

Effect of complex landscape geometry on the invasive species spread: invasion with stepping stones

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Abstract

Spatial proliferation of invasive species often causes serious damage to agriculture, ecology and environment. Evaluation of the extent of the area potentially invadable by an alien species is an important problem. Landscape features that reduces dispersal space to narrow corridors can make some areas inaccessible to the invading species. On the other hand, the existence of stepping stones – small areas or ‘patches’ with better environmental conditions – is known to assist species spread. How an interplay between these factors can affect the invasion success remains unclear. In this paper, we address this question theoretically using a mechanistic model of population dynamics. Such models have been generally successful in predicting the rate and pattern of invasive spread; however, they usually consider the spread in an unbounded, uniform space hence ignoring the complex geometry of a real landscape. In contrast, here we consider a reaction-diffusion model in a domain of a complex shape combining corridors and stepping stones. We show that the invasion success depends on a subtle interplay between the stepping stone size, location and the strength of the Allee effect inside. In particular, for a stepping stone of a small size, there is only a narrow range of locations where it can unblock the otherwise impassable corridor.

Keywords: invasion blocking; dispersal corridors; diffusion-reaction model; Allee effect

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1 Introduction

Invasive species are known to be a major problem in ecology resulting in significant biodiversity loss worldwide [25, 78] and causing serious problems for agriculture, forestry and fishery worth billions of dollars annually [43, 70]. For these reasons, biological invasion has been a major focus of intense empirical and theoretical research for several decades [20, 73, 92] with the number of papers growing with time nearly exponentially [74]. In particular, a variety of invasion scenarios have been identified [37, 39, 69, 85] and considerable progress has been made in understanding how various factors can affect the rate and pattern of species spread into space [57]. Having that said, due to the high complexity of the phenomenon (cf. [77]) many questions remain open and many issues are lacking clarity [14].

Factors affecting the spread depend on the spatial and temporal scales at which the phenomenon is considered. In particular, this bears upon the role of the environmental heterogeneity. Much of the theoretical research has been concerned with invasive spread occurring either in large spatially-uniform areas or in an environment with a small-scale heterogeneity (e.g. in the form of environmental noise). Relevant modelling frameworks are given by reaction-diffusion equations [36, 55, 64, 67, 85, 86, 90], stochastic models [54, 56] including stochastic reaction-diffusion equations [28, 58, 89], and integral-difference equations [46, 48, 63].

Whichever particular model is used to study the invasive spread, it is usually considered in an unbounded space hence neglecting the effect of domain boundaries. However, this assumption of the environmental heterogeneity is restricted to a certain spatial scale and ceases to be valid when the spreading alien population approaches the limits of the corresponding geographic range. On a larger scale, invasive spread can be considered in a fragmented, ‘discrete’ environment where disjoint habitats are connected by dispersal; relevant modelling framework includes coupled map lattices [16, 41, 59] and networks [82].

Interestingly, the intermediate case of environmental heterogeneity occurring on a ‘not too large’ spatial scale, e.g. where the typical spatial size of the heterogeneity is the same as the typical scale of the spreading alien population (e.g. as is given by the variance of the dispersal kernel) has been rarely considered (but see [30, 31]). In particular, the effect of habitat’s boundaries on the invasive species spread remains poorly understood, especially in case of a nontrivial landscape geometry. Meanwhile, in a somewhat more general ecological context, the importance of the boundaries and the habitats shape for the population dynamics is widely recognized [8]. In our recent work, we addressed the above problem by considering invasive spread in a dumbbell-shaped domain where two large habitats are connected by a narrow passage or corridor and showed that the effect of the corridor can be nontrivial and counterintuitive [3]. In this paper, we consider a spatial system with a more complex geometry where the corridor is not uniform but includes a patch with different properties. In case the environment inside the patch is more favourable for the population (e.g. resulting in a higher growth rate or lower mortality

rate) than the rest of the corridor, such a patch can play the role of a ‘stepping stone’ for the invading population [7, 40, 42, 79].

The main goal of this study is to reveal the relation between the ecologically meaningful factors such as the stepping stone patch size, location, and the environment quality inside the patch that can hamper or promote invasive species spread in a complex landscape. The paper is organized as follows. In Section 2, we introduce our modelling framework and consider the effect of stepping stones in a simple one-dimensional system. In Section 3, we consider the effect of stepping stones in a hypothetical two-dimensional H-shaped domain. Last section provide discussion and conclusions.

2 Stepping stone in 1D case

In order to make an inceptive insight into some generic properties of invasive spread with stepping stones, we begin with simple one-dimensional (1D) system.

2.1 Model

We consider a single-species reaction-diffusion model where the local population growth is hampered by the Allee effect. In the 1D space, the model is given by the following equation [55, 62, 91]:

$$\frac{\partial u(x, t)}{\partial t} = \kappa \frac{\partial^2 u}{\partial x^2} + \gamma u(K - u)(u - b(x)), \quad (2.1)$$

where u is the population density of the alien species at position x and time t , κ is the diffusion coefficient, γ is a coefficient quantifying the population growth rate, K is the carrying capacity and b is the measure of the strength of the Allee effect to which we will refer as the Allee threshold [55].

The number of parameters in Eq. (2.1) can be decreased by choosing dimensionless variables:

$$\tilde{u} = \frac{u}{K}, \quad \tilde{x} = x \sqrt{\frac{\gamma K^2}{\kappa}}, \quad \tilde{t} = t \gamma K^2.$$

Equation (2.1) then takes the following form:

$$\frac{\partial u(x, t)}{\partial t} = \frac{\partial^2 u}{\partial x^2} + \hat{\gamma} u(1 - u)(u - \beta(x)), \quad (2.2)$$

where tildes are omitted for the sake of notation simplicity. Here $\beta = b/K$ is the normalized, dimensionless Allee threshold, and $\hat{\gamma}$ is a dimensionless coefficient. In the rest of this section, $\hat{\gamma} = 1$; we keep this factor for convenience, its meaning will become clear in Section 3.3. The Allee effect is called weak for $-1 < \beta \leq 0$ and strong for $0 < \beta < 1$ [91]. In the corresponding nonspatial case, i.e. Eq. (2.2) without the diffusion term, the system has three steady states in the case of strong Allee effect (stable states $u = 0$ and

$u = 1$ and unstable $u = b$) but only two in case of the weak Allee effect (stable $u = 1$ and unstable $u = 0$).

In case the population dynamics is considered in a spatially uniform environment, β is a constant parameter. In an unbounded space, the generic solution of Eq. (2.2) relevant to biological invasion (i.e. for appropriately chosen initial conditions) is then a travelling population front [55, 62] connecting the lower stable steady state $u = 0$ to the upper stable steady state $u = 1$; see Fig. 1. Invasion is successful (the front propagates towards the areas where the invasive species is absent, i.e. to the right in Fig. 1) if $\beta < 0.5$ and invasion fails (the population front retreats, i.e. propagates to the left in Fig. 1) if $0.5 < \beta < 1$ [62]. Below we will refer to the case $\beta > 0.5$ as a ‘very strong’ Allee effect. In case the spatial domain is bounded but sufficiently large, strictly speaking the travelling front solution of Eq. (2.2) is not valid any more but it provides “an intermediate asymptotics” [6]: a good approximation of the actual solution (for relevant initial and boundary conditions) for the time range when the front is sufficiently far away from the domain boundaries.

In the present study, in order to account for the effect of environmental heterogeneity, we consider β to be a function of space. More specifically, we consider the system where the spatial domain is split into a succession of several subdomains or habitats – say, Habitats A, B, C, D and E (see Fig. 2) that differ by their quality. We assume that the quality of the environment is quantified by a single parameter, i.e. by the strength of the Allee effect. Correspondingly, Habitat X is described by the Allee threshold β_X and by its length L_X , $X = A, \dots, E$, where $L_A + L_B + L_C + L_D + L_E = L$ and L is the overall length of the domain. We mention it here that a similar spatial design is often seen in studies on biological invasions in real-world systems, e.g. see [5, 9, 33].

In our choice of values β_X , we focus on the situation where the invasive species in its spread has approached a ‘bad’ area with unfavorable conditions (environment of poor

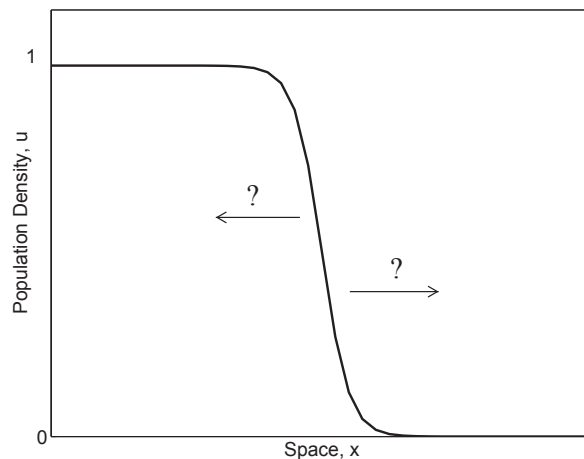


Figure 1: Travelling population front as the generic solution of Eq. (2.2) in a uniform unbounded space. The direction of the front propagation (shown by the arrows) depends on the value of β , as is emphasized by the question marks: the front propagates to the right for $\beta < 0.5$ (successful invasive spread) and to the left for $0.5 < \beta < 1$ (species retreats, invasion failure).

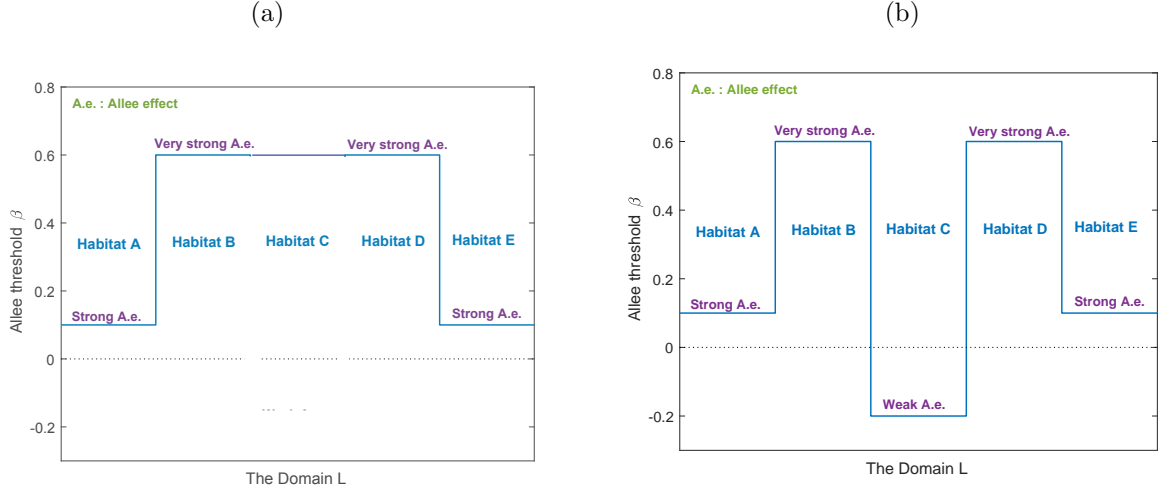


Figure 2: Sketch of the domain structure: (a) a wide ‘barrier’ of unfavourable environment (with a very strong Allee effect, $0.5 < \beta < 1$), as given by combined Habitats A & B & C, separates the invaded Habitat A from potentially invadable but inaccessible Habitat E behind the barrier; (b) the same as in (a) but now with a ‘stepping stone’ of favourable environment (Habitat C) in the middle of the barrier.

quality) where the Allee effect is very strong, $0.5 < \beta < 1$; see combined habitats B, C and D in Fig. 2a. In case the length of this unfavorable area is small, i.e. smaller than a certain critical value [66], the propagating population front will eventually overcome the bad area (sometimes subject to a considerable delay [65]) and continue spreading at the other side, i.e. into favourable Habitat E. In case the length of the unfavorable area is larger than the critical value, the propagating population front will stop at the interface between Habitats A and B, even that the environment behind this barrier is favourable again [66]. The question that we are concerned here with is how this situation may change if there is a domain with favorable conditions (e.g. a weak Allee effect, $\beta < 0$) inside the unfavorable area, see Habitat C in Fig. 2b, to which we refer as the ‘stepping stone’ of invasion.

We assume that the invasive species spreads from left to right; correspondingly, for the initial condition, we consider the situation that the invasive species is present at its carrying capacity in Habitat A but absent from all other habitats, that is

$$u(x, 0) = 1 \quad \text{for} \quad 0 \leq x \leq L_A, \quad u(x, 0) = 0 \quad \text{for} \quad L_A < x < L. \quad (2.3)$$

For the conditions at the external domain boundaries, we consider the zero-flux Neumann condition at the left-hand side boundary and the Dirichlet-type zero function at the right-hand side boundary:

$$\frac{\partial u(0, t)}{\partial x} = 0, \quad u(L, t) = 0. \quad (2.4)$$

2.2 Simulation results

Equation (2.2) with $\beta(x)$ defined as a piecewise-constant function (cf. Fig. 2) was solved by finite differences². The steps of the numerical grid were chosen sufficiently small to avoid numerical artifacts and it was checked that the results do not change with a further decrease of the grid step sizes.

Having performed extensive simulations for various parameter values, we have identified three essentially different invasion regimes that are shown schematically in Fig. 3. In Case 1, the population stops at the boundary between Habitats A and B. The population is at approximately its carrying capacity in A but fast decays to zero outside of Habitat A. In Case 2, the population spills over to Habitat C and establishes there at the population density approximately equal to the carrying capacity, but is blocked at the boundary between Habitats C and D, hence never spilling over to Habitat E (except for an exponentially thin tail). In Case 3, the population first overcomes unfavorable Habitat B and establishes itself in favorable Habitat C (stepping stone) and then eventually spills over to favorable Habitat E. We mention here that, depending on parameter values there may be minor variation in the above scenarios, e.g. the density profile shown in Case 2 may not have the trough or, on the contrary, the density profile shown in Case 3 may have a trough located in Habitat D. Since our main goal is to distinguish between the successful invasion (population overcomes the bad area) and the invasion failure (popu-

²Equation (2.2) was solved in each of the habitats separately and the solutions were then matched together using the conditions of continuity of the function and of the flux at the boundaries separating the habitats.

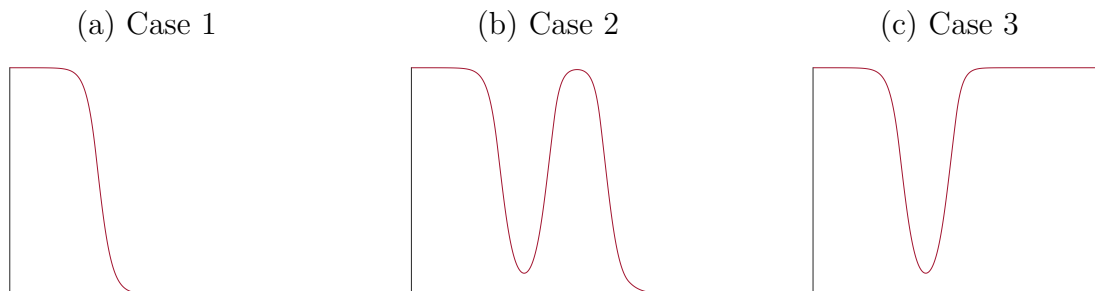


Figure 3: Invasion scenarios in the hypothetical landscape with a ‘stepping stone’ inside the unfavourable area; the solid red curve shows the population density. (a) Invading population is blocked at the interface between habitats A and B. This happens if either L_B is sufficiently large or the Allee effect is very strong in Habitat B (i.e. β_B is close to one) and the conditions are not sufficiently good in the stepping stone Habitat C (β_C is not small enough). (b) Invading population passes through unfavourable Habitat B and establishes in favourable Habitat C but cannot spill over to Habitat E. This happens if either L_D and/or β_D are sufficiently large. (c) Invading population spills over the gap to Habitat E. This happens when neither of L_D or β_D is too large.

lation is blocked by the bad area), here we do not pay much attention to those relatively minor details of the population profile.

We consider L_C and β_C as controlling parameters of the problem and make a more detailed insight into how the properties of the stepping stone Habitat C affect the dynamics of the invasive spread. Our specific goal is to reveal for what parameter values the blocked invasion (Case 1 in Fig. 3) changes to successful invasion (Case 3 in Fig. 3). Apparently, the invading population cannot spill over to Habitat E behind the barrier before establishing in Habitat C first. Indeed, a necessary condition for the population to spread into Habitat E is that it should exceed the Allee threshold β_E at the entrance to the habitat, i.e. at the boundary between Habitats D and E. Correspondingly, it means that the tail of the population density arriving to Habitat E from the left should be larger than β_E . However, it is hardly possible if the population density is low in Habitat C. Therefore, one point to understand is when Case 1 changes to Case 2.

Note that, since the Allee effect in Habitat C is assumed to be weak ($\beta_C < 0$), the population growth is positive there, even for a very small population density. Correspondingly, the decay in the density profile shown in Fig. 3a is not necessarily monotonous but can have a hump at the location of Habitat C. The height of the hump depends on the parameters of Habitats B, C and D (the stepping stone and the two adjoining habitats), in particular on the length L_C . For a small L_C , the hump is hardly visible, but it grows with an increase in L_C . Once L_C exceeds a certain critical value, the height of the hump jumps to a much bigger value with the population density in the middle of Habitat C being approximately equal to the carrying capacity: Case 1 changes to Case 2.

The question remains as to what is the relation between the parameters of the stepping stone that distinguish between the invasion success and invasion failure. This has been addressed through extensive numerical simulations where we fix other parameters as $L_A = L_B = 15$, $\beta_A = \beta_E = 0.3$, $\beta_B = \beta_D = 0.6$ and $L_D = 4$ and vary β_C and L_C in a broad range of values. The corresponding structure of the parameter plane (β_C, L_C) is shown in Fig. 4a. It is readily seen that, for Habitat C to be invaded, either its length must be sufficiently large or the Allee effect must be sufficiently weak (i.e. the quality of the environment should be sufficiently high).

For the parameter values of Fig. 4a, the population cannot proliferate to Habitat E as it is blocked by unfavourable Habitat D. Hence the expectation is that, provided the population establishes in Habitat C, the success of its further spread depends on the parameters of Habitat D, in particular on its length. Intuitively, one can expect that the spread can only be blocked if L_D is sufficiently large. In case L_D is not large enough, successful establishment in Habitat C should inevitably lead to a successful spread to Habitat E, i.e. Case 2 would change to Case 3. This intuitive expectation is confirmed by simulation results. Figure 4b shows parameter plane (β_C, L_C) obtained for a smaller value $L_D = 3$, other parameters being the same as in Fig. 4a. It is readily seen that for this value of L_D Case 2 cannot happen: whenever the population spreads to Habitat C, it spreads to Habitat E too.

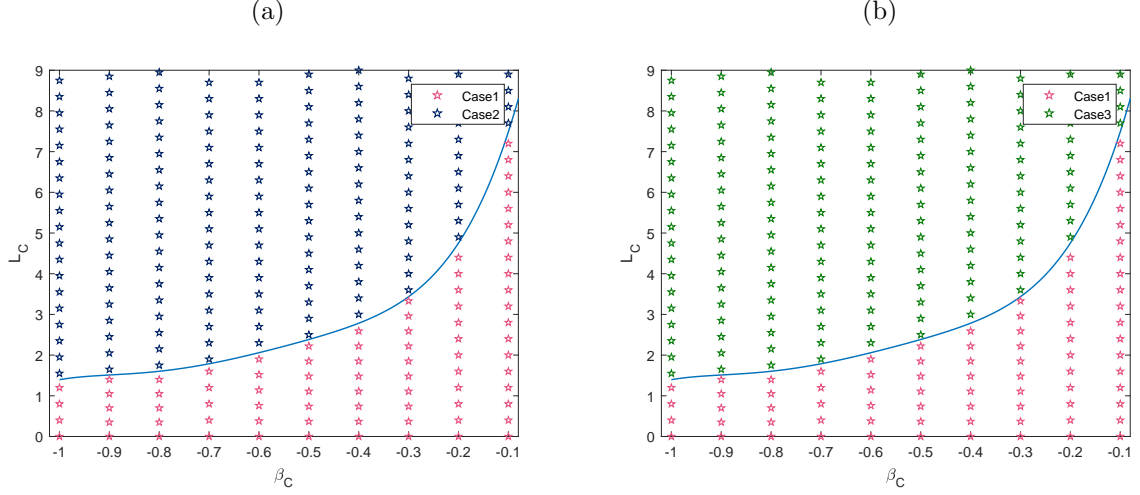


Figure 4: Map in parameter plane (β_C, L_C) where the domains above and below the curve correspond to different invasion scenarios obtained for (a) $L_D = 4$ and (b) $L_D = 3$. Other parameters are $\beta_{A,E} = 0.3$, $\beta_{B,D} = 0.6$ and $L_A = L_B = 15$.

Numerical simulations performed for various values of L_D reveal that, for other parameter values fixed as above, the critical length of Habitat D is approximately 3.7. However, this value is likely to depend on the strength of the Allee effect in the stepping-stone Habitat C. In order to make a more detailed look into this issue, we now fix the length of Habitat C along with other parameters and vary the length of Habitat D. Figure 5 shows the structure of parameter plane (β_C, L_D) . It is readily seen that the dynamics does depend on the strength of the Allee effect, albeit slightly, the main controlling parameter being the length of the bad area L_D .

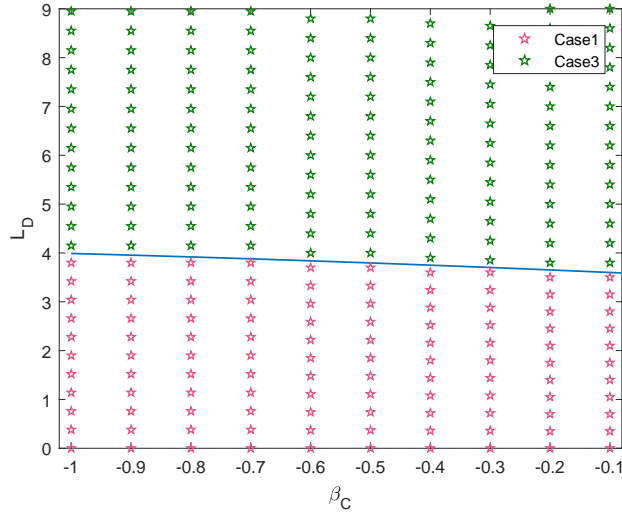


Figure 5: Critical size of Habitat D as a function of the strength of the Allee effect in stepping stone Habitat C (solid curve). For parameters above the curve the population spreads to Habitat E, for parameters below the curve the spread is blocked by bad Habitat D.

3 Stepping stones in 2D case

The results of the previous section provides a first insight into the problem, in particular showing that the outcome of the invasive spread (i.e. success or failure) depends on a subtle interplay between the parameters of the bad area and those of the stepping stone patch, in particular its location and the strength of the Allee effect inside the patch. However, one feature of the dynamics that is completely missed out by the 1D system is the possibility of the spreading population to overcome the bad area by going around it. In this section, we are going to address this issue by considering the problem in a more appropriate 2D layout of the model.

In the 2D space (x, y) , the model is given by the following reaction-diffusion equation:

$$\frac{\partial u(x, y, t)}{\partial t} = \frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} + u(1 - u)(u - \beta(x, y)), \quad (3.1)$$

(in dimensionless units) where notations have the same meaning as in Section 2.1. We consider an H-shaped domain where two large rectangular sub-domains of the same size – say, Habitat 1 and Habitat 2 – are connected by a passage; see Fig. 6 (note that, in order to avoid confusion, we label the habitats differently from the 1D case.) At the boundary of the domain (including the passage boundaries) we use the zero-function Dirichlet type condition; from the ecological perspective, it implies that the areas outside of the H-shaped domain are extremely unfavourable.

Our goal is to consider how the invasion success can be affected by the existence of the stepping stone (cf. Fig. 6) – a patch situated inside either the passage or one of the habitats with more favourable conditions than in the rest of the domain. Inside the patch, we consider the Allee effect to be weak (except for a few clearly stated special

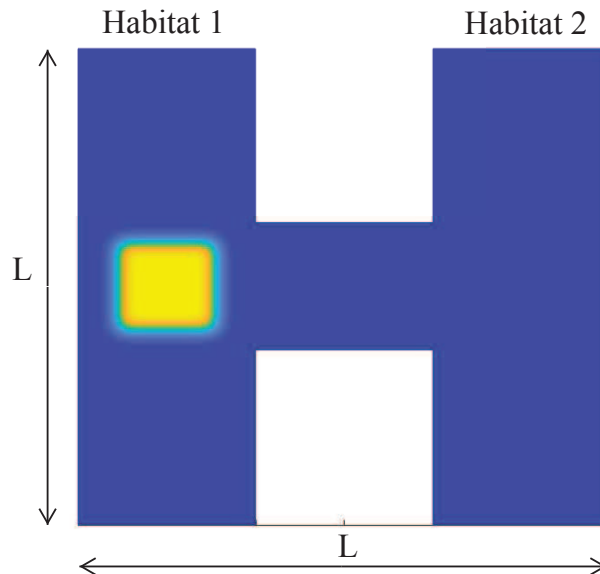


Figure 6: Sketch of the 2D computational domain to study the effect of the favourable patch ('stepping stone', shown by yellow square) on the invasion success.

cases); elsewhere in the domain, we consider it to be strong. The strength of the Allee effect inside and outside the patch is quantified by the value of the Allee threshold as β_w (≤ 0) and β_s (> 0), respectively.

The problem is studied by means of extensive numerical simulations. Equation (3.1) is solved numerically by finite differences. In most cases, we used the simple explicit scheme with mesh steps $\Delta x = \Delta y = 0.1$ and $\Delta t = 0.001$. In all simulations shown below, the overall size of the computational domain is $L = 50$. For the value of the Allee threshold, we fix $\beta_s = 0.1$ but vary β_w using different values (normally, between 0 and -1) in different simulations.

3.1 Establishment

We first consider how the existence of a stepping stone can help the establishment of an alien species in a new environment. For this purpose, we consider the situation where the stepping stone is located inside Habitat 1 (see Fig. 6).

Let us begin with the special case where $\beta_w = \beta_s > 0$ which means that, effectively, there is no stepping stone. We consider that the alien species is introduced into a small square-shaped area to which we for convenience refer as ‘IC-patch’. We assume that, immediately after the introduction, the alien species is distributed uniformly inside the patch with density u_0 . Correspondingly, the initial conditions for Eq. (3.1) are as follows:

$$u(x, y, 0) = u_0 \quad \text{for } (x, y) \in \text{IC-patch}, \quad u(x, y, 0) = 0 \quad \text{otherwise.} \quad (3.2)$$

It is well known that, in case the population growth is affected by the strong Allee effect, the species introduction into a finite area of a uniform space exhibits criticality. The species persists if and only if the initial population density is sufficiently large, i.e. larger than a certain critical value where the latter depends on the size of IC-patch [57, 67]. Simulation results obtained for Eqs. (3.1–3.2) in the case $\beta_w = \beta_s = 0.1$ are shown in Fig. 7a. It is readily seen that a smaller IC-patch does require a higher initial population density to ensure the survival of the alien population as the critical patch size is a monotonously decreasing function of the initial density.

A question now arises as to how this situation may change if the place of the species introduction has more favourable environmental conditions than the rest of the domain, i.e. if the IC-patch effectively coincides with the stepping stone. We mention here that, unlike the case of a uniform space, the problem of species establishment in a nonuniform space has been poorly studied. Figure 7b–d shows simulation results obtained for a few different values of the Allee threshold β_w inside the patch. We observe that the system possesses the properties similar to those shown in Fig. 7a: there exists a critical value of the initial population density, the critical patch size is a decreasing function of the initial population density. Interestingly, for a sufficiently weak Allee effect inside the patch (cf. Figs. 7c,d), the critical patch size exhibits only a weak dependence on u_0 .

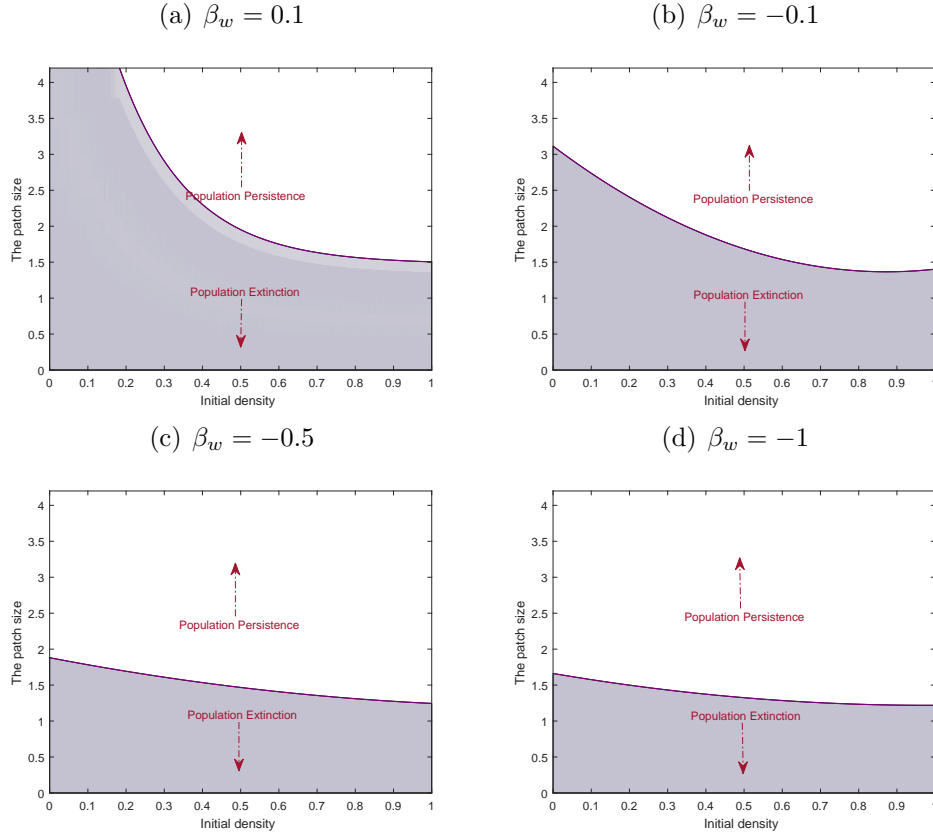


Figure 7: Critical patch size as a function of the initial population density u_0 for a different strength of the Allee effect inside the stepping stone patch. The Allee effect is strong in (a), weak in (b,c) and absent in (d). In the rest of the domain the Allee effect is strong, $\beta_s = 0.1$. Parameters of the passage are $(length, width) = (12, 7.5)$.

To further demonstrate the effect of the stepping stone on species establishment, Fig. 8 shows the dependence of the critical patch size on the strength of the Allee effect inside

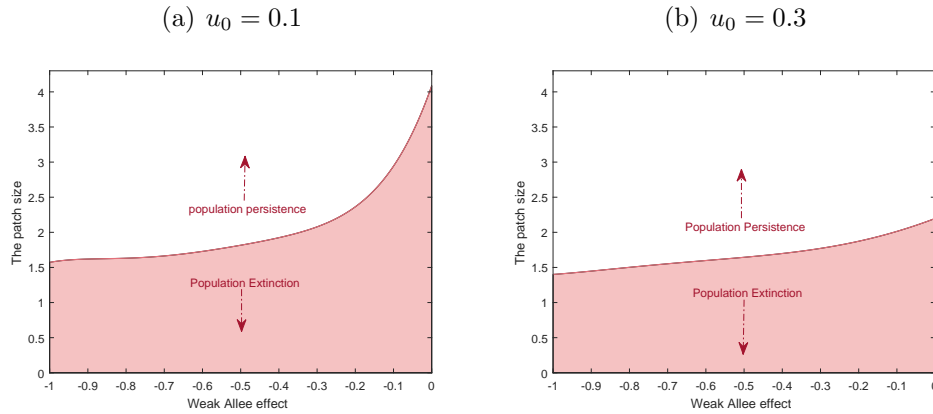


Figure 8: Critical patch size as a function of the strength of the Allee effect inside the stepping stone patch (quantified by β_w) obtained for two values of the initial population density. Other parameters are the same as in Fig. 7.

the patch. We observe that, the weaker the Allee effect is, the smaller the critical patch size is (i.e. the more likely the alien species to persist) and this effect is more prominent for smaller values of the initial population density.

3.2 Spread through the passage

In the rest of Section 3, we consider the situation where the alien species has already invaded Habitat 1. Correspondingly, the initial conditions are used as follows:

$$u(x, y, 0) = 1 \quad \text{for } (x, y) \in \text{Habitat 1}, \quad u(x, y, 0) = 0 \quad \text{otherwise.} \quad (3.3)$$

It has been shown in our previous work that, in case of a uniform environment (β is constant everywhere inside the domain, no stepping stones), the invasion success in the H-shaped geometry is determined by the size of the passage [2, 3]. The alien population spills over to Habitat 2 if and only if either the width of the passage is sufficiently large or the length is sufficiently small; otherwise it is blocked by the passage. Here we are going to consider the effect of the stepping stone (cf. Fig. 9). Our aim is to reveal the relation between the factors that can affect the invasion success (the spill-over of the alien species to Habitat 2), namely, between the size of the patch, the patch location inside the passage (quantified by the distance l_p between the patch and the entrance to the passage from Habitat 1), and the strength of the Allee effect inside the patch.

It was observed in simulations using the model (3.1), (3.3) that, in case of a successful spread, the population spill-over to Habitat 2 is usually well seen by $t = 500$ or so. Correspondingly, for all parameter values where invasion failure is seen (spread blockage), in order to exclude possible long term transients, simulations are run until $t = 4000$.

We begin with the case where there is no stepping stone and the size of the passage is makes it impassable. One such parameter set was identified in simulations as

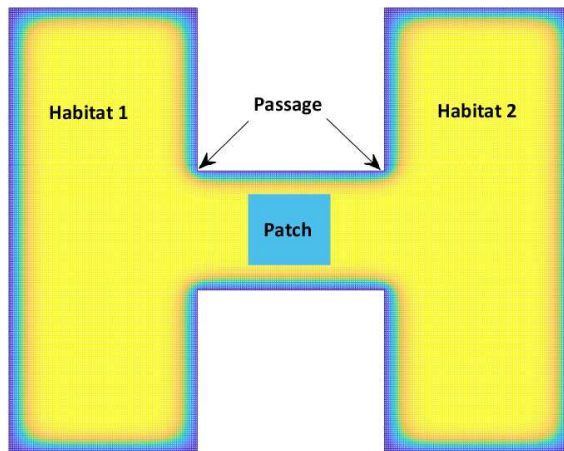


Figure 9: The H-shaped domain with the stepping stone located inside the passage.

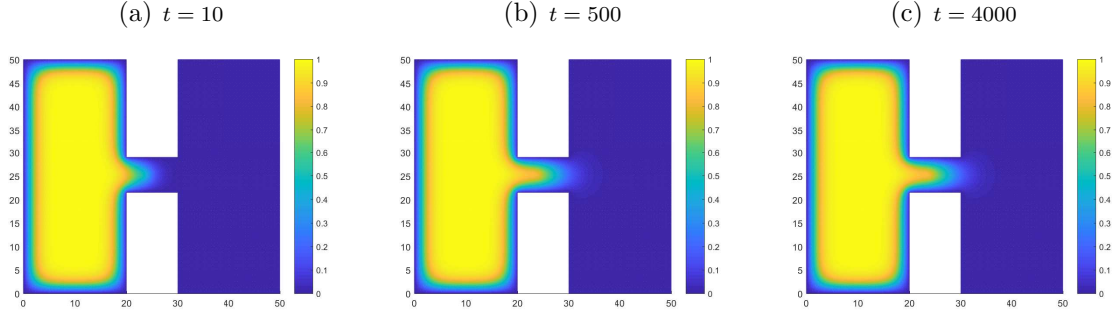


Figure 10: Snapshots of the population distribution over space obtained for the passage size as $(length, width) = (10, 7.5)$, patch size of 2×2 and the patch location $l_p = 2.8$.

$(length, width) = (10, 7.5)$. With the passage of this size, the alien species is blocked and never proliferates into Habitat 2. It is intuitively clear that a small stepping stone is unlikely to unblock the passage, and this is indeed what is seen in simulations. Figure 10 shows the results obtained in the case where there is a 2×2 patch with $\beta_w = -0.5$ located at the distance $l_p = 2.8$ from the passage entrance. It is readily seen that, for this patch size and location, the population spread remains blocked by the passage.

Interestingly, a patch with the same parameters as above but at different location inside the passage can lead to different dynamics changing invasion failure to invasion success. Figure 11 show the results obtained in the case where $l_p = 2.9$, i.e. the patch is located just slightly further away from the passage entrance (other parameters are the same as in Fig. 10). It is readily seen that in this case the passage is unblocked and the population fast spreads to Habitat 2.

In order to provide a comprehensive overview of the system's properties it is therefore necessary to consider the dynamics subject to different parameter combinations. This has been achieved by means of extensive numerical simulations varying all relevant parameters over a broad range. Essential results are shown in Figs. 12-13. Figure 12 shows the map in parameter plane (β_w, l_p) obtained for several different sizes of the stepping stone patch. It is readily seen that, the larger the patch size is, the broader is the range of parameters where invasion is successful. For the patch size of 5×5 or larger, invasion blocking is only

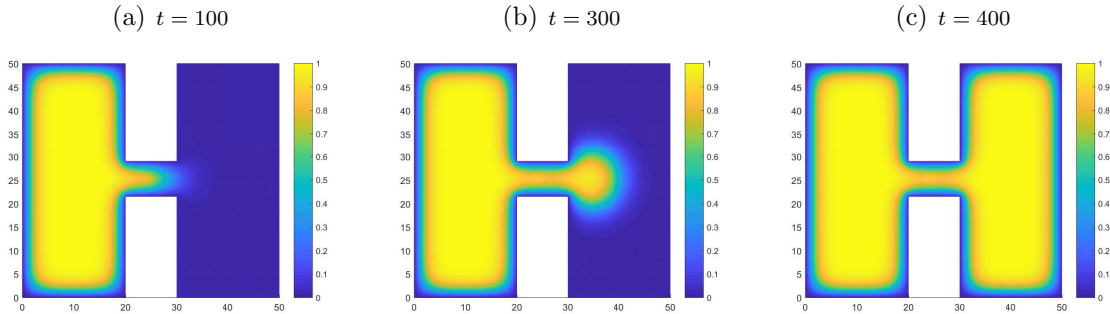


Figure 11: Snapshots of the population distribution over space obtained for the patch location $l_p = 2.9$, other parameters are the same as in Fig. 10.

possible for a few particular combination of parameter values such as values of β_w close to zero and the patch location close to the either passage entrance (i.e. close to Habitat 1) or to the passage exit (close to Habitat 2), see, respectively, the bottom-right and the top-right corners in Fig. 12d. For the stepping stone patch of a small size, see Figs. 12a and 12b, invasion can only be successful if the patch located approximately in the middle of the passage but not at the entrance to the passage. Note that, unless the patch size is large, e.g. equal to or larger than one half of the passage width (cf. Fig. 12c), an increase in β_w will always result in invasion blocking, even that the Allee effect in the patch is still weak and the conditions are favourable.

We want to mention that, for the parameters of Fig. 12, the passage without the stepping stone would block the spread regardless of the strength of the Allee effect inside the patch; see Fig. 9a in [2]. Therefore, the existence of the stepping stone can unblock the otherwise impassable passage.

It is readily seen from Fig. 12 that, for the passage of a fixed size, the parameter domain corresponding to successful invasion (cf. light-blue colored areas in Fig. 12) grows steadily with an increase in the stepping stone patch size. When the patch size approaches the width of the passage, there parameter range where invasion can be blocked shrinks

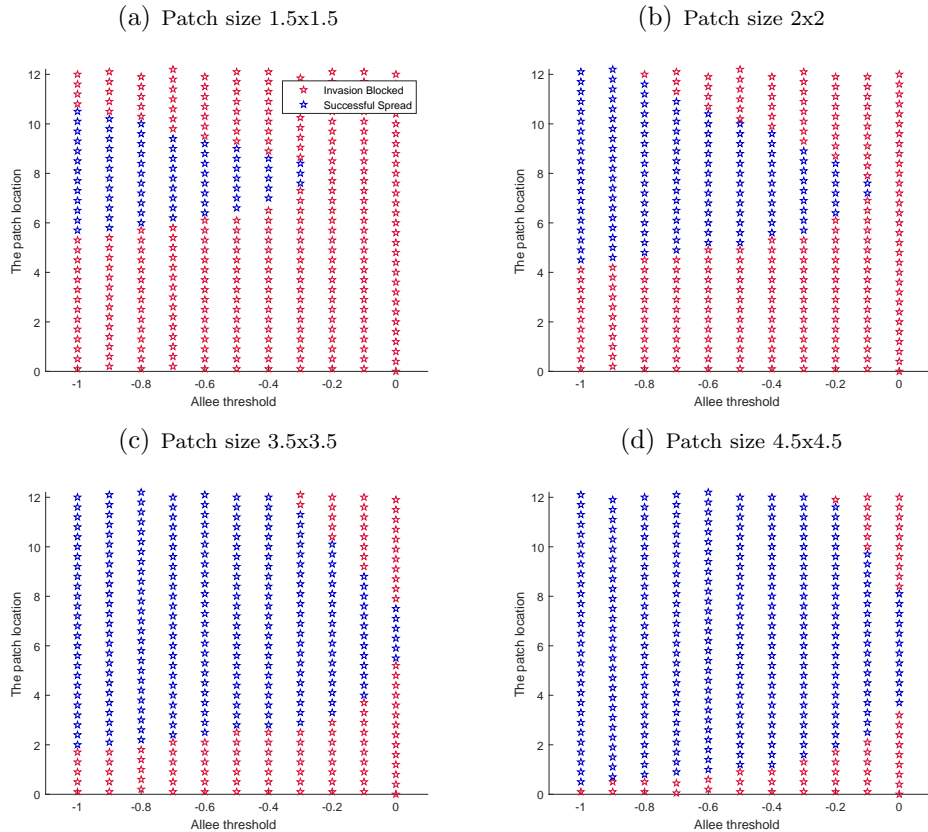


Figure 12: Map in parameter plane (β_w, l_p) showing parameter ranges where the invasion is successful (blue color) and parameter ranges where invasion is blocked by the passage (red color) for the stepping stones of different size. Parameters of the passage are $(length, width) = (12, 7.5)$.

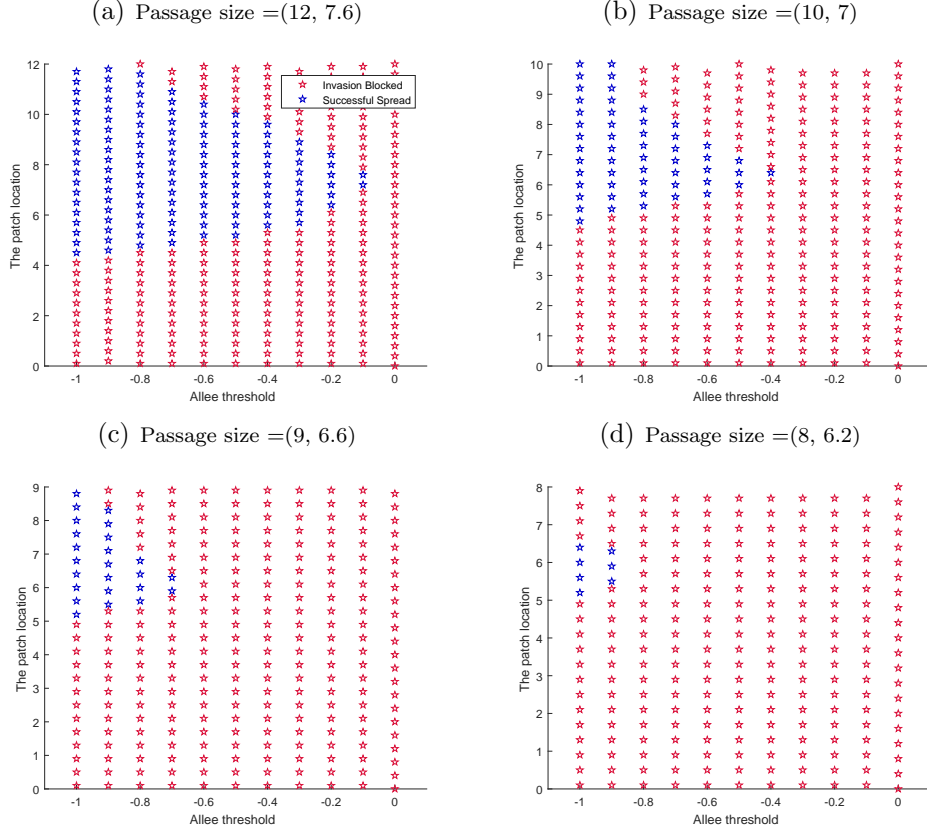


Figure 13: Map in parameter plane (β_w, l_p) showing parameter ranges where the invasion is successful (blue color) and parameter ranges where invasion is blocked by the passage (red color) obtained for the stepping stone 2×2 and the passage of different size.

to zero. A question can arise as to whether the system's dynamics actually depends on the ratio of the passage width and the patch size rather than on these two parameters separately. In order to address this question, we fix the size of the stepping stone patch as 2×2 and perform simulations with the passage of different sizes. The results are shown in Fig. 13. It is readily seen that the parameter domain of successful invasion shrinks along with a decrease in the passage width, hence showing the tendency opposite to that observed in Fig. 12.

3.3 Effects of different growth rate normalization

The above results were obtained under the assumption that normalizing coefficient $\hat{\gamma}$ in Eq. (2.2) (or coefficient γ in original Eq. (2.1)) is constant, i.e. not related to any other species traits. Although this assumption is routinely used in mathematical ecology [19, 62, 85, 91], a closer look reveals that it is in fact not well justified biologically. Indeed, it is readily seen that in this case a change in the value of threshold density β leads to a change in the maximum growth rate and the maximum per capita growth rate [55]. Meanwhile, the properties of the population growth rate at small population densities

(where the Allee effect is especially important) and at intermediate population densities (where the maximum growth rate is reached) are often determined by different factors and processes and hence are not necessarily directly related. Therefore, as an alternative to the simple case $\hat{\gamma} = 1$, now we are going to consider a model where these processes are uncoupled. That requires normalizing coefficient to become a function of the Allee threshold, i.e. $\hat{\gamma} = \hat{\gamma}(\beta)$, where the particular function depends on what property is being preserved.

Namely, we consider the following two cases [55]:

- The maximum growth rate is kept constant (i.e. independent of β). The corresponding expression for the normalizing coefficient is as follows:

$$\hat{\gamma} = 27 / (2(((1 + \beta)^2 - 9\beta/2)(1 + \beta) + ((1 + \beta)^2 - 3\beta)^{3/2})). \quad (3.4)$$

- The maximum *per capita* growth rate is kept constant; the corresponding expression for $\hat{\gamma}$ is

$$\hat{\gamma} = 4 / (1 - \beta)^2. \quad (3.5)$$

We now perform simulations using the 2D model (3.1), (3.3) with $\hat{\gamma}(\beta)$ given by either (3.4) or (3.5) in the H-shaped domain with a stepping stone in the passage; see Fig. 9. Results are summarized in Figs. 14–15.

Figure 14 shows parameter plane (β_w, l_p) of the stepping stone parameters obtained in the case of scaling (3.4) preserving the maximum growth rate. The size of the passage is $(length, width) = (5, 2.6)$. We first check that without the stepping stone this passage is impassable for the population (see also [2]). The presence of the stepping stone assists the spread and can unblock the passage. It is readily seen from Fig. 14 that, although the shape of the map is somewhat different from that obtained in the previous section,

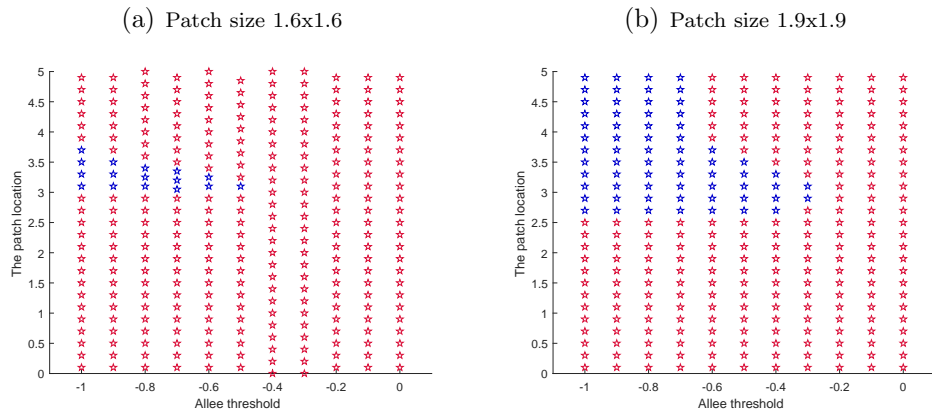


Figure 14: Map in parameter plane (β_w, l_p) showing parameter ranges where the invasion is successful (blue color) and parameter ranges where invasion is blocked by the passage (red color) for the stepping stones of different size and the normalizing coefficient $\hat{\gamma}$ chosen according to Eq. (3.4). Parameters of the passage are $(length, width) = (5, 2.6)$.

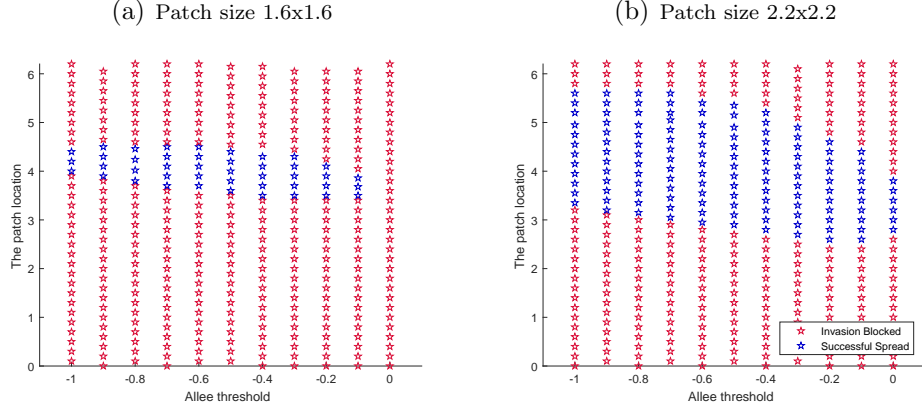


Figure 15: Map in parameter plane (β_w, l_p) showing parameter ranges where the invasion is successful (blue color) and parameter ranges where invasion is blocked by the passage (red color) for the stepping stones of different size and the normalizing coefficient $\hat{\gamma}$ chosen according to Eq. (3.5). Parameters of the passage are $(length, width) = (5, 3.4)$.

the general tendencies remain essentially the same as in the case of $\hat{\gamma} = 1$. The existence of a stepping stone can unblock the otherwise impassable passage; the larger the stepping stone is, the more distinct this effect is (i.e. the broader the corresponding parameter range is). For the stepping stone of a small size (cf. Fig. 14a), it can only unblock the passage if it is located at a certain optimum location approximately in the middle of the passage.

Figure 15 shows parameter plane (β_w, l_p) obtained for the stepping stones of different size in the case where $\hat{\gamma}$ is given by Eq. (3.5) (hence preserving the maximum *per capita* growth rate). The size of the passage is $(length, width) = (5, 3.4)$; note that without the stepping stone this passage is impassable [2]. As well as above, we observe that the stepping stone can assist the spread by unblocking the passage. For smaller patches, there is a certain optimum location but a larger patch unblocks the passage in a broader range of parameters.

4 Discussion and concluding remarks

Biological invasion has been a focus of intense research for several decades because of severe consequences that alien species' spread can cause to biodiversity, environment, forestry and agriculture [20, 25, 43, 70, 78, 92]. Once a new species is introduced and starts spreading, evaluation of the extent of the invadable area becomes an important issue. It is often addressed by means of species distribution modelling (SDM) which attempts to predict the future distribution of invasive species on the basis of the known distribution in their native range by revealing the correlation between the values of the population density (often only the presence/absence data) and relevant environmental parameters such as temperature, precipitation, soil type, land cover, etc. [4]. However,

the capability of SDM to correctly predict the extent of the actually invaded area depends on various factors that can affect species dispersal, such as barriers. Meanwhile, it is well known that dispersal is a limiting factor that affects species distribution; moreover, under certain unfavorable conditions (e.g. under the global climate change) restricted dispersal can endanger species survival altogether [81]. In other words, SDM generally succeeds (subject to the quality of available data) to identify the potential areas where the alien species *can* establish and persist, but it says very little about *how* the alien species will actually get there and whether it will get there at all.

Heterogeneity of the environment often reduces the space accessible to alien species spread to narrow corridors [88]. In conservation programs, corridors are generally regarded as a landscape feature that promotes species persistence [32]. In the context of the invasive spread, however, their effect is different as they tend to slow down the spread [3, 29] or even can block it altogether [2]. Although empirical research into the effect of corridors on invasive species spread remains meagre (arguably, because of considerable technical and methodological difficulties [29]), its tendency to hamper the spread was demonstrated in modelling studies using different models, e.g. see [2, 3, 29].

On the other hand, the importance of stepping stones for species dispersal has long been recognised [7, 40]. It is usually considered as a feature promoting long-distance dispersal [79], i.e. dispersal on a large spatial scale (such as is given, for instance, by an archipelago of small islands [79]). In our study, we endeavored to consider the effect of stepping stones on a much smaller spatial scale by linking them to dispersal corridors. We considered a situation where the corridor connecting two large habitats has got a small area or patch inside that has more favourable conditions than the rest of the environment. In agreement with previous studies, we found that stepping stones promote species spread; the larger is the stepping stone patch, the more noticeable its effect is. However, we also found that their actual efficiency to promote the alien species spread depends significantly on the relation between three factors such as their size, the quality of the environment inside the patch (quantified here as the strength of the Allee effect) and their location. In particular, we found that there exists an optimum location of the stepping stone where even a stepping stone of small size and with relatively poor environmental conditions can unblock the otherwise impassable corridor.

A question may arise here with regard to the generality of our findings. Indeed, in our study we considered the effect of the stepping stones in the particular case of rectangular geometry (as is given by the ‘H-shaped’ domain) and with the zero-function Dirichlet boundary conditions at the boundaries of the passage. In order to check the generality of our findings with regard to the domain shape, we considered the population dynamics described by Eq. (3.1) in a domain with a different ‘keyhole’ geometry; see Fig. 16. We performed a simulation study similar to Section 3.2 with the same aim to reveal how the existence of a favorable patch in the passage (i.e. in the central field) can affect the spread of the invading species from Habitat 1 on the left to Habitat 2 on the right. Interestingly, our findings were essentially the same as above. In particular, we

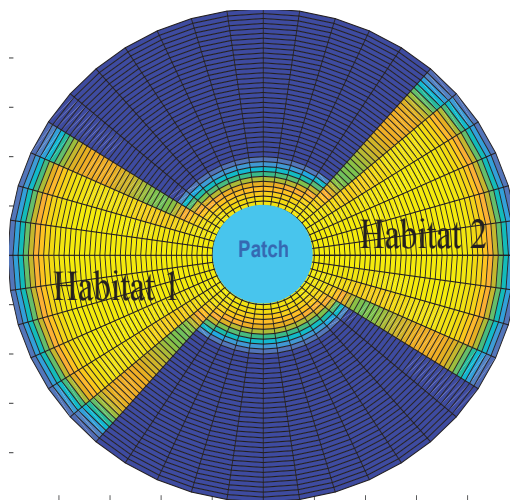


Figure 16: A sketch of the 2D computational domain with polar symmetry with a stepping stone patch (an area with better conditions, i.e. a weaker Allee effect) inside the central field.

observed that the existence of the stepping stone assists the species spread through the otherwise impassable passage. For a small patch, the passage can only be unblocked if the stepping stone is situated at the narrow range of locations (in this case, at the entrance to Habitat 2). For a larger patch, this range of locations grows fast, so that for a sufficiently weak Allee effect inside the patch the stepping stone unblocks the passage at almost any location. Arguably, this apparent similarity between the results obtained for two different geometries suggests that our main conclusions are not too sensitive to the shape of the domain.

With regard to different conditions at the passage boundary, the species spread in the H-shaped domain without a stepping stone was considered in [3]. It was shown there that the spread through the passage can be blocked if the passage is sufficiently narrow but the dynamical mechanisms resulting in the spread blocking and, correspondingly, the conditions of blocking are different for the Dirichlet (zero-function) and the Neumann (zero-flux) conditions at the passage boundaries; see Section 3.1 in [3]. Whilst in the case of Dirichlet conditions the spread is blocked in the middle of the passage, in the case of Neumann conditions the spread is blocked at the exit to Habitat 2. Correspondingly, the effect of the stepping stone is slightly different. In order to unblock the impassable passage, in the case of Neumann conditions the stepping stone must be located inside Habitat 2, not inside the passage. This is readily seen from the heuristic arguments and confirmed by numerical simulations (not shown here for the sake of brevity). Apart from this subtle difference, the effect of the stepping stone in the Neumann case is similar to that in the Dirichlet case: it promotes the spread, the range of stepping stone locations where it unblocks the passage is narrow for a small patch but grows fast with an increase in the patch size.

In this paper, we have considered the effect of habitat's boundaries in the context of

landscape geometry, i.e. aiming to understand how the shape of natural landscape features can affect the spread of invasive species. However, we mention here that a similar problem arises in relation to invasive species control. Indeed, one way to control the spread used in practical applications is to create landscape features – “barriers” – inaccessible for the invader [83, 84]. Arguably, the effect of the boundaries of those human-made structures on the dynamics of the invading population is going to be the same as the effect of natural landscape structures, so that our analysis is fully relevant. Our results therefore may help to provide a more efficient design of the barriers.

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