Received: 18 August 2022 | Revised: 30 May 2023 | Accepted: 17 July 2023

DOI: 10.1002/eap.2910

ARTICLE

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

Introducing desirable patches to initiate ecosystem transitions and accelerate ecosystem restoration

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Funding information
NSF, Grant/Award Numbers: DEB-1556664, DEB-1738041, OIA-1656006; University of Zurich; University Research Priority Program

Handling Editor: Stephen B. Baines

Abstract

Meeting restoration targets may require active strategies to accelerate natural regeneration rates or overcome the resilience associated with degraded ecosystem states. Introducing desired ecosystem patches in degraded landscapes constitutes a promising active restoration strategy, with various mechanisms potentially causing these patches to become foci from which desired species can re-establish throughout the landscape. This study considers three mechanisms previously identified as potential drivers of introduced patch dynamics: autocatalytic nucleation, directed dispersal, and resource concentration. These mechanisms reflect qualitatively different positive feedbacks. We developed an ecological model framework that compared how the occurrence of each mechanism was reflected in spatio-temporal patch dynamics. We then analyzed the implications of these relationships for optimal restoration design. We found that patch expansion accelerated over time when driven by the autocatalytic nucleation mechanism, while patch expansion driven by the directed dispersal or resource concentration mechanisms decelerated over time. Additionally, when driven by autocatalytic nucleation, patch expansion was independent of patch position in the landscape. However, the proximity of other patches affected patch expansion either positively or negatively when driven by directed dispersal or resource concentration. For autocatalytic nucleation, introducing many small patches was a favorable strategy, provided that each individual patch exceeded a critical patch size. Introducing a single patch or a few large patches was the most effective restoration strategy to initiate the directed dispersal mechanism. Introducing many small patches was the most effective strategy for reaching restored ecosystem states driven by a resource concentration mechanism. Our model results suggest that introducing desirable patches can substantially accelerate ecosystem restoration, or even induce a critical transition from an otherwise stable degraded state toward a desired ecosystem state. However, the potential of this type of restoration strategy for a particular ecosystem may strongly depend on the mechanism driving patch dynamics. In turn, which mechanism drives patch dynamics may affect the optimal spatial design of an active restoration strategy. Each of the three mechanisms considered reflects distinct spatio-temporal patch dynamics, providing novel opportunities for empirically identifying key mechanisms, and restoration designs that introduce desired patches in degraded landscapes according to these patch dynamics.

KEYWORDS
ecological modeling, ecosystem restoration, nucleation theory, patch introduction, plant community dynamics, restoration strategy, spatial dynamics

INTRODUCTION

Introducing patches of desired species has become a popular practice in restoration ecology (Angelini & Silliman, 2012; Bechara et al., 2016; Holl et al., 2020; Hulvey et al., 2017; Michaels et al., 2022). Theoretical studies suggest that through a variety of feedback mechanisms, this type of active restoration strategy may provide an effective means to promote the establishment and spread of desired species at the landscape scale (Caughlin et al., 2016; Meron 2016; Michaels et al., 2020). However, we lack a theoretical framework that systematically compares the effects of different feedback mechanisms on patch dynamics that could be observed empirically. As a result, it is difficult to attribute empirical observations of introduced patch dynamics to specific mechanisms (Larsen et al., 2014; Matzek et al., 2017). Such mechanistic understanding is needed to effectively design restoration strategies relying on the introduction of desired species patches (Michaels et al., 2022).

Effective design of restoration strategies is urgently needed to reverse the ecosystem impacts of past land use changes, as recognized by the UN Decade of Ecosystem Restoration (Aronson et al., 2020; Fischer et al., 2020). Passive restoration practices, which include changing land use practices to allow for natural regeneration, may provide a feasible and economically viable strategy to restore ecosystems and their associated functions (Cole et al., 2020; Crouzeilles et al., 2017). However, the time spans needed to achieve ecosystem restoration through natural regeneration may not be sufficient to meet current restoration targets (Bechara et al., 2016; Holl, 2017). Hence, there is an interest in developing active restoration strategies, such as planting schemes, that can enhance the natural regeneration rates of degraded ecosystems (Bechara et al., 2021; Holl et al., 2020; Meli et al., 2017).

Restoration may be even more challenging when the ecosystem degradation process involves a critical transition toward an alternative stable ecosystem state (Michaels et al., 2020; Rietkerk et al., 2004; Suding et al., 2004). In these cases, the degraded state is resilient to typical perturbation regimes, meaning that passive restoration strategies may not be sufficient to initiate regeneration to the desired ecosystem state (Suding et al., 2004). Instead, restoration efforts may need to go beyond restoring abiotic environmental conditions, by reintroducing foundation species in a manner that creates internal feedbacks that are strong enough to drive the system to the desired ecosystem state (Rietkerk et al., 2004; Suding et al., 2004; Angelini & Silliman, 2012). An example of the latter feedback relationships involves foundation plant species that can modulate environmental conditions, promoting their own growth and of other desired species and thereby initiating a development toward the desired ecosystem state (Jones et al., 1994; Rietkerk et al., 2004; Angelini & Silliman, 2012). Initiation of such feedback may require (re-)introducing foundation species above a critical frequency threshold, at which the positive feedback between improved environmental conditions and enhanced growth is activated (Rietkerk et al., 2004; Suding et al., 2004).

Active restoration strategies may involve the introduction of patches of the desired system state within a degraded landscape. This may be a patch of desired plant species planted within an area where an undesired plant community dominates. These desired patches can then serve as foci from which the desired species can reestablish in the landscape. When successful, these patches may not only persist in the landscape, but also create sufficient propagule pressure to enable patch expansion, thereby initiating a transition toward the desired ecosystem state at the landscape scale (Michaels et al., 2020). Within this context, it is important to note the distinction between the spatial scale governing patch edge dynamics, which depends on the interaction neighborhood of the sessile organisms within the vicinity of the patch edge, and the larger landscape scale at which the outcome of the restoration effort is evaluated (Michaels et al., 2020). Spatially averaged, landscape-scale descriptions may obscure leading indicators of ecosystem transitions evident at patch edges (Allstadt et al., 2007; Eppstein et al., 2006). Ignoring leading indicators at the local scale of patch edges could lead to less efficient allocation of management resources (Eppinga et al., 2021; Moody & Mack, 1988). Therefore, theoretical assessments of active restoration strategies require spatially explicit frameworks that enable the modeling of mechanisms considered to be important drivers of local patch dynamics. Such frameworks may elucidate how the effects of driving mechanisms on local patch dynamics are mediated by the initial sizes of the patches themselves, and their position relative to other patches in the landscape (Bernik et al., 2018; Eppinga et al., 2021; Michaels et al., 2020).

The possibility of positive feedback mechanisms driving the dynamics of local patches formed by different plant communities has long been recognized (Eppinga, Rietkerk, et al., 2009; Frenzel, 1983; Wilson & Agnew, 1992). For example, positive feedback may emerge when two plant communities each modify the environment to their own advantage and to the disadvantage of the other, either by changing the same environmental variable in opposite directions, or by changing different environmental variables. In grassland systems, this kind of feedback may occur when competing foundation species of different communities modify the soil environment in ways that stimulate their own growth, by changing the abundance and composition of arbuscular mycorrhizal (AM) fungi (Koziol & Bever, 2019). For forest ecosystems, it has been suggested that similar feedback may occur involving foundational tree species that associate either with AM or ectomycorrhizal fungi (Averill et al., 2022). Due to this type of feedback, the two system states in which one type of foundation species dominates may be alternative stable equilibrium states. Within a restoration context, one of these communities may be considered the desired ecosystem state, while domination of the other plant community may be considered a degraded ecosystem state. In this case, the expansion of patches of the desired plant community may be triggered by an autocatalytic nucleation mechanism (Michaels et al., 2020, 2022). Autocatalytic nucleation can occur when the desired state and the degraded state are alternative stable landscape-scale equilibria, and where the unstable equilibrium point between these states occurs at a frequency of the desired community that is less than 50% across the landscape (Michaels et al., 2020). Under these conditions, the unstable landscape-scale equilibrium point can be related to a critical local patch size above which the desired community is able to expand at the patch edge. Expansion of this local patch can then initiate a transition toward the desired state at the landscape scale (Michaels et al., 2020).

Second, we can distinguish feedback that emerges when only one plant community modifies the environment to its own advantage. A prominently studied example of this feedback involves emerging forest or shrub patches, which may enhance the local seed rain by attracting seed-dispersing animals from the surrounding landscape (Fujita, 2016; Pausas et al., 2006; Toh et al., 1999; Verdu & Garcia-Fayos, 1996). The result of this directed dispersal mechanism is an increase in seed rain that may enhance the colonization of trees and shrubs, which may accelerate the expansion of the patch (Bechara et al., 2021; Caughlin et al., 2016; Cole et al., 2010; Holl, 1998; Holl et al., 2020; Zahawi et al., 2013).

Third, we can distinguish a feedback that emerges when one plant community modifies the environment within the patch to its advantage, while changing the environment in the opposite direction (and thus to its disadvantage) farther away from the patch. A prominently studied example of this feedback involves plant communities in arid ecosystems, which increase water infiltration rates into the soil and thereby direct larger scale surface water flows toward vegetated patches, increasing water uptake in these patches (Rietkerk et al., 2004; Rietkerk & Van de Koppel, 2008). Another example is found in boreal peatland ecosystems, where trees and shrubs may increase evapotranspiration rates and thereby directing larger scale soil water and dissolved nutrient flows toward patches dominated by trees and shrubs storing these nutrients (Eppinga, de Ruiter, et al., 2009; Rietkerk et al., 2004). This resource concentration mechanism improves the community's growth conditions within the patch, but reduces growth conditions at larger spatial scales where resource availability is depleted. The result is a scale-dependent feedback (positive on the short range, negative on the longer range), which may create a landscape containing a spatially regular mosaic with regular spacing between desired patches (Eppinga et al., 2022; Inderjit, Callaway, & Meron, 2021; Rietkerk et al., 2004; von Hardenberg et al., 2001).

Until now, autocatalytic nucleation, directed dispersal, and resource concentration mechanisms have only been studied in separate theoretical frameworks (Caughlin et al., 2016; Michaels et al., 2020; Rietkerk et al., 2004). We thus lack a theoretical framework that systematically compares the effects of these three mechanisms on patch dynamics that could be observed empirically. Such systematic comparisons are needed in order to link empirical observations of patch dynamics to specific mechanisms (Larsen et al., 2014; Matzek et al., 2017). Moreover, it remains uncertain how optimal designs of spatial restoration strategies depend on the specific mechanism driving the dynamics of introduced patches. We aimed to develop a spatially explicit model framework that was flexible enough to include autocatalytic nucleation, directed dispersal, or resource concentration as the driver of patch dynamics. We framed our analyses within a restoration context, in that we considered the introduction of patches dominated by desired foundation species within a landscape dominated by undesired species. Specifically, we utilized this framework to answer the following research questions: (1) How does the rate of patch expansion depend on the driving mechanism governing patch dynamics? (2) To what extent does the driving mechanism of patch dynamics interact with the introduced patch' position, relative to other patches, within the landscape? (3) To what extent does the optimal spatial restoration strategy depend on the driving mechanism governing patch dynamics?

MATERIALS AND METHODS

Description of the general model framework

We developed a stochastic cellular automaton model to describe the expansion of introduced (desired) patches of a particular plant community, within a landscape matrix dominated by another (undesired) resident plant community. Space was discretized as a square-tiled lattice with n rows and columns, in which each tile could be in one of two states: dominated by the introduced community (i.e., the tile state $S = 1$), or dominated by the resident community ($S = 2$). Lattice edges were wrapped into a torus; such periodic boundary conditions are a common choice for the types of models considered here (e.g., Larsen et al., 2016). Following a previous study (Michaels et al., 2020), we focused on plant community patch dynamics that are similar to diffusive spread (i.e., we assume that dispersal and interactions between communities occur on the local scale between adjoining tiles). Within the stochastic cellular automaton framework utilized here, this approach was incorporated by limiting potential state transitions to tiles that occur adjacent to boundaries representing transitions in vegetation (e.g., Eppinga et al., 2013) between the two plant communities during the timestep considered (Figure 1a,c,e). Through this assumption, we thus considered that the establishment of plant communities was constrained by local propagule pressure. This assumption is a simplification, as long-distance dispersal events could also trigger colonization outside of vegetation boundaries and at random locations within the landscape (Caughlin et al., 2016; Eppinga et al., 2013). Hence, our current theoretical framework focuses on landscapes in which the expansion or contraction of patch edges is the dominant driver of vegetation change, compared with background colonization rates within the larger landscape. This focus provides the conditions under which the effects of different mechanisms on spatio-temporal patch edge dynamics can be most clearly observed (Larsen et al., 2014). Following Molofsky and Bever (2002), the transition probability of an individual tile adjacent to vegetation transition boundaries can then be described by:

$$
\begin{aligned}
P_{2\to 1,x_i,y_j,t} = {} & h_{1,x_i,y_j,t}\left(f_{1,x_i,y_j,t}\right) f_{1,x_i,y_j,t}\left(K_I\left(x_i - x', y_j - y'\right)\right) \\
& \left[h_{1,x_i,y_j,t}\left(f_{1,x_i,y_j,t}\right) f_{1,x_i,y_j,t}\left(K_I\left(x_i - x', y_j - y'\right)\right)\right. \\
& \left. + h_{2,x_i,y_j,t}\left(f_{2,x_i,y_j,t}\right) f_{2,x_i,y_j,t}\left(K_I\left(x_i - x', y_j - y'\right)\right)\right]^{-1} \\
& \Omega_{x_i,y_i,t} \qquad (1)
\end{aligned}
$$

It is important to note that the above transition probability is a function of the states of tiles surrounding the focal tile. Here, the number of surrounding tiles that affect the transition probability of the focal tile is determined by the size of the local interaction neighborhood. The vegetation composition within this local interaction neighborhood is incorporated in Equation (1) through $f_{1,x_i,y_j,t}$ and $f_{2,x_i,y_j,t}$, which indicate the frequency of tiles of each community within the interaction neighborhood of the focal tile at row x_i and column y_j of the lattice, at time t. Within the model framework, we assume that the ability of a particular plant community to expand depends on the fitness of a foundation species supporting the other species of the community, possibly through modification of the local environment (e.g., Ellison et al., 2005; Rietkerk et al., 2004). Hence, $h_{1,x_i,y_j,t}$ and $h_{2,x_i,y_j,t}$ indicate the fitness of each community's foundation species, which is based on the frequencies of both types of foundation species within the interaction neighborhood of the focal tile (i.e., $f_{1,x_i,y_j,t}$ and $f_{2,x_i,y_j,t}$). It should be noted that Equation (1) shows that the effects of foundation species on environmental variables were not explicitly modeled, but incorporated into the local spatial density-dependent fitness components of each foundation species. Finally, transitions only occur for those tiles in the lattice that are adjacent to the vegetation transition boundary at time t, indicated with the Boolean operator $\Omega_{x_i,y_j,t}$ in Equation (1). When computing $\Omega_{x_i,y_j,t}$, we used radial kernel smoothing to avoid artifacts in patch expansion dynamics due to the spatial discretization into square tiles (see Appendix S1: Section S1.1 for details). The width of this kernel determined the width around the patch where expansion could occur (i.e., the yellow zones around introduced patches in Figure 1a,c,e). For the default simulations, the kernel was relatively narrow, so that only directly adjacent tiles were selected. In the Supplementary Information, we analyzed how model results were affected by assuming wider kernels allowing for farther spread from the current patch edge and showing general consistency in results (for details see Appendix S1: Section S1.1, Figures S1–S3).

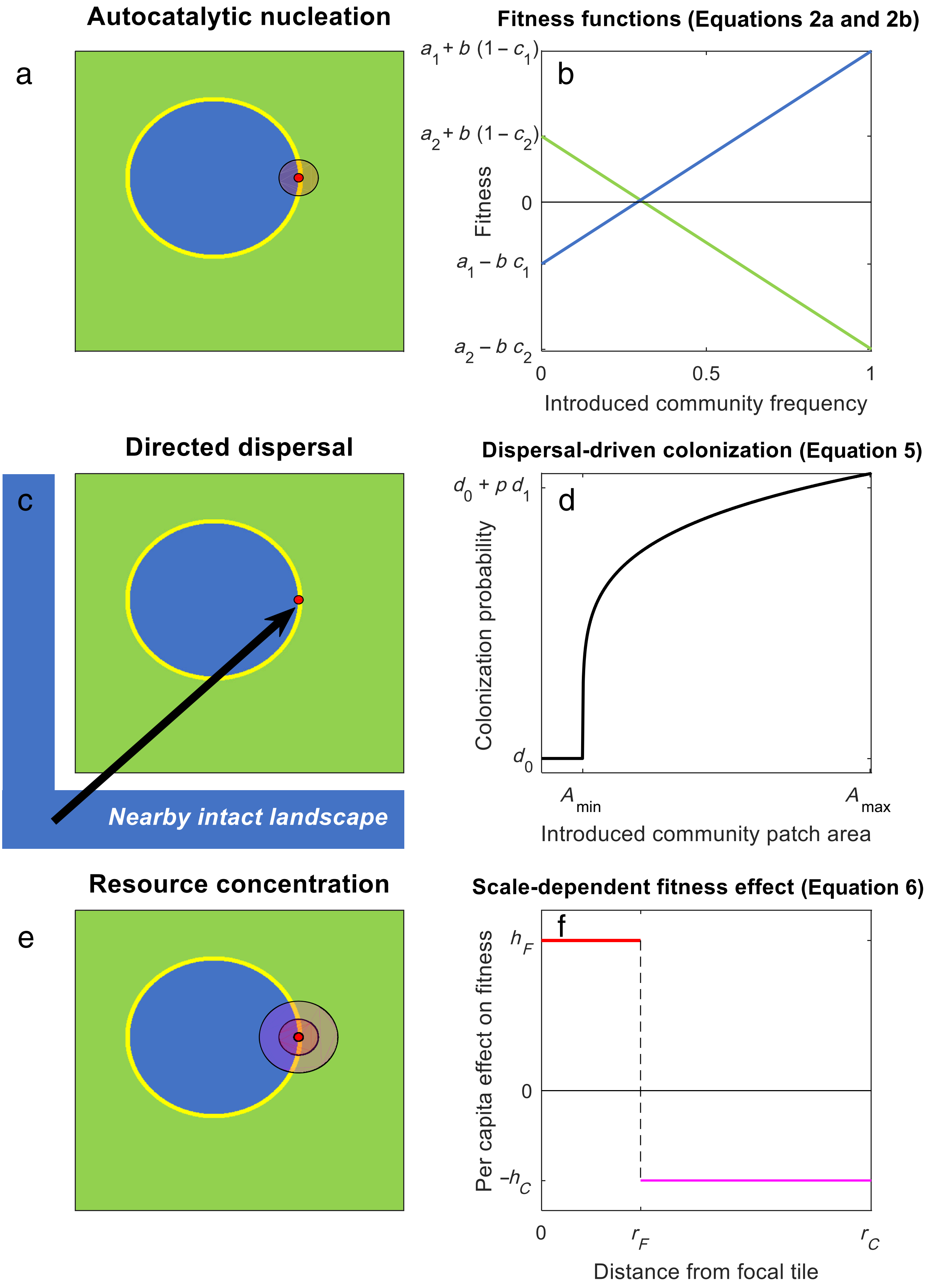

FIGURE 1 Legend on next page.

We assumed that plant community interactions occurred on the same spatial scale for both communities (Molofsky & Bever, 2002). The kernel K_I described this interaction neighborhood around each focal tile. In contrast with previous approaches that used square kernels (e.g., Mack & Bever, 2014; Molofsky & Bever, 2002; Rietkerk et al., 2004), we used radial kernels to mimic that plants' belowground and aboveground biomass typically follow a circular distribution, over which they interact with other plants (Michaels et al., 2020). When none of the three ecological feedback mechanisms was considered, the fitness of the two communities was equal and frequency independent, that is, $h_{0,1} = h_{0,2} = 0.5$. With this parameter setting, Equation (1) reduces to a simple neutral model of two interacting plant communities. In the next subsections, we explain how each of the three ecological feedback mechanisms considered (Figure 1) was included in the model framework through particular adjustments of foundation species' fitness terms. While in real ecosystems multiple feedback mechanisms may occur simultaneously, we focused our simulations on studying the impact of each mechanism in isolation. This approach provided the most straightforward theoretical expectation of how the occurrence of each mechanism would be reflected in emerging system dynamics (Larsen et al., 2014).

Modeling the autocatalytic nucleation mechanism

The autocatalytic nucleation mechanism is driven by local-scale positive feedback (Michaels et al., 2020). Within the context of competitive interactions between plant communities, such feedback can be driven by foundation species that have higher fitness when present in higher densities (e.g., Hulvey & Zavaleta, 2012; Molofsky & Bever, 2002). This type of feedback (Figure 1b; Molofsky & Bever, 2002; Michaels et al., 2020) can be included in the fitness function as:

$$h_{1,x_i,y_i,t} = a_1 + b\left(f_{1,x_i,y_i,t}\left(K_I(x_i - x', y_i - y')\right) - c_1\right), \tag{2a}$$

$$h_{2,x_i,y_i,t} = a_2 + b\left(f_{2,x_i,y_i,t}\left(K_I(x_i - x', y_i - y')\right) - c_2\right). \tag{2b}$$

In which a_i indicate the frequency-independent fitness components, and b indicates the feedback strength. The parameters c_i describe the critical frequencies above which communities reinforce their own growth (Figure 1b; Michaels et al., 2020). The frequencies of the two plant communities, $f_{i,x_i,y_i,t}$, are determined within the local interaction neighborhood of each focal tile, according to:

$$f_{1,x_i,y_j,t} = \frac{1}{n^2}\sum_{k=1}^{n}\sum_{l=1}^{n} H\left(2 - S_{x_k,y_l,t}\right) K_I\left(x_i - x_k, y_j - y_l\right), \tag{3a}$$

$$f_{2,x_i,y_j,t} = \frac{1}{n^2}\sum_{k=1}^{n}\sum_{l=1}^{n} H\left(S_{x_k,y_l,t} - 1\right) K_I\left(x_i - x_k, y_j - y_l\right), \tag{3b}$$

where $H(x)$ indicates the Heaviside step function, that is, $H(x > 0) = 1$ and $H(x \leq 0) = 0$. In Equations (3a) and (3b), K_I is a radial uniform kernel:

$$K_I\left(x_i - x', y_j - y'\right) = H\left(r_I - \sqrt{(x_i - x')^2 + \left(y_j - y'\right)^2}\right). \tag{4}$$

In which r_I indicates the radius of the interaction neighborhood around each focal tile. In a previous study,

FIGURE 1 Overview of the theoretical model framework. The baseline model comprises a neutral competition model between two plant communities, with one community (in blue) being introduced into a landscape dominated by another community (green). Interactions between the two communities occur around the edges of plant community patches (yellow). These interactions are driven by one of three mechanisms: autocatalytic nucleation (top row, a, b), directed dispersal (middle row, c, d) and resource concentration (bottom row, e, f). For each mechanism the left column (a, c, e) illustrates the processes involved in determining the transition probability (toward the introduced community state) of a focal tile at the edge of the introduced patch (red dots). For the autocatalytic nucleation mechanism, this transition probability depends on the fitness of the introduced community, which in turn depends on the frequency of the introduced community around the focal tile (red circle). The higher this frequency, the higher the fitness, as shown by the blue line in the right panel (b). This function is described by the Equations (2a) and (2b) in the main text. For the directed dispersal mechanism, the transition probability depends on the colonization probability of the introduced community at the focal tile, which in turn depends on the seed influx from the nearby intact landscape(s) (black arrow). Seed influx only increases beyond the background rate once the introduced patch exceeds a critical patch size (described by Equation 5 in the main text), as also shown in the right panel. For the resource concentration mechanism, the transition probability depends on fitness of the introduced community in the focal tile, which increases with the frequency of the introduced community within the local interaction neighborhood, following the autocatalytic nucleation mechanism. In this case, however, there is a larger, surrounding neighborhood considered as well, in which individuals of the introduced community exert a negative effect of fitness in the focal tile (described by Equation 6 in the main text). This latter process is thus a long-range negative effect on fitness. The interpretation of parameters on the *x*- and *y*-axes of the panels in the right column is provided in the main text.

Equations (2)–(4) were implemented using a deterministic framework, for which the critical patch size could be derived analytically (Michaels et al., 2020). Introduced patches smaller than the critical patch size will contract and disappear, while introduced patches exceeding the critical patch size will expand until the entire landscape is covered (Michaels et al., 2020). In other words, patch expansion success is a step function of the introduced patch size in the deterministic framework. In the current study, we utilized a stochastic framework instead. Stochasticity will not affect the success of patches that are substantially smaller or larger than the critical patch size. However, for a small range of sizes around the critical patch size, both the patch size and stochasticity will determine whether an introduced patch expands or not. As a result, patch expansion success becomes a sigmoidal function of the introduced patch size (Allstadt et al., 2007). While this sigmoidal function did approach a step function for the stochastic model version of autocatalytic nucleation, complete expansion success was observed for patches that were slightly below the critical patch size predicted analytically for the deterministic model version (for details see Appendix S1: Section S1.2; Figure S2).

Modeling the directed dispersal mechanism

Our approach of including the directed dispersal mechanism in the model framework is based on a previous study by Caughlin et al. (2016), who considered canopy cover dynamics of forested patches within the landscape, and potential feedback effects between canopy cover and seed rain within the patch (Figure 1c). Specifically, as a patch increases in size, seed rain may increase due to higher within-patch seed production or due to increased attraction of seed-dispersing animals (Figure 1d, Bechara et al., 2021; Corbin & Holl, 2012; Holl, 1998; Holl & Zahawi, 2014; Zahawi et al., 2013). When considering dispersal by disturbance-resistant animals such as small birds, directed dispersal may increase relatively rapidly at small patch sizes, because these changes may increase perching habitats that contribute disproportionally to total seed rain (Caughlin et al., 2016; Holl, 1998; Vogel et al., 2017; Zahawi et al., 2013; Zahawi & Augspurger, 2006). However, there may be a minimum patch size below which the directed dispersal mechanism fails, as reflected by seed dispersal and recruitment not exceeding background colonization rates (Cole et al., 2010; Fink et al., 2009; Holl et al., 2020). Under these conditions, the patch would not be acting as a receptor for seeds and subsequent recruitment within the landscape (Figure 1d, Holl et al., 2020). From here, we will therefore refer to this particular patch size threshold as the minimum receptor patch size.

We incorporated these considerations in the model framework by assuming that there was a background colonization rate at the edge of patches of introduced communities, and that these rates increased as a decelerating function of patch size, mimicking directed dispersal by disturbance-resistant animals (Figure 1c,d; Caughlin et al., 2016). In addition, we assumed that the total amount of seeds that can be dispersed into the landscape is unconstrained. We examined the extent to which this latter assumption affected model dynamics, by comparing the model results with scenarios in which the total amount of seeds was constrained (for details see Appendix S1: Section S1.3, Figures S5 and S6). We implemented the processes described above in the model as:

$$P_{2\to 1,x_i,y_j,t} = d_0\left(1+d_1\left(\frac{\max(0,A_{k,t}-A_{\min})}{A_{\max}-A_{\min}}\right)^{d_2}\frac{\mathrm{A}_{\max}}{\left(A_{k,t}+\sum_{l=1}^{n}\sum_{m=1}^{n}\Omega_{k,x_l,y_m,t}\right)}\right). \tag{5}$$

In which d_0 is the background colonization rate at the patch edge, d_1 quantifies the extent to which directed dispersal can accelerate the colonization rate (mimicking the maximum seed deposition rate), and d_2 describes the relationship between patch size and patch attractiveness to dispersers. Furthermore, $A_{k,t}$ indicates the area of the patch that the focal tile is part of, $A_{\min}$ specifies the minimum receptor patch size above which patches attract dispersers, while $A_{\max}$ specifies the patch size at which attractiveness is maximal. Finally, it is assumed that the amounts of dispersed seeds are distributed evenly over the tiles that comprise the current patch as well as the surrounding edge that can be colonized, identified by the Boolean operator $\Omega_{k,x,y,t}$. Because the parameter d_1 is scaled relative to the maximum seed deposition rate (which occurs at the patch size $A_{k,t} = A_{\max}$), the effect on colonization rate needs to be corrected for seeds being distributed among fewer tiles for smaller patches, that is, when $\left(A_{k,t}+\sum_{l=1}^{n}\sum_{m=1}^{n}\Omega_{k,x_l,y_m,t}\right) < A_{\max}$. The last factor on the right-hand side of Equation (5) comprises this correction. Furthermore, in the derivation of Equation (5), it is implicitly assumed that the length and the width of the model domain are relatively small compared with the distance to the seed source (i.e., an intact forest patch inhabited by the seed-dispersing faunal community). We also considered a case in which the model domain was relatively large compared with the distance between the seed source and one edge of the model domain (see Appendix S1: Section S1.4 for details). In this case, colonization probability became a function of the distance to the seed source, and distances to neighboring patches (for details see Appendix S1: Section S1.4, Figure S7). Hence, this additional simulation enabled the investigation of patches acting as stepping stones for further spread of the desired plant community (de la Peña-Domene et al., 2016; Herrera & García, 2009; Simioni et al., 2022).

Modeling the resource concentration mechanism

Our approach of including the resource concentration mechanism in the model framework is based on previous studies by Thiéry et al. (1995) and Rietkerk et al. (2004). Inspired by Conway's Game of Life (Conway, 1976), these studies considered a plant community type that facilitates its own growth at small spatial scales, while negatively affecting its growth at larger spatial scales (Figure 1e). It was shown that this modeling framework could reproduce banded vegetation patterns on slopes (thought to be driven by the spatial redistribution of runoff) as observed in arid ecosystems around the globe (Deblauwe et al., 2008). Subsequently, the approach was extended to also consider flatter areas, showing that the modeling framework could also reproduce spotted patterns, labyrinthine patterns, and gap patterns, as also observed in boreal peatlands (thought to be driven by spatial redistribution of soil nutrients) and other ecosystems (Rietkerk et al., 2004). As noted above, the main modification that we made in the current study is that we used radial, rather than square or rectangular interaction and dispersal neighborhoods. We further assumed that only the foundation species of the introduced community induced and was affected by the resource concentration mechanism. This foundation species' fitness was affected by the two components of the resource concentration mechanism as follows:

$$\begin{aligned} h_{1,x_i,y_i,t} = {} & h_{0,1} + h_F f_{1,F,x_i,y_i,t}\left(K_F(x_i - x', y_i - y')\right) \\ & - h_C f_{1,C,x_i,y_i,t}\left(K_C(x_i - x', y_i - y')\right). \end{aligned} \tag{6}$$

In which $h_{0,1}$ is the default fitness as implemented in the (neutral) baseline model, h_F is the maximum positive (i.e., facilitative) effect of conspecific tiles within the short-range interaction neighborhood, K_F (Figure 1e,f). Similarly, h_C is the maximum negative (i.e., competitive) effect of conspecific tiles within the long-range interaction neighborhood, K_C (Figure 1e,f). In addition, $f_{1,F,x_i,y_i,t}$ and $f_{1,C,x_i,y_i,t}$ represent the frequencies of the introduced communities within the short-range and long-range interaction neighborhoods, respectively. The formulation of these frequencies follows Equations (3), where in this case the specific kernels are defined as:

$$K_F(x_i - x', y_i - y') = H\left(r_F - \sqrt{(x_i - x')^2 + (y_i - y')^2}\right), \tag{7a}$$

$$\begin{aligned} K_C(x_i - x', y_i - y') = {} & H\left(r_C - \sqrt{(x_i - x')^2 + (y_i - y')^2}\right) \\ & - K_F(x_i - x', y_i - y'). \end{aligned} \tag{7b}$$

It should be noted that the above approach models resource concentration phenomenologically, rather than the explicit modeling of resource flows and redistribution across the landscape (e.g., von Hardenberg et al., 2001). Hence, the model framework uses a minimal modeling approach to incorporate scale-dependent feedback (Rietkerk et al., 2004).

Model parameterization

Our aim in the current study was to identify robust, qualitative differences in patch edge dynamics as driven by the three alternative feedback mechanisms considered (following e.g., Eppinga, de Ruiter, et al., 2009; Larsen et al., 2014, 2016). Hence, we did not aim to set model parameters in a way that quantitatively mimics one particular type of ecosystem or field location. Nevertheless, when considering that the foundation species involved include tree species, general constraints on parameter values can still be set (Table 1). For instance, for autocatalytic nucleation it is reasonable to assume the interaction neighborhood of foundation tree species (depending on root and canopy extents) is at least double that of grassland species (i.e., ~4 m, Michaels et al., 2020). Assuming that facilitative effects of resource concentration occur on the same spatial scale, setting the radius for competitive effects to be eight times larger yielded realistic sizes of vegetation patches and bands observed in patterned ecosystems (i.e., 10–30 m, Bastiaansen et al., 2018; Bromley et al., 1997). For the directed dispersal mechanism, previous studies suggested that the minimum receptor patch size was in the order of 50–100 m^2 (Zahawi et al., 2013), which was translated conservatively into a minimum receptor patch radius of 8 m to align with the spatial resolution of our model lattice (i.e., allowing for the introduction of smaller circular patches below the minimum receptor patch size) and other spatial processes considered. Moreover, we assumed that colonization rates due to directed dispersal could increase up to an order of magnitude (Holl et al., 2020),

TABLE 1 Model parameters and their interpretation.

Model mechanism	Symbol	Interpretation	Value	Reference[a]
General model framework	$h_{0,n}$	Basal, density-independent fitness of foundation species *n*	0.001–0.1	1
	$h_{n,x_i,y_j,t}$	Fitness of foundation species *n* at location $\left(x_i,y_j\right)$ at time *t*	Varying	
	$f_{n,x_i,y_j,t}$	Local frequency of foundation species *n* at location $\left(x_i,y_j\right)$ at time *t*	Varying	
	$K_I\left(x_i-x',y_j-y'\right)$	Kernel describing the local interaction neighborhood around location $\left(x_i,y_j\right)$, including all locations (x',y')	0 or 1 (spatially dependent)	
	$\Omega_{x_i,y_j,t}$	Boolean operator identifying whether location $\left(x_i,y_j\right)$ is part of the vegetation transition zone at time *t*	0 or 1 (spatially dependent)	
Autocatalytic nucleation	a_n	Basal, density-independent fitness of foundation species *n*	0.5	2, 3
	b	Strength of density-dependent feedback	1	2, 3
	c_n	Critical frequency of foundation species *n*	0.3–0.7	3
	r_I	Radius of the interaction neighborhood around the nucleating foundation species	16 tiles (~4 m)	3
Directed dispersal	d_0	Background colonization rate at patch edge	0.0005	4
	d_1	Extent to which directed dispersal can accelerate colonization at the patch edge	10	5
	d_2	Shape parameter quantifying the relationship between patch size and attractiveness to dispersers	0.2	6
	$A_{\min}$	Minimum receptor patch area	$\pi r_{\min}^2$ (with $r_{\min}=32$ tiles, ~8 m)	7
	$A_{\max}$	Patch size where attractiveness for dispersers reaches maximum	$\pi r_{\max}^2$ (with $r_{\max}=256$ tiles, ~64 m)	1
	$A_{k,t}$	Size of patch *k* at time *t*	Varying	...
	$\Omega_{A_{k,t}}$	Size of the edge of patch *k* at time *t*	Varying	...
Resource concentration	h_{F}	Maximum positive effect of nearby conspecific tiles	0.4	8, 9
	h_{C}	Maximum negative effect of distal conspecific tiles	−0.35	8, 9
	r_{F}	Radius of the interaction neighborhood in which positive effects occur	16 tiles (~4 m)	8, 9
	r_{C}	Radius of the interaction neighborhood in which negative effects occur	128 tiles (~32 m)	8, 9
	$K_{\mathrm{C}}(x_i-x',y_i-y')$	Kernel describing the local interaction neighborhood in which positive effects occur, around location $\left(x_i,y_j\right)$, including all locations (x',y')	...	...
	$K_{\mathrm{F}}(x_i-x',y_i-y')$	Kernel describing the local interaction neighborhood in which negative effects occur, around location $\left(x_i,y_j\right)$, including all locations (x',y') that are not included in K_C	...	...

Note: Model parameters included in probability calculations are dimensionless. Probabilities are defined for time units that are on the order of a month, so that landscape dynamics occur on the scale of decades. Spatial parameters are expressed in tile numbers, with an approximate length scale in meters.

[a] Reference numbers refer to 1, This study; 2, Molofsky and Bever (2002); 3, Michaels et al. (2020); 4, Aide et al. (1995); 5, Holl et al. (2020); 6, Caughlin et al. (2016); 7, Zahawi et al. (2013); 8, Bromley et al. (1997); 9, Bastiaansen et al. (2018).

and that directed dispersal rapidly increased once patches exceeded the minimum receptor patch size (Caughlin et al., 2016). We simulated patch edge dynamics on a lattice of ~1.5 ha, with time units on the order of 1 month, suggesting that introduced patches could cover the entire landscape in the time span of several decades (e.g., Aide et al., 1995).

Analyses

We first assessed how the rate of patch expansion depended on the driving mechanism governing patch edge dynamics. For each of the three model versions we monitored patch expansion of small, medium, and large circular patches introduced in the center of the lattice. As a measure of expansion, the square root of the area was monitored for the introduced community, which is expected to increase linearly in the standard case of diffusive spread (e.g., Eppinga et al., 2006). Second, we examined to what extent the driving mechanisms differentially affected interactions between multiple introduced patches within the landscape. Specifically, we examined how the expansion of a (circular) patch was affected by the presence of other introduced patches within the landscape. For the additional patches, we varied both size (i.e., small and large), and number (covering two or four cardinal directions) in a full-factorial design. Finally, we evaluated the interaction between the mechanism of patch growth and the success of potential restoration strategies. To this aim, we varied the initial area covered by the introduced community (1%, 2.5%, 5% or 10%), and the number of patches over which this cover was distributed (1, 4, 9, 16, or 25 patches). Using a full-factorial design, this yielded 20 restoration scenarios. We recorded the time needed to cover 50% of the total landscape. This choice was based on the emerging dynamics in the resource concentration scenarios, where a labyrinthine pattern formed (for details see Appendix S1: Section S1.5, Figure S8). All analyses were carried out in MATLAB (v. 9.0, Mathworks, Natick, Massachusetts, USA), with patch properties being computed with the Image Processing Toolbox. An annotated simulation code, which allows for running the three different model versions described, is available online (Eppinga, 2023).

RESULTS

Patch expansion dynamics and the role of patch size

Distinct differences in the absolute and relative rates of introduced patch expansion were observed, depending on the specific mechanism modeled (Figure 2). Sustained accelerated growth of patches over time was only observed for the autocatalytic nucleation mechanism (Figure 2a). For introduced patches that exceeded the critical patch size, the relative expansion rate reached an asymptotic maximum (Figure 2d), which could be explained by the frequency at the patch edge approaching a maximum value of 50% for very large patch sizes. In contrast, introduced patches that were below the critical patch size contracted until the entire patch had disappeared (Figure 2a,d). In the case of directed dispersal, patches expanded regardless of the initial size, but the patch expansion rate drastically increased when the minimum receptor patch size was reached (Figure 2b,e). From Equation (5), it can be inferred that for cases where $d_2 < 0.5$ (as considered in this study), the relative expansion rate of patches exceeding the minimum receptor patch size scales inversely with the patch radius ($\sim \frac{1}{r^{1-2d_2}}$). As a result, the highest relative expansion rates occur when the minimum receptor patch size is reached, and decelerates as the patch (radius) further increases over time (Figure 2e). These dynamics suggest that when the directed dispersal mechanism is activated the time needed to fully cover the landscape could be drastically shortened by introducing patches above the minimum receptor patch size (Figure 2b). When patch dynamics was driven by the resource concentration mechanism, patches of any size were able to expand, although smaller patches experienced an initial phase of slow growth (Figure 2c). This phase was followed by a brief period of accelerated growth, after which longer range negative effects decelerated the expansion of patches (Figure 2c,f). When larger patches were introduced at initialization, only decelerating expansion rates were observed (Figure 2f). We found that the same qualitative differences between simulations occurred when a larger dispersal distance around vegetation transition zones was assumed (see Appendix S1: Section S1.1 for details).

Role of patch position (relative to other patches) in the landscape

The influence of neighboring introduced patches in the landscape differed substantially between the three mechanisms considered (Figure 3). In the case of autocatalytic nucleation, focal patch dynamics were not influenced by neighboring patches, until the merging of expanding patches rapidly increased the focal patch size (Figure 3a). In the case of directed dispersal, the presence of other, large patches in the landscape led to rapid merging with the focal patch, while surrounding smaller patches grew little before being incorporated into the focal patch

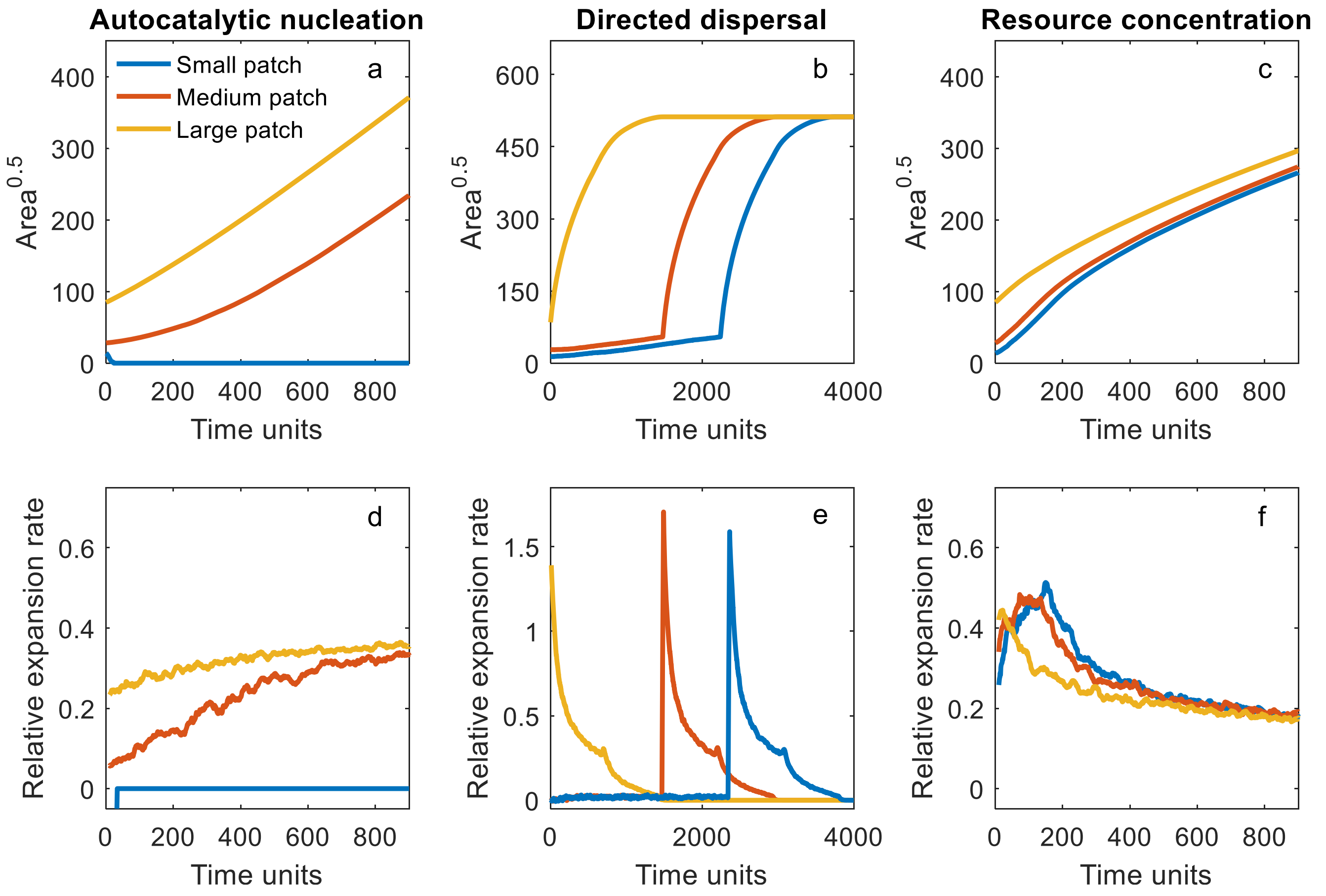

FIGURE 2 Comparison of patch expansion dynamics, as driven by the three ecological mechanisms in the framework. Left column (a, d) indicates the autocatalytic nucleation mechanism, middle column (b, e) the directed dispersal mechanism and the right column (c, f) the resource concentration mechanism. The top row (a–c) indicates the (square root of) the introduced patch area over time, the bottom row (d–f) indicates the relative rate of expansion over time, quantified as the difference in area covered between consecutive timesteps. Parameter values used: $h_{0,1}=h_{0,2}=a_1=a_2=0.001$, $b=1$, $c_1=0.3$, $c_2=0.7$, $d_0=0.005$, $d_1=10$, $d_2=0.2$, $A_{\mathrm{min}}=32^2\pi$, $A_{\mathrm{Crit}}=32^2\pi$, $A_{\mathrm{max}}=256^2\pi$, $h_{\mathrm{F}}=0.4$, $h_{\mathrm{C}}=0.35$, $r_{\mathrm{I}}=16$, $r_{\mathrm{F}}=16$, $r_{\mathrm{C}}=128$.

(Figure 3b). Similar dynamics were observed when the total seed influx into the landscape was constrained (see Appendix S1: Section S1.2 for details). In the case of resource concentration, the presence of other introduced patches in the landscape usually slowed down the expansion of the focal patch, compared with the single-patch scenario (Figure 3c). The only exception occurred in the scenario when the focal patch merged with two large patches present in the landscape (Figure 3c). These predominantly negative effects on the focal patch were stronger in the four-patch scenarios than in the two-patch scenarios (Figure 3c).

Optimal spatial organization of restoration strategies

The time needed for introduced patches to cover 50% of the landscape not only depended on initial cover and patch number, but the effects of these characteristics depended on the specific mechanism driving patch dynamics (Figure 4). In the case of autocatalytic nucleation and high initial cover of the landscape (10%), we found that strategies using many small patches were more effective than strategies using a few large patches (Figure 4a). With decreasing cover, however, the area of patches in many-patch scenarios consequently approached the critical patch size, which led to a slow initial phase of expansion (as described above), thus increasing the total time needed to cover the landscape (Figure 4a). Under the lowest cover classes considered, the patch size in many-patch scenarios fell below the critical patch size, resulting in the loss of the introduced patches (Figure 4a). Thus, with decreasing initial cover, the optimal patch number for rapid restoration needed to decrease as well to ensure that each introduced patch was of sufficient size (Figure 4a).

In the case of directed dispersal, single-patch scenarios most effectively restored the landscape for low initial

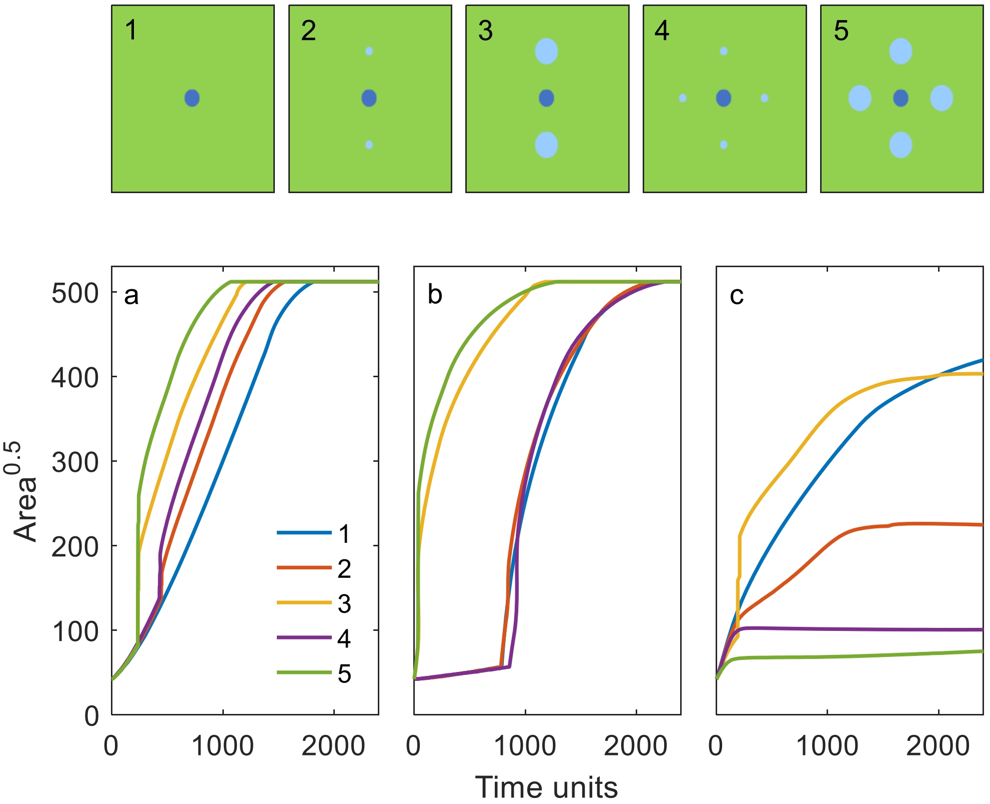

FIGURE 3 Comparison of the role patch position (relative to other patches) in the landscape on patch expansion dynamics. The top row panels show the five different landscape scenarios considered, with the corresponding transient dynamics shown in the bottom row panels (a–c). The bottom left panel (a) shows focal patch dynamics as driven by the autocatalytic nucleation mechanism. The bottom middle panel (b) shows focal patch dynamics as driven by the directed dispersal mechanism. The bottom right panel (c) shows focal patch dynamics as driven by the resource concentration mechanism. Parameters as in Figure 2.

cover (1% or 2.5%), while introducing four patches was most effective for higher initial cover (5% and 10%; Figure 4b). As the directed dispersal mechanism expanded patches at a decelerating rate (as explained above), initial differences in introduced patch sizes led to relatively small differences in restoration time needed to cover 50% of the landscape, provided that introduced patches were close to the minimum receptor patch size (Figure 4b). In contrast, when introduced patches were substantially smaller than the minimum receptor patch size (e.g., in scenarios where 25 patches were introduced), initial differences in introduced patch sizes led to much larger variation in the time needed to cover 50% of the landscape (Figure 4b). Again, we found that similar dynamics occurred in scenarios where the total seed influx was constrained (see Appendix S1: Section S1.3 for details).

When patch dynamics were driven by resource concentration, many-patch scenarios were the most effective in restoring the landscape (Figure 4c). The relatively small patches in these scenarios yielded a relatively low negative impact from within the patch, while only a limited expansion of each patch was needed to cover the landscape. For scenarios with higher initial cover divided over 25 patches, however, competition between neighboring patches led to reduced growth in the later phase of expansion relative to scenarios in which 16 patches were introduced (Figure 4c). Overall, regardless of the initial cover of introduced patches, competition between patches under the resource concentration mechanism yielded little variation in the time needed to cover 50% of the landscape compared with dynamics driven by autocatalytic nucleation or directed dispersal (Figure 4).

DISCUSSION

This model study suggests that the spatio-temporal dynamics of plant community patches reflect the occurrence of key ecological mechanisms that may act as drivers of ecosystem restoration. Depending on which mechanism drives patch dynamics, interactions between competing plant communities at the edge of monodominant patches may substantially differ from expectations based on landscape-scale averages, meaning that patch expansion and contraction may crucially

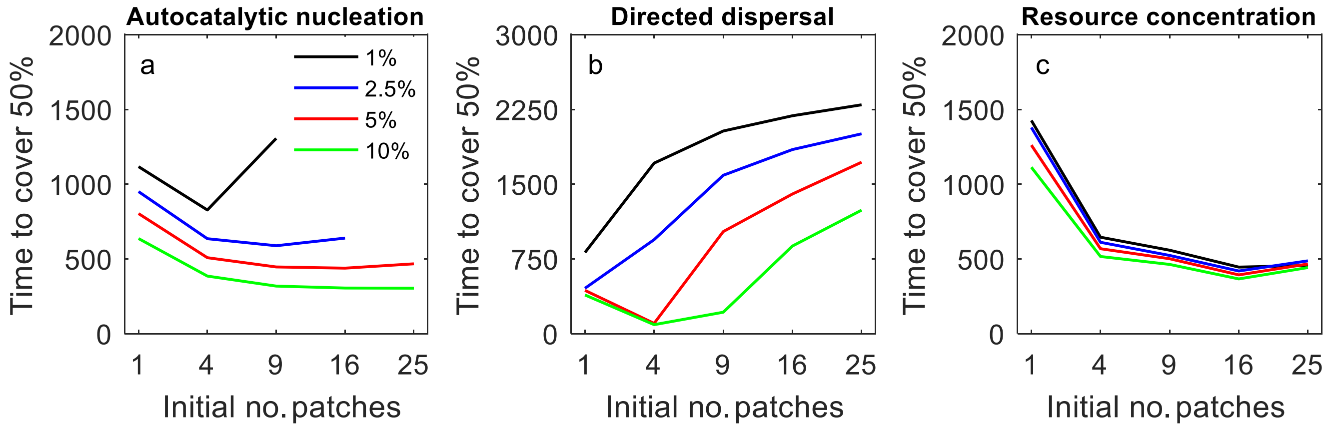

FIGURE 4 Evaluation of the effectiveness of spatial restoration strategies, that is, the introduction of a number of patches of a particular size. Total introduced patch area was varied between 1% and 10%, which was distributed over 1 to 25 patches. Effectiveness was evaluated as the time needed to cover 50% of the landscape (based on the dynamics driven by the resource concentration mechanism, where a labyrinthine pattern formed, see Appendix S1: Section S1.4 for further details). Shorter times indicate more efficient strategies, missing data for specific combinations of initial cover and patch number mean that the introduced patches did not succeed. Results are shown for the autocatalytic nucleation mechanism (a), directed dispersal (b) and resource concentration (c). Parameters as in Figure 2.

depend on local dynamics occurring at the patch edge (Allstadt et al., 2007; Eppinga et al., 2013; Eppstein et al., 2006; Michaels et al., 2020). The dependence of the rates of expansion on initial patch size and number also varied greatly between mechanisms. For example, under autocatalytic nucleation the expansion or contraction of patches depended critically on initial patch size. In contrast, for the directed dispersal and resource concentration mechanisms, we observed that any size of the initial patch expanded, leading to the same outcome (Figure 2). By varying the total cover and number of introduced patches, we also found that the optimal restoration strategy may depend on the specific spatial ecosystem processes driving the patch dynamics (Figure 4). Therefore, identifying such processes is of particular relevance within the context of ecosystem restoration, where spatially explicit restoration strategies may be leveraged to increase the efficiency of interventions (Bechara et al., 2021; Eppinga et al., 2021; Holl et al., 2020; Michaels et al., 2020; Zahawi et al., 2013).

The importance of vegetation communities inducing positive feedback that drives ecosystem dynamics has been recognized in general (Bowman et al., 2015; Rietkerk et al., 2004), and within the context of ecosystem restoration in particular (Byers et al., 2006; Suding et al., 2004; Weidlich et al., 2021). In addition, previous studies have suggested that different types of positive feedback may induce different transient dynamics at the patch scale (Eppinga, Rietkerk, et al., 2009; Wilson & Agnew, 1992). Importantly, while previous studies elucidated the potential for divergent outcomes when introducing patches of different sizes (Angelini et al., 2016; Holl et al., 2020; Michaels et al., 2020, 2022; Robroek et al., 2007), our current study highlights that expansion rates of patches near the critical patch size may strongly depend on the type of feedback involved in patch expansion (Figure 2). For example, patch expansion rates driven by directed dispersal are largest when just exceeding the minimum receptor patch size. In contrast, patch expansion rates driven by autocatalytic nucleation are positive but very low when just exceeding the critical patch size (Figure 2). Moreover, our results highlighted that the proximity of other (simultaneously) introduced patches may strongly constrain patch expansion dynamics in landscapes where a resource concentration mechanism drives patch dynamics (Figure 3). By developing a theoretical framework in which the effect of multiple types of feedback on patch dynamics could be systematically compared, our results suggest novel opportunities to identify positive feedbacks through diagnostic restoration experiments. Additionally, these findings suggest that, for systems where multiple feedbacks are hypothesized to act as drivers of system dynamics, patch introduction experiments can be set up as a means to provide a diagnostic test for potentially important feedbacks (Figures 2 and 3).

Given the feedbacks associated with each mechanism, we also observed distinct signatures in the emergent patch dynamics that may have implications for how we understand ecosystem resilience and the use of patches as a tool for restoration. The autocatalytic nucleation mechanism was characterized by accelerated patch growth over time, and individual patch dynamics that were independent of the patch configuration within the surrounding landscape (Figures 2 and 3). The accelerated patch growth over time could be explained by the frequency of conspecifics at the patch edge asymptotically approaching 50% as the patch increases in size (Allstadt et al., 2007; Michaels et al., 2020). Independence of patch dynamics from the surrounding landscape occurred because the mechanism only considers local-scale feedback and diffusive spread of the plant communities involved (Michaels et al., 2020). These conditions are likely met when there is asymmetric competition between plant communities for resources or when the plant communities locally modify abiotic or biotic components of the environment (Jones et al., 1994; Rietkerk et al., 2004; Michaels et al., 2020).

For patch dynamics driven by the directed dispersal mechanism, our results are consistent with previous models showing that positive feedback between patch size and colonization probability at the patch edge can greatly reduce the time needed for patches to cover the entire landscape (Figures 2 and 3; Caughlin et al., 2016). Where previous work included this positive feedback between patch quality and seed rain more explicitly (Caughlin et al., 2016), we mimicked the onset of this positive feedback as being dependent on a minimum receptor patch size. We also found that, when directed dispersal depends upon the proximity to a dispersal source, large patches near the dispersal sources can be advantageous as they serve as stepping stones (Appendix S1: Section S1.4). Empirical studies of introduced forest patches into degraded landscapes suggest that, indeed, a minimum receptor patch size may be needed to attract seed-dispersing animals toward introduced forest patches (Cole et al., 2010; Holl et al., 2020). Given the long time spans involved in tree maturation and forest succession, it is challenging to observe patch expansion through the establishment of new individuals beyond the introduced patch edges in experiments (Holl et al., 2020; Piaia et al., 2020; Zahawi et al., 2013). In contrast, patch quality resulting from forest successional processes and species turnover within experimental patches is observable on shorter time spans (e.g., Holl et al., 2017), but was not examined in the theoretical framework presented here, as only one state was considered for each plant community (Figure 1). Exploring theoretical frameworks in which changes in species composition could occur through successional processes within patches, as well as expansion of patches at the expense of competing communities, could provide further opportunities to link theoretical predictions of directed dispersal-driven dynamics and empirical observations of long-term experiments (Cole et al., 2010; Holl, 1998; Holl et al., 2020; Piaia et al., 2020; Zahawi et al., 2013).

While patch expansions driven by the resource concentration mechanism involved similar local feedback processes as involved in autocatalytic nucleation, longer range negative effects at larger spatial scales led to interactions between patches not observed under the latter. While autocatalytic nucleation always resulted in one plant community dominating the landscape, under the resource concentration mechanism negative interactions between conspecific patches enabled the formation of stable regular patterns in which both plant communities persisted (Figures 2 and 3). As observed in previous studies (e.g., Rietkerk et al., 2004; von Hardenberg et al., 2001), we observed a sequence of regular spatial patterns emerging, depending on habitat suitability for the introduced plant community (see Appendix S1: Section S1.5 for details). These results are in line with previous empirical studies from patterned ecosystems where the success of introduced patches depended on patch size (Angelini et al., 2016), or the recovery of patch disturbances depended on the habitat suitability for the community forming the disturbed patch (Van Belzen et al., 2017). For instance, while the implications for pattern formation through resource concentration mechanisms have been prominently studied for the restoration of dryland ecosystems (Bera et al., 2021), the restoration perspective taken here highlights the effect of patch size and density on the trajectory toward landscape recovery (Figure 4).

In the current study, we only considered each mechanism of interest occurring in isolation when evaluating effects on emerging patch dynamics. While this is a useful approach to derive hypotheses of how the occurrence of each mechanism may be reflected in empirical data, it is likely that these mechanisms occur simultaneously in real ecosystems, which may additionally lead to interactive effects (Larsen et al., 2014). More empirical studies are needed to reliably quantify model parameters, and hence constrain the relative strengths of the three mechanisms studied, to enable analyses of which combination(s) of mechanisms may be occurring in real ecosystems, and their consequences for the optimal spatial organization of restoration strategies.

It should also be noted that our current modeling exercise implicitly assumed relatively constant environmental conditions. For example, this implicit assumption was reflected by representing critical patch size and minimum receptor patch sizes as parameters that were constant over time. In practice, these minimum sizes may depend on environmental conditions, with more benign conditions for the desired community decreasing critical patch sizes required for successful expansion (Michaels et al., 2020). Within the context of ecosystem restoration, it has been noted that environmental fluctuations may provide windows of opportunity for recovery, examples including forest regeneration during prolonged periods of high precipitation or coastal ecosystem recovery during prolonged periods of reduced hydrodynamic stress (Holmgren & Scheffer, 2001; Hu et al., 2015). While previous research has focused on windows of opportunity for the establishment of individuals of the desired community (van Belzen et al., 2022), our work suggests that this concept could also be applied to entire patches of the desired community. More specifically, patches below the critical patch size needed to survive average environmental conditions may utilize a window of opportunity to expand beyond this critical patch size, meaning that expansion can subsequently be sustained even when environmental conditions return to normal. Parameterizing our model framework for specific case studies that include this potential role of temporal environmental variability on emerging patch dynamics would provide an interesting and important avenue for future research.

The feedback mechanisms considered in this study may occur in a variety of ecosystems. For example, the desired state of many North American prairies includes late successional species that strongly depend on beneficial AM fungi (Burrill et al., 2023; Koziol & Bever, 2015). Yet, agricultural practices and other environmental pressures have shifted many grasslands into an undesired state including early successional species that do not depend on the presence of AM fungi in the soil (Bauer et al., 2015; Wang et al., 2022). Experiments suggest that late successional species are not only more responsive to AM fungi, but are also better hosts for these fungi (Bauer et al., 2015; Burrill et al., 2023; Cheeke et al., 2019). This creates the potential for positive feedback between late successional species density and AM fungi abundance, which has been demonstrated in both field and greenhouse studies (Koziol & Bever, 2019). This positive feedback could initiate an autocatalytic nucleation mechanism when patches with sufficient densities of late successional species and AM fungi are introduced into a degraded grassland (Michaels et al., 2020). Interestingly, a mosaic of late successional and early successional patches is often observed in North American grasslands (Collins, 1990), consistent with the possibility of autocatalytic nucleation dynamics occurring in these systems. Similarly, directed dispersal and resource concentration mechanisms may occur in other types of ecosystems as well (Carlo & Tewksbury, 2014; Michaels et al., 2022; Rietkerk & Van de Koppel, 2008), suggesting a broader relevance of introducing desired patches as an active restoration strategy (Holl et al., 2020; Shaw et al., 2020).

Rapid restoration of ecosystem properties and functions may be key to circumvent extinction debts of past land use change, and curb global biodiversity losses (Strassburg et al., 2020). Introducing patches of the desired vegetation community has been identified as a promising active strategy to accelerate ecosystem restoration (Bechara et al., 2021; Holl et al., 2017; Hulvey et al., 2017; Michaels et al., 2020; Shaw et al., 2020; Zahawi et al., 2013). Our theoretical study suggests that the optimal strategy of patch introduction may depend on the specific type of positive feedback mechanism that drives patch expansion dynamics. More specifically, the introduction of a few large patches may be relatively favorable when aiming to initiate directed dispersal, while many smaller patches may be more effective when dynamics are driven by resource concentration or autocatalytic nucleation. However, for the autocatalytic nucleation mechanism, a more important requirement is that all patches introduced exceed the critical patch size, which may mean that efforts need to be focused on introducing a few large patches when the total amount of patch area that can be introduced is limited (Figure 4). Given that degraded ecosystem states can be relatively resilient and hence require large restoration efforts (Suding et al., 2004), increasing restoration efficiency through the introduction of a sufficient number of patches of an appropriate size informed by its driving feedback mechanism, provides a promising strategy for meeting this challenge.

AUTHOR CONTRIBUTIONS

Maarten B. Eppinga, Theo K. Michaels, Maria J. Santos and James D. Bever conceived the ideas and designed the methodology. Maarten B. Eppinga ran model simulations and wrote the first draft of the manuscript. Theo K. Michaels, Maria J. Santos and James D. Bever contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGMENTS

The research of Maarten B. Eppinga and Maria J. Santos was funded by the University of Zurich's University Research Priority Program in Global Change and Biodiversity. The research of Theo K. Michaels and James D. Bever was funded by NSF grants DEB-1556664, DEB-1738041 and OIA-1656006. Open access funding provided by Universität Zürich.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

No data were collected for this study; all analyses are based on model simulations. An annotated simulation code that allows for running the three different model versions presented in this publication is available in Eppinga (2023) on Figshare at https://doi.org/10.6084/m9.figshare.20509749.v1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Eppinga, Maarten B., Theo K. Michaels, Maria J. Santos, and James D. Bever. 2023. “Introducing Desirable Patches to Initiate Ecosystem Transitions and Accelerate Ecosystem Restoration.” *Ecological Applications* 33(8): e2910. https://doi.org/10.1002/eap.2910