

Regular pattern formation in real ecosystems

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Localized ecological interactions can generate striking large-scale spatial patterns in ecosystems through spatial self-organization. Possible mechanisms include oscillating consumer–resource interactions, localized disturbance-recovery processes and scale-dependent feedback. Despite abundant theoretical literature, studies revealing spatial self-organization in real ecosystems are limited. Recently, however, many examples of regular pattern formation have been discovered, supporting the importance of scale-dependent feedback. Here, we review these studies, showing regular pattern formation to be a general phenomenon rather than a peculiarity. We provide a conceptual framework explaining how scale-dependent feedback determines regular pattern formation in ecosystems. More empirical studies are needed to better understand regular pattern formation in ecosystems, and how this affects the response of ecosystems to global environmental change.

Spatial self-organization

Theoretical ecologists increasingly emphasize that ecosystems can reveal spatial self-organization. Spatial self-organization is the process where large-scale ordered spatial patterns emerge from disordered initial conditions through local interactions. This process is key to understanding ecological stability and diversity [1]. Causal mechanisms explaining spatial self-organization include oscillating consumer–resource interactions leading to spiral waves [2,3], localized disturbance-recovery processes resulting in power laws in the geometry of clusters [4,5], and scale-dependent feedback with ensuing regular patterns [6]. Despite a significant body of theoretical literature on each of these mechanisms [1], there are only a few studies describing spatial self-organization in real ecosystems.

Recently, however, a large body of literature has reported on regular pattern formation across real ecosystems with striking cross-ecosystem similarities. Here, we review these studies to show that scale-dependent feedback between organisms and their environment can explain regular pattern formation in all of these ecosystems. After introducing the principle of scale-dependent feedback, we report on real ecosystems in which scale-dependent feedback leads to regular pattern formation. We uncover the prerequisite of long-distance negative feedback as a unifying principle for regular pattern formation in ecosystems. We also provide possible ways to

measure this mechanism. Finally, we discuss the implications of our conceptual framework for future research, which is needed to understand and predict the dynamics of these ecosystems, including their emergent properties, in relation to global environmental change.

Scale-dependent feedback

Ecosystems consist of organisms and the environment, which interact with each other. These interactions can impose various feedbacks upon the organisms and the environment. The feedback can be negative, for example when organisms deplete resources, leading to competition. Positive feedback can also occur, for example if organisms help others to survive through facilitation, by modifying the environment. If positive and negative feedbacks occur at different spatial scales (i.e. scale-dependent feedback), they might invoke regular pattern formation in ecosystems, even in the absence of underlying environmental heterogeneity [6].

Glossary

Localized disturbance-recovery processes: disturbance occurs primarily close to a site already disturbed (e.g. by wind) and recovery takes place primarily close to a site that is occupied by organisms (e.g. by local seed dispersal).

Long-distance negative feedback: ecological interactions resulting in a net negative feedback between organisms and their environment at a particular distance from the organisms.

Long-range competition: the process where organisms, by depleting resources, constrain the establishment and survival of other organisms over a long range.

Oscillating consumer–resource interactions: cyclic dynamics in a predator population and its prey, caused by strong feeding interactions between the two.

Power laws: any polynomial relationship that exhibits the property of scale invariance, implying that the relation is the same at a range of scales. In the case of the geometry of clusters of organisms, a decreasing linear relation occurs between cluster size and the frequency at which clusters of this size are found when plotted on a double logarithmic scale.

Regular patterns: spatially periodic patterns with a characteristic cluster size (e.g. the spotted coats of leopards).

Resilient: an ecosystem is resilient if it remains in the same domain of attraction and quickly returns to the same state after a disturbance.

Resistant: an ecosystem is resistant if it can withstand environmental change and still remain in the same state.

Scale-dependent feedback: the strength and sign of a feedback between organisms and their environment varies with distance.

Short-distance positive feedback: ecological interactions resulting in a net positive feedback between organisms and the environment near the organisms.

Short-range facilitation: the process where organisms, by creating favourable environmental conditions over a short range, help the establishment and survival of other organisms close-by.

Spatial self-organization: the process where large-scale ordered spatial patterns emerge from disordered initial conditions through local interactions.

Spiral waves: spirals that rotate over time around either meandering or stationary cores.

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Box 1. The activator–inhibitor principle

Turing (Figure 1a) proposed that a chemical substance *A* generates more of itself via an autocatalytic reaction, thereby acting as an activator [7]. This means that the more *A* there is, the more *A* will be produced (autocatalysis; Figure 1a). However, *A* also generates another substance *I*, acting as an inhibitor and therefore balancing the production of *A*. Both *A* and *I* can diffuse at different rates through a medium. Turing showed that, if the diffusion of *I* is faster, the interaction between *A* and *I* generates regular spatial patterning (regular pattern formation; Figure 1b). This is because the inhibitor *I* diffuses rapidly, inhibiting the production of the activator *A* over a long range. This means that the activator *A* will only spread locally, thus forming stable patterns. The formation of patterns is triggered by infinitesimal spatial heterogeneity or disturbance that is amplified in time through the interaction between activation and inhibition at different scales [6]. The net feedback effect of the activator *A* and the inhibitor *I* is scale dependent: positive feedback dominates at short distance, whereas negative feedback dominates at longer distance. The resulting patterns are thus not imposed on the system, but emerge from positive and negative feedback. The emerging patterns are not only regular, but also large-scale as compared with the scale of interactions. So, key to this patterning is that the activation of *A* occurs over a short range whereas the inhibition of *A* by *I* occurs over a longer range.

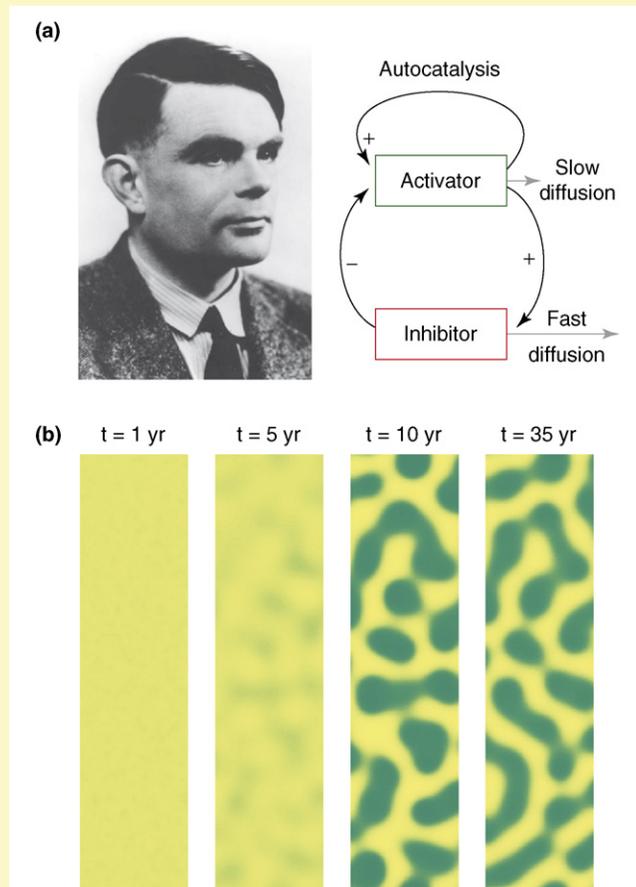


Figure 1. (a) Alan Turing (1912–1954) and autocatalysis in an activator–inhibitor system. The activator generates more of itself through autocatalysis and also activates the inhibitor. The two substances diffuse through the system at different rates, with the inhibitor moving faster. Image of Alan Turing courtesy of the Computer History Museum. (b) An example of how regular patterns form from disordered initial conditions. In this case, the regular patterns consist of vegetation biomass (green) produced by the arid ecosystem model in Ref. [19].

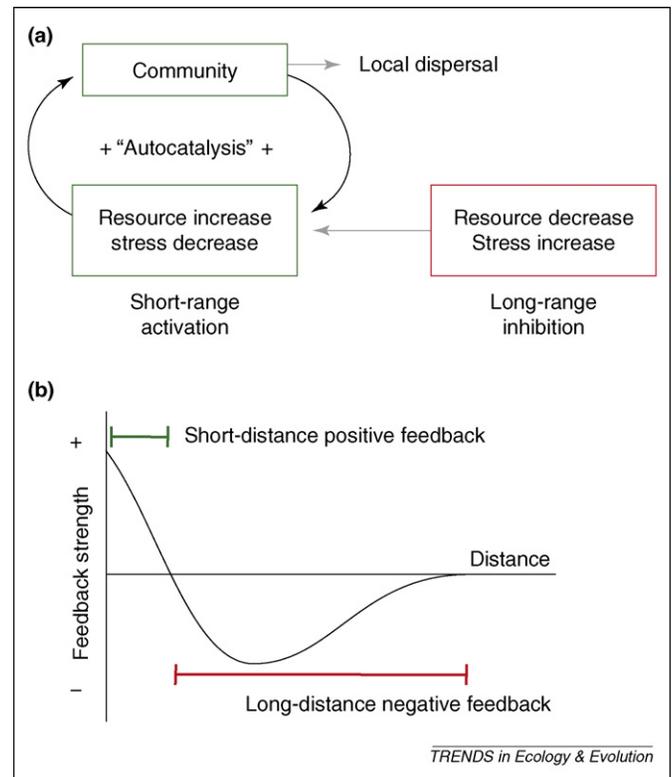


Figure 1. Scale-dependent feedback in ecosystems. (a) Communities reduce stress or increase resource availability through concentration and conservation in the local environment, leading to activation (facilitation) over a short range. Communities and resources move through the ecosystem at different rates, with the resource moving faster and in the opposite direction to the community. This leads to depletion of resources further away, inducing inhibition (competition) over a long range. (b) This results in scale-dependent feedback. A net positive feedback occurs at short distance, whereas net negative feedback takes place at a longer distance. The strength of the feedbacks (y-axis), illustrated by the amplitude, and the scales of their influence (x-axis) can differ depending on the mechanisms involved, and multiple scales of influence might be present simultaneously.

Turing [7] first proposed the possibility of regular pattern formation by scale-dependent feedback in chemical systems. This is explained by the so-called activator–inhibitor principle in Box 1. This activator–inhibitor principle is now a well known universal principle explaining regular pattern formation in chemical [8–10] and physical systems [11,12], as well as morphogenesis in biology (e.g. the striped coats of zebras) [13,14].

Here, we propose that scale-dependent feedback (Figure 1) also explains regular pattern formation in a variety of ecosystems (Figure 2; a more extensive survey is presented as a Google Earth placemark file at: <http://www.nioo.knaw.nl/articles/patterns>). In ecosystems, the scale-dependent feedback emerges mainly from short-range facilitation through modification of the environment and long-range competition for resources. The net effect of this is short-distance positive feedback and long-distance negative feedback (Figure 1), irrespective of the precise mechanisms involved. Often, environmental heterogeneity prevents or obscures such coherent and regular pattern formation in ecosystems. However, evidence for pattern formation linked to scale-dependent feedback in ecosystems is now rapidly increasing, in particular from systems that have little underlying environmental heterogeneity,

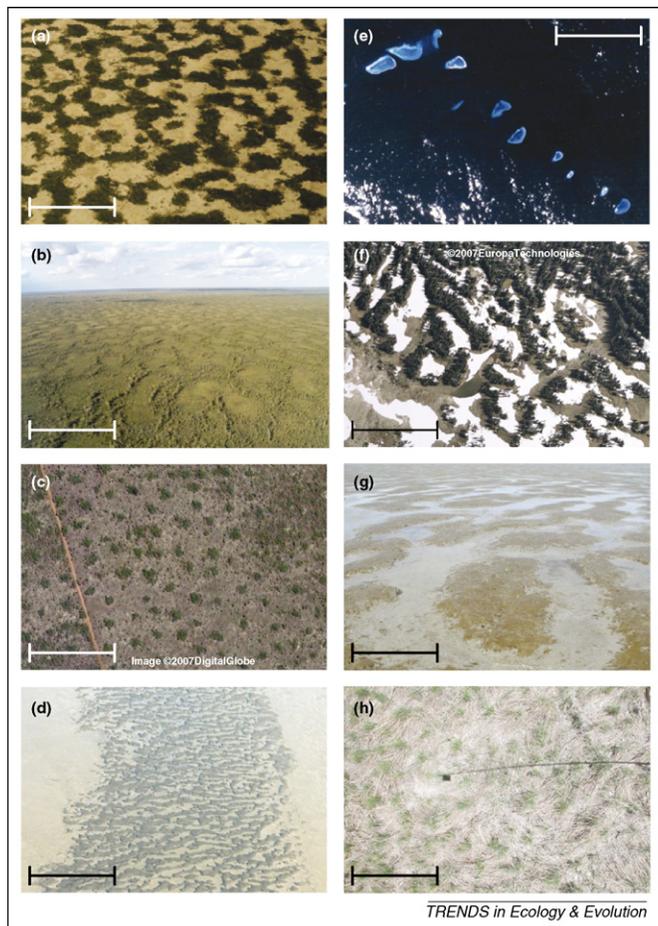


Figure 2. Observations of regular patterns from arid ecosystems, wetland ecosystems, savanna ecosystems, mussel beds, coral reefs, ribbon forests, intertidal mudflats and marsh tussocks. A more extensive survey is presented as a Google Earth placemark file at: <http://www.nioo.knaw.nl/articles/patterns>. (a) Regular maze patterns of shrubs and trees in West Siberia (scale = 100 m). (b) Regular maze patterns of shrubs and trees in West Siberia (scale = 100 m). (c) Spotted pattern of isolated tree patches in Niger ([28], © Google Earth, scale = 200 m). (d) Patterned mussel bank in the Wadden Sea, the Netherlands (scale = 50 m). (e) Reef islands oriented in series along the predominating direction of large-scale currents in Australia (scale = 20 km). (f) Striped pattern of tree lines and snow deposition in ribbon forests in USA ([37,38], © Google Earth, scale = 150 m). (g) Labyrinth pattern of marine benthic diatoms in the Netherlands (scale = 1 m). (h) Regular spaced tussocks of the sedge *Carex stricta* (scale = 2 m). Reproduced, with permission, from Ref. [19] (a), Ref. [26] (b), Ref. [34] (d), Ref. [35,64] (e), Ref. [46] (h).

but also in more heterogeneous systems. These studies highlight scale-dependent feedback as a unifying ecological principle explaining regular pattern formation in real ecosystems.

Real ecosystems

Arid ecosystems

Regular pattern formation in arid ecosystems occurs in the form of stripes ('tiger bush'), labyrinths, spots ('leopard bush') and gaps [15–21] (Figure 2a). Part of the mechanism is short-distance positive feedback between vegetation and soil water availability. Higher vegetation density enables higher water infiltration into the soil. The second part is subsequent redistribution of overland flow driven by differences in rainwater infiltration into the soil. The consequence of this is effective harvesting of water resources by vegetated patches from their bare surroundings. This leads to positive feedback at short distance within

vegetated sites, but a negative feedback at larger distance, thus generating scale-dependent feedback. Other mechanisms leading to the same net effect are lower soil evaporation in shadowy areas under the canopy of shrubs combined with roots that take-up water far beyond the canopy area [22].

Wetland ecosystems

Pattern formation in wetlands includes regular string patterns comprising densely vegetated bands perpendicular to the slope, alternating with wetter zones that are more sparsely vegetated [23–25]. A possible explanation for regular string patterns on slopes is the formation of ponds behind densely vegetated bands owing to lower hydraulic conductivity of the bands [25]. More recent studies have shown regular maze patterns (Figure 2b): densely vegetated bands in a more sparsely vegetated matrix; and tree islands or spots in a matrix of saw grass plains and ridges, emergent marshes and deepwater sloughs [26,27]. The redistribution of limiting nutrients, especially phosphorus, through subsurface water flows generated by transpiration of trees, has been proposed as a general explanation for the formation and maintenance of these patterns [26,27]. Here, the redistribution of nutrients leads to scale-dependent feedbacks.

Savanna ecosystems

Pattern formation in nutrient-poor savannas includes regular isolated spots of trees and shrubs in a matrix of grassland [28] (Figure 2c). The mechanistic base is that plants can have positive effects on each other, and on themselves, by local nutrient accumulation, but compete with each other through long superficial roots that track scarce nutrients from the surroundings [29–31]. The net effect of this is short-distance positive feedback and long-distance negative feedback [28]. New observations (see Google Earth placemark file at: <http://www.nioo.knaw.nl/articles/patterns>) also include labyrinth patterns of trees in a matrix of grassland.

Mussel beds

Regular stripes are found in mussel beds occurring on sediments in the Wadden Sea, the Netherlands (Figure 2d). The striped patterns, oriented perpendicular to the tidal flow, are suggested to be the outcome of scale-dependent feedback. Mussels facilitate each other over short range, because conspecifics are the main substrate for attachment on soft-bottom sediment [32,33]. Competition between mussels occurs for algae, affecting mussel intake and growth, and can occur over long range because water depleted in algal stocks, as a result of the mussels, is carried over the mussel beds by tidal currents [34].

Coral reefs

Patterns in coral reefs vary from fine-scale complex architectures of distinct colonies to large-scale reef distribution patterns. Observed pattern formation ranges from regular spaced coral plates perpendicular to water flow direction on a 0.1-m scale, to reef islands oriented in series along predominant direction of currents on a 1–10-km scale [35] (Figure 2e). The fact that patterns in coral reefs can be

different for colonies of the same species in different environmental conditions suggests that light, water and nutrient flux are important in controlling their formation [36]. Colonies and reefs can develop regular patterns because they obstruct flow and intercept available nutrients, either by enhanced surface roughness or by increased complexity of the path for the flow field [35]. Nutrients enable photosynthetic zooxantellae to provide food and oxygen to the coral organisms. Calcification by the corals produces carbon dioxide that can be subsequently used for photosynthesis of the zooxantellae. The removal of carbon dioxide by photosynthesis enhances calcification, feeding back to increased interception of available nutrients at the scale of coral colonies and reefs. This increased nutrient interception facilitates coral growth over short range, and water carried over the colonies and reefs by predominant currents is depleted in nutrient stocks over long range. New observations (see Google Earth placemark file at: <http://www.nioo.knaw.nl/articles/patterns>) also include labyrinth patterns.

Ribbon forests

Striking spatial patterns have been observed at alpine tree lines in the Rocky Mountains. Stands of Engelmann spruce, *Picea engelmannii*, and sub-alpine fir, *Abies lasiocarpa*, were found to grow in narrow, parallel rows perpendicular to the prevailing winter wind direction (Figure 2f). The rows extend like fingers from the tree line into the tundra vegetation that characterizes higher elevations. These striped patterns have been related to the interaction between wind, trees and snow accumulation, and the effects of snow on the survival of tree seedlings [37,38], but see Ref. [39] for a geomorphic explanation. Wind erodes snow from exposed positions, transports it and deposits it downwind of the tree stripes where wind speed is reduced [37,38]. As a consequence, large amounts of snow accumulate in between the tree stripes, forming snowdrifts up to 7 m in height. These snowdrifts limit seedling establishment by physically damaging the seedlings. Also, the drifts can persist well into August or even September, reducing growing season length [37,38]. Reduced snow accumulation and increased soil moisture promote seedling establishment between and close to the trees [40,41]. Hence, the formation of tree stripes seems to be caused by short-distance positive feedback and long-distance negative feedback, because the trees cause the formation of snowdrifts between the stripes.

Intertidal mudflats

Regular patterns in intertidal mudflats have been reported [42,43], ranging from strongly banded 'ridge and runnel' patterns on mudflats with relatively strong tidal currents to more round-shaped regular microphytobenthos patches where tidal currents are smaller (Figure 2g). The formation of such patterning is strongly related to the presence of diatom biofilms on more elevated ridges or patches. These biofilms produce extracellular polymeric substances (EPS) that enhance sediment cohesiveness and stability [42]. Enhanced drainage of water on the elevated ridges and patches during tidal emergence solidifies the EPS, which reduces erosive losses and favours microphy-

tobenthic growth. Hence, a short-distance positive feedback between sedimentation and diatom growth leads to local elevation of the sediment surface [44]. This, in turn, causes divergence of flowing water into nearby lower parts, which leads to the formation of runnels. These act as drainage structures that remain wet, preventing microphytobenthos from building up a within-biofilm EPS pool. Hence, short-distance positive feedback on ridges leads to negative feedback at larger distance, owing to the divergence of flowing water into runnels. This scale-dependent feedback can explain regular patterning on the mudflats.

Marsh tussocks

In tidal freshwater wetlands in Maine, USA, regularly spaced clumps of the tussock sedge, *Carex stricta*, occur (Figure 2h), which grow on root mounds within a matrix of bare sediment [45,46]. *C. stricta* typically produces large amounts of dead plant material, which falls radially from the tussock and accumulates as wrack between the tussocks. This reduces light availability and limits the growth of seedlings. On top of the mounds, the shading effect of wrack is reduced, because the mound pushes the vegetation through the wrack layer. This leads to long-distance negative feedback: shading is strong at some distance from the tussock, but is alleviated locally within the tussocks [46].

Long-distance negative feedback

The study of the marsh tussocks makes it clear that long-distance negative feedback is essential for regular pattern formation in all of these ecosystems [46]. First, this means that short-distance positive feedback is not essential for regular pattern formation. Second, it implies that short-distance feedback alone, unaccompanied by long-distance feedback, will not be a sufficient condition for regular patterns to form (Figure 1). Indeed, the regularity of a pattern is determined by the spatial extent of the long-distance negative feedback, whereas a short-distance positive feedback might increase the sharpness of the patterns [47] but not shape their regularity. This suggests that all of the studies on regular pattern formation in ecosystems are linked by one single overriding principle, which is that organisms modify their environment, inducing a net negative feedback at a certain distance. The strength of this feedback depends on the density of the organisms. Such a mechanism is likely to be overlooked, because typically only short-distance feedbacks between organisms and their environment are studied. We advocate looking beyond the local scale to study the density-dependent effects of organisms further away, even if these effects would intuitively be beyond the range of influence of the organisms. In Box 2, we outline two possible empirical approaches.

Ecosystem functioning

We reviewed studies from a wide range of ecosystems in which scale-dependent feedback is proposed to explain regular pattern formation. The mechanisms involved all correspond to Turing's scale-dependent activator-inhibitor principle and only differ in the details. The examples from arid ecosystems, wetland ecosystems, savanna ecosystems

and coral reefs involve resource concentration in a so-called activator-depleted substrate system [14]. Here, the activation and inhibition mechanisms are tightly coupled through a biologically mediated flow of resources. Mussel beds also correspond to the activator-depleted substrate system, where the activation and inhibition mechanisms are decoupled (cf. [48]), because the activation results from local cooperative behaviour and the inhibition from resource depletion. In ribbon forests and intertidal mudflats, diversion of snow and shear stress by wind and water flow, respectively, cause short-range activation, but inevitably also generate long-distance inhibition as either snow or water accumulates between the patches [14]. In the marsh tussock system, wrack production generates inhibition of growth at a certain range, but inhibition is alleviated by the tussock mounds. Hence, only long-range inhibition remains and no short-range activation has been observed. One unifying principle emerges from all of these examples: scale-dependence of feedback processes between organisms and their environment leads to regular pattern formation in ecosystems.

Our review reveals the universal appearance of regular pattern formation in real ecosystems. Most of our examples are drawn from ecosystems in relatively homogeneous landscapes, which lack strong environmental gradients. Also, they are generally characterized by adverse environmental conditions where biologically mediated resource concentration or stress alleviation are potentially important processes [31,49]. So, in these ecosystems, there is either a limiting resource or a stress factor constraining establishment and survival of organisms. The organisms themselves can alleviate this constraint locally, but this has repercussions at a certain distance. However, scale-dependent feedback can also be important in structuring ecological communities in more heterogeneous and benign

Box 2. Studying feedbacks at longer distances

One approach to determine the long-distance negative feedback induced by organisms is to remove the organism and detect the effects not only at short distance but also at longer distances. Such a removal experiment was done by Van de Koppel and Crain [46], who removed *Carex stricta* tussock biomass, and studied the performance of transplants with and without removal at longer distances from previous tussock locations (Figure II Figure 1a). They found no effect of *C. stricta* on conspecifics growing within the tussocks, but a strong negative feedback on seedling establishment at 15 cm from the tussock centre, which was alleviated when all aboveground plant material was removed. The long-distance negative feedback results from large amounts of standing dead plant material, which falls radially from the tussocks and accumulates as wrack. So, removing the aboveground tussock vegetation, including the wrack, leads to alleviation of the long-distance negative feedback.

Another approach is to look for significant cross-correlations between the density of the organism and the resource level or stress factor at longer distances. Such a cross-correlation experiment was done by Rietkerk *et al.* [65] who showed that clustered annual vegetation biomass and soil moisture are positively correlated at short distance but negatively at longer distances (Figure 1b). This means that higher annual vegetation biomass is associated with higher soil moisture within vegetated patches, and with lower soil moisture further away, outside vegetated patches. Because vegetation increases rainwater infiltration into the soil and because this association could not be attributed to other factors, such as micro-relief [65], this suggests the presence of scale-dependent feedback.

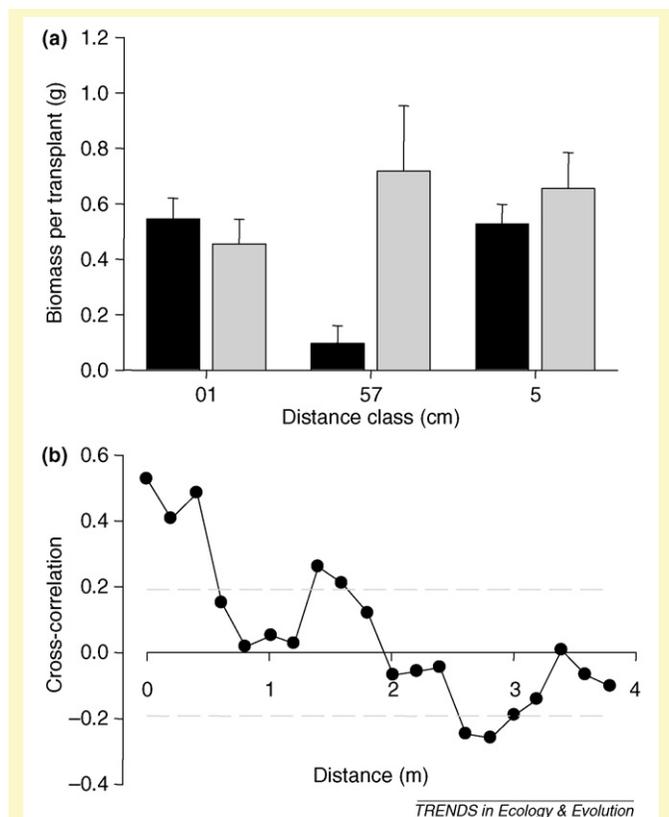


Figure 1. (a) Performance of *Carex stricta* transplants at varying distance. The x-axis represents distance classes (in cm) from tussock centres, with *C. stricta* tussock biomass removed (light bars) and intact (dark bars). *C. stricta* produces large amounts of dead standing plant material, which falls radially from the tussocks, accumulating as wrack, inhibiting the growth of transplants at a certain distance from the tussocks. Long-distance negative feedback is demonstrated because the only significant effect is found at 15 cm from the tussock. The treatment at 15 cm distance with *C. stricta* wrack intact varied significantly from all other treatments (least squares contrast: $F = 25.75$, $df = 1, 44$, $p < .00001$). The bars are standard errors. This treatment is representative of natural intertussock spaces. Reproduced, with permission, from Ref. [46]. (b) Cross-correlograms of annual vegetation biomass and soil moisture demonstrating that biomass (g dm^{-2}) is significantly positively correlated with soil moisture (vol%) at short distance (0–0.5 m) but a significant negative correlation occurs at a longer distance (2.5–3 m). Dashed lines indicate the significance limits of the cross-correlation values for $\alpha = 0.05$ and $N(0) = 105$, which was the number of pairs evaluated at distance = 0 m. A pair consists of a value for vegetation biomass and soil moisture. The distances along the x-axis are the intervals for which the cross-correlation values were calculated. Adapted, with permission, from Ref. [65].

environments. Long-range competition and short-range facilitation determines plant community structure on marine cobble beaches characterized by a strong gradient in wave exposure [50]. Scale-dependent feedback also leads to the formation of regularly spaced barnacle hummocks, especially under benign conditions that enable the formation of dense barnacle beds, inducing strong competition [51]. More research is needed to further understand how scale-dependent feedback spatially organizes communities in such environments.

Recent evidence shows that short-distance positive feedback between plants and their local environment gives rise to spatial self-organization revealed by power-law clustering of vegetation in arid ecosystems [52,53]. This is in line with our assertion that short-distance positive feedback alone does not produce regular pattern formation, but that a long-distance negative feedback is essential for the

regularity to form. Power laws in the geometry of clusters in ecosystems might also be the result of localized disturbance-recovery processes; for example, in wave-disturbed mussel beds [4], and in wind-disturbed [54] and fire-disturbed [55] forests. Both the observation of regular pattern formation and power-law clustering now provide a strong indication of the omnipresence of spatial self-organization in real ecosystems [1]. Alternative explanations for regular pattern formation in ecosystems include noise [56,57] and pre-determined regularity related to geophysical processes [12,39,58]. Despite this, our review shows increasing evidence linking regular pattern formation to scale-dependent feedback between organisms and their environment.

Models predict that regular pattern formation has important emergent effects on ecosystem functioning. Ecosystems with regular patterns might be more resilient to disturbance and resistant to global environmental change as compared with homogeneous ecosystems [19,34,59]. This can be most intuitively explained by the resource concentration mechanism in ecosystems corresponding to the activator-depleted substrate system mentioned earlier. Organisms concentrate resources in their local environment, enabling persistence even when mean field resource levels become too low for their survival; for example, as a consequence of increased aridity. Linked to this, several studies suggest that regular pattern formation leads to resource optimization [18,60,61] having positive consequences for productivity and diversity [28,62,63]. The potential application and relevance of regular pattern formation for global environmental change, ecosystem adaptation and restoration involves transplanting organisms so that they reach a certain threshold density, to induce short-range facilitation, and arranging them spatially in a way to make optimal use of limiting resources [49,60,62]. Indeed, mimicking regular patterns in arid ecosystems or coral reefs is an intuitive strategy to aid ecosystem restoration, because the patterns increase the interception of resources that flow past and spatially optimize their exploitation [49,61]. An outstanding research question is whether a change in regular patterns can indicate loss or gain of resilience or resistance in real ecosystems, or even act as a warning signal for an abrupt loss of the patterns altogether. Further research is needed to better understand and predict regular pattern formation in ecosystems, and how this affects the response of ecosystems to global environmental change.

Acknowledgements

M.R. is supported by a personal VIDI grant from the Netherlands Organization of Scientific Research, Earth and Life Sciences (NWO-ALW). We thank David Bercovici, Wladimir Bleuten, Norbert Dankers, Chris Klausmeier, Brian Helmuth, David Jupp, Elena Lapshina, Olivier Lejeune, Roland Thar and Martin Wassen for sharing their photographs. Stefan Dekker, Maarten Eppinga, Jo Gascoigne, Erez Gilad, Frédéric Guichard and Sonia Kéfi provided comments and ideas that significantly improved the article.

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