Anthropogenic habitat loss accelerates the range expansion of a global invader

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Abstract

**Aim:** Understanding the patterns and correlates of the range expansion of established alien species is crucial for predicting invasion impacts and developing effective control strategies. With accelerating globalization, it is key to identify the interactions of different global change processes, such as how land-use change may influence range expansion, yet empirical studies remain limited.

**Location:** Liuji Town, Jiangsu Province, China.

**Methods:** We first divided the study area into 128 grids with a resolution of 1 x 1 km and conducted visual encounter surveys over two years for a total of 492 water bodies to explore the establishment and range expansions of a global notorious invader, the American bullfrog *Lithobates catesbeianus* (Shaw, 1802) (= *Rana catesbeiana* (Shaw, 1802)) using generalized linear mixed models. Then, we investigated the residence time of the established bullfrogs in each water body based on a questionnaire survey. We quantified the habitat loss and range expansion of the past 30 years via GIS-based spatial analysis and explored their temporal dynamics using the breakpoint regression technique.

**Results:** We found that the area of suitable habitats was the most important variable positively related to the bullfrog establishment. There was a similar temporal trend of the range expansion and habitat loss, although the optimal time of habitat loss was slightly earlier than that of the great increase in bullfrog range expansion. Overall, the bullfrogs tended to expand faster with greater habitat loss after controlling for temporal non-independence.

**Main conclusions:** Our results demonstrated that loss of suitable habitats may facilitate invaders with faster range expansion to occupy the remaining limited resources. Alien species might thus accelerate invasions under human-induced land-use modifications in the era of global change. The time lag between range expansion and habitat loss is the golden window for preventing the spread of established alien species in disturbed habitats.
1 | INTRODUCTION

Invasive alien species (IAS) are homogenizing the biodiversity of our planet with high ecological, economic and public health impacts worldwide (Blackburn et al., 2019; Simberloff et al., 2013). Along the three main invasion stages of the “introduction-establishment-expansion” continuum (Blackburn et al., 2011; Richardson & Pyšek, 2012), range expansion after establishment is recognized as a key stage determining the magnitude of IAS impacts (Blackburn et al., 2011). Therefore, understanding the pattern and determinants of IAS range expansion is critically important to develop effective control strategies (Hastings et al., 2005; Neubert & Parker, 2004). For alien invertebrates, such as insects, great efforts have been made to estimate the range expansion rates of established alien populations, mainly owing to the relatively abundant monitoring data (Kadoya & Washitani, 2010; Roques et al., 2016). However, the overall quantification of alien species expansion rates has always been a challenge largely due to the lack of long-term spatiotemporal data on the dynamics of established alien populations and complex models for stochastic situations (Hastings et al., 2005; Kot et al., 1996), which can limit our ability to prevent and manage invasion impacts. It is particularly true for vertebrate invaders despite some successful examples on the invasive cane toad (Rhinella marina (Linnaeus, 1758)) in Australia based on long-term observation data or radio-tracked data (Lindstrøm et al., 2013; Phillips et al., 2006; Urban et al., 2008).

The dispersal of IAS is generally determined by a series of key characteristics of invaded communities (Blackburn et al., 2011; Richardson & Pyšek, 2012). These factors consist of abiotic environmental conditions (such as the availability and heterogeneity of suitable habitats), human activities and interactions with other native and co-occurring alien species (Duncan et al., 2003; Kolbe et al., 2016; Urban et al., 2008). A suitable habitat is a fundamental factor for the establishment of alien species, which often expand to more suitable habitats (Pyšek et al., 2010). Environmental heterogeneity among suitable habitats is also an important predictor variable of alien species range expansion (Melbourne & Hastings, 2009). For example, heterogeneous habitats can create many dispersal barriers, such as inhospitable corridors, slowing the dispersal of established populations of alien species (Liu et al., 2014; Tingley et al., 2013). However, these barriers may be circumvented by human-assisted jump dispersals (Wilson et al., 2009). Human activities can also increase range expansion by eliminating natural enemies and competitors (Banks et al., 2015). However, the effects of species interactions among native and alien species on invasion outcomes are typically very complex (Jackson, 2015; Liu et al., 2018) and depend on several covariants, such as relative population densities, functional equivalence and trophic positions (Ballari et al., 2016; Nyström et al., 2001). For instance, increasing evidence has emerged that a positive relationship exists between earlier alien species invasion and the probability of later alien species establishment according to the invasion-meltdown hypothesis (Adams et al., 2003; Redding et al., 2019), whereas “founder takes all” hypothesis predicts that earlier alien colonizers may fill available biotopes and prevent establishment of later migrants (Waters et al., 2013). Additionally, all these potential correlates, including habitat suitability, environmental heterogeneity and biotic interactions, might be strongly influenced by anthropogenic modification of land use, which may greatly influence the process of alien species invasions (Dukes & Mooney, 1999; Early et al., 2016). For example, disturbed habitats facilitate the establishment of alien species by decreasing native predators and competitors, thereby creating vacant niches that can be filled by invaders (Díez et al., 2012). The relationship between land-use change and species invasion outcome has thus been of particular concern recently due to the increasing degree of land-use change across the globe (Newbold et al., 2015). Nevertheless, at the range expansion level, except for large-scale modelling analyses (Ficetola et al., 2010), few field studies have explicitly examined the relationship between land-use change and range expansion of IAS across temporal scales. Furthermore, the natural dispersal pattern of established alien species might be confounded by some anthropogenic factors such as human intentional releases (Liu et al., 2012) and multiple introduction events (Liu et al., 2014). Therefore, it is key to control for these confounding effects to explore the natural expansion patterns of established alien species more accurately.

The American bullfrog Lithobates catesbeianus (Shaw, 1802) (= Rana catesbeiana (Shaw, 1802), hereafter the bullfrog) provides one ideal study species to address these scientific questions. First, its distinct loud call is very different from that of native amphibians in China, and the villagers around each invaded pond can estimate the approximate year when the bullfrog was first established (Li et al., 2011), providing a unique opportunity to estimate establishment time and expansion rate. Second, the invasion pathway of the bullfrog in China is clear (Liu et al., 2010) and primarily includes aquaculture for food and religious release activities (Liu & Li, 2009; Liu et al., 2012). We can thus select those regions with only one historical aquaculture event and without Buddhist temples to account for the potential influences of multiple introductions and human-assisted secondary introductions. Third, since the 1960s, when the bullfrog was introduced into China (Liu et al., 2010), China has been undergoing rapid development, and significant land-use changes have occurred, providing opportunities to explore the relationship between land modification and IAS range expansion. Finally, the bullfrog is a particularly troublesome invasive species because amphibians are arguably the most threatened vertebrate taxonomic group on the planet (Hoffmann et al., 2010), and their declines have been linked to human-assisted movement of alien species, such as the bullfrog and their pathogens (Liu et al., 2013; O’Hanlon et al., 2018).

KEYWORDS
biological invasion, global change, invasion success, invasive alien species, land-use change
Here, based on two-year field surveys and questionnaires, we conducted a detailed analysis of the patterns and correlates of the range expansion of the established bullfrogs in an invaded region of eastern China, where there is only one historical aquaculture event and no evidence of religious bullfrog releases. We also used remote sensing image information combined with the spatial analysis function in Geographic Information Systems (GIS) and the breakpoint regression technique to explore the role of land-use change on the observed variations in expansion patterns across years.

2 | MATERIALS AND METHODS

2.1 | Study species

The bullfrog *Lithobates catesbeianus* (Shaw, 1802) (= *Rana catesbeiana* (Shaw, 1802)) is an invasive frog species introduced to China in 1959 (Liu et al., 2010). Bullfrogs were widely distributed across the whole country in the 1990s and have now established naturalized populations in central, east and southwest China. Due to their great impacts on native amphibians through predation, competition, hybridization and transmission of notorious wildlife diseases, such as chytrid fungi (Kats & Ferrer, 2003; Kraus, 2015; Measey et al., 2016), bullfrogs have been listed as one of the world’s 100 worst IAS (Lowe et al., 2000).

2.2 | Study area

We conducted field surveys on water bodies in Liuji town (32°26′N, 119°15′E), a flat region of Yangzhou city, Jiangsu Province, eastern China (Figure 1). This study area is ideal to explore the spread of bullfrogs for the following reasons. First, there are diverse aquatic habitats, including paddy fields, irrigation channels, rivers and other aquatic habitats (Figure 1). For instance, there are many patchily distributed artificial ponds that were constructed to store water for rice

![Image](image_url)
cultivation, providing bullfrogs with potentially ideal habitats for establishment and dispersal corridors (Wang & Li, 2009). Second, the introduction history of bullfrogs in the study area is clear, starting with a failed aquaculture event in Yuqiao Reservoir (32°26′3.05″N, 119°16′21.31″E) in 1991 (G90 grid in Figure 1). All bullfrogs escaped from their enclosures, and no other farmers have raised bullfrogs since then. Finally, few Buddhist temples are located in the study area, and ceremonial animal release activities were not observed during the two years of our field surveys or collected from questionnaire surveys around each village (Text S1 and S2).

2.3 | Field survey

We divided Liuji town into 128 grids with a resolution of 1 km x 1 km through ArcGIS (ESRI), and we numbered the grids from 1 to 128 in order from north to south and west to east (Figure 1). A total of 492 water bodies that were randomly distributed among the 128 grids were surveyed using standard visual encounter surveys (Jaeger, 1994) in August and September of 2019 and 2020. The location of each water body was recorded using a hand-held GPS (Magellan eXplorist210) and mapped in ArcGIS. We categorized the water bodies as permanent lentic water bodies preferred by bullfrogs or other water body types (Wang & Li, 2009) and estimated the area of suitable bullfrog habitats in each grid using ArcGIS. After excluding inaccessible areas, two observers simultaneously searched line transects for bullfrogs, native frogs and crayfish (Procambarus clarkii (Girard, 1852)) and recorded the number of encountered individuals in each transect at night (19:00–22:00) with the aid of an electric torch. In addition, a dipnet was used to sample eggs, tadpoles and froglets in the water bodies along the transect for evidence of bullfrog establishment (Jaeger, 1994). The identification of native frogs was based on a guidebook of Amphibians of China (Fei et al., 1999). We also recorded any observations of human animal release activities to validate the natural dispersal assumption given the absence of temples in our study area.

2.4 | Questionnaire survey for bullfrog residence time

We obtained the approximate time of bullfrog establishment in invaded water bodies based on questionnaire surveys (Li et al., 2011). The questions were designed to address potential biases of interview surveys in ecological and conservation research (White et al., 2005, see Text S1). We interviewed at least two residents around each water body to obtain the information of the earliest time when they saw the bullfrog or heard calls of adult bullfrogs (Text S1). To guarantee the quality of the bullfrog residence time data, we obtained this information from middle-aged or older people who lived in the village before bullfrog aquaculture in Liuji town (the average age of the interviewees was 62.8, range: 50–75). In 57.82% (85/147) of the invaded water bodies, we obtained the same residence time from different interviewees (Text S2). For the 40.82% (60/147) of invaded water bodies for which the interviewees did not provide consistent time information (Text S2), we calculated the mean residence time. We assumed that the water bodies were invaded by bullfrogs for one year in the cases (1.36%, 2/147) when we were told that the water bodies were not invaded (Text S2), but we observed tadpoles or subadults of bullfrogs during our field surveys. In total, the residence times for bullfrogs in our study area ranged from 2 to 29 years with an average (± SE) of 14.3 years (± 0.34).

2.5 | Satellite image interpretation of land-use changes in the study area

We obtained satellite image data from China’s Multi-Period Land Use Land Cover Remote Sensing Monitoring Dataset (CNUCC). This dataset is one of the most accurate remote sensing monitoring data products of land use in China and has been widely used in national land resource surveys, hydrology and ecological research (Ning et al., 2018). Since bullfrog introductions occurred in the 1990s, we interpreted all satellite images in 1990, 1995, 2000, 2005, 2010, 2013, 2015, 2018 and 2020 when the satellite data were available based on the Project and Union functions of ArcGIS. The land-use types of each of the 128 grids were divided into 5 categories: (1) paddy fields, (2) reservoirs and ponds, (3) settlement residential areas, (4) drylands and (5) forests and bushes (Figure 1).

2.6 | Statistical analyses

To explore the correlation of range expansion with changes in bullfrog habitats, we first used generalized linear mixed models (GLMMs) to evaluate the role of permanent still water bodies [i.e. suitable habitats identified in previous studies (Maret et al., 2006; Wang & Li, 2009; Werner & Mcpeek, 1994)] in influencing the establishment of naturalized bullfrog populations in our study area. We conducted GLMM analyses with a binomial error structure and a logit link function using the lmer function in the lme4 package (Bates et al., 2015) in R (Version 4.0.3, R Development Core Team, 2020), with the presence of a feral bullfrog population in each of the 128 grids as the binary response variable, and included the area of suitable habitats quantified by the sum of the paddy field, reservoir and pond areas, the presence of the red swamp crayfish, the number of native frog species and settlement residential area of local people as the independent variables. These variables have all been identified as potentially important factors influencing bullfrog establishment in invaded ranges in China (Liu et al., 2018). In particular, the residential area of local people can reflect the potential influence of human activities on bullfrog establishment and range expansion. In addition, we also added the number of water bodies surveyed in each grid as a random effect to account for the potential pseudoreplication such that there may be a higher probability of bullfrog establishment in grids with more...
water bodies (Bolker et al., 2009). We applied multi-model inference based on information theory (Akaike’s information criterion, AIC) to evaluate the relative importance of the different predictor variables using the dredge and model.avg functions in the MuMIn package (Bartoń, 2020).

To quantify the rate of range expansion of the bullfrog and explore its temporal trend with years, we applied breakpoint regressions using the segmented package in R (Muggeo et al., 2017). We fitted a generalized linear regression and two breakpoint regression models including the left-horizontal regression and two-slope regression that are widely used in ecological and biogeographical studies, and an AIC-based approach was used to identify the best model and optimal breakpoint year when the substantial change of the bullfrog range expansion occurred (Chen et al., 2020; Lomolino & Weiser, 2001; Wang et al., 2018). The regression slope was quantified as the expansion rate of the bullfrogs, which is regarded as a robust method to measure a reasonable expansion rate when the explicit historical dispersal route is commonly not available (Preuss et al., 2014). Furthermore, in order to explore the relationship between the range expansion of the bullfrogs and the rate of habitat modification, we first quantified the proportion of suitable habitats in each grid for different years using GIS spatial analyses based on satellite image interpretation and found that the area of suitable habitat decreased every year with intensive anthropogenetic pressures. For instance, although a small number of previously terrestrial lands have been transformed into reservoirs and ponds (9.78%), a majority of suitable habitats were transformed into settlement residential areas to satisfy the needs of local human population increases. Therefore, we calculated the loss of suitable bullfrog habitats for each grid with available satellite data for 1995, 2000, 2005, 2010, 2013, 2015 and 2018 relative to that in 1990. We then explored the temporal dynamics of habitat loss over time using the linear regression and breakpoint regression (see above), and applied the AIC-based approach to identify the optimal breakpoint year when the rate of habitat loss increased sharply and compared it with the estimated breakpoint of the bullfrog range expansion. We also analysed the correlation between the average expansion distance of the bullfrog and the average loss of suitable habitats for each grid with bullfrog establishment data over time using the Pearson correlation analysis. There may be a temporal non-independence issue given that the positive correlation between expansion distance and habitat loss may result from their synchronous increases over time. We therefore conducted further separate analyses for individual years along east–west–north–south directions to test whether a close association existed between expansion distance and spatial variation in habitat loss within the same year by combining data along four directions for each individual year. This supplementary analysis was focused on three years (i.e. 2000, 2005, and 2010), when relatively more bullfrog establishment data were available to estimate and compare the expansion distances in four directions (but bullfrog establishment data were only available for three directions for the year 2010).

3 | RESULTS

3.1 | Establishment and range expansion pattern of bullfrog populations

Our field surveys showed that bullfrogs established feral populations in 29.9% of the waterbodies (147/492), accounting for 50% (64/128) of all grids. Based on different arrival times, we observed a trend of further spread to peripheral areas with a 5-year interval (Figure 1). The population with the largest dispersal distance appeared in grid 3, which was 8.70 km from the original aquaculture site, where the bullfrog was established in 2015 based on the interview survey (Figure 1, Text S2).

3.2 | Correlates of bullfrog population establishment

Model averaging analysis based on GLMMs after accounting for the number of water bodies in each grid showed that the suitable habitat area in each grid was indeed the most important factor that was positively correlated with the presence of bullfrog established populations in our study area (relative importance value based on Akaike weights, $W_p$: 0.98, GLMM estimate + SE: 4.25 ± 2.10, $p = .044$). In addition, bullfrogs were likely to establish populations in grids with the occurrence of red swamp crayfish ($W_p$: 0.92, estimate + SE: 1.19 ± 0.46, $p = .011$). However, we did not find an important effect of the residential area of local people ($W_p$: 0.42, estimate + SE: 2.61 ± 2.65, $p = .329$) or native frog richness on the occurrence of established bullfrog populations ($W_p$: 0.39, estimate + SE: -0.34 ± 0.30, $p = .2561$).

3.3 | Expansion rate of bullfrog populations and its relationship with habitat loss

Model selection analysis based on AIC$_c$ showed that breakpoint regressions performed better than the generalized linear regression (Table 1, Figure 2). The best model was observed for the two-slope breakpoint regression with the breakpoint time of the greatest increase of the bullfrog expansion occurring around the year of 2009 (Table 1a, Figure 2a). Since then, there was a faster bullfrog expansion on average of 0.36 km/year according to the regression slope of the second segment of the two-slope breakpoint regression mode (Table 1a, Figure 2a) than that before 2009 (on average 0.20 km/year, Table 1a, Figure 2a). The best model quantifying the loss of suitable habitat (i.e. permanent still water bodies) over time was observed for the left-horizontal regression with the optimal breakpoint time of suitable habitat loss (approximately 2005, Table 1b, Figure 2b) slightly earlier than that of the greatest increase in the distance of bullfrog range expansion.

Overall, the average expansion distance of the established bullfrogs increased with the average loss of suitable habitats for all
residence years (Figure 3a; Pearson $r^2 = .711; p < .001$). After we accounted for potential temporal non-independence, separate analyses focusing on three individual years along four directions (i.e. east, west, north and south) showed consistent results (Figure 3b). Specifically, an increasing trend of the average expansion distance of the established bullfrogs with the average degree of suitable habitat loss for each individual year was noted (Figure 3b for the year of 2000, $r^2 = .840$; 3c for 2005, $r^2 = .554$; and 3d for 2010, $r^2 = .833$).

### 4 | DISCUSSION

By combining fieldwork, questionnaire surveys, GIS technique and breakpoint regressions, we quantified the factors that influenced the spatial patterns of bullfrog established populations, evaluated the approximate expansion rate and linked the observed expansion pattern with temporal land-use change. Our results support previous concerns on the faster dispersal of the pioneer invasive populations observed from cane toads in Australia (Lindström et al., 2013; Phillips et al., 2006; Urban et al., 2008), implying the potential generality of accelerating the invasion velocity of IAS. Nevertheless, whether the bullfrog invasion front populations in our study area have also evolved similar rapid shifts in morphology (Phillips et al., 2006) and immune responses (Brown et al., 2015) with dispersal as seen in cane toads remains to be explored in the future.

Compared with previous studies focusing on environmental and landscape variables (e.g. Urban et al., 2008), our main aim was to explore the potential interactions between land-use change and range expansion. Previous modelling studies using large-scale historical land-use data predicted the spread of invasive bullfrogs in Europe and identified that land-use change could significantly increase model predictive performance (Ficetola et al., 2010). Our present study provided further novel evidence on the important role of land-use change in promoting the spatial expansion of the bullfrog based on field survey and GIS analyses at the local scale. We observed a largely similar temporal dynamic of the bullfrog expansion and habitat loss and a positive relationship between the average expansion distance and the degree to which suitable habitats decreased, indicating that IAS may accelerate invasion rates in disturbed environments to occupy the remaining limited resources. This result enforced previous concerns on the potential positive interactions of habitat loss and alien species invasions (Didham et al., 2007). We also found that there might be a time lag between bullfrog range expansion and the loss of suitable habitat, which is reasonable, as bullfrogs may need some time to respond to changing environments (Crooks, 2005).

We found that the probability of bullfrog establishment was higher in water bodies with the presence of invasive crayfish, supporting the invasion-meltdown hypothesis (Adams et al., 2003) and previous findings on the positive relationship between the distribution of these co-occurring aquatic invaders (Bissattini et al., 2018; Liu et al., 2018). Therefore, recent crayfish introductions may be an alternative explanation of the bullfrog expansions observed in our study. However, we argued that this might not be the truth. Our study area was near the city of Nanjing, which is the first city in which crayfish were introduced in 1929 long before the introduction of the bullfrog in China (Cai et al., 2010). Previous studies have confirmed that crayfish are widely distributed in all major water bodies across the country, especially in the middle and lower reaches of the Yangtze River, where the study area is located (Wang et al., 2010). Therefore, considering the time and site of its historical introduction, we hypothesize that there is a high likelihood that crayfish invasion in Liuji town occurred much earlier than the bullfrog introduction in the 1990s.

We detected a negative relationship between bullfrog establishment and native frog richness although this effect is relatively

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**TABLE 1** Results of linear and breakpoint regression models exploring the variations in the bullfrog range expansion (a) and the rate of suitable habitat loss (b) over time

| Models formula | Parameter estimate | Model selection |
|----------------|-------------------|-----------------|
| (a) Bullfrog range expansion | | |
| $D = c + z_1 \cdot Y$ | $c = -479.837$, $z_1 = 0.241$ | $K = 3$, $AIC_c = 413.914$, $\Delta_i = 4.1788$, $w_i = 0.110$ |
| $D = c + (Y > T) \cdot z_1 \cdot (Y - T)$ | $c = 2.444$, $z_1 = 0.290$, $T = 2001.218$ | $K = 4$, $AIC_c = 435.790$, $\Delta_i = 26.056$, $w_i = 0.000$ |
| $D = c + (Y \leq T) \cdot z_1 \cdot Y + (Y > T) \cdot [z_1 \cdot T + (z_2 - z_1) \cdot (Y - T)]$ | $c = -396.615$, $z_1 = 0.200$, $z_2 = 0.360$, $T = 2009.289$ | $K = 5$, $AIC_c = 409.735$, $\Delta_i = 0.000$, $w_i = 0.890$ |

| (b) Rate of habitat loss | | |
| $P = c + z_1 \cdot Y$ | $c = -635.954$, $z_1 = 0.318$ | $K = 3$, $AIC_c = 7936.552$, $\Delta_i = 3.355$, $w_i = 0.120$ |
| $P = c + (Y > T) \cdot z_1 \cdot (Y - T)$ | $c = 0.054$, $z_1 = 0.473$, $T = 2004.450$ | $K = 4$, $AIC_c = 7933.197$, $\Delta_i = 0.000$, $w_i = 0.644$ |
| $P = c + (Y \leq T) \cdot z_1 \cdot Y + (Y > T) \cdot [z_1 \cdot T + (z_2 - z_1) \cdot (Y - T)]$ | $c = -43.236$, $z_1 = 0.022$, $z_2 = 0.473$, $T = 2004.784$ | $K = 5$, $AIC_c = 7935.212$, $\Delta_i = 2.015$, $w_i = 0.235$ |

Notes: The performance of each model in each section was assessed by using the Akaike information criterion based on a small sample size ($AIC_c$). The best model that predicted the time threshold of range expansion and habitat loss is marked in bold. Abbreviations: c, intercept; D, the range expansion distance for Table 1a; K, number of estimable parameters; P, rate of habitat loss for Table 1b; T, breakpoint; w, Akaike weight; Y, year; z, slope; $\Delta_i$, Akaike difference.
weak based on the model averaging analyses, generally supporting the impacts of the invasive bullfrog on native frogs but may have complex effect with the presence of the other co-occurring invaders such as the alien crayfish here, which may have density-dependent and complex interspecific interactions that can generate uncertain outcomes on native species (Bissattini et al., 2018; Liu et al., 2018).
However, given that our study was based on only correlative analysis and we did not have long-term population dynamic data on the native species after the bullfrog invaded, this result could not distinguish whether the bullfrogs were responsible for the decline in local species or whether bullfrogs were more likely to colonize habitats where there was low native frog richness due to decreased biotic resistance, which warrants further investigation.

Our results suggest that settlement residential areas exert minimal influence on the occurrence of the established bullfrog populations, implying that human activities may not have great effects on the invasion outcome of the bullfrogs in our study area, which further validated our initial assumption that our study could largely reflect the natural dispersal process. Finally, when comparing the range expansion rate over time, a potential issue was the possibility of a population density-dependent dispersal rate with residence time (Enfjäll & Leimar, 2009). We thus compared the densities of the bullfrog populations in each grid between the first and the last 15 years when the bullfrog started to represent a faster range expansion based on the breakpoint regression and found that there was no significant difference in bullfrog density between these two time stages (Kruskal–Wallis test, p < .05), indicating that the observed increase of the bullfrog expansion rate might not be due to the variations in population densities over time.

It has been clear that close interactions exist among different components of global environmental changes (Dukes & Mooney, 1999). The present study reinforced this argument by demonstrating that the degradation of suitable habitats may not only facilitate establishment but also accelerate the spread of established populations to more recipient habitats, which may further exacerbate the impacts of invasive species on native species in human-modified habitats. Our findings contribute to a deeper understanding of how habitat modification may influence invasion dynamics, which could enable better prediction and management of established alien species in response to ongoing land-use modifications during the Anthropocene. Importantly, the observed time lag between the accelerating range expansion and suitable habitat loss indicates that we may have a golden window for managing the dispersal of established alien species under land-use change, which may be key to develop early prevention and control strategies against alien species invasions.

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CONFLICT OF INTEREST

The authors declare no competing interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All relevant data supporting the results are available from the Dryad: https://datadryad.org/stash/share/xFBE29kFPP8BuEbUzwFtP...V8zuzK0Uqqo44GR6U, https://doi.org/10.5061/dryad.2bqg83bqf.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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