

# Quantifying the Effect of Land-cover Change on the Endangered Farmland Green Treefrog (*Zhangixalus arvalis*) in an Agricultural Landscape: Implications for Conservation

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Habitat loss and fragmentation have a significant negative effect on amphibian species, particularly those with specialized habitat requirements. The endangered farmland green treefrog (*Zhangixalus arvalis*) primarily inhabits woodlands of agricultural landscapes in central Taiwan. Recently, due to increased demands for pineapple products, many woodlands, particularly bamboo plantations, were converted to pineapple fields. This study aimed to quantify the effect of habitat loss and fragmentation on *Z. arvalis* due to changes in land cover in an agricultural landscape. The study area contained 34,243 50 m × 50 m grids. In 2006 and 2014–2015, we used acoustic surveys to survey the occurrence of *Z. arvalis* in each grid. We obtained satellite images of the study area for 2006 and 2014, and we assigned the land-cover type of each grid to one of the following six types: woodland, brushland, cropland, bareland, manmade structures and water body. We examined whether *Z. arvalis* preferred a certain land-cover type by comparing the proportion of cover types available and the proportion of cover types used by the frogs. Furthermore, we used occurrence records for 2006 and 2014–2015 and applied the Maximum Entropy Model to predict suitable habitat for the respective years. We mapped the loss of suitable habitat and used six indices to quantify habitat fragmentation within the 8 years. We also tested the prediction that the occupancy rate of *Z. arvalis* in different-sized habitat patches was a function of patch size. *Zhangixalus arvalis* exhibited a strong preference for woodland, but avoided cropland and manmade structures. From 2006 to 2014–2015, the suitable habitat decreased 4.1%, and all six indices showed an increase in habitat fragmentation. The occupancy rate of different-sized woodland patches was positively correlated with patch size. Mapping suitable habitat and identifying the potential gaps in functional habitat connectivity can be used to guide effective measures for conserving *Z. arvalis*.

**Key words:** Farmland, Habitat connectivity, Habitat specialist, Metapopulation, Species distribution model.

## BACKGROUND

Anthropogenic factors, such as habitat loss and fragmentation, overexploitation, invasive species, pollution, spread of pathogens and climate change,

have driven declines in global biodiversity (Pereira et al. 2012; Pimm et al. 2014; O’Hanlon et al. 2018). Among the terrestrial fauna, amphibians are the most imperiled taxa (Stuart et al. 2004; Monastersky 2014); it was estimated that ≥ 40% of the described amphibian

species are currently threatened (Monastersky 2014). Amphibians generally have a complex life-history, a relatively poor dispersal capability, and a permeable skin (Duellman and Trueb 1986); those characteristics make amphibians susceptible to environmental changes (Rowe et al. 2003; Hopkins 2007). In the last few centuries, humans have altered massive areas of natural environments such as forests and wetlands to fulfill their needs for food, shelter, livelihoods and transportation (Goldewijk 2001; Gallant et al. 2007), which has caused habitat loss and fragmentation for many species. For amphibians, it is widely recognized that habitat loss and fragmentation are among the main causes of extinction and population declines (Gallant et al. 2007; Hof et al. 2011; Green et al. 2020). Habitat loss directly reduces the habitat that is required for populations to persist. Habitat fragmentation further compromises amphibian populations, and it has resulted in a reduction in functional habitat connectivity (Cushman 2006; Schivo et al. 2020), genetic diversity (Dixo et al. 2009; Rivera-Ortiz et al. 2015), and species diversity (Becker et al. 2007; Almeida-Gomes et al. 2016).

With the rapid growth of the human population, the demand for food continues to rise (Tilman et al. 2011); the human population will reach approximately 9.1 billion by 2050, and the demand for food will increase 70% (FAO 2009). Consequently, the agricultural landscape is expected to expand in the future, particularly in developing countries (Molotoks et al. 2018). Agricultural landscapes are often a mosaic of different modified land covers and scattered patches of fragmented forest (Bennett et al. 2006). In some cases, modified farmlands can create a highly heterogeneous environment and host high levels of amphibian biodiversity (Mendenhall et al. 2014; Collins and Fahrig 2017). However, the composition and configuration of land cover within agricultural landscapes might change frequently due to crop harvesting, crop rotation (Bullock 1992), or changes from less profitable crops to more profitable ones (Chang et al. 2008). Responses of amphibian species to changes in agricultural land-cover are often species-specific (Todd et al. 2009; Suárez et al. 2016; Nowakowski et al. 2017). Some amphibian species have tolerated land-cover change and remained abundant in modified farmlands (Todd et al. 2009; Hansen et al. 2019). However, some species, especially those with specialized habitat requirements and narrow habitat tolerance, are more sensitive to habitat modification (Gibbs 1988). For those amphibians with high sensitivity to habitat modification, it is important to understand their species-specific habitat requirements and evaluate how land-cover changes might affect their habitat availability and habitat connectivity (Gibbs 1988; Hansen et al. 2019).

The endangered farmland green treefrog (*Zhangixalus arvalis*, Jiang et al. 2019; formerly as *Rhacophorus arvalis*, Lue et al. 1995) is endemic to Taiwan, and it has a small distribution range that is restricted to the plains of Yunlin, Chiayi, and Tainan counties (Lue and Chou 2004). In the Yunlin area, *Z. arvalis* primarily inhabits bamboo plantations and secondary forests that are close to rivers (Chang et al. 2008; Ciou 2010). Adults rest in trees during the day (Chuang 2000). During the reproductive season, males climb down the trees after sunset, aggregate near water pools, and exhibit lekking behavior (Hsieh 2004), in which multiple males vocalize and display at breeding sites (leks) to attract females (Bradbury 1981). Males do not move between the leks and exhibit a high lek fidelity with an average activity range of 139.8 m<sup>2</sup> (maximum convex polygon area,  $n = 34$ , Hsieh 2004). Females, on the other hand, travel among leks to seek mating opportunities (Hsieh 2004). After amplexus, a female carries a male an average of  $10.3 \pm 8.5$  (mean  $\pm 1$  SD) m to find an oviposition site and to lay eggs in a foam nest on the ground with a thick layer of litter (Chuang 2000).

*Zhangixalus arvalis* had a limited activity range during the reproductive season (Hsieh 2004). Successful breeding largely depends on the availability of a thick layer of litter substrate that prevents the foam nests from desiccating and temporary water pools that allow aquatic larvae to live and develop. Water pools that remained  $\geq 18$ –24 days are required for successful metamorphosis of tadpoles (Chen 2005). Temperature and precipitation significantly influenced the vocal and breeding activities of *Z. arvalis* (Chen 2005). In central Taiwan, high precipitation during summer creates temporary pools on the ground of bamboo plantations and other woodlands. In addition, farmers sometimes irrigate bamboo plantations (Chen 2005). Taken together, lowland woodlands, particularly bamboo plantations, provide good habitats and breeding sites for *Z. arvalis*. However, the specialized habitat requirement of lekking at breeding sites makes *Z. arvalis* highly susceptible to land cover change. In Yunlin County, Chang et al. (2008) reported a substantial critical habitat loss for *Z. arvalis* within 5 years due to conversion of bamboo plantations to coffee or tangerine fields. More recently, because of the increased popularity of fresh pineapples and pineapple cakes, many bamboo plantations and remnant forests in an agricultural landscape of the Chiayi area were converted to pineapple fields (Council of Agriculture 2015). Pineapple fields are arid and considered inhospitable for tadpoles to survive and for adults to breed and disperse. It is imperative that we quantify the effects of changes in land-cover on *Z. arvalis* due to changes in crop types

to guide effective measures for conservation.

To assess the effect of habitat loss and fragmentation on a certain species, one fundamental step is to understand the spatiotemporal changes in habitat. However, it is often challenging to identify all the habitats occupied by a species due to a limited investigational effort. In addition, for some rare or cryptic species low detectability might yield false absence data. Recently, several species distribution models (SDMs), such as DOMAIN (Carpenter et al. 1993), artificial neural networks (Manel et al. 1999) and the maximum entropy model (Maxent, Phillips et al. 2004), have been developed to derive spatially explicit predictions of habitat suitability for species. In general, SDMs are quantitative tools that combine species occurrence with environmental variables to predict species distribution across space and time (Elith and Leathwick 2009). Among the SDMs, Maxent is widely used to map the suitable habitats of a species and provide applications in wildlife conservation and management (e.g., Angelieri et al. 2016; Preau et al. 2018). Maxent is advantageous because it uses presence-only data and thus can avoid errors from false absences (Phillips et al. 2006). Additionally, in contrast to most SDMs where predictive accuracy decreases with small sample sizes (Wisniewski et al. 2008), Maxent has a good predictive ability even with small sample sizes (Pearson et al. 2007; Wisniewski et al. 2008).

This study aimed to quantify the degree to which the habitat of *Z. arvalis* was lost and fragmented due to agricultural land cover changes at a regional landscape scale. We collected empirical occurrence data for *Z. arvalis* in 2006 and 2014–2015 in the Chiayi area, central Taiwan. We first examined whether *Z. arvalis* exhibited preference for a certain type of land cover by comparing the proportion of land-use types used with the proportion of land-use types that were available. Then, we used the Maxent model to predict the distribution of suitable habitat for *Z. arvalis* in 2006 and 2014–2015, and examined the loss of suitable habitat over the 8 years. Additionally, we used six indices to quantify habitat fragmentation. Considering the negative impacts of fragmentation and the limited movement capability of *Z. arvalis*, extinction of a subpopulation in an isolated habitat patch is more likely to occur in small patches than in large patches. Thus, we tested the prediction that the occupancy rate of *Z. arvalis* in different-sized habitat patches was a function of patch size. Our data that mapped the suitable habitat and identified the potential gaps in functional habitat connectivity can be used to determine strategic locations for habitat preservation, enhancement, and/or connection.

## MATERIALS AND METHODS

### Study area and occurrence records

We conducted this study in the Chiayi area, central Taiwan (Fig. 1). The study area contains a mosaic of different types of land cover, which included bamboo plantations, orchards, secondary forest, single species tree plantations, sugar cane plantations, shrubs, rice fields, pineapple fields, fallow farmland, bareland, houses, roads, and water bodies. We conducted this study from May to August 2006 and June to September 2014 and 2015. During the study periods, the average temperatures were  $27.8 \pm 1.1^\circ\text{C}$  (mean  $\pm$  1 SD),  $29.1 \pm 0.7^\circ\text{C}$  and  $28.7 \pm 1.2^\circ\text{C}$ , respectively, in 2006, 2014 and 2015; the total precipitations were 1777.5 mm, 949.2 mm and 1184.0 mm, respectively, in 2006, 2014 and 2015 (Data obtained from Chiayi Weather Station,  $23^\circ29'\text{N}$ ,  $120^\circ25'\text{E}$ , 26.9 m a.s.l.).

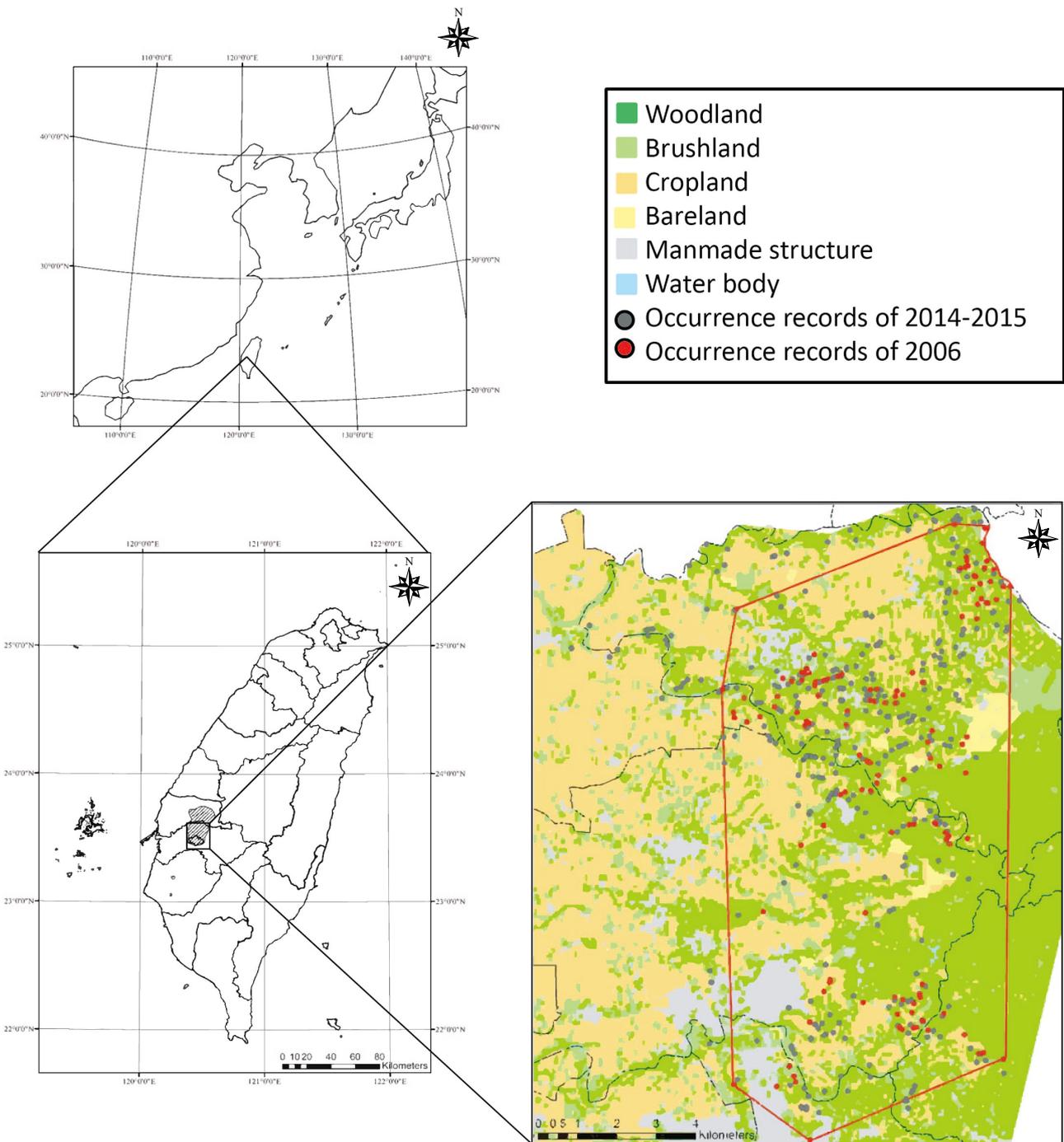
In 2006, one of the co-authors, M.-H. Chuang, trained volunteers from the Chiayi branch of the Society of Wilderness to investigate the distribution of *Z. arvalis* in the Chiayi area. Field surveys were conducted at night from May to August. In each survey, one or two trained volunteers rode scooters slowly along roads and paths, detecting the presence of *Z. arvalis* acoustically. When calls of *Z. arvalis* were detected, the volunteers recorded the coordinates as close to the frog's location as possible using GPS (Garmin eTrex Vista, USA). In 2006, we conducted a total of 20 surveys. The area of extent of occurrence (EOO) of *Z. arvalis* (8,560.7 ha, equivalent to  $34,243\ 50\ \text{m} \times 50\ \text{m}$  grids) was used to examine habitat loss and fragmentation over time (Fig. 1).

During the breeding seasons (June–September) of 2014 and 2015, we used the same acoustic surveys to survey for the presence of *Z. arvalis*. We conducted 23 surveys in 2014 and 37 surveys in 2015. Each of the aforementioned 34,243 grids was surveyed once per year. Field surveys started immediately after sunset and finished within 4 hours. Hsieh (2004) showed that vocalizations of *Z. arvalis* were significantly influenced by precipitation. Our observations also showed that *Z. arvalis* substantially reduced vocalizations when it rained heavily or when it did not rain for  $\geq 3$  consecutive days. Thus, we stopped field surveys when either of these two situations occurred. When we detected *Z. arvalis*, we recorded the coordinates of the frog's location using a GPS (Garmin GPSMAP 62stc, USA). In addition, we recorded land-cover type used by *Z. arvalis*.

### Preference for land-cover type

We purchased satellite images of the study area that were taken in July 2006 and August 2014 by FORMOSAT (resolution: 2 m) and SPOT-6 (resolution: 1.5 m) satellites, respectively. We manually determined

the land-cover type of each 50 m × 50 m grid in ArcGIS 10.1. If a grid included several land-cover types, the type with the most percentage cover was represented. Because we were unable to distinguish some land-cover types with 100% accuracy using satellite images, we pooled some cover types together. For example, we



**Fig. 1.** Study site in the Chiayi area, Taiwan. The different colors in the background indicate the distribution of the six land-cover types in 2014. Red and black filled circles are occurrence records of *Zhangixalus arvalis* surveyed in 2006 and 2014–2015, respectively. The red-line polygon is the area of extent of occurrence of *Z. arvalis* from 2006.

pooled bamboo plantation, secondary forest, orchard, and single species tree plantation together into the category “woodland.” Similarly, we pooled sugar cane plantation and shrub into “brushland,” and rice fields, pineapple fields, and fallow farmlands into “cropland.” Eventually, we assigned each grid into one of the following six types of land-cover: woodland, brushland, cropland, bareland, manmade structure (house and roads), and water body. After determining the land-cover type of each grid for 2006 and 2014, we created a land-cover transfer matrix to examine the changes in area of each land-cover type between the two study periods.

Using occurrence records obtained from 2014–2015, we performed a Jacob’s index (Jacobs 1974) to examine preferences for types of land-cover. The Jacob Index was calculated as:

$$J = (r-p)/[(r+p)-2rp]$$

where “ $r$ ” represents the proportion of a certain land-use type used and “ $p$ ” refers to the proportion of that land-use type that was available. The Jacob index value ranges between 1 and -1, indicating a strong preference or a strong avoidance, respectively.

### Species distribution model and quantifying habitat loss

We used occurrence records from 2006 and 2014–2015 and Maxent 3.3.3 (source: <http://www.cs.princeton.edu/~schapire/maxent/>) with a resolution of 50 m × 50 m to predict the distribution of suitable habitats over the years. For model simulations, we used five variables as environmental predictors: land-cover type, distance to the nearest river, elevation, slope, and aspect. For “distance to the nearest river,” we obtained the data layer of the Taiwan river shapefile from governmental open data (source: <https://data.gov.tw/>) and calculated the distance from river to the center of the grid using ArcGIS. Elevation data were generated from an open data, global digital elevation model (GDEM, 20 m grids) (source: <https://data.moi.gov.tw/>). The data for slope and aspect of each grid were acquired from elevation in ArcGIS 10.1. Due to the relatively small scale of our study area, we did not include climatic variables.

The number of grids occupied by *Z. arvalis* in 2006 and 2014–2015 was not equal, so for each year we randomly chose 100 occupied grids as subset data for simulations. We chose 70% of the subset data randomly for model training and the remaining 30% for validation. We used the area under the Receiver Operating Characteristic curves (AUC) to evaluate the

performance of the model (Fielding and Bell 1997). AUC values range from 0.5 to 1.0, and a value > 0.75 is considered potentially useful (Elith 2002). We used jackknife resampling to examine the contribution of each variable to the model. The output of Maxent models generated a map with values that ranged from 0 to 1 in each grid to represent that grid’s habitat suitability. For each of the two survey periods, we performed simulations 10 times. We used the average of the “tenth percentile training presence” as a threshold to produce a binary habitat suitability map. This threshold selection method has been used in several studies for amphibians (e.g., Rödder et al. 2009; Kafash et al. 2018). Grids with a probability above the threshold were classified as “suitable habitat,” and other grids were classified as “unsuitable habitat.” We determined habitat loss as the amount of predicted suitable habitat that was reduced between 2006 and 2014–2015.

### Quantifying habitat fragmentation

After generating the distribution of suitable habitat, we performed six common fragmentation indices to quantify the changes in habitat fragmentation between 2006 and 2014–2015. All analyses were performed using FRAGSTATS 4.2 (McGarigal and Marks 1995). We employed a 4-neighbor rule in FRAGSTATS whenever it was applicable. The six indices were: 1) number of patches (NP; McGarigal and Marks 1995)—a patch was defined by the 4-neighbor rule. A higher NP indicates greater fragmentation. 2) mean patch size (MPS; McGarigal and Marks 1995). MPS = total area of all patches/number of patches. MPS decreased with increasing fragmentation. 3) largest patch index (LPI; McGarigal and Marks 1995). LPI = (area of the largest patch/total area of all patches) × 100. LPI ranged between close to 0 and 100. A smaller LPI indicates greater fragmentation. 4) percent of landscape (PLAND; McGarigal and Marks 1995). PLAND = (total area of habitat patches/total landscape area) × 100. PLAND lies between close to 0 and 100. A smaller PLAND indicates greater fragmentation. 5) mean shape index (MSI; McGarigal and Marks 1995). MSI = (perimeter of patch/4area of patch)/number of habitat patches. A larger MSI indicates greater fragmentation. Finally, 6) mean Euclidean nearest neighbor distance (MENN; McGarigal et al. 2002). MENN = (distance between two patches/number of comparisons between two patches). ENN was the shortest straight-line distance between two patches. A larger MENN indicates greater fragmentation.

We used occurrence records and woodland patches obtained from 2014–2015 to test the prediction that occupancy rate of *Z. arvalis* in different-sized

habitat patches was a function of patch size. We focused on small patches with patch size  $\leq 2$  ha to emphasize the effect of habitat fragmentation. We divided all the habitat patches  $\leq 2$  ha into 20 size classes at 0.1-ha intervals. For a given patch size class, we determined the “occupancy rate” as the number of patches occupied by *Z. arvalis* divided by the total number of patches. We performed a regression analysis to test for the correlation. Statistical significance was set at  $P < 0.05$ .

## RESULTS

### Occurrence records

We found *Z. arvalis* in 127 grids from the 20 surveys of 2006 and in 336 grids from the 60 surveys of 2014–2015 (Fig. 1). We used the area of extent of occurrence of *Z. arvalis* from 2006 to examine habitat loss and fragmentation over time. Only 291 occurrence records from 2014–2015 were within this area (Fig. 1). Among them, our field observations showed that 172 (59.1%) were found in bamboo plantations, 52 (17.9%) in secondary forests, 14 (4.8%) in single species tree plantations, 15 (5.2%) in orchards, 19 (6.5%) in brushland, three (1.0%) in sugar cane plantations, four (1.4%) in fallow farmlands, one (0.4%) in a pineapple field, and 11 (3.8%) in gardens of houses. The only occurrence in a pineapple field was in close proximity to a bamboo plantation.

### Land-cover preference

Based on the satellite image of 2014, woodland was the most abundant land-cover type, accounting for 54.7% of the total grids, followed by cropland (28.0%), manmade structures (7.5%), brushland (7.0%), bareland (2.6%) and water body (0.1%). Among the 291 grids occupied by *Z. arvalis*, the vast majority (83.6%) were in woodlands; other land-cover types occupied by *Z. arvalis* included croplands (8.5%), brushlands (7.1%), barelands (0.4%) and manmade structures (0.4%) (Table 1). The only occurrence in a manmade structure was found in the garden of a house. Accordingly, *Z. arvalis*

showed a preference for woodland (Jacobs index = 0.617), but exhibited an avoidance for manmade structures (Jacobs index = -0.916), bareland (Jacob index = -0.764), and cropland (Jacobs index = -0.612) (Table 1).

### Predicted suitable habitats and habitat loss

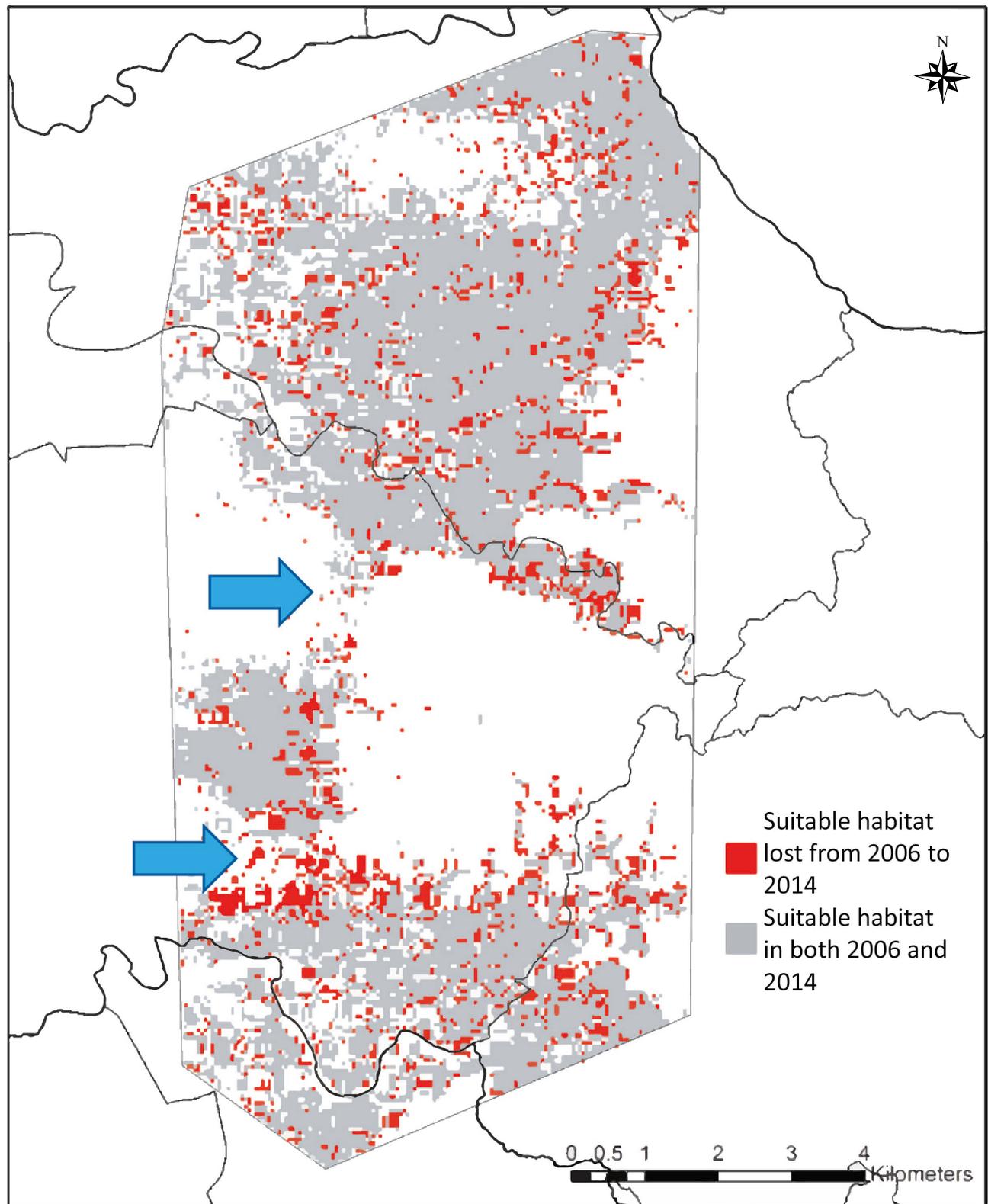
The AUC of the Maxent models were  $0.867 \pm 0.026$  for 2006 ( $n = 10$ ) and  $0.886 \pm 0.021$  ( $n = 10$ ) for 2014–2015, indicating good model performances in both years. Among the five environmental variables used in the models, the “nearest distance to the river” was the largest contributor to the model, contributing 43.8%, followed by elevation 38.6% and type of land cover 11.7%. The thresholds used to determine suitable habitat (*i.e.*, tenth percentile training presence) were 0.365 for 2006 and 0.298 for 2014–2015. In general, the predicted suitable habitat included three major areas, which included two large areas on the north and south of the study area and a relatively small area in the middle (Fig. 2). From 2006 to 2014–2015, suitable habitats were reduced by 148.5 ha from 3,651.4 ha to 3,502.9 ha, which was a loss that represented 4.1% of the total suitable habitat area. The loss of suitable habitat was spread over the study area; some patches located between the three major areas disappeared, which may have reduced connectivity among habitat fragments (Fig. 2). From 2006 to 2014–2015, the result of land-use transfer matrix showed that 235 ha of woodland were converted to cropland or other habitat types; however, 45.1 ha of other types of land cover became woodland. As a result, woodland area decreased by 189.9 ha. Cropland area, on the other hand, increased 186.3 ha in 8 years (Table 2).

### Habitat fragmentation

Of the six habitat fragmentation indices used in 2006 and 2014–2015, the values of three increased: NP increased from 264 to 278, MSI increased slightly from 1.28 to 1.30, and MENN increased from 99.3 to 101.1 (Table 3). The values of the other three indices decreased: MPS decreased from 15.75 to 14.08, LPI

**Table 1.** Test for land-cover preference of *Zhangixalus arvalis* in the Chiayi area, Taiwan, using Jacobs index based on occurrence records of 2014–2015 and satellite images from 2014

	Woodland	Cropland	Brushland	Bareland	Manmade structures	Water body
Land cover available (%)	54.7	28.0	7.0	2.6	7.5	0.1
Land cover used (%)	83.6	8.5	7.1	0.4	0.4	0
Jacobs index	0.617	-0.612	0.006	-0.764	-0.916	-



**Fig. 2.** Distribution of suitable habitats of *Zhangixalus arvalis* in the Chiayi area, Taiwan, in 2006 and 2014. Gray areas refer to the suitable habitat in both 2006 and 2014. Red areas are suitable habitat lost from 2006 to 2014–2015. The blue arrows indicate the locations of high priority for habitat construction and/or connection.

from 19.12 to 18.37, and PLAND from 43.0 to 40.46. All six indices indicated there was an increase in habitat fragmentation from 2006 to 2014–2015.

*Zhangixalus arvalis* preferred the woodland type of land cover. Thus, we examined whether occupation rates of *Z. arvalis* in different-sized woodland patches was a function of patch size. In 2014–2015, the study sites contained 1,903 woodland patches with a patch size  $\leq 2.0$  ha, and the occupation rate increased significantly in larger patch sizes (Fig. 3,  $R^2 = 0.71$ ,  $P < 0.01$ ).

## DISCUSSION

### Habitat loss

The vast majority (~82%) of amphibian species are forest-dependent (Stuart et al. 2004). Even in agricultural landscapes, woodlands are used by some amphibian species as important habitats or refuges (Weyrauch and Grubb 2004; Boissinot et al. 2015; Collins and Fahrig 2017). In our study site, woodlands were important to *Z. arvalis* for three reasons. First, adults are arboreal and largely depend on woodlands in which to live and to display lekking behavior. Second, the thick layer of litter on the ground of woodlands helps to keep the foam nests moist. Third, temporary water pools that persist for 18–24 days are required for

aquatic larvae to survive and to develop (Chen 2005). The relatively dense canopy of woodlands could prevent water pools from rapid desiccation.

Our results showed that the agricultural land-cover alteration due to changes in crop types resulted in a 4.1% habitat loss for *Z. arvalis* over 8 years. Habitat loss directly led to amphibian population declines (Cushman 2006). For a species like *Z. arvalis* that has a global distribution of  $< 1,000$  km<sup>2</sup> (Lue and Chou 2004), a small proportion of habitat loss could have a significant effect on its population abundance, especially when the total amount of remaining habitat falls below a critical threshold level (Swift and Hannon 2010). Additionally, in our study, because some predicted suitable habitats were not actually inhabited by *Z. arvalis*, we expected that the proportion of habitat loss would be much higher if only area of occurrence (AOO) was examined. Unfortunately, we were not able to identify all the grids occupied by *Z. arvalis* due to a limited investigational effort. Notably, although some croplands and other land-cover types were converted to woodlands/bamboo plantations during the two survey periods (Table 2), it normally takes a few years for newly planted woodland to increase shade cover and to generate litter substrate before it can be used by *Z. arvalis* as a breeding site. The degree of habitat loss presented in our study was presumably underestimated. Nonetheless, our results that mapped the spatiotemporal changes in suitable habitat provide important information for identifying

**Table 2.** Land cover transfer matrix in the region where *Zhangixalus arvalis* was surveyed in the Chiayi area, Taiwan, from 2006 to 2014

Land-cover area in 2006 (ha)	Land-cover area in 2014 (ha)						
	Woodland	Cropland	Brushland	Bareland	manmade structures	Water body	Total
Woodland	2646.4	191.0	16.9	5.6	17.8	3.7	2881.4
Cropland	20.5	3071.0	17.4	13.1	25.3	1.1	3148.5
Brushland	10.6	41.0	535.3	4.1	7.7	1.6	600.3
Bareland	4.9	18.9	9.9	309.7	14.7	0.5	358.6
Manmade structures	8.7	11.8	0.9	1.0	1496.8	0.6	1519.8
Water body	0.3	1.2	0.1	0.0	0.0	50.5	52.0
Total	2691.5	3334.8	580.5	333.6	1562.4	57.9	8560.7

**Table 3.** Values of six fragmentation indices for suitable habitat of *Zhangixalus arvalis* in the Chiayi area, Taiwan, in 2006 and 2014

Year	NP	MPS	LPI	PLAND	MSI	MENN
2006	264	15.75	19.12	43.00	1.28	99.26
2014	278	14.08	18.37	40.46	1.30	101.09

Note: NP: number of patches, MPS: mean patch size, LPI: largest patch index, PLAND: percent of landscape, MSI: mean shape index, MENN: mean Euclidean nearest neighbor distance.

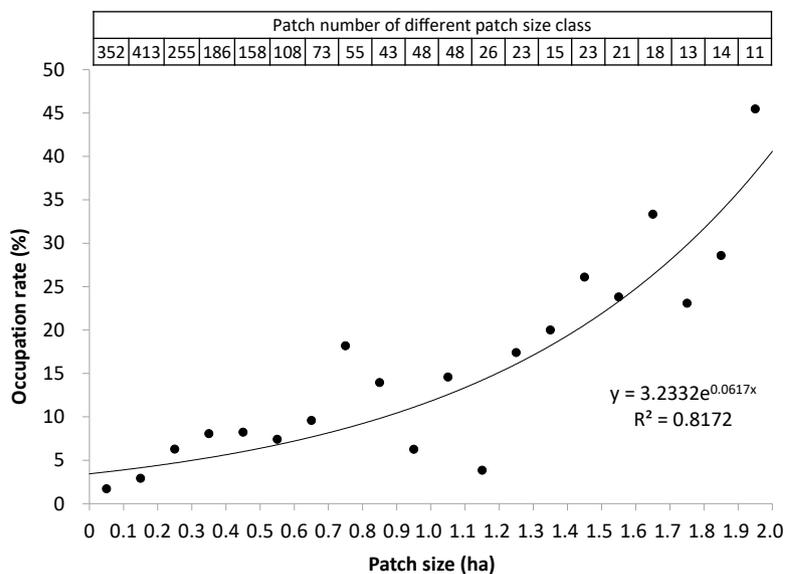
habitat management units and for making better habitat management decisions.

**Habitat fragmentation**

Numerous studies have reported the adverse effects of habitat fragmentation on amphibians, such as reducing species richness (e.g., Almeida-Gomes et al. 2016). For individual species, populations in fragmented habitat had a smaller population size and a lower genetic diversity compared to populations in the more continuous habitat (Johansson et al. 2007; Dixo et al. 2009). *Zhangixalus arvalis* resided in discontinuous habitat patches embedded within a matrix of less suitable habitats. We found that in our study site the degree of habitat fragmentation increased over time; specifically, both the number of small patches and the distance between patches increased (Table 3). As habitat connectivity deteriorated, the relative ease of movement between isolated habitat patches was reduced. Consequently, fragmentation reduced the chance of recolonization by dispersal and the probability of gene flow (Dixo et al. 2009). Although the dispersal capability of *Z. arvalis* has never been investigated, *Z. arvalis* adults had a small activity range (Hsieh 2004). The maximum dispersal distance of amphibians varied among species from < 20 m in *Leiopelma hochstetteri* (Tessier et al. 1991) to > 1 km in several amphibian species (reviewed by Smith and Green 2005). In some amphibians, juvenile dispersal plays a predominant role in population connectivity (e.g.,

Preisser et al. 2001; Rothermel 2004). Future work can focus on the dispersal capability of *Z. arvalis* and quantify the influences of habitat structure on gene flow and population connectivity using molecular genetic analysis (Cushman 2006). Furthermore, the increased interpatch distance due to fragmentation could also increase the risks of roadkill or predation when frogs move among isolated patches (Carr and Fahrig 2001). Lu (2005) reported that several female *Z. arvalis* were killed on roads. The potential effect of roadkill warrants further investigation.

In our study area, *Z. arvalis* likely formed a metapopulation, where the persistence of subpopulations in isolated patches was determined by the local extinction and recolonization (Smith and Green 2005). We found that the occupation rate of *Z. arvalis* decreased with decreasing patch size (Fig. 3). This suggested that habitat fragmentation affected the persistence of subpopulations in small isolated patches (Todd et al. 2009). For the common frog *Rana temporaria* in an agricultural landscape, its probability of occurrence was positively correlated with woodland surface (Boissinot et al. 2015). Vos and Chardon (1998) also reported that pond size had a positive effect on occupation probability in the moor frog *Rana arvalis*. Small population size and low genetic diversity in fragmented habitat could result in higher risks of genetic drift and inbreeding, and a lower evolutionary potential (Johansson et al. 2007; Pabijan et al. 2020). As a consequence, subpopulations in small patches had a higher extinction probability in contrast to subpopulations in large patches (Collins and



**Fig. 3.** Occupation rate of *Zhangixalus arvalis* in the Chiayi area, Taiwan, in different-sized woodland patches based on data obtained from 2014–2015. Habitat patches ≤ 2 ha were divided into 20 size classes at 0.1-ha intervals. The numbers on the top refer to the numbers of patches in each size class.

Fahrig 2017). In our study, although a small proportion of small-sized patches was occupied by *Z. arvalis*, without immigration of individuals from nearby patches, we expect that these subpopulations will eventually go extinct.

In addition to the aforementioned effects, habitat fragmentation could also affect amphibians through edge effects, such as highly fluctuating air temperatures, drier soils, lower relative humidity, and stronger winds (Cushman 2006). These edge effects could shorten the lifespan of temporary water bodies. Because adults of *Z. arvalis* have little cutaneous resistance to evaporative water loss (Liu and Hou 2012), and the survival of tadpoles depends heavily on temporary water bodies (Chen 2005), changes in microenvironments mediated by edge effects could potentially reduce the suitability of habitats.

### Conservation implications

With the threats from habitat modification, effective measures for conservation of *Z. arvalis* are needed. We suggest these conservation strategies. First, preserve large-sized woodlands, particularly bamboo plantations. Our results provided empirical occurrence records and a map of suitable habitat for *Z. arvalis* showing that occupation rates increased with increasing patch size (Fig. 3). These results can provide useful information for the authorities to determine strategic locations for habitat preservation or management. For example, habitat patches > 1.4 ha (occupation rate > 20%) and habitat suitability > 50% can be used as criteria to set priorities for habitat preservation.

Second, encourage farmers to participate in treefrog-friendly farmland practices. Because most of the bamboo plantations in our study area were private properties, farmers' attitudes towards preserving bamboo plantations are key to the success of *Z. arvalis* conservation. To increase farmers' willingness to participate in conservation efforts, an effective means is to increase their incomes. In the Yunlin area, subsidies given directly to farmers were used to maintain bamboo plantations. Unfortunately, the subsidy program failed because the farmers broke the agreement and changed their crop types to more profitable coffee and tangerines (Chang et al. 2008). Since 2018, the Taiwan Forestry Bureau Chiayi District Office has worked with a consulting team led by one of our co-authors (M.-S. Chuang) to promote eco-friendly agricultural practices in local communities in the Chiayi area to encourage farmers to preserve bamboo habitats. In this program, the governmental agency provided funds, and the consulting team held workshops to increase farmers' awareness of conservation and provide technical support

for eco-friendly agricultural practices. The participating farmers agreed to not use pesticides and to manage their bamboo plantations in ways that were friendly to *Z. arvalis*, such as maintaining a thick layer (3–5 cm) of litter on the ground and maintaining temporary water pools for  $\geq 18$  days. Currently, the consulting team is working to develop a treefrog-friendly label to promote the sale of bamboo shoots to increase farmers' revenue. By the end of 2020, 13 farmers had joined the program with a total area of 8.02 ha (M.-S. Chuang, pers. commun.).

Third, functional habitat connectivity to facilitate dispersal is crucial for recolonization of subpopulations in small isolated habitats and maintain the regional viability of *Z. arvalis* populations. Thus, on a relatively large scale, we suggest that corridors or stepping-stone habitats be established in the two regions that we identified where habitat connectivity could be lost due to habitat destruction (Fig. 2). Corridors or stepping-stone habitats can enhance structural connectivity among habitat patches (Crooks and Sanjayan 2006). If corridors or stepping-stone habitats were established, a long-term post-construction monitoring should be conducted to examine its effectiveness. On a relatively small scale, the increased interpatch distance might impede the dispersal of individuals. Empirical studies on dispersal capability of *Z. arvalis* and movement rates among patches will be useful to determine their dispersal threshold. Further study can also create a more detailed corridor map for the entire study area using corridor models (Sahlean et al. 2020).

Fourth, temperature and precipitation significantly influence the activity of *Z. arvalis* (Chen 2005). The success of breeding and metamorphosis of larvae depends on the availability and sustainability of water pools (Chen 2005). Water sources appear to be a critical environmental variable that affects the distribution of *Z. arvalis*. This is supported by our result that the "nearest distance to the river" was the most important environmental predictor in our simulations. In Taiwan, high precipitation during summer creates temporary rain water pools on the ground of woodlands and provides *Z. arvalis* with good lekking and breeding sites. Typhoons often bring heavy rains and sometimes floods, which were suggested to be important factors facilitating passive dispersal (Lu 2005). In the future, *Z. arvalis* might be threatened by changes in temperature, typhoon and precipitation patterns, moisture and hydroperiod associated with climate change (Li et al. 2013). Thus, farmers should be encouraged to manage habitats—specifically to increase shade cover—to generate litter substrate, and to maintain water pools to enhance water availability. In this study, we used SDMs to investigate the spatiotemporal changes of suitable habitat over

time. We also encourage future studies to use SDMs to predict changes in *Z. arvalis* populations and to monitor the effectiveness of conservation measures in response to climate change (Zellmer et al. 2020).

## CONCLUSIONS

The vast majority of studies that have investigated the effects of habitat loss and fragmentation on amphibians in agricultural landscapes have focused on ground-dwelling and pond-breeding species (e.g., Hansen et al. 2019; Jeliakov et al. 2019). Less attention has been paid to arboreal species. Our study focused on the endangered *Z. arvalis*, an arboreal tree frog that prefers woodlands, particularly bamboo plantations, to live, court, and breed. The changes in crop type from bamboo plantations to pineapple fields not only resulted in habitat loss, but also produced smaller and more isolated habitat patches. The result that the occupation rate decreased with decreasing patch size suggests that subpopulations in small isolated patches might have a relatively high risk of extinction. In agricultural landscapes, farmers might change crop types frequently to maximize their revenues. This could further jeopardize *Z. arvalis*, which are already threatened.

Recently, the pathogenic fungus *Batrachochytrium dendrobatidis* has caused extinction and population declines in a great number of amphibian species worldwide (O'Hanlon et al. 2018). Although *Z. arvalis* has been exempt from the ravages of this fungal disease thus far, threats such as habitat loss, habitat fragmentation, and climate change continue to threaten their populations' sustainability. Our results mapped the areas of suitable habitat loss and identified the potential gaps in habitat connectivity. To conserve *Z. arvalis*, we suggest preserving large-sized patches, encouraging farmers to adopt treefrog-friendly practices and enhancing water availability through habitat management, and to construct corridors or stepping-stone habitats in the regions that have lost habitat connectivity.

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