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RESEARCH ARTICLE

Surviving the winds through pattern formation: Mathematical modelling of heather stripes in Scotland

Toyo Vignal[1,2] | Mara Baudena[3,4] | Jonathan Sherratt[1] | Angeles G. Mayor[5]

[1]Maxwell Institute for Mathematical Sciences, University of Edinburgh, Edinburgh, UK

[2]Integrative Community Ecology Unit, Okinawa Institute of Science and Technology Graduate University, Onna, Okinawa, Japan

[3]Institute of Atmospheric Sciences and Climate, National Research Council, Turin, Italy

[4]National Biodiversity Future Center, Palermo, Italy

[5]Department of Biodiversity, Ecology and Evolution, Complutense University of Madrid, Madrid, Spain

Correspondence
Toyo Vignal
Email: t.vignal@oist.jp

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Abstract

1. Remarkable patterns of heather (*Calluna vulgaris*) and soil can be observed in some areas of Scotland. Bands of vegetation regularly alternate with bands of bare ground, with the whole pattern slowly moving in a direction perpendicular to the stripes. While previous studies have proposed that strong winds may play a role in shaping these patterns, the underlying mechanisms—particularly the initiation of the patterning—remain poorly understood.
2. In this study, we develop a simple mathematical model based on two partial differential equations to capture local interactions between wind, soil and vegetation. Using dynamical systems theory and numerical simulations, we identify the conditions necessary for pattern formation and provide insight into how these patterns emerge and disappear. Furthermore, we derive a parametrisation, informed by existing literature, that produces results with realistic order of magnitude for pattern amplitude, wave length and travelling wave speed.
3. Our model demonstrates that basic interactions between wind, soil and vegetation are sufficient to generate solutions consisting of moving bands of vegetation, closely resembling the observed real-world patterns.
4. Our analysis reveals the role of *Calluna vulgaris* as an ecosystem engineer, facilitating its survival in harsh, wind-exposed environments by forming spatial patterns that extend its habitat range. Notably, our findings indicate that pattern onset does not require pre-existing soil patterning.
5. *Synthesis*: Our results suggest that simple interactions between wind, soil and vegetation can drive the formation of periodic biogeomorphological patterns in wind-blasted ecosystems. This modelling approach has potential applications for understanding other ecosystems subject to strong winds and may contribute to conservation efforts for these sensitive habitats.

KEYWORDS
advection–diffusion model, biogeomorphological patterns, ecosystem engineer, partial differential equations, plant–plant facilitation, Scottish Highlands, wind-driven vegetation pattern formation

Jonathan Sherratt and Angeles G. Mayor are co-senior authors.

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1 | INTRODUCTION

Spatial patterns emerging through self-organisation, without direct human intervention, are widespread in nature. They can arise in otherwise homogeneous conditions, taking various forms—including strikingly regular arrangements—and occurring across diverse climates, environments and types of organisms (Deblauwe et al., 2008; Eppinga et al., 2010; Martinez-Garcia et al., 2022). These patterns are closely linked to ecosystem functioning and resilience: Spatial patterns have been shown to enhance ecosystem productivity compared to homogeneous distributions, further allowing ecosystems to maintain functionality up to certain stress levels (Aguiar & Sala, 1999; Kéfi, Génin, et al., 2024; Rietkerk et al., 2021). Spatial patterns are also increasingly recognised as potential indicators of resilience loss and early warning signals of tipping points—sudden, often irreversible transitions to alternative ecosystem states under environmental stress (Dakos et al., 2024; Kéfi et al., 2007; Rietkerk et al., 2004).

Vegetation patterns are particularly common and well studied in drylands, where water scarcity leads plants to form patches separated by bare soil. Mathematical models have been instrumental in uncovering the mechanisms behind these patterns, inspired Turing's (1952) seminal work on pattern formation and incorporating processes such as resource redistribution, ecosystem engineering and plant–plant facilitation (Deblauwe et al., 2008; Gilad et al., 2004; Klausmeier, 1999; Rietkerk et al., 2002).

Wind-driven spatial patterns are another compelling example of emergent structures in nature. Models of wind-driven landform dynamics, such as sand dunes, incorporate fluid dynamics and sediment transport to describe the interplay between wind, sand and sometimes vegetation (Bagnold, 1941; Durán et al., 2010; Falcone & Finzi Vita, 2020; Kroy et al., 2002). In vegetated dune models, vegetation contributes to pattern formation by mitigating wind-driven sand erosion (Baas & Nield, 2010). Another type of wind–vegetation interaction drives the so-called 'tree regeneration waves', or *shimagare* in Japanese, where trees on mountain slopes are sorted into stripes according to their developmental stage. In this case, the main driver of patterning is the wind's impact on vegetation mortality. Tree regeneration waves have been successfully modelled using grid-based approaches, capturing local asymmetrical plant–plant facilitation, where windward trees provide shelter to leeward ones (Puigdefábregas et al., 1999; Sato & Iwasa, 1993; Schlicht & Iwasa, 2006).

In addition to sand dunes and *shimagare*, less-studied biogeomorphological patterns have been reported in montane, subarctic and arctic regions. These soil-vegetation formations are thought to result from interactions between wind, frost and topography (Gallart et al., 1993; Selkirk-Bell & Selkirk, 2013). However, the precise mechanisms behind many of these patterns remain unclear, with mathematical models only beginning to address such complex systems. This study focuses on the spectacular heather (*Calluna vulgaris*) patterns found in the Scottish Highlands (Ballantyne, 2019; Bayfield, 1984; Metcalfe, 1950; Watt, 1947). Sometimes referred to as 'wind-striped heath' or 'wind stripes', the patterns consist of alternating bands of vegetation and bare soil (see Figure 1a). Housing a rich diversity of lichens and bryophytes (Britton & Fisher, 2007; Gilbert & Fox, 1985), these formations occur on flat or gently sloped terrain. The soil surface exhibits ripples with an asymmetric profile: convex on the bare side and concave on the vegetated side (Bayfield, 1984) (see Figure 1c). The dynamics of the vegetation bands were described in an early paper from Scottish botanist and plant ecologist Watt (1947) as a striking example of spatially ordered vegetation phases, with heather linearly sorted following its life phases (building, mature, degenerate and dead) across the stripe. Furthermore, the bands migrate slowly, approximately 1 cm per year (Bayfield, 1984), in the direction perpendicular to the stripes, thought to be that of prevailing winds, resulting in a space–time mosaic of heather growth phases (Watt, 1947). Consistent with wind-driven formation hypotheses, these patterns are found in areas subject to exceptionally strong winds. Despite these associations, understanding the precise role of wind in heather stripe formation remains challenging due to coarse wind data and complex local topographic influences (Wagenbrenner et al., 2016). In his 1984 study focusing on the dynamics of heather stripes, Bayfield (1984) used spray-painted gravel to track soil movement, supporting the role of wind in stripe migration. However, with only three measurements over 1 year, longer term trends remain unverified.

The heather stripes literature is very scarce, consisting of few, decades-old descriptions of the phenomenon (Bayfield, 1984; Metcalfe, 1950; Watt, 1947). To date, no mechanistic model has specifically addressed the formation of heather stripes or evaluated whether strong winds alone can account for these patterns. Furthermore, key questions about the onset of heather stripes remain unresolved. Competing hypotheses exist (Bayfield, 1984), suggesting either vegetation colonisation of bare ground pre-moulded by wind into ripples, or heather dieback at the most exposed points of pre-moulded ground during harsh weather. These uncertainties highlight the suitability of mathematical modelling to determine the processes sufficient and necessary for pattern formation and migration.

Here, we introduce a simple mathematical model of soil and heather dynamics subject to strong prevailing winds, appropriately parametrised and calibrated, to answer the following questions: (i) How does environmental stress influence the persistence of heather, and do spatial patterns contribute to the persistence of stressed heather? (ii) What environmental conditions trigger the formation of spatial patterns in heathland? (iii) Specifically, is pre-patterned ground a prerequisite for the formation of heather stripes, or does heather act as an ecosystem engineer by triggering pattern formation? (iv) What environmental changes lead to the disappearance of heather patterns?

2 | METHODS

2.1 | Model description

Our model consists of two coupled partial differential equations, representing the change in time (t) of the heights of heather and soil surface, respectively denoted by C and S, across a one-dimensional spatial domain (x). We consider prevailing winds blowing in the positive x direction, with

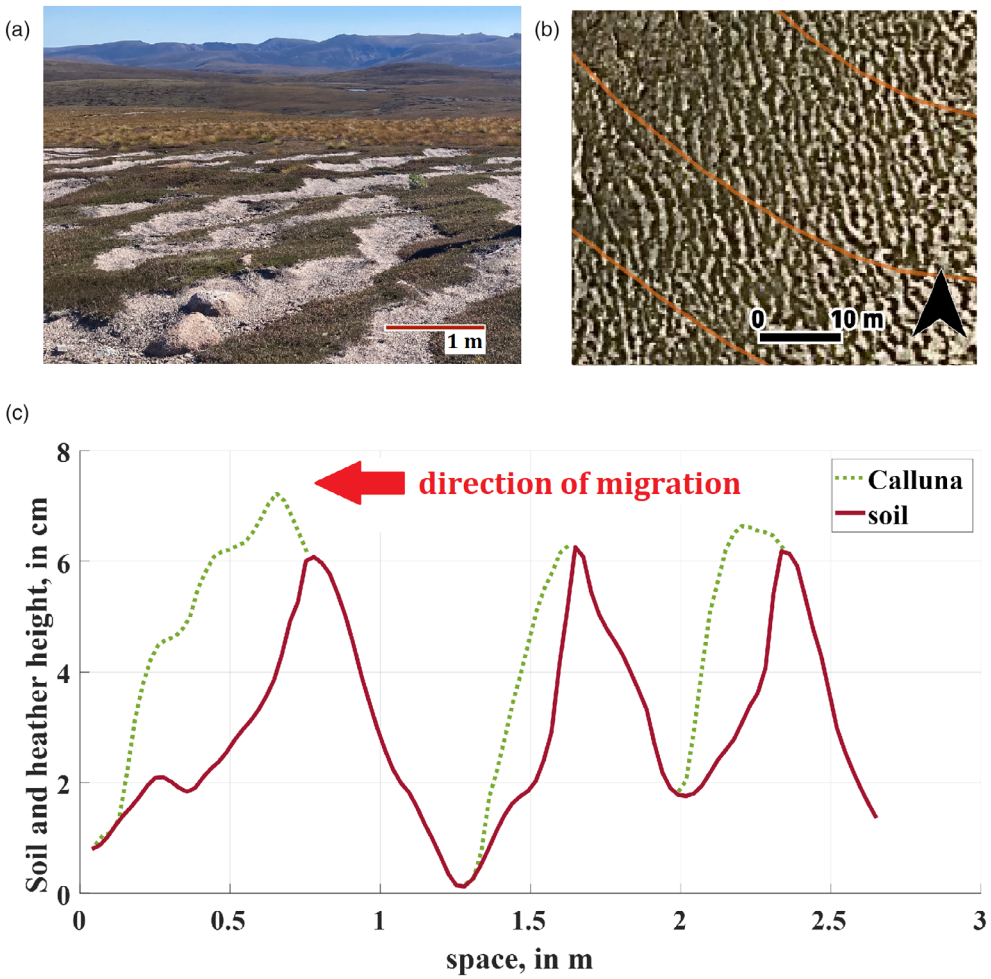


FIGURE 1 (a) Picture of heather stripes in Bynack More, Cairngorms, Scotland, September 2023. (b) Aerial view of a striped area in Hoy, Orkney, Scotland (Getmapping, 2013c). The orange elevation contour lines (Ordnance Survey [GB], 2024a), evidence that the stripes bearing does not match the slope bearing. (c) Pattern profile with the relative heights of soil surface and heather. Data taken from Bayfield (1984), using graphreader.com.

constant speed w. We do not include terrain slope, as we assume that it is not a pattern driver. Empirical data (see Figure 1b; Figure S6) show that, unlike the vegetation stripes patterns found in drylands (a.k.a. 'tiger bush') (Bromley et al., 1997), heather stripes do not necessarily align with elevation contour lines. The choice of a one-dimensional space is motivated by our goal to produce regular bands oriented perpendicularly to the prevailing wind direction, and mathematical tractability. The choice of modelling heather height, rather than biomass or density, is motivated by the physical processes driving the system. Transported soil particles are intercepted by the vertical structure of the plants, so taller heather more effectively reduces soil erosion, as observed in field studies (Imeson, 1971). Furthermore, modelling heather height facilitates empirical validation. First, it is easily measured in a non-invasive way and was the variable recorded in Bayfield's transect study (Bayfield, 1984). Second, for the soil variable, height is the most logical choice, since it is the elevation of the surface that shelters downwind plants. By modelling both variables as heights, we can plot them together and directly compare their spatial profiles—visually and quantitatively—with field observations. Finally, note that plants above-ground biomass and stand height are typically correlated (Proulx, 2021).

$$\underbrace{\frac{\partial C}{\partial t}(x;t)}_{\text{heather height dynamics}} = \underbrace{D_c \frac{\partial^2 C}{\partial x^2}}_{\text{dispersal}} + \underbrace{\frac{rCS}{S+k_1}\left(1-\frac{C}{k_2}\right)}_{\text{soil-dependent logistic growth}} \underbrace{-mC}_{\text{baseline mortality}} \underbrace{-Cwk_3F\left(\frac{\partial S}{\partial x}\right)}_{\text{wind-induced extra mortality}} \quad (1)$$

$$\underbrace{\frac{\partial S}{\partial t}(x;t)}_{\text{soil surface height dynamics}} = \underbrace{D_s \frac{\partial}{\partial x}\left\{\frac{k_4 k_5}{C+k_4}\frac{\partial S}{\partial x}\right\}}_{\text{redistribution, mitigated by the presence of heather}} \underbrace{-\frac{\partial}{\partial x}\left\{S\frac{k_4 k_5 w}{C+k_4}\right\}}_{\text{wind-driven advection, mitigated by the presence of heather}} \quad (2)$$

In the heather equation, Fickian diffusion represents the spread of plants in all directions, as a result of adventitious rooting and/or seed dispersal. We assume that heather has a carrying capacity height, k_2, above which its growth rate becomes negative. Our model also captures that heather requires soil to grow, with a half-saturation parameter k_1, and that heather decays, at a constant baseline rate m. This parameter m captures the effects of mortality, metabolic expenses and all isotropic stresses (i.e. stresses that are equal in all directions), on the plants' height. In addition to m, which we refer to as the *baseline mortality* rate from now on, plants suffer extra, anisotropic and therefore space-dependent, stress induced by strong prevailing winds, at a rate $wk_3F\left(\frac{\partial S}{\partial x}\right)$. The function $F\left(\frac{\partial S}{\partial x}\right)$, defined in the Supporting Information, is the 'softplus' function, a smooth approximation of the ramp function $\max\left(0;\frac{\partial S}{\partial x}\right)$. This function captures how only plants on windward-exposed sides of the microtopography suffer extra wind-induced damage and mortality, at a rate proportional to the wind speed w (Crabtree & Ellis, 2010; Gimingham, 1960). Plants on the leeward side of the soil ripples are sheltered and suffer only the baseline mortality rate m. Bayfield's (1984) field measurements evidence the impact of microtopography on local wind speeds, showing that wind speeds atop the crests of patterned ground are approximately double those recorded above troughs, indicating a significant sheltering effect from the windward slope. The constant k_3 is a physiological parameter specific to the plant, which gives the magnitude of the impact of prevailing wind-induced stress. Empirical observations show that strong winds can damage the heather canopy, and cause desiccation through modified evapotranspiration rates. There is an observed decrease in canopy height with wind speed (Crabtree & Ellis, 2010; Gimingham, 1960; Pears, 1967).

Similar to previous work on wind-driven dryland patterns (Zhang et al., 2017), our soil equation captures two types of sediment redistribution. First, Fickian diffusion captures dispersal in all directions, due to non-prevailing winds and other non-directional factors, at a rate D_s. Second, soil is also exclusively displaced in the positive x direction by strong prevailing winds, with a displacement rate monotonously increasing with wind speed w. Both types of soil redistribution were empirically observed by Bayfield (1984) with his spray-painted gravel experiment. The dimensionless constant k_5 depends on soil type, and represents the soil displaceability, while k_4 is the local height of heather that halves the wind erosion speed. Both the isotropic and directional erosion rates are decreased by the local presence of heather. This negative correlation between heather height and soil displacement rates has been empirically observed (Imeson, 1971).

We adopt a quasi-steady-state approximation for soil formation processes, considering these slow changes negligible compared to the faster physiological processes of heather growth and soil transport. Under this assumption, no soil is created nor destroyed, and the total soil height integrated over space remains constant. Consequently, the dynamics of soil surface height reduce to a pure transport equation, governed by a flux, J. A simple expression for this flux, capturing how vegetation slows down soil erosion, is $J = -\frac{k_4k_5D_s}{k_4+C}\frac{dS}{dx} + wS\frac{k_4k_5}{k_4+C}$. Applying the conservation law $\frac{dS}{dt} + \frac{d}{dx}(J) = 0$ (Murray, 1993), we obtain our transport equation for soil surface height (details are given in the Supporting Information). It is a non-linear generalisation of the classical advection–diffusion equation, with both diffusion and advection coefficients depending on the local vegetation state $C(x,t)$. Finally, we define the zero soil surface height $S = 0$ as the absolute minimum value that the soil surface height can take, representing conditions where there is no soil particle to displace, and heather cannot grow. A more detailed description of the parameters, their units and the values chosen for the simulation are given in the parametrisation section of the Supporting Information.

2.2 | Analysis

We analyse our model using both dynamical system theory and numerical simulations in order to answer our research questions. To address question (i) (How does environmental stress affect the persistence of heather, and do patterns contribute to the persistence of stressed heather?), we begin by considering the effects of isotropic stress (i.e. stress applied equally in all directions) on heather persistence. This is achieved by examining the spatially homogeneous steady states of the system as the baseline mortality rate, m, increases. These steady states are derived by solving the following equations, which neglect spatial processes:

$$\frac{\partial C}{\partial t}(x;t) = 0 = \frac{rCS}{S+k_1}\left(1-\frac{C}{k_2}\right) - Cm \tag{3}$$

$$\frac{\partial S}{\partial t}(x;t) = 0. \tag{4}$$

Subsequently, we incorporate spatial processes, including the directional stress imposed by strong prevailing winds. We explore numerically how the combined effects of isotropic and directional stress influence heather survival and pattern formation.

To answer question (ii) (What environmental conditions trigger spatial patterning in heathland?), we conduct a Turing instability analysis. By applying linear stability techniques and Fourier decomposition, we determine the conditions under which a spatially homogeneous vegetated steady state becomes unstable and gives rise to spatial patterns (Murray, 1993; Van Gorder, 2021). However, it is important to note that Turing instability analysis alone does not establish whether the spatial patterns are stable or transient, nor does it define the duration of any transient dynamics. In some instances, Turing patterns occur on timescales too brief to be observed in nature (Krause et al., 2024). To address this limitation, we perform numerical simulations with realistic parametrisation (Supporting Information). The model is run over extended periods (i.e. 300 years) to assess the timescale over which patterns predicted by our model persist.

For question (iii) (Is pre-patterned ground a prerequisite for the formation of heather stripes, or does heather act as an ecosystem engineer by triggering pattern formation?), we examine the combined insights from Turing analysis and numerical simulations starting with a completely flat soil surface to investigate the onset of

pattern formation. This analysis sheds light on whether heather acts as an ecosystem engineer, facilitating pattern formation even in the absence of pre-existing soil structures.

Finally, we address question (iv) (What environmental changes lead to the disappearance of heather patterns?) through the same realistically parametrised numerical simulations. We identify the environmental conditions under which patterns degrade and ultimately vanish to either bare ground or a homogeneous heather cover.

Detailed parameter values and derivation are provided in the Supporting Information. Unless otherwise stated, simulations are conducted with periodic spatial boundary conditions.

3 | RESULTS

3.1 | Persistence of heather under environmental stress, and the role of patterns in sustaining survival

Examining the spatially homogeneous steady states of our system provides insight into the equilibrium height of heather under isotropic stress. Solving the system (Equations 3 and 4) yields two families of spatially uniform steady states:

1. Bare ground equilibria: These states correspond to vegetation height $C = 0$ and soil height $S = S_0$.
2. Vegetated equilibria: These states are characterised by vegetation and soil heights (C_{eq}, S_{eq}), where the equilibrium vegetation height C_{eq} is given by:

$$C_{eq} = k_2 \left\{ 1 - m \frac{(S_{eq} + k_1)}{rS_{eq}} \right\}. \tag{5}$$

We obtain families of steady states (i.e. continuous curves in the $C - S$ plane) rather than discrete points because soil is a conserved quantity. There is no creation or loss of soil, and the conserved soil height can take any positive value, represented as S_0 in the bare ground equilibrium and S_{eq} in the vegetated equilibrium (note that $S_{eq} = S_0$ when $C_{eq} = 0$).

From expression (Equation 5), we see that the spatially homogeneous vegetated steady state is subject to the condition of existence

$$\frac{rS_{eq}}{S_{eq} + k_1} > m, \tag{6}$$

which imposes two requirements: (1) the maximum growth rate r of heather must exceed its baseline mortality rate m, and (2) the soil surface height S_{eq} must surpass a minimal threshold $S_{min} := \frac{mk_1}{r-m}$, necessary for plants' growth. Linear stability analysis shows that the condition for the existence of the spatially uniform vegetated steady state also determines its (temporal) stability to spatially uniform perturbations. When condition (6) is satisfied, C_{eq} is positive, and the vegetated equilibrium (C_{eq}, S_{eq}) is stable, while the bare ground equilibrium $(0, S_0)$ is unstable. Conversely, when condition (6) is not met, C_{eq} becomes negative, and thus ecologically irrelevant. In this case, the bare ground equilibrium $(0, S_0)$ is stable (Figure 2). Importantly, C_{eq}, the heather height at the uniform vegetated equilibrium, decreases as the baseline mortality rate m increases. There is a critical value $m_{crit} := \frac{rS_{eq}}{S_{eq} + k_1}$ at which C_{eq} reaches zero, marking the transition to stable bare ground equilibrium. In ecological terms, increasing isotropic stress, represented by a rise in m, gradually reduces heather height until bare ground is reached at the critical stress threshold m_{crit}. This decline in C_{eq} aligns with field observations: as environmental stress increases, heather height decreases (Gimingham, 1960; Grant & Hunter, 1962). Under stress, heather adopts a low, prostrate form, while in less stressed environments, it grows in an upright, erect form (Gimingham, 1960) (see Figure 2 for illustrations of these growth forms). Figure 2 presents a bifurcation diagram showing the relationship between C_{eq} and m, capturing the stability regime of the spatially uniform system.

We now examine the original system (Equations 1 and 2), incorporating spatial processes in heather and soil surface height dynamics, notably anisotropic, wind-induced heather mortality.

To compare with the spatially uniform case, we define $\overline{m}$ as the spatially averaged heather mortality rate, accounting for both the baseline rate m and the anisotropic wind-induced mortality rate $wk_3F\left(\frac{\partial S}{\partial x}\right)$. Using numerical simulations, we compare the trajectories of two systems with the same $\overline{m}$: one fully isotropic ($\overline{m} = m$), and the other incorporating anisotropic mortality due to strong directional winds. Figure 3 illustrates how heather, as modelled by our system (Equations 1 and 2), can survive mortality rates $\overline{m}$ exceeding the critical baseline mortality rate m_{crit}, provided the isotropic component of $\overline{m}$ remains below m_{crit} and additional mortality is anisotropic. In this case, instead of collapsing to bare ground, the system stabilises into spatial patterns of asymmetrical soil ripples and alternating bare and vegetated bands, resembling

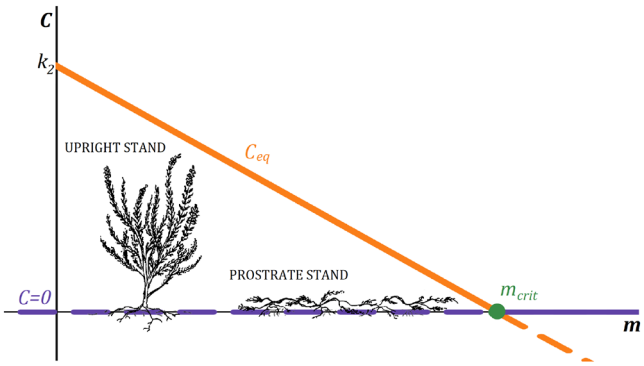


FIGURE 2 Bifurcation diagram for the spatially uniform model: Heather height at equilibrium as a function of baseline mortality rate. S_{eq} and all parameters other than m are fixed. Solid (resp. dashed) lines represent stable (resp. unstable) steady states. Purple (resp. orange) lines represent the bare (resp. vegetated) steady state. Heather height at uniform equilibrium, C_{eq} decreases linearly with baseline mortality m, reaching bare ground at the critical threshold m_{crit} where the stability of the system switches.

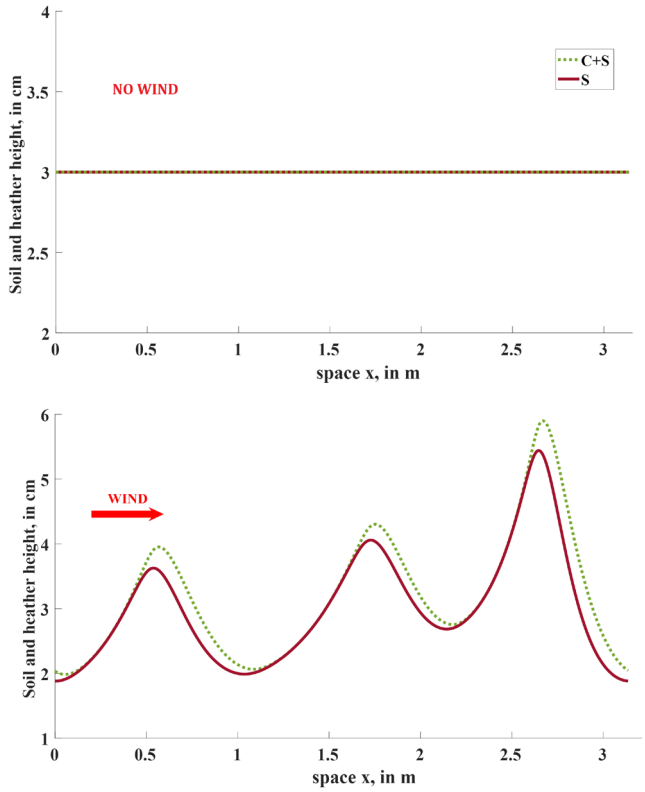


FIGURE 3 Comparing two systems with the same spatially averaged mortality rate, $\overline{m}$, starting from identical random initial condition for C and uniform soil height. Heights are in centimetres, and space x is in metres. Heather is plotted atop the soil surface ($S + C$). *Top*: Mortality is isotropic (i.e. uniform in all directions) and exceeds m_{crit}, leading to stabilisation at the bare ground state $C = 0$. *Bottom*: With baseline mortality rate $m < m_{crit}$, and extra anisotropic mortality applying windward (where the soil slope is positive), for wind blowing in the positive x direction. Vegetation avoids extinction by forming patterns.

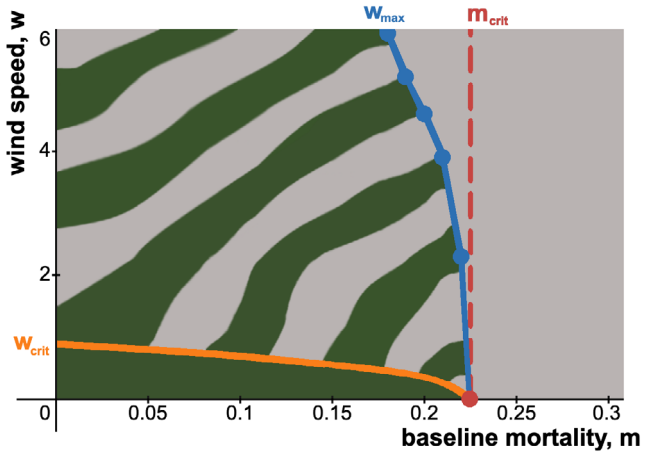


FIGURE 4 Stable homogeneous or patterned solution in the parameter space of wind speed (vertical axis) w and baseline mortality m (horizontal axis). All other parameters and S_{eq} are fixed. The plot shows whether each (m, w) pair yields the stable uniformly vegetated solutions (green), patterned solutions (striped green and grey) or bare ground (grey). The orange curve $w_{crit}(m)$ is derived analytically and represents the critical wind speed above which patterns form, as a function of the baseline mortality rate. The blue curve $w_{max}(m)$ is derived numerically, and represents the maximal wind speed above which patterns turn to bare ground, as a function of the baseline mortality rate. The bare ground area extends indefinitely to the top right of the blue curve. Note that the striped depiction of the patterned region is a graphical choice to distinguish it from the uniform regions; it does not imply a single fixed pattern wavelength. In reality, this region typically supports a range of pattern wavelengths.

field observations (compare the bottom of Figure 3 with Figure 1c, noting that in both cases, it is the quantity $S + C$ that is plotted, rather than C, since heather lies atop the soil surface in real life).

3.2 | Environmental conditions triggering pattern formation

A Turing instability analysis of system (Equations 1 and 2) allows us to identify the critical wind speed, which we call w_{crit}, above which the uniformly vegetated state becomes unstable to spatially heterogeneous perturbations (see the Supporting Information for details of the Turing analysis, and the formula for w_{crit}). Long-term simulations with realistic parametrisation indicate that these perturbations result in patterns that persist over relevant timescales (hundreds of years). Our mechanistic model suggests that pattern formation under high wind speeds results from two interacting processes. First, strong winds directly damage vegetation, preventing uniform plant cover. Second, they increase soil erosion, but this erosion is spatially modulated by the presence of vegetation—less erosion under plant patches and more in bare zones. This differential erosion generates a microtopography that provides shelter to downwind plants, initiating a local positive feedback. In this way, vegetation and soil co-modulate each other's dynamics and create conditions reinforcing spatial heterogeneity.

Importantly, the critical wind speed w_{crit} decreases with increasing baseline mortality rate m (see Figure 4), suggesting that already stressed heather forms patterns under weaker winds compared to less stressed heather.

Furthermore, Turing instability analysis indicates that all patterned solutions are travelling wave solutions, as illustrated in Figure 5, which shows patterns migrating with constant shape and speed in the direction of the prevailing winds. This behaviour aligns with field observations and supports the prevailing view that patterns slowly move downwind (Bayfield, 1984). We find very good agreement between empirically measured pattern migration speed (Bayfield, 1984) and the speed of our simulated solutions. Furthermore, for a fixed wave number, the migration speed of the patterns near equilibrium is directly proportional to the prevailing wind speed w and to the soil displaceability (or erodibility) parameter k_5 (see the Supporting Information for details). This relationship is only valid for a linear approximation of the solution's behaviour near the equilibrium (C_{eq}, S_{eq}). However, our numerical simulations still show that the speed of the travelling wave further away from equilibrium keeps increasing monotonously with w and k_5, as intuitively expected (see Figure 5; Figure S7).

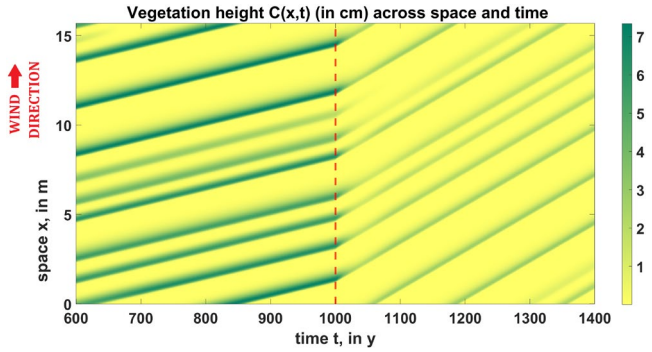


FIGURE 5 Periodic travelling wave solution for two different wind speeds. Plotting the soil profile over space and time reveals the periodic travelling wave nature of the patterns. The wave's shape remains constant, as indicated by the consistent colouring representing vegetation height along the lines of movement. The straightness of these lines confirms the constancy of the wave's speed. At time $t = 1000$ (red dashed line), we change the wind speed, from $w = 4$ to $w = 8$. This change in wind speed directly affects the travelling wave speed, as can be seen from the change in direction of the lines of movement. We can observe that the change in wind speed also directly affects the frequency, amplitude and bandwidth of patterns, as further described in Section 3.4. The soil solution S also forms a periodic travelling wave with the same wave number, exhibiting similar space–time behaviour.

3.3 | The role of heather as an ecological engineer during pattern onset

To investigate the role of heather and pre-existing soil structures in pattern formation, we initiate our simulations with a spatially uniform soil cover, and nearly uniform heather cover (see top left plot in Figure S3). The results reveal that the initially flat soil surface evolves into periodic patterns, driven by interactions with the non-uniform vegetation cover. This behaviour illustrates how heather modulates soil erosion rates, thereby promoting the formation of spatial patterns. In this context, heather acts as an ecosystem engineer: By locally slowing down erosion, it creates shelter that allows it to establish and persist, thereby extending its habitat into wind-blasted environments.

This finding suggests that pre-patterned ground is not a prerequisite for heather stripe formation. Figure S3 illustrates the emergence and stabilisation of fully developed biogeomorphological patterns from initially uniform soil and nearly uniform vegetation cover under strong directional winds. Crucially, the processes of soil sheltering vegetation and vegetation stabilising soil create an indirect, scale-dependent, positive plant–plant feedback loop. This feedback promotes the spontaneous emergence and persistence of biogeomorphological patterns under strong directional winds.

3.4 | Two pathways to patterns disappearance

Existing patterns of soil and heather can disappear through two contrasting pathways: either transitioning to bare ground or to uniform vegetation cover, depending on the direction of environmental changes.

3.4.1 | Transition from patterns to bare ground

In the absence of strong prevailing winds, vegetation collapses to bare ground when isotropic stress exceeds the critical threshold, $m > m_{crit}$. Additionally, simulations show that patterns transition to bare ground when wind speed exceeds a critical threshold, $w_{max}(m)$, which depends on the baseline mortality rate m.

As this threshold is approached—through an increase in m or w—the disappearance of patterns occurs through three concurrent processes: (1) *Decrease in frequency*: Fewer vegetated bands form across the landscape. (2) *Decrease in amplitude*: Vegetation height within the bands declines. (3) *Decrease in bandwidth*: Vegetated bands narrow, reducing the overall area covered by vegetation.

At high wind speeds $(w > w_{max}(m))$, patterns eventually vanish, leaving bare ground. Figure 6 illustrates changes in patterned heather and soil height as wind speed increases. Similarly, Figures S4 and S5 depict the disappearance of the patterns through the same three concurrent mechanisms as isotropic stress rate m is increased. A real-world example of pattern disappearance with increasing combined isotropic and anisotropic stress $(\overline{m})$ is provided in Figure S6.

We numerically investigated the boundary $w_{max}(m)$ that separates patterned ground from bare ground in the m-w parameter space, as shown in Figure 4. For seven different isotropic stress levels m, we gradually increased the wind speed w until the vegetation went extinct. Vegetation was considered absent when its height fell below 0.5 cm. Unlike the analytically derived boundary between uniform vegetation cover and patterned ground, this numerically obtained estimate provides a coarse assessment of the upper limit in m-w space where patterns can persist.

3.4.2 | Transition from patterns to uniform vegetation cover

Patterns can also disappear in favour of uniform vegetation cover when environmental conditions become less stressful. This occurs when m and/or w decrease to the point where the lower boundary $w_{crit}(m)$ for pattern formation is crossed (Figure 4). Reduced stress enables vegetation to colonise previously bare ground, leading to uniform vegetation cover.

4 | DISCUSSION

Our simple mechanistic model provides robust support for the prevalent hypothesis (Ballantyne, 2019; Bayfield, 1984; Watt, 1947) that heather stripes in the Scottish Highlands are primarily driven by strong winds. In doing so, it offers novel perspectives on geomorphological pattern formation. Unlike previous work on wind-driven vegetation and soil patterns, which predominantly focused on dry ecosystems (Mayaud et al., 2017; Zhang, 2021; Zhang et al., 2017), our parsimonious model relies solely on the interplay between wind-stressed vegetation and displaced soil to generate patterns

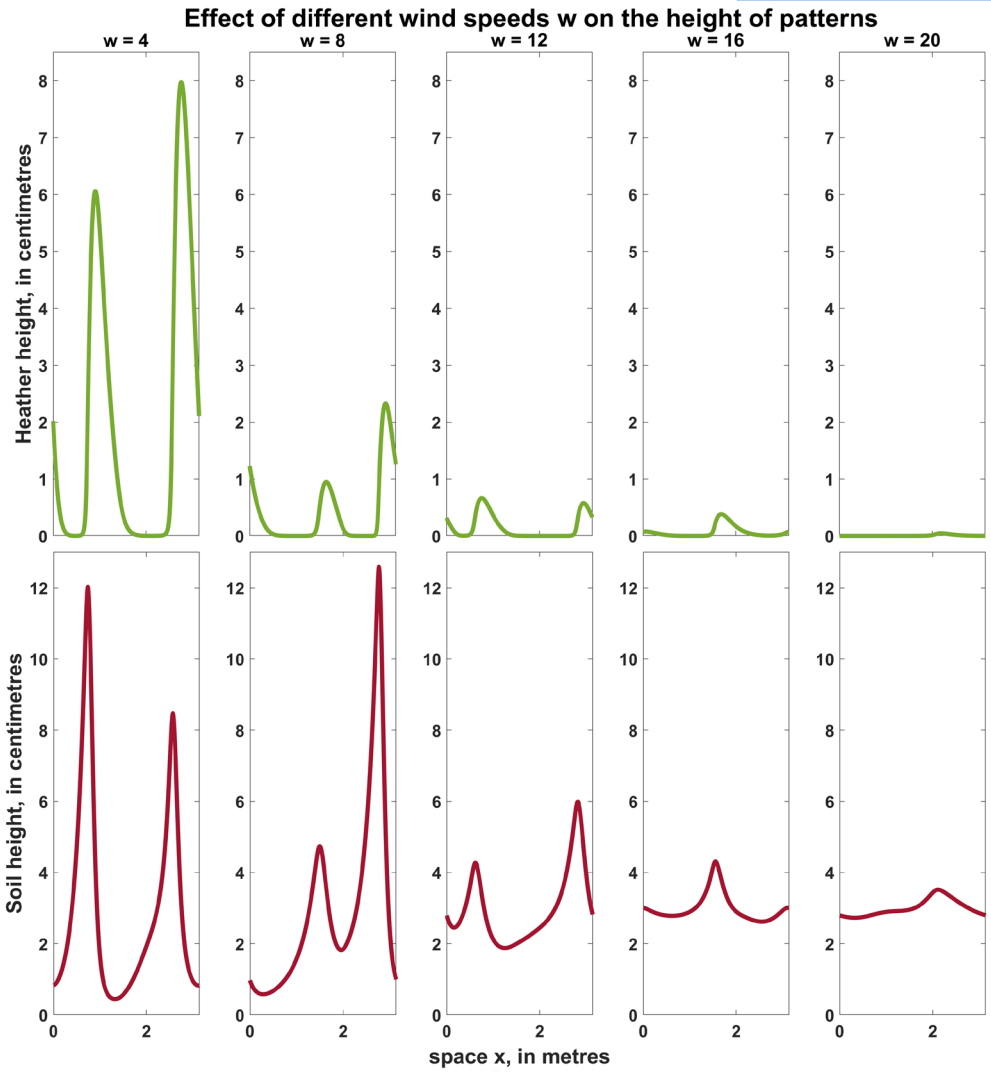


FIGURE 6 Disappearance of heather stripes through three concurrent processes as wind speed is increased. Numerical simulations show the progressive disappearance of the pattern through a decrease in frequency, amplitude and bandwidth, as the wind speed w is increased. Heather gradually goes extinct, while the soil rippling disappears towards a more uniform distribution as wind increases and vegetation disappears. The bare ground soil distribution will eventually flatten out to uniform, thanks to soil diffusion.

that closely resemble the characteristic asymmetrical distributions observed in the field. Our findings emphasise how heather acts as an ecosystem engineer, enabling its persistence in wind-blasted environments. Heather patterns are found at the limit of the plants' habitat: Along gradients of combined wind-driven and isotropic environmental stress, patterns succeed to uniform vegetation. As stress increases, the patterns' amplitude and frequency decrease down to bare soil, when a threshold of combined environmental stress is crossed, marking the end of heather's habitat.

Using mathematical analysis, supported by numerical simulations, we have demonstrated that fundamental interactions between soil, wind and heather—namely (1) advection and (2) diffusion of the soil, both slowed down by the local presence of heather, coupled with (3) heather diffusion, (4) logistic, soil-dependent growth of heather, (5) natural decay and (6) extra, anisotropic, wind-induced mortality—are sufficient to give rise to long-lasting periodic travelling wave solutions akin to the patterns seen in the field. Furthermore, our literature-based parametrisation yields solutions with realistic orders of magnitude for pattern amplitude, frequency and wave speed, closely matching field observations.

In contrast to similar PDE-based models of wind-driven patterns (Zhang et al., 2017), the soil variable in our model is purely transported, reflecting that patterns emerge at a considerably faster scale than soil formation. Another distinction from existing PDE models for vegetation pattern formation (Hillerislambers et al., 2001; Klausmeier, 1999; Rietkerk et al., 2002), including those that incorporate wind effects (Zhang et al., 2017), is that ours does not rely on water scarcity for pattern formation. Moreover, in our model, periodic patterns cannot form in the absence of heather. This is a main difference with existing sand dune models, which typically reproduce the regular patterning of bare soil through processes like saltation (wind-driven movement of sand grains), creep (slow surface movement due to grain collisions) and avalanches (sudden downslope movement when the angle of repose is exceeded) (Bagnold, 1941; Durán et al., 2010; Kroy et al., 2002). Our

model does not require such detailed soil processes, which are, moreover, limited to relatively coarse-grained soils.

In elucidating the conditions sufficient for pattern formation, our model highlights the facilitative role of *Calluna* in pattern formation. Contrary to previous hypotheses that pre-existing soil ripples are required (Bayfield, 1984), our model indicates that heather stripes can develop on initially flat terrain. Rather than heather colonising or dying off on pre-formed soil ripples, vegetation and soil jointly organise into patterns under strong prevailing winds. Specifically, heather modulates soil erosion by reducing soil dispersal and advection, with stabilisation rates increasing in proportion to heather stand height—results that align with empirical observations (Imeson, 1971). The anisotropic effects of wind-induced mortality and soil transport then enable vegetation to shelter behind redistributed soil. This facilitative process is absent in fully isotropic conditions, underscoring the importance of directional drivers in heather pattern formation. These mechanisms share commonalities with facilitative processes observed in dryland ecosystems, where vegetation within patterns locally reduce the environmental stress, promoting the establishment and survival of seedlings, ultimately fostering vegetation persistence in resource-scarce environments (Kéfi, Lortie, & Cavieres, 2024; Qiu et al., 2025). In both types of systems, facilitation acts as a key driver of pattern formation, which enables vegetation to withstand harsh conditions.

While facilitative interactions are generally associated with enhanced ecosystem resilience—by mitigating climate stress and promoting biodiversity (Kéfi, Génin, et al., 2024)—our findings align with broader evidence suggesting that such positive feedback can have dual consequences. On one hand, facilitation enables persistence under stress; on the other, it increases the difficulty of a system to recover once degraded. For instance, in drylands, because of facilitation-driven hysteresis, systems hardly recover from desertification, even under active restoration (Mander et al., 2017; Rietkerk et al., 2021; Saco et al., 2018). Similarly, our model predicts that once heather patterns degrade to bare soil, the soil surface ripples smoothen out, leading to a loss of shelter for recolonising heather. The positive feedback hampers heather re-establishment, not because of bistability—which is absent from our model—but because of the loss of local facilitation mechanisms. Thus, while facilitation fosters persistence through pattern formation under certain conditions, it is also a manifestation of the system's vulnerability and its difficulty to recover from degradation.

Even though our model does not involve any process specific to the heather family (Ericaceae), we argue that our formulation is particularly well suited to representing these types of plants. The combination of plant diffusion and the absence of a minimal height requirement for plant survival is well suited to represent heather's capacity to form mats of prostrate individuals in harsh environments (MacDonald et al., 1995). This phenotype is linked to heather's capacity for reproduction through adventitious rooting, also known as *layering reproduction*, with the prostrate stand exhibiting many branching nodes (MacDonald et al., 1995). Plants unable to undergo this type of reproduction would not be well captured by our model and would require, for example, the representation of adult plants and seedlings separately, or an Allee effect, to capture the impact of wind on lower height individuals not evolved to develop a prostrate stand and layering reproduction mode.

While our model effectively demonstrates how wind can drive heather stripe formation, we acknowledge its limitations and highlight areas that could be made more realistic. Firstly, we assumed a linear relationship between the anisotropic wind-induced mortality and the soil gradient $\frac{\partial S}{\partial x}$. We chose this relationship for simplicity, and retained it because it produced the desired patterns, with realistic orders of magnitude. Future iterations of the model might explore alternative formulations for the wind-induced mortality function, $F\left(\frac{\partial S}{\partial x}\right)$.

Secondly, we did not account for the sheltering effect of windward plants on leeward plants (Carlsson & Callaghan, 1991). This could be incorporated by using $F\left(\frac{\partial C}{\partial x}, \frac{\partial S}{\partial x}\right)$ instead of $F\left(\frac{\partial S}{\partial x}\right)$ in Equation (1), which would introduce positive direct plant–plant feedback. However, our aim was to demonstrate that such feedback is not necessary for pattern formation, which is why we omitted the plants sheltering effect. Incorporating plants sheltering would require adding a parameter to account for differences in sheltering effects between soil and heather, making the model not only more realistic but also more complex. This more detailed representation could be enhanced by using field data that relate heather height to wind speed, as reported in Crabtree and Ellis (2010) in their figure 5.

Another natural extension of our model would involve considering two-dimensional space, allowing the integration of multiple wind directions and the interaction between wind and ground slope. We expect the addition of a second spatial dimension to enable the modelling of less regular, more patchy or labyrinthine patterns of heather observed in the field (as seen in Figure S1). Furthermore, including steep ground slope dynamics would also allow modelling fellfield (slope) ecosystems, such as the 'terracettes' (Veyret & Coque-Delhuille, 1989) and 'turfed bank terraces' (Ballantyne, 2019) that can be observed near heather stripes, or the critically endangered *Azorella macquariensis* found on subantarctic Macquarie Island (Bergstrom et al., 2015; Selkirk-Bell & Selkirk, 2013). *Azorella macquariensis* forms regular patterns (Bergstrom et al., 2015), and facilitates other species in the harsh fellfield environment (Bergstrom et al., 2015). While some of its patterns are very similar in shape to heather stripes, others rather consist of patches and terraces (Selkirk-Bell & Selkirk, 2013), which we expect to be captured by the combined effects of wind and slope on plants and soil dynamics.

Future work could also extend our single-species model to multiple species, reflecting the diversity observed empirically within heather mats. Prostrate heather mats have been shown to support other species, including lichens, mosses, vascular plants such as *Juncus trifidus* and *Arctostaphylos uva-ursi*, among others (Bayfield, 1984; Crabtree & Ellis, 2010), with species often exhibiting zonation patterns within the stripes (Metcalfe, 1950; Watt, 1947) (see Figure S2). A number of rare lichen, in particular, reach their maximum development in heather stripes, their presence following the growth and decay cycle of the taller plants (Gilbert & Fox, 1985). This spatial arrangement aligns with Watt's

(Watt, 1947) concept of a 'space–time mosaic' of coexisting successional phases within the heather stripes. We postulate that the mixture of open area and shelter provided by the stripes plays a critical role in the local biodiversity. While the transition from patterned to full vegetation cover discussed in answer to research question (iv) results in greater overall vegetation cover, it may however lead to loss of biodiversity due to the homogenisation of the landscape, consistent with observations of ecological trade-offs (Britton et al., 2009, 2017). For instance, long-term monitoring of Scottish alpine habitats shows significant increases in alpine *Calluna vulgaris* cover, concomitant with decreases in cover of characteristic alpine lichen species and a loss of β-diversity (Britton et al., 2017). Biodiverse heather stripes represent a great case-study to investigate how facilitation and spatio-temporal patterning can allow coexistence of competing species in a harsh environment.

Heathland is a vulnerable and often highly managed environment (Matt Davies et al., 2010). A deeper understanding of the growth and death processes of heather, a keystone species in these environments, is essential to address the challenges they face. Given the rapid transformations occurring in heathlands due to climate change and human activity (Britton et al., 2009, 2017), advancing our understanding of heather stripe dynamics is increasingly important. Their dynamic nature, sensitivity and position at the stress limits of heather's range make them particularly valuable as ecological indicators. For instance, changes in the amplitude or band width of these stripes could provide crucial insights into environmental shifts and ecosystem responses. These insights could inform conservation strategies and contribute to sustaining the unique biogeomorphological features of heathlands. Furthermore, the relevance of studying Scottish heather stripes extends to similar fragile non-arid patterned ecosystems world-wide, such as the Azorella cushion-plant stripes of Macquarie Island, a World Heritage Site. It is currently undergoing catastrophic decline, the cause of which has not yet been clearly elucidated (Bergstrom et al., 2015). By studying and preserving biogeomorphological patterns, we can better understand and protect the interconnected biodiversity and landscapes they support.

AUTHOR CONTRIBUTIONS

Toyo Vignal: Conceptualisation (lead); methodology (lead); formal analysis (supporting); investigation (equal); writing—original draft (lead). **Mara Baudena:** Conceptualisation (supporting); investigation (equal); supervision (equal); writing—review and editing (equal). **Jonathan Sherratt:** Conceptualisation (supporting); formal analysis (lead); methodology (supporting); supervision (equal); writing—review and editing (equal). **Angeles G. Mayor:** Conceptualisation (supporting); investigation (equal); supervision (equal); writing—review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

We have no conflict of interest to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The authors have nothing to report.

ORCID

Toyo Vignal https://orcid.org/0000-0003-0309-8245

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SUPPORTING INFORMATION

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

Figure S1. Patchy heather patterns observed in Papa Stour, Shetland, Scotland.

Figure S2. Zonation between heather (*Calluna vulgaris*) and bearberry (*Arctostaphylos uva-ursi*) on patterned ground, Bynack More, Cairngorms National Park.

Figure S3. Simulated pattern onset and stabilisation.

Figure S4. Numerical simulations showing the height of vegetation on patterned ground, for different baseline mortality rates m, all other parameter fixed (wind speeds $w = 6$).

Figure S5. Numerical simulations showing the soil height corresponding to the vegetation dynamics.

Figure S6. Aerial view of a gradient in vegetation cover on the isle of Hoy, Orkney, Scotland, and on Ronas Hill, Shetland, Scotland, with superimposed elevation contour lines.

Figure S7. Influence of erodibility parameter k_5 on travelling wave speed.

Table S1. Parameters of the biogeomorphological patterns model.

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