*. According to the results, breeding sites of *R. japonica* were more widely distributed in paddy-field areas of low elevations than in forest areas. A total of 53.8% of adults of *R. japonica* were found at the edge of the forest in the Tama Hills, as reported by Osawa and Katsuno (2001). Besides, it has been validated that individuals of *R. japonica* occur in paddy-field areas in Niigata (Tojo, 1976); similar results for this species were reported by other groups (Natuhara and Kanbara 2001; Osawa and Katsuno 2001). Whereas, breeding sites of *R. ornativentris* were widely distributed at middle and high elevations (150–720 m) with surrounding forests, which is consistent with the report that this species inhabits forests (Osawa and Katsuno 2001).

The habitat isolation between two *Rana spp*. (*R. japonica* and *R. ornativentris*) and *B. japonicus formosus* might be retained by the differences in a typical water environment. *B. japonicus formosus* is known to breed in ponds and wetlands (Kusano et al. 1995), such as ponds with plentiful aquatic vegetation; this is following the results on *B. japonicus formosus*. In contrast, the two *Rana spp*. were not found in wetlands.

2.4.2 Effects of spatial variables on frog breeding

It is generally accepted that many frogs and toads move between aquatic and terrestrial environments. They are susceptible to change in landscape that influences their habitats over a range of scales (Vos and Stumpel 1996). Discussing which spatial variables affect frog distribution in different scales can also provide insights into the mechanisms underlying these effects (Knutson et al. 1999). I found that forest area had a consistent positive relationship with species' breeding selection. Forest areas can provide a more favorable context than open habitats (Tomioka, 1990), particularly, as forests are an essential environment for tadpoles and frog juveniles to avoid the risk of desiccation (Osawa and Katsuno 2001; Rothermel and Semlitsch 2002). The effects of forest area appeared to be most reliable at the 100 m scale for *R. japonica*, at the 500 m scale for *R. ornativentris,* and at the 50 m scale for *B. japonicus formosus* (see Table 2-6). Forest is the required habitat for *R. ornativentris* (Osawa and Katsuno 2001). Several previous studies have suggested that the dispersal distances of *R. japonica* and *R. ornativentris* are within the range of ~ 220–500 m (Osawa and Katsuno 2001; Kato et al. 2010). Moreover, many researchers have demonstrated that the migrating distances of individual *B. japonicus formosus* ranged from ~100–504 m (Yano 1978; Okuno 1985). These were mostly consistent to the trend expectation of the movement distances, which this study indicated that the most influential scale was 500 m radius for all three species. Nonetheless, less forest cover has additional effects on frogs as it translates into habitat degeneration.

The results of this chapter indicated that elevation had a consistent negative relationship with breeding site selection of *R. japonica* and *B. japonicus formosus*, whereas the relationship between elevation and breeding site selection of *R. ornativentris* was neutral (Fig. 2-2a; Table 2-6). Contrary to the results, however, *R. ornativentris* and *B. japonicus formosus* have widely been observed in lowland to montane areas, but tend to dwell at higher elevations (Sasaki et al. 2005). In particular, Otake and Shimada (2016) surveyed calls of *R. ornativentris* and *B. japonicus formosus* many times at high elevations in Toyota city. Furthermore, compared with the investigations of historical distribution in Aichi Prefecture (Aichi Prefectural Government 1996; Ota 2000; Otake and Shimada 2016; Takatsu 1998), my analysis demonstrated the number of egg masses of the three species is scarce not only in urban zones but also at high elevations. Such a phenomenon was also registered in other sites of central Japan (Osawa et al. 2013; Katayama et al. 2015).

2.4.3 Effects of different spatial scales on frog breeding

According to the results of model selections based on the lowest AIC values (see Table 2-5), the number of egg masses of three frog species were affected by the same spatial scale (500-m-radius buffer). This was mostly consistent to the trend expectation of the movement distances of adults from the breeding sites to forest habitats (Kusano et al. 1995; Osawa and Katsuno 2001; Kato et al. 2010). The different ages and genders of *B. japonicus formosus* distributed explain movement distances reported in previous article (Kusano et al. 1995).

The concordance of the effective spatial scales and migration distances reported for these three frog species suggests that amphibian abundance is influenced by the process of adult habitat use (Ficetola et al. 2009). For example, most individuals exhibit site-fidelity, meaning that they were absent at some potentially suitable sites. Nevertheless, they utilize a particular range including breeding sites and nearby forests throughout their lives.

2.4.4 Effects of local variables on frog breeding

The percentage of concrete revetment was the primary variable driving population reduction in the three frog species. This implies that agricultural intensification, especially in paddy-field areas, causes degradation and split breeding habitats for these frogs (Kidera et al. 2018). The average water depth harmed breeding of *R. japonica*, possibly because this species prefers to lay eggs in shallow/intermediate water habitats (Kidera et al. 2018) where there are no fish.

My study showed that water depth played an essential role in breeding sites for frogs. This is consistent with previous studies that *R. japonica* and *B. japonicus formosus* prefer to use the relatively intermediate water, and *R. ornativentris* prefer to use the relatively deep water to lay eggs during breeding season (Maeda and Matsui 1989; Kato et al. 2010), a feature also reported for other amphibian groups (Watson et al. 2003; Matsushima and Kawata 2005).

Many previous studies have reported that aquatic habitat areas play an essential role in amphibian distribution (Naito 2012; Osawa et al. 2013; Kidera et al. 2018). Meanwhile, these studies have also indicated that the water management regime and water areas were critical factors for conservation biodiversity. My findings support the hypothesis that increasing the water area may be a primary variable affecting the number of egg masses of three species.

The results of this chapter also confirmed that *B. japonicus formosus* lays eggs in wetlands/ponds with dense aquatic vegetation coverage because these suitable oviposition sites provide favorable breeding conditions such as aquatic vegetation and water physical conditions, promoting hatching success and larval growth (Kusano et al. 1995).

2.5 Tables

Table 2-1. The operational definition of each predictor variable, range of values in the data set, and data sources.

Explanatory variables	Operational definition	Range of values	Data source
Spatial variables			
FC	Total forest area proportion of vegetation cover within four scales of the center of the study site	2.80–98.50 %	Ministry of the Environment, Biodiversity Center of Japan, 2008
GA	Total grassland area of vegetation cover within four scales of the center of the study site	0–95070.00 m^2	(http://www.biodic.go.jp/copyright/index.html)
LA		0–111149.50 m^2	
WA		0–19462.30 m^2	
PA		0–287073.58 m^2	
APA		0–21256.01 m^2	
DFA		0–126058.60 m^2	
RVA		0–247099.77 m^2	
CA		0–410047.47 m^2	
OWA		0–186196.40 m^2	
ELV	Recorded values of center of study site	27–927 m	GPS, 2018
TRD	Total road density of buffer areas within four scales of the center of the study site	0–15.04 %	Geospatial Information Authority of Japan, 2015
ELD	The difference value between maximal elevation and minimum elevation within three scales of the center of the study site	0–224.21 m	(https://fgd.gsi.go.jp/download/menu.php)

Table 2-1. (Continued)

Explanatory variables	Operational definition	Range of values	Data source
Local variables			
AWD	An average water depth value	1.6–500 cm	Field surveys, 2018
PT	Presence of trees on the soil levees of the habitats	0/1	
CAV	Emergent + Submerged vegetation = Total Aquatic Vegetation	0–100 %	
PCR		0–100 %	
CEV		0–100 %	
WA		6.8–759687.67 m^2	

Notes: Spatial variables: Forest cover (FC), grassland area (GA), lawn area (LA), wetland and riverside area (WRA), paddy-field area (PA), abandoned paddy-field area (APA), dry field area (DFA), residential region with much vegetation area (RVA), city area (CA), open water area (OWA), elevation (ELV), total road density (TRD), elevation difference (ELD); Local variables: average water depth (AWD), presence of trees (PT), cover of aquatic vegetation (CAV), percentage of concrete revetment (PCR), cover of embankment vegetation (CEV), and water area (WA).

Table 2-2. Information of spearman correlation coefficients (Spearman's rho, ρ).

Table 2-2-1. Spearman correlation coefficients (Spearman's rho, ρ) between the local variables.

	WA	AWD	PCR	CEV	CAV
WA	1.00	0.45	-0.21	0.17	0.05
AWD		1.00	-0.07	0.13	-0.12
PCR			1.00	-0.22	-0.23
CEV				1.00	0.40
CAV					1.00

Notes: Coefficients in bold denote strong correlations (|ρ| > 0.7).

Water area (WA), average water depth (AWD), percentage of concrete revetment (PCR), cover of embankment vegetation (CEV), and cover of aquatic vegetation (CAV).

Table 2-2-2. Spearman correlation coefficients (Spearman's rho, ρ) between the spatial variables.

	FA	GA	LA	WRA	PA	APA	DFA	RVA	CA	OWA	ELV	TRD	ELD
50 m													
FA	1.00	0.03	-0.15	0.06	**-0.73**	0.03	-0.11	-0.32	-0.04	0.02	0.04	-0.36	NA
GA		1.00	-0.02	-0.03	-0.21	-0.05	-0.03	-0.06	-0.05	-0.06	0.07	0.06	NA
LA			1.00	-0.01	0.03	-0.03	0.48	-0.03	0.31	-0.03	-0.15	0.15	NA
WRA				1.00	-0.06	-0.04	-0.03	-0.05	-0.05	-0.05	0.20	-0.10	NA
PA					1.00	-0.10	-0.10	-0.09	-0.09	-0.24	0.08	0.32	NA
APA						1.00	-0.05	-0.10	-0.08	-0.09	-0.22	-0.17	NA
DFA							1.00	-0.06	0.11	-0.06	-0.18	0.14	NA
RVA								1.00	-0.10	0.27	-0.18	0.06	NA
CA									1.00	0.10	-0.03	0.00	NA
OWA										1.00	-0.20	-0.21	NA
ELV											1.00	0.39	NA
TRD												1.00	NA
ELD	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
100 m													
FA	1.00	0.04	-0.09	-0.02	-0.69	0.05	-0.07	-0.37	-0.13	-0.08	0.06	-0.45	0.10
GA		1.00	-0.05	0.21	-0.13	-0.08	-0.05	-0.05	-0.04	0.11	0.21	0.28	-0.06
LA			1.00	-0.04	0.01	-0.05	0.22	-0.08	0.20	-0.08	-0.24	-0.04	-0.04
WRA				1.00	0.03	-0.07	-0.04	-0.10	0.10	0.09	0.27	0.12	0.15
PA					1.00	-0.08	-0.06	0.00	-0.05	-0.19	0.10	0.35	-0.05
APA						1.00	-0.05	-0.06	-0.13	-0.06	-0.18	-0.25	-0.06
DFA							1.00	0.02	0.05	-0.08	-0.18	0.05	-0.04
RVA								1.00	0.01	0.19	-0.27	0.20	0.11
CA									1.00	0.00	-0.04	-0.01	-0.09
OWA										1.00	-0.20	-0.11	0.02
ELV											1.00	0.36	0.03
TRD												1.00	0.04
ELD													1.00
250 m													

Table 2-2-2. (Continued)

	FA	GA	LA	WRA	PA	APA	DFA	RVA	CA	OWA	ELV	TRD	ELD
FA	1.00	-0.13	-0.23	-0.07	-0.45	0.15	-0.17	-0.46	-0.34	-0.17	0.23	-0.55	0.09
GA		1.00	-0.04	0.24	-0.01	-0.22	-0.08	-0.14	0.08	0.09	0.26	0.15	0.22
LA			1.00	-0.06	-0.09	-0.12	0.05	-0.02	0.25	-0.12	-0.21	0.10	-0.15
WRA				1.00	0.10	-0.12	-0.09	-0.14	0.09	0.20	0.32	0.19	0.12
PA					1.00	-0.07	-0.02	-0.07	-0.02	-0.12	0.11	0.12	0.20
APA						1.00	0.16	-0.03	-0.10	0.09	-0.24	-0.29	-0.26
DFA							1.00	0.12	0.09	0.07	-0.34	0.08	-0.27
RVA								1.00	-0.04	0.10	-0.46	0.42	-0.24
CA									1.00	0.06	-0.04	0.33	-0.16
OWA										1.00	-0.26	0.03	-0.30
ELV											1.00	0.11	0.50
TRD												1.00	-0.07
ELD													1.00
500 m													
FA	1.00	-0.24	-0.23	0.06	-0.22	-0.03	-0.31	-0.50	-0.65	-0.31	0.49	**-0.70**	-0.09
GA		1.00	0.03	0.13	-0.04	-0.18	0.13	-0.10	0.25	0.16	0.15	0.10	-0.04
LA			1.00	-0.11	-0.13	-0.04	0.03	0.04	0.26	0.01	-0.12	0.14	-0.17
WRA				1.00	0.01	-0.13	0.02	-0.13	0.01	0.12	0.20	-0.03	0.13
PA					1.00	-0.07	0.04	-0.07	-0.08	-0.24	0.00	-0.07	0.54
APA						1.00	0.00	0.06	0.08	0.11	-0.37	0.06	-0.19
DFA							1.00	0.20	0.29	0.13	-0.27	0.27	0.02
RVA								1.00	0.12	0.16	-0.63	0.59	-0.06
CA									1.00	0.32	-0.31	0.56	-0.03
OWA										1.00	-0.43	0.20	-0.16
ELV											1.00	-0.46	0.15
TRD												1.00	-0.19
ELD													1.00

Notes: Coefficients in bold denote strong correlations ($|\rho| > 0.7$).

Forest area (FA), grassland area (GA), lawn area (LA), wetland and riverside area (WRA), paddy-field area (PA), abandoned paddy-field area (APA), dry field area (DFA), residential region with much vegetation area (RVA), city area (CA), open water area (OWA), elevation (ELV), total road density (TRD), elevation difference (ELD).

Table 2-3. The egg-masses number of the three species in different habitats.

Species	Wetlands	Paddy fields	Ponds	Abandoned paddy fields	Total
Rana japonica	0	15	9	6	30
Rana ornativentris	0	16	11	11	38
Bufo japonicus formosus	2	0	8	15	25

Table 2-4. Steel–Dwass test results (statistical significance, *P*) of between-habitat group differences (Statistically significant values indicated in bold).

Comparison of habitat type	*R. japonica*		*R. ornativentris*		*B. japonicus formosus*	
	t	*P*	t	*P*	t	*P*
Wetlands : Paddy fields	1.9811	0.1951	2.0674	0.1639	3.1574	**0.0087**
Wetlands : Ponds	1.8530	0.2486	2.1008	0.1528	0.2570	0.9940
Wetlands : Abandoned paddy fields	1.4314	0.4796	2.0624	0.1655	0.9290	0.7893
Paddy fields : Ponds	0.4131	0.9762	0.2479	0.9947	3.6576	**0.0015**
Paddy fields : Abandoned paddy fields	0.9863	0.7573	0.0227	1.0000	5.1552	**<0.001**
Ponds: Abandoned paddy fields	0.5778	0.9388	0.1557	0.9987	1.3138	0.5541

Table 2-5. Results of model selections based on AIC. Selected scale of each explanatory variable, AICs and ΔAICs (the difference between each AIC value and the smallest value) are indicated for the models with ΔAICs less than 2: models with ΔAICs < 2 are often considered plausible.

Species Model	Selected scale (m) for each variable																
	APA	RVA	CA	ELD	ELV	FA	DFA	GA	LA	OWA	PA	TRD	WRA	logLik	AIC	ΔAICs	Weight
Rana japonica																	
(50 m) Best model					**-7.34**									-173.37	**352.70**	0.00	**0.013**
2nd					-7.47				-11.76					-172.45	352.90	0.20	0.012
3rd			-0.62		-7.55									-172.59	353.20	0.50	0.011
4th					-7.41			-0.94						-172.78	353.60	0.90	0.011
5th					-7.54			-0.96	-11.69					-171.83	353.70	1.00	0.011
6th			-0.56		-7.63				-11.29					-171.86	353.70	1.00	0.010
7th		0.23			-7.86									-172.91	353.80	1.10	0.010
8th			-0.63		-7.63			-0.98						-171.95	353.90	1.20	0.009
9th					-8.14	-0.26			-12.13					-171.95	353.90	1.20	0.009
10th					-7.07							-11.63		-172.96	353.90	1.20	0.009
11st		0.24			-8.02				-11.83					-171.96	353.90	1.20	0.009
12nd			-0.78		-7.82						-0.19			-171.98	354.00	1.30	0.008
13rd			-0.71		-7.25							-14.05		-172.00	354.00	1.30	0.008
14th					-7.90	-0.22								-173.01	354.00	1.30	0.008
15th					-7.52						-0.14			-173.01	354.00	1.30	0.008
16th					-7.65				-11.78		-0.14			-172.10	354.20	1.50	0.007
17th		0.23	-0.62		-8.09									-172.15	354.30	1.60	0.007
18th			-0.82		-7.92			-1.15			-0.22			-171.19	354.40	1.70	0.007
19th			-0.57		-7.71			-0.99	-11.29					-171.20	354.40	1.70	0.007
20th					-7.26				-11.39			-8.85		-172.21	354.40	1.70	0.006

Table 2-5. (Continued)

Species Model	Selected scale (m) for each variable																
	APA	RVA	CA	ELD	ELV	FA	DFA	GA	LA	OWA	PA	TRD	WRA	logLik	AIC	∆AICs	Weight
21st					-7.22								-16.03	-173.22	354.40	1.70	0.006
22nd			-0.62		-8.11	-0.22								-172.24	354.50	1.80	0.006
23rd	-0.17				-7.60									-173.26	354.50	1.80	0.005
24th					-7.36				-11.74				-16.00	-172.31	354.60	1.90	0.004
(100 m) Best model		**0.70**			**-7.41**	**7.24**								-168.49	**347.00**	0.00	**0.011**
2nd		0.49			-8.54	7.62						33.10		-167.53	347.10	0.10	0.010
3rd		0.44			-8.53	7.54		-1.17				37.30		-166.57	347.10	0.10	0.010
4th		0.68			-7.58	7.15			-0.94					-167.72	347.40	0.40	0.009
5th					-9.22	5.62		-1.38				55.79		-167.76	347.50	0.50	0.009
6th		0.68			-7.29	7.09		-0.85						-167.78	347.60	0.60	0.009
7th		0.48			-8.66	7.51			-0.87			32.06		-166.81	347.60	0.60	0.008
8th		0.43			-8.67	7.43		-1.19	-0.87			36.29		-165.83	347.70	0.70	0.008
9th					-9.35	5.55		-1.39	-0.93			54.42		-166.97	347.90	0.90	0.008
10th					-9.32	5.43						53.39		-168.99	348.00	1.00	0.008
11st		0.66			-7.46	7.00		-0.88	-0.94					-166.99	348.00	1.00	0.007
12nd		0.69	-0.23		-7.63	7.38								-168.14	348.30	1.30	0.007
13rd		0.42		-2.09	-8.44	7.47		-1.19				39.11		-166.14	348.30	1.30	0.007
14th		0.47		-1.93	-8.45	7.54						34.63		-167.16	348.30	1.30	0.006
15th				-2.47	-9.10	5.72		-1.39				56.68		-167.20	348.40	1.40	0.006
16th		0.49	-0.19		-8.71	7.71						32.24		-167.28	348.60	1.60	0.005
17th		0.40		-2.13	-8.57	7.35		-1.20	-0.87			38.11		-165.38	348.80	1.80	0.005
18th		0.45		-1.97	-8.58	7.44			-0.87			33.62		-166.43	348.90	1.90	0.004

Table 2-5. (Continued)

Species Model	Selected scale (m) for each variable																
	APA	RVA	CA	ELD	ELV	FA	DFA	GA	LA	OWA	PA	TRD	WRA	logLik	AIC	ΔAICs	Weight
(250 m) Best model		**0.32**			**-8.50**	**11.33**		**-0.42**						-167.00	**346.00**	0.00	**0.013**
2nd		0.42		-1.87	-7.94	13.02		-0.39			0.36			-165.12	346.20	0.20	0.011
3rd		0.46		-1.88	-8.10	14.10					0.38			-166.26	346.50	0.50	0.010
4th		0.35			-8.69	12.23								-168.30	346.60	0.60	0.009
5th		0.39			-8.62	12.87		-0.36			0.23			-166.38	346.80	0.80	0.009
6th		0.39			-8.79	13.64					0.27			-167.40	346.80	0.80	0.008
7th		0.45		-2.23	-8.95	15.00				-0.29	0.43			-165.40	346.80	0.80	0.008
8th		0.33		-1.14	-7.97	10.95		-0.44						-166.43	346.90	0.90	0.008
9th		0.34			-8.86	11.16		-0.45	-0.42					-166.46	346.90	0.90	0.008
10th					-8.84	11.06		-0.40				2.93		-167.56	347.10	1.10	0.007
11st		0.44		-2.29	-8.54	14.08		-0.34		-0.22	0.40			-164.61	347.20	1.20	0.007
12nd		0.25			-8.83	12.42		-0.40				1.45		-166.74	347.50	1.50	0.006
13rd		0.33			-9.38	12.70				-0.23				-167.75	347.50	1.50	0.006
14th		0.39		-1.14	-8.18	12.20								-167.80	347.60	1.60	0.006
15th		0.33			-8.89	11.88		-0.37		-0.13				-166.81	347.60	1.60	0.006
16th		0.35		-1.23	-8.30	10.79		-0.47	-0.44					-165.82	347.60	1.60	0.006
17th		0.36			-8.99	12.17			-0.37					-167.88	347.80	1.80	0.005
18th		0.36		-1.80	-8.20	14.03		-0.37			0.36	1.26		-164.90	347.80	1.80	0.005
19th					-7.85	6.55		-0.40						-168.90	347.80	1.80	0.005
20th	0.32	0.34		-1.49	-8.75	14.55				-0.33				-165.90	347.80	1.80	0.005
21st		0.39			-9.43	14.19				-0.20	0.27			-166.92	347.80	1.80	0.005
22nd		0.32			-8.38	11.21		-0.42					-7.88	-166.94	347.90	1.90	0.005
23rd					-9.09	11.83						3.03		-168.94	347.90	1.90	0.005

Table 2-5. (Continued)

Species Model	Selected scale (m) for each variable																
	APA	RVA	CA	ELD	ELV	FA	DFA	GA	LA	OWA	PA	TRD	WRA	logLik	AIC	ΔAICs	Weight
24th		0.38			-8.57	12.65	0.25	-0.46			0.35			-165.95	347.90	1.90	0.005
25th		0.39		-1.81	-8.44	15.36					0.39	1.50		-165.95	347.90	1.90	0.005
(500 m) Best model				**3.59**	**-9.96**	**8.02**		**-0.49**					**0.35**	-146.85	**307.70**	0.00	**0.015**
2nd				3.22	-9.63	7.34		-0.47						-147.89	307.80	0.10	0.014
3rd				3.25	-10.17	7.03		-0.52	-0.41					-146.93	307.90	0.20	0.014
4th		0.28	0.28	3.65	-9.51	13.67		-0.49					0.61	-144.95	307.90	0.20	0.013
5th		0.29	0.29	3.61	-9.74	13.01		-0.53	-0.39				0.59	-143.99	308.00	0.30	0.013
6th				3.61	-10.37	7.54		-0.53	-0.36				0.33	-146.03	308.10	0.40	0.012
7th			0.19	3.59	-9.50	10.25		-0.51					0.41	-146.09	308.20	0.50	0.012
8th				2.40	-10.07	7.71		-0.45			0.57			-147.17	308.30	0.60	0.011
9th			0.20	3.57	-9.78	9.49		-0.55	-0.38				0.39	-145.19	308.40	0.70	0.011
10th		0.19		3.68	-10.05	9.53		-0.46					0.45	-146.30	308.60	0.90	0.009
11st		0.29	0.29	2.67	-9.38	13.47		-0.45			0.47		0.57	-144.35	308.70	1.00	0.009
12nd				2.58	-10.47	7.38		-0.49	-0.35		0.52			-146.42	308.80	1.10	0.008
13rd		0.21		3.57	-10.31	8.41		-0.52	-0.37				0.45	-145.51	309.00	1.30	0.008
14th		0.30	0.30	2.79	-9.59	12.99		-0.49	-0.34		0.42		0.57	-143.54	309.10	1.40	0.007
15th					-9.26	6.88		-0.39			1.03			-148.59	309.20	1.50	0.007
16th			0.10	3.13	-9.25	8.10		-0.48						-147.67	309.30	1.60	0.007
17th				2.98	-10.44	7.54		-0.50	-0.32		0.39		0.31	-145.69	309.40	1.70	0.006
18th		0.10		2.99	-9.93	7.37		-0.49	-0.42					-146.74	309.50	1.80	0.006
19th				3.05	-9.48	7.04	-0.06	-0.46						-147.79	309.60	1.90	0.006
Rana ornativentris																	
(50 m) Best model													**-10.65**	-222.55	**451.10**	0.00	**0.008**

Table 2-5. (Continued)

Species Model	Selected scale (m) for each variable																
	APA	RVA	CA	ELD	ELV	FA	DFA	GA	LA	OWA	PA	TRD	WRA	logLik	AIC	∆AICs	Weight
2nd														-223.69	451.40	0.30	0.007
3rd									-6.18				-10.15	-222.16	452.30	1.20	0.004
4th											0.12		-10.48	-222.26	452.50	1.40	0.004
5th									-5.62					-223.31	452.60	1.50	0.004
6th		-0.23											-10.65	-222.31	452.60	1.50	0.004
7th								-0.36					-10.68	-222.34	452.70	1.60	0.004
8th											0.13			-223.36	452.70	1.60	0.004
9th							-0.33						-10.68	-222.36	452.70	1.60	0.004
10th					0.48								-10.38	-222.41	452.80	1.70	0.004
11st			0.13										-10.49	-222.47	452.90	1.80	0.003
12nd		-0.23												-223.47	452.90	1.80	0.003
13rd								-0.35						-223.49	453.00	1.90	0.003
(100 m) Best model				**-3.65**										-222.38	**450.80**	0.00	**0.007**
2nd				-3.70				-0.53						-221.53	451.10	0.30	0.006
3rd														-223.69	451.40	0.60	0.005
4th								-0.52						-222.89	451.80	1.00	0.004
5th				-3.66						-0.20				-222.03	452.10	1.30	0.003
6th				-3.68							0.12			-222.09	452.20	1.40	0.003
7th				-3.72				-0.55		-0.22				-221.12	452.20	1.40	0.003
8th				-3.67					-0.43					-222.13	452.30	1.50	0.003
9th				-3.67			-0.32							-222.17	452.30	1.50	0.003
10th		-0.13		-3.62										-222.20	452.40	1.60	0.003
11st				-3.72				-0.54	-0.44					-221.26	452.50	1.70	0.003

Table 2-5. (Continued)

Species Model	Selected scale (m) for each variable																
	APA	RVA	CA	ELD	ELV	FA	DFA	GA	LA	OWA	PA	TRD	WRA	logLik	AIC	∆AICs	Weight
12^{nd}				-3.65	0.40									-222.29	452.60	1.80	0.003
13^{rd}				-3.72			-0.34	-0.54						-221.30	452.60	1.80	0.003
14^{th}		-0.15		-3.67				-0.55						-221.30	452.60	1.80	0.003
15^{th}				-3.63								-5.84		-222.34	452.70	1.90	0.003
(250 m) Best model												**-48.16**		-222.36	**450.70**	0.00	**0.006**
2^{nd}														-223.69	451.40	0.70	0.005
3^{rd}				1.63										-222.70	451.40	0.70	0.004
4^{th}							-0.31					-48.21		-221.81	451.60	0.90	0.004
5^{th}				1.06								-37.63		-222.01	452.00	1.30	0.003
6^{th}									0.21			-51.15		-222.07	452.10	1.40	0.003
7^{th}										-0.15		-43.77		-222.10	452.20	1.50	0.003
8^{th}										-0.22				-223.11	452.20	1.50	0.003
9^{th}							-0.30							-223.17	452.30	1.60	0.003
10^{th}	-0.11											-51.16		-222.21	452.40	1.70	0.003
11^{st}				1.97					0.27					-222.24	452.50	1.80	0.003
12^{nd}		-0.07										-46.24		-222.25	452.50	1.80	0.003
13^{rd}			0.07									-55.73		-222.25	452.50	1.80	0.003
14^{th}						1.56								-223.27	452.50	1.80	0.003
15^{th}								0.07				-51.61		-222.28	452.60	1.90	0.002
(500 m) Best model	**0.24**					**3.38**				**-0.40**				-202.29	**412.60**	0.00	**0.013**
2^{nd}	0.20				-0.84	4.70				-0.45				-201.73	413.50	0.90	0.008
3^{rd}	0.24					4.16	0.11			-0.37				-201.82	413.60	1.00	0.008
4^{th}					-1.06	4.47				-0.37				-202.82	413.60	1.00	0.008

Table 2-5. (Continued)

Species Model	Selected scale (m) for each variable																
	APA	RVA	CA	ELD	ELV	FA	DFA	GA	LA	OWA	PA	TRD	WRA	logLik	AIC	∆AICs	Weight
5th	0.22									-0.43				-203.83	413.70	1.10	0.008
6th						2.92				-0.28				-203.93	413.90	1.30	0.007
7th	0.24					3.38		0.06		-0.42				-202.15	414.30	1.70	0.006
8th	0.22	0.05				3.65				-0.41				-202.18	414.40	1.80	0.005
9th	0.25					3.20				-0.38	0.08			-202.21	414.40	1.80	0.005
10th										-0.31				-205.22	414.40	1.80	0.005
11st	0.23		0.04			3.69				-0.41				-202.25	414.50	1.90	0.005
Bufo japonicus formosus																	
(50 m) Best model						**2.76**								-118.96	**243.90**	0.00	**0.007**
2nd					-1.19	2.20								-118.07	244.10	0.20	0.006
3rd			0.38			2.24								-118.13	244.30	0.40	0.006
4th						2.79							-13.92	-118.13	244.30	0.40	0.006
5th		0.41	0.43			2.19								-117.25	244.50	0.60	0.005
6th					-1.30	2.11	-7.24							-117.28	244.60	0.70	0.005
7th			0.37			2.27							-14.98	-117.34	244.70	0.80	0.005
8th					-1.07	2.27							-14.31	-117.42	244.80	0.90	0.004
9th		0.40	0.42			2.23							-15.97	-116.49	245.00	1.10	0.004
10th		0.40	0.43			2.15	-7.86							-116.67	245.30	1.40	0.004
11st						2.59				0.21				-118.68	245.40	1.50	0.004
12nd			0.43			1.95				0.28			-16.01	-116.76	245.50	1.60	0.004
13rd		0.34				2.76	-7.33							-117.82	245.60	1.70	0.004
14th						2.28					-0.10			-118.83	245.70	1.80	0.004
15th						2.62				0.20			-14.46	-117.88	245.80	1.90	0.003

Table 2-5. (Continued)

Species Model	Selected scale (m) for each variable																
	APA	RVA	CA	ELD	ELV	FA	DFA	GA	LA	OWA	PA	TRD	WRA	logLik	AIC	∆AICs	Weight
(100 m) Best model				**-18.65**	**-1.69**	**4.91**								-118.19	**246.40**	0.00	**0.003**
2nd				-18.20	-1.78	4.90	-7.41							-117.22	246.47	0.07	0.003
3rd				-17.92	-1.57	4.86							-9.07	-117.43	246.90	0.50	0.003
4th				-19.00	-1.66	4.85	-7.63						-9.36	-116.46	246.90	0.50	0.003
5th					-1.71	4.77								-119.52	247.00	0.60	0.002
6th					-1.55	4.80							-9.20	-118.57	247.10	0.70	0.002
7th					-1.79	4.77	-7.39							-118.61	247.20	0.80	0.002
8th					-1.64	4.79	-7.38						-9.19	-117.64	247.30	0.90	0.002
9th				-21.49			-5.51				-0.31		-6.29	-117.73	247.50	1.10	0.002
10th							-5.25				-0.31		-6.06	-118.75	247.50	1.10	0.002
11st				-21.70	-1.87	5.07	-8.38	-0.34						-116.75	247.50	1.10	0.002
12nd				-21.68	-1.78	5.07		-0.33						-117.75	247.50	1.10	0.002
13rd				-19.67		3.41					-0.24		-9.66	-117.81	247.60	1.20	0.002
14th				-21.10		3.51					-0.24			-118.82	247.60	1.20	0.002
15th			0.16	-19.19	-1.52	4.68								-117.83	247.70	1.30	0.002
16th											-0.30		-6.58	-118.89	247.80	1.40	0.002
17th				-20.14		3.43	-7.98				-0.26			-117.94	247.90	1.50	0.002
18th						3.22	-8.01				-0.26		-9.79	-117.98	248.00	1.60	0.002
19th			0.17	-19.98	-1.39	4.61							-8.98	-117.04	248.10	1.70	0.001
20th				-21.62	-1.46	4.24	-8.654				-0.10			-117.08	248.20	1.80	0.001
21st				-19.08	-1.83	5.13						6.30		-118.13	248.30	1.90	0.001
(250 m) Best model							**-0.58**				**-0.31**		**-4.86**	-117.10	**244.20**	0.00	**0.009**
2nd			-0.27				-0.51		0.45		-0.32		-5.04	-115.58	245.20	1.00	0.008

Table 2-5. (Continued)

Species Model	Selected scale (m) for each variable																
	APA	RVA	CA	ELD	ELV	FA	DFA	GA	LA	OWA	PA	TRD	WRA	logLik	AIC	∆AICs	Weight
3rd											-0.32		-5.64	-118.60	245.20	1.00	0.008
4th			-0.15				-0.55				-0.39		-9.32	-116.66	245.30	1.10	0.008
5th			-0.32						0.48		-0.34		-8.02	-116.73	245.50	1.30	0.007
6th					-0.77		-0.65				-0.24		-8.02	-116.85	245.70	1.50	0.007
7th							-0.57		0.20		-0.26		-6.75	-116.86	245.70	1.50	0.005
8th			-0.19								-0.43		-9.32	-117.90	245.80	1.60	0.005
9th							-0.58				-0.33	-15.89	-8.04	-116.95	245.90	1.70	0.005
10th		0.09					-0.57				-0.26		-8.07	-116.95	245.90	1.70	0.005
11st	-0.10						-0.53				-0.30		-7.29	-116.99	246.00	1.80	0.005
12nd						1.19	-0.56				-0.33		-9.12	-117.02	246.00	1.80	0.005
13rd							-0.59	-0.07			-0.31		-9.27	-117.03	246.10	1.90	0.004
(500 m) Best model		**0.25**		**-5.36**		**5.83**	**0.34**		**0.38**		**0.47**		**-5.24**	-97.06	**210.10**	0.00	**0.012**
2nd		0.38		-5.21		3.33	0.33			-0.28			-5.26	-98.34	210.70	0.60	0.009
3rd		0.23		-4.20		5.42	0.30		0.33				-5.38	-98.43	210.90	0.80	0.008
4th		0.32		-5.82		4.89	0.33		0.30	-0.17	0.46		-5.14	-96.53	211.10	1.00	0.008
5th		0.41		-6.06		3.34	0.36			-0.29	0.40		-5.15	-97.53	211.10	1.00	0.008
6th		0.33		-5.02			0.25			-0.28			-4.93	-99.67	211.30	1.20	0.007
7th		0.26		-5.18		7.15	0.32	0.13	0.48		0.54		-5.55	-96.71	211.40	1.30	0.006
8th		0.32		-4.83		4.45	0.31		0.22	-0.19			-5.27	-97.75	211.50	1.40	0.006
9th	-0.13	0.30		-5.67		5.39	0.33		0.40		0.49		-7.28	-96.76	211.50	1.40	0.006
10th		0.28		-4.87	-1.54	5.11	0.34			-0.38			-5.17	-97.76	211.50	1.40	0.006
11st	-0.34			-4.60	-4.75	6.70	0.38			-0.46			-5.51	-97.80	211.60	1.50	0.006
12nd	-0.29	0.24		-5.02	-3.42	6.18	0.36			-0.45			-5.50	-96.83	211.70	1.60	0.006

Table 2-5. (Continued)

Species Model	Selected scale (m) for each variable																
	APA	RVA	CA	ELD	ELV	FA	DFA	GA	LA	OWA	PA	TRD	WRA	logLik	AIC	∆AICs	Weight
13^{rd}		0.35		-5.80		6.57	0.32	0.18	0.41	-0.21	0.59		-5.12	-95.93	211.90	1.80	0.005
14^{th}		0.35		-5.77			0.27			-0.29	0.36		-5.14	-98.94	211.90	1.80	0.005
15^{th}	-0.33			-4.36	-4.27	8.22	0.35		0.25	-0.34			-6.14	-96.98	212.00	1.90	0.005
16^{th}				-5.17		3.99	0.29		0.42		0.50		-5.23	-99.00	212.00	1.90	0.005
17^{th}		0.25	-0.05	-5.45		5.25	0.34		0.39		0.45		-5.24	-97.02	212.00	1.90	0.005

Notes: Abandoned paddy-field area (APA), residential region with much vegetation area (RVA), city area (CA), elevation difference (ELD), elevation (ELV), forest area (FA), dry field area (DFA), grassland area (GA), lawn area (LA), open water area (OWA), paddy-field area (PA), total road density (TRD), wetland and riverside area (WRA).

Table 2-6. The best models were explaining the number of egg masses by the spatial variables. The estimated coefficients (Coefficient) and standard errors (SE) are shown for each species.

Species with scales	Variable in the best model	Coefficient	SE
Rana japonica			
50 m	Elevation	-7.34	0.90
	(Intercept)	17.67	2.05
100 m	Residential region with much vegetation area	0.70	0.24
	Elevation	-7.41	0.92
	Forest area	7.24	2.01
	(Intercept)	-13.77	8.99
250 m	Residential region with much vegetation area	0.32	0.16
	Elevation	-8.50	1.04
	Forest area	11.33	3.35
	Grassland area	-0.42	0.23
	(Intercept)	-1.70	6.28
500 m	Elevation	-9.96	1.30
	Elevation difference	3.59	1.14
	Forest area	8.02	2.78
	Grassland area	-0.49	0.16
	Wetland and riverside area	0.35	0.29
	(Intercept)	-28.81	15.42
Rana ornativentris			
50 m	Wetland and riverside area	-10.65	1860.03
	(Intercept)	-1.37	559.93
100 m	Elevation difference	-3.65	1.91
	(Intercept)	0.76	0.61
250 m	Total road density	-48.16	20.79
	(Intercept)	-11.43	5.68
500 m	Forest area	3.38	2.11
	Open water area	-0.40	0.12
	Abandoned paddy-field area	0.24	0.12
	(Intercept)	-17.41	12.24
Bufo japonicus formosus			
50 m	Forest area	2.76	1.11
	(Intercept)	-10.03	4.02
100 m	Elevation	-1.69	0.77
	Elevation difference	-18.65	2914.15
	Forest area	4.91	2.00
	(Intercept)	-22.93	877.29

Table 2-6. (Continued)

Species with scales	Variable in the best model	Coefficient	SE
250 m	Dry field area	-0.58	0.31
	Paddy fields area	-0.31	0.13
	Wetland and riverside area	-4.86	686.87
	(Intercept)	-0.78	206.77
500 m	Residential region with much vegetation area	0.25	0.10
	Elevation difference	-5.36	0.85
	Forest area	5.83	3.03
	Dry field area	0.34	0.10
	Lawn area	0.38	0.15
	Paddy fields area	0.47	0.20
	Wetland and riverside area	-5.24	412.74
	(Intercept)	-29.55	125.50

Table 2-7. Model-averaged (full-model averaging is the preferred approach) estimates for explaining the number of egg masses by the spatial variables. The estimated coefficients (Coefficient), standard errors (SE), Adjusted SE (AS), *z* values (*z*), and *P* values (*P*) are shown for each species (statistically significant values indicated in bold). The candidate models with △AICs < 4 are considered plausible in the model averaging.

Species with scales	Spatial variables	Coefficient	SE	AS	*z*	*P*
Rana japonica						
50 m	ELV	-0.02	<0.01	<0.01	6.20	**<0.001**
	LA	-3.71	8683000.00	8773000.00	<0.01	1.0000
	RVA	0.09	0.20	0.20	0.45	0.6510
	CA	-0.23	0.39	0.39	0.59	0.5570
	GA	-0.31	0.55	0.55	0.57	0.5720
	PA	-0.05	0.13	0.13	0.40	0.6930
	TRD	-0.01	0.04	0.04	0.29	0.7730
	OWA	-0.09	0.23	0.23	0.39	0.7000
	WRA	-1.33	1670000.00	1687000.00	<0.01	1.0000
	DFA	-0.01	0.14	0.14	0.09	0.9280
	FA	0.03	0.41	0.41	0.07	0.9470
	APA	0.00	0.10	0.10	0.03	0.9760
	(Intercept)	3.27	2662000.00	2689000.00	<0.01	1.0000
100m	ELV	-0.02	<0.01	<0.01	6.00	**<0.001**
	RVA	0.33	0.27	0.27	1.20	0.2290
	LA	-10.58	15420000.00	15580000.00	<0.01	1.0000
	CA	-0.60	0.42	0.42	1.43	0.1530
	GA	-0.88	0.60	0.60	1.46	0.1450
	TRD	-0.09	0.08	0.09	1.07	0.2860
	PA	-0.21	0.20	0.20	1.04	0.2980
	OWA	-0.36	0.35	0.35	1.04	0.2990
	FA	0.63	1.26	1.27	0.50	0.6200
	WRA	-12.41	5515000.00	5572000.00	<0.01	1.0000
	DFA	-0.09	0.41	0.41	0.22	0.8290
	APA	-0.12	0.32	0.33	0.36	0.7190
	(Intercept)	3.25	2773000.00	2801000.00	<0.01	1.0000
250 m	RVA	0.27	0.22	0.22	1.21	0.2283
	ELV	-8.64	1.26	1.28	6.77	**<0.001**
	FA	12.44	4.14	4.17	2.99	**0.0028**
	GA	-0.22	0.26	0.27	0.82	0.4148
	ELD	-0.65	1.10	1.10	0.60	0.5521

Table 2-7. (Continued)

Species with scales	Spatial variables	Coefficient	SE	AS	*z*	*P*
	PA	0.12	0.20	0.20	0.59	0.5523
	OWA	-0.07	0.16	0.16	0.42	0.6726
	LA	-0.07	0.22	0.22	0.35	0.7303
	TRD	0.80	1.76	1.77	0.45	0.6520
	APA	0.03	0.11	0.11	0.27	0.7913
	WRA	-1.18	1684000.00	1701000.00	<0.01	1.0000
	DFA	0.01	0.11	0.11	0.04	0.9722
	(Intercept)	-3.75	506800.00	512100.00	<0.01	1.0000
500 m	ELD	2.59	1.64	1.65	1.57	0.1164
	ELV	-9.69	1.47	1.49	6.50	**<0.001**
	FA	8.86	3.66	3.70	2.39	**0.0167**
	GA	-0.47	0.17	0.17	2.74	**0.0062**
	WRA	0.24	0.32	0.32	0.76	0.4474
	LA	-0.16	0.24	0.25	0.66	0.5100
	RVA	0.08	0.16	0.16	0.53	0.5934
	CA	0.09	0.15	0.16	0.60	0.5489
	PA	0.29	0.45	0.45	0.65	0.5168
	DFA	-0.01	0.07	0.07	0.14	0.8895
	OWA	<0.01	0.07	0.07	0.05	0.9605
	APA	<0.01	0.06	0.06	0.01	0.9945
	(Intercept)	-34.30	21.63	21.84	1.57	0.1163
Rana ornativentris						
50 m	WRA	-6.48	1185000.00	1197000.00	<0.01	1.0000
	LA	-1.51	3786000.00	3825000.00	<0.01	1.0000
	FA	-0.29	0.77	0.77	0.37	0.7090
	PA	0.04	0.12	0.12	0.34	0.7330
	RVA	-0.04	0.16	0.16	0.27	0.7860
	GA	-0.05	0.23	0.23	0.24	0.8130
	DFA	-0.04	0.21	0.21	0.21	0.8360
	CA	0.03	0.15	0.15	0.19	0.8520
	APA	-0.02	0.13	0.13	0.14	0.8920
	TRD	<0.01	0.02	0.02	0.05	0.9580
	OWA	<0.01	0.11	0.11	0.02	0.9810
	ELV	<0.01	<0.01	<0.01	0.41	0.6810
	(Intercept)	-0.39	1194000.00	1207000.00	<0.01	1.0000
100 m	ELD	-2.59	2.33	2.34	1.11	0.2690
	GA	-0.21	0.33	0.33	0.62	0.5370
	OWA	-0.04	0.13	0.13	0.31	0.7550

Table 2-7. (Continued)

Species with scales	Spatial variables	Coefficient	SE	AS	*z*	*P*
	PA	0.02	0.07	0.07	0.22	0.8260
	LA	-0.07	0.26	0.27	0.28	0.7830
	DFA	-0.05	0.20	0.20	0.24	0.8070
	RVA	-0.02	0.09	0.09	0.19	0.8520
	ELV	0.01	0.29	0.29	0.05	0.9630
	TRD	-0.67	5.54	5.58	0.12	0.9040
	APA	<0.01	0.09	0.09	0.06	0.9560
	CA	0.01	0.08	0.08	0.08	0.9390
	WRA	-0.01	0.14	0.14	0.08	0.9370
	FA	<0.01	0.22	0.22	0.01	0.9910
	(Intercept)	0.76	2.01	2.02	0.37	0.7090
250 m	TRD	-25.23	29.07	29.16	0.87	0.3870
	ELD	0.42	0.87	0.87	0.48	0.6300
	DFA	-0.06	0.17	0.17	0.35	0.7280
	LA	0.04	0.16	0.16	0.27	0.7880
	OWA	-0.03	0.11	0.11	0.30	0.7630
	APA	-0.01	0.07	0.07	0.11	0.9120
	RVA	-0.01	0.07	0.07	0.19	0.8490
	CA	<0.01	0.05	0.05	0.08	0.9370
	FA	0.13	0.74	0.75	0.18	0.8610
	GA	<0.01	0.06	0.06	0.05	0.9620
	ELV	-0.01	0.33	0.34	0.04	0.9680
	WRA	<0.01	0.11	0.11	0.03	0.9740
	PA	<0.01	0.05	0.05	0.03	0.9770
	(Intercept)	-6.35	8.05	8.08	0.79	0.4320
500 m	APA	0.14	0.15	0.15	0.92	0.3583
	FA	3.31	2.92	2.95	1.12	0.2618
	OWA	-0.39	0.14	0.14	2.78	**0.0055**
	ELV	-0.34	0.77	0.78	0.44	0.6618
	DFA	0.03	0.07	0.08	0.33	0.7403
	GA	0.01	0.06	0.06	0.24	0.8108
	RVA	0.01	0.05	0.05	0.17	0.8665
	PA	0.01	0.07	0.07	0.19	0.8508
	CA	0.01	0.05	0.05	0.17	0.8683
	WRA	0.01	0.11	0.11	0.13	0.8952
	LA	-0.01	0.07	0.07	0.10	0.9233
	ELD	-0.01	0.22	0.23	0.04	0.9718
	(Intercept)	-16.21	16.37	16.52	0.98	0.3266

Table 2-7. (Continued)

Species with scales	Spatial variables	Coefficient	SE	AS	*z*	*P*
Bufo japonicus formosus						
50 m	ELV	<0.01	<0.01	<0.01	1.57	0.1170
	FA	0.02	0.01	0.01	1.37	0.1700
	DFA	-2.73	471.72	476.57	0.01	0.9950
	CA	0.14	0.25	0.25	0.55	0.5800
	WRA	-2.50	702.36	709.60	<0.01	0.9970
	LA	-0.43	387.82	391.81	<0.01	0.9990
	TRD	0.01	0.04	0.04	0.22	0.8220
	PA	-0.02	0.10	0.10	0.17	0.8670
	APA	-0.01	0.10	0.10	0.10	0.9250
	RVA	-0.01	0.10	0.10	0.06	0.9550
	GA	<0.01	0.13	0.13	0.03	0.9770
	OWA	0.01	0.11	0.11	0.12	0.9050
	(Intercept)	-2.13	276.74	279.60	0.01	0.9940
100 m	ELD	-20.08	3920000.00	3961000.00	<0.01	1.0000
	ELV	-0.96	1.03	1.04	0.93	0.3540
	FA	3.68	2.69	2.71	1.36	0.1730
	DFA	-3.62	1114000.00	1126000.00	<0.01	1.0000
	WRA	-4.44	961000.00	971000.00	<0.01	1.0000
	PA	-0.09	0.16	0.16	0.59	0.5570
	GA	-0.07	0.21	0.21	0.31	0.7580
	CA	0.04	0.13	0.13	0.31	0.7590
	OWA	-0.01	0.09	0.10	0.06	0.9550
	APA	-0.01	0.09	0.09	0.12	0.9080
	TRD	0.80	6.90	6.95	0.12	0.9080
	LA	<0.01	0.17	0.17	0.03	0.9770
	RVA	0.01	0.10	0.11	0.11	0.9150
	(Intercept)	-21.79	1259000.00	1272000.00	<0.01	1.0000
250 m	ELV	<0.01	<0.01	<0.01	1.30	0.1950
	DFA	<0.01	<0.01	<0.01	1.56	0.1180
	PA	<0.01	<0.01	<0.01	0.89	0.3730
	WRA	<0.01	1.02	1.03	0.00	0.9970
	CA	<0.01	<0.01	<0.01	0.57	0.5720
	OWA	<0.01	<0.01	<0.01	0.32	0.7520
	ELD	<0.01	0.01	0.01	0.30	0.7620
	FA	<0.01	0.02	0.02	0.13	0.8990
	RVA	<0.01	<0.01	<0.01	0.18	0.8580
	APA	<0.01	<0.01	<0.01	0.20	0.8420

Table 2-7. (Continued)

Species with scales	Spatial variables	Coefficient	SE	AS	*z*	*P*
	TRD	<0.01	0.07	0.07	0.07	0.9420
	LA	<0.01	<0.01	<0.01	0.09	0.9250
	(Intercept)	0.61	1.68	1.69	0.36	0.7160
500 m	RVA	0.23	0.17	0.17	1.38	0.1667
	ELD	-5.08	1.06	1.07	4.76	**<0.001**
	FA	4.57	3.62	3.65	1.25	0.2104
	DFA	0.31	0.12	0.13	2.47	**0.0136**
	LA	0.21	0.22	0.22	0.97	0.3330
	PA	0.23	0.28	0.28	0.84	0.4018
	WRA	-4.74	3112.00	3160.00	<0.01	0.9988
	OWA	-0.19	0.19	0.19	0.99	0.3236
	GA	0.02	0.07	0.07	0.26	0.7922
	APA	-0.06	0.13	0.13	0.47	0.6390
	ELV	-0.88	1.53	1.54	0.57	0.5684
	CA	<0.01	0.05	0.05	0.08	0.9349
	(Intercept)	-19.08	937.10	951.50	0.02	0.9840

Notes: Abandoned paddy-field area (APA), residential region with much vegetation area (RVA), city area (CA), elevation difference (ELD), elevation (ELV), forest area (FA), dry field area (DFA), grassland area (GA), lawn area (LA), open water area (OWA), paddy-field area (PA), total road density (TRD), wetland and riverside area (WRA).

Table 2-8. Results of model selections based on AIC. Selected scale of each explanatory variable, AICs and △AICs (the difference between each AIC value and the smallest value) are indicated for the models with △AICs less than 2: models with △AICs < 2 are often considered plausible.

Species Model	Selected scale (m) for each variable									
	AWD	PT	CAV	PCR	CEV	WA	logLik	AIC	△AIC	Weight
Rana japonica										
Best model	**-1.67**			**-0.02**		**1.16**	-156.73	**323.50**	0.00	**0.053**
2nd				-0.02		1.06	-157.75	323.50	0.00	0.052
3rd				-0.02			-158.81	323.60	0.10	0.049
4th	-1.48			-0.02			-158.07	324.10	0.60	0.038
5th	-1.98					1.19	-158.15	324.30	0.80	0.035
6th				-0.02	-0.01	1.36	-157.33	324.70	1.20	0.029
7th						1.20	-159.34	324.70	1.20	0.029
8th			0.01	-0.03			-158.45	324.90	1.40	0.026
9th	-1.98						-159.50	325.00	1.50	0.025
10th	-1.83	0.85		-0.02			-157.51	325.00	1.50	0.025
11st		0.56		-0.03			-158.55	325.10	1.60	0.024
12nd			0.02	-0.03	-0.02		-157.55	325.10	1.60	0.024
13rd	-1.55			-0.02	-0.01	1.34	-156.56	325.10	1.60	0.023
14th	-1.50		0.01	-0.03			-157.59	325.20	1.70	0.023
15th							-160.61	325.20	1.70	0.022
16th			0.02	-0.03	-0.02	1.09	-156.63	325.30	1.80	0.022
17th	-1.81	0.38		-0.02		1.00	-156.64	325.30	1.80	0.022
18th	-1.66		<0.01	-0.02		1.04	-156.68	325.40	1.90	0.021
19th					-0.01	1.48	-158.68	325.40	1.90	0.021
20th			<0.01	-0.02		0.97	-157.72	325.40	1.90	0.020

Table 2-8. (Continued)

Species Model	Selected scale (m) for each variable									
	AWD	PT	CAV	PCR	CEV	WA	logLik	AIC	∆AIC	Weight
Rana ornativentris										
Best model				**-0.02**		**2.60**	-211.82	**431.60**	0.00	**0.117**
2^{nd}			-0.02	-0.02		2.75	-210.84	431.70	0.10	0.115
3^{rd}			-0.02	-0.03	-0.02	2.72	-209.90	431.80	0.20	0.107
4^{th}				-0.02	-0.02	2.53	-210.92	431.80	0.20	0.105
5^{th}		0.35		-0.02		2.69	-211.72	433.40	1.80	0.048
6^{th}		0.30	-0.01	-0.02		2.83	-210.75	433.50	1.90	0.046
7^{th}	0.37		-0.01	-0.02		2.75	-210.77	433.50	1.90	0.045
8^{th}		1.03				2.74	-212.78	433.50	1.90	0.045
Bufo japonicus formosus										
Best model	**-0.04**	**1.79**	**0.03**	**-0.05**		**0.96**	-127.74	**269.50**	0.00	**0.225**
2^{nd}	-0.04	1.60	0.03	-0.05			-129.46	270.90	1.40	0.109
3^{rd}	-0.05	1.84	0.03	-0.05	-0.01	0.99	-127.64	271.30	1.80	0.091
4^{th}		1.41	0.03	-0.05			-130.69	271.40	1.90	0.086

Notes: Average water depth (AWD), presence of trees (PT), cover of aquatic vegetation (CAV), percentage of concrete revetment (PCR), cover of embankment vegetation (CEV), and water area (WA).

Table 2-9. Model-averaged (full-model averaging is the preferred approach) estimates for estimating the number of egg masses of three species, their estimated coefficients (Coefficient), standard errors (SE), Adjusted SE (AS), *z* values (*z*), and *P* values (*P*) in the model averaging. The candidate models with △AICs < 4 are considered plausible in the model averaging. Statistically significant values indicated in bold.

Species	Variables in model averaging	Coefficient	SE	AS	*z*	*P*
Rana japonica						
	AWD	-0.8465	1.0393	1.0451	0.8100	0.4180
	PT	0.1327	0.4802	0.4872	0.2720	0.7850
	CAV	0.0033	0.0091	0.0092	0.3620	0.7180
	PCR	-0.0166	0.0145	0.0146	1.1400	0.2540
	CEV	-0.0038	0.0092	0.0093	0.4080	0.6830
	WA	0.6341	0.7301	0.7352	0.8620	0.3880
	(Intercept)	1.7284	1.6189	1.6305	1.0600	0.2890
Rana ornativentris						
	AWD	0.1210	0.4119	0.4133	0.2930	0.7696
	PT	0.1746	0.4661	0.4684	0.3730	0.7093
	CAV	-0.0061	0.0093	0.0094	0.6470	0.5177
	PCR	-0.0173	0.0136	0.0136	1.2740	0.2028
	CEV	-0.0058	0.0101	0.0101	0.5700	0.5690
	WA	2.6425	0.4216	0.4254	6.2120	< **0.001**
	(Intercept)	-3.4247	1.1341	1.1412	3.0010	**0.0027**

Table 2-9. (Continued)

Species	Variables in model averaging	Coefficient	SE	AS	*z*	*P*
Bufo japonicus formosus						
	AWD	-0.0289	0.0292	0.0294	0.9820	0.3263
	PT	1.4823	0.8036	0.8084	1.8340	0.0667.
	CAV	0.0286	0.0098	0.0099	2.8950	**0.0038**
	PCR	-0.0510	0.0159	0.0160	3.1860	**0.0014**
	WA	0.5371	0.6342	0.6373	0.8430	0.3993
	CEV	-0.0007	0.0057	0.0057	0.1290	0.8972
	(Intercept)	-1.7489	1.4848	1.4932	1.1710	0.2415

Notes: Average water depth (AWD), presence of trees (PT), cover of aquatic vegetation (CAV), percentage of concrete revetment (PCR), cover of embankment vegetation (CEV), and water area (WA).

2.6 Figures

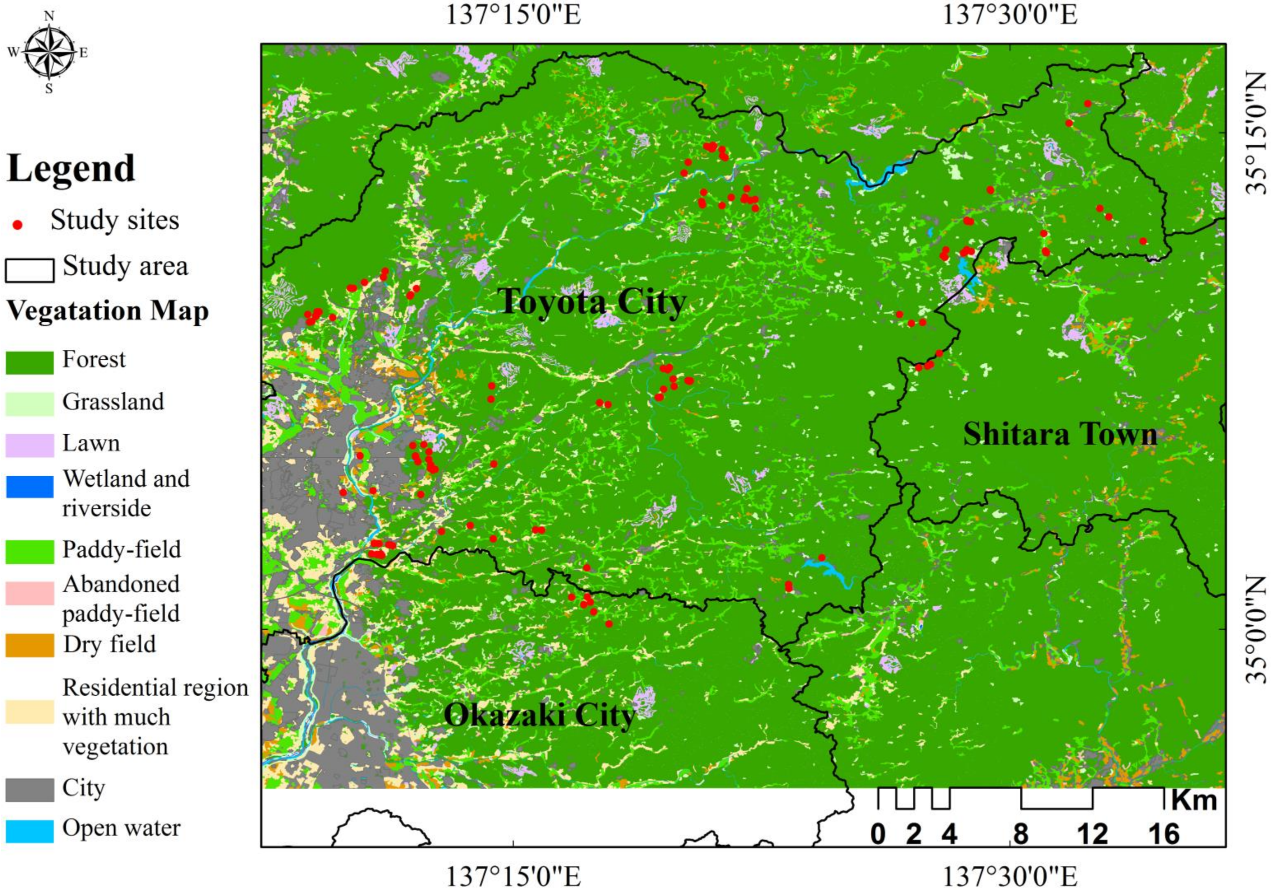
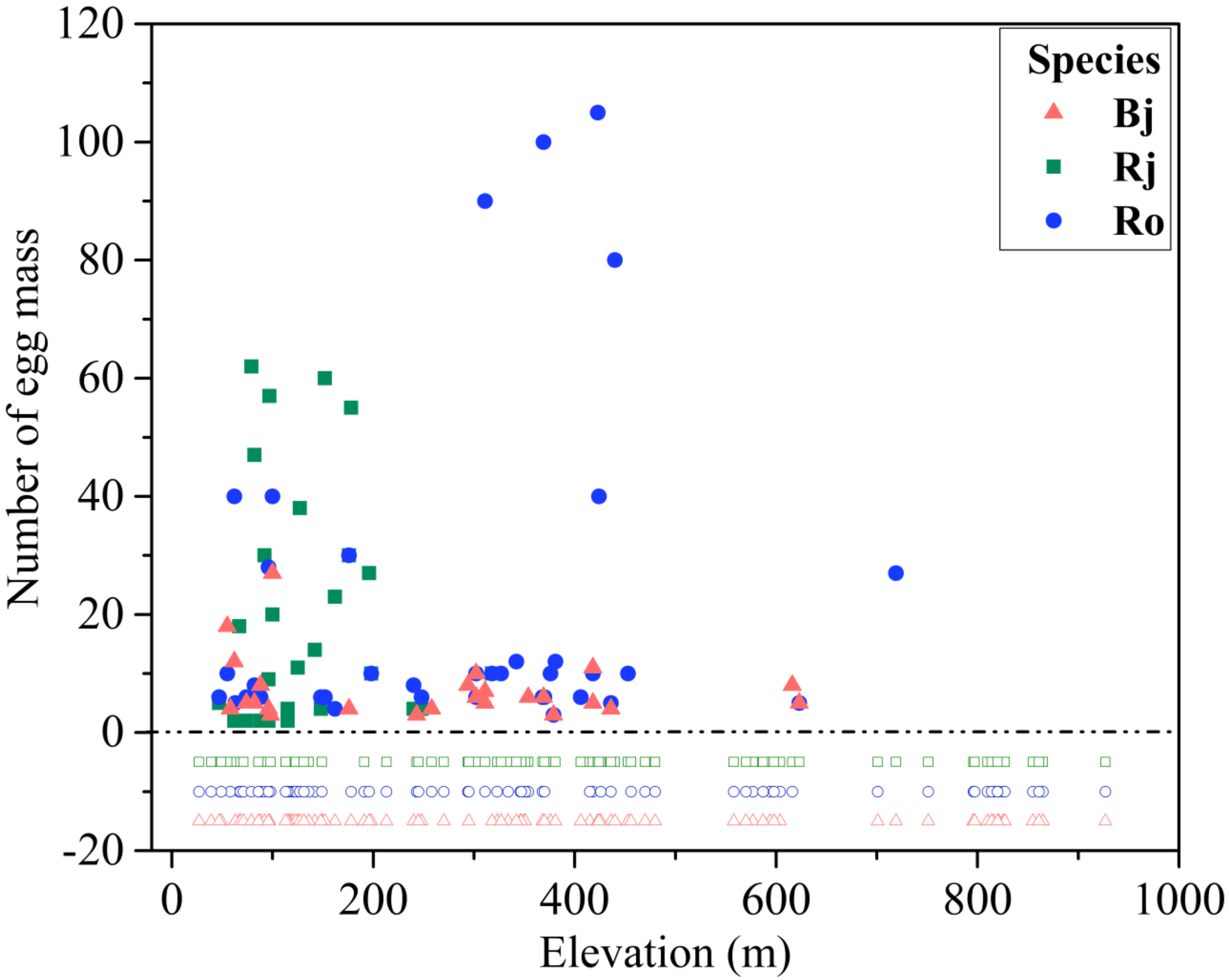
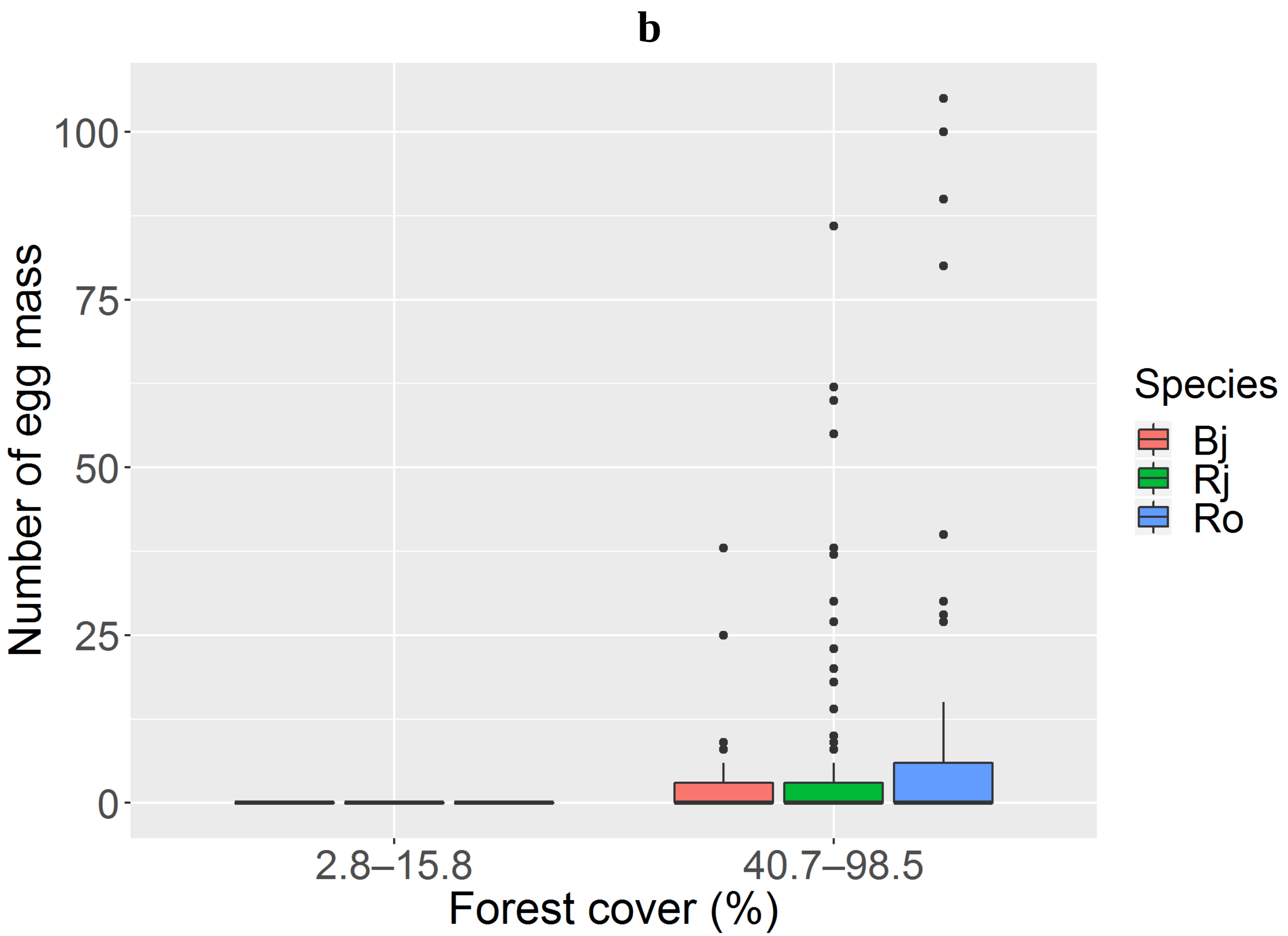


Fig. 2-1 A vegetation map of study sites.

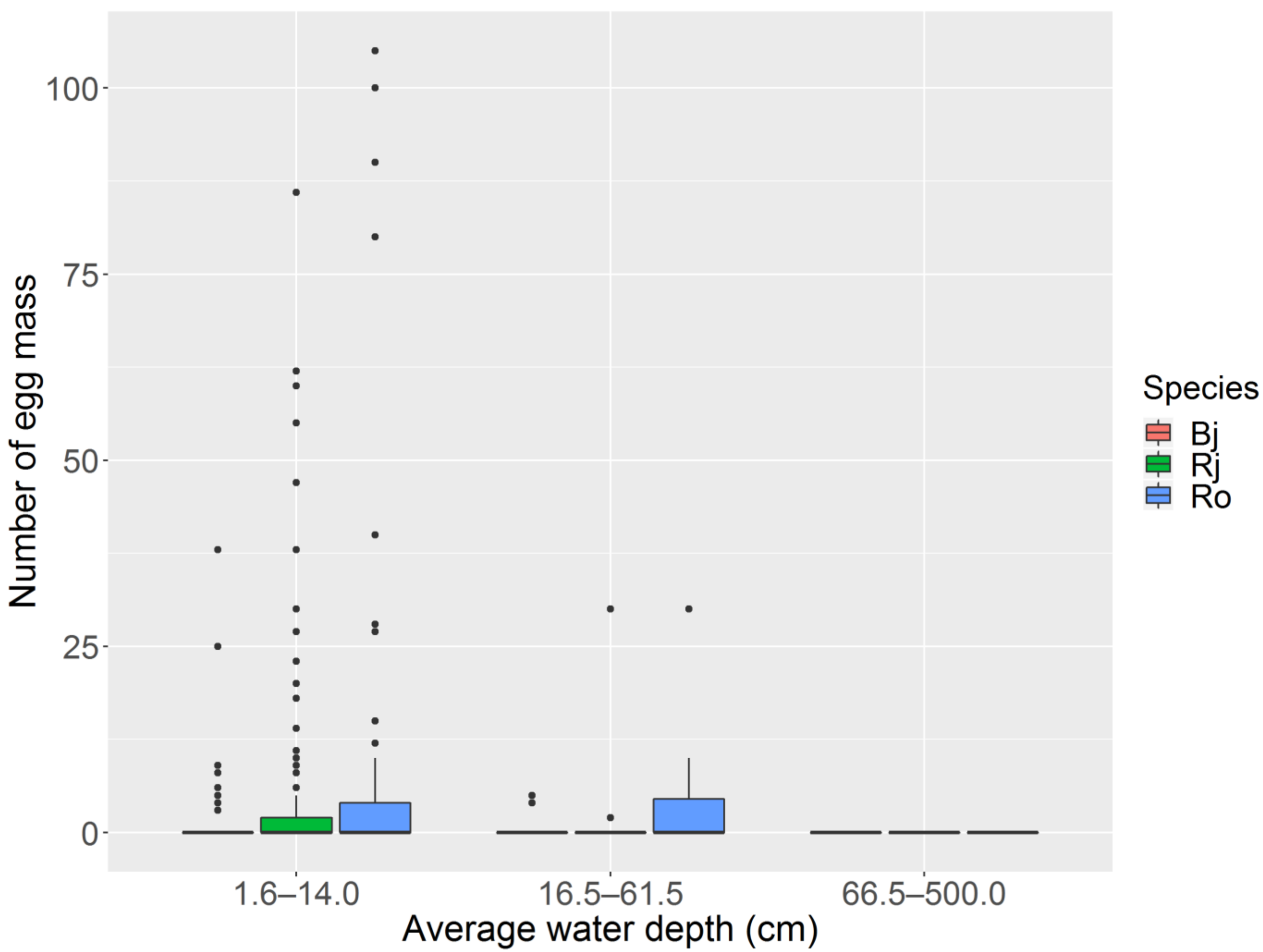
a



Species
Bj
Rj
Ro
Number of egg mass
Elevation (m)
120
100
80
60
40
20
0
-20
0
200
400
600
800
1000


b
100
75
50
25
0
Number of egg mass
2.8–15.8
40.7–98.5
Forest cover (%)
Species
Bj
Rj
Ro

c



100
75
50
25
0
Number of egg mass
1.6–14.0
16.5–61.5
66.5–500.0
Average water depth (cm)
Species
Bj
Rj
Ro

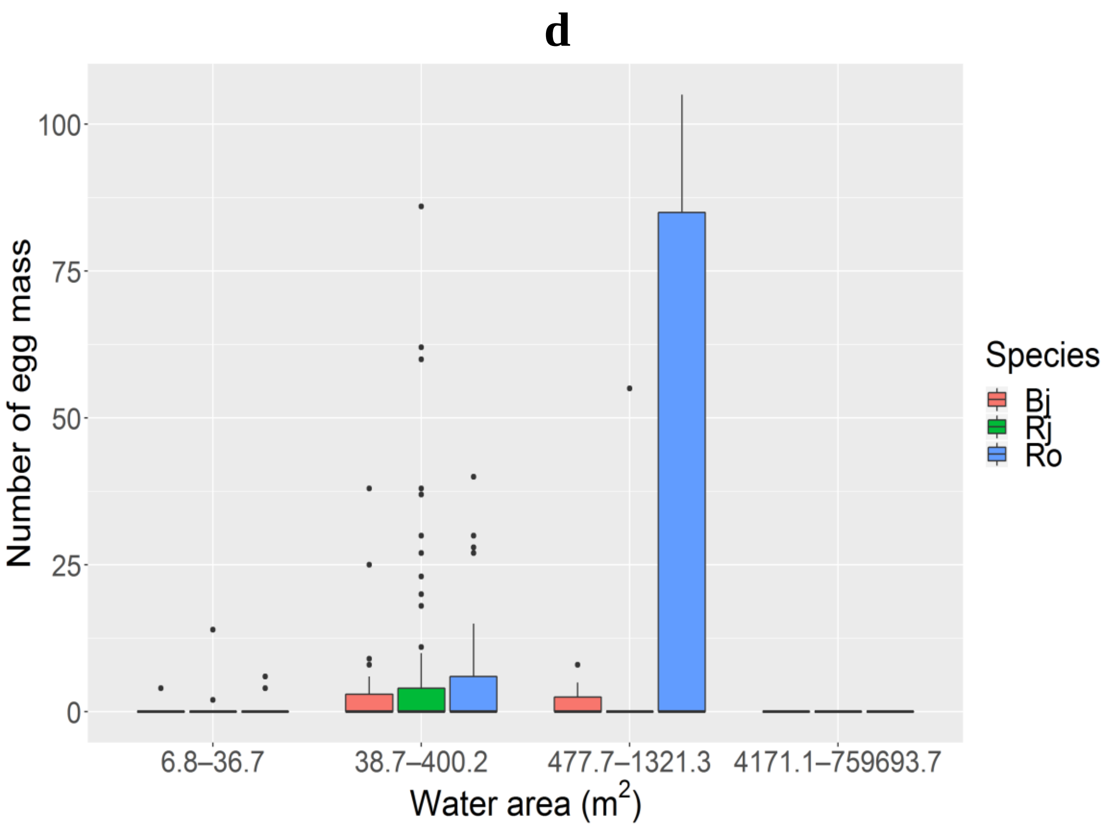


Fig. 2-2 Relationships between the number of egg masses of the three amphibian species (*Rana japonica* (Rj), *Rana ornativentris* (Ro) and *Bufo japonicus formosus* (Bj)) and elevation (a); forest cover within a 500-m-radius (b); average water depth (c); and water area (d) at all of the survey sites. The black circles represent the outlier values for each species in the box plots. The geometrical points which were higher than zero represent the number of egg masses surveyed in the study area.

Chapter 3: Landscape and local correlates with two tree frogs, *Rhacophorus* (Amphibia: Rhacophoridae) in two different habitats, central Japan

3.1 Introduction

Agricultural landscapes have undergone a massive change over the past 70 years due to agricultural intensification and abandonment (Krebs et al. 1999; Kidera et al. 2018), leading to habitat degradation and loss of amphibian communities (Hamer and Parris 2011). Previous studies have indicated that the living environment of many amphibian species depends on agricultural landscapes (Bennett et al. 2006; Kidera et al. 2018). Frogs are considered as representative indicator species in the agricultural landscapes of Japan (Naito et al. 2012). Urban infrastructures, including roads, buildings, and fences present barriers that could cause the decrease of amphibian communities in urban agricultural landscapes owing to the loss and fragmentation of habitat, and the degradation of habitat quality (Vos and Chardon 1998).

Paddy fields provide significantly essential habitats for many species, such as insects, birds, and amphibians (Washitani 2001; Kobori and Primack 2003). However, paddy fields in Japan have been suffering intensification as part of farmland improvements. For example, modern drainage ditches of paddy have been constructed with deep concrete levees by paddy-field improvements. Agricultural intensification and abandonment of paddy fields have caused habitat changes and biodiversity loss. It has been revealed that ponds and wetlands are vital habitats for breeding of amphibians (Kato et al. 2010; Ribeiro et al. 2017). Amphibian communities are easily damaged by the modification of landscape structure, which is attributed to urbanization and agricultural intensification. Amphibians are sensitive to the environment and require specific habitats to survive (like spawning, growing, foraging, and sheltering), and it is urgent to enhance the habitat quality and establish enough space with abundant resources both in aquatic and terrestrial districts (Pope et al. 2000; Niemi and McDonald 2004; Hamer and Parris 2011).

To explore the practical conservation actions, studies have made great efforts to seek factors that affect the dispersal of organisms in paddy fields (Mukai et al. 2005; Fujimoto et al. 2008). As a result, water management and intensifying connection between paddy fields and wetlands are useful restoration practices. In Japan, rural landscape consists of a fine-scale mosaic of forests, paddy fields, ponds, wetlands, roads, and residential housings (Kobori and Primack 2003), which should be comprehensively involved for the research. The habitat changes of frogs, from breeding sites to their terrestrial habitats, are widely investigated by the scientific community. Previous articles concluded that the terrestrial land-cover has a strong effect on frog distribution or biodiversity in different habitats (Marsh and Trenham 2001; Pulsford et al. 2019). Therefore, studying multi-scale limiting variables will beneficial to see the protective measures for the target species (Kato 1955).

According to the latest Japanese Red List, *Rhacophorus schlegelii* and *Rhacophorus arboreus* have been listed in red books by local government to be under threat of extinction by local governments (Association of Wildlife Research and Envision Conservation Office 2012). Additionally, many ecologists are drawn to study them because of their peculiar spawning behavior (e.g., arboreal spawning of *R.arboreus* and foam nests under the soft soil of *R. schlegelii*) (Fukuyama 1991;

Kusano et al. 2005). Generally, research works for these two species concentrate in several aspects, including spawning systems, acoustic characteristics, ecological functions, and DNA analysis, *etc* (Mizuhira et al. 1986; Fukuyama 1991; Matsui and Wu 1994; Wilkinson et al. 1996; Kusano et al. 2006; Matsui et al. 2019). Although the numbers of both species are declining in Japan owing to habitat transformation and agricultural intensification (Ise 2006), a few studies have been done to compare the influence of landscape and local factors on *R. schlegelii* and *R. arboreus* in different habitats. These two species demonstrate site fidelity in forests across years in breeding and non-breeding season (Maeda and Matsui 1990; Kusano et al. 2006); it is of great importance to survey geographic distribution relationship of the two species.

The purpose of this chapter is to identify the landscape and local factors that are responsible for choice of the breeding sites of two green tree-frogs, *Rhacophorus*. Finally, to conserve the biodiversity of frogs in a varied landscape, I discussed on the importance of the combination of paddy fields and other landscape elements to preserve and restore.

3.2 Materials and methods

3.2.1 Site description and field surveys

Field surveys were conducted at 138 sites in paddy fields (118), and ponds (20) located on Toyota City, Okazaki City, and Shinshiro Town (34°51′38″–35°17′24″N, 137°2′24″–137°40′35″E; elevation: 100–827 m), Aichi Prefecture, Japan (Fig. 3-1). I set long distances between each study site to avoid overlaps among large buffer circles. The landscape of surveys consisted mostly of paddy fields and forests, ranging from forest-dominated hilly rural zones to paddy-dominated plains along an ecological gradient. All study sites consisted of water bodies.

I surveyed the adults of *Rhacophorus schlegelii* by calls and with the naked eye, together with the egg masses/adults of *Rhacophorus arboreus*, to determine their presence during their reproductive season (from mid-May to late- June, 2018). In the April–June of 2017, the presence or absence of *R. schlegelii* and egg masses /adults of *R. arboreus* in paddies and ponds was surveyed by the preliminary investigation. Besides, I conducted survey of the egg masses/adults of *R. arboreus* at absent sites in early-July of 2019 to confirm the population accuracy. The data of 2019 have been included in the 2018 surveys.

I recorded the egg-mass number/calls of *R. arboreus*, which were identified visually/auditorily, by walking along the ways surrounding the habitats, as *R. arboreus* lays foamed egg masses that are easy to identify.

3.2.2 Land uses around the study sites

Landscape factors were analyzed by ArcGIS Spatial Analyst (Version 10.5). The composition of the surrounding area (50 m, 100 m, 250 m, and 500 m radii), which includes total areas (m^2) of forest, grassland, lawn, wetland and riverside, paddy fields, abandoned paddy fields, dry fields, residential area with rich vegetation, city, and open water were extracted within a buffer zone using a digital 1/25,000 vegetation map downloaded from J-IBIS (Japan Integrated Biodiversity Information System; Ministry of the Environment, Biodiversity Center of Japan, 2008; http://www.biodic.go.jp/index.html). I extracted the total road density (%) and elevation difference (m) using a digital map downloaded from GIAJ (Geospatial

Information Authority of Japan, 2015; https://fgd.gsi.go.jp/download/menu.php). The elevation (m) of all study sites was recorded using GPS.

3.2.3 Local factors

To explore the effects of environmental changes on the frogs' distribution, I measured seven local factors. The presence of trees on the soil levees of the habitats was recorded. I measured water depth at eight different points randomly along the periphery of each site, acquiring an average water depth value, and measured the water area of ponds using a tape measure (for small water areas) or Google Earth (in June 2018). Concrete revetments of ponds are constructed due to modernization of agriculture and urbanization/safety, *etc*. Thus, for each type of habitat, non-soil levees were included in a proportion of concrete revetment surrounding the habitats. Proportion of aquatic vegetation/rice crop (i.e., emergent/rice crop + submerged vegetation = total aquatic vegetation/rice crop), and the proportion of embankment vegetation were estimated based on visual observations by walking around the habitats. It should be pointed out that the 'presence of fishes' was only recorded in ponds. Other water-quality measures, such as water agrochemical contamination, pH, dissolved oxygen, salinity, and conductivity, are known to have little effect on amphibians (Yoshida et al. 2006). I examined the local models using 46 study sites with an elevation of higher than 400 m for *Rhacophorus arboreus*.

3.2.4 Descriptive statistics

I tested the normality assumption for each independent variable before GLMs analysis and compared the habitat types to the two tree-frogs' distribution using the

Pearson's Chi-Square test at $P < 0.05$. I also checked the multicollinearity by Variance Inflation Factor (VIF) test. If VIF was < 4.0, which manifested that there were no multicollinearity problems (Miles and Shevlin 2001) (Table 3-1). The logarithm of the survey area was used as an offset term to consider over-dispersion. Then, I examined the effects of landscape and local features on the presence of the two tree-frogs using the generalized linear models (GLMs) with binomial error distribution and log-link function.

All of the independent factors were categorized at two different levels: landscape factors and local factors. In the GLM models, the presence of either species (presence, 1; absence, 0) was supposed to the response variable. Seven factors were used to represent the local level. Spatial models included 13 spatial explanatory variables in buffers around each study site at four scales: 50m, 100 m, 250 m, and 500 m.

I tested all combinations of explanatory variables to examine the most influential buffer scale using model selection based on the Akaike Information Criteria (AIC) with GLMs. The best model with the lowest AIC was selected for each species. Then, to distinguish landscape and local factors affecting the dispersal of each species, models with ΔAICs < 2.0 were considered to have similar performance, which selected variables are stable among the models (Burnham and Anderson 2003). The total statistical analyses were performed using the package 'MuMIn' in the statistical software R (ver. 3.6.1) (Team RC 2013).

3.3 Results

I found *Rhacophorus schlegelii* at 88 study sites, in paddy fields (71), and ponds (17), mainly in rural areas and none in urban areas of the study area (Fig. 3-1a).

Egg masses of *Rhacophorus arboreus* were distributed at 32 sampling sites, in paddy fields (24), and ponds (8) in mountain areas with high elevation (Fig. 3-1b). Distributions of *R. schlegelii* and *R. arboreus* were divided by the elevation although these two species coexisted at some sites in the higher elevation. *R. schlegelii* was recorded a significantly more frequent in the paddy fields than ponds (P = 0.0278, Pearson's Chi-Square test), whereas *R. arboreus* was recorded nearly the same rate between paddy fields and ponds (P = 0.4176, Pearson's Chi-Square test). The adults of *R. schlegelii* were not found at low elevation in urban areas with lower elevation ((Fig. 3-1a). *Rhacophorus arboreus* were widely distributed at high elevations of 406–827 m in the study area (Fig. 3-1b).

3.3.1 Effects of landscape factors at different spatial scale

The most influential scale for the distribution of *R. schlegelii* was 250 m radius, compared by AIC value (Table 3-2). In the best model, forest cover and elevation difference were affected positively on the presence of this species, whereas the total road density was negatively. However, models in the 50-m-radius buffer, elevation and forest cover affected positively and the residential area with rich vegetation and dry field area affected negatively on the distribution of this species. In the 100-m-radius buffer, elevation and forest cover were found to have positive effects on the frogs' distribution (Table 3-3). The 50% presence of *R. schlegelii* was observed at an elevation of higher than 380 m (Fig. 3-2a). Forest cover composed more than 70% of the surrounding environment at half of the sites where *R. schlegelii* was observed (Fig. 3-2b). Within the 500-m-radius buffer, total road density was negatively related to the presence of *R. schlegelii*.

The most influential scale for *R. arboreus* was 500 m radius (Table 3-2). In the best model, elevation, forest cover, dry field area, and paddy-field area affect positively and the residential area with rich vegetation affect negatively on the distribution of this species. Elevation and paddy-field area were consistently selected in the best models of all scales, but the residential area with rich vegetation, forest cover, and dry field area are not selected in other scales. Wetland and riverside area was selected in the best models of 50 m, 100 m, and 250 m scales. Seventy-five percent of the present sites of *R. arboreus* were located at an elevation of higher than 580 m (Fig. 3-2c). The presence of *R. arboreus* significantly increased with paddy-field area within a 250-m-radius and 500-m-radius (Table 3-3). I found that the 50% presence of *R. arboreus* appeared in forest covers of more than 85% (Fig. 3-2d).

3.3.2 Effects of local factors

The water depth of paddy fields did not influence the distributions of *R. schlegelii*. Therefore, I removed the 'average water depth' from the GLMs analysis. In the best model for the adult distribution of *R. schlegelii* in paddy fields (AIC = 97.50) (Table 3-4), the presence of trees and the proportion of embankment vegetation were found to be the most positively affecting factors (Table 3-5). The high proportion of embankment vegetation means that many soil levees are surrounding the paddy fields. In the best model for the distribution of *R. schlegelii* in ponds, the presence of trees and the proportion of embankment vegetation were incorporated as explanatory factors (AIC = 17.70) (Tables 3-4 and 3-5).

In the best model that explains the presence of *Rhacophorus arboreus* in paddies (AIC = 46.40) (Tables 3-4 and 3-5), only the presence of trees was incorporated as an explanatory variables.

3.4 Discussion

This chapter provides essential implications for paddy-field and forest protection, especially in rural landscapes. Also, I have compared the influence of various landscape (13 variables) and local (7 variables) factors on *R. schlegelii* and *R. arboreus* in different habitats. In Japan, rural landscape consists of a fine-scale mosaic of forests, paddy fields, wetlands, residential housings, *etc*. Mosaic structure in a Satoyama landscape is thought to enhance biodiversity by providing composite habitats to amphibians that undergo ontogenetic habitat changes (Washitani 2001; Kobori and Primack 2003). Therefore, the outcomes of protection measures in particular paddy fields are likely to differ depending on the surrounding landscape structure, but few previous studies have been done with such a context-dependent view.

3.4.1 Effects of landscape factors at different spatial scale

Rhacophorus arboreus breed in paddy fields surrounded by forests, in mountain areas at higher elevation. The results are consistent with previous studies (Maeda and Matsui 1990; Kato et al. 2010).

According to the results of model selections based on the lowest AIC values, the most influential scale on breeding sites of *R. schlegelii* (250 m) is smaller than *R. arboreus* (500 m) was affected by different spatial scales. It was inconsistent with the prediction of the movement distance of adults from aquatic to terrestrial habitats, i.e., *R. schlegelii* is known to show a longer travel distance than *R. arboreus* (~ 300–1000 m, Osawa and Katsuno 2000; 120 m, Kusano 1998). Some frogs revealed an actual spatial scale similar to their movement distance (Houlahan and Findlay 2003), whereas others have exhibited an uncertain actual spatial scale than their movement distance (Herrmann et al. 2005; Kato et al. 2010). The above phenomena indicate that ecological processes are intrinsic in the species themselves at the landscape scale. Some works so far have suggested that amphibian distribution is affected by the process of adult habitat use on landscape characteristics (Van Buskirk 2005; Ficetola et al. 2009).

3.4.2 Effects of local factors

The proportion of embankment vegetation on the soil levees was the positive factor to influence the distribution of *R. schlegelii*. This is consistent with earlier study that demonstrated *R. schlegelii* constructs its foam nests under the soil (Maeda and Matsui 1990). Furthermore, the adults of *R. schlegelii* prefer to inhabit the trees or embankment vegetation (Maeda and Matsui 1990).

3.5 Tables

Table 3-1. Variance Inflation Factor (VIF) test for multicollinearity evaluation.

Table 3-1-1. Variance Inflation Factor (VIF) test between the local factors.

Species	Habitats	PCR	PEV	PT	PAV	AWD	WAP	PF
R. schlegelii	Paddy fields	1.03	1.07	1.10	1.05	–	–	–
	Ponds	**6.33**	3.47	2.84	2.97	2.94	**8.61**	**11.08**
R. arboreus	Paddy fields	1.03	1.03	1.10	1.11	1.14	–	–

Notes: Coefficients in bold denote strong correlations (VIF > 4.0);

Proportion of concrete revetment (PCR), proportion of embankment vegetation (PEV), presence of trees (PT), proportion of aquatic vegetation/rice crop (PAV), average water depth (AWD), water area of pond (WAP), presence of fishes (PF).

Table 3-1-2. Variance Inflation Factor (VIF) test between the landscape factors.

Species Scale	FC	GA	LA	WRA	PA	APA	DFA	RAV	CA	OWA	TRD	ELV	ED
R. schlegelii													
50 m	1.69	1.30	1.00	1.00	1.99	1.17	1.23	1.28	1.34	1.24	1.30	1.22	_
100 m	2.13	1.17	1.27	1.00	1.77	1.25	1.09	1.61	1.26	1.20	1.69	1.37	1.09
250 m	3.35	1.19	1.82	1.00	1.96	1.35	1.21	2.35	1.49	1.30	2.96	2.30	1.45
500 m	**6.03**	1.21	1.14	1.35	1.20	1.18	1.30	3.79	1.64	1.66	**5.21**	3.98	2.01
R. arboreus													
50 m	3.88	1.24	1.00	1.00	3.77	1.00	1.00	1.00	2.50	1.40	1.54	1.92	_
100 m	4.00	1.17	1.73	1.00	3.52	1.08	1.48	1.00	3.93	1.60	2.81	1.85	1.00
250 m	**4.13**	1.63	1.01	1.00	**6.03**	1.01	1.67	1.00	**4.45**	2.74	**10.13**	**8.23**	1.50
500 m	**9.19**	1.17	1.07	1.19	1.27	1.32	1.52	3.85	1.78	1.62	**7.31**	**4.65**	2.47

Notes: Coefficients in bold denote strong correlations (VIF > 4.0);

Forest cover (FC), grassland area (GA), lawn area (LA), wetland and riverside area (WRA), paddy fields area (PA), abandoned paddy fields area (APA), dry fields area (DFA), residential area with rich vegetation (RAV), city area (CA), open water area (OWA), total road density (TRD), elevation (ELV), elevation difference (ED).

Table 3-2. Results of best model summary selections based on AIC. Selected scale of each explanatory factor, AICs and △AICs are indicated for the best models.

Species Model	Selected scale (m) for each variable														
	APA	RAV	CA	ED	ELV	FC	DFA	GA	LA	OWA	PA	TRD	WRA	logLik	AIC	△AICs
R. schlegelii																
(250 m) Best model				**0.0144**		**0.0265**						**-0.2584**		-59.7400	**127.50**	0.00
(500 m) Best model	0.2327			0.0094							-0.6462	-4.2070		-62.57	135.10	0.00
(100 m) Best model					0.0022	0.0442								-66.11	138.20	0.00
(50 m) Best model		-0.2821			0.0023	0.0295	-0.4330							-70.71	151.40	0.00
R. arboreus																
(500 m) Best model		**-0.5292**			**0.0236**	**0.1672**	**0.6216**				**1.4740**			-12.76	**37.50**	0.00
(250 m) Best model					0.0261						0.8239		4.1420	-15.37	38.70	0.00
(100 m) Best model					0.0254						0.6727		4.5610	-15.87	39.70	0.00
(50 m) Best model					0.0255						0.7563		6.2210	-16.02	40.00	0.00

Table 3-3. Results for GLM analyses of the effects of the surrounding landscape on the presence of two tree-frog species. Factors, their estimated coefficients (Coefficient), standard errors (SE) in the best models are shown for each species.

Spatial scale (m)	Factor in the best model	Coefficient	SE
Rhacophorus schlegelii			
50 m	Residential area with rich vegetation	-0.2821	0.1541
	Elevation	0.0023	0.0010
	Forest cover	0.0295	0.0094
	Dry field area	-0.4330	0.3070
	(Intercept)	-0.6253	0.3769
100 m	Elevation	0.0022	0.0011
	Forest cover	0.0442	0.0092
	(Intercept)	-1.4317	0.3913
250 m	Elevation difference	0.0144	0.0106
	Forest cover	0.0265	0.0143
	Total road density	-0.2584	0.1459
	(Intercept)	0.4117	1.4950
500 m	Abandoned paddy-field area	0.2327	0.1227
	Elevation difference	0.0094	0.0062
	Paddy fields area	-0.6462	0.4963
	Total road density	-4.2074	1.3559
	(Intercept)	6.0295	2.5280
Rhacophorus arboreus			
50 m	Elevation	0.0255	0.0056

Table 3-3. (Continued)

Spatial scale (m)	Factor in the best model	Coefficient	SE
	Paddy fields area	0.7563	0.3965
	Wetland and riverside area	6.2208	855.5437
	(Intercept)	-13.6240	257.5707
100 m	Elevation	0.0254	0.0057
	Paddy fields area	0.6727	0.3616
	Wetland and riverside area	4.5607	705.7081
	(Intercept)	-14.1161	212.4722
250 m	Elevation	0.0261	0.0058
	Paddy fields area	0.8239	0.4202
	Wetland and riverside area	4.1423	618.2234
	(Intercept)	-15.6187	186.1511
500 m	Residential area with rich vegetation	-0.5292	0.3449
	Elevation	0.0235	0.0066
	Forest cover	0.1672	0.0881
	Dry field area	0.6216	0.3744
	Paddy fields area	1.4736	0.5937
	(Intercept)	-32.0936	11.7132

Table 3-4. Results of model selections based on AIC. Selected scale of each explanatory factor, AICs and △AICs (the difference between each AIC value and the smallest value) are indicated for the models with △AICs less than 2: models with △AICs < 2 are often considered plausible.

Species Model	Habitats	Selected scale (m) for each factor										
		AWD	PCR	PT	PAV	PEV	WAP	PF	df	logLik	AIC	△AICs
R. schlegelii												
Best model	Paddy fields		**-0.02**	**3.71**		**0.02**			4	-44.75	**97.50**	0.00
2^{nd}			-0.02	3.84	0.01	0.02			5	-43.94	97.90	0.40
3^{rd}				3.75		0.02			3	-46.29	98.60	1.10
4^{th}				3.88	0.02	0.02			4	-45.36	98.70	1.20
5^{th}			-0.02	3.67					3	-46.84	99.70	2.20
Best model	Ponds			**2.60**		**0.04**			3	-5.84	**17.70**	0.00
2^{nd}				2.23					2	-7.04	18.10	0.40
3^{rd}						0.03			2	-7.38	18.80	1.10
4^{th}									1	-8.45	18.90	1.20
5^{th}		0.39		2.47		0.04			4	-5.79	19.60	1.90
6^{th}				2.62	0.00	0.04			4	-5.83	19.70	2.00
R. arboreus												
Best model	Paddy fields			**1.71**					2	-21.22	**46.40**	0.00
2^{nd}				1.53	0.03				3	-20.58	47.20	0.80
3^{rd}			-0.03	1.65					3	-20.70	47.40	1.00
4^{th}		0.16		1.84					3	-20.84	47.70	1.30
5^{th}									1	-22.92	47.80	1.40
6^{th}					0.03				2	-21.92	47.80	1.40

Table 3-4. (Continued)

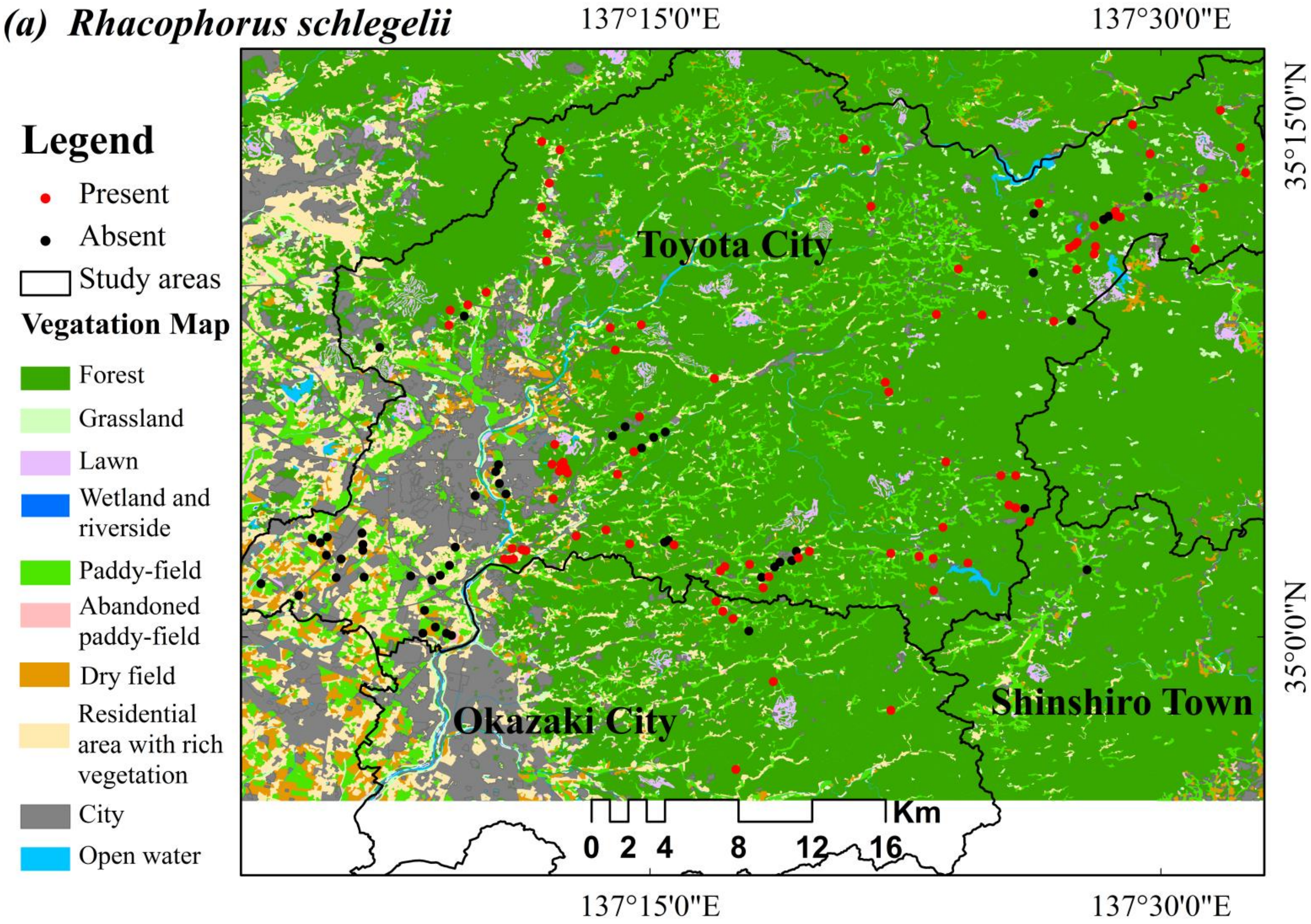
Species Model	Habitats	Selected scale (m) for each factor										
		AWD	PCR	PT	PAV	PEV	WAP	PF	df	logLik	AIC	ΔAICs
7th		0.25		1.72	0.03				4	-19.94	47.90	1.50
8th				1.66		0.01			3	-21.18	48.40	2.00

Notes: average water depth (AWD), proportion of concrete revetment (PCR), presence of trees (PT), proportion of aquatic vegetation/rice crop (PAV), proportion of embankment vegetation (PEV), water area of pond (WAP), presence of fishes (PF).

Table 3-5. Results for GLM analyses of the effects of the local factors on the presence of two tree-frog species in different habitats. Factors, their estimated coefficients (Coefficient), standard errors (SE) in the best models are shown for each species.

Species	Habitat types	Factor in the best model	Coefficient	SE
Rhacophorus schlegelii	Paddy fields	Proportion of concrete revetment	-0.0240	0.0142
		Presence of trees	3.7103	0.6272
		Proportion of embankment vegetation	0.0247	0.0125
		(Intercept)	-2.0610	0.9572
	Ponds	Presence of trees	2.5952	1.6419
		Proportion of embankment vegetation	0.0388	0.0262
		(Intercept)	-2.3828	2.0986
Rhacophorus arboreus	Paddy fields	Presence of trees	1.7047	0.9594
		(Intercept)	-0.6931	0.8660

3.6 Figures



(a) Rhacophorus schlegelii
137°15'0"E
137°30'0"E
35°15'0"N
35°0'0"N
Legend
Present
Absent
Study areas
Vegatation Map
Forest
Grassland
Lawn
Wetland and riverside
Paddy-field
Abandoned paddy-field
Dry field
Residential area with rich vegetation
City
Open water
Toyota City
Okazaki City
Shinshiro Town
Km
0 2 4 8 12 16

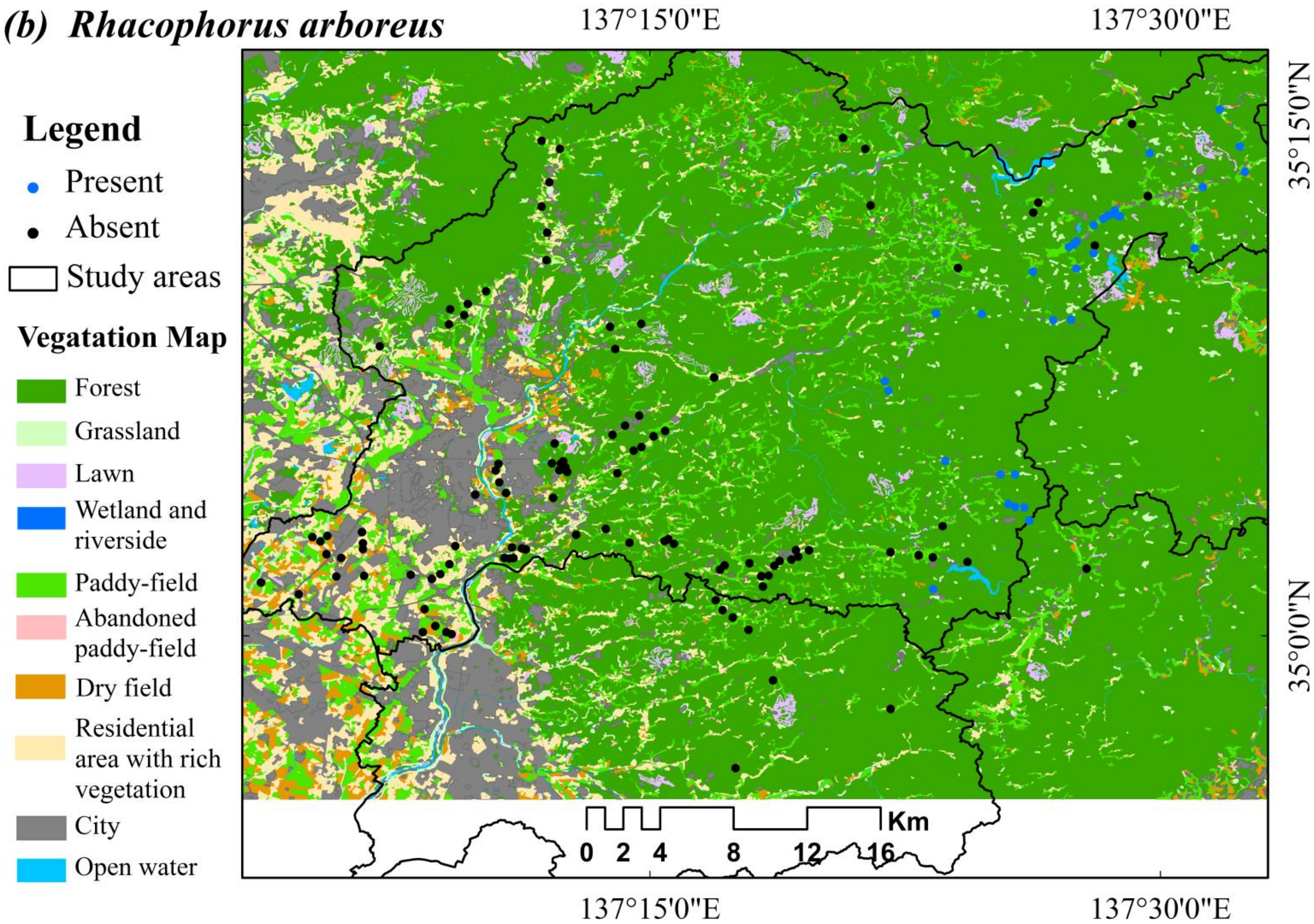


Fig. 3-1 Distribution maps of *Rhacophorus schlegelii* (a) and *Rhacophorus arboreus* (b) in the study area were located in Toyota City, Okazaki City, and Shinshiro Town.

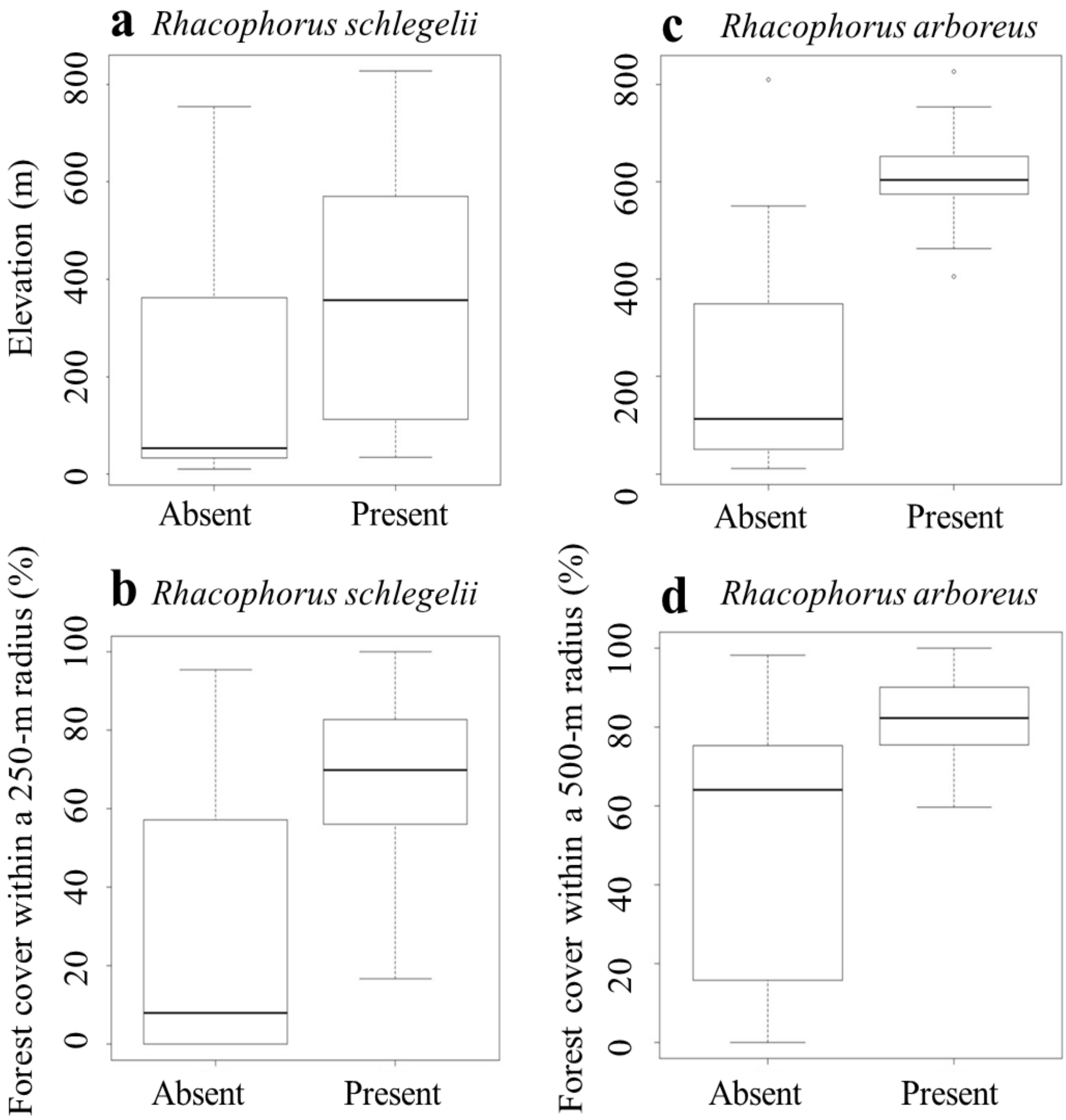


Fig. 3-2 Effects of elevation and forest cover on the presence of *Rhacophorus schlegelii* and *Rhacophorus arboreus*. The box plot represents the 75th, 50th, and 25th percentiles; the top bar ranges from the 75th to the 90th percentiles, and the bottom bar ranges from the 25th to the 10th percentiles. Open circles represented the outlier values in the box plots.

Chapter 4: Ecological impacts of the midsummer drainage and drainage system modernization on tadpoles of *Rhacophorus arboreus* in Japanese paddy fields

4.1 Introduction

In Japan, more than 60 % of natural wetlands have been converted mainly into paddy fields over the past 100 years (Geospatial Information Authority of Japan, 2000). A large portion of paddy fields are connected to various habitats, such as forests, wetlands, and irrigation ponds, through irrigation systems (Naito et al. 2012). Based on the above circumstances, paddy fields have long been used as critical habitat for several aquatic plants (Yamaguchi and Umemoto 1996), aquatic organisms (Mukai et al. 2014), fishes (Amilhat and Lorenzen 2005), loach (Tanaka 1999), water birds (Fasola et al. 1996; Marques 1999; Pierluissi 2010), and amphibians (Fujioka and Lane 1997; Natuhara and Kanbara 2001; Osawa and Katsuno 2001; Tsuji et al. 2011; Naito et al. 2012).

However, since the 1950s, agricultural modernization has altered the environment of the paddy-field, and many previously common species are now endangered. In particular, the modern-style drainage systems which have been constituted of concrete-sided ditches may lead to biodiversity loss in paddy fields in Japan (Fujioka and Lane 1997).

I classified three types of drainage system of paddy fields, traditional-style, intermediate-style, and modern-style. Traditional drainage systems consist of earth-sided ditches, shallow/permanent water bodies, and unlined irrigation ditches (Katayama et al. 2011). Intermediate-style drainage systems consist of concrete revetment surrounding the paddies, which were supplied with water and drained by plastic pipes/concrete ditches. These features of an intermediate-style drainage system cause tadpoles could not move to catchment ditch were near the habitat for refuging by the irrigation water inlet or the drainage water outlet (Fig. 4-1). Additionally, modern-style drainage systems consist mainly of under-drainage systems below paddy fields, and the water is typically supplied through underground pipes via taps and is drained into deep ditches (Fujioka and Lane 1997; Katayama et al. 2011; Fujita et al. 2015). Therefore, the under-drainage systems are easily identified because their water taps project from the ground.

Over the past 70 years, ~ 80% of paddy fields have been converted to the modern-style irrigation system in Japan (Fujioka and Lane 1997). The modern-style drainage system has increased the dryer areas of paddy fields in midsummer (Donald 2004), which has negatively affected on aquatic organisms (Fujioka and Lane 1997; Naito et al. 2012). Modern drainage systems negatively influence on loach (Katayama et al. 2011), frogs (Naito et al. 2012), birds (Lane and Fujioka 1998; Fujita et al. 2015), and midsummer drainage impact on other aquatic organisms (Yamazaki et al. 2003). Numerous studies have suggested that the populations of paddy-dwelling frogs were negatively affected by the modern-style drainage systems (Tsuji et al. 2011; Naito et al. 2012; Fujita et al. 2015).

In general, farmers irrigate paddy fields in April just before the rice planting and temporarily drain about six weeks after the planting (Naito et al. 2012). The breeding season of frogs using paddy fields is divided into three in Japan; *Rana japonica* breeds in February before the irrigation, *Perophylax spp.* breed in April and

May after the irrigation, and *Rhacophorus arboreus* breeds in June. Tadpoles of *R. arboreus* stay at the paddy fields after the midsummer drainage. During midsummer drainage, the tadpoles may move primarily towards the traditional-style irrigation systems with a catchment ditch, which is filled with water for refuge. Flooded fallow fields and abandoned paddies can serve as suitable growing habitats for tadpoles and birds during the period of midsummer drainage (Fujioka et al. 2001; Maeda 2001). However, the modern-style irrigation systems may have caused a large number of tadpoles to decline/die (Blaustein and Wake 1990; Fujioka and Lane 1997).

The rice-transplanting season varies by region. In the hilly and mountainous area of Toyota City, the rice-transplanting is early in June, and the mid-summer drainage starts in mid-July. The rice fields are drained for a week or two until mid-July. Indeed, some farmers do not drain paddy fields in this season (Natuhara 2013).

This chapter focuses on the ecological impacts of the midsummer drainage and drainage system modernization on the tadpoles of the forest green tree frog, *Rhacophorus arboreus*, which mainly breeds from June to July in Toyota City (Otake and Shimada 2016). Most of the frogs in Japan seldom use lakes and ponds for breeding. However, *R. arboreus* more often use ponds in and near the forests than rice fields for breeding. An early article reported that amphibians breed in various aquatic habitats with different levels of drying risk (Richter‐Boix et al. 2011), which may lead to selection for breeding in permanent water bodies, rather than in rice fields with a high risk of desiccation (i.e., midsummer drainage).

The tadpoles of *R. arboreus* metamorphose in about 1.5 months (Matsui and Seki 2008). However, no study has compared the influence of midsummer drainage and irrigation systems on the tadpoles of *R. arboreus*.

I hypothesized that the intermediate style irrigation system causes larger mortality of tadpole death than those the traditional drainage system does during the period of midsummer drainage. Considering the refuge surrounding the traditional-style irrigation systems, I hypothesized that the tadpoles of *R. arboreus* would move to the catchment ditch/ shallow earth ditches near the paddies. Finally, I discuss different types of irrigation systems, how these systems have affected the status of tadpoles by the midsummer drainage in the study sites.

4.2 Materials and methods

4.2.1 Study area

This work was conducted at 20 spawning sites (17 paddy fields, 1 abandoned paddy-field, 1 fallow paddy-field, and 1 corn field) of *Rhacophorus arboreus* located within Northeast Toyota City, Aichi prefecture, central Japan (Fig. 4-2; 35°3′51.98″–35°14′10.72″N, 137°23′24.36″–137°32′29.04″E; altitude: 400-660 m). All sites were filled with water in the spawning season. The study sites consisted mostly of paddy fields, creeks, forests, and other farmlands.

4.2.2 Field surveys

I surveyed the study sites to verify the drainage system (traditional-style: 0; intermediate-style: 1), water source/supply of paddies with egg masses of *R. arboreus* by the preliminary survey, which carried on the 18th and 21st of June, 2019, and obtained the detailed date for the midsummer drainage from local farmers (Fig. 4-3).

At each study site, I recorded living tadpoles of *R. arboreus* were present in refuge biotope surrounding the traditional-style irrigation systems, abandoned paddy-field, fallow paddy-field, corn field, and paddy fields, including shallow water and dried places in paddies. All of the surveys were carried out on 9, 10, 15, and 19 of July in 2019, during the midsummer drainage of water management (Fig. 4-3). I also visited each site 2–3 times to confirm water levels and recording of died tadpoles.

4.2.3 Statistical analysis

Fisher's exact test (Bryan et al. 1995; Bower 2003) was used to check whether significant differences in levels of died tadpoles occurred between the drainage system modernization.

4.3 Results

No modern-style irrigation system was found. Among all study sites, I observed *Rhacophorus arboreus* bred mainly from June to early-July. The water depths in paddies are drained for 10–14 days from ~ eighth to 20th in July 2019.

Four paddy fields (sites 5, 11 were with traditional-style drainage system, and sites 4, 17 were with intermediate-style drainage system), fallow paddy (site 9) and abandoned paddy (site 15) with traditional-style drainage system were not drained, whereas other 14 paddies were drained (Table 4-1).

I recorded the presence of the water pools (i.e., shallow water and intermediate water) in or next eight paddy fields among the 14 drained paddies. These water pools may have reduced the negative impacts on tadpoles for growing (Table 4-1). A lot of died tadpoles were confirmed after midsummer drainage in 6 paddies, including sites

2, 6, 14, 16, 18, 19, where the water depths were dried thoroughly. The tadpoles survived in 6 sites where without midsummer drainage (Table 4-1). I recorded egg masses at site 6 in both 2018 and 2019. This site was paddy-field in 2018 while it was converted to corn field in 2019.

The Tadpoles died at 2 of 11 traditional drainage system and 3 of 6 intermediate-style's system. The indirect effect of drainage system modernization on the incidence of tadpoles death (P = 0.046, Fisher's exact test), as showed in Table 4-1. Four out of six study sites with died tadpoles of *R. arboreus* in habitat within intermediate-style drainage system, which indicated that died tadpoles were more abundant in the above drainage system. This result tested the first hypothesis stated in the introduction.

4.4 Discussion

In this chapter, quite a few breeding sites for *R. arboreus* are counted in paddy fields. It was consistent with a previous study (Kato et al. 2010). Paddy fields seem to be the main habitats due to the total area available for breeding (Kato et al. 2010). Tadpoles appear to suffer from less crowding in paddy fields than in small ponds and temporal water bodies (Brady and Griffiths 2000).

The combined harmful effects of midsummer drainage and drainage system modernization on aquatic organisms are suspected (Fujioka and Lane 1997; Donald 2004; Naito et al. 2012). Such influences on tadpoles of *Rhacophorus arboreus*–a particular breeding season in paddy-field ecosystems in Japan–have been suggested, but there has been no direct evidence of them thus far. My findings demonstrated that the occurrence of died tadpoles of *R. arboreus* directly associated with midsummer drainage. This is the first case of evidence that indicates the impact of water management for agricultural purposes on growing tadpoles of *R. arboreus* through water-level control during the midsummer drainage period. Moreover, I also report the second case of the indirect negative effect of drainage system modernization on tadpoles.

Results of the survey demonstrate that many died tadpoles of *R. arboreus* were found in site 6, due to the paddy has been converted into a corn field. *R. arboreus* show site fidelity in breeding sites across years (Maeda and Matsui 1990; Kusano et al. 2006). Crop rotation negatively affected tadpole survival.

4.5 Table

Table 4-1. A summary of some characteristics of midsummer drainage, drainage systems, and habitats in 20 study sites.

Study sites	Midsummer drainage (No: 0; Yes: 1)	Situation of tadpoles (not died: 0; died:1)	Drainage systems (traditional-style: 0; intermediate-style: 1)	Habitat types
1	1_Shallow water	0	0	Paddy
2	1_No water	1	0	Paddy
3	1_Intermediate water	0	0	Paddy
4	0	0	1	Paddy
5	0	0	0	Paddy
6	1_No water	1	1	Paddy–> Corn field
7	1_Intermediate water	0	0	Paddy
8	1_Intermediate water	0	0	Paddy
9	0	0	0	Fallow paddy
10	1_Shallow water	0	0	Paddy
11	0	0	0	Paddy
12	1_Intermediate water	0	1	Paddy
13	1_Shallow water	0	0	Paddy
14	1_No water	1	1	Paddy
15	0	0	0	Abandoned paddy
16	1_No water	1	1	Paddy
17	0	0	1	Paddy
18	1_No water	1	0	Paddy
19	1_No water	1	1	Paddy
20	1_Shallow water	0	0	Paddy

4.6 Figures

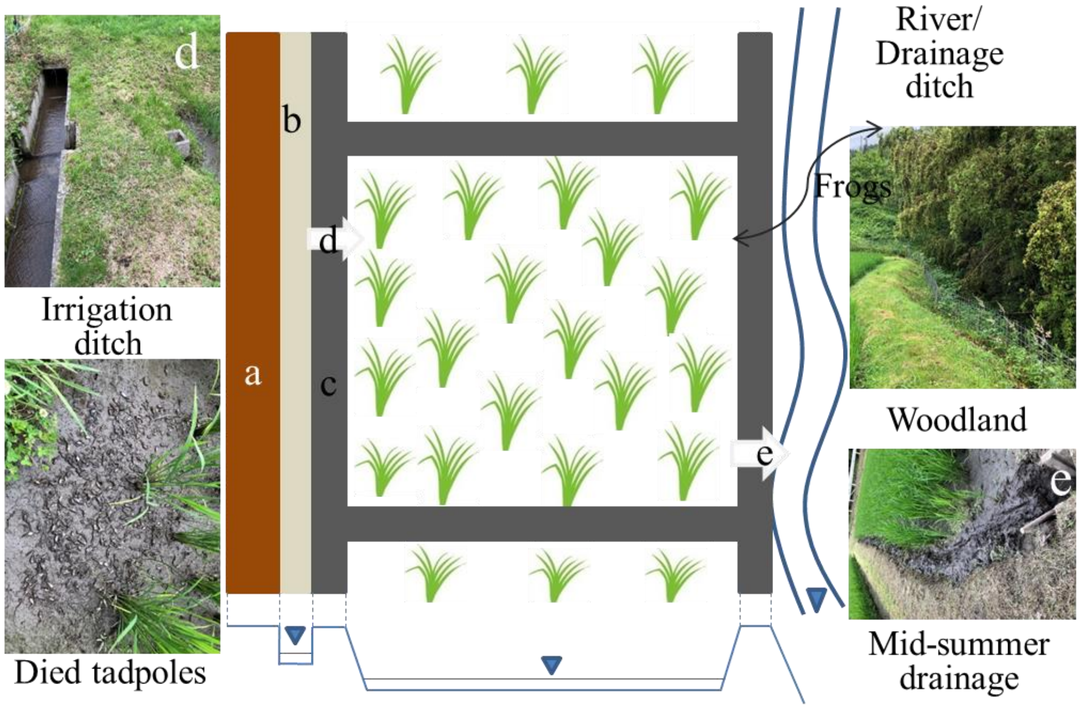


Fig. 4-1 Cross-section of the paddy-field after land consolidation and improvement projects. The irrigation channel is the U-shaped, concrete type. Note: (a) farm road, (b) irrigation ditch, (c) levee, also used as a walking path surrounding the paddy-field, (d) irrigation water inlet, (e) drainage water outlet. Photographs of the woodland and died tadpole, *etc*, were displayed in this figure.

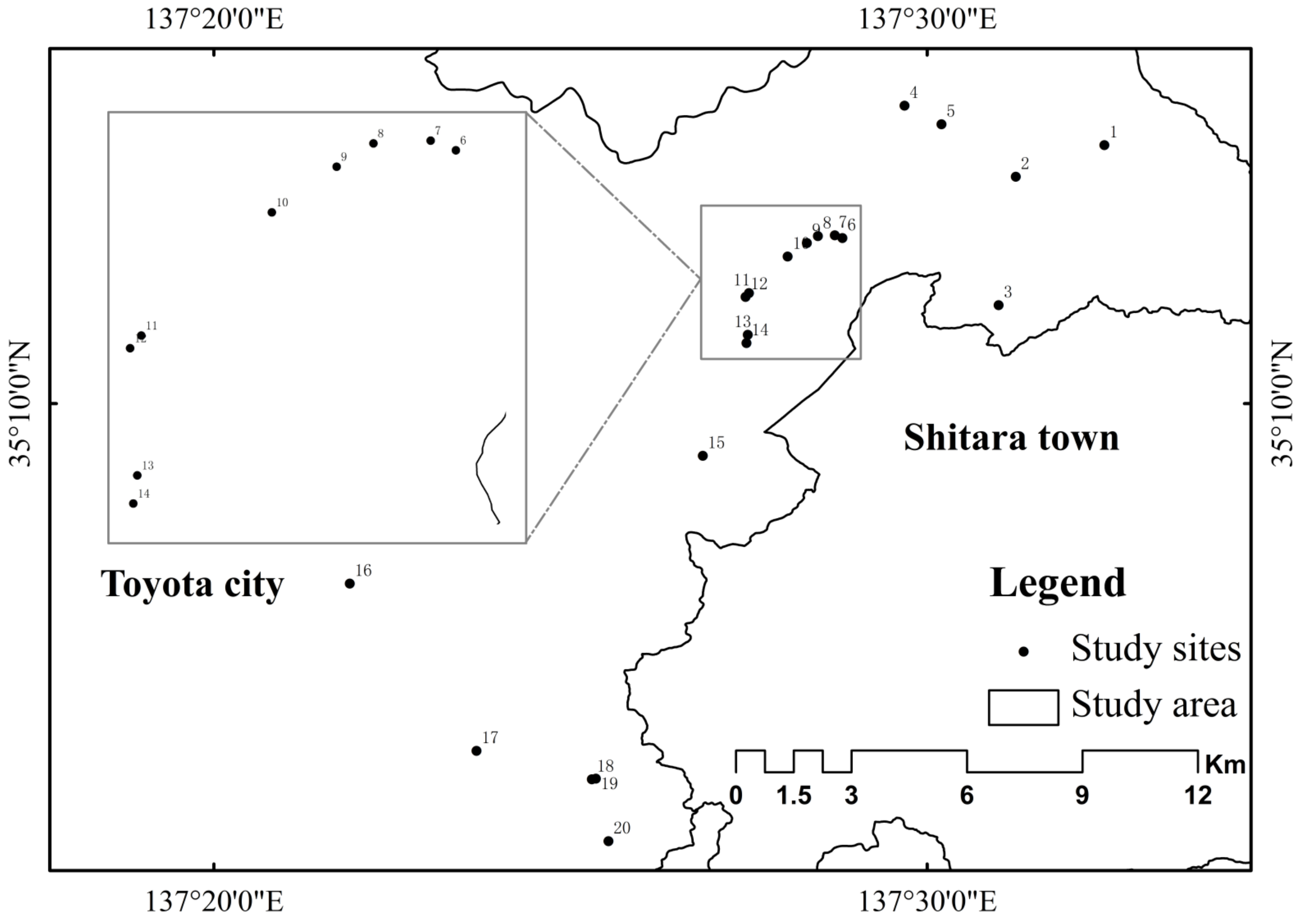


Fig. 4-2 Geographical locations of the study sites.

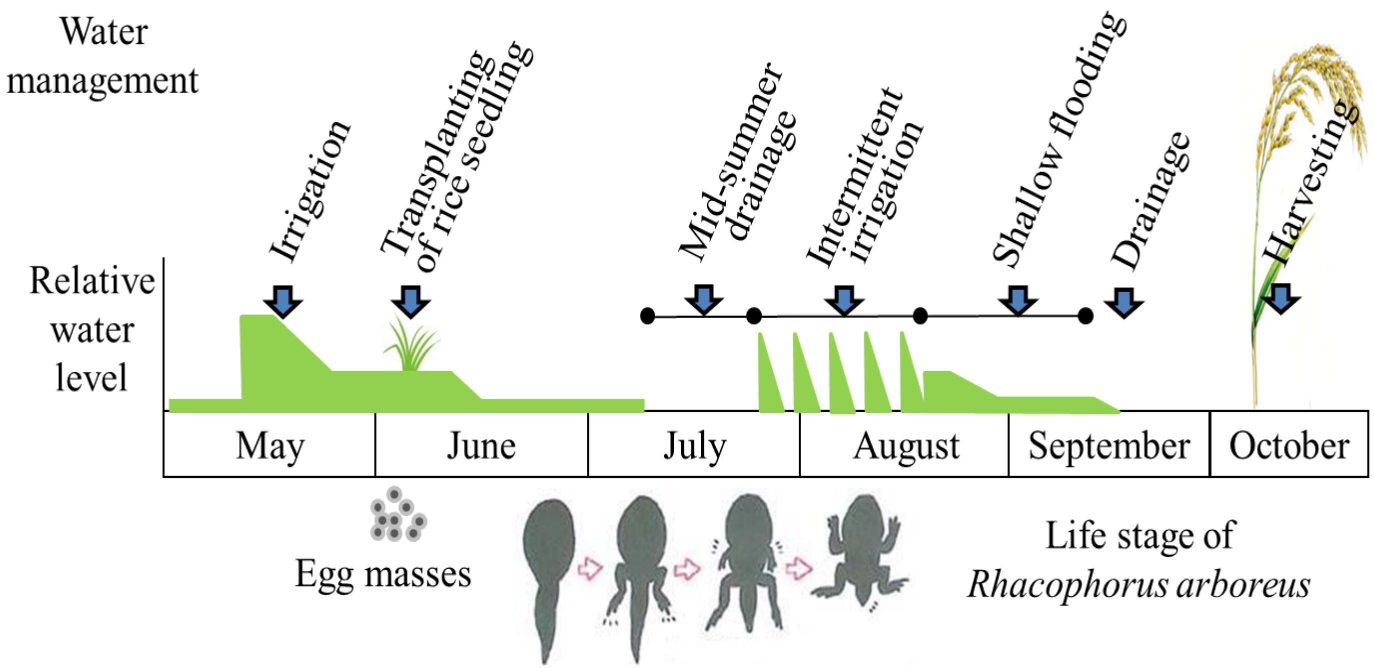


Fig. 4-3 Schematic figure of a typical water management taken at landscape of paddy fields for *Rhacophorus arboreus* in the study area.

Chapter 5: Thesis summary and conclusions

In chapter 2, I concluded that *Rana japonica* was distributed in lower elevation, and threatened by prevalence of concrete revetment on the levee of paddy fields. *Rana ornativentris* was widely breeding in ponds, abandoned paddy fields, and paddy-field areas with surrounding forests. Hence, there was a difference in susceptibility to human activities between *R. japonica* and *R. ornativentris.* Likewise, these driving factors have also probably influenced other amphibian species (Naito 2012) and aquatic insects, such as diving beetles (Nishihara et al. 2006). Together, these reports indicate that spatial heterogeneity, as well as local conditions such as appropriate modern water management measures, play irreplaceable roles in biodiversity conservation. Long-term data monitoring may help us understand population declines resulting from environmental changes or natural elements (Houlahan et al. 2000; Kidera et al. 2018). The effects of competition and the predation interactions on amphibian fitness must also be studied. The results of chapter 2 verified that the egg masses of the three species depend not only on water conditions but also on the terrestrial conditions of breeding sites, such as dense vegetation cover.

In chapter 3, I concluded that *Rhacophorus schlegelii* and *Rhacophorus arboreus* were positively affected by forest cover, and the latter was also affected by elevation. Similar studies for Asian, American, and European amphibians have indicated that tree-frog species were more abundant in habitats with more surrounding forest cover and higher elevation (Guerry and Hunter Jr 2002; Houlahan and Findlay 2003; Porej et al. 2004; Van Buskirk 2005; Gagné and Fahrig 2007; Tsuji et al. 2011).

I also concluded that, at the local level, the presence of trees and the proportion of embankment vegetation have positive effects on *R. schlegelii.* Also, *R. schlegelii* was threatened by habitat fragmentation because of road density. I did not have multiple-year data for these two green tree-frogs in my field, but previous studies reported that these two species demonstrate site fidelity in forests across years in breeding and non-breeding season (Maeda and Matsui 1990; Kusano et al. 2006; Toda 2013). Thus, I believe that my data with single-year did not cause seriously biased estimation of suitable habitats for these two tree-frogs.

In chapter 4, I concluded that the tadpole survival of *Rhacophorus arboreus* in paddy fields was negatively affected by the midsummer drainage and intermediate-style drainage system. Paddy fields are the basis of Japanese culture, while some functions of the ecosystem in paddy fields have deteriorated due to agricultural intensification.

The present work shows a clear relationship between the distribution of five frog species and the environment variables. This dissertation has significant implications for habitat conservation and restoration management both in urban and rural landscapes. Previous studies have focused on the declination and extinction of amphibian populations, resulting from the isolation of habitats caused by agricultural landscape modification and fragmentation (Natuhara and Kanbara 2001; Eterovick et al. 2016; Westgate et al. 2018). The isolation indicates that population decline and/or extinction of the five species could happen if no conservation policies are implemented.

To protect amphibians' diversity in agricultural lands, ecologists, policymakers, land managers, and even civilians should pay more attention to interspecies differences in susceptibility to human activities (Tsuji et al. 2011), e.g., agricultural abandonment and urbanization. In Japan, most species of frogs use paddy-field as breeding site. In particular, *Rana japonica*, *Rana ornativentris,* and *Bufo formosus japonicus* lay eggs in wet paddy fields in spring. Yet, during the breeding season of these species, only a few paddy fields are filled with water. Reserving water in winter and proper water management practices are undertaken to enhance or restore biodiversity (Maeda and Yoshida 2009; Takuya et al. 2009). Thus, this dissertation suggests that reserving water in winter could enhance the abundance of the frog species. Habitat with certain water depth could also promote an increase in frog breeding density (Fong et al. 2016; Kidera et al. 2018). Additionally, for *R. ornativentris* and *B. japonicus formosus*, constructing more aquatic organisms and connectivity among habitats should be considered. Chapter 2 showed that the use of concrete revetment on banks of paddy fields had substantial adverse effects on breeding of *R. japonica*, *R. ornativentris*, and *B. formosus japonicas*. We should conserve the traditional paddy-field areas with vegetated levees and soil drainage ditches.

For amphibians with high site fidelity, such as *R. schlegelii and R. arboreus*, conservation efforts should be focused on reducing habitat loss and degradation (Tsuji et al. 2011). Chapter 3 indicated that *R. schlegelii* was threatened by habitat fragmentation because of road density. This result suggests that urbanization could negatively affect the abundance of *R. schlegelii*. Likewise, reviving cultivation in abandoned paddy fields and protecting the traditional paddy fields surrounded by forests could enhance these two tree-frogs' abundance.

Chapter 4 indicates that we need to choose a favorable paddy-field concerning water management and construct suitable ecological engineering, such as catchment ditch and semi-natural habitats for target species. It needs to try our best to harmonize with rice production in modern-style paddy systems.

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