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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.

Keywords
bet-hedging, biogeomorphology, disturbances, edge effects, restoration, risk mitigation, spatial dispersion, uncertainty
The worldwide degradation of ecosystems by human activities has had major consequences for human livelihood and has spawned an ongoing pursuit for large-scale ecosystem restoration (Barbier et al., 2011; Beck & Airolidi, 2007; Costanza et al., 1997) 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 (Bayraktarov et al., 2015; de Groot et al., 2013; Lotze et al., 2006; Wolters et al., 2005; Zedler, 2000). The conventional approach to restoration of a degraded landscape (where seeding 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; Bean et al., 2004; de Groot & van Duin, 2013; Lewis & Streever, 2000; 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; van 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; Cao et al., 2018; Friess et al., 2012). Managers may take advantage of this through clustering pioneering organisms together to reduce attrition (Layton et al., 2019; Michaels et al., 2020; Silliman et al., 2015; van Katwijk et al., 2016). 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; Cohen, 1966; Kelly, 1956; 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 shortcomings 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 are explored using a 2D grid simulation model based on previous theoretical (Huang et al., 2008; Kéfi et al., 2007; Scanlon et al., 2007) and empirical work (Bouma et al., 2009; Schwarz et al., 2011; Silliman et al., 2015) 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 neighbouring 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, is derived by tracing the outcome of a single vegetation configuration through 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 describes its tendency towards risk-seeking or risk-averse characteristics in colonization.

We developed a simple cellular automaton (Balzter, 2000; Balzter et al., 1998; Pascal & Guichard, 2005) that mimics clonal vegetation patch dynamics (Bouma et al., 2009; Bruno & Kennedy, 2000; Huang et al., 2008; Kéfi et al., 2007; Scanlon et al., 2007; Schwarz et al., 2011; Silliman et al., 2015) from 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 describes its tendency towards risk-seeking or risk-averse characteristics in colonization.
cover. The use of a constant initial cover was chosen both (a) to reflect a common initial starting state for restoration projects using transplanted vegetation and (b) 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'.

2.2 | Initial vegetation configurations

The intensity of spatial dispersion in the pattern of vegetation was tuned by determining (a) the number of patches and (b) 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. To create clustered and regular patterns, we used an algorithm roughly approximating a magnetic field extending out from each vegetation patch's centre 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 timesteps. Quantitative characterization of the spatial heterogeneity of vegetation was measured using the variance-to-mean ratio (VMR) method (Equation 1, Hoel, 1943).

\[
VMR = \frac{\sigma^2}{\mu}
\]

where \(\sigma^2\) is the variance of vegetation and \(\mu\) is the mean number of vegetation pixels found within the spatial pattern, when divided into ten 10 x 10 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.

2.3 | Disturbances

Disturbances in this model degrade the vegetation in a patch from the outer edge inward by preferentially destroying vegetated cells with fewer vegetated neighbouring 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 neighbouring eight cells in alignment with the concept of conspecific facilitation between individual plants (Bertness & Leonard, 1997; Bruno & Kennedy, 2000; Cao et al., 2018; Friess et al., 2012). Here, the maximum disturbance strength is tuned so that fully vegetated cells that are surrounded by fully vegetated neighbours 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 neighbours). 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 timestep. 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.

2.4 | 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.
2.5 | Statistical analyses

The correlation between the VMR metric and (a) a pattern’s probability to experience restoration failure as well as (b) the average interval required to achieve 100% cover in successful trials were calculated using third-order polynomial linear regressions (Figure S1). Both the y- and x-variables were log-transformed to account for some of the nonlinearity 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 first-, second- and third-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 modelling and analyses were performed in R version 3.6.0 (R Core Team, 2020).

3 | RESULTS

3.1 | 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: (a) 1,000 patches of the smallest possible size placed in a regular gridded pattern (Figure 1a), (b) the same 1,000 patches placed at random (Figure 1b) and (c) 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 timesteps. 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 1,468 timesteps to achieve complete colonization, which is nearly 10 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.

3.2 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 (a) the likelihood of restoration success ($F_{3,421} = 5154, n = 425, R^2 = 0.9733, p < 0.0001$, Figure S1a) and (b) 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 and 3 for visualizations of the pattern spectrum). Note that the optimal value varies depending on the environment, favouring more clustered patterns as the average environmental conditions become increasingly hostile.

3.3 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 edge/area ratio (Figure 3). Patches with large edge/area ratios have a larger proportion of their vegetation actively contributing to...
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 neighbouring patches. The initial arrangement of many patches in space affects 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 neighbouring 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 behaviour intrinsic to spatially variable patterns demonstrates the central advantage of taking a ‘diversified hedging’ approach.
4 | DISCUSSION

4.1 | Main findings

This study demonstrates the important consequences of the spatial arrangement of transplanted vegetation in a restoration project. Creating both (1) a spectrum of patch sizes and (2) a spectrum of inter-patch distances is key to finding a proper balance between risk mitigation and growth efficiency under the uncertainty imposed by erosive disturbances, common to coastal and arid systems. 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.
4.2 | Overcoming human tendencies to favour 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 towards 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 towards 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 (Bouma et al., 2009; Schwarz et al., 2018; Temmerman et al., 2007; van de Vijsel et al., 2020). Schwarz 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, 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; Crotty et al., 2018; Tews et al., 2004). 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).

4.3 | 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 300 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 & Zedler, 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. modelling, performing pilot studies and conducting laboratory 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.

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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.

**AUTHORS’ CONTRIBUTIONS**

G.S.F., J.v.B. and T.J.B. conceived the ideas and designed the methodology; G.S.F. wrote and ran the simulations and performed the analyses of results; G.S.F., R.J.M.T., K.D., W.L., T.v.d.H. and T.J.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

**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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