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Effects of landscape heterogeneity and breeding habitat diversity on rice frog abundance and body condition in agricultural landscapes of Yangtze River Delta, China

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Abstract

Amphibians play a key role in structuring biological assemblages of agricultural landscapes, but they are threatened by global agricultural intensification. Landscape structure is an important variable influencing biodiversity in agricultural landscapes. However, in the Yangtze River Delta, where a "farmland-orchard-fishpond" agricultural pattern is common, the effects of landscape construction on anuran populations are unclear. In this study, we examined the effects of agricultural landscape parameters on the abundance and body condition of the rice frog (*Fejervarya multistriata*), which is a dominant anuran species in farmland in China. Employing a visual encounter method, we surveyed rice frog abundance for 3 years across 20 agricultural landscapes. We also calculated the body condition index (BCI) of 188 male frog individuals from these agricultural landscapes. Landscape variables, comprising landscape compositional heterogeneity (using the Shannon diversity index of all land cover types except buildings and roads), landscape configurational heterogeneity (using landscape edge density), breeding habitat diversity (using the number of 5 waterbody types available as breeding habitats), and areas of forest were also measured for each 1-km radius landscape. We found that the amount of forest in each agricultural landscape had a significant positive relationship with rice frog abundance, and breeding habitat diversity was positively related to the BCI of male rice frogs. However, body condition was negatively impacted by landscape configurational heterogeneity. Our results suggested the importance of nonagricultural habitats in agricultural landscapes, such as waterbodies and forest, to benefit rice frog population persistence.

Key words: agriculture, amphibian conservation, edge density, frog, waterbody type diversity

Agricultural landscapes are essential habitats for maintaining and improving wildlife biodiversity due to natural habitat loss, fragmentation, and degradation of habitat quality caused by human activity (Benton et al. 2003; Fraterrigo et al. 2009; Fahrig et al. 2011). Many amphibians exist in these environments and some species are able to use them for foraging, breeding, and overwintering (Donald 2004). Agricultural intensity is often associated with natural habitat loss, high agrochemical use, large farms with cropped fields, and high levels of mechanization (Koumaris and Fahrig 2016), and is an important threat to amphibian biodiversity (Cushman 2006). For example, agrochemicals have negative effects on anuran life stages in farmlands (Mann et al. 2009), and large areas of cropped fields can affect anuran movement due to the decrease in landscape connectivity in farmland (Suárez et al. 2016). Although amphibian conservation in farmlands has been a research hot-topic, to the best of our knowledge, only a few studies have focused on how to protect and improve amphibian biodiversity in agricultural landscapes in East Asia, which are undergoing a change from traditional farming patterns to intensive agriculture (Kato et al. 2010; Katayama et al. 2013; Kidera et al. 2018). This is particularly important in China, which is experiencing not only the rapid development of intense agriculture (Li et al. 2019), but also relevant decreases in amphibian biodiversity (Nanjing Institute of Environmental Sciences 2018). In 2018, farmland in China accounted for >1.3 million km^2, and agricultural landscapes (20.2% of the total abundance) hosted more amphibians than forest landscapes (17.7% of the total abundance) according to the biodiversity survey in China during 2011–2017 (Nanjing Institute of Environmental Sciences 2018).

Understanding the relationship between landscape structure and biodiversity in agricultural landscapes is a pressing conservation issue (Benton et al. 2003; Tscharntke et al. 2005; Fahrig et al. 2011). Traditional Chinese farming in the Yangtze River Delta, which includes a diverse range of crops and semi-natural (nonagricultural) habitats, is defined as a "farmland-orchard-fishpond" pattern and has been conducted for millennia. This heterogeneous agricultural landscape comprises a mosaic of numerous field crops, orchards, and fishponds and/or lotus ponds managed by farmers, as well as a diverse range of nonagricultural waterbodies and forests. Five anuran species (*Fejervarya multistriata, Pelophylax plancyi, Pelophylax nigromaculata, Microhyla fissipes,* and *Bufo gargarizans*) are widely distributed in the agricultural landscape of Shanghai, and rice frogs (*F. multistriata*), as a dominant anuran species in farmlands (Li et al. 2017), tend to use various agricultural waterbodies as their breeding habitats (Li et al. 2019). Although various studies have been conducted in North America, South America, and Europe (da Silva et al. 2012; Collins and Fahrig 2017; Boissinot et al. 2019; Ribeiro et al. 2019), few have investigated the relationship between the agricultural landscape structure and amphibian biodiversity within these environments in China, which has a mosaic of crop and nonagricultural habitats (especially a diverse range of waterbodies) and is facing a rapid decrease of amphibian biodiversity. Such investigations could suggest a possible conservation strategy if specific landscape variables have significant effects on amphibian populations.

Morphology characteristics (e.g. body size, body mass, and body condition) of individual animals are often used to evaluate amphibian population dynamics (Eterovick et al. 2016; Li et al. 2016; Li et al. 2019). For example, body condition is used as an indicator for conservation and habitat quality, and several specific methods have been developed for its assessment (Schulte-Hostedde et al. 2005). Body condition is based on the weight and body size of individuals,

reflecting their physiological and nutritional status, and even their possible future extinction rate (Cooke et al. 2019). Previous studies tested the effects of habitat type, temperature, altitude, age, and season on the body condition of amphibians (e.g. Băncilă et al. 2010; Matías-Ferrer and Escalante 2015; Ribeiro et al. 2017). In addition, body condition is associated with amphibian movement and survival, with individuals with higher body condition showing better movement ability and higher survival rates compared with those with poorer body condition (Lowe 2003; Lowe et al. 2006; Scott et al. 2007). Population size is the most common indicator used to represent the amphibian population status, but some studies have suggested that body condition is a stronger predictor of amphibian population dynamics and can be used to assess the quality of their habitats (Ousterhout et al. 2015; Li et al. 2016, 2019).

Landscape heterogeneity is defined as the number and proportions of different cover types (compositional heterogeneity) and their complex spatial arrangement (configurational heterogeneity) in the landscape (Fahrig and Nuttle 2005). Landscape heterogeneity in agricultural landscapes is related to the diversity and pattern complexity of agricultural habitats (e.g. farmland with different crop productions) and/or nonagricultural habitats (e.g. woodland, grassland, and diverse waterbody types) (Fahrig et al. 2011). Previous studies have indicated that higher landscape heterogeneity significantly increases the species diversity and/or abundance of amphibians in agricultural landscapes (Guerra and Aráoz 2015; Collins and Fahrig 2017). However, few studies have considered the effects of the landscape structure on the body condition of amphibians. Food availability is an important predictor that affects the physiology and morphology of organisms (Sumner et al. 1999; Matías-Ferrer and Escalante 2015). Arthropods are the main food of amphibians and they are more abundant in agricultural landscapes with higher landscape heterogeneity (Molina et al. 2014; Fahrig et al. 2015). Thus, landscapes with higher compositional heterogeneity could provide more resources for a single species, such as an amphibian (Fahrig et al. 2011). However, anurans have limited dispersal ability (Ribeiro et al. 2019), and might have to frequently cross inhospitable land-use types to move to suitable foraging, breeding, or shelter environments in agricultural landscape. Anuran in agricultural landscapes with higher landscape heterogeneity may consume more energy and their body condition may decline.

Some nonagricultural habitats are crucial for amphibian population persistence in agricultural landscapes (Knutson et al. 2004). Most wetlands have been lost through the conversion of wetlands to agricultural fields (van Asselen et al. 2013); agricultural intensity has also reduced waterbody cover and breeding habitat diversity for amphibians in agricultural landscapes. Given the importance of waterbodies for the amphibian life cycle (especially during the breeding season), studies have investigated the effect of waterbody characteristics on amphibian species richness and abundance in agricultural landscapes (Ribeiro et al. 2017; Boissinot et al. 2019; Sawatzky et al. 2019). Li et al. (2019) found a difference in rice frog abundance and morphology (especially body condition) in 3 different waterbody types from 30 agricultural landscapes in Shanghai. However, whether both anuran abundance and body condition increase with more breeding habitat types in the same agricultural landscape remains untested. In addition, some amphibian species depend on forests for foraging, hibernating, and migration (Marty et al. 2005). Several studies in North America, South America, and Europe reported that forest cover in agricultural landscapes benefits amphibian diversity (Boissinot et al. 2015; Oda et al. 2016; Collins and Fahrig 2017) and body condition (Scheele et al. 2014); however,

it is unclear whether forest patches would have significant effect on anurans, given the traditional Chinese farming pattern, which is characterized by small farm sizes (i.e. more farmland edges) and diverse crop and nonagricultural habitats.

The Yangtze River Delta has the highest level of urbanization and human population density in China, and Shanghai City is one of the centers of this area. Current studies have reported a rapid decline in the species diversity (i.e. abundance and species richness) and individual physiological status of amphibians in Shanghai because of rapid urbanization over the past 30 years (Li et al. 2016; Zhang et al. 2016). Studies also indicated that agricultural landscapes have greater potential to support amphibian biodiversity compared with the urban environment in this study (Zhang et al. 2016; Li et al. 2017). However, it remains unknown how landscape structures caused by farm patterns in the Yangtze River Delta might influence anuran abundance and body condition. Such information would be useful for designing appropriate landscapes to improve amphibian biodiversity in Yangtze River Delta.

In this study, we surveyed rice frog abundance and measured the body condition index (BCI) of male rice frogs from 20 agricultural landscapes in Shanghai characterized by a mosaic of crop and nonagricultural habitats, and measured the landscape structure of these agricultural landscapes. Our objectives were to investigate how the landscape structure, especially landscape heterogeneity and breeding habitat diversity, affects rice frog abundance and body condition in agricultural landscapes in the Yangtze River Delta. We hypothesized that there would be higher rice frog abundance in agricultural landscapes with higher landscape heterogeneity because the higher landscape heterogeneity should provide more resources for rice frogs (Collins and Fahrig 2017). In contrast, higher landscape heterogeneity may decrease rice frog body condition due to the

need to consume more energy to frequently move across diverse inhospitable land-use types, with anurans known have limit dispersal ability (Ribeiro et al. 2019). Additionally, more breeding habitat types in agricultural landscapes would also benefit anurans by providing more breeding habitat selection and some nonagricultural waterbodies could support anurans with higher body conditions than farmland waterbodies based on our previous study (Li et al. 2019).

Material and Methods

Study sites

Shanghai is located on the alluvial plain formed by natural deposition of the Yangtze River, and had an agricultural area of 3,589 km² in 2014. Rice, wheat, and various vegetables and fruits are farmed in the Shanghai agricultural areas. We chose 20 1-km radius agricultural landscapes in rural Shanghai (Figure 1), where the total amount of farmland was >40%. We selected 1 km as our study scale because it was considered a reasonable representation of the average dispersal and migration movements of rice frogs (Li et al. 2019). Previous studies have shown that certain agricultural landscape variables can affect anuran biodiversity at this scale (Knutson et al. 2004; Collins and Fahrig 2017). To ensure spatial independence, the minimum distance between each sampled landscape was at least 3 km (Li et al. 2019).

A single anuran survey transect was established along farmland irrigation ditches in each landscape (Figure 1), which is the common habitat of breeding rice frogs in the agricultural landscapes of Shanghai (Li et al. 2019). A total of 20 survey transects were established in this study. The survey-transect lengths were 300–500 m, with a width of 5 m due to the differences in farmland irrigation ditch lengths in each landscape.
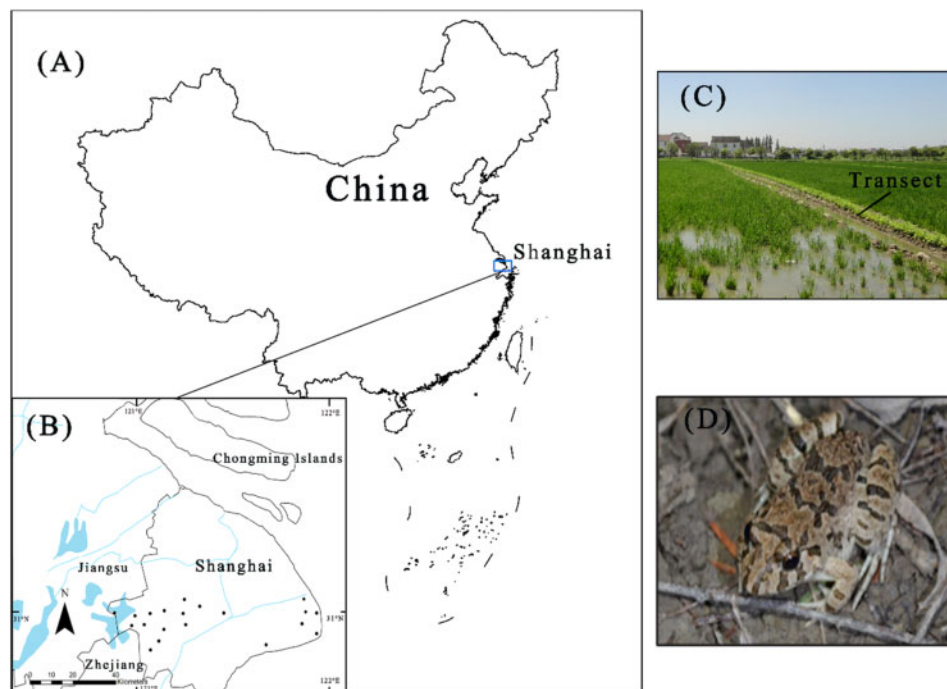
Figure 1. (**A**) The map of China from National Geomatics Center of China (http://ngcc.sbsm.gov.cn/ngcc/). (**B**) The study location of the 20 agricultural landscapes (black points) with a radius of 1 km in rural Shanghai, China. (**C**) General view of the transect set along farmland irrigation ditches (300–500 m) in each agricultural landscape. (**D**) The picture of rice frog recorded in each transect.

Study species

We chose the rice frog as our study species because it is an ideal model organism for investigating the influences of agricultural landscape structure on anuran abundance and body condition. The rice frog is the dominant amphibian in Shanghai farmlands, making it easier to get a large enough sample size for data analysis (Li et al. 2016, 2017). Specimens of rice frogs use a diverse range of breeding habitats (i.e. ditches and ponds) in agricultural landscapes during the breeding season in April to August (Fei et al. 2009), and they are easily affected by environmental changes in breeding habitats (Li et al. 2019). Finally, this frog has a huge demand for food resources and low movement ability, also the agricultural types and practices contribute to the arthropod abundance and landscape connectivity (Clough et al. 2007; Diekötter et al. 2010; Fahrig et al. 2011).

Anuran surveys

We conducted 6 visual surveys following the method of Crump and Scott (1994) along the same transect in the 20 agricultural landscapes between April to July (breeding season) in 2014 (twice), 2016 (3times), and 2017 (once). Surveys were performed during the night (from 19:00 to 24:00 h) when there was no rain and strong winds (<30 km/h). Surveys were performed by groups of 2–3 researchers who walked each transect at a steady speed of 1 km/h to search for anurans with flashlights. To account for the variation in survey conditions (i.e. time, temperature, humidity, interannual variation, and transect lengths) (Mazerolle et al. 2007), the average anuran population density (individuals per meter) detected in the 3 surveys with the largest counts among all 6 surveys across the 3 years was used to represent the rice frog abundance of each landscape.

BCI

During the 2016 surveys, we captured 188 male rice frogs randomly across the 20 landscapes and placed them into individual bags to determine anuran body condition (range from 7 to 12 individuals in each landscape). Although anuran surveys were conducted 6 times during 3 years, to avoid recapturing the same frog sample in subsequent surveys and reduce the effect of different weather conditions (especially temperature and humidity) in different years on frog body condition (Reading and Clarke 1995; Reading 2007), all anuran individuals in each agricultural landscape were captured in a single survey from the 3 anuran surveys of 2016. We used male frog data because of differences in the egg-laying period among female frogs (Fei et al. 2009) and the absence of juvenile data in the breeding season according to our surveys. The presence of nuptial pads was used to sex male frog individuals (Fei et al. 2009).

The BCI for each one of the 188 male frogs was estimated based on the measurement of body mass (W) and snout–vent length (SVL), where W was recorded with a portable electronic balance (0.01 g) and SVL was measured with an electronic digital caliper (0.1 mm). The BCI of each rice frog was calculated with a simple regression using log W and log SVL across all male frog individuals and its residual value (Li et al. 2016, 2019).

Landscape variables

Land use data were obtained from Formosat-2 satellite images in 2012 (2-m resolution). We defined 13 land cover types comprising farmland (including the areas of grain, and a variety of vegetables and fruits), orchards (including peach and citrus trees), woodland, grassland, buildings, roads, uncultivated land, rivers, ponds, fishponds, lotus ponds, streams, and ditches (Figure 2). All landscape

Figure 2. Example land cover map for a 1-km radius agricultural landscape sampled in Shanghai, China.

Table 1. Description of the landscape predictive variables used in this study

Variable	Description
Landscape compositional heterogeneity	The Shannon diversity index of land cover types (except roads and buildings) in each agricultural landscape. SHDI $= -\sum_{i=1}^{m} \text{Piln(Pi)}$, where Pi = proportion of the landscape occupied by patch land cover type (class) i
Landscape configurational heterogeneity	The edge density of land cover types at the landscape level in each agricultural landscape. $ED = \frac{E}{A}$, where E = the total length of the edge in each agricultural landscape (m), A = the area of each agricultural landscape (ha)
Breeding habitat diversity	The number of breeding habitat types available for rice frogs in each agricultural landscape
Forest area	The proportion of forest cover in each agricultural landscape (%)

contents were determined by visual interpretation and we combined aerial photographs with ground surveys to distinguish the land cover types if they were hard to define.

We measured 4 potential landscape predictor variables within each 1-km radius landscape (Table 1): landscape compositional heterogeneity, landscape configurational heterogeneity, and breeding habitat diversity (including 5 waterbody types that were available for rice frogs as breeding habitats: ponds, fishponds, lotus ponds, streams, and ditches) (Table 2), and forest area (including woodlands and orchards). Landscape compositional heterogeneity was measured as the Shannon diversity index for all land cover types except buildings and roads (hereafter landscape Shannon diversity) and landscape configurational heterogeneity was measured as the edge density of the land cover types within each landscape (hereafter landscape edge density) (Li et al. 2018). Breeding habitat diversity was represented by the number of waterbody types available for rice frogs as breeding habitats from the 5 waterbody types in each landscape (Bickford et al. 2010). Rice frogs rarely finish their breeding life-history in rivers (Fei et al. 2009), and paddy fields are not high-

Table 2. Description of breeding habitat types available for rice frogs in 20 agricultural landscapes in Shanghai, China

| Category	Description	Usage
Pond	Still water $\leq 500\,\mathrm{m}^2$	Natural or semi-natural landscape
Fishpond	Still water $>500\,\mathrm{m}^2$	Aquaculture
Louts pond	Still water $>500\,\mathrm{m}^2$	Aquaculture and aquatic vegetables (especially lotus root and seeds)
Stream	Running or still water $>500\,\mathrm{m}$ long and $>4\,\mathrm{m}$ wide	Artificial landscape
Ditch	Running or still water $\leq 500\,\mathrm{m}$ long and $\leq 4\,\mathrm{m}$ wide	Agricultural irrigation for farmland and/or orchard

quality breeding habitats for rice frogs due to the high agrochemical-use in temporary waterbodies in February to April (Li et al. 2019), and therefore rivers and paddy fields were not listed as suitable breeding habitats for rice frogs in agricultural landscapes. The forest area was calculated as the proportion of forest cover in the landscape. ArcMap version 10.0 and Fragstats version 4.2 (McGarigal et al. 2012) were used to obtain and analyze the landscape structure data in this study.

Statistical analysis

Rice frog abundance and the average BCI of male rice frogs in the breeding season (at least $N>7$, range: 7–12 individuals) from each agricultural landscape were used as the response variables to test the influence of landscape structure (especially landscape heterogeneity and breeding habitat diversity due to our hypothesis) on rice frog abundance and body condition. Four predictor variables (landscape Shannon diversity, landscape edge density, breeding habitat diversity, and forest area) were log transformed to increase their linear relationships with response variables. Given that rice frog abundance was represented by count data in this study, generalized linear models (GLMs) were run with the Poisson distribution. GLMs were used with the Gaussian distribution for rice frog body condition.

Pearson correlation tests were used to analyze pairwise correlations between the predictor variables, and $|r|=0.7$ was considered to be the maximum collinearity threshold (Dormann et al. 2013). To further assess the collinearity among the 4 predictor variables, their variance inflation factors (VIFs) were also estimated, $\mathrm{VIF}>4$ indicating a possible collinearity (Neter et al. 1996). To further check for the potential spatial autocorrelation of 2 response variables, we calculated Moran's I using ArcGIS version 10.0 and GeoDa software (Anselin et al. 2006).

We used a multi-model inference approach using Akaike's Information Criterion corrected for small sample sizes ($\mathrm{AIC_C}$) to estimate and compare standardized model-weight mean coefficients of the direction and relative importance of the predictor variables on 2 response variables. Differences in $\mathrm{AIC_C}$ ($\triangle\mathrm{AIC_C}$) were used to choose the set of candidate models. All models with $\triangle\mathrm{AIC_C} <4$ were considered to be equally suitable for making inferences (Burnham and Anderson 2004; Burnham et al. 2011). Akaike weights (w_i) were also calculated to further estimate whether any model was clearly the best among the candidate models ($w_i > 0.9$) (Anderson et al. 2001). The global model of rice frog abundance and BCI with 4 predictor variables was used to perform model
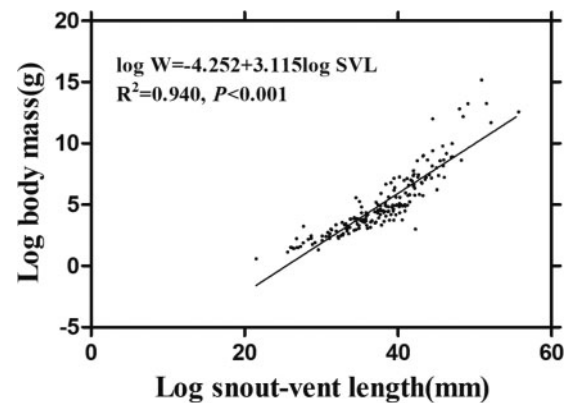
Figure 3. Relationship between $\log_{10}$-transformed body mass and SVL in male rice frogs ($n = 188$) captured from the 20 agricultural landscapes used in this study.

selection, and model averaging of all candidate models was performed to provide model coefficients and variances.

All statistical analyses were conducted using R version 3.6.1 (R Core Team 2019). The "AICcmodavg" package (Mazerolle 2017) was used for model selection and averaging. We did not identify any problems with over-dispersion and heterogeneity of variance upon examination of the dispersion parameter and residuals from the models.

Results

We observed 3,641 rice frogs across all 6 surveys over the whole survey period during 2014, 2016, and 2017. The population density of this species in the 20 agricultural landscapes ranged from 0.040 to 0.250 individuals per meter [mean 0.127 ± 0.107 standard deviation (SD)]. The BCI of each frog was $\log \mathrm{W}=-4.252+3.115 \log \mathrm{SVL}$ ($R^2 = 0.940$, $P < 0.001$) (Figure 3). The average BCI of male rice frogs was 0.012 ± 0.015 SD, ranging from -0.077 to 0.093 across the 20 agricultural landscapes.

The landscape variables of the 20 agricultural landscapes are shown in Table S1 of the Supplementary Material section. The pairwise correlations between the 4 predictor variables ($|r|$) were all <0.7 (Supplementary Material, Table S2). The VIFs for the 4 predictor variables were all <4 (Supplementary Material, Table S3), which suggested no severe collinearity between the 4 predictor variables in the analysis. No significant spatial autocorrelation was found for 2 response variables ($P > 0.1$) (Supplementary Material, Table S4).

Forest area was the most important predictor in the top 5 models ($\triangle\mathrm{AIC_C} < 4$) for rice frog abundance, but the null model was also listed among the candidates in the best model set (Supplementary Material, Table S5). Model averaged coefficients showed that forest area was significantly and positively related to rice frog abundance [estimate mean $\pm$ standard error (SE) $= 0.086 \pm 0.014$, 95% confidence interval (CI) $= 0.059 - 0.113$] (Figure 4A).

Breeding habitat diversity and landscape edge density were the 2 main predictors in the top 6 models ($\triangle\mathrm{AIC_C} <4$) for male rice frog BCI (Supplementary Material, Table S6). Model averaged coefficients suggested a significant positive relationship between breeding habitat diversity and male rice frog BCI (estimate mean $\pm$ SE $= 0.278 \pm 0.114$, 95% CI $= 0.055 - 0.501$); however, landscape edge density had a significant negative relationship with male rice frog BCI (estimate mean $\pm$ SE $= -0.252 \pm 0.121$, 95% CI $= -0.489 - -0.015$) (Figure 4B).
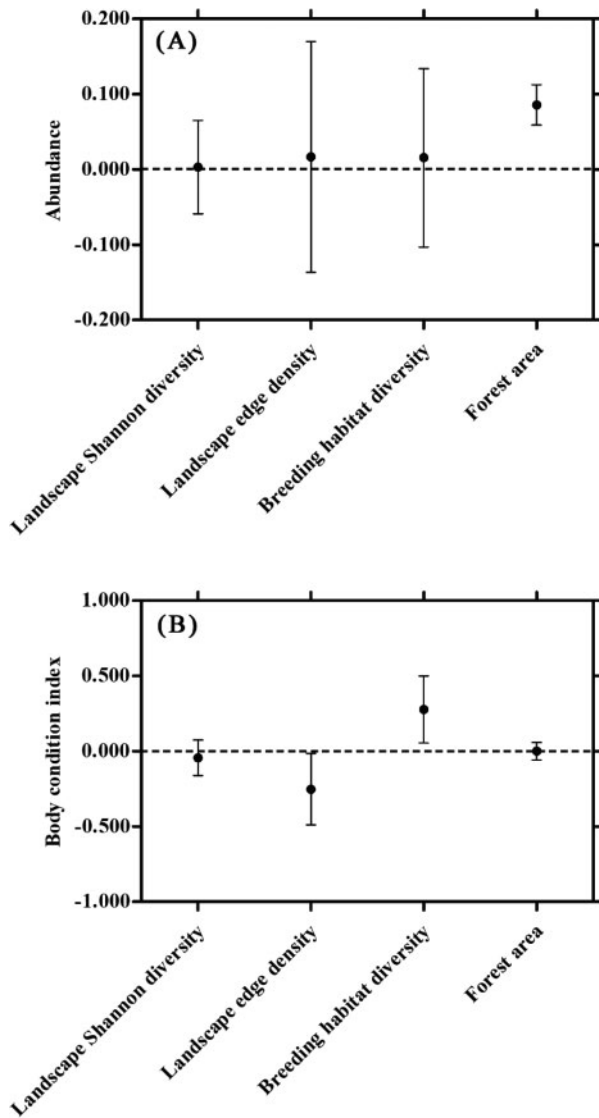
Figure 4. Model-weighted mean standardized coefficients and 95% CIs for the direction and relative magnitude of the effect of 4 predictor variables from the top models ($\triangle AIC_C < 4$) based on rice frog abundance (**A**) and male rice frog BCI (**B**) in 20 agricultural landscapes in Shanghai. The models for rice frog abundance and BCI using GLMs.

Discussion

We found that forest area had a significant positive relationship with rice frog abundance despite the null model ($w_i = 0.08$) being listed as the best model, which may indicate that the other best models were not very informative. In addition, breeding habitat diversity was positively correlated with the BCI of male rice frogs in the agricultural landscape. However, landscape configurational heterogeneity using landscape edge density in agricultural landscape was negatively correlated with male rice frog BCI.

Forest area was the only significantly positive predictor for rice frog abundance in agricultural landscapes in this study (Figure 4A). Forest is considered to be an important habitat for many animal taxa in agricultural landscapes (Harvey et al. 2006). Several studies have shown that forest cover is positively related to anuran species richness, occurrence, and abundance in agricultural landscapes in North America, South America, and Europe (Boissinot et al. 2015;

Oda et al. 2016; Collins and Fahrig 2017), but few similar studies have been conducted in East Asia, with its different farming patterns. Anurans use forest habitats for foraging, migratory movement, and as overwintering sites (Marty et al. 2005), and many anuran species use temporary and permanent waterbodies in forest areas as breeding habitats (Guerry and Hunter 2002; Suárez et al. 2016). Previous studies have shown that rice frogs in rural Shanghai would use forest areas and forest irrigation ditches for foraging and breeding, respectively (Li et al. 2019). In addition, anurans have a strong dependence on waterbodies and little tolerance to water loss because their highly permeable skins can easily lose water and their low movement ability limits their ability to move from dry to humid environments (Withers et al. 1984). High-quality microhabitats and shelters provided by forests may decrease the negative effect of temperature and hygrometric variations on anurans (Denoël and Ficetola 2008). Therefore, we concluded that forest is an essential habitat for rice frogs in agricultural landscapes, and that the provision of some terrestrial and aquatic habitats (such as forest irrigation ditches or temporary ponds in forests) related to forest area could benefit rice frogs in agricultural landscapes.

Male rice frog BCI was higher in agricultural landscapes with higher breeding habitat diversity (Figure 4B), which supported our hypothesis that the variety of waterbodies in agricultural landscapes benefited anurans by providing more types of breeding habitat. We also found a positive relationship between rice frog abundance and breeding habitat diversity although it was not statistically significant. Previous studies have indicated that more types of breeding habitat in a landscape increased anuran species richness and abundance in natural (Bickford et al. 2010) and urban environments (Li et al. 2018). Our previous study also found that nonagricultural waterbodies would benefit the rice frog body condition in the agricultural landscapes of Shanghai (Li et al. 2019). However, few studies have focused on the effect of breeding habitat diversity on anuran body condition in agricultural landscapes. The diverse range of breeding habitats in agricultural landscapes provides different hydroperiods and agrochemical exposures, and may also increase the resources available for anurans. Farmland irrigation ditches are managed by farmers and impacted by weather condition, and rice frogs may therefore face changes in humidity, water depth, and food resources due to farm patterns and climate change. Maintaining a diversity of permanent and semi-permanent breeding habitats, with different hydroperiods, will reduce the negative influences of environmental change on anurans (McCaffery et al. 2014), not only by providing several complementary breeding habitats for them to maintain population dynamics, but also enabling them to avoid water loss and provide enough food resource for their population physiological status. Previous studies have indicated that agrochemicals have a negative effect on anuran life stages (Mann et al. 2009), stimulate anuran compensation/detoxification systems (Costa and Nomura 2016), and even decrease anuran food intake in crophabitats (Ribeiro et al. 2017). In Shanghai, farmland irrigation ditches are the most common habitats for rice frogs in farmlands (Li et al. 2017, 2019). However, agrochemical use in this habitat is higher than in other waterbodies (e.g. ponds, steams, and rivers) in the agricultural landscape (Yao et al. 2010), which could have negative effects on anuran body conditions when they have few breeding habitats.

Importantly, our results showed that configurational heterogeneity in agricultural landscapes, measured as landscape edge density, had a negative effect on rice frog BCI (Figure 4B), which was consistent with our prediction that higher landscape heterogeneity

would decrease rice frog body condition by making their movement more different. Previous studies have demonstrated the positive effects of landscape configurational heterogeneity on anuran abundance in agriculture landscapes (Collins and Fahrig 2017; Ribeiro et al. 2017). However, few previous studies have investigated the relationship between landscape heterogeneity and the body condition of anurans. Agricultural landscapes with higher edge density might have a greater food availability and provide more refuge habitats for anurans (Nowakowski et al. 2013; Molina et al. 2014). It has also been hypothesized that anuran species might benefit from smaller field edge habitats, which could facilitate movement through the landscape and decrease energy consumption (Collins and Fahrig 2017). However, we suggest that rice frogs in the agricultural landscape of Shanghai were negatively affected by the higher edge density because Chinese traditional farming patterns are based on small farms and a diversity of nonagricultural habitats, and farmland managers have used farmland edge habitats to densely plant terrestrial vegetation and crops (Figure 1). Thus, rice frogs might consume large amounts of energy to move across these edge habitats. In addition, our results showed that rice frog abundance was positively related to agricultural landscape configurational heterogeneity (Figure 4A). Ousterhout et al. (2015) found negative relationship between anuran density and their body size, and intraspecific interaction was a stronger predictor of anuran morphology than habitat characteristics; therefore, we expected that a large rice frog density in the high configurational heterogeneity landscape would decrease their body condition.

Landscape Shannon diversity had no significant effect on both rice frog abundance and body condition in this study. However, landscape compositional heterogeneity was positively related to rice frog abundance in the agricultural landscape (Figure 4A), possibly because some anurans may inhabit more habitats and access more resources in landscapes with higher Shannon diversity index (Collins and Fahrig 2017). In addition, Shannon diversity decreased with male rice frog body condition in agricultural landscapes during the breeding season (Figure 4B). We hypothesized that rice frogs consume more energy when moving across varied habitats, given that this species is less mobile than other amphibians, such as toads (Zhang et al. 2016).

In the Yangtze River Delta, farmland managers usually change crop type, but seldom change crop area in farmlands during different years. Thus, we did not investigate the effect of structural complexity of crop areas (especially crop compositional and configurational heterogeneity) on the rice frog population. However, future field studies could investigate whether changing waterbody and forest areas in agricultural landscapes to land-use types with more economic value, such as orchards, fishponds, or lotus ponds, and whether these land-use types could also become important habitats for anurans and would not decrease anuran abundance and body condition.

Our results emphasized the importance of the positive effects of nonagricultural habitats, especially waterbodies and forests, on rice frog abundance and body condition in the agricultural landscape in Shanghai. In addition, we revealed a negative relationship between landscape configurational heterogeneity (using landscape edge density) and rice frog body condition. Whereas frog abundance may benefit from higher landscape heterogeneity in agricultural landscapes (Suárez et al. 2016; Collins and Fahrig 2017), the amount of different habitats we used to calculate landscape edge density (including many anthropogenic land-use types) may be detrimental to frog body condition. We suggest increasing forest cover and the diversity of waterbody types to benefit rice frogs in agricultural landscapes in Shanghai. Additionally, further studies are needed to explore the edge effect (represented as the edge density of a diverse range of crops and nonagricultural habitat edges or the vegetation characteristics of various habitat edges) of farming patterns of the Yangtze River Delta on anuran communities in agricultural landscapes.

Author Contributions

B.L. and T.W. designed the experiment. B.L., W.Z., and H.X. performed the experiments. B.L. performed the data analyses. B.L. and T.W. wrote the paper. Z.W., X.Y., and E.P. provided the valuable suggestions. All authors read and approved the final manuscript.

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Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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