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ORIGINAL ARTICLE

Habitat loss-induced tipping points in metapopulations with facilitation

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Abstract

Habitat loss is known to pervade extinction thresholds in metapopulations. Such thresholds result from a loss of stability that can eventually lead to collapse. Several models have been developed to understand the nature of these transitions and how they are affected by the locality of interactions, fluctuations or external drivers. Most models consider the impact of grazing or aridity as a control parameter that can trigger sudden shifts, once critical values are reached. Others explore instead the role played by habitat loss and fragmentation. Here we consider a minimal model incorporating facilitation between the individuals of the same species along with habitat destruction, with the aim of understanding how local cooperation and habitat loss interact with each other. A mathematical model incorporating facilitation and habitat destruction is derived, along with a spatially explicit simulation model. It is found that a catastrophic shift is expected for increasing levels of habitat loss, but the bifurcation becomes continuous when dispersal is local. Under these conditions, spatial patchiness is found and the qualitative change from discontinuous to continuous results are in agreement with previous studies on ecological systems. Our results suggest that species exhibiting facilitation and displaying short-range dispersal will be markedly more capable of avoiding catastrophic tipping points.

KEYWORDS

computational ecology, dispersal, metapopulations with facilitation, spatial dynamics, tipping points

1 | INTRODUCTION

A major threat to the viability of many extant ecosystems is connected to their susceptibility to habitat loss. Among the potential problems associated with this process, a great concern exists in relation to the tempo of ecosystems collapse. A growing consensus among scientists is that species diversity might face the presence of the so-called *catastrophic shifts*, namely discontinuous transitions from a diverse to a poor (or fully extinct) community once parametric thresholds are crossed (Rockström et al., 2009; Scheffer et al., 2001; Scheffer 2009; Solé 2011). In this context, prediction

of future scenarios becomes an issue, given the ongoing degradation of habitats associated with climate change, demographic pressures and the potentially irreversible nature of tipping points (Barnosky et al. 2012; Barnosky & Hadly 2016; Scheffer et al., 2001).

Mathematical and computational models of ecosystem responses against different classes of damage have been developed in the last decades. Some of these models concern the impact of habitat loss and fragmentation, indicating the existence of destruction levels leading to species extinctions (Bascompte & Solé 1996; Hanski 1999; Nee & May 1992; Solé et al. 2002; Tilman et al. 1994). Others incorporate the

impact of increasing aridity levels, which damages soil crusts and reduces the quality of soil and vegetation resilience (Maestre et al. 2015). The effective impact level of these two classes of perturbations is tied to the nonlinearities associated with individual interactions. In standard models of habitat destruction, vegetation reacts as a logistic-like growth shape which, combined with linear decay, creates the conditions for smooth extinction thresholds (Levins 1969).

On the other hand, when individuals interact in nonlinear ways, responses to increasing levels of aridity or grazing also lead to extinction thresholds, although the nature and speed of the decay toward extinction is very different. A specially relevant example involves the future of semi-arid ecosystems (Kéfi S, Rietkerk M, Alados CL, et al. 2007; Kéfi S, Rietkerk M, van Baalen M, et al. 2007; Rietkerk & van de Koppel 1997; Scanlon et al. 2007; Solé 2007) where warming, steady declines in rainfall and increased grazing are likely to promote a sudden shift to a desert state (Foley et al. 2003). The analysis and modeling of spatial patterning in semi-arid habitats consistently supports the fact that rapid shifts might occur in a near future (Kéfi S, Rietkerk M, Alados CL, et al. 2007; Kéfi S, Rietkerk M, van Baalen M, et al. 2007; Solé 2011).

Several types of models have been proposed to explain ecosystem responses under different environmental stresses. When dealing with drylands, a key factor appears to be the presence of *facilitation processes*, that is, positive pairwise interactions between individuals leading to the benefit of at least one of the interacting partners (Brooker et al. 2008). A specially relevant example involves positive interactions where one organism makes the local environment more favorable for another (which can belong or not to the same species). This positive effect can occur either directly or indirectly. An example of the former includes shading mechanisms that reduce water or nutrient stress. The later would include removing competitors or deterring predators (see Bruno et al. 2003). Since both facilitation and habitat loss can occur together and they have distinct types of dynamics: What is the impact of habitat destruction on an ecological system involving facilitation? How does this effect interact with the nonlinearities associated with facilitation? What kind of tipping points (i.e., catastrophic or smooth) are found under habitat loss and facilitation?

Here, we explore this problem by presenting a minimal model that captures both components, as well as the spatially extended counterpart under different dispersal regimes and facilitation processes. The mean-field (well-mixed) version is built from a microscopic description based on the underlying rules of facilitation: colonization and extinctions involving loss of the population. It predicts that first-order (catastrophic) transitions will occur for increasing levels of habitat loss. However, the spatially explicit versions of the model reveal a

rather interesting phenomenon: the transition becomes continuous when interactions are local, confined to nearest neighbors, becoming catastrophic after a given dispersal range is exceeded. This seems to be a rather generic phenomenon, associated with the universal properties of complex systems exhibiting phase transitions (Villa Martín, Bonachela, Levin, & Muñoz, 2015; Weissmann & Shnerb 2014). A detailed analysis of the effects of dispersal is presented and the potential implications for ecosystems' fate are discussed.

2 | MATERIALS AND METHODS

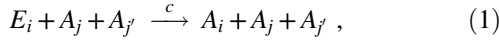
In this section, we introduce the mathematical and computational models developed to investigate the dynamics of facilitation under habitat destruction. The program codes used in this work are available as online supplementary material as well as upon request.

2.1 | Master equation and mean field model

Our goal is to develop a spatial generalization of metapopulations with facilitation under habitat destruction. The system introduced here aims to model the colonization and extinction dynamics of sessile organisms, particularly within the context of drylands and rangelands. Here we consider an individual-based description where interactions are considered in an explicit way. From that microscopic description, average population equations are obtained. We begin by building a formal lattice model using a master equation considering the processes of facilitation, colonization and decay of the individuals. The basic conceptualisation is summarized in Figure S2a–d, where a toy picture of the lattice is provided by a 2×2 system, to be defined as compositions of the three possible site states. Here, transitions between states are shown in (a–c) with the respective transition probabilities that can be indicated as $\omega(alb)$ or $\omega(a \leftarrow b)$. When we take one of these lattice states (b in this case) the master equation includes all the in- and out- transitions from these state, as summarized in the diagram (d). From this set of equations it is possible to obtain the dynamics of global quantities, such as the vegetation cover. To get there, a proper set of transition probabilities needs to be defined.

This type of model has been used in different contexts (Chopard and Droz, 1998) including field theoretic models of biogeography (Azaele et al. 2016; O'Dwyer et al. 2010; Pigolotti et al. 2018). Let us consider a given habitat described as a two-dimensional grid of size L^2 , as a simple way to simulate spatial ecological interactions. Three discrete state variables are defined per site: $A_i, E_i, D_i \in \{0, 1\}$ with $i \in \{1, \dots, L^2\}$. These local variables correspond to the occupied, empty and destroyed states of a site, respectively. For example, a site i is said to be occupied at a given time t if $A_i = 1$

and $E_i = D_i = 0$. In order to avoid degeneracy, a state constrain is imposed: $A_i + E_i + D_i = 1$ for all sites. The following reaction rules determine the dynamics of the system:



Here, reaction (1) denotes the process of colonization: a site with an occupied state $A_j = 1$ interacts with an occupied neighboring site $A_{j'}$ and colonizes an empty site E_i at a probability rate c . Hereafter, we will use the notation $\{j, j'\}_i$ to refer to immediate next neighbors of site i . Reaction (2) corresponds to the extinction process, where an occupied site A_i becomes empty at a rate e . This is all we need to define the stochastic mathematical description from which average vegetation cover will be derived. The reader not looking for the mathematical details can go to Equation (5).

Consider a compact notation by introducing local vector states $\vec{X}_i \equiv (A_i, E_i, D_i)$, and a state vector for global configurations $\sigma \equiv (\vec{X}_1, \dots, \vec{X}_L)$. Now, it is possible to define the ensemble of time-evolving configuration probabilities characterized by a distribution function $P(\sigma; t)$. Considering reactions (1)–(2), it can be shown that the probability distribution evolves under the following master equation (see Section S3.1). This equation is described, in general terms, as follows (Méndez et al. 2014, van Kampen 1981):

$$\frac{dP(\sigma; t)}{dt} = \sum_i \omega_{\sigma_i \leftarrow \sigma'_i} P(\sigma'_i; t) - \sum_i \omega_{\sigma'_i \leftarrow \sigma_i} P(\sigma_i; t), \quad (3)$$

where the normalization condition $\sum_{\sigma} P(\sigma; t) = 1$, holds. Here, the whole set of transitions between different probabilistic configurations are taken into account. The first term at the right hand side of Equation (3) includes all the favorable transitions towards $P(\sigma; t)$ whereas the second term stands for all changes going out from it. In our mathematical framework, the state space incorporates the lattice description. For the specific set of rules given by reactions (1)–(2), it can be shown (see Section S3.1) that the resulting master equation is given by:

$$\begin{aligned} \frac{dP(\sigma; t)}{dt} = & \sum_i \left[\left(c \sum_{\{j, j'\}_i} A_j A_{j'} (1 - E_i) + e(1 - A_i) \right) \right. \\ & \times P(\dots, (1 - A_i, 1 - E_i, D_i), \dots; t) \\ & \left. - \left(c \sum_{\{j, j'\}_i} A_j A_{j'} E_i + e A_i \right) P(\sigma; t) \right]. \end{aligned}$$

Averages of any (local or global) observable magnitude, namely \mathcal{O} , may now be computed as $\langle \mathcal{O} \rangle(t) = \sum_{\sigma} \mathcal{O} P(\sigma; t)$.

Furthermore, the time-derivatives of a macroscopical observable $\langle \mathcal{O} \rangle(t)$ can be derived from Equation (3). Thus, for the average activity of the system we obtain

$$\frac{d}{dt} \langle A_i \rangle(t) = c \sum_{\{j, j'\}_i} \langle A_j A_{j'} E_i \rangle - e \langle A_i \rangle. \quad (4)$$

Finally, we perform first order calculations on Equation (4) by ignoring all spatial correlations. This process will lead us to a so-called mean field theory, upon which a simple analysis becomes feasible. Recalling the non-degeneracy constrain $E_i = 1 - D_i - A_i$, and breaking correlations by assuming that the three-point functions may be approximated as $\langle \mathcal{O}_i \mathcal{O}_j \mathcal{O}_k \rangle \sim \langle \mathcal{O}_i \rangle \langle \mathcal{O}_j \rangle \langle \mathcal{O}_k \rangle$, then Equation (4) turns into the following dynamical equation associated to the vegetation abundance and given by

$$\frac{dx}{dt} = cx^2(1 - D - x) - ex, \quad (5)$$

where we have introduced the following notation: $\langle A_i \rangle = x$ and $\langle D_i \rangle = D$. Effectively, by this procedure we are mixing the system, or, alternatively, connecting all the sites together. Hence, Equation (5) does not reflect any intrinsic spatial effects. The last equation can be considered as a modified version of Levins' metapopulations model with habitat destruction (see Section S1). The nonlinear term on population growth and colonization for this model is interpreted as a process of autocatalysis, where the reproduction (given by cx^2) is not exponential but hyperbolic. When no habitat fragmentation is considered, that is, $D = 0$, then it becomes equivalent to an autocatalytic replicator with exponential degradation (see Fontich & Sardanyés 2008, Sardanyés & Solé 2007, Windus & Jensen 2007).

2.2 | Spatial stochastic computational model

Following methods of stochastic spatial systems we will implement the dynamics tied to reactions (1) and (2) using a cellular automaton (CA). This computational approach has been previously used to investigate the spatial dynamics of two-species metapopulations with exponential colonization under habitat destruction (Dythan 1995). The CA is given by a square L^2 lattice of side size L and periodic boundary conditions (see Figure 1). The states of the CA are given by sites that can be occupied (S_a); empty (S_e) or destroyed (S_d). The fraction of destroyed sites (D) is implemented by randomly distributing the given number of S_d states over the grid during the lattice initialisation (see below). The states S_d

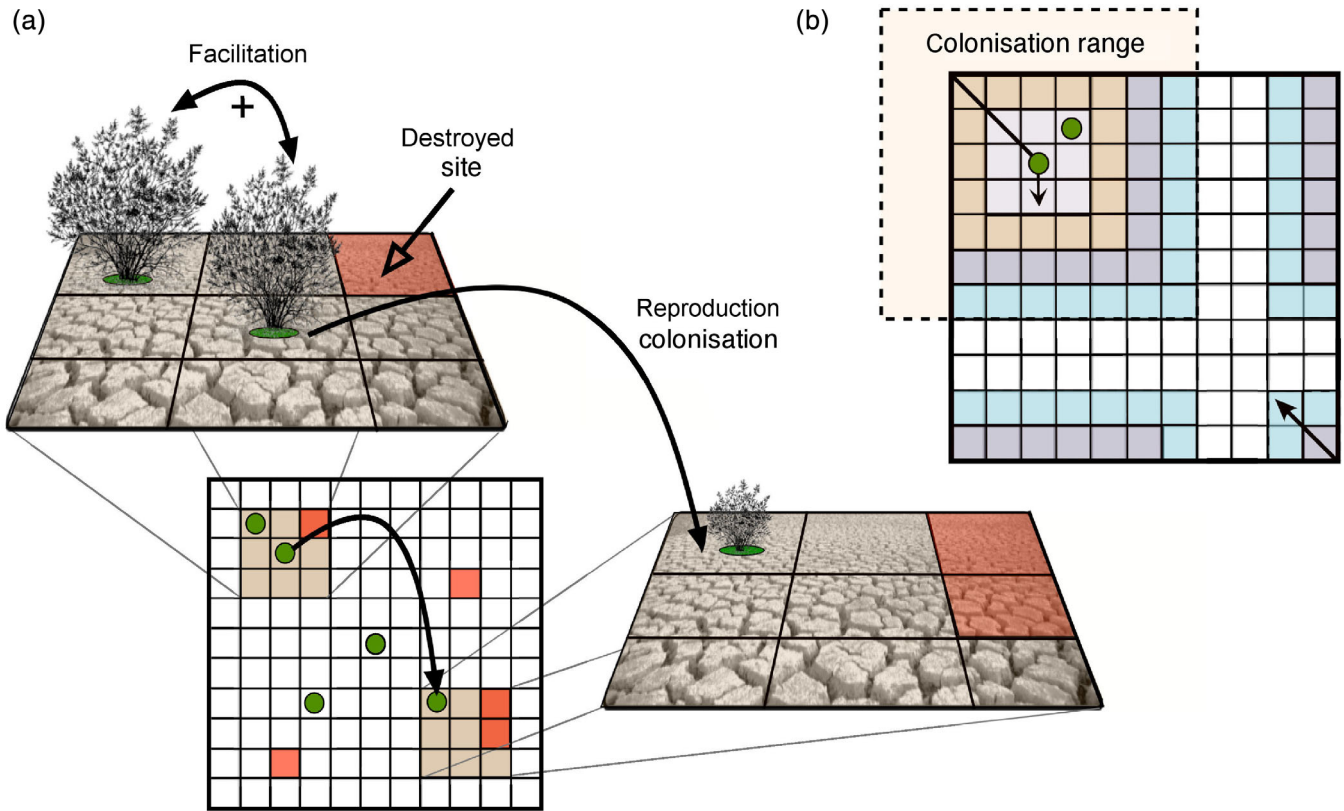


FIGURE 1 Schematic diagram of the ecological system with facilitation in reproduction under habitat destruction illustrated with the cellular automaton (CA) model. The individuals can grow and reproduce due to the cooperation with neighboring individuals. (a) The CA is a square lattice and has three states: sites occupied by an individual (green circle), empty sites that can be colonized (white and brown cells) and destroyed sites (red sites) where no establishment or growth of an individual is possible. The dynamics of reproduction involves facilitation, that is, an individual can reproduce if a neighboring place is occupied. Once an individual reproduces, can colonize another empty site of the lattice. If the colonized site is destroyed the individual can not grow. The lattice is assumed to have toroidal boundary conditions. In (b), we display two possible colonization scenarios: Local (short thin arrow) and long-range (solid arrow) dispersal

do not follow any dynamics, that is, once the system is initialized, only the nondestroyed sites evolve dynamically.

The CA algorithm works as follows: at each time generation, τ , $L \times L$ random sites are chosen and a stochastic version of the state-transitions rules following reactions (1) and (2) is applied. This updating process ensures that, on average, all cells in the lattice will be updated once every generation. The state-transition rules are:

- **Reproduction and colonization:** a site, say S_i , is randomly chosen. If S_i is empty or destroyed nothing happens. If S_i contains a species (is occupied), a random nearest neighbor (using the eight nearest neighbors that is, Moore neighborhood) is selected, say $S_{j \neq i}$. If $S_{j \neq i}$ contains another species, the species in S_i reproduces and colonizes another randomly chosen neighbor site $S_{k \neq i, j}$, placed within a given colonization distance, δ (see below). Colonization occurs with probability $c \in [0, 1]$. If $S_{k \neq i, j}$ is a destroyed or an occupied site, no colonization takes place.

- **Extinction:** a random cell is chosen. If the cell is occupied by a species, it dies with probability $e \in [0, 1]$.

The CA is initialized with a random distribution of empty and occupied states, if not otherwise specified. Then, a fraction of destroyed sites (D) is introduced randomly over the lattice.

The previous rules consider that the process of reproduction and further colonization of a given individual (occupied site) occurs whenever it is surrounded by other individuals that facilitate this process (Figure 1). Alternatively, it is possible to postulate a different type of facilitation process by considering that facilitation takes place after colonization, that is, supposing that seeds establishment is limited by the presence of neighbors around the colonized site. For this case, reproduction is not density-dependent. We briefly discuss this alternative model in the last part of Section 3. A full description of this model can be found in Section S4 (see also Figure S8).

As mentioned above, colonization is implemented considering a given dispersal distance, varying from local (closest neighbors) to long-range (any lattice site) ranges. The former would be more limited to shorter dispersal, while the latter may colonize over longer distances. In order to consider the full spectrum between these two extremes we use the approach by Wodarz & Levy (2011). Here, authors used a function to obtain the distance (labeled δ) over which colonization can take place, given by:

$$\delta = 1 - k \log \left[e^{-m/k} + R \left(1 - e^{-m/k} \right) \right]. \quad (6)$$

This function provides a random number between 1 and m , where m is the maximum distance that can be achieved during colonization. Since the CA model has periodic boundary conditions we shall assume that $m = L/2$. R is a uniformly distributed random number, and the parameter k determines how steep the distribution of δ is (see Figure S3). If $k \rightarrow 0$, the distribution of δ is very steep and the probability of colonization declines very fast with distance. When $k = 0$, $\delta = 1$ and thus colonization occurs within the nearest neighbors (local range colonization). On the other hand, for large k the distribution of δ tends to be uniform and any position in the lattice has the equal chance of being colonized (long-range colonization). The latter is equivalent to a perfect mixing extreme modeled by Equation (5). Intermediate values of k allow for a continuum between these two extremes.

In the spatial simulations developed in this work, k will be used as a control parameter to test how the nature of the transition towards the extinction of the metapopulation depends on the colonization ranges (see Figure 1b). Since k does not provide clear information about the colonization distance, we use mean colonization distance for any given value of k , namely $\bar{\delta}(k)$, as $\bar{\delta}(k) = \sum_{\delta=1}^m \delta(k) P(\delta, k)$. Here $P(\delta, k)$ is computed via the probability distribution derived from expression (6). The variation of $\bar{\delta}(k)$ is displayed in Figure S3. Notice how for small values of k the mean distance is close to k . For example, for $k = 5$, $\bar{\delta}(k) \approx 5.5$.

3 | RESULTS

Two distinct objectives are simultaneously addressed to characterize the metapopulation dynamics with facilitation under habitat destruction: (a) the impact of spatial correlations and distinct dispersal ranges (distances) of colonization; and (b) the effect of stochasticity in the metapopulation dynamics. However, before exploring these features, we will analyze Equation (5). This simple nonspatial model, which does not consider stochasticity, will provide clues about the nature of the transitions involving metapopulations collapses

under habitat degradation and pair-wise (facilitated) interactions.

As previously mentioned, two similar spatial models will be investigated. The first model considers facilitation during the process of plant reproduction and further colonization, and the establishment of the seeds in the new colonized sites will not depend on the nearest neighbors at the colonizing site. The second model will consider the process of facilitation necessary for the establishment of seeds in the colonized sites, being the reproduction of the plants not dependent on the density of the nearest neighbors.

3.1 | How facilitation determines metapopulation dynamics and extinction transitions in well-mixed populations under habitat destruction

The calculation of an explicit, closed solution $x(t)$ is not possible for Equation (5), as a difference from the classical Levins' metapopulation model with habitat destruction (see Section S1). However, it is possible to qualitatively investigate the dynamics of the model incorporating facilitation. To do so, we will compute the equilibrium points and their stability, as well as a potential function. The equilibrium points of this model are obtained from $f(x) = cx^2(1 - D - x) - ex = 0$, which gives three solutions, namely $x_0^* = 0$ and the pair

$$x_{\pm}^* = \frac{1}{2} \left(1 - D \pm \sqrt{(1 - D)^2 - 4r} \right),$$

where $r \equiv e/c$. Notice that the pair x_{\pm}^* will be biologically meaningful whenever $(1 - D)^2 - 4r \geq 0$. Indeed, when $(1 - D)^2 - 4r = 0$ both equilibrium points x_+^* and x_-^* have the same value, which occurs for the critical threshold

$$D_c = 1 - 2\sqrt{r},$$

associated with a catastrophic shift, as shown in Figure 2a. For $D > D_c$ the two equilibria x_{\pm}^* do not exist in the biologically-meaningful domain, involving a catastrophic shift towards extinction. This shift occurs through a saddle-node bifurcation (to be compared with the Levins' model with habitat destruction, for which the extinction of the metapopulation is smooth and continuous, see Section S1).

Generically, the (linear) stability of an equilibrium point x^* in a one-variable dynamical system can be obtained by means of the sign of $\lambda(x^*) = df(x^*)/dx$. The equilibrium point involving metapopulation extinction is a local attractor since $\lambda(x_0^*) = -e$. This means that the stability of the origin does not depend on D , which plays the key role in the

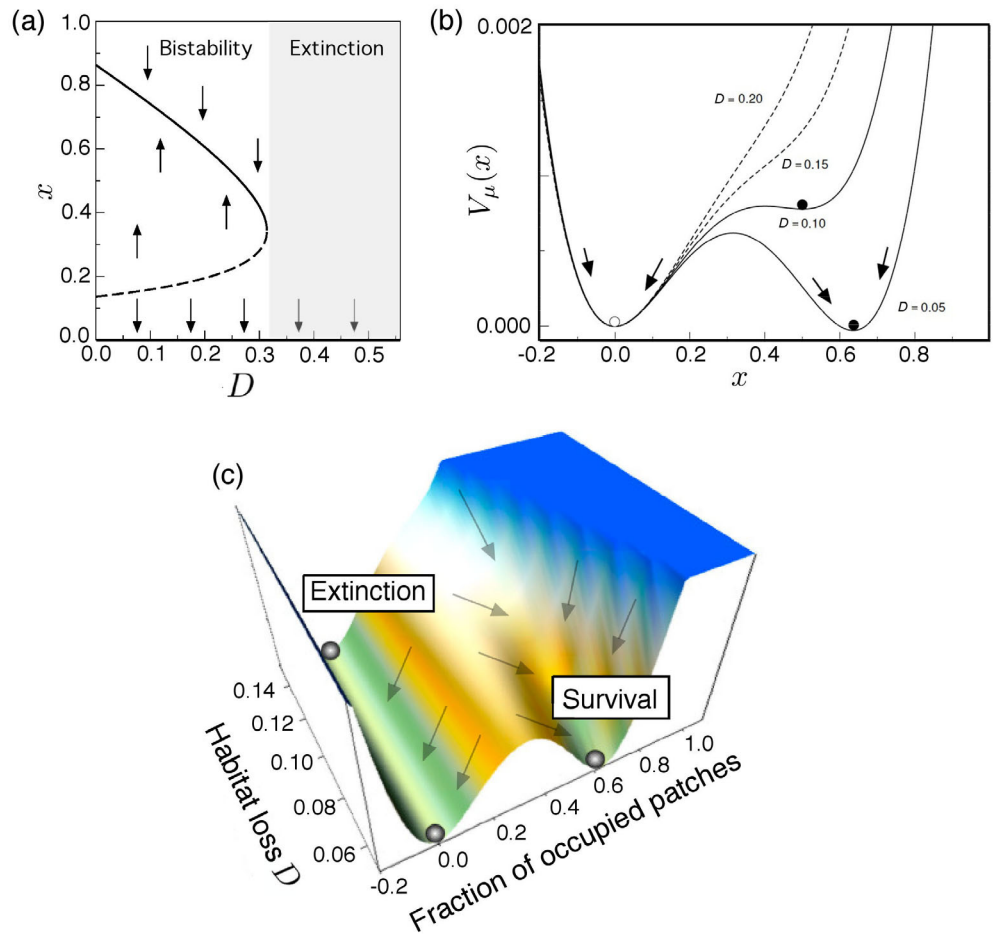
FIGURE 2 Catastrophic shift due to habitat destruction in metapopulations with facilitation identified in the mathematical model given by Equation (5).

(a) A tipping point is found as the fraction of habitat destroyed, D , increases beyond the bifurcation value D_c (here with

$D_c = 1 - 2\sqrt{e/c} \approx 0.314$ since $c = 0.85$ and $e = 0.1$) causing a saddle-node bifurcation.

(b) Another approach to this type of bifurcation diagram is provided by the potential function $V(x)$ associated with the dynamics.

Values of D below the bifurcation value (solid lines) display bistability, while for $D > D_c$ a single, stable state is found at $x^* = 0$. In (c), we show a more complete picture of the role played by D in changing the shape of $V(x)$



bifurcation described above. We refer the reader to Section S2 for further analyses on the stability of the equilibrium points x_{\pm}^* .

This model also allows for an explicit calculation of the associated potential landscape, described by the function $V(x) = - \int f(x)dx$, which for Equation (5) gives:

$$V(x) = -cx^2 \left(-\frac{r}{2} + \frac{1-D}{3}x - \frac{1}{4}x^2 \right).$$

The potential is displayed in Figure 2b for several values of D . For $D < D_c$ (solid lines) two wells are found, corresponding to the two stable states (x_0^* and x_+^*) resulting in bistability, that will be achieved depending on the initial conditions. Evidences of multiple states have been recently identified in semi-arid ecosystems (Berdugo et al. 2017). Also, a complete fold bifurcation diagram has been experimentally built with cooperative yeast strains (Dai et al. 2012). Once the fraction of habitat destroyed surpasses its critical values D_c , a single well is found (dashed lines). This single stable state is given by the equilibrium point $x^* = 0$, and involves the extinction of the metapopulation. A three-dimensional visualization of the function $V(x)$ is plotted for

different values of D in Figure 2c. Here, it is possible to see the dependence of the initial conditions (fraction of occupied sites) in the asymptotic dynamics under the bistable scenario (survival and extinction).

3.2 | Spatially-explicit dynamics and transitions to extinction with facilitation in reproduction under habitat destruction

In this section we will further extend the results obtained from the mean field model, which assumed well-mixed dynamics and determinism. Here we will use the CA models to include explicit spatial correlations and stochasticity. In what follows we will denote the normalized population of individuals (occupied sites) at generation τ as $\rho(\tau)$. The term ρ^* will denote population at equilibrium (i.e., large τ). We first investigate the dynamics of facilitation during the process of reproduction and colonization. This means that seeds can occupy non-destroyed empty sites, but their growth and further reproduction will be determined by facilitation provided by the presence of closer neighbors. This mode of facilitation involves that a given individual needs from other individuals in its surroundings to further reproduce and colonize. Such neighboring individuals may retain water and

provide good conditions for the growth and reproduction of the species after the arrival of seeds by dispersion. The dependence of neighbors for reproduction might also be representative of dioecious species such as mediterranean shrubs, for example, *Pistacia lentiscus* (Quezel 1981) or *Juniperus sp.* (Adams 2004), as well as plants of the *Salix* genus (Newsholme 2003) or African teaks, for example, *Baikiaea plurijuga*, *Milicia excelsa*, *Pericopsis elata* or *Pterocarpus angolensis*, among others. For these cases, the reproduction and colonization term will be density-dependent (non-linear), as modeled by Equation (5), since it is assumed that plants will be fertilized by the surrounding ones (assuming short-range fertilization).

We first analyze two extreme scenarios of colonization: (a) the new individuals are dispersed to any random site of the lattice; (b) the new individual colonizes the nearest neighbor of the selected site (a neighbor at distance 1). Scenario (a) is closer to the mean field model analyzed above, since here spatial correlations are only considered during the process of facilitation, but then colonization can take place to any site of the lattice (similar to the break of the spatial correlations). For this type of colonization, a catastrophic shift is found, as predicted by the mean field model (see

Figure 2a). Figure 3 displays the mean population density $\bar{\rho}^*$ for different values of habitat destruction and colonization probabilities. The system with long-range colonization displays a catastrophic shift and bistability, as predicted by the mean field model. Figure 3a displays the abrupt change from survival to extinction, which takes place at increasing D and at decreasing c . The time series in Figure 3a.1–a.2 shows the bistability of the system in the survival scenario: low initial conditions give place to metapopulations extinctions (Allee effect), while large initial populations allow the survival of the metapopulation (see also Figures S3–S6).

The same analysis allowing only for local colonization ($k = 0$, $\bar{\delta}(k) = 1$) reveals a continuous transition toward extinction (Figure 3b). For this case, bistability is not found, since all initial conditions in the survival scenario allow the persistence of the metapopulation (see the time series in Figure 3b.1–b.2). Our results suggest that the dispersal distance is crucial in metapopulations with facilitation, since it can determine if transitions due to, for example, habitat destruction is catastrophic or continuous. An example of the abrupt transition occurring when dispersal is completely random and the associated spatio-temporal patterns are displayed in Figure 4. Here, we plot the mean population value,

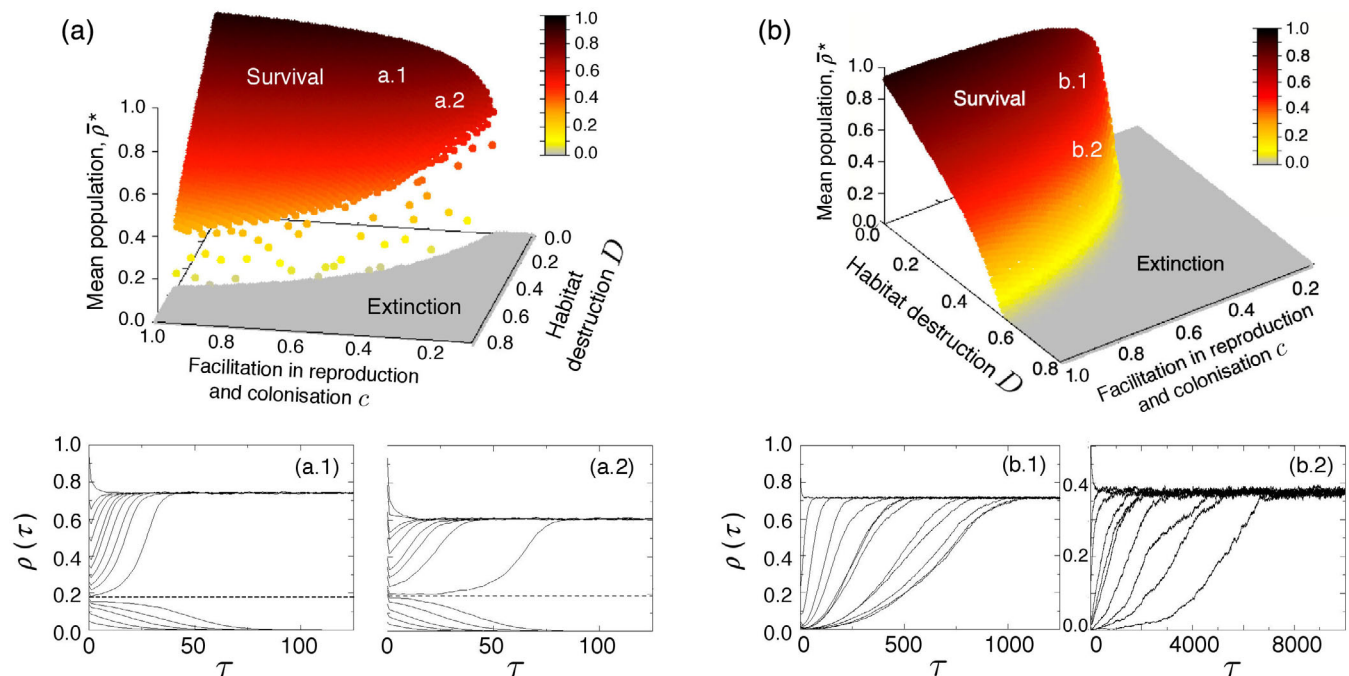


FIGURE 3 Transitions due to habitat destruction in the spatial model with facilitation in reproduction before colonization for (a) long-range (using $k = 10^4$, $\bar{\delta}(k) \approx L/2$) and (b) local dispersal (using $k = 0$, $\bar{\delta}(k) = 1$), respectively. The surface are the stationary population values for different values of D and c (here we use $e = 0.05$). Each data point is an average over 25 independent replicates at $\tau = 5 \times 10^4$ using $L = 100$. Below we display two examples of the time dynamics for both long-range and local dispersal using a battery of different initial conditions, using the combination of parameters (c , D) placed on the surfaces with letters a and b in white. For long-range colonization, the dynamics depends on the initial conditions, since for the same value of c and D , survival or extinction can be achieved due to bistability, in agreement with the mean field model (panels a.1 and a.2). For the local dispersal, however, the system becomes monostable and undergoes a continuous transition (panels b.1 and b.2)

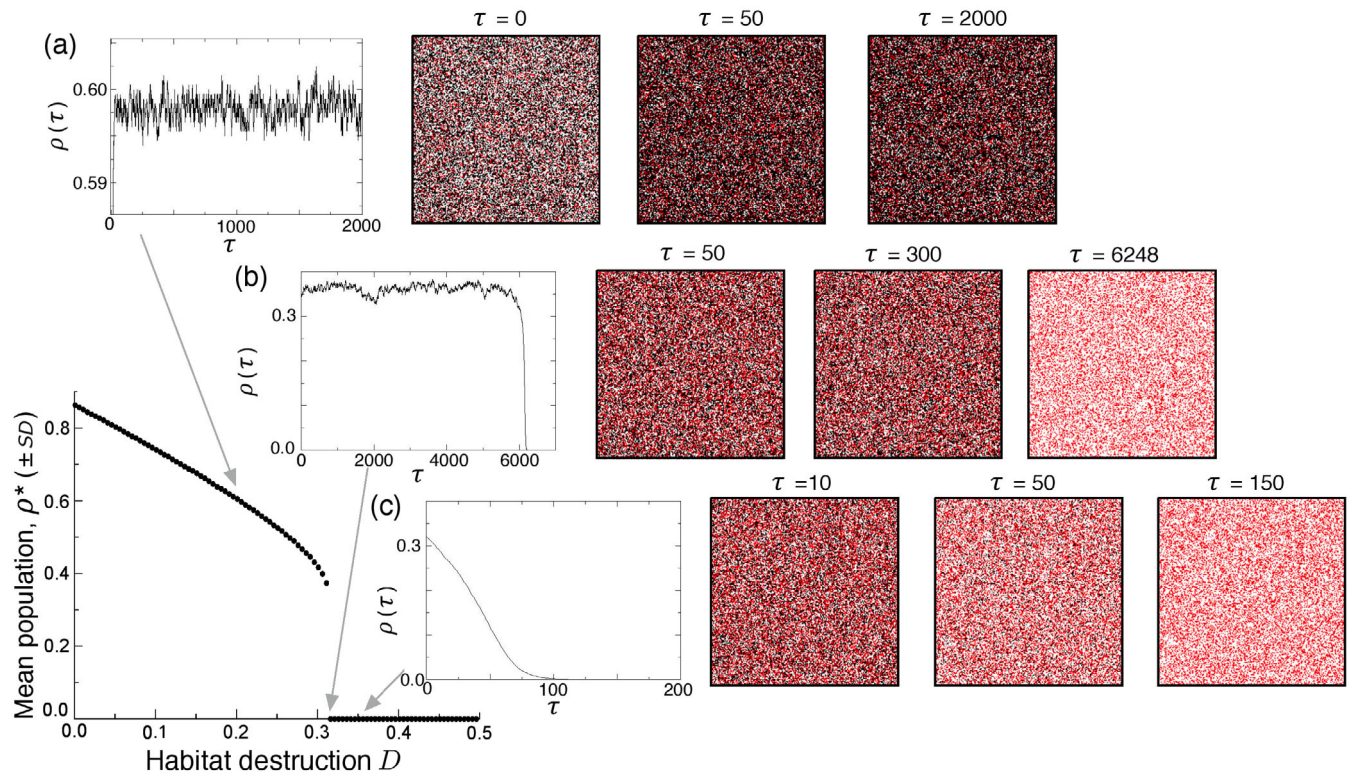


FIGURE 4 Spatio-temporal dynamics of facilitation considering random colonization (using $k = 10^4$ that is, any lattice site can be colonized with equal probability) setting $c = 0.85$, $e = 0.1$ and $L = 200$ (see figure S4a for the same analysis using smaller lattice sizes). The mean equilibrium population values ($\bar{\rho} \pm SD$, error bars are smaller than the points) are computed averaging 25 independent runs at $\tau = 5 \times 10^4$. We display three examples of different fractions of habitat destruction, D , with: (a) $D = 0.2$, (b) $D = 0.3122 \approx D_c$ and (c) $D = 0.35$. The spatial patterns display several snapshots at different generations of the CA. Here, we represent the sites occupied by an individual (black), the destroyed sites (red) and the empty sites (white)

$\bar{\rho}^*$, at increasing the fraction of habitat destruction, D , setting $L = 200$ (Figures S3a displays the same analysis using lattices of sizes $L = 50, 100$ and 150). For low values of D , the metapopulation is able to persist, and the observed spatial patterns are well-mixed. However, even for low D values, extinction can occur if the initial population values are low (see Figures S3a, S4a and S6). This is due to the existence of a separatrix corresponding the unstable branch identified with the mean field model (given by the repulsor point x_-^*). Section S3.2.1 explains how this separatrix can be systematically computed in the CA model (see below). Once the critical value of D_c is surpassed, the metapopulation suffers the catastrophic shift. Notice that near D_c the metapopulation suffers a long transient (with plateau shape, as can be seen in the mid time series of Figure 4) before collapsing. This is a fingerprint of saddle-node or fold bifurcations, where delayed transitions are known to occur near bifurcation thresholds (Fontich & Sardanyés 2008; Sardanyés & Solé 2007). Once D grows beyond D_c the transient to extinction becomes very short.

The metapopulations with local colonization form patchy aggregations, which become more disconnected and

dispersed as D approaches to the critical threshold. Figure 5 displays the same results of Figure 4 but now simulating local colonization. Here, although extinction occurs for a similar D_c value compared with the long-range colonization analysis, the transition is smooth (see also Figure S5). Similar analysis using lattices with $L = 50, 100$ and 150 are displayed in Figure S4b. The algorithm used to find the separatrix in the CA has been also applied for local colonization. Here, the separatrix has not been found, suggesting that the system under local colonization becomes monostable.

3.3 | How does the range of seed dispersal influence the extinction transitions with facilitation in reproduction under habitat destruction

The previous results have focused on two extreme cases of colonization given by purely random (long-range) colonization and local dispersal (involving the colonization of the nearest neighbors). However, several interesting questions arise from the previous results: how does the nature of the transition to extinction depend on the range of dispersal?

What is the impact of the extinction probability (e) on the nature of the transitions for different ranges of dispersal?

To address these questions we will simulate the spatial dynamics setting $k > 0$ ($\bar{\delta}(k) > 1$). Figure 6a displays results on the mean population values increasing the fraction of destroyed habitat, D (notice that we focus on a range of D values close to the extinction threshold). As mentioned, the results for $k = 0$ the transition is smooth and the critical D value is about $D_c \approx 0.35$ (Figure 6a), since the density of individuals decreases in a flat manner. However, when $k = 6$ ($\bar{\delta}(k) \approx 6.5$) the transition becomes more abrupt, being $D_c \approx 0.32$. The inset in Figure 6a displays the same results for $k = 7$ ($\bar{\delta}(k) \approx 7.5$) and $k = 11$ ($\bar{\delta}(k) \approx 11.5$), where more abrupt transitions are found. Figure S5a displays the same results for $k = 0, \dots, 11$. The previous results also indicate that the critical value D_c , which is tied to transitions of different nature, can change for different distances of colonization (see Figure 6a,b, and Figures S5a and S6). Although the differences are not very large, increasing the range of dispersal decreases D_c . However, this is not a general trend, since increasing e can reverse this situation (compare Figure 6a with Figure 6b). This effect is discussed in more detail below.

In order to distinguish between continuous and abrupt transitions several strategies could be followed. One possible approach, as previously mentioned, could be the computational search of the so-called separatrix, which is given by the unstable branch in the bistability scenario before the saddle-node bifurcation (see dashed line in Figure 2a, and Figures S3a and S4). The separatrix divides the basins of attraction of the extinction and the persistence attractors. We have developed an algorithm for finding this separatrix in the CA model. The description of this method can be found in Section S3.2.1. For the probabilities of colonization and extinction ($c = 0.85$ and $e = 0.1$) analyzed, the change from continuous to catastrophic transition is shown to take place at $k = 6$ ($\bar{\delta}(k) \approx 6.5$, see Figure S7 and Section S3.2.1 for the explanation of these results.

Up to now, we have determined that the nature of the transitions can change depending on the distance of dispersal. However, as we have previously seen, these transitions can also depend upon the model parameters (i.e., colonization or extinction probabilities). In order to explore the impact of the model probabilities we will focus on the impact that extinction probability e has in the critical D_c values and in the nature of the transitions. Figure 6b

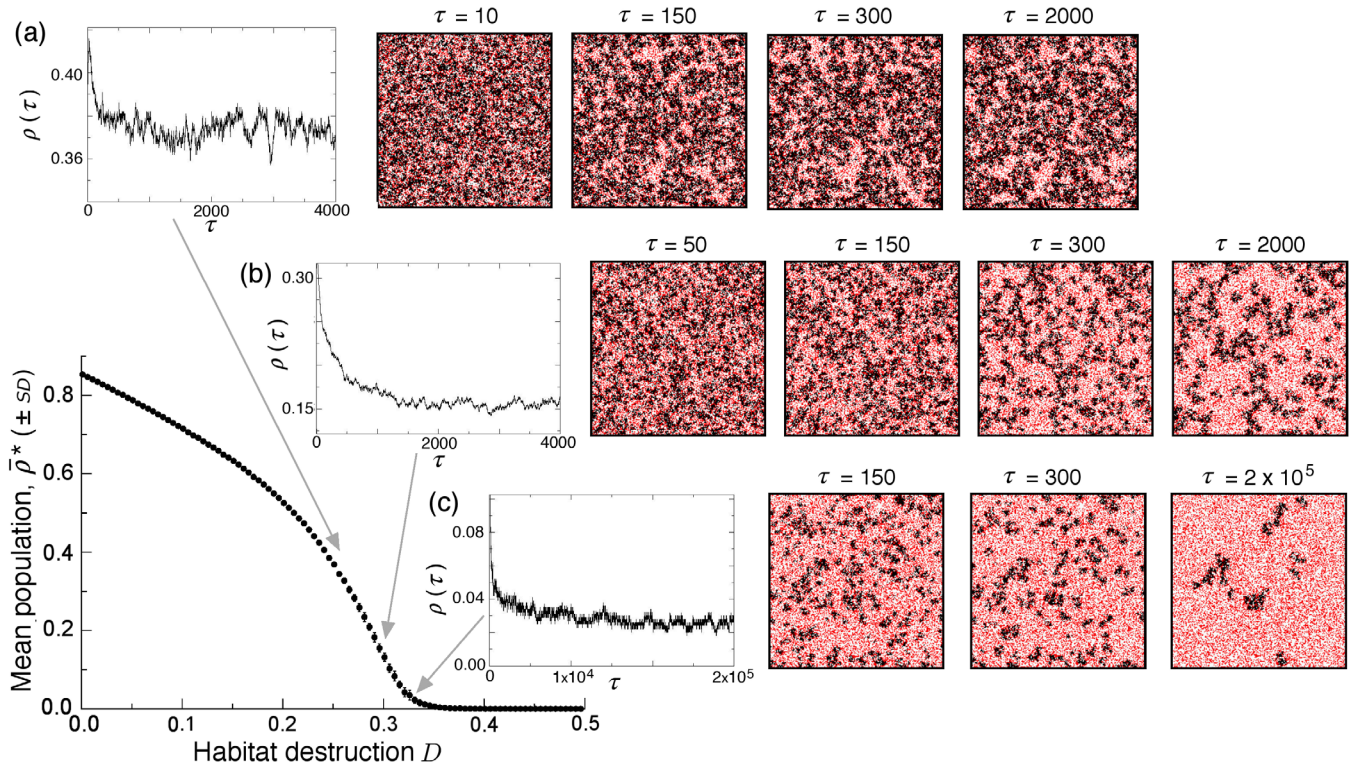


FIGURE 5 Same as in Figure 4 now considering facilitation and local colonization within the nearest neighbors (setting $k = 0$). Here we also used $c = 0.85$, $e = 0.1$ and $L = 200$ (see figure S4b for the same analysis using smaller lattice sizes). We also display several examples of the spatio-temporal dynamics for four different fractions of habitat destruction, D , with: (a) $D = 0.25$, (b) $D = 0.3$ and (c) $D = 0.33$. At increasing D , patchiness appears and become more sparse

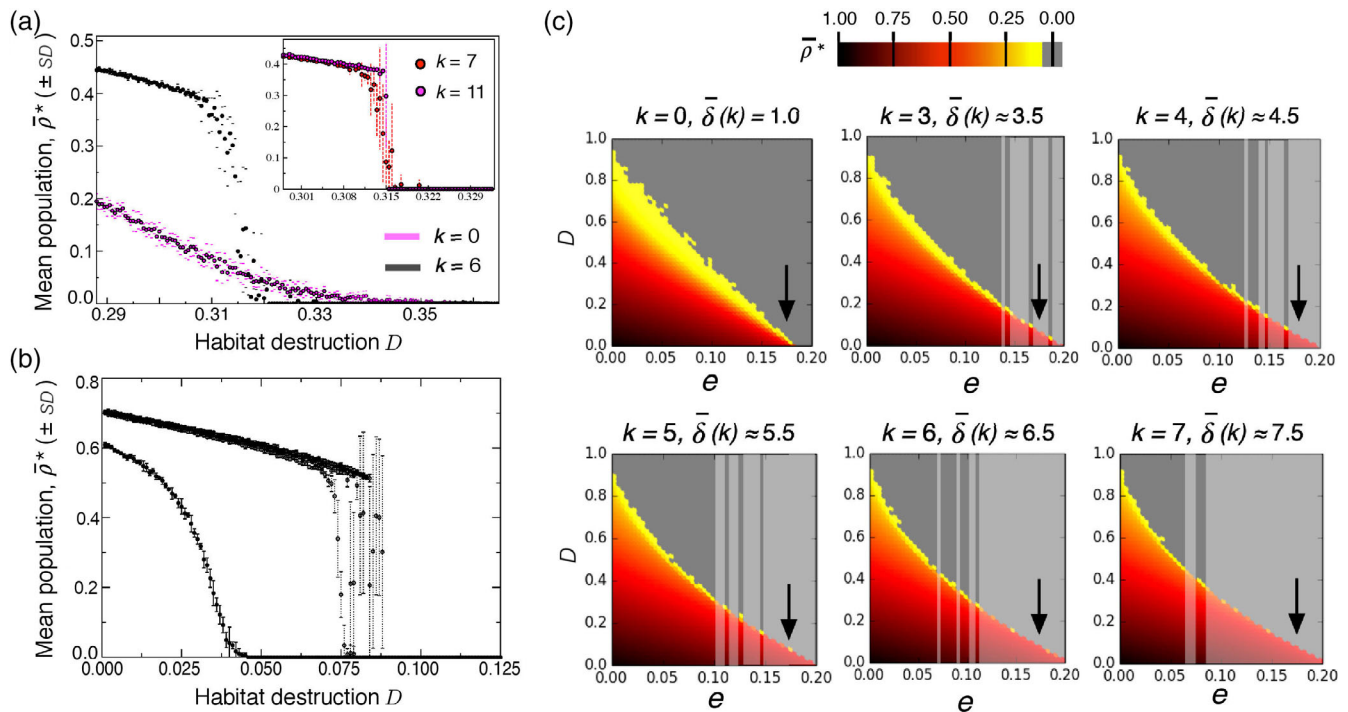


FIGURE 6 (a) Transitions toward extinction at increasing the fraction of destroyed sites using several colonization ranges changing k , with $c = 0.85$ and $e = 0.1$. Here, each data point is the mean population \bar{p}^* (and the small lines are the extremes of the $\pm SD$) averaged over five independent replicas at $\tau = 2 \times 10^5$. The main panel displays the values for $k = 0$ (local colonization) and $k = 6$, while the inset displays the same results for $k = 7$ and $k = 11$ (here the SD is displayed with dashed lines). Notice that for this combination of c and e probabilities, the continuous transition becomes discontinuous $k \approx 6$ (see Figure S6b for the same analyses using $k = 0, \dots, 11$). (b) Same as in (a) using $e = 0.175$ and different colonization ranges (from left to right): $k = 0$ ($\bar{\delta}(k) = 1$); $k = 3$ ($\bar{\delta}(k) \approx 3.5$); $k = 4$ ($\bar{\delta}(k) \approx 4.5$); $k = 5$ ($\bar{\delta}(k) \approx 5.5$); $k = 6$ ($\bar{\delta}(k) \approx 6.5$) and $k = 7$ ($\bar{\delta}(k) \approx 7.5$). (c) Mean population values in the parameter space (e, D) using $c = 0.85$ and six different values of k ($k = 0, 3, 4, 5, 6, 7$). Here, each data point is also the average of five independent runs now setting $\tau = 2 \times 10^4$. The overlapped gray bands enclose the regions where abrupt transitions are found. Notice that the change from yellow to gray corresponds to the continuous transition, while the change from red (orange) to gray accurately displays the sharp transition. In all of the plots we used $L = 200$

displays the mean population values also tuning D for different values of $\bar{\delta}(k)$, using a larger extinction probability $e = 0.175$. For local colonization (with $\bar{\delta}(k) = 1$) the transition is continuous and metapopulation extinction occurs at $D_c \approx 0.04$. However, the increase in the dispersal distance changes the continuous transition towards a more abrupt one, and the value of D_c increases up to $D_c \approx 0.08$ (Figure 6b). This counterintuitive result highlights the importance of the difficulties in predicting the changes of the system under nonlinearities together with spatial and stochastic dynamics.

Figure 6c displays the impact of the dispersal distance and extinction probabilities (analyses in the parameters space $[e, D]$) in the mean density of the metapopulation as well as in the nature of the transitions. For local colonization, the transition is shown to be continuous for all the analyzed ranges of e , here with $0 \leq e \leq 0.2$. Notice that a continuous transition occurs in the boundaries of the triangle inside the space (e, D) with yellow color, since yellow color indicates close to zero values and thus no catastrophic jump

is found. For all of the boundaries with orange or red color the jump can be considered abrupt. Specifically, those values of e causing a catastrophic transition have been framed with a transparent gray area in Figure 6c. The arrows in the panels of Figure 6c indicate the transitions for $e = 0.175$, which are displayed in Figure 6b plotted with standard deviation indicated with dashed lines. Finally, in Figure S6b we display the change in the mean population values at increasing the extinction probability considering local colonization. Here we must notice that the catastrophic shift only takes place for $D = 0$. Once the habitat starts to be destroyed the transition switches to a continuous one.

3.4 | Spatially-explicit dynamics and extinction transitions with facilitation in seeds establishment under habitat destruction

A second model considering facilitation during the establishment after colonization is analyzed here. In the previous model, seeds were able to colonize non-destroyed, empty

sites and then reproduce in a density-dependent manner. In the system investigated here, facilitation will enhance the establishment of the seeds, finding good conditions for its establishment. However, reproduction will not depend on facilitation (see Figure S8 for a schematic diagram of this system). As we will show below, the dynamics for this system is similar to the one previously analyzed, although some differences in the extinction transitions are found.

Now the CA model needs to be slightly modified to simulate these ecological processes. The state-transition rules of this model are explained in Section S4.1. Although similar to the previous model, facilitated establishment becomes more sensitive to extinction. For instance, the impact of extinction rates, e , in the mean population is stronger compared to the system previously analyzed. In Figure S9, we plot the mean population of occupied sites increasing extinction probabilities using different fractions of habitat destruction. The extinction thresholds are found for lower values of e and the same tendencies are observed for decreasing values of D . We notice that transitions for $D > 0$ are also continuous, while the extinction for $D = 0$ is abrupt, as we found in the previous model with facilitation in reproduction. The value at which the catastrophic shift takes place for this second model is $e \approx 0.164$, compared to the value obtained for the model with facilitated reproduction given by $e \approx 0.184$.

The differences in the critical values of the probabilities causing metapopulation extinction for this second model are also observed tuning the fraction D of habitat destruction. These differences can be seen in Figures S9 and S10, where we plot the mean population of occupied sites increasing D . These data are shown overlapped to the same analysis obtained with the model considering facilitation in reproduction (displayed with small gray circles). Figure S9 displays the results for long-range colonization. For this particular analysis, the extinction occurs at $D \approx 0.26$ for the model with facilitated establishment, while the critical D value for the model with facilitated reproduction is $D \approx 0.315$. The spatial patterns for long-range colonization are also random like distributions of the occupied sites (Figure S10). This second model with local colonization also displays patches of occupied sites, although the distribution of these patches is sparser compared with the same analyses developed for the model with facilitated reproduction (Figure 5) due to the higher sensitivity of this second system (see Figure S11).

4 | DISCUSSION

Local facilitation among individuals in a spatially-extended landscape pervades the presence of strong nonlinearities and the potential for tipping points (e.g., extinction transitions due to ecological or environmental changes such as increased aridity or global warming). These extinctions, as

some theoretical models incorporating facilitation between plants indicate, could be discontinuous as the ecological or environmental parameter changes. One particularly relevant case study is provided by semi-arid ecosystems. As grazing or aridity increase, vegetation and soil quality levels decay until bifurcations are reached, resulting in catastrophic shifts (Kéfi S, Rietkerk M, Alados CL, et al. 2007; Kéfi S, Rietkerk M, van Baalen M, et al. 2007). On the other hand, habitat loss and fragmentation interact with other types of nonlinearities associated with the presence of facilitation effects. In this paper we brought together both habitat loss and positive interactions with the goal of exploring the potential transitions to extinction. Both well-mixed (non-spatial, mean field) and spatially extended models are considered.

We have built a minimal theoretical model incorporating positive interactions due to facilitation and fragmentation, also including competition between individuals and extinction processes. This model, which resembles to the classical Levins model and includes a nonlinear colonization function due to facilitation effects, allows to understand the expected impact of both habitat loss (as given by the D parameter) and facilitated colonization (given by constant c) in the dynamics and the transitions of this system. A closed analytical result of the potential function predicts a sudden shift once a habitat destruction threshold is reached, being this threshold different from the one predicted by the standard Levins model with habitat loss. In the later the transition is smooth and continuous, whereas in our model it leads to a discontinuous (catastrophic) shift.

The importance of spatial correlations on the dynamical outcomes in evolutionary ecology (Bascompte and Solé 1995; Dytham 1995; Berdugo et al. 2017) and pathogens dynamics (Sato et al. 1994; Wodarz & Levy 2011) has been a matter of debate and intensive research over the last decades. By extending our model to a spatial, stochastic scenario, a different type of transition has been found. When long-range dispersal is considered, a discontinuous shift is still found. Departures from the mean field predictions are known to occur when the role played by space becomes explicit (see for example, Bascompte and Solé 1996; Mendonça 2018). However, in this case the difference goes far beyond a displacement of the parameters associated with the transitions: the nature of the transition itself is changed and no catastrophic shift is observed separating the survival from the extinction phases. Such qualitative change in the nature of the transition resulting from short versus long dispersal is likely to be similar to those found in the study of other nonlinear systems under dimensionality changes. This has been studied in models of trimolecular reactions (Prakash & Nicolis 1996, 1997, Provata et al. 1993, Windus and Jensen 2007). More recently, a theoretical analysis of the so called

Ginzburg-Landau model (Weissmann and Shnerb, 2014), given by:

$$\frac{dx}{dt} = -\alpha x + \beta x^2 - \gamma x^3 = \Gamma(x),$$

has been studied in order to explore catastrophic desertification (Weissmann et al. 2017) as well as potential ways of avoiding catastrophic shifts (Villa Martín et al. 2015). Clearly our model belongs to this general class. Mapping our parameters into the previous ones as follows: $\alpha \rightarrow e$, $\beta \rightarrow c(1 - D)$, $\gamma \rightarrow c$, one obtains Equation (5). By expanding this model into a stochastic spatial counterpart, it is possible to actually explore the effect of different factors on the nature of transitions (Goldenfeld 2018). This was done by analyzing the behaviour of

$$\frac{\partial x(r, t)}{\partial t} = \Gamma(x(r, t)) + D \nabla^2 x(r, t) + \eta(r, t), \quad (7)$$

where the two last terms at the right hand side of Equation (7) are the diffusion and noise terms associated with the spatiotemporal dynamics, r being a spatial coordinate. Equation (7) predicted that limited diffusion (which they can treat as a continuous parameter) can transform the catastrophic shift into a continuous phase change, as it occurs in our model. Local colonization in our system can be interpreted as a limited diffusion process since new individuals establish in the surrounding of the reproducing plants that is, their diffusion is rather small. This strategy has been widely described in semiarid ecosystems (see below).

In our study, instead, we can actually look at this in an adaptive context (see also Kéfi et al. (2008) for an evolutionary analysis of facilitation and dispersal in arid ecosystems). The risks associated with vegetation loss due to grazing or aridity (factors increasing soil degradation) might have pushed species living in semi-arid conditions to evolve local dispersal that will lead to patchiness while effectively removing the presence of a catastrophic bifurcation. In this sense, many examples of plants exhibiting short-range colonization (engychory) have been described in arid and semi-arid ecosystems. The community-specific soil water conditions have been suggested to strongly determine colonization and reproductive mechanisms (Hensen 1997). The presence of short-range plant dispersal strategies is well established in different communities with low precipitation and extreme habitat conditions such as for example, in the xeromorphic dwarf-shrublands (e.g., *Fagonia bruguieri* community) and rock deserts (e.g., *Gimnocarpus decandrus* community) in the Arabian Peninsula (Frey & Kürschner 1987). Also, engychory has been described in multiple species in xerothermic grasslands (e.g., *Stipetum capillatae* s.l., *Adonido-Brachypodium*

pinnati community) (Hensen 1997). This community is typically found in parts of Central and Northeastern Germany.

Finally, we want to note that a smooth transition would not only prevent severe population extinctions but also favor the identification of species approaching to extinction. For the discontinuous extinction the population goes from a large equilibrium density to extinction in a sudden manner. This is not the case for a continuous transition, where one may detect how the population approaches to extinction gradually.

The take-home message of our investigations is two-fold. First, facilitation processes introduce positive feedbacks in colonization that change the smooth transition of the Levins model with habitat degradation to a catastrophic shift. Second, local dispersal strategies can revert the catastrophic nature of the transition to a continuous one. Hence, our predictions indicate that ecosystems with facilitation in plants undergoing long-distance dispersal (more prone to suffer a catastrophic shift) should be monitored more carefully under slight changes in habitat destruction.

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