The Implementation of Habitat Destruction Methods That Promote Native Survival Under Invasion

Yinghui Yang
Southwest Jiaotong University
Haoqi Liu (✉ liuhaoqi1986@yeah.net)
Zhejiang Agriculture and Forestry University https://orcid.org/0000-0003-1897-8691

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The implementation of habitat destruction methods that promote native survival under invasion

Yinghui Yang[a], Haoqi Liu[b,*]

[a]School of Mathematics, Southwest Jiaotong University, Chengdu 611756, China, ORCiD IDs: https://orcid.org/0000-0002-3139-6277;

[b]College of Mathematics and Computer Science, Zhejiang Agriculture and Forestry University, Hangzhou 311300, China[1], ORCiD IDs: https://orcid.org/0000-0003-1897-8691;

Abstract: Controlling invasive alien species invasion and maintaining the survival of native species have attracted increasing attention, and habitat destruction can be used to achieve these aims. However, it remains unclear whether and how to promote the long-term survival of indigenous species facing invaders through the use of habitat destruction. In this study, we developed a spatially explicit simulation model and exposed invaders and residents from this model to habitat destruction with different properties. The results showed that (1) introducing habitat destruction could promote the long-term survival of native species facing invaders; however, the promoting effect of habitat destruction occurred only over a period of time after introduction, and habitat destruction substantially weakened indigenous species before that. (2) Intermediate levels of habitat destruction were the most beneficial to the protection of native species.

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[*]Corresponding author at: College of Mathematics and Computer Science, Zhejiang Agriculture and Forestry University, 666 Wusu Street, Linan District, Hangzhou 311300, China. Tel.: +17502018855.

E-mail address: liuhaoqi1986@yeah.net (H.Q. Liu).

(3) Even if not considering the proportion of destroyed habitats, introducing spatially dispersed habitat destruction at an earlier time and shortening the interval between two habitat destruction events were very beneficial to the protection of residents. These insights can help facilitate the protection of residents under invasion by adjusting the implementation method of habitat destruction.

Keywords: Invasion inhibition, habitat destruction and fragmentation, native resistance, competitive invasion, survival advantage

1. Introduction

Biological invasions have attracted much attention from the political, scientific, and social public and are considered one of the most difficult environmental problems (Wolfe 2002; Blackburn et al. 2019; Pysek et al. 2020). Invaders can suppress resident populations, decrease local richness, and alter ecosystem processes (Liao et al. 2008; Vila et al. 2010; Wardle et al. 2011). Part of the key drivers of these influences are the competitive superiority of invaders (Ortega and Pearson 2005; Maron and Marler 2008) and their greater ability to disperse in recipient communities (Pysek and Richardson 2008; Murray and Phillips 2010; Flores-Moreno et al. 2013). Specifically, when exotic species, especially those that are functionally similar to native species, arrive at the native community, they might have great niche overlaps with natives and hence pose as strong competition (Maron and Marler 2008; Hänfling et al. 2011). Due to their advantage of utilizing resources, the abundance of the resident populations will dramatically decline. By establishing in empty habitat or available space, exotic species may inhibit the seedling germination of natives (Crawley et al. 1999; Yurkonis and

Meiners 2004). Given the dramatic invasion-caused impact on native species, ecological studies should focus more on issues of protecting native populations.

Habitat destruction has been documented to play certain roles in the outcome of biological invasions (With 2004; Newbold et al. 2015). Normally, habitat destruction is expected to enhance biological invasions (Alpert et al. 2000; Marvier et al. 2004; Alofs and Fowler 2010; Kumschick et al. 2015). For example, exotic species with better dispersal abilities were assessed as benefitting more from habitat destruction (With 2004; Pearson and Dawson 2005); additionally, for native western grey tree squirrels, tree canopy loss provided a competitive advantage to alien tree squirrels (Jessen et al. 2018). Moreover, recent field surveys of the American bullfrog *Lithobates catesbeianus* indicated that habitat destruction has facilitated the expansion and occupation of invaders among the remaining limited resources (Wang et al. 2021).

Although habitat destruction could promote the invasion process to some degree, this influence would not always occur at each site. In some cases, it could even inhibit the expansion of invaders and be utilized as a conservation practice for biodiversity. For example, Bartuszevige et al. (2006) empirically explored woodlot invasion by *Lonicera maackii* and found no possible relationship between landscape connectivity and invasion. In central Texas, fragmented patches of herbaceous vegetation were shown to slow the spread of invaders with limited dispersal (Alofs and Fowler 2010). When habitat destruction intensity increases to a sufficient level, species may persist (Dytham 1995). In addition to field studies, Liu et al. (2012) built a metapopulation model and suggested that habitat destruction could inhibit invaders when there was competition pressure and habitat destruction. Other theoretical models have provided similar insights and have indicated that habitat destruction helps to inhibit the spread of invasive populations (Brown et al. 2012; Barron et al. 2020; Bozzuto et al. 2021). Therefore, habitat destruction is regarded as possibly being effective in preventing the invasion process.

In fact, totally understanding the relationship between habitat destruction and invasion processes is a challenge (Alofs and Fowler 2010). The above literature has paid the most attention to the effects of invader attributes, but native population resistance has largely been ignored. Total area loss, patch isolation, or frequent exposure to edge effects, which arise from habitat destruction, could initiate long-term changes in any population (Haddad et al. 2015; Hertzog et al. 2019), even indigenous and exotic populations. Some species benefit from habitat destruction, while others may suffer from it (Henle et al. 2004; Rybicki et al. 2020). Research on the use of habitat destruction for the management of biological invasion should examine the full response of all species in the system, especially native and/or endangered species. Additionally, considering only habitat destruction on one factor (e.g., amount levels) is not enough. The influence of habitat destruction is complicated. For example, random landscape removal would decrease richness more than when area is lost in spatial aggregation (Yin et al. 2021). Habitat destruction could also be referred to as a dynamic process (Fahrig 2017; May et al. 2019). As a result, it should generally be considered as the combined consequence of multiple distinct factors, such as destruction intensity, extent, frequency, spatial configuration of habitat removal, or beginning time of destruction events (Kinzig and Harte 2000; Roxburgh et al. 2004; Didham et al. 2012; Rybicki et al. 2020).

Considering the above contents of the review, we established a spatially explicit simulation model to explore the influence of habitat destruction on invasion expansion and native survival. The simulation model is a simple two-species competition system. One of these species is regarded as the invader and is assigned invasion dominant attributes, such as competition invasion or survival rate superiorities. Destruction events are then introduced into this competition system. By calculating the equilibrium conditions across parameter ranges and considering the inhibited properties of habitat destruction through four aspects, including the spatial structure, interval between two destructing events, total destruction proportion, and introduction time, we mainly attempted to address the following two questions: (1) does habitat destruction prevent resident extinction; (2) what are the properties of habitat destruction in relation to the long-term survival of native species facing invaders?

2. Models and Methods

We first simulated the invasion processes, and the invasion model included two species. Species 1 was defined as an invasive alien species that had superior competitive abilities or a higher ability to occupy empty habitats. In addition, we introduced habitat destruction events into the invasion model.

2.1 Invasion model

The species dynamics were simulated by a spatially discrete and a time-discrete process. We assumed a two-dimensional landscape and scape with 100×100 cells and periodic boundary conditions. System dynamics occurred on this landscape. Individuals possessed limited dispersal abilities and only interacted with their nearest neighbours (von Neumann neighbourhood with $z = 4$). There were three states of habitat: 0, 1, and 2, which represented empty cells, cells occupied by invasive alien species and cells occupied by resident species, respectively. The parameter descriptions are provided in Table 1.

At each time step, the individuals of species i naturally die at a natural rate m_i (i =1, 2) (Hiebeler et al. 2016). Parameters α_{ii} and α_{ij} quantify extra deaths caused by intra- and interspecific competing forces, respectively, and values with a higher magnitude indicate more intense competition. Moreover, the sign of α_{ij} represents the direction of species competition. If species i has a competing force on species j, we set $\alpha_{ij} > 0$, and $\alpha_{ij} = 0$, implying no interaction. The final competition superiority was decided by combined items, such as net competing force and neighbouring individuals of their population. When offspring were sent to neighbouring sites, they could not survive on the already occupied sites. We set the colonization rate of species i as r_i, which was still proportional to their individual number among the nearest neighbours (see Table 2 for details). Details of the transition rules can be found in Table 2. We ran the dynamic system until all global densities reached equilibrium.

Table 1 Parameters and variables

Parameter	Description	Value
m_i	Mortality rate of species i $(i = 1,\ 2)$	0.01
r_2	Colonization rate of native species 2	0.1
r_1	Colonization rate of alien species 1	er_2
e	Dispersal advantage of native species 1	$e \in [1,3]$
α_{ii}	Intraspecific competitiveness within population of species i $(i = 1,\ 2)$	0.01
α_{21}	Interspecific competitiveness from species 2 to species 1	0.03
α_{12}	Interspecific competitiveness from species 1 to species 2	$\theta\alpha_{21}$
θ	Competition advantage of alien species 1	$\theta \in [1,3]$
D_{μ,t_ζ}	Proportion of destructed habitats at step t_ζ for random habitat destruction	
D_{ν,t_ζ}	Proportion of destructed habitats at step t_ζ for contagious habitat destruction	
$D_{\mu,\mathrm{end}}$	Total proportion of destructed habitats for random habitat destruction	
$D_{\nu,\mathrm{end}}$	Total proportion of destructed habitats for contagious habitat destruction	
x_μ	Probability that each intact habitat becomes destructed at each step for random habitat destruction	0.025
x_{i,t_ζ}	Probability that each habitat in group i $(i = 0,1,\dots,8)$ becomes destructed at step t_ζ for contagious habitat destruction	

n_{μ,t_ζ}	Total number of intact habitats at step t_ζ for random habitat destruction
n_{i,t_ζ}	Total number of habitats in group i $(i = 0,1,\ldots,8)$ at step t_ζ for contagious habitat destruction
t_η	Introduction time of habitat destruction
t_κ	Interval between two habitat destruction events
β_i	A sequence of constants which was used to describe the degree to which habitat destruction is contagious, and $i = 0,1,\ldots,8$

Table 2 Updating probabilities of cellular automation from the states along the rows to the states along the columns.

	Empty 0	**Species 1**	**Species 2**
Empty 0	$1 - r_1\frac{\sum sp_1}{z} - r_2\frac{\sum sp_2}{z}$	$r_1\frac{\sum sp_1}{z}$	$r_2\frac{\sum sp_2}{z}$
Species 1	$\Delta_1 := m_1 + \alpha_{11}\frac{\sum sp_1}{z} + \alpha_{21}\frac{\sum sp_2}{z}$	1-Δ_1	—
Species 2	$\Delta_2 := m_2 + \alpha_{12}\frac{\sum sp_1}{z} + \alpha_{22}\frac{\sum sp_2}{z}$	—	1-Δ_2

Note: $\sum sp_i$ $(i = 1, 2)$ is the total number of species *i* among the nearest z number of neighbours.

2.2 Habitat destruction process

To simulate the habitat destruction process, we built discrete habitat destruction models in time and space, i.e., a random and contagious habitat destruction model. As described in Section 2.1, the landscape included 100×100 cells with equal area and shape. Initially, all cells were considered to be intact, but if habitat destruction occurred in an intact cell, it became destroyed. The models were defined as follows.

For random habitat destruction, each intact cell was destroyed with equal and fixed probability x_{μ} (the value is given in Fig. 1). The proportion of destroyed cells at step t_{ζ} ($t_{\zeta} = 0,1,2,\ldots$) is denoted by $D_{\mu,t_{\zeta}}$, and it is calculated as follows:

$$D_{\mu,t_{\zeta}} = 1 - \left(1 - x_{\mu}\right)^{t_{\zeta}},\ D_{\mu,0} = 0. \tag{1}$$

For contagious habitat destruction, we used the global forest data reported by Boakes et al. (2010) to build the model. At step t_{ζ}, the proportion of destroyed cells is denoted by $D_{\mu,t_{\zeta}}$. According to the Moore neighbourhood (Boakes 2010), all intact cells were divided into nine groups, and each cell in group i ($i = 0,1,\ldots,8$) had i destroyed neighbours. If an intact cell had more destroyed neighbours (i.e., i was larger), the probability that the cell becomes destroyed was higher. Thus, if $x_{i,t_{\zeta}}$ represents the destruction probability of group i at step t_{ζ}, we obtained $x_{i,t_{\zeta}} < x_{j,t_{\zeta}}$ ($i < j$). To compare the two types of models, we assumed that all intact cells were destroyed at a constant rate as follows:

$$n_{\mu,t_{\zeta}} x_{\mu} = \sum_{i=0}^{8} n_{i,t_{\zeta}} x_{i,t_{\zeta}}. \tag{2}$$

where $n_{\mu,t_{\zeta}}$ denotes the total number of intact cells at step t_{ζ} for random habitat destruction, and $n_{i,t_{\zeta}}$ denotes group i when contagious habitat destruction occurs. In addition, we obtained the following:

$$D_{\mu,t_{\zeta}} = \left(\sum_{j=1}^{t_{\zeta}} \sum_{i=0}^{8} n_{i,j} x_{i,j}\right)/10000. \tag{3}$$

where 10000 is the total number of cells in the landscape (see Section 2.1). From Equation (2), we obtained the values of $x_{i,t_{\zeta}}$ (see “Supplementary results” for details). The processes described by the random and contagious habitat destruction model are given in Fig. 1.

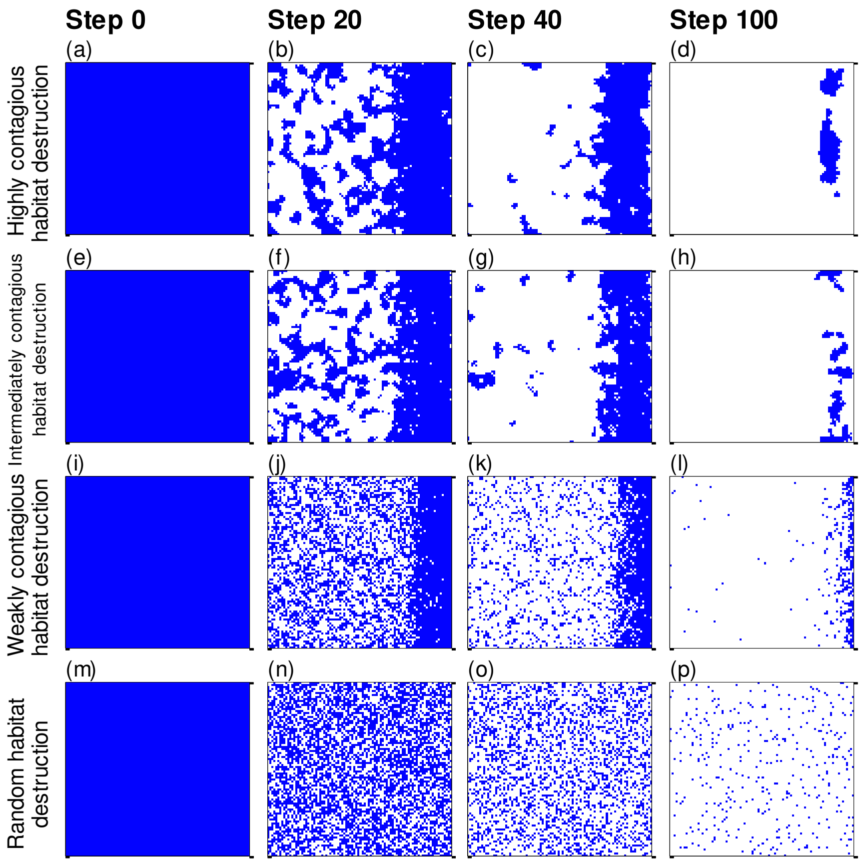

Fig. 1 Examples of highly, intermediately, and weakly contagious habitat destruction and random habitat destruction processes. The blue areas are intact cells, and the white areas are destroyed cells. Parameters: $x_{\mu} = 0.025$, $\beta_0 = 1$. Highly contagious habitat destruction: $\beta_1 = 200$, $\beta_2 = 800$, $\beta_3 = 1{,}501$, $\beta_4 = 3{,}000$, $\beta_5 = 10{,}000$, $\beta_6 = 41{,}200$, $\beta_7 = 130{,}001$, and $\beta_8 = 560{,}000$. Intermediately contagious habitat destruction: $\beta_1 = 19$, $\beta_2 = 65$, $\beta_3 = 90$, $\beta_4 = 207$, $\beta_5 = 490$, $\beta_6 = 1{,}976$, $\beta_7 = 4{,}980$, and $\beta_8 = 16{,}789$. Weakly contagious habitat destruction: $\beta_1 = 2.16$, $\beta_2 = 2.454$, $\beta_3 = 2.248$, $\beta_4 = 2.643$, $\beta_5 = 3.377$, $\beta_6 = 3.733$, $\beta_7 = 4.876$, and $\beta_8 = 5.556$.

2.3 Implementation method and data processing

We set the species death rates as $m_1 = m_2 = 0.01$. The intrinsic growth rate of native species 2 was $r_2 = 0.1$. By giving the value of the intrinsic growth rate of invader species 1 proportional to native species 2, namely $r_1 = e * r_2$ $(e \in [1, 3])$, we could control the gradient of growth superiority. A larger value of e means a larger difference between the two species, and $e = 1$ corresponds to equal spreading abilities. The other important parameters of the system are the intraspecific and interspecific competition coefficients between species i and j α_{ij} $(i, j = 1,2)$, and $\alpha_{11} = \alpha_{22} = 0.01$. We fixed the competing force from native species 1 to invader species 2 $\alpha_{21} = 0.03$ and assumed that invaders had competitive superiority $\alpha_{21} < \alpha_{12} = \theta * 0.03$ $(\theta \in [1,3])$. When θ=1, α_{21} equals α_{12}, i.e., competitive symmetry occurred.

The simulation processes of invader and resident dynamics and habitat destruction were implemented as follows: (1) we set the parameter values; (2) we let invaders and residents dynamically change in the landscape; (3) if introducing habitat destruction, we let invaders and residents change in the destroyed landscape until step 3000; (4) if not introducing habitat destruction, we let invaders and residents continue changing until the final step 3000. More details about the implementation are provided in the "Supplementary results".

To eliminate stochasticity, ten independent replicated simulations were run, and we made the figures in Section 3 based on the 10 replications. Specifically, the parameter range where indigenous species densities were positive in the equilibrium state for at least 6 replications was the species coexistence region, and the other parameter value cases were considered native extinction. The mean density for residents was measured from the 10 replicated simulations. For the proportion of species or cells in the neighbours of residents, we also measured the mean among the 10 replicated simulations. The relative size of the parameter coexistence area is the ratio of the parameter range of invaders that native species can survive under invasion in at least 6 replicates to the whole parameter range.

3. Results

In Section 3.1, we investigated whether habitat destruction could enhance the probability of survival for native species. In Sections 3.2-3.4, we investigated the optimal measures for promoting the long-term survival of indigenous species based on the spatial structure of habitat destruction, the interval between two destruction events, the introduction time of habitat destruction, and the proportion of destroyed habitat.

3.1 Habitat destruction can enhance native survival facing invaders

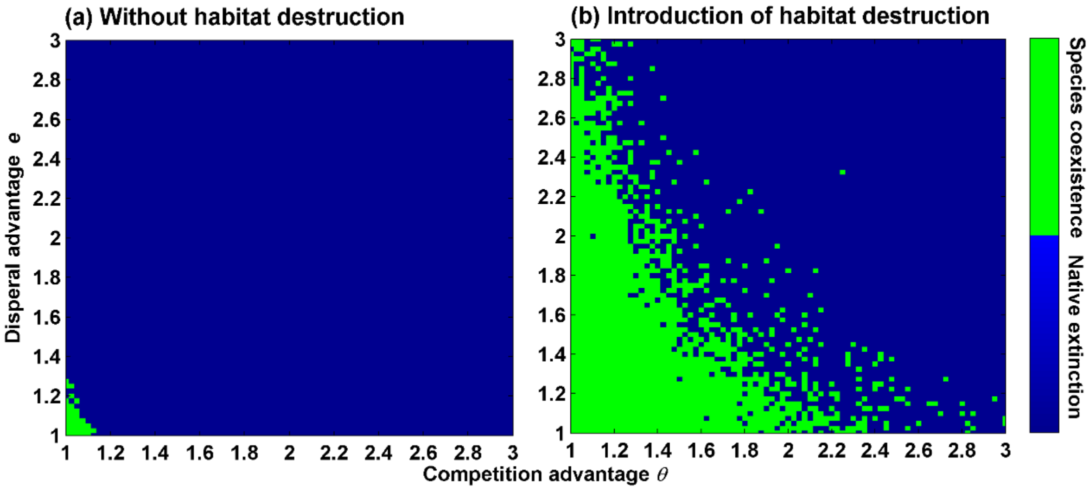

Fig. 2 Habitat destruction can protect residents from extinction due to invasion. Panels (a-b) show the parameter (axis of dispersal advantage e and competition advantage θ of invaders) ranges for species coexistence, namely, native species can coexist with alien species (see Section 2.3 for definition) and native extinction, respectively, when not introducing (a) or introducing (b) random habitat destruction. The parameters of the invasion model are listed in Table 1. Most of the parameters for the habitat destruction model are shown in Fig. 1, and the other parameters are $D_{\mu,\text{end}} = 50\%$, $t_{\eta} = \text{step } 150$, and $t_{\kappa} = 10$ steps.

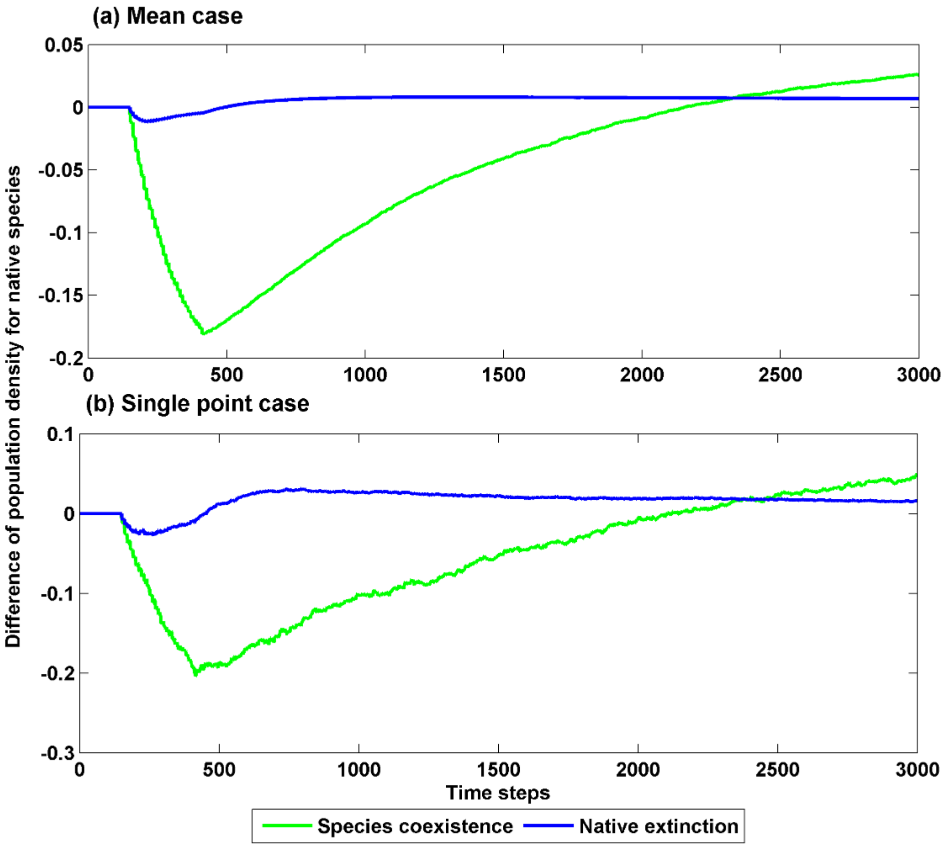

Fig. 3 Habitat destruction is adverse to residents for quite a long time after introduction. The curves in the figure show how the density difference of native species 2 with and without habitat destruction changes along the time axis. Green curves present the native populations that can coexist with invaders, while blue curves correspond to the natives who suffer from invasion-caused extinction. Panels (a) and (b) are the results of the mean (see Section 2.3 for definition) and a certain point ($\theta = 1$, $e = 1.05$ (green curve) or $\theta = 1.2$, $e = 1.3$ (blue curve)) case, respectively. We then introduced random habitat destruction. The parameters of the invasion model are shown in Table 1. Most of the parameters for the habitat destruction model are shown in Fig. 1, and the other parameters are $D_{\mu,\mathrm{end}} = 50\%$, $t_\eta = \mathrm{step}\ 150$, and $t_\kappa = 10$ steps.

Fig. 2a illustrates that if habitat destruction is absent, when competition advantage θ and dispersal advantage e are larger than approximately 1.15 or 1.2, the invasive alien species will drive the native species to extinction. However, if habitat destruction is introduced, e.g., at 150 time steps, even when the competition advantage θ and dispersal advantage e reach approximately 2.3 or 2.8, respectively, the native species still possibly survives (Fig. 2b). Therefore, habitat destruction can protect native species from extinction to some extent. This result is also in line with previous studies that have suggested that habitat destruction can be used to control biological invasions (Alofs and Fowler 2010; Barron et al. 2020; Bozzuto et al. 2021).

Protecting native species from extinction under the threat of invaders (Fig. 2) does not mean that habitat destruction is beneficial for all ecological processes of native species. Thus, we analysed whether habitat destruction is always beneficial for residents. Fig. 3a shows that compared with the case without habitat destruction, the native species density decreased due to destruction (curves located below zero) over a long period. This degree of decline was much more obvious for the residents that could coexist with invaders without habitat destruction (green curve) than for the others (blue curve). Additionally, Fig. 3a demonstrates that after a long enough time period, habitat destruction could finally allow the resident density to exceed the density in the case without destruction. This trend was still more significant for the native species that were strong enough to coexist with invaders (green curve). As a result, after the introduction of habitat destruction, the density of residents immediately declined, and the promoting effects of habitat destruction on residents occurred only after a long period. The above results from a parameter value case (Fig. 3b) also support this trend.

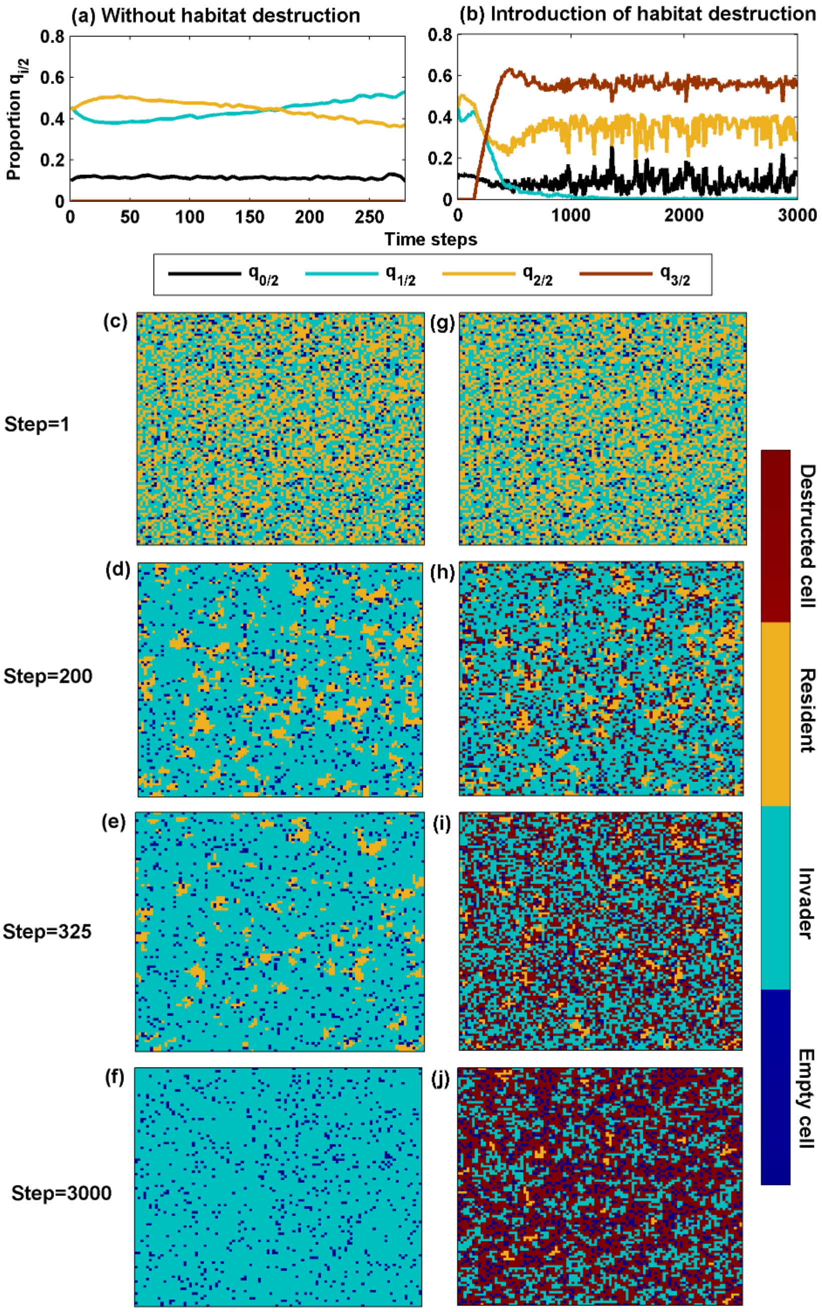

Fig. 4 Habitat destruction can separate invaders from native species. Panels (a-b) show the relationships between the proportions of empty habitats ($q_{0/2}$), invaders ($q_{1/2}$), native species ($q_{2/2}$), or destroyed habitats ($q_{3/2}$) in the neighbours of native species (see Section 2.3 for definition) that can coexist with invaders when introducing habitat destruction and time steps when not introducing habitat destruction (a) or when introducing habitat destruction (b). For the residents and habitats facing invaders with $\theta = 1.2$ and $e = 1.3$, panels (c-j) show the spatial distribution of species and

habitats when habitat destruction was not introduced (c - f) or when it was introduced (g - j). Here, we introduced random habitat destruction. Most of the parameters for the habitat destruction model are shown in Fig. 1, and the other parameters are $D_{\mu,\mathrm{end}} = 50\%$, $t_{\eta} = \mathrm{step}\ 150$, and $t_{\kappa} = 10$ steps. The parameters of the invasion model are shown in Table 1.

In Fig. 4, we analysed the detailed spatial evolution of each population. As shown, the main way in which habitat destruction protects native species from extinction when facing invaders is by separating invader individuals from resident individuals. Specifically, without habitat destruction, native species would be largely surrounded by alien species. We determined that the proportion of invasive individuals among native neighbours was approximately 40% and even up to 55% at its peak (Fig. 4a). Thus, the native population experienced many competing forces. However, if habitat destruction was introduced (Fig. 4b), this proportion gradually declined to almost 0, and the proportion of destroyed habitats in the neighbours of native species gradually reached approximately 60%. That is, compared with the situation in which habitat destruction was not introduced, if introducing habitat destruction, alien invaders would be gradually replaced by destroyed habitats, thereby gradually separating alien invaders from residents. In this case, alien invaders could neither compete to occupy the empty cells neighbouring native species nor directly increase the mortality rate of native species (see Section 2.1 for how invaders drive native species to extinction). The spatial distributions of residents, invaders, and destroyed habitats could further demonstrate that the destroyed habitats gradually encompassed residents and separated out invaders from residents (Fig. 4c - j).

The reasons why the native species density declined slightly during a short time period are that once habitat destruction occurs in an intact habitat, the individual living in it immediately dies (see Section 2.3 for this process), and thus, the native species is hurt. During habitat destruction there was a period of time from the appearance of the first destruction event to the last event. After this time, the positive effects of habitat destruction (i.e., separating out invaders from native species) appeared and enhanced the long-term survival of native species.

3.2 Random habitat destruction can better enhance native survival

In this section, we explored how the spatial structure of habitat destruction influenced the long-term survival of native species facing invaders. Fig. 5a illustrates that when introducing highly contagious habitat destruction, if the competition advantage θ and dispersal advantage e of invaders are larger than approximately 1.3 or 1.5, respectively, the native species have a small chance of survival. If the habitat destruction is less contagious, the native species facing the invasive alien species with competition advantage θ 1.4 or 2 and dispersal advantage e 1.7 or 2.8 still have a chance to survive (Fig. 5b and c). If random habitat destruction is introduced, even when the competition advantage θ and dispersal advantage e reach approximately 2.3 or 3, respectively, the native species can also survive (Fig. 5d). From highly contagious habitat destruction to random habitat destruction, the spatial distribution of destroyed habitats became more dispersed (Fig. 1). As a result, if habitat destruction is more dispersed, it will more vigorously promote the long-term survival of native species.

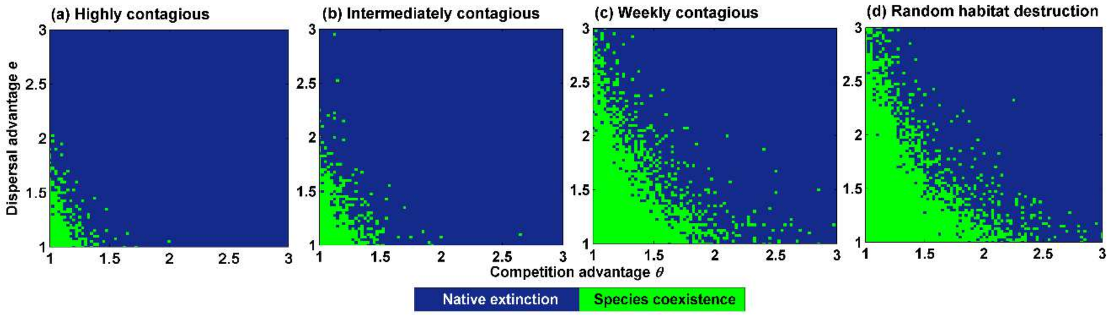

Fig. 5 Introducing random habitat destruction will better protect native species facing invaders. Panels (a-d) show whether native species can coexist with invasive alien species (see Section 2.3 for definition) based on the dispersal advantage e and competition advantage θ of the invasive alien species when introducing highly (a), intermediately (b), and weakly (c) contagious habitat destruction and random habitat destruction (d). The parameters of the invasion model are shown in Table 1. Most of the parameters for the habitat destruction model are shown in Fig. 1, and the other parameters are $D_{\mu,\mathrm{end}} = D_{\nu,\mathrm{end}} = 50\%$, $t_\eta = \text{step } 150$, and $t_\kappa = 10$ steps.

3.3 Habitat destruction will protect the residents better if it can work earlier

In this section, we calculated the relative proportion of coexisting area in the whole parameter range space and investigated how it changed with the interval between two habitat destruction events and the introduction time of habitat destruction. Fig. 6 shows that when the interval between two destruction events was very long (i.e., 40 steps), the relative size of the parameter coexistence area was only approximately 0.1, and if the interval decreased, the parameter coexistence area increased rapidly, irrespective of whether the introduction time was earlier or later. The top even reached approximately 0.67 when the introduction time was very early (i.e., earlier than step 40), and the bottom was also larger than 0.2 when the introduction time was very late (i.e., step 200). In addition, Fig. 6 demonstrates that when the interval was 1, the relative size of the parameter coexistence area sharply increased from approximately 0.2 to approximately 0.67 if the introduction time decreased from a very late step (step 200) to a very early step (step 5). The parameter coexistence area also increased with decreasing introduction time in other interval value cases. As a result, if the interval between two habitat destruction events is shorter or if the introduction time of habitat destruction is earlier, the native species has a greater chance of survival under invasion.

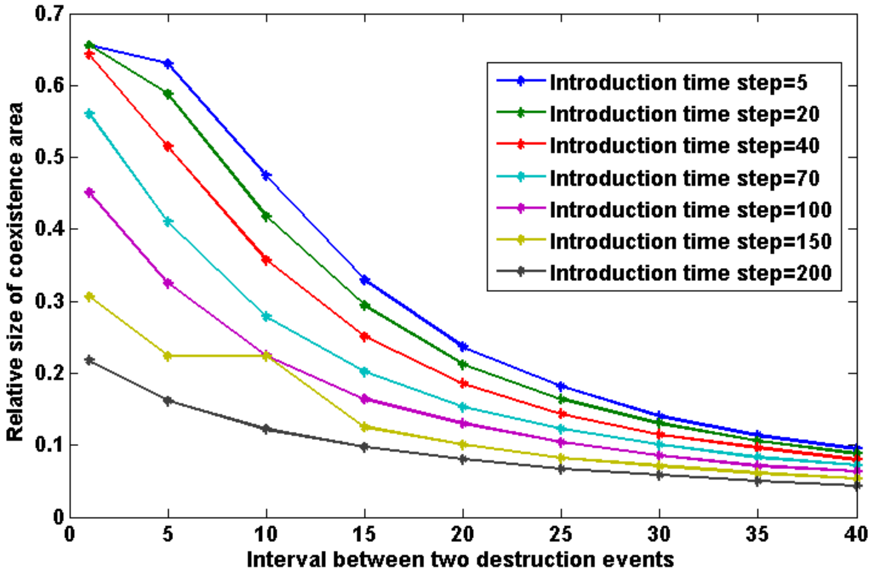

Fig. 6 Habitat destruction will better enhance the survival of native species when the interval between two destruction events is shorter or when the introduction time is earlier. The panel shows the relationships between the relative size of the parameter coexistence area (see Section 2.3 for definition) and the interval between two destruction events or introduction time when introducing random habitat destruction. Curves with different colours correspond to various introduction time step cases. The parameters of the invasion model are shown in Table 1. Most of the parameters for the habitat destruction model are shown in Fig. 1, and the other parameter is as follows: $D_{\mu,\text{end}} = 50\%$.

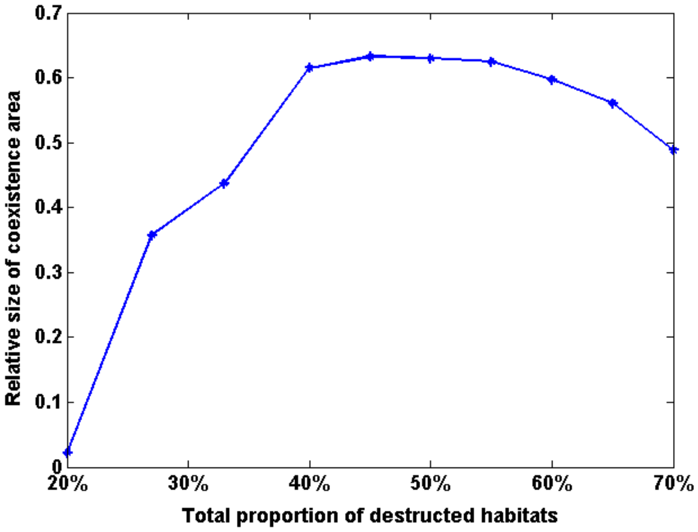

Fig. 7 An intermediate level of habitat destruction can better protect residents from extinction under invasion. The panel shows the relationship between the relative size of the parameter coexistence area (see Section 2.3 for definition) and the proportion of the destroyed habitats when introducing random habitat destruction. The parameters of the invasion model are shown in Table 1. Most of the parameters for the habitat destruction model are shown in Fig. 1, and the other parameters are t_η = step 5 and $t_\kappa = 6$ steps.

3.4 The intermediate level of habitat destruction has a better protection effect

In this section, we explored how the proportion of destroyed habitat influenced the survival of native species facing invaders. Fig. 7 illustrates that when the proportion of destroyed habitat was very low (approximately 20%), the relative size of the parameter coexistence area was less than approximately 0.02, and if the proportion of destroyed habitat increased, the parameter coexistence area also increased and reached a maximum value (approximately 0.62) when the proportion of destroyed habitat was intermediate (approximately 45%). It then decreased and was already less than approximately 0.5 when the proportion of destroyed habitat was very high (approximately 70%). As a result, if introducing an intermediate level of habitat destruction, native species will obtain the best protection.

4 Discussion

By building an invasion model and habitat destruction model, we exposed residents and alien invaders to different types of habitat destruction. The results suggest that habitat destruction is a key factor influencing the survival of indigenous species. Specifically, after the introduction of habitat destruction, although the residents became weakened during quite a long time, habitat destruction could still promote the coexistence of residents with alien invaders. An intermediate level of habitat destruction was the most beneficial to maintaining the long-term survival of indigenous species. Even if the proportion of destroyed habitat remained constant, the survival of indigenous species was greatly influenced by habitat destruction. If habitat destruction was more dispersed, residents had a higher chance of survival. Decreasing the interval between two habitat destruction events could better promote the coexistence of residents with alien invaders, and introducing habitat destruction at an earlier time was more beneficial for the long-term survival of residents.

In this study, we could not find any evidence that habitat destruction could enhance the competition or dispersal abilities of native species. Moreover, compared with not introducing habitat destruction, residents were harmed first over the long term after introduction (Fig. 3). However, habitat destruction could still promote the long-term survival of residents by gradually separating alien invaders from residents (Fig. 3) so that the harm of alien invaders to residents gradually decreased and eventually disappeared. In addition, separating alien invaders from residents could explain why the habitat destruction with the following properties could protect resident better: the proportion of destroyed habitat was intermediate (Fig. 7), the destroyed habitat was dispersed in the invaded range (Fig. 5), habitat destruction was introduced at an earlier time, and the interval between two habitat destruction events was very short (Fig. 6); these properties of habitat destruction may better separate alien invaders from residents. These results also suggest that habitat destruction may have positive effects on biodiversity, although habitat destruction has been identified as a major threat to biodiversity conservation (Pimm and Raven 2000; Gonçalves-Souza et al. 2020; Dri et al. 2021). As a result, we need to study the effect of habitat destruction on biodiversity from a more comprehensive view.

Previous studies have focused on how habitat destruction affects invaders (Bartuszevige et al. 2006; Didham et al. 2007; Achury et al. 2021), and even if invaders and residents were exposed to habitat destruction, these studies only suggest that the spread of invaders will be slowed (Alofs and Fowler 2010) and that the density of residents remaining in undisturbed habitats will increase (Bolger et al. 2008). We explored whether habitat destruction could enhance the long-term survival of residents when invaders and residents were simultaneously exposed to habitat destruction. The results indicated that habitat destruction could maintain the long-term survival of residents by separating alien invaders from residents, but this influence occurred only part of the time after the introduction of habitat destruction. Furthermore, we investigated how to protect local species by adjusting the method of habitat destruction and found that the intermediate level of habitat destruction should be dispersed in the invaded range. Additionally, if habitat destructed was introduced at an earlier time and if the interval between habitat destruction events was shorter, the protective influence was stronger , which was in contrast with previous studies that focused only on whether habitat destruction could maintain the survival of local species (Alofs and Fowler 2010; Liu et al. 2012). In addition, most previous studies have used spatially random habitat destruction models (Brown et al. 2012; Liu et al. 2012), and although spatial heterogeneity has been introduced in some previous models (With 2004; Kinezaki et al. 2010), these models are static in time. Therefore, when and in what order habitat destruction should occur has not been investigated in these studies (Kinezaki et al. 2010; Liu et al. 2012). However, the processes of habitat destruction are dynamic in time and spatially non-random (Boakes et al. 2010), and as we have shown, habitat destruction will significantly influence local species under invasion.

Several of our results add weight to previous studies. Previous studies have suggested that habitat destruction can inhibit the invasion process (Liu et al. 2012; Barron et al. 2020). Our findings that habitat destruction reduces indigenous species extinction risk driven by invasive alien species (Fig. 2 and 3) offer support for this hypothesis. For the indigenous species under invasion, after the occurrence of habitat destruction, the density in the undisturbed habitats was higher than before (Bolger et al. 2008). Our findings found that, compared with not introducing habitat destruction, habitat destruction led to an increase in the density of indigenous species over a period of time after introduction (Fig. 3), and this result offered support for this hypothesis.

Previous results have emphasized the importance of considering the spatial structure of habitat destruction when investigating alien species invasion and have suggested that spatially dispersed habitat destruction is adverse to the spread of invasive alien species (With 2004). Our study suggests that spatially dispersed habitat destruction can better promote the long-term survival of indigenous species facing invaders (Fig. 3).

There are some interesting directions in which our study could be extended. First, we included only one indigenous species in this study. In nature, alien invaders always pose threats to many indigenous species and can even threaten a whole ecosystem (Cybèle et al. 2021; Zubek et al. 2022). Thus, we need to extend our model to a multispecies system in future researcher. Additionally, in this study, the invasive alien species could invade successfully due to its stronger dispersal and competition abilities. Moreover, alien species can spread rapidly and seriously threaten indigenous species by preying on or living on local species (Chalkowski et al. 2018; Taillie et al. 2021), and they sometimes form mutualistic relationships with certain residents (Xu and Chen 2021). Therefore, we will introduce these characteristics into the invasion model and study the effects of habitat destruction on the survival of residents in the future. Finally, but most importantly, much of the invasiveness of invasive alien species comes from its rapid evolution in the new environment (Novak 2007; Prentis et al. 2008). After introduction, environmental pressures, founder effects, genetic drift, and other factors drive alien species to evolve rapidly (Lee 2002; Colautti and Lau 2015; Hagan and Gloag 2021). During these processes, many alien species can adapt to the environment of the invaded range, strengthen dispersal abilities, and gain a competitive advantage over indigenous species (Hänfling and Kollmann 2002; Qin et al. 2013; Szűcs et al. 2017). As a result, we will introduce an evolution to this invasion model and study how habitat destruction affects the evolution of invasive alien species, and then we will study how these effects influence the long-term survival of indigenous species.

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Data availability: Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

Declarations

Conflict of interest: The authors declare that they have no conflict of interest.

Consent to participate: All authors consent in participate in this manuscript.

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Supplementary Files

- Supplementaryresults.docx