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Increasing spatial dispersion in ecosystem restoration mitigates risk in disturbance-driven

environments

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Abstract

1. Many vegetated ecosystems, including drylands, coastal dunes, salt marshes and seagrass meadows, inhabit environments frequently disturbed by the erosive forces of wind and water. Once degraded, the restoration of these systems entails a high-risk of failure due to the uncertainty in timing and intensity of future disturbances. Risk-mitigation strategies like bet-hedging (i.e., spreading risk over diverse options) have been proven in cross-disciplinary contexts to optimize yield when uncertainty is high. Yet restoration designs commonly homogenize resources by planting vegetation of similar sizes in grid-like patterns. This decision may unwittingly contribute to the high rate of restoration failure in these environments.

2. Using numerical simulations mimicking vegetation patch dynamics, we demonstrate how avoiding uniform planting designs substantially improves the likelihood of restoration success.

3. These simulations also suggest that the intrinsic risk of failure associated with any planting pattern can be identified *a priori* by calculating the variance-to-mean ratio of vegetation cover.

4. *Synthesis and applications.* By introducing a level of spatial overdispersion (variance in vegetation clustering) into restoration planting designs, projects will insure themselves against the uncertainty imposed by disturbances, limited by their willingness to accept a lower rate of recolonization.

Introduction

The worldwide degradation of ecosystems by human activities has had major consequences for human livelihood and has spawned an on-going pursuit for large-scale ecosystem restoration (Costanza *et al.*

1997, Beck 2007, Barbier et al. 2011) as highlighted UN's call to action in the 'Decade of Restoration' (Waltham et al. 2020). While the restoration of many ecosystems has been widely successful, those found in physically dynamic environments, such as coastal and arid 'biogeomorphic' landscapes, are notoriously difficult to restore (Zedler et al. 2000, Wolters et al. 2005, Lotze et al. 2006, de Groot et al. 2013, Bayraktarov et al. 2015). The conventional approach to restoration of a degraded landscape (where seedling establishment is rare) often involves direct transplantation of pioneer organisms in their adult life-stage into bare areas, when they are least sensitive to environmental stress (Friess et al. 2012), so that they may clonally diffuse into the surrounding area (Bainbridge et al. 1995, Lewis & Streever 2000, Bean *et al.* 2004, de Groot & van Duin 2013, Mor-Mussery *et al.* 2013). Yet in highly dynamic physical settings, disturbances tend to inflict heavy losses on isolated individuals, which strongly curtail the effectiveness of this approach (Bergin 1994, Katwijk *et al.* 2016). In such cases, conspecific-facilitation between individual plants often plays a key role in enhancing the persistence of pioneers (Bertness & Leonard 1997, Bruno & Kennedy 2000, Friess *et al.* 2012, Cao *et al.* 2018). Managers may take advantage of this through clustering pioneering organisms together to reduce attrition (Silliman *et al.* 2015, Katwijk *et al.* 2016, Layton *et al.* 2019, Michaels *et al.* 2020). Clustering, however, comes at a cost, reducing the potential for fast recolonization due to the edge-dependent nature of diffusive expansion (Layton *et al.* 2019).

Understanding how to balance the trade-off between dividing vegetation patches into ever-smaller units to maximize expansion rates, while maintaining sufficiently large patches to withstand disturbances of unpredictable timing and magnitude, is in essence an investment trade-off problem. Here, we address this problem to improve the likelihood of restoration success using the concept of 'diversified bet-hedging' (Einum & Fleming 2004, Olofsson *et al.* 2009). Bet-hedging is a class of risk-management strategies effective at maximizing yields when uncertainty about the future is high (Bernoulli 1954, Kelly 1956, Cohen 1966, Walters *et al.* 2016), commonly used in both financial practice (al-Binali 1999) and as a tool to understand the effectiveness of biological life histories (Frank & Slatkin 1990).

'Diversified' bet-hedging is a method to reduce risk by making investments in many categories so that the successful investment in one will account for the short-comings of the other, depending on the future circumstances that arise. This study explores one application of this technique to demonstrate the benefit of employing risk mitigation strategies both in this specific scenario and in a more general sense for ecological restoration.

Here, the consequences of applying a constant initial cover of transplanted vegetation in variable arrangements is explored using a 2-D grid simulation model based on previous theoretical (Kéfi *et al.* 2007, Scanlon *et al.* 2007, Huang *et al.* 2008) and empirical work (Bruno *et al.* 2009, Silliman *et al.* 2015, Schwarz *et al.* 2011) from dryland and coastal systems. In our model, clonal vegetation expands diffusively from initial patches and is destroyed by randomly generated disturbances (mimicking physical disturbances such as erosion or burial). Vegetation loss from disturbances is mitigated depending on the amount of neighboring vegetation. These rules together model the expansion and degradation of clonal pioneering grasses such as salt marsh, seagrass, and dune grass pioneers. Using this framework, we demonstrate how initial configurations of varying spatial dispersion modify the probability of successful re-colonization and the maximum potential speed at which it can be achieved. The effect of environmental disturbances, for which the timing and intensity are highly uncertain, are derived by tracing the outcome of a single vegetation configuration though many randomly generated scenarios. We furthermore describe a practical means by which to introduce variation into a design so that it reflects a desired level of risk. By quantifying a pattern of vegetation in terms of the variance-to-mean ratio in vegetation cover (VMR, also known as the index of dispersion, Hoel 1943), managers will be able to place it along a risk-spectrum that accurately describe its tendency toward risk-seeking or risk-averse characteristics in colonization.

Materials and Methods

Model framework

We developed a simple cellular automaton (Balzter et al. 1998, Balzter 2000) that mimics clonal vegetation patch dynamics (Bruno & Kennedy 2000, Kéfi *et al.* 2007, Scanlon *et al.* 2007, Huang *et al.* 2008, Bouma et al. 2009, Schwarz *et al.* 2011, Silliman *et al.* 2015) where the growth and loss of vegetation occur predominantly at the patch margin. Within a square grid, cells of vegetation are distributed through space from a limited pool of available transplant material that then grow outward diffusively. Cells containing vegetation joined adjacently to other vegetated cells form a larger unit of vegetation called a 'patch'. The rate of vegetative diffusion is constant throughout all trials with a single cell contributing new growth to itself and its 8 surrounding neighbors in proportion to its own vegetation density. Cells with the maximum vegetation density, 1, do not benefit from growth. Disturbances of varying intensity occur stochastically in time, over the entire grid, destroying any vegetation that lacks a threshold amount of neighboring vegetation such that small, isolated patches, and the edges of larger patches, are most vulnerable. The disturbance tolerance rules assume that plant biomass and tolerance to erosion correlate linearly, an assumption that has been supported in experimental trials (Cao *et al.* 2018) and used in similar models of establishment in disturbance-driven environments (Hu *et al.* 2015).

To test the response of a spatial pattern of vegetation in a disturbance-driven environment with high future-uncertainty, we simulated growth from a 100x100 cell starting grid of 10% cover. The use of a constant initial cover was chosen both (1) to reflect a common initial starting state for restoration projects using transplanted vegetation, and (2) to emphasize the impact of spatial patterning when available resources are fixed. The growth of the vegetation was simulated in 100 randomly generated disturbance scenarios where the intensity of the disturbance environment was pulled from a random (uniform) pool. The vegetation cover was then traced through time as it attempted to fully colonize the grid. Given sufficient time, all simulations reached an equilibrium at either 0% or 100% cover. As such, the final cover could be used to classify each simulation as either a 'success' or 'failure'.

Initial vegetation configurations

The intensity of spatial dispersion in the pattern of vegetation was tuned by determining (1) the number of patches and (2) the size of each patch. First, a random number of vegetated cells were spread over the grid. Circular patches then expanded from these initial cells through diffusion until they reached a desired size. Initial patch sizes were drawn from a log-normal distribution, where increasing the standard deviation parameter of the distribution increased the intensity of variation between patch sizes. Additionally, the spatial dispersion of the patches was modified by perturbing the position of patches in relation to one another to create a spectrum of patterns, which were biased either to be more regularly spaced or to cluster. In order to create clustered and regular patterns we used an algorithm roughly approximating a magnetic field extending out from each vegetation patch's center of mass that either attracted or repulsed nearby vegetation according to the inverse-square law. The intensity of the restructuring of the pattern of vegetation was determined by running the algorithm for more or fewer time steps. Quantitative characterization of the spatial heterogeneity of vegetation was measured using the variance-to-mean ratio (VMR) method (Equation 1, Hoel 1943).

$$VMR = \sigma^2/\mu \qquad \qquad \textit{Equation 1}$$

where σ^2 is the variance of- and μ is the mean number of vegetation pixels found within the spatial pattern, when divided into ten 10x10 pixel sample quadrats (see Figure 3 for visual representation of this spectrum). In total we tested 428 patterns ranging between a VMR of 0.166 and 72, where a ratio of 1 represents an unbiased random Poisson pattern.

Disturbances

Disturbances in this model degrade the vegetation in a patch from the outer edge inward by preferentially destroying vegetated cells with fewer vegetated neighboring cells. During disturbances, cells containing vegetation may be returned to a bare state depending on the amount of vegetation contained in their own cell and in the neighboring eight cells in alignment with the concept of conspecific-facilitation between individual plants (Bertness & Leonard 1997, Bruno & Kennedy 2000, Friess *et al.* 2012, Cao *et al*. 2018). Here, the maximum disturbance strength is tuned so that fully vegetated cells that are surrounded by fully vegetated neighbors cannot be destroyed in disturbances. The disturbance magnitude ranges between the values 0 and 1, representing the amount of nearby vegetation required to resist it, divided by the maximum possible tolerance (a fully vegetated cell surrounded by eight fully-vegetated neighbors). Protective benefits also extend over the repeating boundary condition. Each simulation is initiated with a specific disturbance probability distribution from which the disturbance magnitude is randomly drawn at each time step. We chose to use a log-normal distribution to describe the likelihood of disturbances of greater intensity. Long-tailed distributions of many kinds would have been equally valid in this simulation; however using the log-normal distribution made it possible to set the intensity of the disturbance environment using only one parameter, the standard deviation, ignoring the mean because of the re-scaling of the distribution to within the vegetation tolerance range of 0 and 1. The average (mean-log) disturbance intensity of each simulation is quantified in terms of the tolerance required to survive an average event (a value between 0 and 1, see Figure 1). Here, the value 0.5 indicates a simulation featuring severe disturbances where a vegetated cell must be at least halfway surrounded by fully vegetated cells to survive an average disturbance. Here, increasing the frequency of disturbances is effectively equivalent to lowering the rate of diffusive expansion, since in either case the plant would be exposed to a larger number of harsh events before reaching a given size.

Monte Carlo simulations: Patch dynamics under varying disturbance scenarios

With these simple dynamics at play, we imposed a variety of initial configurations of transplant material onto each grid, simulating growth in disturbance-prone environments until either the entire grid became saturated with vegetation or until all vegetation was lost. These simulations were then repeated 100 times for each configuration, drawing disturbances stochastically from a unique regime in each 'Monte Carlo' trial (He & Mladenoff 1999, Klenner *et al.* 2000). All configurations experienced the same series of random trials. For each trial the disturbance environment parameter (standard deviation) was selected from a uniform distribution ranging between 0.25 and 2.5. These extreme values either led to a 100% chance of destruction of all possible configurations, or such weak disturbances that all configurations consistently achieved their maximum speed of colonization. The interval between these minimum and maximum values represented the entire range of relevant disturbances conditions and the flat (uniform) distribution assumed that no prior information was known about the tendency of the environment.

Statistical analyses

The correlation between the VMR metric and (1) a pattern's probability to experience restoration failure as well as (2) the average interval required to achieve 100% cover in successful trials, were calculated using 3rd-order polynomial linear regressions (Figure S1). Both the y- and x-variables were log-transformed to account for some of the non-linearity in the relationship between these quantities before fitting the regressions. The chosen linear models were selected from a group of potential models through AIC model comparison (including 1st-, 2nd-, and 3rd-order polynomial fits, with logged and unlogged variables). The chosen regression model had an AIC value of -1054, which was a significant improvement from the second-best model at -938 and the worst model at 2401 (here a more negative AIC value represents a stronger fit). All modeling and analyses were performed in R version 3.6.0 (R Core Development Team, 2008).

Results

Pattern characteristics driving risk mitigation

To showcase how the spatial arrangement of vegetation in restoration designs impacts the recolonization process, we consider three strongly contrasting archetypal patterns: (1) 1000 patches of the smallest possible size placed in a regular gridded pattern (Figure 1a), (2) the same 1000 patches placed at random (Figure 1b), and (3) a configuration that places all vegetation into a single, massive circular-patch (Figure 1c). When exposed to an identical series of 100 random disturbance-environments, these three patterns display strongly divergent responses in the survival and expansion of vegetation. A comparison between the regularly-spaced patches and the random (Poisson) arrangement shows that random patch-displacement increases the overall probability of restoration success from 32 % to 65 %, but also increases the minimum period required for colonization to take place from 101 to 152 time steps. Meanwhile, the single large patch has an even greater probability of eventual colonization, at 86%, but this comes at a severe cost to speed, requiring a minimum interval of 1468 time steps to achieve complete colonization, which is nearly ten-times longer. These differences in response demonstrate how patterns that prime vegetation to expand quickly, trade away their overall likelihood to survive disturbances and ultimately succeed in landscape colonization, and vice versa.

Trade-off between risk and reward

The extreme costs associated with exaggerated investment into either patch consolidation or regularization, demonstrated between the above archetypes, give an indication that design efficiency may be maximized by an intermediate pattern somewhere between these two opposing cases. To probe this question in depth, we generated a set of 428 patterns along a spectrum between the opposing archetypes. When exposing these patterns to the same series of 100 random disturbance-environments, it becomes clear that the extent of spatial clustering or regularity in the design strongly correlates with both (1) the

likelihood of restoration success ($F_{3,421}$ = 5154, n = 425, R^2 = 0.9733, p < 0.0001, Figure S1a) and (2) the

speed of colonization ($F_{3,421}$ = 3159, n = 425, R^2 = 0.9572, p < 0.0001, Figure S1b). The extent of spatial

clustering we measure using the variance-to-mean ratio (VMR) of the vegetation cover within the pattern

(see methods for details). When the trade-off between risk and reward is displayed as a Pareto-frontier,

where the speed and likelihood of restoration success are plotted against each other (Figure 2), we find

that extreme investment into either patch consolidation or regularization yields strongly diminishing

returns. At high VMR values, heavily clustered vegetation patterns continue to drastically diminish the

rate of colonization without strongly impacting the overall probability of colonization success.

Meanwhile, perfectly regularized gridded patterns have an extremely high risk of failure while yielding

only minor further benefits to speed. Designs that more efficiently balance the diminishing returns lie

roughly within the VMR range between 2.5 and 11, which is representative of slightly clustered random

pattern (see Figures 2-3 for visualizations of the pattern spectrum). Note that the optimal value varies

depending on the environment, favoring more clustered patterns as the average environmental conditions

become increasingly hostile.

Patch-scale mechanisms driving risk-reward trade-off

The strong correlation between spatial pattern characteristics and risk-reward responses is ultimately

governed by patch-scale dynamics at work within the patterns. When considering the size and shape of a

single patch, both the capacity for quick patch-expansion and vulnerability to degradation are invariably

linked to the patch's the edge/area-ratio (Figure 3). Patches with large edge/area ratios have a larger

proportion of their vegetation actively contributing to colonization but are simultaneously more

vulnerable to disturbances. Due to the stochastic nature of disturbances, a high edge/area-ratio can lead to

situations in which the colonization of the landscape happens very quickly, even in environments that

tend on average to be hostile due to the occurrence of unusual periods of calm (i.e. 'windows of

opportunity', Balke *et al.* 2014). Yet in hostile environments in particular, the use of exclusively small

patches maximizes the vulnerability of the vegetation, which more often leads to equally rapid patch-degradation. Ultimately, this concurring tendency for fast growth and fast degradation means that the results of restoration projects in erosive environments will be more erratic the smaller and more uniform patches are in size.

The same trade-off pervades at larger spatial scales in the dynamics between neighboring patches. The initial arrangement of many patches in space effects their developmental trajectory by either biasing the patches to avoid contact, or by facilitating early patch-linking events. Patch linking occurs when the edges of neighboring patches grow together. This event abruptly lowers the edge/area-ratio of the merging patches by eliminating the patch-edges that collide. This increases the overall disturbance-resistance of the vegetation pattern while also decreasing the amount of vegetation contributing to expansion. The choice to utilize regular spacing, as in gridded project designs, delays patch linking and maintains a large cumulative edge-length throughout the colonization process (Figure 4a). This exaggerates the early period of vulnerability while prolonging the period of strongest growth. When inter-patch distances are instead highly variable, some patches link up earlier than others and contribute progressively to a risk-averse pattern while other more isolated patches retain their vulnerable status and continue to contribute to rapid growth. When viewed at the scale of the entire pattern, variability in patch-spacing leads to the development of disturbance-refuges inside vegetation patches of many different sizes. This allows spatially variable patterns to survive disturbances of large magnitude while also retaining much of their capacity to expand in the case that disturbances do not appear (Figure 4b & c). This self-balancing behavior intrinsic to spatially variable patterns demonstrates the central advantage of taking a 'diversified bet-hedging' approach.

Discussion

Main findings

This study demonstrates the important consequences of the spatial arrangement of transplanted vegetation in a restoration project. In a frequently disturbed erosive environment, such as is common to coasts and arid landscapes, creating both a spectrum of patch sizes and a spectrum of inter-patch distances is key to finding a proper balance between risk mitigation and growth efficiency under uncertainty. The VMR metric can help to quantify the extent of dispersion in a chosen pattern which is useful in distinguishing the relative utility of different patterns in the same environment. However, there are limits to its practical application since environmental data remain necessary to determine the 'optimally' balanced pattern in each new setting. Instead, this theoretical model should encourage managers to think about spatial arrangements as consequential aspects of a project design, rather than as an arbitrary feature. In particular, we have demonstrated that the widely standardized practice of performing transplantations at even distances on a grid is the theoretically worst design choice in the face of disturbances. Even a small divergence in the arrangement of vegetation away from this design appears to drastically improve the resilience of the transplanted vegetation. As a rule of thumb, we suggest the use of a Poisson random pattern as a replacement in standard practice because it is both theoretically resilient and practically manageable to produce. As an example, a Poisson random pattern (with a VMR roughly equal to 1) can be produced by preselecting the positions at which transplanted vegetation is placed using pairs of latitude and longitude coordinates determined at random, likely with the aid of random number generator.

Overcoming human tendencies to favor uniform designs

In contrast to most natural processes, like seed dispersal, that tend to form Poisson random patterns, humans tend to prefer to create uniform designs. It has been demonstrated that the public consensus of what a 'random pattern' should look like is biased toward more uniform patterns that intentionally avoid clustering (Bar-Hillel & Wagenaar 1991, Falk *et al.* 2009). In practice, this means that even when planting designs do not have the specific goal of achieving uniformity, planters will generally produce

biased uniform patterns simply out of habit. Thus, making a conscious shift toward utilizing any kind of clustering random patterns will require some effort. Likewise, there may be further logistical or practical impediments during project construction and monitoring as a consequence of using non-Euclidian designs. Nevertheless, in the majority of cases the increased likelihood of restoration success, demonstrated here, should be a motivating force for practitioners to meet and overcome the novel logistical challenges. Furthermore, in nature, uniform patterns are the outlier and there is mounting evidence that the non-uniformity of landscape patterns is critical to the creation of productive and resilient ecosystems – utility beyond what has been explored here. Overdispersion in the distribution of vegetation has for instance been demonstrated to accelerate the formation of certain types of natural infrastructure that are developed by scale-dependent feedback processes (Temmerman *et al.* 2007, Bouma *et al.* 2009, Schwarz *et al.* 2018, van de Vijsel *et al.* 2020). Schwartz *et al.* (2018) demonstrated that tidal channel formation in salt marshes is accelerated when vegetation clustering is intensified, and that the distribution of vegetation can also alter the final structure of the channels that service the marsh. Dune-building grasses have even been shown to employ Levy-walks (strongly uneven patterns in rhizome extension), which naturally produce patchy clone-structure, in order to maximize dune formation with limited resources (Reijers *et al.* 2019). Variation in vegetation patch sizes has furthermore been found to enhance biodiversity at higher trophic levels (Bonte *et al.* 2004, Tews *et al.* 2004, Crotty *et al.* 2018). Meanwhile, restored natural systems that have incorporated uniform or Euclidean patterns due to past management policies are commonly more impoverished in biodiversity and less resilient than their historical precursors (Beck & Airoldi 2007, de Groot & van Duin 2013, Lawrence *et al.* 2018).

Accepting uncertainty allows us to approach problems differently

The broader question of how to appropriately deal with uncertainty transcends disciplines. Work on uncertainty that began three hundred years ago (Bernoulli 1954, *translation of Bernoulli 1738*) has had a major impact on the way we understand the evolution of life histories (Cohen 1966, Frank & Slatkin

1990) and account for risk in daily life (al-Binali 1999). Yet although many of the methods developed to address risk, like bet-hedging, may appear ubiquitously throughout biology, their application in biological contexts, such as restoration, is not common practice (except see a few examples in Doherty *et al.* 2015, Davies *et al.* 2018). Instead, when information is lacking, researchers tend to seek out solutions that remove, rather than accept, the uncertainty in complex problems (i.e., modeling, performing pilot studies, and conducting lab experiments to understand mechanisms). While such methods have been irrefutably effective in the scientific discipline, these approaches have a hidden cost, which is that the research itself requires an uncertain investment of time and resources before perfect information is achieved. More so, in cases where processes change more quickly than they can be studied, attainment of perfect information may not be achievable, a problem of growing prescience in our current era of global change (Polasky *et al*. 2011). Comparatively rare are solutions that attempt to flip the problem on its head, and address uncertainty by increasing the robustness of plans against many potential outcomes. A change in mindset that asks how we can mitigate risk rather than reduce uncertainty may yet open up an untapped well of solutions to old and tired problems that allow us to effectively achieve goals where time, resources, and information are limited.

Authors' contributions

GSF, JvB, & TJB conceived the ideas and designed methodology; GSF wrote and ran the simulations and performed the analyses of results; GSF, RJMT, KD, WL, TvH, & TJB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability statement

The scripts used to perform the analyses that appear in this study are archived and publicly available via 4TU.Research Data. https://doi.org/10.4121/18133766 (Fivash *et al.* 2022).

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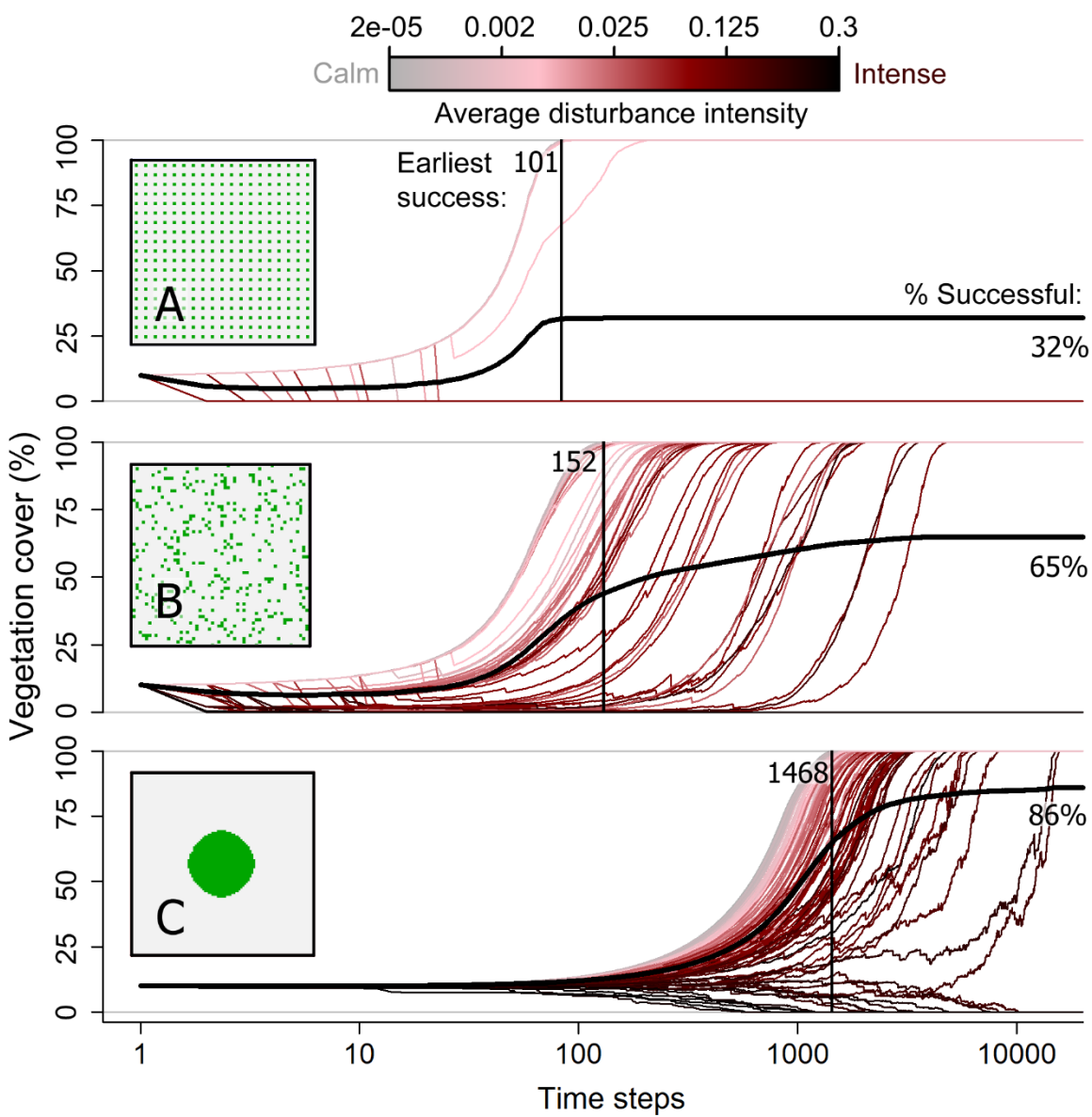
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patches (a) represents the most risk-seeking, fast-growing spatial arrangement of vegetation. When the same vegetation patches are placed at random (b), the likelihood of successful colonization doubles. In the most risk-averse case (c), the probability for a single large circular patch to withstand disturbances and colonize the entire grid is even more likely, but requires at a minimum nearly 10-times as long as the random pattern to fully colonize the grid.
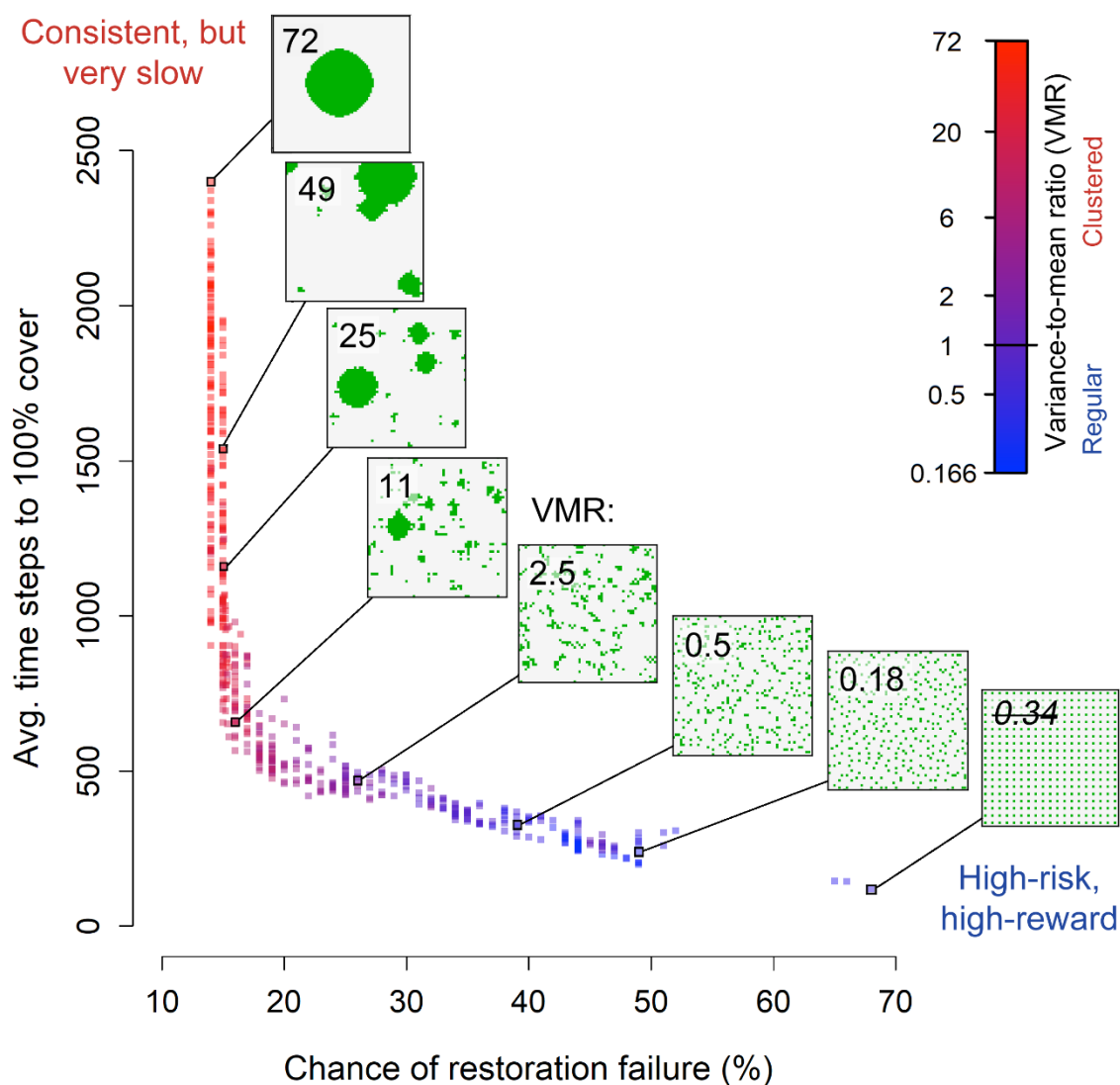
Fig 2. The trade-off in pattern design between maximizing the speed of colonization and the minimizing the risk of restoration failure is displayed as a Pareto frontier. The extent of spatial clustering in each pattern (measured as the variance-to-mean ratio, VMR) is depicted by the point colors between blue (regular) and red (clustered). The concave shape of the Pareto frontier demonstrates that both extremely regular and clustered patterns have accentuated disadvantages, in the form of either a slow colonization rate or a high risk of failure. In our model trials, these negative consequences are minimized in intermediately clustered random spatial patterns with a VMR-value roughly between 11 and 2.5. Note that

our VMR quantification technique fails to adequately characterize highly uniform patterns, which should,

but do not, approach a VMR of 0 (see inflated VMR of gridded pattern).
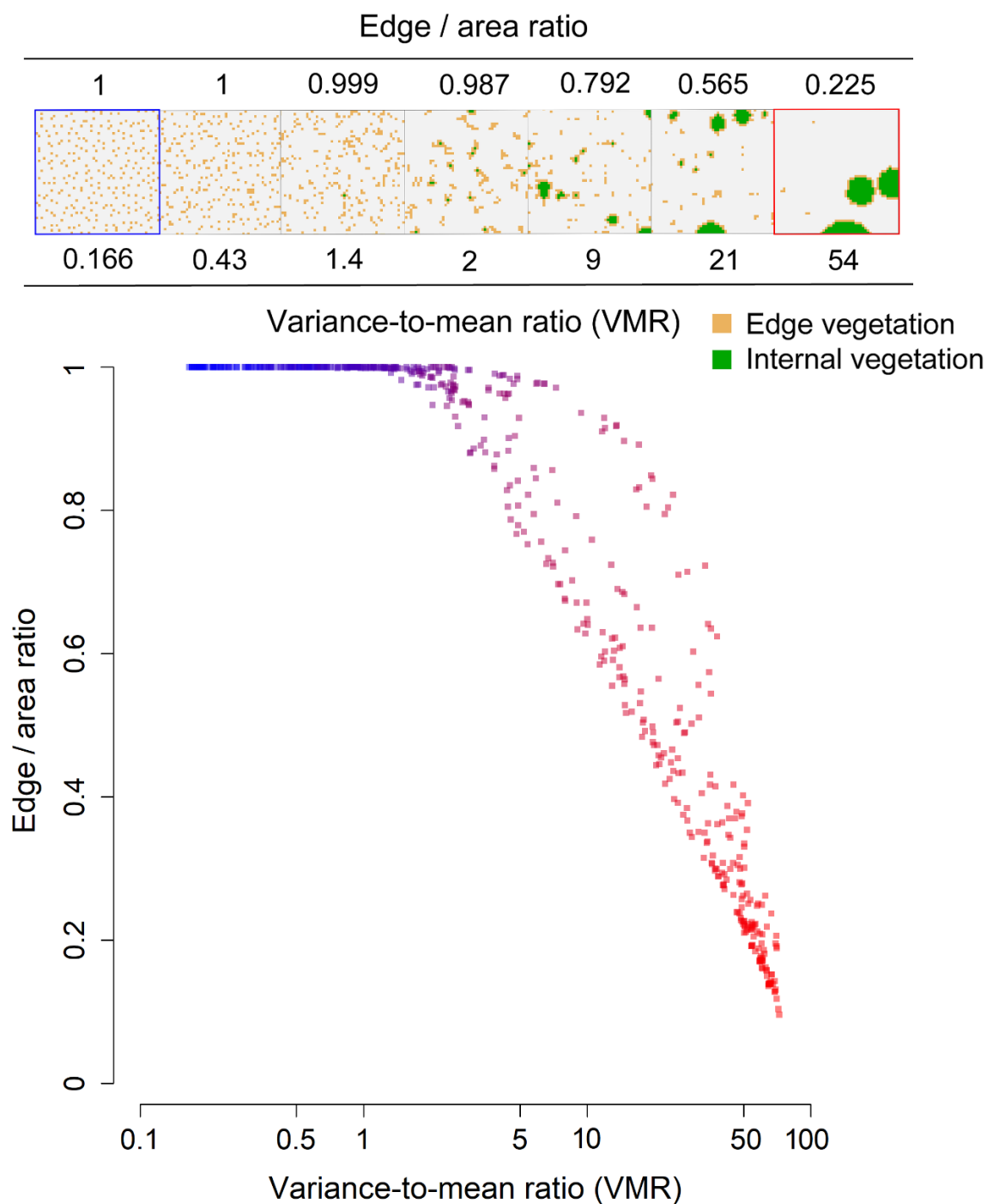
Fig 3. The change in the edge/area ratio is displayed for a series of vegetation patterns across the spectrum of spatial heterogeneity, measured by the variance-to-mean ratio. In our simulations, patches grow diffusively and are impacted by disturbances only at their edge. Internal vegetation, denoted in green, acts as insurance, buffering the magnitude of both positive and negative changes in total vegetation

cover, because it cannot be directly destroyed by disturbances, but also does not contribute to expansion.

The red-blue point color scheme displays each point's VMR value (also on the x-axis) corresponding to
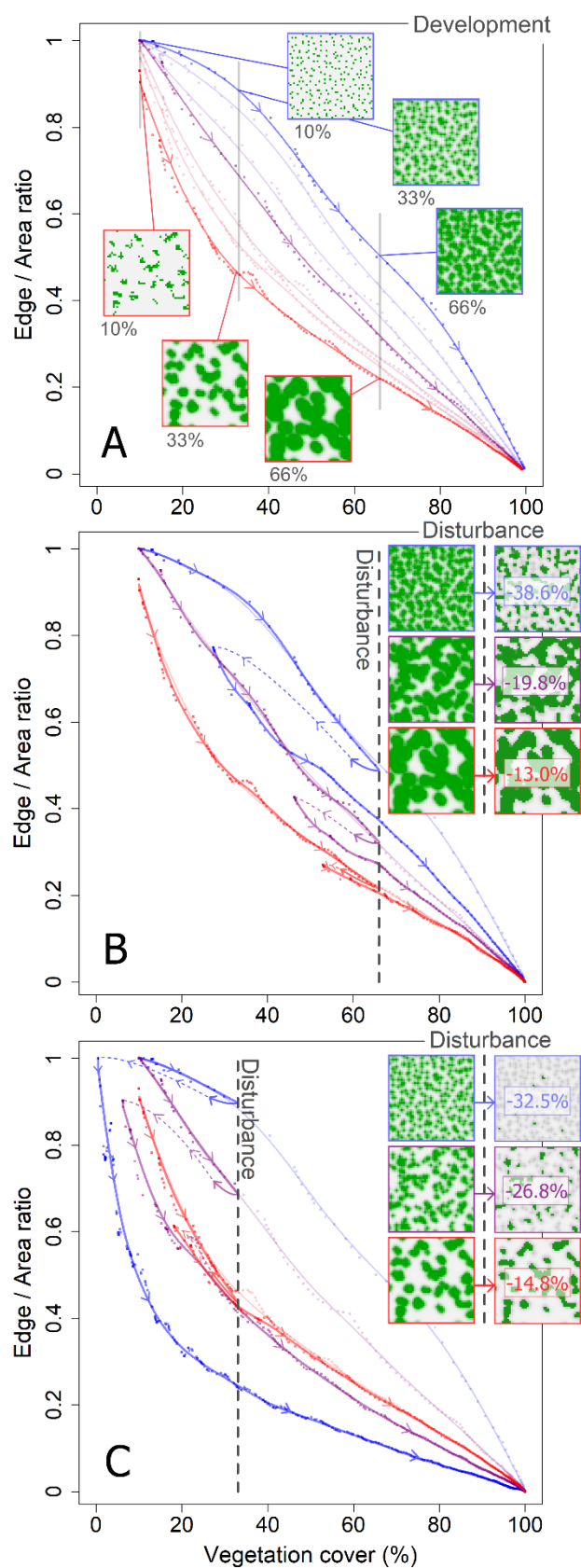
the point colors seen in Figure 2.

Fig 4. The change in edge/area ratio is displayed for three contrasting spatial patterns as they

increase in total vegetation cover. In panel A, vegetation develops without disturbances, while in panel B and C, a single disturbance event occurs once vegetation cover has reached a threshold value (B: 33%, C: 66%). The colored points and lines correspond to the characteristics of the special pattern: clustered (red), regular (blue), Poisson random (purple). Points are fit with smooth splines to aid visualization. Clustered patterns achieve low edge/area ratios sooner due to early patch-linking events that consolidate vegetation into fewer large patches. In contrast, regular patterns delay linking and maintain a large edge surface at higher total cover (panel A). The removal of vulnerable vegetation with high-growth potential in the aftermath of the disturbances (panel B & C) shifts edge/area development to follow more conservative trajectories that achieve a low edge/area ratio, sooner. The patterns most vulnerable to disturbances both lose the most vegetation cover and are most strongly altered in character, in the wake of a disturbance.