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When patches grow themselves: from analogy to autocatalytic processes, the relevance of ecological nucleation for restoration practices

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Choosing restoration strategies may depend on ecosystem's stability properties. When degraded ecosystems do not self-perpetuate, natural regeneration can lead to system recovery, and restoration interventions are often designed to accelerate the natural regeneration process. However, when degraded systems self-perpetuate, reestablishing functional ecosystems depends on overcoming resistance thresholds that impede recovery. In both scenarios, concentrating restoration efforts in patches of the desired state may enhance ecosystem recovery. Introducing patches of a desired state has been motivated by two frameworks: autocatalytic nucleation and the analogy to nucleation. When restoration depends on overcoming resistance thresholds, autocatalytic nucleation lowers restoration barriers by initiating a local positive feedback mechanism that is only successful when desired patches are introduced above a critical patch size. In contrast, the analogy to nucleation accelerates natural regeneration whereby desired patches interact with landscape scale factors often through directed dispersal. We compare nucleation frameworks, and discuss their applications for restoration practices.

Key words: alternative stable states, critical patch size, directed dispersal, nucleation, positive feedbacks, restoration barriers

Implications for Practice

- Introducing patches of a desired state as a restoration strategy has been motivated by two frameworks: autocatalytic nucleation and the analogy to nucleation.
- Autocatalytic nucleation lowers restoration barriers, facilitating transitions between alternative stable states. It requires a local positive feedback mechanism that is only successfully leveraged when patches of the desired state are introduced above a critical patch size, otherwise the restoration will fail.
- The analogy to nucleation accelerates regenerative recovery. Patch size may influence the rate of patch maturation but is less influential on patch spread, and should instead consider how the mechanism of dispersal interacts with the patch and landscape scale factors.
- Overlooking these differences can lead to failure to reach restoration goals.

Introduction

Fingerprints of human activity have modified Earth's ecosystems. Given rapid rates of environmental degradation, ecosystem restoration is an increasingly necessary and challenging task (Hobbs & Cramer 2008) that requires innovative restoration techniques. Restoration ecology is seeing a growing movement of spatially explicit restoration strategies (Shaw et al. 2020; Michaels et al. 2022). Spatial dynamics can play an important role in dictating ecosystem recovery behavior, wherein small spatial scale interventions can initiate spatial dynamics that drive changes at larger spatial scales. Restoration strategies harnessing spatial dynamics, advocate for introducing desired vegetation patches into degraded landscapes which act as focal points for ecosystem recovery. Not only can these strategies be cost effective, but unlike traditional restoration practices they may increase ecosystem heterogeneity, and address transitions barriers between degraded and desired ecosystem states (Michaels et al. 2020; Shaw et al. 2020). While spatially explicit restoration strategies show promise, few studies highlight how they interact with ecosystem stability properties that dictate recovery trajectories between degraded and desired ecosystem states.

Whether management strategies successfully initiate ecosystem recovery strongly depends on the stability properties of

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the current degraded and the desired ecosystem states. When the desired ecosystem state is a globally stable equilibrium, the degraded state is not self-perpetuating, and the desired state can be reached through natural regeneration (Fig. 1A; Crouzeilles et al. 2017). In many cases natural regeneration strategies may be slow to meet restoration goals, and active restoration practices are needed to enhance the rate of natural regeneration (Hobbs & Cramer 2008).

A fundamentally different situation occurs when the current degraded state is a locally stable equilibrium (Fig. 1B). In this case, perturbations or interventions need to be large enough to overcome resistance thresholds, above which the system can develop toward the desired, alternative stable state, which is also a locally stable equilibrium (Fig. 1B). The possibility of alternative, locally stable states arise through positive feedbacks (Scheffer & Carpenter 2003; Suding et al. 2004; Kéfi et al. 2016). As a result, degraded alternative stable states may resist restoration practices that simply try to reinstate historic abiotic conditions. To reach restoration goals, restoration practices need to initiate the positive feedbacks that drive ecosystem state transitions (Suding et al. 2004). Thus, understanding the stability properties of a system can clarify whether interventions should aim for accelerating regeneration or overcoming resistance thresholds.

Ecosystem stability properties can interact with spatially explicit restoration strategies, as seen in the example of nucleation. Nucleation has come to embody two distinct definitions predicated on different sets of assumptions about the stability property of a given ecosystem. The concept of nucleation stems from physical chemistry to describe material phase transitions between alternative stable states, in which local perturbations spread over space, such as droplets formed through vapor condensation (e.g. Lothe & Pound 1962). When introduced to the ecological literature, nucleation was first used as an analogy to describe the establishment of vegetation patches acting as focal points for seedling recruitment and subsequent patch growth (Yarranton & Morrison 1974). This interpretation was later extended to restoration (Corbin & Holl 2012). Evolving beyond this analogy, a recent ecological definition of nucleation was derived from its chemical application; autocatalytic nucleation describes how spatial applications of local scale positive feedback can drive transitions between alternative stable states (Michaels et al. 2020).

While these definitions of nucleation differ in important ways, there has not been a systematic comparison, limiting our ability to apply nucleation restoration strategies that match the stability properties of the degraded system. Here we (1) define autocatalytic nucleation and describe its application to overcome resistance thresholds in restoration to reach a desired ecosystem state, (2) describe the analogy to nucleation as it has been predominately used in restoration for accelerating natural regeneration, with a focus on directed dispersal as the catalyzing mechanism (Shaw et al. 2020), and (3) compare and contrast the conditions for, and dynamics of, autocatalytic nucleation and the analogy to nucleation. Understanding the distinctions between autocatalytic nucleation and the analogy to nucleation will help restoration practitioners identify strategies appropriate for their system and restoration goals.

Autocatalytic Nucleation

For systems currently residing in a locally stable, degraded state, autocatalytic nucleation can initiate critical ecosystem transitions toward an alternative, desired, stable state. Consistent with nucleation as defined in physical chemistry (e.g. Lothe & Pound 1962), conditions for autocatalytic nucleation require that a patch of the desired state generates local positive feedback, that species disperse locally, and that the patch can produce and maintain continuous habitable space (Michaels et al. 2020).

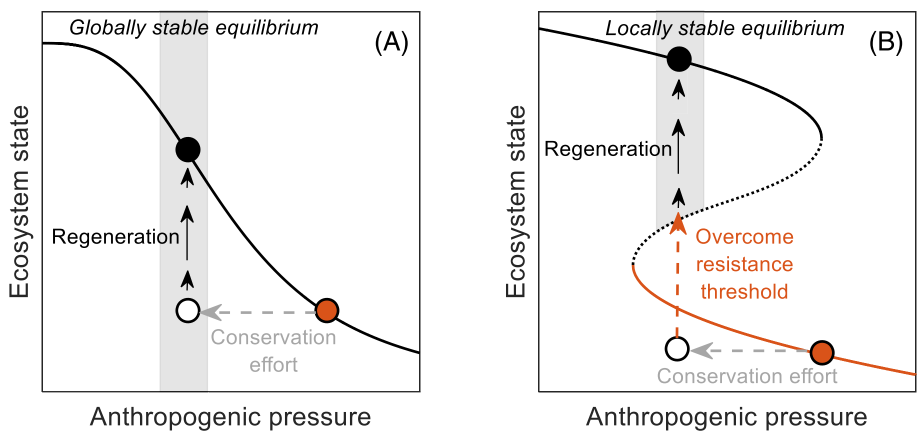

Figure 1. Stability properties of the desired restoration target state may constrain the set of viable management strategies. (A) In cases where the restoration target comprises a globally stable equilibrium, reduction of anthropogenic pressures may be a sufficient strategy to initiate natural regeneration processes toward the restoration target. (B) In cases where the restoration target comprises a locally stable equilibrium, reducing anthropogenic pressures alone may not be sufficient. Instead, successful strategies may need to include interventions that overcome resistance thresholds associated with the degraded ecosystem states. Solid black lines indicate stable restoration target states, the solid red line indicates a stable degraded ecosystem state, and the dashed black line indicates an unstable ecosystem state. Dashed arrows indicate management interventions and solid arrows indicate regeneration, that is state changes toward the restoration target state driven by internal ecosystem processes.

To explain, we will consider an initial patch of vegetation representing a desired state surrounded by a degraded state (Fig. 2). We assume these two states disperse locally and generate local positive feedback (Michaels et al. 2020). A local positive feedback mechanism can involve a single type of organism, or two or more different types of organisms whose interactions alter environmental conditions as to promote their own growth and the development toward the desired state (Eppinga et al. 2009; Koziol & Bever 2019). Initiating local positive feedbacks depends on the organism(s) involved exceeding a critical occupancy (e.g. Rietkerk et al. 2004). If the organism exceeds the critical occupancy at the patch edge, the patch will expand. If not, the patch will contract. Larger patches have higher local occupancy at the patch edge (Allstadt et al. 2007; Michaels et al. 2020). Thus, the conditions to initiate positive feedback can be translated to a critical patch size needed for successful establishment and spread of the desired ecosystem state (Michaels et al. 2020). Following this, when the patch of the desired state is below a critical size, it will contract and disappear (Fig. 2). However, when the patch exceeds the critical patch size, it will expand, and importantly, the expansion rate will accelerate as patch size increases (Fig. 2).

The utility of autocatalytic nucleation for restoration relies on introducing patches of the desired state that embody a positive feedback mechanism at a size larger than the critical patch size (Box 1). Examples of such mechanisms include mutualistic

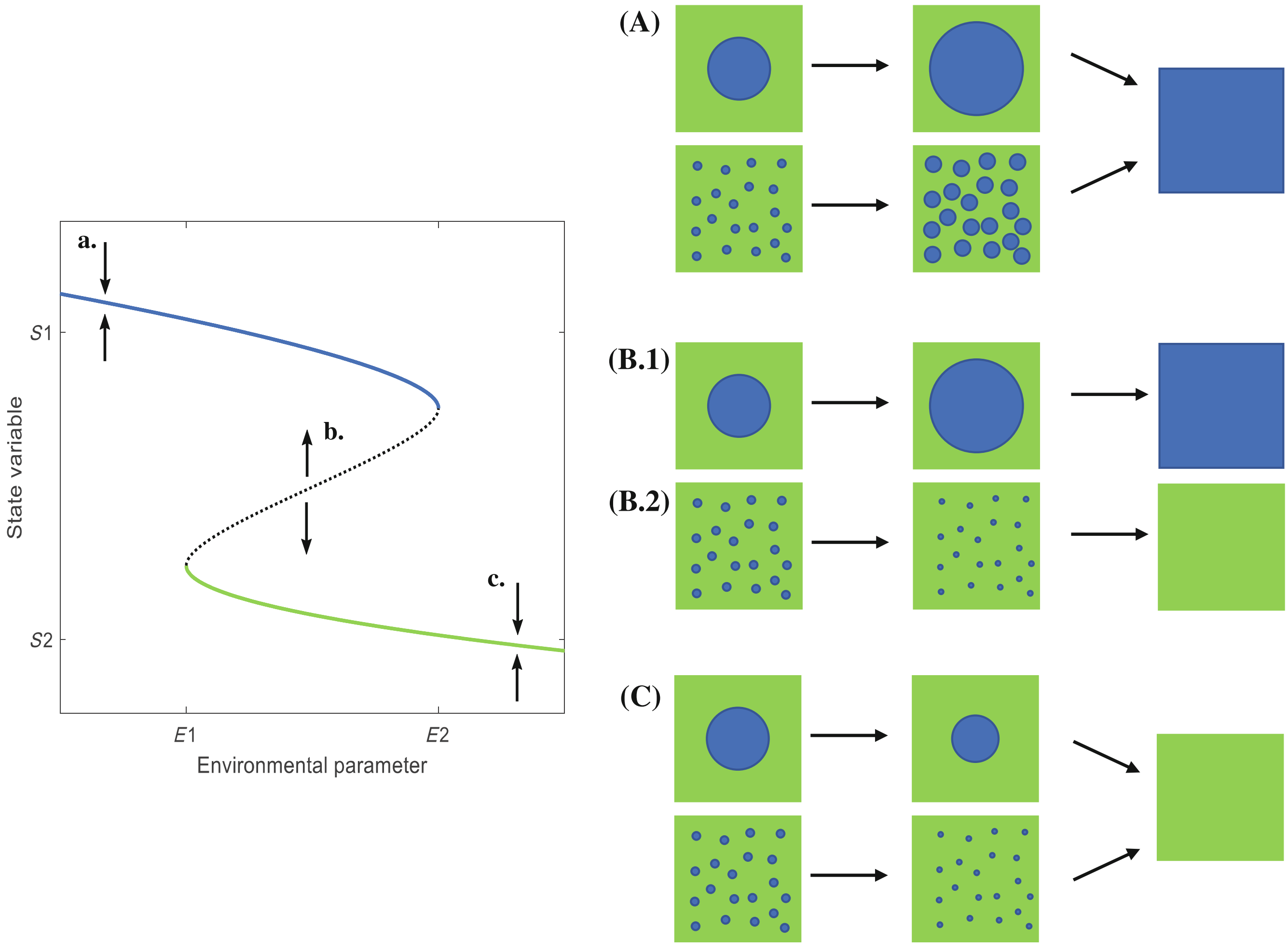

Figure 2. *Source*: Adapted from Suding et al. (2004) and Michaels et al. (2020). In systems characterized by local feedback dynamics, the challenge of transitions between alternative stable states may be addressed by leveraging autocatalytic nucleation. On the left side of the figure is a generic mean field depiction of the transition between alternative stable states, with solid lines representing stable equilibria and the dotted line represents an unstable equilibrium. For low values of the environmental parameter (*E*), the system will be stably maintained at the high value equilibrium (represented here by the blue line). If the environment is perturbed past *E*2 then the system collapses to a lower equilibrium, represented by the green line. Under the traditional alternative stable states model, ecosystem recovery requires reducing the environmental parameter below *E*1. On the right side of the figure, is a conceptual depiction of autocatalytic nucleation that considers the spatial characteristics of the patch of the desired state. For values of the environmental parameter where only one equilibrium is possible (e.g. at points a and c), the system of mixed states will go to that equilibria regardless of the spatial configuration of the state patches, as depicted by panels (A) and (C) respectively. However, for intermediate values of the environmental parameter where two stable equilibria are possible (e.g. at point b), a system will go to either the high or the low equilibrium depending upon the initial proportion of the two patch types and the spatial structure of those patches (panel B.1, B.2). The single large patch of the desired state is more likely to result in autocatalytic nucleation and trigger a landscape-scale transition (panel B.1).

Box 1 Autocatalytic nucleation dynamics for restoration: an example from tallgrass prairies.

Here we illustrate how autocatalytic nucleation dynamics can be harnessed to overcome thresholds of degraded ecosystem states using tallgrass prairie restoration as an example. Tallgrass prairies and their associated degraded systems, meet the conditions under which autocatalytic nucleation would apply as the appropriate restoration technique. First, local positive feedbacks are an important process shaping this system, which are generated between plants and arbuscular mycorrhizal (AM) fungi. Late successional plants are very responsive, and good hosts for, their beneficial fungal partners, which in turn generate strong local positive feedback (Cheeke et al. 2019; Koziol & Bever 2019). In contrast, early successional species are not as dependent on, and are not sensitive to, AM fungi, generating weak positive feedback dynamics (Cheeke et al. 2019; Koziol & Bever 2019). These locally driven differential feedbacks are important in maintaining prairie systems and driving transitions between early and late succession (Bauer et al. 2015). Second, they exhibit characteristics of locally stable equilibrium associated with alternative stable states. Post-agricultural systems can remain stuck in alternative, early successional, stages of recovery due to resistance thresholds associated with degraded plant–AM fungal feedback relationships (Koziol & Bever 2017). Because agricultural practices reduce mutualistic fungal partners, the resulting degraded fungal community selects for early successional and non-native plant species that are less sensitive to AM fungi, which inhabit the establishment of late successional species, thereby reinforcing the degraded state (Koziol & Bever 2017).

Under these conditions, restoration techniques that reintroduce plants without addressing the local positive feedback mechanism will not suffice. To restore this system using autocatalytic nucleation techniques, we need to employ a patch of the desired state and its associated local positive feedback mechanism. We can utilize the late successional plant–AM fungal feedbacks to catalyze patch growth by introducing a patch of late successional plants and their associated AM fungal partners (e.g. via inoculation, Middleton & Bever 2012), into a post-agricultural degraded state. To recall, autocatalytic nucleation necessitates a patch larger than the critical patch size for patch growth. Thus, as long as the introduced patch is larger than the critical patch size, beneficial AM fungi spreading from the patch will positively influence late successional plants adjacent to the patch, giving them greater fitness and the patch of desirable late successional species will expand the patch outward. With expansion of the patch, the desired result of the restoration will be reached (Fig. 2B.1). However, if the patch is smaller than the critical patch size, the degraded AM fungal community surrounding the patch will have more influence on the plants near the patch edge, resulting in greater fitness for early successional species, and the patch of the late successional species will contract. Patch contraction of the desirable plants will result in restoration failure (Fig. 2B.2).

In this restoration scenario employing autocatalytic nucleation, we note that patch expansion via local positive feedback is distinct from the process of diffusion, which might result if the likelihood of establishment and fitness of the plants in the desired patch did not depend on the successional stage of their neighbors. In the case of diffusion, expectations are that local dispersal will blur the border of the patch over time, but the patch will not expand. Like diffusion, directed dispersal, the mechanism most commonly associated with the analogy to nucleation (Fig. 3), does not assume plant fitness dependence on neighbors, as patch expansion is driven by differential patterns of dispersal.

relationships between arbuscular mycorrhizal fungi and late successional prairie plants (Koziol & Bever 2019), facultative relationships between mussels and salt marsh plants (Derksen-Hooijberg et al. 2017), and plants directly or indirectly altering abiotic properties such as hydrology (Robroek et al. 2009), and nutrient cycling (Eppinga et al. 2011). As we have highlighted, these local positive feedbacks are only successfully leveraged when introduced patches exceed the critical patch size which depends on the strength of feedback and environmental stress of the degraded state (Michaels et al. 2020).

Nucleation as Analogy

For systems currently residing in an unstable degraded state, processes analogous to nucleation can enhance the rate of regeneration. A process that has received considerable attention within this context is directed dispersal (Pausas et al. 2006; Fujita 2016). Consider the establishment of a single tree or patch of trees characteristic of the desired state within a degraded landscape (Fig. 3). The establishment of this individual or patch may initiate a process that enhances the local seed rain by attracting seed-dispersing animals from the surrounding landscape, which may increase the arrival of desired plant species, thereby promoting patch development and expansion (Slocum 2001; Zahawi & Augspurger 2006; Caughlin et al. 2016; Holl et al. 2020). A prerequisite for the analogy to nucleation is that the landscape harbors vegetation of the desired state, such that directed dispersal acting at the landscape scale connects remnant vegetation to regenerating patches leading to rapid ecosystem recovery (de la Peña-Domene et al. 2016; Zahawi et al. 2021).

As a restoration strategy, the analogy to nucleation suggests that establishing patches of the desired state in a degraded landscape, bypasses the initial stages of establishment, thereby jumpstarting the regenerative process (Corbin & Holl 2012). Established patches can range from a single tree (Toh et al. 1999), to single size patches (Rey Benayas et al. 2015), to patches varying in size and species composition, all of which manifest directed dispersal, and increase the rate of recovery (Zahawi & Augspurger 2006; Holl et al. 2020).

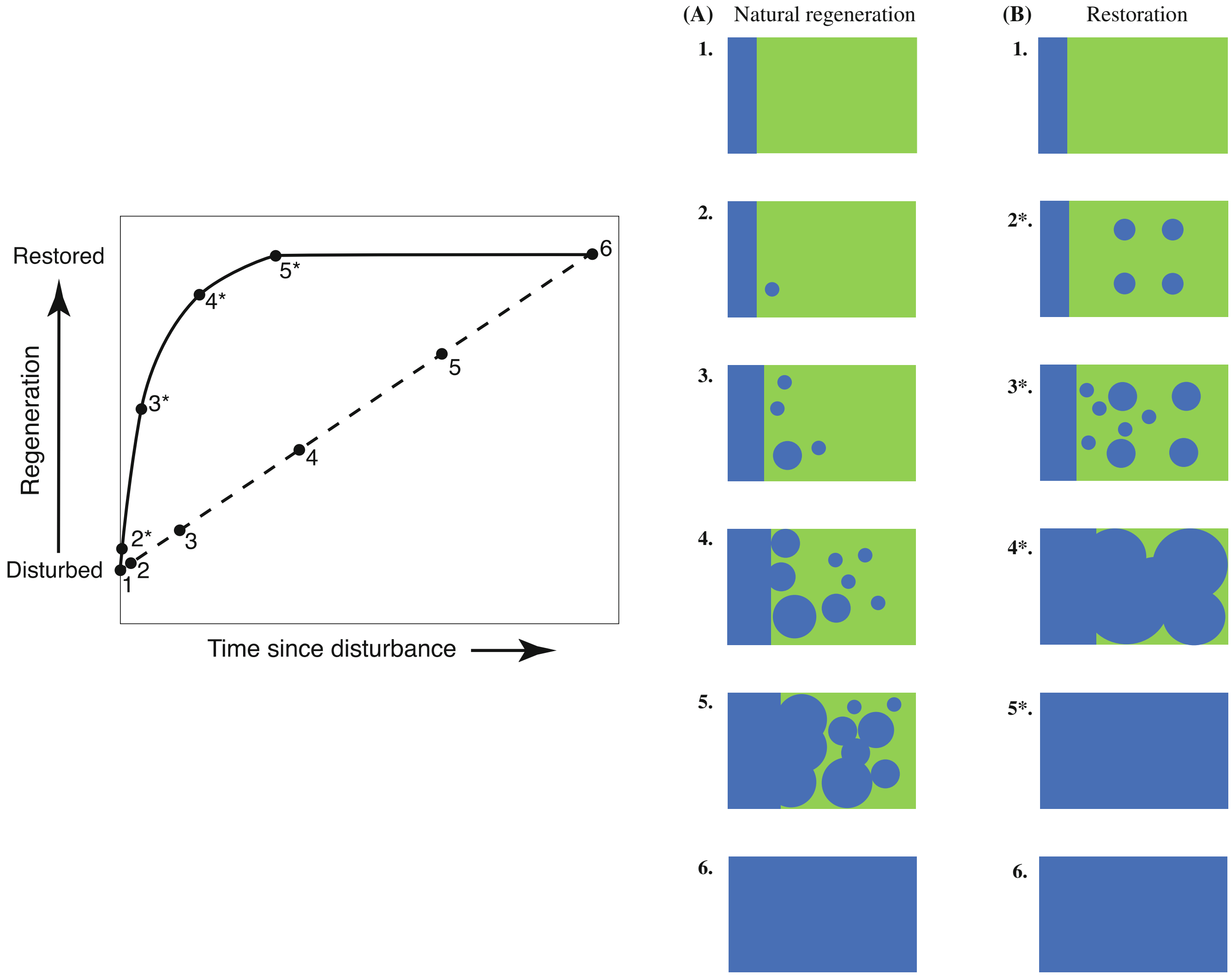

Figure 3. Here, we demonstrate the analogy to nucleation using directed dispersal as the primary mechanism in a forest ecosystem. Directed dispersal is presented in terms of both natural regeneration (A) and restoration that utilizes principles analogous to nucleation (B). The two columns represent a pictorial description of these dynamics. Each starts out with the desired state in blue, here a forest represented as a blue rectangle, and the degraded state in green (1A, 1B). Full recovery has occurred when the whole rectangle is blue (6A, 5*B, and 6B). In the column labeled natural regeneration (A), a dispersal event initiates the first patch of forest in the degraded landscape (2A) followed by directed dispersal events that give rise to subsequent patches (3–6A) which expand and coalesce overtime. In contrast, the column labeled restoration has employed dynamics analogous to nucleation; instead of waiting for a dispersal event to occur, patches are preemptively established to attract dispersal agents to the degraded area (2*B). Along with the addition of new patches, the initial patches will expand and again coalesce overtime (3*–5*B). In each scenario, these regenerating forest patches grow at the same rate as the remnant forest. The graph on the left synthesizes (A) and (B), with time since disturbance is on the x-axis and regenerating state on the y-axis, showing how employing principles analogous to nucleation will initially result in accelerated recovery that decelerates over time as the desired state is approached.

Discussion

As we have highlighted, initiating patches of a desired state has utility for restoration efforts employing both autocatalytic nucleation and the analogy to nucleation. However, these two concepts of nucleation differ in significant ways, with autocatalytic nucleation lowering barriers to facilitate transitions between alternative stable states, while the analogy to nucleation accelerates regenerative recovery to a globally stable desired state. These concepts differ in patch size dependence and feedback dynamics. Recognizing these differences is essential to optimally meeting restoration challenges.

The Relative Importance of Patch Size

Autocatalytic nucleation and the analogy to nucleation differ with the relative importance of patch size. For autocatalytic nucleation, the local positive feedback mechanism is only successfully leveraged when introduced patches exceed the critical patch size (Michaels et al. 2020). Studies show that a critical patch size is necessary for lowering barriers to achieve restoration goals; without the critical patch size, the degraded system remains stagnant in an early stage of recovery, or collapses back into the degraded state (Robroek et al. 2009; Angelini & Silliman 2012). Additionally, for autocatalytic nucleation patch size is expected to grow at an accelerating rate (Michaels et al. 2020), which has been observed in multiple ecosystems (Vidondo et al. 1997; Cappuccino 2004).

In contrast, for the analogy to nucleation, desired ecosystem transitions do not depend on a critical patch size to initiate recovery. While larger patches may enhance patch development and coalescence, even a small patch can accelerate spatial dominance of the desired state (Slocum 2001; Holl et al. 2020). Instead, patch size can contribute to patch maturation—that is change within patch, rather than patch expansion. Studies show larger patches enhance bird visitation rates and duration times, increasing the chance of seed dispersal to the patch (Fink et al. 2009; Cole et al. 2010). This may lead to greater patch complexity in plant composition, canopy structure and cover (Slocum 2001; Fink et al. 2009). Thus, with strategies leveraging the analogy to nucleation, patch size may influence the rate of patch maturation but is less influential on patch spread, while for autocatalytic nucleation the optimal restoration strategy necessarily includes patches larger than the critical patch size, otherwise the restoration will fail.

Relationship Between Mechanism and Spatial Scale Dynamics

Another key difference between autocatalytic nucleation and the analogy to nucleation is the spatial dynamics at which the mechanisms driving ecosystem recovery act. A principal condition for autocatalytic nucleation is a local positive feedback mechanism that can catalyze growth at the patch edge. In salt marsh systems, Cordgrass (*Spartina alterniflora*) patches rebound from disturbance and expand in the presence of the cordgrass mutualism with mussels (*Geukensia demissa*). When this mutualism is disrupted, recovery is significantly reduced (Derksen-Hooijberg et al. 2017). These results are consistent with alternative stable state transitions driven by local positive feedback as described by autocatalytic nucleation. As the local positive feedback mechanism is directly associated with individual patch dynamics, this mechanism is independent from its position in the landscape (Eppinga et al. 2021).

In contrast, the analogy to nucleation depends on access to nearby, intact elements in the landscape that can be deposited to near the patch. Understanding the behavioral ecology of the dispersal agent could play an important role in leveraging the analogy of nucleation. Landscape scale characteristics such as distance from intact forest to the patch, and patch connectivity, can dictate disperser behavior thereby shaping patch development (de la Peña-Domene et al. 2016; Cadavid-Florez et al. 2019). The optimal restoration strategy for analogy to nucleation then necessarily considers how the mechanism of dispersal interacts with patch and landscape scale factors, whereas for autocatalytic nucleation the priority is to introduce a local scale positive feedback mechanism with an adequately large patch.

The Future of Nucleation for Restoration Challenges

Autocatalytic nucleation and the analogy to nucleation each serve to advance ecosystem recovery. However, it is important to recognize the ways in which these mechanistic frameworks differ from one another. Given the stability properties of a degraded system, overlooking these differences can lead to a mismatch between restoration barriers and nucleation strategy. Restoration practitioners should first assess the likelihood that the current degraded state is locally stable in order to identify the appropriate nucleation framework. The nucleation framework will affect priorities for initiating patches and choice of attributes to evaluate restoration objectives. Practitioners utilizing autocatalytic nucleation will want to initiate sufficiently large patches that include the positive feedback mechanism, and track the rate and direction of patch edge expansion. When implementing the analogy to nucleation partitioners will want to consider the location of the patch relative to the seed source and may consider evaluating species richness and composition within the desired patch, as well as rates of patch expansion.

The UN Decade of Ecosystem Restoration (2021–2030) highlights the urgency of ecosystem restoration (Fischer et al. 2021). When designing restoration strategies, we need to address the potentially nonlinear recovery behavior of degraded states, and shift our restoration strategies to meet, and manage for, ecosystem complexity. Autocatalytic nucleation and the analogy to nucleation provide innovative ways to restore ecological integrity to degraded landscapes and use our human fingerprint to help patches grow themselves.

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